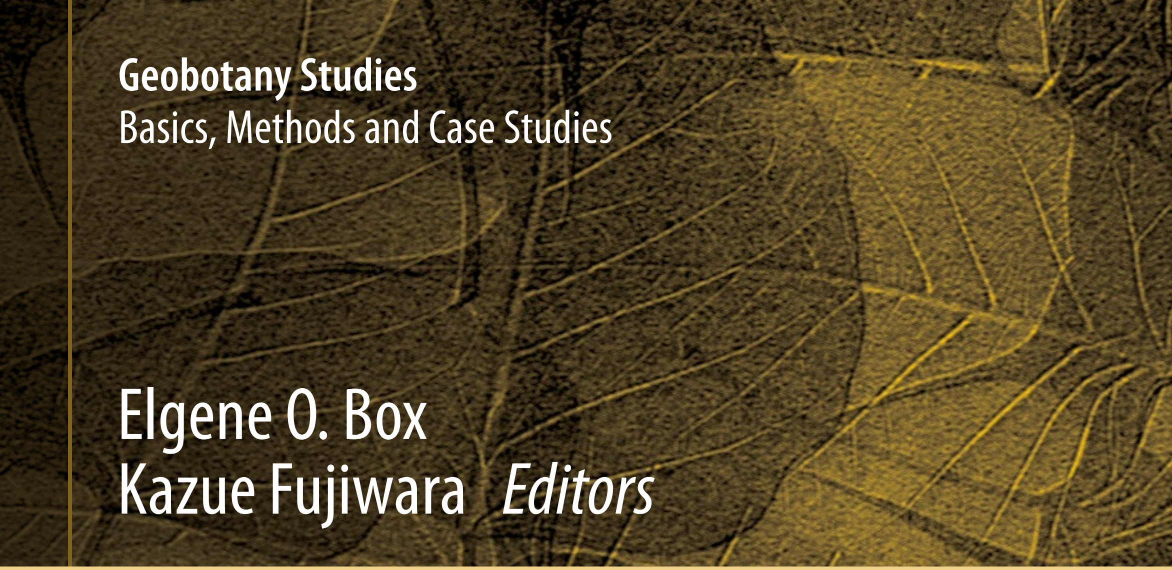


Geobotany Studies
Basics, Methods and Case Studies

Elgene O. Box
Kazue Fujiwara *Editors*

Warm-Temperate Deciduous Forests around the Northern Hemisphere

Springer

Geobotany Studies

Basics, Methods and Case Studies

For further volumes:
http://www.springer.com/series/10526

About the Series

The series includes outstanding monographs and collections of papers on a given topic in the following fields: Phytogeography, Phytosociology, Plant Community Ecology, Biocoenology, Vegetation Science, Eco-informatics, Landscape Ecology, Vegetation Mapping, Plant Conservation Biology and Plant Diversity. Contributions are expected to reflect the latest theoretical and methodological developments or to present new applications at broad spatial or temporal scales that could reinforce our understanding of ecological processes acting at the phytocoenosis and landscape level. Case studies based on large data sets are also considered, provided that they support refinement of habitat classification, conservation of plant diversity, or prediction of vegetation change. “Geobotany Studies: Basics, Methods and Case Studies” is the successor to the journal *Braun-Blanquetia*, which was published by the University of Camerino between 1984 and 2011 with the cooperation of the Station Internationale de Phytosociologie (Bailleul-France) and the Dipartimento di Botanica ed Ecologia (Università di Camerino, Italy) and under the aegis of the Société Amicale Francophone de Phytosociologie, the Société Française de Phytosociologie, the Rheinold Tüxen Gesellschaft, and the Eastern Alpine and Dinaric Society for Vegetation Ecology. This series aims to promote the expansion, evolution and application of the invaluable scientific legacy of the Braun-Blanquet school.

Elgene O. Box • Kazue Fujiwara
Editors

Warm-Temperate Deciduous Forests around the Northern Hemisphere

Springer

Editors
Elgene O. Box
Geography Department
University of Georgia
Athens, Georgia
USA

Kazue Fujiwara
Yokohama City University
Yokohama
Japan

ISSN 2198-2562 ISSN 2198-2570 (electronic)
ISBN 978-3-319-01260-5 ISBN 978-3-319-01261-2 (eBook)
DOI 10.1007/978-3-319-01261-2
Springer Cham Heidelberg New York Dordrecht London

Library of Congress Control Number: 2014957871

© Springer International Publishing Switzerland 2015
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed. Exempted from this legal reservation are brief excerpts in connection with reviews or scholarly analysis or material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work. Duplication of this publication or parts thereof is permitted only under the provisions of the Copyright Law of the Publisher's location, in its current version, and permission for use must always be obtained from Springer. Permissions for use may be obtained through RightsLink at the Copyright Clearance Center. Violations are liable to prosecution under the respective Copyright Law.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
While the advice and information in this book are believed to be true and accurate at the date of publication, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Preface

The basic worldwide geographic framework for understanding relations between climate and plant or vegetation types involves the recognition of regular bioclimatic zones, such as tropical, temperate, and further subdivisions. In global bioclimatic zonation, one zone is the warm-temperate, which has generally warm (if not hot) summers and relatively mild winters, but with some frost, which distinguishes this zone from the tropical climates. Many warm-temperate climates are also generally humid, with year-round rainfall. As a result, the "zonal" (i.e., potential natural) vegetation of the warm-temperate zone is considered to be evergreen broad-leaved forest, such as the "laurel forests" of East Asia, southern Brazil, and the cloud belt of some parts of the Canary Islands. The trees typically have quite pliable, often glossy, thin-leathery evergreen leaves; build relatively deep root systems; and grow rapidly under the good climate conditions.

In some parts of the Northern Hemisphere, though, some more "southern" deciduous temperate (summergreen) forests, mostly oak forests, extend into the warm-temperate zone, where winters are just a bit too cold for the broad-leaved evergreen trees, though summers are still quite warm. That deciduous forests may occur regularly in the warm-temperate zone, under such conditions, was first recognized by the Japanese ecologist Tatsuō Kira, who called these forests "warm-temperate deciduous." This book represents the first attempt to recognize and describe "warm-temperate deciduous forests" as a consistent forest type representing a consistent response to similar climatic situations around the entire Northern Hemisphere. Most of the chapters included herein are from papers presented in 2011, in a special session on warm-temperate deciduous forests (also a first), held at the annual meeting of the International Association for Vegetation Science in Lyon.

Forest composition, structure, and environmental relations are treated in this book in various ways, some emphasizing bioclimatic relationships, some following traditional phytosociological analysis, plus some other methodologies. Some chapters on more specialized aspects are also included, in particular on various aspects of two prototype warm-temperate deciduous tree species, namely, downy oak (*Quercus pubescens*) from southern Europe and Chinese cork oak (*Quercus variabilis*) from East Asia. The book begins with a general overview chapter on the concept of warm-temperate deciduousness, and there is an attempt at the end to quantify the climatic limits of potential temperate forest regions and to map them accordingly, around the entire Northern Hemisphere.

As in any large area with diverse language and cultural regions, there are problems of terminology. The terms used herein for bioclimatic zonation represent what appears to be the global consensus on concepts, types, and names. The official Chinese national classification system is quite different, however, and some terms are in direct conflict. For example, in the Chinese system, *all* temperate deciduous forests have been called "warm-temperate" (despite winter temperatures to -30°C or lower), and all evergreen broad-leaved forests are usually assigned to the "subtropical" zone (if not tropical). For this book, only the more globally consistent terminology is used. This is explained in the "Overview" chapter, along with an attempt to explain the Chinese discrepancy.

Another difference involves people's names. In East Asia the family name comes first, followed by given names. For Japanese, there is no problem, because Japanese scientists follow the Western order quite consistently when using Western languages. Chinese and Korean names, on the other hand, are shown much less consistently, and it has become fashionable among eager young Chinese researchers to use the Western name order consistently, even when not dictated by their publishers. This can be quite confusing for people not familiar with Chinese and Korean names. Family names in both Chinese and Korean are normally of one syllable, followed usually (but not always) by two given names. The problem comes when there is only one given name (one syllable), but even this can be overcome simply by observing the pattern used for other names in the particular publication. In this book, Chinese and Korean names are given in their natural order (family name first), with the two given names hyphenated; Japanese names are given in Western order. The only exception is in some registered names of phytosociological syntaxa, which may be idiosyncratic.

Literature references are given in the direct, common-sense format used formerly by the Ecological Society of America. In this format, the first author (of multiples) has the family name first and subsequent authors follow with given and family names in their normal order – without inversions and without all those unnecessary, obfuscating commas that make the gothic, but now “accepted” format so difficult to read. Note that, in the format used herein, there is no comma in any Chinese or Korean name because there can be no inversions of family and given names.

Diacritical marks are unavoidable in order to retain some correct meanings and pronunciations, especially in Japanese. For long vowels, a macron is used on o (ō) and u (ū), while the other long vowels are indicated (as in written Japanese) by doubling the vowel, i.e., aa or ii, or by the convention “ei” for long e. Although it has recently become fashionable in Japan to omit macrons in Romanization, the difference between long and short vowels is not trivial. It represents different spellings, difference in syllable stress, and often quite different meanings. For example, short *o* means small (小) but long *ō* means large (大). Other things being equal, a syllable with a long vowel is much more likely to be stressed than one with only a short vowel – as also in English and most languages. In Chinese, each syllable carries one of four possible tones. Tone marks, though, are usually not shown herein, since these do not represent differences in spelling, either in *pinyin* (the Chinese phonetic Romanization system) or in Western renditions.

Finally, understanding some place names, especially in China, will be much easier if the reader is willing to learn just three East Asian words. A mountain (or mountains) is *shan* in Chinese and *san* in both Japanese and Korean; *ling* (Chinese) is a range of mountains. Thus, [the] Changbai-Shan is the mountains along the border between China and North Korea, Fuji-san is Mt. Fuji, and the Da Xing An Ling (Chinese) is the Greater Hinggan mountain range that separates Inner Mongolia (to the west) from Chinese Manchuria (to the east).

Sadly we must also note that Tatsuō Kira passed away in 2011, at age 91. He once told me (Box) that he kept his imagination young by dividing his scientific career into roughly 10-year segments, in each one of which he studied something entirely different from before. Perhaps this is a good model for many of us – his life was a model for all of us. It seems fitting, therefore, that we dedicate this book to his memory.

Athens (Georgia), USA — Elgene O. Box
Yokohama, Japan — Kazue Fujiwara

Contents

Introduction: Why Warm-Temperate Deciduous Forests?

Elgene O. Box and Kazue Fujiwara

Warm-temperate deciduous forests would seem to be an enigma. In the various global (and globally aware) bioclimatic zonation systems, warm-temperate climates are generally construed as humid temperate climates with warm summers, mild winters (no lasting snow cover), and evergreen broad-leaved forest as the zonal (i.e. climatic potential) vegetation type. This is the general conceptualization both in global treatments of vegetation and climate, as by Rübel (1930), Schmithüsen (1968), and Walter (1968, 1970, 1985); and in regional systems, such as by Kira and others for East Asia (cf Kira 1945, 1949, 1977, 1991; Suzuki 1953; Miyawaki 1967). Such zonal evergreen broad-leaved forests occur in East Asia (often called "laurel forests") as well as in southern Brazil, northern New Zealand, parts of eastern Australia, in montane belts of tropical Asia (and even the Canary Islands), and, where topography permits, in small areas of the warm-temperate southeastern USA. Thermally, some mediterranean climates are also warm-temperate and may carry evergreen broad-leaved forests, albeit with sclerophyll rather than laurophyll foliage.

Even so, Tatsuō Kira (1949) recognized that deciduous forests may also occur as stable forests in some warm-temperate areas, if winters are too cold for evergreens. For these forests, especially some in interior Honshū (the largest island of Japan), he coined the term 'warm-temperate deciduous forest'. These deciduous forests occur not only as successional stages but may remain as permanent vegetation, even in some areas where winters are milder. In this sense, warm-temperate deciduous forests can be conceived as:

- "southern" temperate deciduous forests;
- occurring where summers are warm but winters are too cold for evergreens;
- occurring not only in Japan but also mainland East Asia, southeastern USA, and perhaps elsewhere; and
- including perhaps the "thermophilous" and "submediterranean" deciduous forests of southern Europe.

Why do such deciduous forests persist in warm-temperate areas? Are they anomalies, or are they a natural alternative in a consistent global zonation?

Warm-temperate deciduous forests (and more open woodlands) are a Northern Hemisphere phenomenon, resulting, like the boreal forest, from the continentality of the large Northern land masses (cf Troll 1948; Box 2002). Kira recognized the warm-temperate deciduous forests of Japan by observing that some deciduous *Quercus* species in Japan do not occur in either of the adjacent climatic zones, the cool-temperate to the north or the subtropical zone to the south. Indeed, throughout the Northern Hemisphere, warm-temperate deciduous forests are overwhelmingly oak forests. In East Asia these forests are composed especially of deciduous *Quercus serrata*, *Q. variabilis*, *Q. aliena* and *Q. dentata*. These species form forests in the drier climates of interior Honshū, such as around Nagano, where summers are warm but winters are colder. Minimum winter temperature in these areas can go below −15°C (not below −20°C), mean January temperature is around 0°C, and values of Kira's Coldness Index are below −10°C. Average annual precipitation may be 900–1100 mm, which is low for Japan.

Similar deciduous forests also occur in the relatively warm climates of north-central to eastern China and the more southern lowlands of Korea; analogous deciduous forests beyond Asia appear to include the *Quercus pubescens* forests of the Mediterranean area and the oak-hickory (*Quercus-Carya*) forests of interior southeastern North America. In East Asia, the main warm-temperate

---

E.O. Box (✉)
Geography Department, University of Georgia, Athens, Georgia 30602, USA
e-mail: boxeo@uga.edu

K. Fujiwara
Yokohama City University, Yokohama 236-0027, Japan
e-mail: kazue@ynu.ac.jp

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*,
Geobotany Studies, DOI 10.1007/978-3-319-01261-2_1,

deciduous species generally occur on relatively dry sites and are the same species that form the canopy of successional deciduous forests that are eventually replaced by zonal evergreen broad-leaved forests. In eastern North America, some deciduous tree species have distinctly northern or southern ranges, making the concept of warm-temperate deciduousness relatively clear. Areas of potential warm-temperate deciduous forest around the Northern Hemisphere can be suggested from climatic considerations, as shown in the last chapter of this book (Box). In the Southern Hemisphere, temperate deciduous forests occur naturally only in the southern Andes, but the climate is much too cool to consider them warm-temperate.

Most chapters in this book come from papers presented at the 2011 annual IAVS meeting, in Lyon, in a special session on warm-temperate deciduous forests, which was the idea of the second author. The purpose of that session was to try to clarify some of the climatic and related questions about warm-temperate deciduous forests as a true forest type. Local and regional specialists were invited to present descriptions of the warm-temperate deciduous forests in their areas, with whatever further analysis seemed appropriate. This session was the first to focus on warm-temperate deciduous forests as a recognized type within a global framework. Some initial goals were to:

- Document the composition and structure of these forests, as well as their landscape dynamics
- Examine and compare their environmental situations, including but not limited to their Climatic similarities (and differences)
- Understand why these deciduous forests are not replaced by evergreen broad-leaved forests.

Particular questions include the following:

- What are warm-temperate climates?
- What is a warm-temperate deciduous forest (composition, ecology, etc.)?
- What are the relative advantages of evergreen and deciduous trees in such climates?
- Why do deciduous forests persist and evergreens not dominate if the climate is warm enough for them?
- Are there significant differences among ‘thermophilous’, ‘submediteranean’ and ‘warm-temperate’ deciduous forests, in Europe or elsewhere?

The chapters in this book are mostly from papers presented at the Lyon meeting, but a few papers were added later, since they expanded on the topic.

The first chapter (Box and Fujiwara), after this brief introduction, provides a world overview of warm-temperate deciduous forest areas, including attempts to define the term. This is followed by regional treatments, starting with East Asia, proceeding through Europe to eastern North America, and ending with the drier west-side situations of California and parts of the Middle East. In East Asia, the national climatic classification system of China also uses the term ‘warm-temperate deciduous forest’ but in a different sense, since their classification is based mainly on the growing season and not on the climate of the whole year. As a result, Chinese usage is not equivalent to our global concept of warm-temperate deciduous forest, although warmer parts of the Chinese deciduous forest region probably are warm-temperate. This is explained in the overview chapter and elsewhere (e.g. Box 1995a; Box and Fujiwara 2012).

The next chapter, by Fujiwara and Harada, presents a detailed phytosociological comparison of East Asian temperate deciduous forests, including those from many areas in China, based on extensive fieldwork and analysis of relevé data. These temperate forests are mainly dominated by beech (*Fagus*) or oaks (*Quercus*), but the warm-temperate deciduous forests are overwhelmingly oak forests. This chapter represents one of the few truly comprehensive treatments of any forest type across East Asia as a whole (cf Fujiwara et al. 2008), comparing forest composition, environmental limitations, and identifying many new phytosociological syntaxa (and reinterpreting some existing syntaxa). This chapter also includes a map of current actual warm-temperate deciduous forest locations and another showing where these forests are permanent or successional to evergreen forests. There is also an extensive list of references to East Asian literature, most of which was conceived within national borders. This chapter represents a major phytosociological synthesis of information on deciduous *Quercus* forests of East Asia.

In East Asia, *Quercus variabilis* (Chinese cork oak) is a prototypic warm-temperate deciduous tree species, occurring from north-central China to Korea and Japan. It occurs both as a secondary tree and as the dominant or co-dominant of persisting warm-temperate deciduous forests. Despite some confusing terminology (cf Preface), *Quercus variabilis* does seem to be a truly warm-temperate deciduous tree. The situations and phytosociological units in which it occurs are described in detail by Tang et al. (herein), who offer an ordination and define several new alliances as well as a new order and class. At the end of this chapter is the suggestion that the southern boundary of the Chinese zone called warm-temperate be moved further south, which would bring it more in line with global zonations. This should be accompanied, though, by a southward shift of the northern boundary of this zone (and perhaps of the “temperate” zone itself).

The largest part of the book treats southern Europe, where *Quercus pubescens*(downy oak) can be considered a prototypic warm-temperate deciduous tree. It occurs from northern Iberia to the Black Sea region, with some outliers beyond. Within southern Europe, we begin with a description by Costa et al. (herein) of vegetation mosaics in the transition, in Portugal, between the Euro-Siberian nemoral forests to the north and the Mediterranean, or at least submediterranean, vegetation to the south. Deciduous forests over much of Europe involve *Q. robur*, the most widely occurring species. In central Portugal, forests of *Q. robur* ssp. *broteroana* (in a Viburno tini – Querceto roboris) are seen as warm-temperate deciduous, and forests of an Arisaro-Quercetum broteroi as intermediate between warm-temperate deciduous and Mediterranean, i.e. submediterranean.

The Iberian peninsula represents a fairly broad transition from nemoral to Mediterranean conditions, and northern Spain has some fairly extensive areas of deciduous oak forest. Various features of Iberian oaks are described and interpreted by Garcia-Mijangos et al. (herein) as adaptations to the nemoral, submediterranean or Mediterranean climatic conditions. Marcescence, in particular, seems not to be a lingering vestige of the evergreenness that it suggests, but rather a characteristic of submediterranean conditions. Other adaptations are also considered, such as semi-evergreenness, as well as advantages of evergreenness and deciduousness in transitional situations. All of these phenological adaptations occur also in other oaks in other climates: what do they have in common?

Downy oak (*Quercus pubescens* s. l.) is a prototypic warm-temperate deciduous tree species in Europe and is treated in three chapters. Its distribution and ecology in Italy, as well as its polymorphisms and difficult taxonomic history, are considered by Guarino et al. (herein), who note that the widest range of forms and ecological conditions is found in Sicily, where some commonly competing trees are missing. Differences in Sicily do not seem to be related to clear ecological or geographical discontinuities. *Q. pubescens* is also an important species in the long-managed landscapes of interior central Italy, where it occurs mainly in coppices. Its potential in the Marche region, at landscape scale, is considered by Cianfaglione (herein). Finally, taxonomic and other, mainly historical problems of *Q. pubescens* and related taxa are treated by Wellstein and Spada, based on a comprehensive literature review including the classic monographs on European oaks. *Q. pubescens* has long been considered a “species complex”, but the actual species status of some other well known, named oaks in southern Europe is also questioned.

Two other oak species are also treated in detail. One is *Quercus petraea*, which occurs widely in deciduous forests of Europe and looked quite like a “southern” species when its climatic range was projected to North America (Box and Manthey 2006). Its situation as a potential warm-temperate deciduous species is considered by Pedrotti (herein) in the transitional forests of northern Italy. *Quercus suber*, on the other hand, is evergreen but may lose some foliage in winter and is interestingly related to some of the deciduous oaks of southern Europe. Its long history and possible occurrence much further east than at present are considered in a deeply researched chapter by Schirone et al. (with Spada, Simeone, Vessella, herein) that suggests a model for historical study of other Mediterranean species as well. The same co-authors (mostly) also provide an interesting perspective on forest refugia in Europe during the last glacial period (Schirone, Spada, Piovesan and Simeone, herein).

Eastern North America may have the world’s largest area of warm-temperate deciduous forests, in roughly the southern half of its eastern deciduous forest area. The deciduous forests of the interior southeastern USA occur under conditions of warm summers and milder winters than at comparable latitude and geographic position in East Asia, where forests are usually broad-leaved evergreen. The forests of the interior southeastern USA are deciduous, however, because of infrequent but extreme low-temperature events (cf Box 1995a). Various types of American warm-temperate deciduous forest are described (Box, herein), with relevé data and with climatic data provided in the Appendix to this book.

Regional coverage concludes with two chapters covering drier, west-side situations, in which the vegetation is generally not closed forest. Both chapters are from Blumler, who has studied the advantages of deciduousness in mediterranean climates for many years (e.g. Blumler 1991). The first chapter (Blumler, herein) concerns California, where deciduous oaks occur and dominate, mainly in open woodlands, under submediterranean and sometimes truly Mediterranean-like climatic conditions. The second region involves parts of the interior Middle East, which is treated by Blumler and Plummer (herein) in comparison with California. Large areas from the Levant to Iran have (interior) Mediterranean climatic conditions but are dominated by deciduous trees, usually in open woodlands or scrub, rather than the evergreen sclerophyll scrub of other areas with mediterranean climate.

Finally, in the last chapter (Box, herein), an attempt is made to delimit warm-temperate deciduous and other temperate climatic regions quantitatively and to map their geographic areas based on postulated climatic envelopes (cf Box 1981, 1995b, c). It is seen in the “overview” chapter (Box and Fujiwara, herein) that the thermophilous and submediterranean deciduous forests of southern Europe occur under distinctly cooler summer conditions than in East Asia and eastern North America. This does not disqualify them as warm-temperate deciduous forests but suggests that the concept must be seen as relative to conditions over the whole of the particular large regions concerned.

Taken together, these chapters represent a first attempt to recognize warm-temperate deciduous forests as a consistent, alternative forest type in the Northern warm-temperate zone and to explore what they have in common. With global warming, warm-temperate deciduous forest areas may well become battlegrounds between deciduous and evergreen elements, as suggested by the 'laurophyllization' phenomenon described already in southern Switzerland (Klötzli and Walther 1999). So knowledge of these areas is important, and we hope this comparison will be useful.

References

Blumler, M. A. 1991. Winter-deciduous versus evergreen habit in mediterranean regions: a model. In: *Proceedings of the Symposium on Oak Woodlands and Hardwood Rangeland Management*, October 31–November 2, 1990, Davis (R. B. Standiford, tech. coord.), pp. 194–197. USDA, Forest Service, Gen. Tech. Rep. PSW-126, Berkeley.

Blumler, M. A. (herein). Deciduous woodlands in mediterranean California. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Blumler, M. A., and J. C. Plummer (herein). Deciduous woodlands in the Near-Eastern Fertile Crescent and a comparison with California. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). GeobotanicalStudies.

Box, E. O. 1981. *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Tasks for Vegetation Science, vol. 1. The Hague: Dr. W. Junk BV. 258 pp

Box, E. O. 1995a. Climatic relationships of the forests of East and South-East Asia. In: *Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and Southeast Asia* (E. O. Box et al., eds.), pp. 23–55. Kluwer Academic Publishers, Dordrecht

Box, E. O. 1995b. Factors determining distributions of tree species and plant functional types. *Vegetatio*, 121:101–116.

Box, E. O. 1995c. Global Potential Natural Vegetation: Dynamic Benchmark in the Era of Disruption. In: *Toward Global Planning of Sustainable Use of the Earth – Development of Global Eco-engineering* (Sh. Murai, ed.), pp. 77–95. Amsterdam: Elsevier

Box, E. O. 2002. Vegetation analogs and differences in the Northern and Southern Hemispheres: a global comparison. *Plant Ecology*, 163:139–154 (appendix missing! – request from author)

Box, E. O. (herein). Warm-Temperate Deciduous Forests of Eastern North America. In: *Warm-Temperate Deciduous Forests around the Northern Hemishere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O. (herein). Quantitative Delimitation of Warm-Temperate Deciduous Forest Areas. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O. (herein). Appendix: Climatic Data for Representative Humid-Temperate Sites around the Northern Hemisphere,with Climate Type Predicted from an Envelope Model and Mapped In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O., and K. Fujiwara 2012. A comparative look at bioclimatic zonation, vegetation types, tree taxa and species richness in Northeast Asia. *Botanica Pacifica* (Vladivostok), 1:5–12.

Box, E. O., and K. Fujiwara (herein). Warm-Temperate Deciduous Forests: Concept and Global Overview. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O., and M. Manthey 2006. Conservation of deciduous tree species in Europe: Projecting potential ranges and changes. In: *Nature Conservation: Concepts and Practice* (D. Gafta and J. Akeroyd, eds.), pp. 241–253. Springer-Verlag, Berlin.

Cianfaglione, K. (herein). On the potential of *Quercus pubescens* and other *Quercus* species in Camerino. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Costa, J. C., T. Monteiro-Henriques, P. Bingre, and D. Espírito-Santo (herein). Warm-temperate deciduous forests of central Portugal: a mosaic of syntaxa. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Fujiwara, K., and A. Harada (herein). Character of warm-temperate forests in Asia. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Fujiwara, K., You H.-M., Tang Q., A. Harada, Wang Zh.-X., and Wang L. 2008. Deciduous *Quercus* and *Fagus* Forests in Asia. In: *Integrated Vegetation Mapping of Asia* (K. Fujiwara, leader), pp 111–129. Report to Japan Society for Promotion of Science

García-Mijanos, I., J. A. Campos, I. Biurrun, M. Herrera, and J. Loidi (herein). Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Guarino, R., G. Bazan, and B. Paura (herein). Downy-oak woods of Italy: Phytogeographical remarks on a controversial taxonomic and ecologic issue. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Kira, T. 1945. *Nōgyō Chirigaku-no Kisō to shite no Tō-A no Shin Kikō Kubun* (A new classification of climate in eastern Asia, as a basis for agricultural geography.) Horticult. Inst., Kyoto University. 23 pp (in Japanese).

Kira, T. 1949. Nippon-no shinrin-tai [Forest zones in Japan]. *Ringyō Kaisetsu*, 17:105–141. Nippon Ringyō Gijutsu Kyōkai, Tokyo; reprinted in Kira 1971, pp 105–141 (in Japanese).

Kira, T. 1977. A Climatological Interpretation of Japanese Vegetation Zones. In: *Vegetation Science and Environmental Protection* (A. Miyawaki, ed.), pp. 21-30. Maruzen, Tokyo.

Kira, T. 1991. Forest ecosystems of East and Southeast Asia in a global perspective. *Ecol. Research* (Japan), 6:185–200. Reprinted: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 1–21. Kluwer, Dordrecht.

Klötzli, F., and G.-R. Walther 1999. Recent Vegetation Shifts in Switzerland. In : *Recent Shifts in Vegetation Boundaries of Deciduous Forests, especially due to general global warming* (F. Klötzli and G.-R. Walther, eds.), pp 15–29. Birkhäuser, Basel

Miyawaki, A. 1967. [Vegetation of Japan, compared with other parts of the world]. [Encyclopedia of Science and Technology], vol. 3. Gakken, Tokyo. 535 pp (in Japanese).

Pedrotti, F. (herein). Chorology and phytosociology of *Quercus petraea* in Trentino-Alto Adige. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Rübel, E. F. 1930. *Pflanzengesellschaften der Erde*. Verlag Hans Huber. 464 pp.

Schirone, B., F. Spada, M. C. Simeone, and F. Vessella (herein). *Quercus suber* L. distribution revisited. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Schirone, B., F. Spada, G. Piovesan, and M. C. Simeone (herein). Phenorhythms and Forest Refugia. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Schmithüsen, J. 1968. *Allgemeine Vegetationsgeographie*. 3rd edition. Walter de Gruyter, Berlin. 463pp.

Suzuki, T. 1953. The forest climaxes of East Asia. *Japanese J. Botany*, 14:1-12.

Tang Q., K. Fujiwara, and You H.-M. (herein). Phytosociological Study of *Quercus variabilis* Forest in Warm-Temperate China. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Troll, C. 1948. Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- und Südhalbkugel. *Jahresbericht des Geobotanischen Instituts Rübel* (1947):46–83.

Walter, H. 1968. *Die Vegetation der Erde in ӧko-physiologischer Betrachtung*. Vol. II: Die gemäβigten und arktischen Zonen. Jena: VEB Gustav-Fischer-Verlag. 1002 pp.

Walter, H. 1970. *Vegetationszonen und Klima*. Verlag Eugen Ulmer, Stuttgart. 382 pp. (3rd ed. 1977, 309pp)

Walter, H. 1985. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*. 3rd edition. Springer-Verlag, New York. 318 pp (1st edition 1970)

Wellstein, C, and F. Spada (herein). The status of *Quercus pubescens* Willd. in Europe. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Warm-Temperate Deciduous Forests: Concept and Global Overview

Elgene O. Box and Kazue Fujiwara

Abstract

The zonal vegetation of [humid] warm-temperate regions is normally considered to be evergreen broad-leaved forest, such as the “laurel forests” of East Asia, southern Brazil, and much of New Zealand. Observing the vegetation of Japan and other parts of East Asia, however, Kira noted in 1949 that some deciduous *Quercus* species do not occur in either the cool-temperate (deciduous) or the subtropical (evergreen) zone and eventually proposed the concept of warm-temperate deciduous forest, composed especially of *Quercus* species. These species occur in the drier climates of interior Honshū, especially around Nagano, where summers are warm enough but winters are too cold for evergreen broad-leaved forest. This concept also fits parts of middle-eastern China and lowland Korea, where most of the same *Quercus* species also occur. Analogous warm-temperate deciduous forests beyond Asia appear to include, *inter alia*, the *Quercus*-*Carya* forests of interior southeastern North America and the *Quercus pubescens* forests of southern Europe. In East Asia, some main deciduous species are *Quercus variabilis*, *Q*. *serrata*, *Q*. *aliena* and *Q*. *dentata*, all occurring on mesic to dry sites. These species also form the canopy of secondary deciduous forests that are eventually replaced by the zonal warm-temperate evergreen broad-leaved (laurel) forests. In eastern North America, some *Quercus* and other deciduous taxa (including *Fagus*) have wide north-south ranges, but deciduous *Q*. *falcata*, *Q*. *nigra*, and others have distinctly southern ranges. This southern area is in the warm-temperate zone and has mean winter temperatures significantly higher than in East Asia (albeit with unusual lower extremes). Warm-temperate deciduous forest analogs around the Northern Hemisphere can be identified from climatic considerations but also from phytosociological analysis (and ordinations) based on relevé data, suggesting that this is a consistent subzonal forest type.

Keywords

Absolute minimum temperature • Climatic zonation • Cool-temperate climate • Deciduousness • Evergreenness • Kira index • Summer warmth threshold • Submediterranean climate • Thermophilous deciduous forest • Typical temperate climate • Warm-temperate climate • Zonal vegetation

1 Introduction

The idea of warm-temperate deciduous forest derives from Tatsuō Kira, the imaginative Japanese ecologist who made the first modern climatic zonation system for much of East Asia (Kira 1945) and used it to explain potential forest

---

E.O. Box (✉)
Geography Department, University of Georgia, Athens, Georgia 30602, USA
e-mail: boxeo@uga.edu

K. Fujiwara
Yokohama City University, Yokohama 236-0027, Japan
e-mail: kazue@ynu.ac.jp

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_2,

Table 1 Forest zones of humid East Asia as defined by Kira's warmth index and coldness index

	Warmth Index	Coldness Index	Mean annual temperature
Arctic	0–15°		
Subarctic (evergreen conifer)	15–45°		
Cool-temperate			
Deciduous broadleaf	45–85°		
Mixed broadleaf + conifer	>45°		
Warm-temperate			
Evergreen broadleaf	85–180°	>−10°	>20°
Deciduous broadleaf	>85°	<−10°	
Subtropical	180–240°		20–25°
Tropical	>240°		>25°

The Warmth Index is defined as the annual sum of monthly mean temperatures above a 5°C threshold; the Coldness Index is the annual sum of monthly mean temperatures below 5°C. Warm-temperate evergreen and deciduous are differentiated by the degree of winter cold. No climatic distinction is specified between cool-temperate deciduous and mixed forest zones. All values are in degrees Celsius or equivalent annual temperature sums.
Source: Kira (cf 1977, 1991)

zones, initially in Japan (Kira 1949, 1977). The system was quantified by means of Warmth and Coldness Indices (WI, CI), which represent temperature sums above and below a growth threshold of 5°C (see Table 1). With WI and CI values it was possible to distinguish tropical, subtropical, warm-temperate (evergreen), cool-temperate (deciduous), and subarctic (boreal) zones and their potential (zonal) vegetation, including some belts in mountains. The system was also applied to Korea (Yim 1977; Yim and Kira 1975–1976) and eventually to much of mainland East Asia (Kira 1991), in order to explain vegetation patterns for all of East Asia first described by Suzuki (1952, 1953).

Even so, Kira (1949) also recognized that some deciduous *Quercus* species do not occur in the cool-temperate deciduous zone but rather in the warm-temperate zone, in which the zonal vegetation was supposed to be evergreen broad-leaved "laurel forest" (the *Lorbeerwald* of Rübel 1930; Schmithüsen 1968, and other European writers). For these warmer-climate deciduous *Quercus* species Kira coined the term 'warm-temperate deciduous forest' to refer to stable deciduous forests occurring under conditions warm enough for warm-temperate broad-leaved evergreens but with winter temperatures too low for evergreens. These forests are composed especially of *Quercus* species and occur in the drier, somewhat more continental climates of interior Honshū, especially around Nagano and Ueda, where summers are warm enough (WI > 85°) but winters are too cold (CI < −10°) for evergreen broad-leaved forest. Minimum winter temperatures in these areas can go below −15°C (but not below −20°C); mean annual temperature is around 11°C, and average annual precipitation may be 900–1100 mm, which is low for Japan.

This description also fits some regions in middle China and southern Korea, and seems to describe some areas beyond Asia, such as large parts of the interior southeastern USA and parts of southern Europe. Included in particular might be the deciduous oak-hickory (*Quercus-Carya*) forests and "Southern mixed hardwoods" (Quarterman and Keever 1962) of the southeastern coastal plain of the USA (cf Braun 1950; Greller 1989); and the 'thermophilous' (e.g. Čarni et al. 2009) and 'submediterranean' (e.g. Meusel and Jäger 1989) deciduous forests across southern Europe from the Iberian peninsula to the Hyrcanian region. Note that this is not the Chinese sense of 'warm-temperate', a term applied to all temperate deciduous forests (see, *inter alia*, Hou 1983; Zhao 1986).

The collection of papers in this book, designed originally for *Braun-Blanquetia*, is from the 2011 meeting of the International Association for Vegetation Science in Lyon, as presented in a special session dedicated to understanding "warm-temperate deciduous forests" and why they occur. This current paper attempts to provide a background for this discussion by presenting relevant climatic zonation and posing questions about the ecology of such forests. For example, what are warm-temperate deciduous forests, why do they occur, why do evergreens not dominate in these forests, and what are the relative advantages of evergreenness and deciduousness in warm-temperate climates? Finally, an initial attempt is made to identify the apparent boundaries of warm-temperate deciduous forests, both climatically and in terms of the vegetation.

2 Climatic Zonation

Climatic zonation began with the basic division of the world into torrid (tropical), temperate and frigid (polar) regions by Aristotle, around 350 BC. The Earth is still usually divided in this way, into 'tropical' regions with no frost

Table 2 Basic concepts of humid temperate and adjacent climates

Main world divisions, based on frost severity and occurrence		
Tropical	No frost ever	Always warm, little temperature seasonality
Temperate	Seasonal frost	Warm summers, colder winters, frost slight to severe
Polar	Frost all year	Even summer frost; extreme day-length variation
Temperate climates, based on summer and winter temperatures		
	Warm summer	*Cool summer*
Mild winter	Warm-temperate	cool-temperate
Cold winter	Typical temperate	cool-temperate
Resulting zonation, with zonal vegetation types		*Forest type*
Boreal	Continental, with severely cold winters and pleasant summers	Coniferous
Temperate	Four distinct seasons, summers cool to quite warm, significant winter frost; generally 4 months or more >10°C	
Cool-temperate	Cool summers, winters mild to cold	Deciduous/mixed
Typical temperate	Largest region, generally subcontinental, with warm season usually 5–6 months	Deciduous
Warm-temperate	Warmer, still longer summers, usually 6–8 months; winters mild enough for evergreens (mean temperatures >0°C)	Evergreen mixed/ broad-leaved
Subtropical	Almost tropical, i.e. almost frost-free and warm [almost] all year	Evergreen broad-leaved

The three-part division in part (a) was first suggested by Aristotle and has provided the basic global framework for climate classification ever since. Humid temperate climates (part b) can be divided based on summer and winter temperature levels. Typical temperate climates are subcontinental, with warm summers and cold winters. Warm-temperate requires a milder winter, as may occur at lower latitudes or near the coast, as well as a fairly warm summer. Cool-temperate has cooler summers, which may derive from higher latitudes or oceanic effects (winters may be mild, e.g. oceanic, to quite cold). To the north (part c), boreal climates generally have more severe winters and summers not warm or long enough for temperate-zone broad-leaved trees. To the south, subtropical climates are almost tropical but still may have light frost occasionally, perhaps only a few times in a century. Some other temperature limits are suggested in the main text.

(at least in lowlands), mid-latitude or 'temperate' regions with frost increasing poleward, and 'polar' regions with frost possible at almost any time of year (Table 2). The transitions between these regions are called 'subtropical' and 'subpolar'.

Modern climate classifications are normally based either on quantitative indices for separating climate types (e.g. Köppen 1931) or on the mechanisms of atmospheric circulation that generate particular climate types (e.g. Walter 1977; cf Flohn 1950). In higher to middle latitudes of the Northern Hemisphere, both the quantitative and genetic (i.e. mechanistic) approaches recognize a polar zone with very cool, short summers (not frost-free); a boreal zone with long, severely cold winters but short, pleasant summers too warm to be truly subpolar; and a temperate zone with warm summers but still significant frost in winter (e.g. Troll and Paffen 1964; Walter 1968, 1977, 1985; Hämet-Ahti et al. 1974; Box and Fujiwara 2005, 2013).

Except in drier continental interiors, the most typical temperate climate is expressed as a humid subcontinental climate with warm summers, cold winters with significant frost, and four characteristic seasons of roughly equal length. One can also recognize subtypes based on the relative warmth or coldness of the summers and winters:

- a cool-temperate climate, with cooler summers (often oceanic, with mild or cold winters); and
- a warm-temperate climate, with milder winters, warmer summers, and a longer growing season.

Forests in the typical-temperate and cool-temperate regions are usually deciduous, while forests in warm-temperate regions are at least potentially evergreen (broad-leaved), unless winters are too cold. Mild winters generally have mean temperatures above freezing (perhaps well above) and no persisting snow cover. Winters too cold for evergreen forest generally have mean temperatures below about −1°C (Fujiwara 1982) or absolute minima below about −15°C (Woodward 1987; Box 1995; cf Sakai 1971).

On the other hand, Japanese writers traditionally recognized only two temperate subdivisions, warm and cool, though a "middle temperate zone" was also suggested (e.g. Yamanaka 1956). The Chinese zonation also recognizes two subdivisions, cold-temperate and warm-temperate, but uses the terms quite differently. The global zonation of Walter (1977) also recognized only two types, warm-temperate and nemoral, with the latter corresponding more to the cooler, higher-latitude climates of Europe.

On continental east sides, mid-latitude climates tend to be more continental and the humid temperate zone broader (cf Box 1995; Box and Fujiwara 2013). Both vegetation and climatic patterns over the large north-south extent of deciduous forests, especially in eastern North America and most of East Asia, argue strongly for the division into three sub-zones:

- a cool-temperate zone with cooler summers (due to higher latitude or oceanic influence), usually with significant admixtures of non-boreal conifers such as *Pinus koraiensis* or *P. strobus*;
- a main, generally subcontinental 'typical temperate' zone, with four seasons of roughly equal expression and more completely deciduous forests (without conifers at maturity); and
- a warm-temperate zone with milder winters, quite warm-sultry summers, and normally evergreen broad-leaved forests as the zonal vegetation, unless winters are too cold.

Logic suggests that the typical temperate should represent the widest portion, with cool and warm-temperate as smaller sub-zones possessing some transitional character.

This three-part zonation is used here because it conforms better to all parts of the Northern Hemisphere. By this scheme, most of Hokkaidō is cool-temperate and the northern half of Honshū is typical temperate (i.e. the range of lowland or foothill *Fagus* forests); Manchuria (including the Russian Far East) and subhumid southeastern (Chinese) Mongolia are mostly cool-temperate and much of North China is typical temperate; Korea is mainly cool-temperate in the north and typical temperate in the middle and south. To the south, much of eastern China, southern Japan, and the southern coast of Korea are warm-temperate, with evergreen broad-leaved forests unless winters are too cold. Eastern North America fits this three-part scheme well, with a large typical-temperate region in the middle (cf Greller 1989); it would not fit the two-part scheme because cool-temperate (cool summers) would apply only to New England and adjacent, but mild winters (warm-temperate) do not appear (southward) until one reaches the southeastern coastal plain, leaving a large (typical temperate) gap in between. Europe is mostly cool-temperate north of the Alps, due to the higher latitude and oceanic influence, but typical temperate to warm-temperate in the submediterranean south. In mountains of the temperate zone, the montane belt corresponds generally to cool-temperate (with mixed forests) in the typical temperate zone and to typical temperate (with more completely deciduous forests) in the warm-temperate zone. Subalpine belts correspond generally to boreal (with conifer forests), and alpine belts (above treeline) correspond to the polar zone, with treeless vegetation.

3 Warm-Temperate Regions

Warm-temperate climates are thus normally understood to be mostly humid temperate climates with:

- warmer summers and a longer growing season; and
- milder winters, with mean temperatures above freezing and no persistent snow cover.

The warm-temperate climate was included in Walter's system of world climate types, but as a type V that could occur on both the west and east sides of continents (cf Walter and Lieth 1960–1967). Various authors have recognized this one (and only) logical flaw in Walter's system and have separated type V into a 'marine west-coast' climate resulting from pervasive oceanic influence at higher latitudes on the windward west sides of land masses; and a warmer, truly 'warm-temperate' type found at lower latitudes on east sides of land masses. Our concept herein is the latter, involving zonal laurophyll forests, as in East Asia, southern Brazil, northern New Zealand, and even some montane belts in the Canary Islands and small topogenic areas of the southeastern USA. The relative positions of these and all the Walter climate types are shown on an "Ideal Continent" in Fig. 1, and a full global zonation scheme based on Walter has been given by Box (2002; cf Box and Fujiwara 2005).

Within warm-temperate regions of the Northern Hemisphere (see Table 3), one can also recognize the following subdivisions and transitions (with Walter-based notations):

- a main warm-temperate region (Ve), with evergreen broad-leaved forests;
- a subtropical transition (Ve-II), with milder but also drier winters (generally still evergreen);
- a poleward transition (Ve-VI and VI-Ve), with more significant frost (becoming deciduous); and
- a transition toward drier continental interiors (Ve-VII), with somewhat colder winters and conditions generally too dry for closed forest (e.g. the evergreen oak woods of central Texas).

On continental west sides, mediterranean climates represent a thermal counterpart to warm-temperate (and subtropical), but with dry summers. Up to the point where summers become too dry, the transition from nemoral to mediterranean (VI-IV) produces 'submediterranean' conditions that can involve deciduous forest and can be quite similar to our warm-temperate deciduous concept. Submediterranean climates were characterized by Sánchez de Dios et al. (2009) as involving lower winter mean temperatures than mediterranean (-1° to +3°C) and temperatures in general, as well as annual and summer precipitation amounts, that are intermediate between nemoral and mediterranean.

In Japan, Korea, and the Russian Far East, zonation schemes have largely followed global concepts and terminology (cf Box and Fujiwara 2005, 2013; Box and Choi 2003).

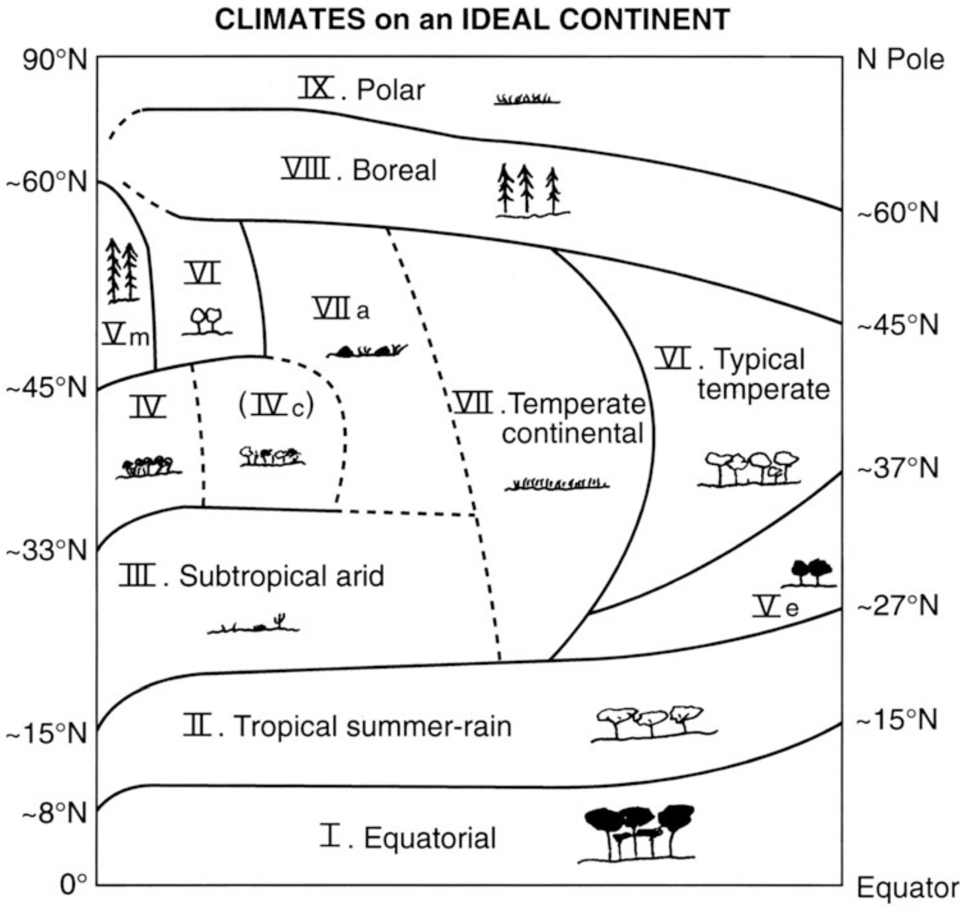


Fig. 1 Climatic regions on an ideal continent. The climates are the genetic climate types of Walter (1977; cf 1968, 1973, 1985), modified by splitting the original Walter V climate into marine west-coast (Vm) and warm-temperate east-coast (Ve) types, due to the quite different atmospheric mechanisms which produce them

Walter climate types:

I	Equatorial	Ve	Warm-temperate (east)
II	Tropical summer-rain	VI	Typical temperate
III	Subtropical arid	VII	Temperate continental
IV	Mediterranean	VIIa	Temperate arid
	c. continental	VIII	Boreal
Vm	Marine west-coast	IX	Polar

In Southern Hemisphere: Boreal does not occur and types may occur slightly closer to the Equator.

The Chinese national zonation system is quite different, however, focusing on the growing season and not the climate of the whole year (see English-language summaries by Tietze and Domrös 1987 and by Zhao 1986). The Chinese system was developed in the 1950s (Physical Regionalization Committee 1958–1959), influenced by the more northern perspective of Russian thinking of that time. The Chinese system (e.g. China Natural Geography Editorial Commission 1984) includes zones called liáng wên (温, = cool-warm), translated as cool-temperate, and nuăn wên (暖温, = warm-warm), translated as warm-temperate. The problem arises when 'cool-temperate' is applied to the zone of boreal conifer forests and 'warm-temperate' for the zone of temperate deciduous forests, including places like northern (Chinese) Manchuria, where January mean temperatures are around −20°C and extremes drop to around −40°C (see Appendix). This is not the mild winter of a warm-temperate climate and may not even seem very "temperate" at all. The climate is so ultra-continental, in fact, that the nemoral forest zone (with 4–5 warm months) is truncated in some places by the sudden appearance of permafrost and boreal forests, with no transition (Box et al. 2001).

Table 3 Types of warm-temperate climate and corresponding woody vegetation

Warm-temperate type	Walter climate	Vegetation	Examples
Humid warm-temperate (classic concept)	Ve	Evergreen broad-leaved "laurel" forests of mainly temperate tree taxa	East Asia, S Brazil, Florida (except south)
Mediterranean (thermally warm-temperate)	IV	Evergreen woods/scrub	Mediterranean region, most of California (cf submediterranean Europe, IV-VI)
Warm-temperate deciduous	VI-Ve	Deciduous forests composed of "southern" or "thermophilous" taxa	Interior Japan, interior northern-eastern China, interior southeastern USA, southern Europe
Warm-temperate mixed	Ve-VI	"Mixed" semi-evergreen forests (e.g. "southern mixed hardwoods")	Central-interior southern China, SE US coastal plain, parts of southern Europe (cf submediterranean)
Dry warm-temperate	Ve-VII	Woodlands of mainly evergreen broad-leaved trees (e.g. oaks)	Central Texas; much of Australia
Humid subtropical	Ve-II	Evergreen broad-leaved "laurel" forests of mainly (sub)tropical tree taxa	Southern China, mountains of SE Asia

The Roman numerals represent the climate types of Heinrich Walter, the most widely used genetic system of global climate types (see Walter 1977; Walter and Lieth 1960–1967; Walter and Box 1976). Warm-temperate climates (Ve) are the east-side portions of Walter's original type V, with the west-side portion called marine west-coast (Vm) (see Fig. 1; cf Box 2002; Box and Fujiwara 2013). Warm-temperate climates include the main warm-temperate zone (Ve) plus its transitions: to subtropical, with drier winters (Ve-II); to typical temperate, with still mild winters (Ve-VI) or cooler winters (VI-Ve, more completely deciduous); and to drier temperate continental (Ve-VII). Thermally, mediterranean climates are also generally warm-temperate, at least on their poleward side (subtropical toward the equator). Submediterranean climates (IV-VI) that are still humid enough for forest or woodlands may thus also represent a kind of warm-temperate climate.

Furthermore, the term 'subtropical' is applied to the entire southern half of eastern China, beginning where January mean temperatures are below 5°C.

A very useful summary of the Chinese system has been provided more recently by Fang et al. (2002), explaing how the system developed from a basis in mean temperatures through 'accumulative temperatures', potential evaporation, and heat sums such as Kira's indices. All of these, however, focus on the warm season, without reference to the low temperatures that actually limit many vegetation types and zones. General concepts and terminology should reflect conditions over the entire year, not just seasons of particular interest, such as agricultural growing seasons. Terminology and classifications should also respect the meanings of the words used: for example, regions called 'sub' should not be larger than their base regions. Some of these Chinese terms are inappropriate and out of step with global zonation systems.

Another problem involves the delimitation of the warm-temperate versus humid subtropical zones, since both normally have evergreen broad-laurophyll forests with very similar physiognomy. The difference is in the floras, as suggested in Table 4. Mature evergreen forests are composed mainly of (sub)tropical taxa in the subtropical zone but mainly of temperate taxa (e.g. *Castanopsis*, *Cyclobalanopsis*, *Persea*, *Magnolia*) in the warm-temperate zone. The transition from one flora to the other is gradual in China, making delimitation difficult. In Florida, on the other hand, the temperate flora is replaced almost completely by a subtropical flora within the north-south distance of about 100 km, beginning just south of a town appropriately named Frostproof (Crumpacker et al. 2001). In addition, after disturbance (and after some deciduous pioneers such as *Mallotus*), the secondary forest vegetation in the subtropical zone is mainly evergreen and also composed mainly of (sub)tropical taxa. The secondary forest vegetation in the

Table 4 Subtropical versus warm-temperate humid climates and vegetation

	Zonal forest (terminal stage)	Secondary forest (after pioneers)
Subtropical (Tabmin > −2°C)	Evergreen (tropical taxa)	Evergreen (tropical taxa)
Warm-temperate (Tabmin > −15°C)	Evergreen (temperate taxa)	Deciduous (temperate taxa)

Humid subtropical and warm-temperate climates both generally have evergreen broad-leaved forest as the zonal vegetation type. In addition to their limits for extreme low temperatures (Tabmin, absolute minimum temperature), these zones may also be differentiated by their secondary vegetation and their floras. In the subtropical zone, the secondary (woody) vegetation that arises after disturbance (after an initial stage of pine or other conifers) is mainly evergreen and composed of (sub)tropical taxa. In the warm-temperate zone, the secondary woody vegetation is largely deciduous and composed of temperate taxa, including many of the main trees of permanent warm-temperate forests (cf Miyawaki and Fujiwara 1983).

Table 5 Warm-temperate deciduous regions and some main taxa, especially oaks

Region	Main species	Locations	References
East Asia	*Quercus serrata*, *Q. variabilis*, *Q. aliena*, *Q. acutissima*; plus *Aphananthe aspera*, *Celtis sinensis*	Central Honshū (Japan)	Kira 1949; Karizumi 1956; Yamanaka 1956; Miyawaki et al. 1971; Miyawaki 1980–1989
		Eastern-central China	Wang 1961; Wu 1980; Chen 1995; Tang et al. 2008; You et al. 2008
		Interior Korean peninsula	Yim 1995; Kim 1990
Eastern N America	*Quercus falcata*, *Q. nigra*, *Q. phellos*, *Q. laevis*, *Q. texana* (red group); *Q. muehlenbergii* (white group); *Liquidambar*	Interior coastal plain of southeastern USA	Braun 1950; Quarterman and Keever 1962; Christensen 1988; Greller 1989; Box and Manthey 2006
Southern Europe (+ N Africa)	*Quercus pubescens*, *Q. cerris*, *Q. petraea*		Quézel and Médail 2003; Ozenda 1994
	west: *Q. broteroi*, *Q. canariensis* (semi-decid); *Q. pyrenaica*, *Q. faginea* (marcescent)	Northern Iberian peninsula	Morla and Pineda 1985; Moreno et al. 1990; Sánchez de Dios et al. 2009
	N Afr: *Q. afares* (+ *Q. can.*, *Q. pyr.*)	Interior northern-central Italy	Blasi et al. 1999; Pignatti 1998
		Maghreb mountains	Quézel and Médail 2003; Tessier et al. 1994
	east: *Q. frainetto*	Interior Balkan peninsula	Horvát et al. 1974; Bergmeier et al. 2004; Čarni et al. 2009; cf Horvát 1959
Euxino-Hyrcanian region	*Quercus iberica*, *Q. macranthera*, *Q. pontica*; *Q. castaneifolia*; + *Q. pubesc.*, *Q. petraea*, *Q. cerris*; plus *Pistacia*, *Amygdalus*, *Crataegus*, *Pyrus*, *Cerasus*, *Celtis* spp. *Zagros*: *Q. brantii*, *Q. infectoria*, *Q. libani*		Zohary 1973–1974; Browicz 1978–1988,
		Northern & eastern Turkey	Ugurlu and Gökhan Senol 2005; Kavgaci et al. 2010; Kargioglu et al. 2011; Ugurlu et al. (in press)
		Colchis, S slopes of Caucasus southern Azerbaijan	Nakhutsrishvili 2012; Klein and Lacoste 1989; Scharnweber et al. 2007
		Hyrcanian Iran	Akhani et al. 2010; Zohary 1963
		"Zagros gap"	Blumler (herein - a)
California-Oregon	*Quercus lobata*, *Q. douglasii*, *Q. kelloggii*, *Q. garryana*; *Q. engelmannii* (semi-evergr.)	Foothills around central valley and in southern Oregon	Barbour et al. 2007; Mensing 2005–2006; Blumler (herein - b)
Mexico	*Quercus xalapensis*, *Q. eduardii* (red group); *Q. insignis* (white group); *Liquidambar*, *Carpinus*	Mid-elevations of Sierra Madre Oriental	Kappelle 2006; Borchert et al. 2005; Rzedowski 1978; Miranda and Sharp 1950

The East Asian species dominate both permanent warm-temperate deciduous forests and secondary stages leading to zonal evergreen laurel forests. In the US, *Q. phellos* and *Q. nigra* are both "tardily deciduous" (the latter semi-evergreen toward the south). In the Middle East, *Q. macrolepis* and *Q. ithaburensis* are both at least semi-evergreen.

warm-temperate zone, on the other hand, is mainly deciduous and involves temperate taxa such as *Quercus serrata* and *Q. variabilis* in East Asia or *Q. nigra* in Florida, which are also major species of the (persisting) warm-temperate deciduous forests in these regions (cf Miyawaki et al. 1971).

4 Warm-Temperate Deciduous Regions and Taxa

Warm-temperate climates differ from "typical temperate" or nemoral climates by having milder winters, which permit evergreen broad-leaved forests to be seen as the zonal vegetation type, as in the case of the laurel forests of East Asia and southern Brazil. Warm-temperate deciduous forest areas with colder winters, however, do occur and can be expected in transitions from nemoral climates with deciduous forests (e.g. the Euro-Siberian region) to warmer, more southern regions with evergreen broad-leaved vegetation. The main potential regions of warm-temperate deciduous forest are shown in Table 5 and include East Asia, southeastern North America, and southern Europe; the Southern Hemisphere has no warm-temperate deciduous forests because summers are too cool. Also shown in Table 5 are the main deciduous (including semi-deciduous) tree taxa and literature descriptions of the local vegetation.

The most important single taxon is the deciduous oaks (*Quercus*, s.s.), which are the canopy dominants or co-dominants in all of the warm-temperate deciduous forest regions. Oaks are apparently well adapted to these climates, perhaps because their somewhat thicker, more reinforced leaves (usually with a distinct cuticle) permit exploitation of the margins (especially autumn) of the potentially longer growing season. Canopy trees in these transitional forests are largely deciduous, but understoreys (and occasionally canopies) may have evergreen elements. In Japan, the warm-temperate deciduous forest zone was conceived as occupied mainly by deciduous *Quercus* forests, and a

Castanea crenata-Quercus serrata association was recognized in central Honshū (Karizumi 1956). Major warm-temperate deciduous species in East Asia include *Q. acutissima*, *Q. aliena*, *Q. serrata* and *Q. variabilis*, plus *Q. wutaishanica* (s.l.) in China (see also Menitsky 2005 for all Asian oaks).

In eastern North America, some tree species span the entire north-south range of deciduous forests, including *Fagus grandifolia*, *Quercus alba* and *Q. rubra*, several *Carya* species, and *Acer rubrum*. Other species have distinctly "northern" or "southern" ranges, in genera including *Quercus*, *Acer*, *Fraxinus* and *Tilia* (cf Daubenmire 1978). For example, *Quercus rubra* (northern red oak) is replaced southward by *Q. falcata* (southern red oak). Many other such examples of northern and southern species can be found among the range maps of Little (1971–1978). The same is true of *Fagus*, *Quercus*, and some other deciduous tree genera in Japan. Even so, there appear to be few real vicariant oak species between East Asia and eastern North America. *Q. aliena* is called 'Oriental white oak' in English but has a much more limited north-south range than 'white oak' (*Q. alba*) in eastern North America. Furthermore, many of the warm-temperate deciduous candidates in eastern North America, including *Q. coccinea*, *Q. falcata* and *Q. velutina*, are in the red-oak group *Erythrobalanus*, which is endemic to the Western Hemisphere (see Miller and Lamb 1985 for North American oaks). *Liquidambar styraciflua* also seems to be a good warm-temperate deciduous candidate in eastern North America (cf *L. formosana* in southeastern China).

In Europe, the two main oak species over much of the continent are *Quercus robur* and *Q. petraea*, the ranges of which overlap widely except for the extension to the Ural Mountains by *Q. robur*. If the climatic envelope of *Q. petraea* is projected onto eastern North America, it spans the typical temperate and warm-temperate deciduous areas, almost as widely as does *Q. alba* (Box and Manthey 2006). This, and its range in Europe, both suggest that Q. *petraea*, like *Q. alba*, is not exclusively a warm-temperate deciduous species, although both can function as such (see also Pedrotti herein). *Q. pubescens*, on the other hand, and despite its complicated taxnomy (see Guarino et al. herein;Wellstein and Spada herein), seems to be a true warm-temperate deciduous species, along with other candidates such as *Q. cerris*, *Q. pyrenaica*, *Q. faginea*, and *Q. frainetto*. The climatic envelopes of these species generally project onto eastern North America as "southern" species, as shown in Fig. 2 for *Q. pubescens*. Mosaics involving *Q. robur* and the more southern *Quercus* species are described from Portugal by Costa et al. (herein). Geographic distribution types of Mediterranean-central European taxa were described by Jäger (1970).

Several features of deciduous oaks can be seen as possible adaptations to the intermediate position of warm-temperate deciduousness. One such feature is marcescence, by which trees (mainly oaks) retain withered brown leaves through the winter (e.g. *Q. pubescens*, *Q. pyrenaica*, *Q. faginea*). This may have functional value in submediterranean climates, as explained by García-Mijanos et al. (herein) and commented on by other authors in this book. Another possible adaptation, in the southeastern USA, is the "tardy deciduousness" shown by *Quercus nigra* and *Q. phellos*, whose leaves do not turn completely brown and drop (if at all) until December. These two species have entire leaves, however, like most evergreen oaks, and may represent a more truly transitional position between evergreenness and deciduousness. Finally, irregular or incomplete deciduousness has also been suggested as a more general characteristic of some deciduous oaks, including semi-deciduous *Q. canariensis* and even *Q. suber* (cork oak, normally considered evergreen) in some Mediterranean areas (see Schirone et al. herein). Sclerophylly and semi-deciduousness were interpreted by Sánchez de Dios et al. (2009) as mediterranean features, marcescence as submediterranean, and truly deciduous leaves as Euro-Siberian, i.e. nemoral. (Note that the marcescent oaks are called semi-deciduous, however, by del Río and Penas 2006, and probably also by some others.) The spread of deciduous oaks in Europe since the last glaciation has been summarized by Brewer et al. (2002).

Evergreenness versus deciduousness is essentially a functional tradeoff involving the potentially higher photosynthetic rates of malacophyllous deciduous leaves versus the potentially longer growing season of evergreen leaves. This calculus is tempered, though, by several other factors, such as the greater nutrient requirements for building deciduous leaves; the extra energy storage required to do this each spring (before photosynthetic gains can be realized); the potentially longer lifespans and water-loss control of evergreen leaves; and the inhibition at low temperatures of the water uptake needed by evergreens in winter (e.g. Chabot and Hicks 1982; Aerts 1995; Givnish 1986, 2002; Villar and Merino 2001). Such 'physiological drought' can occur at low but above-freezing temperatures and may mark the northern limit, for example, of "southern pines" in the eastern USA (Hocker 1956). Of course, climatic winter dryness may limit many evergreen trees on their tropical side, as in the monsoonal climates of south and southeast Asia. Insights into physiological advantages of evergreenness versus deciduousness have been given recently, among many others, by Cavender-Bares et al. (2005) and by Baldocchi et al. (2010). Growth and phenological patterns have been explained by Tessier et al. (1994) and by Dhaila et al. (1995); topographic effects have been demonstrated by Isogai (1994). Particular advantages of evergreenness have been summarized by Aerts (1995) and of deciduousness in mediterranean environments by Blumler (1991). A general

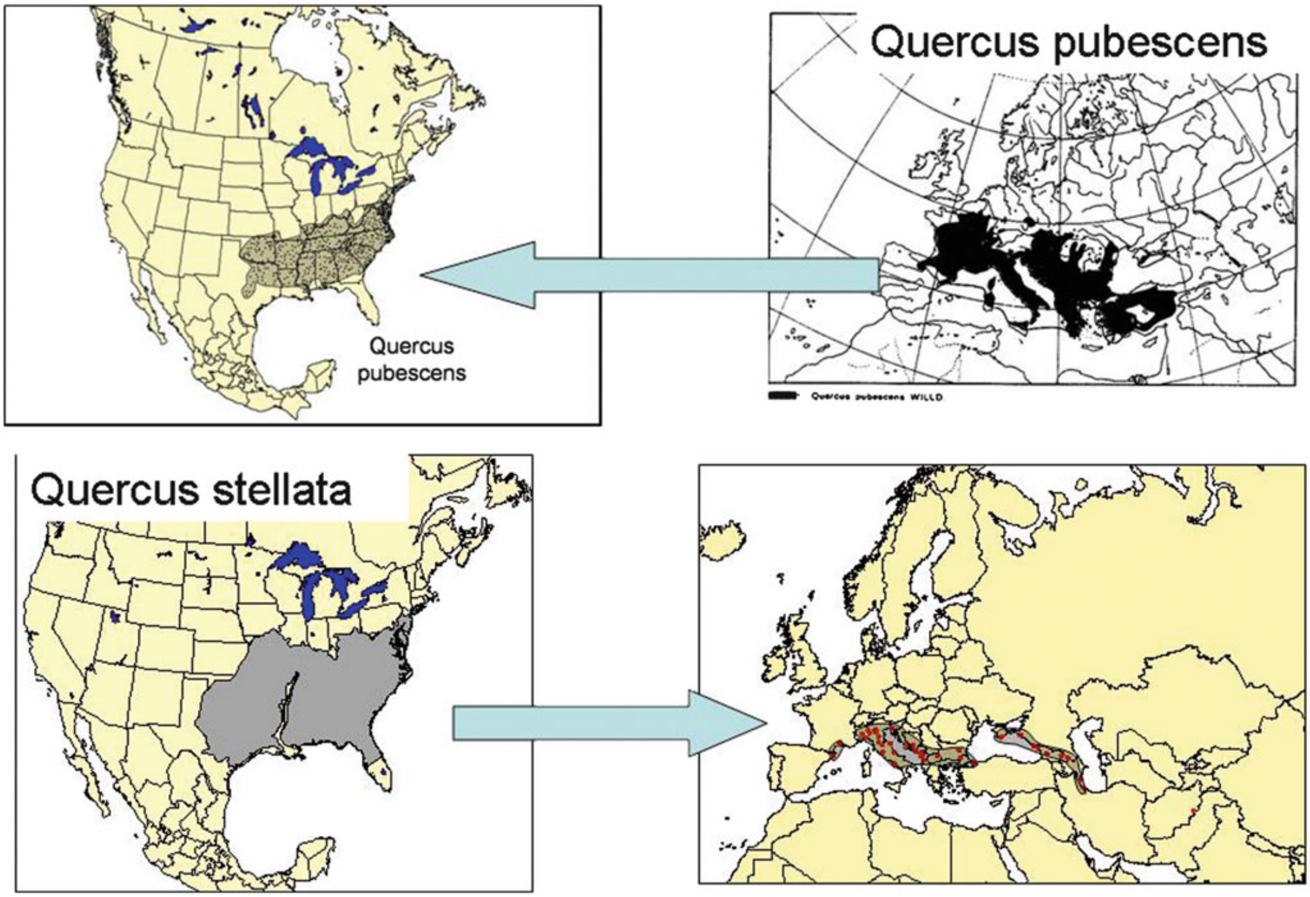


Fig. 2 Cross-projections of oak species between Europe and eastern North America. The top portion shows *Quercus pubescens* from mainly southern Europe. When its climatic envelope is projected onto North America, it appears as a largely "southern" species, corroborating its designation as perhaps the quintessential warm-temperate deciduous species of Europe. The bottom portion shows *Quercus stellata*, which spans the typical and warm-temperate regions in eastern North America but co-dominates only in drier areas further west (Missouri, eastern Oklahoma, eastern Texas). The projection of its climatic envelope onto Europe covers only a small area, coinciding with areas often called submediterranean. This projection of climatic envelopes is explained in Box and Manthey (2006), where other cross-projections are also shown

"solution" to the "triple paradox" of evergreen versus deciduous leaves has been proposed by Givnish (2002). Some of these ideas and other relative advantages and disadvantages of evergreen versus deciduous habits are listed in Table 6 and will be discussed by other authors in this book.

5 Vegetation Boundaries in Temperate Forest Regions

Hypothesized regions of warm-temperate deciduous forest and their main canopy tree species were shown in Table 5. These include not only East Asia and the southeastern USA but also some deciduous forests in warmer areas of southern Europe and in the Middle East, and perhaps even North Africa. Such forest regions should be recognizable by vegetation boundaries as well as by climatic conditions.

In Japan there is a clear difference between cool-temperate (into typical temperate) regions dominated by *Fagus* or by *Quercus crispula* (= *Q. mongolica* var. *grosseserrata*) to the north and more southern regions where deciduous forests are dominated by other oak species, especially those that may be replaced eventually by evergreen (broad-leaved) trees in the warm-temperate zone. These latter oaks include *Q. serrata*, *Q. variabilis*, *Q. aliena*, and *Q. acutissima*. In Manchuria and parts of northern China there is also a cool-temperate (to typical temperate) region of dominance by *Q. mongolica* (*s.s.*) and a region to the south (across north-central China) involving the same group of "warm-temperate" oaks as in Japan, plus *Q. wutaishanica* (which now includes *Q. liaotungensis*). These regions have been identified from extensive fieldwork and are shown on the map by Fujiwara and Harada (herein; cf Fujiwara et al. 2008; You et al. 2008). A recent attempt has been made (Zhao and Tian 2001; cf Wu and Raven 1999) to combine

Table 6 Advantages and disadvantages of deciduousness

Advantages
Dropping leaves avoids water loss in unfavorable season: cold winter or tropical dry season; may also permit evasion of late-summer drought (if enough reserves stored)
Softer leaves (malacophylls), with higher gas-exchange rates: thus higher photosynthesis and potential growth rates (may be especially important for establishment of young plants)
Leaflessness reduces water loss in winter/dry season, leaving more water in soil for beginning of growing season
Malacophylls are generally more shade-tolerant, so deciduous can grow up under sclerophylls and conifer (coriaceous) and replace them
Disadvantages
Deciduous plants are not "present" at beginning of the growing season and may lose their space to evergreens
Deciduous plants must produce new leaves each year and thus do not use the whole growing season for positive photosynthesis and net growth
Malacophylls require more nutrients to build, especially nitrogen, than do most evergreen leaves, which are lignin-rich but nutrient-poor
Malacophylls decompose faster and may facilitate faster net loss of nutrients from systems
Soft malacophylls need more water than "harder" evergreen leaves (except laurophylls)
Malacophylls are generally intermediate in shade tolerance and so can be replaced by highly shade-tolerant laurophylls

For more consideration of the advantages and disadvantages of the deciduous versus evergreen habit, see *inter alia*, Baldocchi et al. 2010; Sánchez de Dios et al. 2009; Cavender-Bares et al. 2005; Givnish 2002; Damesin et al. 1998; Zobel and Singh 1997; Aerts 1995; Dhaila et al. 1995; Isogai 1994; Tessier et al. 1994; Blumler 1991; Meusel and Jäger 1989; Monk 1966.

these last two taxa with *Q. mongolica* into a single species, but this may not have considered their ecological differences sufficiently.

In eastern North America, the major discontinuity is suggested graphically by a figure (from Daubenmire 1978, pp. 121, 132) that depicts typical ranges for "northern" tree species such as *Acer saccharum* (sugar maple, as on the Canadian national flag) versus "southern" species such as *Q. laurifolia* (more evergreen in the southern part of its range). The southern deciduous forests have been called the Oak-Hickory-Pine region (Braun 1950), 'southern mixed hardwoods' (Quarterman and Keever 1962), 'warm-temperate mixed forests' (Lieth 1975), and the 'deciduous-evergreen-coniferous region' (Greller 1989). Some "southern" deciduous species also reappear disjunctly in montane belts of the Sierra Madre Oriental of eastern Mexico, where they can be almost evergreen (Rzedowski 1978; Velázquez et al. 2000; cf Borchert et al. 2005). Warm-temperate deciduous and evergreen woods overlap in many places, including central Texas (van Auken et al. 1981).

In southern Europe, deciduous forests in warmer areas have been called 'thermophilous' (e.g. Dimopoulos et al. 2005; Čarni et al. 2009) or, where summers are drier, 'submediterranean' (e.g. Schmithüsen 1968; Meusel and Jäger 1989; Sánchez de Dios et al. 2009). In Europe, the major discontinuity in deciduous forests is between forests of *Fagus sylvatica* or *Q. robur* to the north and the more southern deciduous forests dominated mainly by *Q. pubescens*, *Q. cerris*, or *Q. petraea* (or by *Q. broteroi* or *Q. pyrenaica* in Iberia, by *Q. frainetto* in the Balkans, or by *Q. iberica* in Georgia). The idea that these species are more "southern" or thermophilous was corroborated by projecting their climatic envelopes onto eastern North America, where they coincided largely with the ranges of "southern" American species (see Fig. 2; Box and Manthey 2006). The main regions of these warmer-climate deciduous forests in southern Europe are across northern Iberia (where not too dry); from submediterranean southern France to Insubria and southward into interior peninsular Italy; in lower and more southern parts of the Balkan Peninsula; and in small areas of the Euxine-Hyrcanian region. In these areas, the deciduous oak forests involving species other than *Q. robur* are to be found especially on south-facing slopes (Franco Pedrotti, personal communication). Perhaps the most detailed description of Balkan thermophilous forest, with phytosociological tables, has been given in the recent book on *Forest Vegetation of the Galičica Mountain Range*, in Slavic northern Macedonia, by Matevski et al. (2011).

6 Recognizing Temperate Climatic Subregions

Most of the climatic factors that limit regional ranges of warm-temperate deciduous trees involve aspects of temperature, especially winter mean temperatures and absolute minima (cf Wolfe 1979). The ranges of putative warm-temperate deciduous species also correlate with summer mean temperatures, although this apparent threshold effect may be only a surrogate for the longer warm period. In some cases forests are limited by drier conditions, usually toward continental interiors. Where winters become milder in East Asia, the deciduous trees are simply replaced by evergreen (broad-leaved) tree species. In Manchuria and northern Japan (and upward in mountains), warm-temperate deciduous trees are limited mainly by cooler, shorter summers (but also in some cases by colder winters). In the southeastern USA, the situation is similar except that winter mean temperatures are much higher than at the same latitudes in East Asia and there is never any persisting snow cover. Evergreen broad-leaved trees are precluded in the southeastern USA mainly by unusual low-temperature events (Box 1995 and herein). Even so, warm-temperate deciduous trees also occur much less where extremes go below about −24°C. Finally, the higher latitude and windward west-side position of Europe mean that its summers are somewhat cooler than in East Asia or eastern North America. These relationships, for selected temperate-zone sites, can be seen from the climatic data in the Appendix at the end of this book.

Along temperature gradients from north to south, areas of relatively rapid temperature increases may also suggest climatic boundaries. Identifying such climatic "breaks" can be useful, especially since quantitative values for climatic variables will be necessary for modeling and mapping climatic regions. Climatic data for representative sites in the three main temperate forest regions of the Northern Hemisphere are given in Tables 7, 8 and 9. The data include temperature levels, values of Kira's Warmth and Coldness Indices, the number of consecutive warm months (mean above 10°C), and the annual climatic moisture balance (precipitation versus potential evapotranspiration). The three main deciduous forest regions are considered below, with the sites in Tables 7, 8 and 9 also showing the climate type suggested.

(a) **East Asia**

In Japan (see Table 7: top section of sites), southern Hokkaidō is significantly warmer than most of the island, which does not reach 21°C for the warmest month (Tmax), has only 4–5 warm months (Lwarm), and has much colder winters (cf Tmin and Tabmin). There is an even larger "break", though, between southern Hokkaidō and the northern tip of the main island Honshū, where warm-month mean temperatures immediately exceed 23°C, there are at least 6 warm months, and WI exceeds 70 (and soon exceeds Kira's threshold of 85 for warm-temperate). Another "break" appears in central Honshū, at around 25°C for Tmax, south of which there are at least 7 warm months, mean January temperature is above freezing, and WI exceeds 100, except at inland sites like Nagano (which was Kira's prototype for warm-temperate deciduous). Taken together with vegetation patterns, these thresholds suggest the following scheme:

- Cool-temperate if Tmax is below 22°C (perhaps 21°C), WI is below 60, only 4–5 months are warm (mean above 10°C), and winter mean temperatures are well below freezing; this is the zone of *Quercus crispula* woods (*Q. mongolica* var. *grosseserrata*) over most of lowland Hokkaidō (although with no *Fagus*) and corresponds to the mainland zone of *Q. mongolica* with *Pinus koraiensis*;
- Typical temperate if Tmax is above 22°C but below 25°C, WI is > 60 and there are 6 warm months but cold-month means are still below freezing (e.g. Hakodate, Aomori, Sendai); this is the zone of *Fagus* forests over southernmost Hokkaidō and most of lowland Tōhoku (northern half of Honshū), including also the lower and middle elevation of mountains; and
- Warm-temperate if Tmax approaches or exceeds 25°C, WI is above Kira's threshold of 85 (mostly above 90 or more), at least 7 months are warm, and winter monthly mean temperatures are generally above freezing; this is the zone of evergreen broad-leaved forests dominated by various *Castanopsis* spp and *Machilus* (*Persea*) *thunbergii* – except for sites like inland Nagano, where Tmin is still below freezing.

Let us compare this scheme with the other regions.

In Manchuria (Russian Far East, Heilongjiang, and northernmost Korea), Tmax is < 22°C, WI is < 60, only 4–5 months are warm, and Tmin is far below freezing, generally below -15°C; this is the cool-temperate mixed forest zone with *Quercus mongolica*, often *Pinus koraiensis*, and species-rich mesophytic forests of "Manchurian species" where the climate is truly humid (cf Box and Fujiwara 2013).

In peninsular Korea Tmax is generally < 25°C in the north and > 25°C in the middle and south, with WI, warm months and winter mean temperatures generally following the patterns suggested above. This divides peninsular Korea into a typical-temperate north and middle, with deciduous *Quercus* forests (still recovering slowly from the Korean War); and a warm-temperate deciduous south, with *Q. serrata*, *Q. variabilis*, and other typically warm-temperate oaks, as in Japan and China. Only the south-coastal strip is warm-temperate evergreen (e.g. Pusan), where mean cold-month temperatures are above freezing and the absolute minimum does not go below about -15°C.

In northeastern China, most of Jilin and Liaoning have Tmax > 22°C, with at least 5 warm months, and so can be called typical temperate; *Q. mongolica* still occurs here, but other oaks also appear as one goes southward. Southernmost Liaoning is already much less severely cold in the winter and summers become warmer (WI > 85, usually 6 warm months), with Tmax surpassing 25°C (and with 7 warm months) in Shandong, around Beijing, and westward through Shanxi and Shaanxi (cf Xian); this is a region of warm-temperate deciduous oak forests (e.g. Wu et al. 1980, Chen 1995; Fujiwara et al. 2008). *Q. mongolica* occurs throughout most of northern China and has been considered both a cool-temperate and typical-temperate species (Box and Fujiwara 2013). Finally, southern China has Tmax generally > 27°C, at least 8 warm months, WI > 120, and mean winter temperatures above freezing; this is the region of evergreen broad-leaved forests, which appear climatically to be warm-temperate (WI below Kira's 180 threshold and

Table 7 Climatic data and interpreted climate types for selected sites in East Asia

	Lat	Elev	Tmax	Tmin	Tabmin	WI	CI	Lwarm	MIy	Type
Asahikawa (Hokkaidō)	43.8	114	20.8	−9.2	−41.0	60	−50	5	2.01	Cool
Sapporo (SW Hokkaidō)	43.0	17	21.4	−5.5	−28.5	65	−35	6	1.91	Typical
Hakodate (S peninsula)	41.8	33	21.9	−3.7	−21.7	68	−27	6	2.00	Typical
Aomori (N tip Honshū)	40.8	3	23.5	−2.7	−24.0	79	−23	6	2.22	Typical
Sendai (N Pacif Honshū)	38.3	39	24.7	0.7	−20.2	94	−10	6	1.74	WT-decid
Yamagata (N Honshū)	38.3	153	25.1	−1.4	−20.0	93	−18	6	1.81	WT-decid
Nagano(central Honshū)	36.7	418	25.6	−1.3	−17.0	98	−16	7	1.41	WT-decid
Tōyama (Japan Sea side)	36.7	9	26.5	2.0	−13.1	110	−5	8	2.90	EG-BL
Yokohama (Tōkyō Bay)	35.4	39	26.5	4.6	−8.2	120	−0.5	8	1.92	EG-BL
Kyōto(Kansai)	35.0	41	26.8	2.9	−11.9	114	−3	8	1.87	EG-BL
Blagoveshchensk (Amur)	50.3	132	21.5	−23.9	−45.0	57	−114	5	0.97	Cool
Hailar (Khingan Mtns)	49.2	650	20.2	−27.3	−49.3	50	−134	4	0.69	Cool
Khabarovsk (Amur)	48.5	86	21.2	−21.8	−43.0	59	−100	5	1.11	Cool
Harbin (Heilongjiang)	45.7	151	23.1	−19.6	−42.4	69	−87	5	0.92	Typical
Nikolsk-Ussuriysk (Prim)	43.8	46	21.1	−19.8	−36.8	59	−85	5	1.16	Typical
Vladivostok (Primorye)	43.1	138	20.3	−13.7	−31.0	56	−63	4	1.39	Cool
Hyesan (NE Korean mtns)	41.4	714	20.6	−16.7	−35.8	58	−74	5	1.13	Cool
Kimchaek (NE coast)	40.7	19	22.1	−5.8	−23.8	70	−33	6	1.21	Typical
Pyongyang (N peninsula)	39.0	36	24.3	−7.8	−30.0	90	−36	6	1.40	Typical
Seoul AP (mid-peninsula)	37.6	18	25.3	−3.6	−24.4	100	−21	7	1.92	WT-decid
Pusan (S Korea)	35.1	69	25.8	2.4	−14.0	113	−4	8	1.75	EG-BL
Shenyang (Liaoning)	41.8	45	24.7	−12.3	−33.1	87	−55	5	1.09	Typical
Dalian (S Liaoning)	38.9	97	24.2	−5.0	−21.1	92	−28	6	0.92	Typ/WT-d
Beijing	39.9	52	26.1	−4.5	−27.4	107	−25	7	0.83	WT-decid
Qingdao (Shandong)	36.1	79	25.2	−1.3	−17.6	101	−15	7	0.95	WT-decid
Xuzhou (N Jiangsu)	34.3	4	27.3	−0.2	−18.3	122	−11	7	0.93	WT-decid
Xian (Shaanxi)	34.3	412	27.0	−0.6	−20.6	116	−12	7	0.72	WT-decid
Nanjing (Jiangsu)	32.0	15	27.9	2.3	−13.8	129	−4	8	1.11	EG-BL
Shanghai	31.2	12	27.6	3.3	−12.1	128	−2.3	8	1.25	EG-BL
Wuhan (Hubei)	30.6	23	28.9	3.5	−13.0	141	−1.5	9	1.23	EG-BL
Fuzhou (Fujian)	26.1	20	29.0	11.1	−6.0	180	0	12	1.17	EG/Subtrop
Guangzhou (Guangdong)	23.1	18	28.5	13.5	−2.0	203	0	12	1.29	Subtrop
Chengdu (Sichuan)	30.7	498	25.8	5.8	−6.0	137	0	9	0.99	EG-BL
Chongqing (W-central)	29.6	259	29.2	8.1	−3.1	165	0	9	0.99	EG-BL
Kunming (Yunnan)	25.0	1893	19.9	8.4	−7.0	119	0	10	1.12	EG-BL
Simao (S Yunnan plateau)	22.8	1300	22.5	12.8	−2.5	163	0	12	1.35	Subtrop

Climate types are interpreted, based on apparent threshold values in the data:
Cool = Cool-temperate (deciduous, with Tmax < 21°C)
Typical = Typical temperate (deciduous, with Tmax ≥ 21°C)
WT-decid = Warm-temperate deciduous (with Tmax > 24°C; at least 6, usually 7 warm months)
EG-BL = Warm-temperate evergreen (with Tabmin ≥ −15°C but lower Tmax threshold, as at Kunming)
Subtrop = Subtropical (with Tabmin ≥ −3°C but also a lower Tmax threshold, as at Simao)
Other abbreviations:
Lat = latitude
Elev = elevation (m)
Tmax (Tmin) = mean temperature of warmest (coldest) month (°C)
Tabmin = absolute minimum temperature (°C, coldest ever measured; ! = estimated lower)
WI (CI) = Kira's warmth (coldness) index
Lwarm = number of consecutive warm months (monthly means > 10°C)
MIy = annual moisture index (precipitation / potential evapotranspiration)

absolute minima still below about -3°C) until one reaches Guangdong, perhaps southern Fujian, and the lowlands south of the Yunnan Plateau. In China, unlike Florida, there is not enough information to show a clear discontinuity between the temperate flora of the warm-temperate zone and the (sub)tropical flora of the subtropical zone.

Table 8 Climatic data and interpreted climate types for selected sites in Eastern North America

	Lat	Elev	Tmax	Tmin	Tabmin	WI	CI	Lwarm	MIy	Type
Québec (SE Québec)	46.8	90	19.5	−11.8	−36.7	54	−64	5	2.15	Cool
Montréal (S Québec)	45.5	57	21.2	−9.9	−33.9	67	−51	5	1.77	Typical
Boston, Massachusetts	42.4	6	21.8	−2.6	−27.8	76	−23	6	1.73	Typical
Hartford, Connecticut	41.9	53	23.0	−3.5	−32.2	84	−24	6	1.73	Typical
New York (city)	40.8	39	24.3	−0.4	−26.1	95	−15	7	1.62	Typ/WT-d
Baltimore, Maryland	39.3	4	25.7	1.5	−21.7	110	−8	7	1.35	WT-decid
Charlottesville, Virg.	38.0	265	24.7	2.0	−23.3	110	−7	7	1.45	WT-decid
Raleigh-Durham, N Car.	35.9	132	25.6	4.7	−22.8	123	−0.3	9	1.28	WT-decid
Columbia, S Carolina	34.0	74	27.1	7.9	−18.9	152	0	9	1.08	WT-decid
Athens, Georgia	33.9	246	26.5	5.7	−20.0	138	0	9	1.27	WT-decid
Cape Hatteras, N Carol.	35.3	2	25.6	7.7	−14.4	140	0	9	1.44	EG-BL
Charleston, S Carolina	32.8	3	27.7	10.1	−12.2	168	0	12	1.09	EG-BL
Savannah, Georgia	32.1	15	27.6	10.5	−16.1	171	0	12	1.08	EG-BL
Pensacola (NW Florida)	30.5	36	27.5	11.4	−15.0	179	0	12	1.30	EG-BL
Gainesville (N Florida)	29.6	29	27.3	12.7	−14.4	187	0	12	1.08	EG-BL
Tampa (mid-Gulf Florida)	28.0	8	27.9	15.9	−7.8	206	0	12	0.96	EG-BL
Miami (S Florida)	25.8	3	28.2	19.8	−2.8	231	0	12	1.03	Subtrop
Banner Elk (N Carolina)	36.2	1143	19.1	0.5	−35.0	70	−12	6	2.20	Cool
Bluefield (W Virginia)	37.3	881	21.3	−0.7	−29.4	86	−13	7	1.48	Typical
Toronto (Ontario)	43.7	116	20.8	−5.1	−32.8	67	−35	5	1.40	Cool
Madison, Wisconsin	43.1	263	22.4	−8.2	−38.3	76	−43	6	1.29	Typical
Pittsburgh, Pennsylvania	40.5	367	23.2	−1.1	−30.0	90	−16	7	1.36	Typical
Indianapolis, Indiana	39.7	243	24.0	−2.9	−32.8	94	−19	7	1.46	Typ/WT-d
Cincinnati, Ohio	39.1	232	24.5	−1.4	−27.2	103	−15	7	1.42	WT-decid
Kansas City, Missouri	39.3	312	25.7	−2.5	−30.6	101	−18	7	1.28	WT-decid
St.Louis, Missouri	38.7	174	26.3	−0.4	−30.6	112	−13	7	1.24	WT-decid
Lexington, Kentucky	38.0	298	24.6	0.5	−29.4	105	−10	7	1.49	WT-decid
Nashville, Tennessee	36.1	180	26.7	4.3	−27.2	129	−0.7	8	1.28	WT-decid
Little Rock, Arkansas	34.7	78	27.7	3.9	−25.0	139	−1.1	9	1.31	WT-decid
Oxford, Mississippi	34.4	116	26.7	5.2	−25.0	137	0	9	1.39	WT-decid
Montgomery, Alabama	32.3	67	27.6	8.1	−20.6	160	0	10	1.23	WT-decid
Mobile, S Alabama	30.7	66	27.3	10.6	−18.3	173	0	12	1.40	WT-decid
Biloxi, S Mississippi	30.4	5	27.8	10.9	−17.2	177	0	12	1.31	EG-BL
Baton Rouge, Louisiana	30.5	20	27.8	11.3	−16.7	180	0	12	1.25	EG-BL
Tulsa, Oklahoma	36.2	206	28.5	2.2	−26.7	133	−4	8	1.06	WT-decid
Dallas, N Texas	32.8	134	30.0	7.2	−22.2	168	0	9	0.82	WT-decid
Austin, central Texas	30.3	193	29.3	9.7	−18.9	182	0	11	0.68	WT-decid

Climate types are interpreted, based on apparent threshold values in the data:
Cool = Cool-temperate (deciduous, with Tmax < 21°C)
Typical = Typical temperate (deciduous, with Tmax ≥ 21°C)
WT-decid = Warm-temperate deciduous (with Tmax > 24°C; generally at least 7 warm months)
EG-BL = Warm-temperate evergreen (with Tabmin ≥ −15°C but lower Tmax threshold)
Subtrop = Subtropical (with Tabmin ≥ −3°C but also a lower Tmax threshold)
The other abbreviations are as in Table 7. Sites are grouped, generally from north to south, within the following regions: north Atlantic, middle and south Atlantic, southern Appalachians, northern interior, interior South, and southern Plains

(b) Eastern North America

On the east side of North America, climatic patterns (see Table 8) are much the same at corresponding latitudes as in East Asia. In the northern Atlantic area, the main break comes at around Tmax = 22°C, which separates eastern Canada and northern New England to the north (WI < 85) from the more moderate climates of southern New England, with their longer warm periods (6–7 months) and warmer summers (WI > 85). Eastern Canada and northern New England are areas of deciduous "northern hardwood" forests, especially with *Acer saccharum*, and mixed forests with admixtures of *Pinus strobus* (five soft needles, cf *P. koraiensis*), plus other more northern taxa such as *Q. rubra* and *Betula* spp. (see, for example, Barbour and Billings 1988). Southern New England already has significantly more tree

Table 9 Climatic data and interpreted climate types for selected sites in Europe

	Lat	Elev	Tmax	Tmin	Tabmin	WI	CI	Lwarm	MIy	Type
Uppsala (Sweden)	59.9	21	16.6	−4.6	−39.5	42	−40	4	1.08	Cool
Greenwich (London)	51.5	7	17.1	4.0	−14.1!	61	−1.9	6	0.98	Cool
Krakow (S Poland)	50.1	213	19.4	−3.0	−26.6	66	−23	5	1.06	Cool
Paris-Le Bourget	49.0	66	18.7	2.6	−17.0	72	−5	7	0.94	Cool
Wien (Vienna, E Austria)	48.2	203	19.6	−1.4	−22.6	71	−17	5	1.02	Cool
Dijon (Bourgogne)	47.3	222	19.8	1.7	−22.0	73	−8	6	1.10	Cool
Genève (W Switzerland)	46.2	416	18.7	−0.6	−18.4	62	−14	5	1.46	Cool
Lyon (Rhône/France)	45.7	200	20.5	2.1	−24.6	79	−7	7	1.18	Cool
Toulouse (S France)	43.6	152	21.2	4.6	−19.2	91	−0.4	7	0.92	Typical
Avignon (Rhône/S France)	43.9	20	23.4	5.2	−16.0	107	0	7	0.75	Mediterr
Nice (Provence)	43.6	4	22.9	7.3	−7.5	118	0	9	0.92	Mediterr
Marseille (Provence)	43.4	6	22.8	6.5	−16.8	111	0	8	0.69	Mediterr
Barcelona (Catalonia)	41.4	175	24.3	9.2	−6.7	135	0	11	0.62	Mediterr
Trento (NE Italy)	46.1	312	22.8	0.8	−16.5!	97	−8	7	1.35	Thermoph
Torino (NW Italy)	45.2	301	22.7	0.2	−16.2!	92	−10	7	1.22	Thermoph
Milano (N Italy)	45.4	107	23.9	1.1	−16.2!	100	−8	7	1.31	Thermoph
Firenze (Toscana)	43.8	40	24.9	5.4	−10.6	116	0	8	0.97	WT-d/Med
Roma	41.9	45	25.0	6.7	−5.4	125	0	9	0.91	Mediterr
A Coruña (Galicia)	43.4	58	18.8	10.2	−5.5	109	0	12	1.20	Cool
Vitoria (N Spain)	42.8	550	19.2	4.7	−17.8	79	−0.3	6	1.29	Cool
Burgos (N meseta)	42.4	894	18.8	2.4	−22.0	67	−6	6	0.92	Cool
Bragança (N Portugal)	41.8	691	21.2	4.6	−12.0	87	−0.4	7	1.02	Typical
Salamanca (meseta)	41.0	782	21.6	3.9	−18.1!	86	−1.5	7	0.57	Dry Temp
Segovia (central mtns)	40.9	1005	21.5	3.2	−13.2	82	−3.4	6	0.72	Typical
Madrid (meseta)	40.4	657	24.8	5.0	−10.1	107	0	7	0.52	Dry WT
Cuenca (meseta)	40.1	945	22.1	3.6	−17.8	85	−2.3	6	0.77	Typical
Lisboa (W Portugal)	38.7	95	22.0	10.6	−1.7	132	0	12	0.74	Mediterr
Evora (central Portugal)	38.6	321	23.9	8.9	−3.6	129	0	10	0.68	Mediterr
Cluj-Napoca (Transylvania)	46.8	410	19.2	−4.4	−29.8	66	−27	5	0.98	Cool
Ljubljana (Slovenia)	46.2	385	19.2	−1.1	−23.0	68	−17	6	2.32	Cool
Zagreb (Croatia)	45.8	163	21.4	−0.1	−30.5	85	−11	7	1.31	Typical
Beograd (Serbia)	44.8	132	22.1	−0.2	−25.5	91	−11	7	0.94	Typical
Bucuresti (Romania)	44.4	82	22.9	−2.9	−30.0	89	−19	7	0.85	Thermoph
Split (Dalmatian coast)	43.5	122	25.6	7.4	−11.4!	132	0	9	0.87	Mediterr
Plovdiv (Bulgaria)	42.1	179	23.3	1.0	−31.5	97	−8	7	0.72	Thermoph
Skopje (N Makedonia)	42.0	238	23.3	0.3	−25.0	97	−10	7	0.71	Thermoph
Istanbul (NW Türkiye)	41.0	40	23.6	5.4	−16.1	110	0	8	0.83	WT-d/Med
Ioannina (NW Greece)	39.7	466	24.7	5.1	−10.0	113	0	8	1.41	WT-d/Med
Moskva (central Russia)	55.7	156	18.5	−10.2	−42.0	50	−59	5	1.13	Cool
Kyyiv (Kiev, Ukraine)	50.4	180	20.5	−5.5	−40.0	69	−37	5	0.97	Cool
Rostov-na-Donu (S Russ)	47.2	77	23.0	−5.4	−33.0	82	−34	5	0.81	Typical
Yalta (S Crimea)	44.5	14	23.7	3.8	−14.5	98	−2.3	7	0.71	WT-d/Med
Zakataly (Azerbayjan)	41.6	500	24.8	2.9	−22.0	103	−5	7	1.27	WT-decid

Climate types are interpreted, based on apparent threshold values in the data:
Cool = Cool-temperate (deciduous, with Tmax < 21°C)
Typical = Typical temperate (deciduous, with Tmax ≥ 21°C)
Thermoph = Thermophilous (i.e. warmer-deciduous but with Tmax near only 23°C)
WT-decid = Warm-temperate deciduous (with Tmax above 23°C)
Mediterr = Mediterranean, i.e. essentially EG-BL but dry summer or dry year-round (not necessarily forest)
Dry Temp = Typical temperate but too dry for forest (MIy < 0.6); similarly for Dry WT (dry warm-temperate)
Other abbreviations are as in Tables 7 and 8. Exclamation marks with Tabmin mean the measured value (perhaps over only a few years) was replaced by a lower estimate (see Methodology section of main text)

species, including some with more southern ranges. In the middle and south-Atlantic region, Tmax is generally > 25°C, WI is >110, there are at least seven warm months, and Tmin is > 0°C, meaning that there is no persistent winter snow cover. From the South Carolina coast on southward, all 12 months can be above 10°C. This is a region of "southern hardwood" forests, especially so-called oak-hickory (*Quercus-Carya*) forests, with persistent, secondary "southern pines" (called 'heliophilic' by Box 1981). These southern forests correspond very well to the warm-temperate deciduous forests of East Asia, in climatic parameters as well as in vegetation structure and main tree taxa (see Box, herein - a).

In the Appalachians, patterns follow elevation (cf Greller 1988). Above the lowland warm-temperate deciduous forests in the South, on the (leeward) Atlantic side, are more typical-temperate foothill and lower-montane forests, originally with much *Castanea dentata* but now (after decimation by the chestnut blight) with co-dominance by *Quercus prinus*, *Q. alba* and *Q. rubra*. This is the Oak-Chestnut forest of Braun (1950). On the wetter western side are the richest forests, the Mixed Mesophytic Forest of Braun, with no dominant species but as many as 10 canopy co-dominants, sometimes reaching more than 40 m in height (cf Bluefield in Table 8). Above this is a belt of truly montane, cool-temperate mixed forest (cf Banner Elk) involving mainly "northern hardwoods", *Pinus strobus* (not originally native to the southern Appalachians), and some admixtures of the two local subalpine conifers, especially *Picea rubens* (as in eastern Canada) plus endemic *Abies fraseri* at higher elevations.

In the interior lowland (between the Appalachians and the drier Great Plains), zonation is much the same but with more continental temperature regimes. In the north, Toronto (on Lake Erie) has Tmax < 21°C but most other sites are above 22°C, with WI > 70 and have at least 6 warm months (to 7 in the Ohio River valley); Tmin is always below 0°C, though, and there is often a persistent winter snow cover (at least before global warming). This region has *Acer-Tilia* forests (especially Wisconsin) and *Fagus-Acer* forests (especially Ohio), plus more continental oak-hickory forests further west (e.g. Missouri; see Braun 1950 or Box, herein - a). South of the Ohio River, Tmax is generally 26–28°C, WI exceeds 100, at least 7 months are warm, and there is no winter snow cover (Tmin > 0°C). This is a large region of warm-temperate deciduous forest, including the Western Mesophytic Forest in Kentucky-Tennessee and Oak-Hickory-Pine Forest further south (Braun 1950); the latter extends westward to its dryness limit in eastern Oklahoma and Texas, where the canopy is typically only about 15 m tall and only two (eastern) oaks remain as co-dominants, *Q. stellata* and *Q. marilandica*, joined in central Texas especially by *Q. texana*.

(c) **Europe**

Although summers in Europe are cooler than in the other two regions, the warm period (≥ 10°C) can be just as long. Summers in southern Europe, though, are often drier than in the nemoral region to the north, due to the higher temperatures (thermophilous) or to reduced summer precipitation (submediterranean).

In Europe (see Table 9), most of the area north of the Alps is cool-temperate, with Tmax generally below about 20°C and WI < 80 (though usually with at least 5 if not 6 warm months – the Atlantic influence). In the Rhône valley of southern France there is an abrupt jump in Tmax from 20.5°C at Lyon to 23.4°C at Avignon, with a similar increase in Tmin (2.1–5.2°C). This suggests a more typical-temperate climate to the south, as well as in northern Italy (Tmax at least 22°C); these areas all have at least 7 warm months and WI > 90, albeit with the increasingly dry Mediterranean summer. In the Iberian Peninsula, Galicia and the north coast are cool (Tmax < 20°C) but with mild winters and absolute minima that could perhaps permit broad-leaved evergreens. On the *meseta* (generally above 500 m, including northeastern Portugal), Tmax is typically 21–22°C but the colder winters still have cold-month means well above freezing; much of this area, though, is too dry for forest except in valleys or other more humid sites. In all of this western Mediterranean area, Tmax does not reach 24°C (cf. Milano, Barcelona, Madrid, Firenze) until after absolute minimum temperatures have risen well above -10°C (with means well above freezing), i.e. high enough to permit broad-leaved evergreens. As a result, there is no warm-temperate deciduous climate with the same summer temperature levels as in East Asia or eastern North America—it is already warm enough for evergreens; the same is true in Portugal, though at lower summer temperatures (cf Moreno et al. 1990).

In the mountainous, more continental Balkan area, warm-month means are typically 21–24°C but without any clear north-south break. Absolute minima are lower than in the western Mediterranean area, and winter means are as in central Europe. Here also a warm-month mean of 24°C is generally not reached (except near the coast), and some warm-month means are distinctly lower, sometimes < 20°C. This occurs already at elevations not so much higher (see values in the Appendix), as at Cluj-Napoca (410 m, in Transylvania), Ljubljana (385 m), Sofiya (586 m) and Ioannina (466 m, in NW Greece). Also here, there are thus no large areas for warm-temperate deciduous forest with summers as warm as on continental east sides. The warmer 'thermophilous' and 'submediterranean' deciduous forests of southern Europe appear to occur in thermal regimes that, elsewhere, would be considered typical temperate. Of course these conditions are still significantly warmer than in central to northern Europe and do not preclude recognition as warm-temperate deciduous woods, with thermophilous species such as *Q. pubescens*. These occur especially on the many warmer south-facing slopes.

Finally, in eastern Europe, there does seem to be a significant southward jump in summer mean temperatures between the 20.5°C at Kyyiv (Kiev) and the means of 23.0°C at Sochi and Rostov-na-Donu, and 23.7°C at Yalta on the Crimean south coast (although mean winter temperatures stay below freezing until near the coast). Although Moskva (Moscow) and Kazan both have 5 warm months, and Kazan (at the same latitude but further east) has *Q. robur* forest, both must be considered cool-temperate, as also Kyyiv. Southernmost Russia (e.g. Rostov) and Ukraina could be warm-temperate deciduous, except that they are generally too dry for forest. Zakataly (Azerbaijan) and some small areas on lower southern slopes of the Caucasus in northeastern Georgia (with no climate data) could both be seen as warm-temperate deciduous; the Georgian forests are co-dominated by *Fraxinus*, *Tilia*, *Carpinus*, *Acer*, and *Quercus iberica*, and can be very species-rich (cf Nakhutsrishvili 2012; see relevés in Box et al. 2000).

7 Conclusions and Questions

The temperature data and apparent thresholds identified in the previous section, for the three regions, show that the 'thermophilous' and 'submediterranean' deciduous forests of southern Europe occur at lower summer temperatures than in the warm-temperate deciduous forest areas of East Asia and eastern North America. This follows a general pattern of lower mid-latitude temperatures on continental west sides (e.g. Europe), due to the greater oceanic effect on the windward west sides. The lower summer temperatures in southern Europe do not necessarily mean that the European 'thermophilous' and 'submediterranean' forests cannot be called warm-temperate. Rather it means that the concept of warm-temperate deciduous forest, and perhaps of the warm-temperate climate in general, may need to be understood in relation to the general temperature levels of the particular regions. An attempt to show this discrepancy geographically is made in the last chapter of this book (Box, herein - b), by mapping potential regions based on apparent climatic limits identified in this chapter.

In East Asia and eastern North America, temperature levels are quite comparable and the concept 'warm-temperate deciduous' seems to identify, quite well, those areas with warmer summers and no continuing winter snow cover, even though winter temperatures (means or extremes) are too low for broad-leaved evergreens. These are the southernmost areas of deciduous forest, dominated by deciduous trees that also occur well into the warm-temperate evergreen areas further south, usually as the main canopy species of secondary forests. In Europe (and perhaps small areas of the northwestern USA), 'warm-temperate deciduous' also seems to identify the southernmost deciduous forests, also involving more thermophilous species, even if the actual summer temperatures are lower. Where summers are humid these forests are called thermophilous, where summer is drier they are called submediterranean. Note that this is not a vindication of Walter's climate type V, which involved west-side areas occurring much further north (marine west-coast climates, from 40° to 55° of latitude, in some cases to 60° N latitude) and with much more oceanic precipitation regimes.

Values for Kira's Warmth Index are not significantly lower in southern Europe than in East Asia or eastern North America. Furthermore, the length of the warm period is often even longer (7 months) in the thermophilous deciduous regions of southern Europe, due to the greater oceanic effect on the continental west side. Lengths of warm and wet periods were suggested already by Wang (1941) and by Lauer (1952, cf Lauer and Rafiqpoor 2002) as effective indicators of climate types and potential vegetation regions. Length of a warm-wet period (instead of a P/PET ratio) and of the warm period (instead of particular temperature thresholds) may indeed be better indicators and are being explored.

Given the above interpretation and the similar results on continental east sides, it does seem that warm-temperate deciduous forest represents a consistent and useful concept in corresponding regions on different continents, with similar climatic thresholds except for summer temperatures in Europe. Warm-temperate deciduous forests do appear to have clear climatic constraints, but these forests are also distinct in terms of their vegetation, especially the combinations of canopy dominant or co-dominant tree species involved. There may also, however, be unknown factors, involving perhaps evolutionary or more recent history, effects of topography and substrate on water balance, and aspects of microclimate not captured by a macroclimate approach. Some of these factors may be identified by the subsequent chapters in this special-session volume.

References

Aerts, R. 1995. The advantages of being evergreen. *Trends Ecol. Evol.*, 10:402–407.

Akhani, H., M. Djamali, A. Ghorbanalizadeh, and E. Ramezani 2010. Plant biodiversity of Hyrcanian relict forests, N Iran: an overview of the flora, vegetation, paleoecology and conservation. *Pakistan J. Botany*, 42:231–258.

Baldocchi, D. D., Ma Si-Yan, S. Rambal, L. Mission, J.-M. Ourcival, J.-M. Limousin, J. Pereira, and D. Papale 2010. On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. *Ecological Applications*, 20 (6):1583–1597.

Barbour, M. G., and W. D. Billings 1988. *North American Terrestrial Vegetation*. Cambridge University Press. 434pp (2nd edition 2000, 708 pp).

Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr 2007. *Terrestrial Vegetation of California*. 3rd ed. University of California Press, Berkeley. 712pp. (1st ed.: Barbour & J. Major 1977, Wiley & Sons).

Bergmeier, E., P. Dimopoulos, K. Theodoropoulos, and E. Eleftheriadou 2004. Zonale sommergrüne Laubwälder der südlichen Balkanhalbinsel – eine Übersicht. *Tüxenia*, 24:89–111.

Blasi, C., M. L. Carranza, L. Filesi, A. Tilia, and A. Acosta 1999. Relation between climate and vegetation along a Mediterranean-Temperate boundary in central Italy. *Global Ecology Biogeogr.*, 8:17–27.

Blumler, M. A. 1991. Winter-deciduous versus evergreen habit in mediterranean regions: a model. In: Proceedings Symposium on Oak Woodlands and Hardwood Rangeland Management (R. B. Standiford, techn.coord.), pp 194–197. US Forest Service Genl. Techn. Report PSW-126. Berkeley (California).

Blumler, M. A. (herein - a). Deciduous woodlands in the Near-Eastern Fertile Crescent and a comparison with California. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Blumler, M. A. (herein - b). Deciduous woodlands in mediterranean California. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Borchert, R., K. Robertson, M. D. Schwartz, and G. Williams-Linera 2005. Phenology of temperate trees in tropical climates. *V Internat. J. Biometeorology*, 50:57-65.

Box, E. O. 1981. *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Tasks for Vegetation Science, vol. 1. The Hague: Dr. W. Junk BV. 258 pp.

Box, E. O. 1995. Climatic relationships of the forests of East and South-East Asia. In: *Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and southeast Asia* (E. O. Box et al., eds.), pp. 23–55. Kluwer Academic Publishers, Dordrecht.

Box, E. O. 2002. Vegetation analogs and differences in the Northern and Southern Hemispheres: a global comparison. *Plant Ecology*, 163:139–154 (appendix missing! – request from author).

Box, E. O. (herein - a). Warm-Temperate Deciduous Forests of Eastern North America. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O. (herein - b). Quantitative Delimitation of Warm-Temperate Deciduous Forest Areas. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O., and J. N. Choi 2003. Climate of Northeast Asia. In: *Forest Vegetation of Northeast Asia* (J. Kolbek et al., eds.), pp. 5–31. Kluwer, Dordrecht.

Box, E. O., and K. Fujiwara 2005 (2nd ed. in press). Vegetation Types and their Broad-Scale Distribution. In: *Vegetation Ecology* (E. van der Maarel, ed.), pp. 106–128. Blackwell, Oxford.

Box, E. O., and K. Fujiwara 2013. A comparative look at bioclimatic zonation, vegetation types, tree taxa and species richness in Northeast Asia. *Botanica Pacifica* (Vladivostok), 1:5–12.

Box, E. O., K. Fujiwara, G. Nakhutsrishvili, N. Zazanashvili, R. J. Liebermann, and A. Miyawaki 2000. Vegetation and landscapes of Georgia (Caucasus), as a basis for landscape restoration. *Bull. Inst. Environm. Sci. Technol.*, Yokohama Natl. University, 26(1):69–102.

Box, E. O., and M. Manthey 2006. Conservation of deciduous tree species in Europe: Projecting potential ranges and changes. In: *Nature Conservation: Concepts and Practice* (D. Gafta and J. Akeroyd, eds.), pp. 241–253. Springer-Verlag, Berlin.

Box, E. O., You Hai-Mei, and Li Dong-Liang 2001. Climatic ultra-continentality and the abrupt boreal- nemoral boundary in northern Manchuria. In: *Studies on the Vegetation of Alluvial Plains* (Assn. Commemorate Retirement of Prof. Okuda, eds.), pp. 183–200. Yokohama.

Braun, E. L. 1950. *Deciduous Forests of Eastern North America*. Philadelphia: Blakiston Co. 596 pp.

Brewer, S., R. Cheddadi, J. L. de Beaulieu, and M. Reille 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management*, 156:27–48.

Browicz, K. 1978–88. *Chorology of Trees and Shrubs in Southwest Asia*. 5 vols. Institute of Dendrology, Polish Academy of Sciences. Warszawa.

Čarni, A., P. Košir, B. Karadžić, V. Materski, S. Redžić, and Ž. Škvorc 2009. Thermophilous deciduous forests in southeastern Europe. *Plant Biosystems*, 143(1):1–13.

Cavender-Bares, J., P. Cortes, S. Rambal, R. Joffre, B. Miles & A. Rocheteau 2005. Summer and winter sensitivity of leaves and xylem to minimum freezing temperatures: a comparison of co-occurring Mediterranean oaks that differ in leaf lifespan. *New Phytologist*, 168:597–612.

Chabot, B. F., and D. J. Hicks 1982. The ecology of leaf lifespans. *Ann. Rev. Ecol. Systematics*, 13:229–259.

Chen L.-Zh. 1995. Deciduous Broad-Leaved Forests in North-Central China. In: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 255–271. Kluwer, Dordrecht.

China Natural Geography Editorial Commission (eds.) 1984. [*China Natural Geography: Climate*]. Academia Sinica. Science Press, Beijing. 161 pp (in Chinese).

Christensen, N. L. 1988. Vegetation of the Southeastern Coastal Plain. In: *North American Terrestrial Vegetation* (M. G. Barbour and W. D. Billings, eds.), pp. 317–363. Cambridge University Press.

Costa, J. C., T. Monteiro-Henriques, P. Bingre, and D. Espírito-Santo (herein). Warm-temperate deciduous forests of central Portugal: a mosaic of syntaxa. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Crumpacker, D. W., E. O. Box, and E. D. Hardin 2001. Temperate-subtropical transition areas for native trees and shrubs in Florida: Present locations, predicted changes under climatic warming, and implications for conservation. *Natural Areas Journal*, 21(2): 136–148.

Damesin, C., S. Rambal, and R. Joffre 1998. Co-occurrence of trees with different leaf habit: a functional approach on mediterranean oaks. *Acta Oecologica*, 19:195–204.

Daubenmire, R. 1978. *Plant Geography, with special reference to North America*. Academic Press, New York. 338pp.

del Río, S., and A. Penas 2006. Potential distribution of semi-deciduous forests in Castile and Leon (Spain) in relation to climatic variations. *Plant Ecology*, 185:269–282.

Dhaila, S., S. P. Singh, G. C. S. Negi, and Y. S. Rawat 1995. Shoot-growth phenology of co-existing evergreen and deciduous species in an oak forest. *Ecol. Research* (Japan), 10:151–159.

Dimopoulos, P., E. Bergmeier, K. Theodoropoulos, and E. Eleftheriadou 2005. Thermophilous deciduous forests in Greece – a preliminary survey. *Botanika Chronika*, 18(1):83–100.

Fang J.-Y., Song Y.-Ch., Liu H.-Y., and Piao Sh.-L. 2002. Vegetation-climate relationship and its application in the division of vegetation zones in China. *Acta Botanica Sinica*, 44(9):1105–1122.

Flohn, H. 1950. Neue Anschauungen über die allgemeine Zirkulation der Atmosphäre und ihre klimatische Bedeutung. *Erdkunde*, 4:141–162.

Fujiwara, K. 1982. [Phytosociological investigations of evergreen broad-leaved forests of Japan: II. Regional distribution of the evergreen broad-leaved forest]. *Bull. Inst. Environm. Sci. Techn., Yokohama National University*, 8:121–150 (in Japanese).

Fujiwara, K., and A. Harada (herein). Character of warm-temperate forests in Asia. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Fujiwara, K., You H.-M., Tang Q., A. Harada, Wang Zh.-X., and Wang Lin 2008. Deciduous *Quercus* and *Fagus* Forests in Asia. In: Integrated Vegetation Mapping of Asia (K. Fujiwara, leader), pp 111–129. Report to Japan Society for Promotion of Science.

García-Mijanos, I., J. A. Campos, I. Biurrun, M. Herrera, and J. Loidi (herein). Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Givnish, T. J. (ed.) 1986. *On the Economy of Plant Forms and Function*. Cambridge Univ. Press, New York.

Givnish, T. J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica*, 36:703–743.

Greller, A. M. 1988. Deciduous Forests. In: *North American Terrestrial Vegetation* (M. G. Barbour and W. D. Billings, eds.), pp 287–316. Cambridge University Press.

Greller, A. M. 1989. Correlation of warmth and temperateness with the distributional limits of zonal forests in eastern North America. *Bull. Torrey Botan. Club*, 116:145–163.

Guarino, R., G. Bazan, and B. Paura (herein). Downy-oak woods of Italy: Phytogeographical remarks on a controversial taxonomic and ecologic issue. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Hämet-Ahti, L., T. Ahti, and T. Konen 1974. A scheme of vegetation zones for Japan and adjacent regions. *Ann. Bot. Fennica*, 11:59–88.

Hocker, H. W. 1956. Certain aspects of climate as related to the distribution of Loblolly Pine (*Pinus taeda*). *Ecology*, 37:824–834.

Horvát, I. 1959. Sistematski odnosi termofilnih hrastovih i borovih suma Jugoistocne Evrope. *Biol. Glasn.* (Zagreb), 12:1–40.

Horvát, I., V. Glavač, and H. Ellenberg 1974. *Vegetation Südosteuropas*. Geobotanica Selecta, vol. 4. Gustav-Fischer-Verlag, Stuttgart. 768 pp.

Hou X.-Y. 1983. Vegetation of China with reference to its geographical distribution. *Ann. Missouri Bot. Garden*, 70:509–548.

Isogai, T. 1994. [Distribution of evergreen and summergreen broad-leaved secondary forests and its causal factors in a small drainage basin in the southern Izu Peninsula, central Japan]. *Eco-Habitat*, 1:15–31 (in Japanese).

Jäger, E. J. 1970. Charakteristische Typen mediterran-mitteleuropäischer Pflanzenareale. *Feddes Repert.*, 81:67–92.

Kappelle, M. (ed.) 2006. *Ecology and Conservation of Neotropical Montane Oak Forests*. Springer-Verlag, New York. 483 pp.

Kargioglu, M., A. Serteser, C. Senkul, and M. Konuk 2011. Bioclimatic characteristics of oak species *Quercus macrantha* ssp. *syspirensis* and *Quercus petraea* ssp. *pinnatiloba* in Turkey. *J. Environm. Biology*, 32(1):127–131.

Karizumi, N. 1956. Noziri-ko biwa-jima-no shokusei [Vegetation of Biwa Island in Noziri Lake]. *Japanese Forestry Society*, 38(8): 306–310.

Kavgaci, A., A. Čarni, B. Tecimen, and G. Ozalp 2010. Diversity and ecological differentiation of oak forests in NW Thrace (Turkey). *Arch. Biolog. Sci. Beograd*, 62(3):707–720.

Kim J.-W. 1990. A syntaxonomic scheme for the deciduous oak forest of South Korea. *Abstracta Botanica*, 14:51–81.

Kira, T. 1945. *Nōgyō Chirigaku-no Kisō to shite no Tō-A no Shin Kikō Kubun* (A new classification of climate in eastern Asia, as a basis for agricultural geography.) Horticult. Inst., Kyōto University. 23 pp (in Japanese).

Kira, T. 1949. Nippon-no shinrin-tai [Forest zones in Japan]. *Ringyō Kaisetsu*, 17:105-141. Nippon Ringyō Gijutsu Kyōkai, Tokyo (in Japanese).

Kira, T. 1977. A Climatological Interpretation of Japanese Vegetation Zones. In: *Vegetation Science and Environmental Protection* (A. Miyawaki, ed.), pp. 21–30. Maruzen, Tokyo.

Kira, T. 1991. Forest ecosystems of East and Southeast Asia in a global perspective. *Ecol. Research* (Japan), 6:185–200. Reprinted: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 1–21. Kluwer, Dordrecht.

Klein, J. C., and A. Lacoste 1989. Les chênaies à *Quercus macranthera* F. & M. dans le massif dell'Alborz (Iran) et les chaines limitrophes (Grand et Petit Caucase). *Ecolog. Mediterranea*, 15(3/4) :65–93.

Köppen, W. 1931. *Grundriss der Klimakunde*. Walter de Gruyter, Berlin.

Lauer, W. 1952. Humide und aride Jahreszeiten in Afrika und Südamerika und ihre Beziehungen zu den Vegetationsgürteln. *Bonner Geogr. Abhandl.*, 9 :15–98.

Lauer, W., and M. D. Rafiqpoor 2002. *Die Klimate der Erde*. Franz Steiner Verlag, Stuttgart. 271pp.

Lieth, H. 1975. Primary Production of the Major Vegetation Units of the World. In: *Primary Productivity of the Biosphere* (H. Lieth & R. H. Whittaker, eds.), pp 203–215. Springer-Verlag, New York.

Little, jr., E. L. 1971–1978. *Atlas of United States Trees*. Misc. Publs., US Forest Service. US Govt. Printing Ofc., Washington. 5 vols.

Matevski, V., A. Čarni, O. Avramovski, N. Juvan, M. Kostadinovski, P. Košir, A. Marinšek, A. Paušić, and U. Šilc 2011. *Forest Vegetation of the Galičica Mountain Range in Macedonia*. Založba ZRC, Ljubljana. 200pp.

Menitsky, Yu. L. 2005. *Oaks of Asia*. Science Publishers (Enfield, NH, and Plymouth, UK). 549pp (translated from Russian, originally published 1984 by Komarov Botanical Institute, Leningrad).

Mensing, S. A. 2005–06. The history of oak woodlands in California. *California Geographer*, 45:1–38; 46:1–31.

Meusel, H., and E. J. Jäger 1989. Ecogeographical differentiation of the Submediterranean deciduous forest flora. *Plant Systematics and Evolution*, 162:315–329.

Miller, H., and S. Lamb 1985. *Oaks of North America*. Naturegraph, Happy Camp (California). 327pp.

Miranda, F., and A. J. Sharp 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology*, 31(3): 313–333.

Miyawaki, A. (ed.) 1980–1989. *Nihon Shokusei-Shi* (Japan Vegetation Record). 10 vols., each 400–600pp, with color maps and tables. Shibundō, Tokyo (in Japanese; German, English summaries).

Miyawaki, A., K. Fujiwara, et al. 1971. Zushi-shi-no shokusei – nippon-no jōryoku kōyō rin-ni tsuite [Vegetation of Zushi city: about Japanese evergreen broad-leaved forest]. Tokyo. 151 pp (in Japanese).

Miyawaki, A., and K. Fujiwara 1983. Evergreen broad-leaved forests and secondary forests in the Bōsō Peninsula (SE part of Kantō region). *Bull. Inst. Envl. Sci. Techn. Yokohama Natl. Univ.*, 9:63–76.

Monk, C. D. 1966. An ecological significance of evergreenness. *Ecology*, 47:504–505.

Morla, C., and F. D. Pineda 1985. The woody vegetation in the Mediterranean-Atlantic boundary in the north west of the Iberian Peninsula. *Candollea*, 40:435–446.

Moreno, J. M., F. D. Pineda, and S. Rivas-Martínez 1990. Climate and vegetation at the Eurosiberian-Mediterranean boundary in the Iberian Peninsula. *J. Vegetation Science*, 1:233–244.

Nakhutsrishvili, G. 2012. *The Vegetation of Georgia* (*South Caucasus*). Geobotany Studies. Springer-Verlag, Heidelberg. 235pp.

Ozenda, P. 1994. *Végétation du Continent Européen*. Delachaux et Niestlé, Paris.

Pedrotti, F. (herein). Chorology and phytosociology of *Quercus petraea* in Trentino-Alto Adige. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Physical Regionalization Committee 1958–59. [General Natural Divisions of China]. Science Press, Beijing (In Chinese).

Pignatti, S. 1998. *I Boschi d'Italia*. UTET, Torino. 677pp.

Quarterman, E., and Ch. Keever 1962. Southern mixed hardwood forest: climax in the southeastern coastal plain, U.S.A. *Ecol. Monogr.*, 32:167–185.

Quézel, P., and F. Médail 2003. *Écologie et Biogéographie des Forêts du Bassin Méditerranéen*. Elsevier, Paris.

Rübel, E. F. 1930. *Pflanzengesellschaften der Erde*. Verlag Hans Huber. 464 pp.

Rzedowski, J. 1978. *Vegetación de México*. Limusa, Mexico (city). 432pp.

Sakai, A. 1971. [Frost hardiness of evergreen and deciduous broadleaved trees native to Japan]. *Low-Temperature Science* (Japan), series B, 35:15–43 (in Japanese, with English summary).

Sánchez de Dios, R., M. Benito-Garzón, and H. Sainz-Ollero 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology*, 204:189–205.

Scharnweber, T., M. Rietschel, and M. Manthey 2007. Degradation stages of the Hyrcanian forests in southern Azerbaijan. *Archiv Naturschutz Landschaftsforschung*, 2007:133–156.

Schirone, B., F. Spada, M. C. Simeone, and F. Vessella (herein). *Quercus suber* L. distribution revisited. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Schmithüsen, J. 1968. *Allgemeine Vegetationsgeographie*. 3rd edition. Walter de Gruyter, Berlin. 463pp.

Suzuki, T. 1952. *Tou-A no Shin-Rin Shokusei* [Forest Vegetation of East Asia]. Kokon Shōin, Tokyo. 137 pp (in Japanese).

Suzuki, T. 1953. The forest climaxes of East Asia. *Jap. J. Bot.*, 14:1–12.

Tang Q., K. Fujiwara, and You H.-M. 2008. Warm-Temperate Deciduous *Quercus* Forest in China. In: Integrated Vegetation Mapping of Asia (K. Fujiwara, project leader), pp 102–110. Report to Japan Society for Promotion of Science.

Tessier, L., P. Nola, and F. Serre-Bachet 1994. Deciduous *Quercus* in the Medierranean region: tree-ring/climate relationships. *New Phytologist*, 126:355–367.

Tietze, W., and M. Domrös 1987. The climate of China. *GeoJournal*, 14(2):265–266.

Troll, C., and K. H. Paffen 1964. Karte der Jahreszeitenklimate der Erde. *Erdkunde*, 18:5–28.

Ugurlu, E., and S. Gökhan Senol 2005. *Quercus*-dominated vegetation units in the Aegean region of Turkey. *Botanika Chronika*, 18(1): 283–291.

Ugurlu, E., J. Roleček, and E. Bergmeier (in press). Oak woodland vegetation of Turkey – a first overview based on multivariate statistics. Applied Vegetation Science.

Van Auken, O. W., A. L. Ford, and J. L. Allen 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. *Amer. J. Bot.*, 68(9):1249–1256.

Velázquez, A., V. M. Toledo, and I. Luna 2000. Mexican Temperate Vegetation. In: *North American Terrestrial Vegetation*, 2nd edition (M. G. Barbour and W. D. Billings, eds.), pp 573–592. Cambridge University Press.

Villar, R., and J. Merino 2001. Comparison of leaf construction costs in woody species with differing leaf lifespans in contrasting ecosystems. *New Phytologist*, 151:213–226.

Walter, H. 1968. *Die Vegetation der Erde in öko-physiologischer Betrachtung*. Vol. II: Die gemäßigten und arktischen Zonen. Jena: VEB Gustav- Fischer-Verlag. 1002 pp.

Walter, H. 1973. *Die Vegetation der Erde in ökophysiologischer Betrachtung*. Vol. I: Die tropischen und subtropischen Zonen. 3rd edition. Gustav-Fischer-verlag, Stuttgart. 743pp.

Walter, H. 1977. *Vegetationszonen und Klima*, 3rd edition. Verlag Eugen Ulmer, Stuttgart. 309 pp.

Walter, H. 1985. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*. 3rd edition. Springer–Verlag, New York. 318 pp (1st edition 1970).

Walter, H., and E. O. Box 1976. Global classification of natural terrestrial ecosystems. *Vegetatio*, 32:75–81.

Walter, H., and H. Lieth 1960–67. *Klimadiagramm-Weltatlas*. Stuttgart: Gustav-Fischer-Verlag.

Wang Chi-Wu 1961. *The Forests of China, with a Survey of Grassland and Desert Vegetation*. Maria Moors Cabot Foundation Publ. no. 5. Harvard University, Cambridge (Mass.). 313 pp.

Wang, T. 1941. Die Dauer der humiden, ariden und nivalen Zeiten des Jahres in China. *Tübinger Geogr. Geolog. Abhandlungen*, 2(7):1–33.

Wellstein, C, and F. Spada (herein). The status of *Quercus pubescens* Willd. in Europe. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. US Geolog. Survey (Washington), Professional Paper No. 1106. 37 pp.

Woodward, I. 1987. *Climate and Plant Distribution*. Cambridge University Press. 174 pp.

Wu Zh.-Yi and committee (eds.) 1980, 1995. *Zhongguo Zhibei* [Vegetation of China]. Science Press, Beijing.1375 pp + 339 B/W photos; 1382 pp + photos (in Chinese; Latin-Chinese species lists).

Wu Zh.-Yi and P. H. Raven (eds.) 1999. *Flora of China*. 4 vols. Science Press, Beijing. 374pp.

Yamanaka, Ts. 1956. Shikoku chihō-ni okeru dantai-rin kara ontai-rin e no ikō-ni tsuite [On the transition from the warm-temperate to the cool-temperate forest region in Shikoku]. Kōchi Daigaku Gakujutsu Kenkyuu Hōkoku [Kōchi University Science Research Report], 5(20) (in Japanese).

Yim, Y.–J. 1977. Distribution of forest vegetation and climate in the Korean Peninsula. Parts 3 and 4. *Jap. J. Ecol.*, 27:177–189, 269–278.

Yim, Y.-J., and T. Kira 1975-76. Distribution of forest vegetation and climate in the Korean Peninsula. Parts 1 and 2. Jap. J. Ecol., 25:77-88, 26:157-164.

Yim, Y.-J. 1995. Composition and Distribution of Deciduous Broad-Leaved Forests in Korea. In: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 273–298. Kluwer, Dordrecht.

You H.-M., K. Fujiwara and Tang Q 2008. *Quercus liaotungensis* Forest in China. In: Integrated Vegetation Mapping of Asia (K. Fujiwara, project leader), pp 91–101. Final Report to Monbushō for grant #16255003, Yokohama National University.

Zhao S.-Q. 1986. *Physical Geography of China*. Science Press, Beijing (with John Wiley & Sons). 209 pp + 64 color photos and 11 Landsat images.

Zhao Y.-Zh. and Tian H. 2001. [Taxonomic revision and floristic analysis of *Quercus* in Inner Mongolia]. Inner Mongolia University Study Reports, 32(4):470–472 (in Chinese).

Zobel, D. B., and S. P. Singh 1997. Himalayan forests and ecological generalizations. *BioScience*, 47:735–745.

Zohary, M. 1963. On the geobotanical structure of Iran. *Bull. Res. Council Israel*, 11D (suppl):1–113.

Zohary, M. 1973–74. *Geobotanical Foundations of the Middle East*. Geobotanica Selecta, vol. 3 Gustav-Fischer-Verlag, Stuttgart. 2 vols: 683 + 738 pp.

Character of Warm-Temperate *Quercus* Forests in Asia

Kazue Fujiwara and Atsuko Harada

Abstract

The concept of warm-temperate deciduous forest was re-proposed, from mid-temperate forest (Mid-Zone of Tanaka 1887), by Kira (1949, 1991, 2011), based on climatic data and values of his Warmth and Coldness Indices. T. Suzuki (1966) recognized this as the intermediate-temperate zone (Tsugion sieboldii). What kind of forests are warm-temperate forests in Asia? This chapter treats deciduous forests in eastern Asia, especially deciduous *Quercus* forests, and compares them, based on forest composition and climate data, with more typical temperate and cool-temperate *Quercus* forests. *Quercus serrata* forests, in most of eastern Asia, occur in drier, warmer climates than do *Fagus* forests and in climates that are colder in winter than the evergreen forest area. In Japan such forests are composed mainly of deciduous *Quercus serrata*, *Q. acutissima, Q. variabilis, Castanea crenata*, *Carpinus tschonoskii,* and *C. laxiflora*. This kind of forest occurs mainly as secondary forest preceding evergreen broad-leaved forest, in both Japan and Korea. *Q. serrata* and *Q. variabilis* forests occur naturally and secondarily in Korea and China too, the latter in particular as natural forest in Chinese protected areas. In Japan there is a natural *Quercus serrata* forest region in inland Honshū, around Nagano and Ueda, as mentioned by Kira (1949) and described by Wada (1977, 1982a, b). We compared these drier, warmer deciduous *Quercus* forests with *Quercus* forests in cooler climatic zones, dominated mainly by *Q. mongolica* var. *crispula, Q. mongolica,* and *Q. wutaishanica.* As a result, it appears that *Quercus* forests can be classified into ten forest types (see main text), which can be grouped into three broader forest classes: (1) warm-temperate forests, with *Q. serrata*, *Q. brevipetiolata Q. variabilis, Q. acutissima* and *Q. aliena*; (2) temperate forests, with *Q. mongolica* var. *crispula* and *Q. dentata* in Japan, *Q. mongolica* in the Beijing area and southern Chinese Manchuria, and *Q. wutaishanica* in drier southern Inner Mongolia and the northern Qinling Mts.; and (3) cool-temperate forests, especially mixed forests of *Q. mongolica* and conifers (*Pinus koraiensis*, *Abies holophyla* and *A. homolepis*) on the Asian mainland (China, Korea and Russia), plus *Q. mongolica* var. *crispula* and *Abies sachalinensis* in Japan. Under human impact, species from the warm-temperate *Quercus serrata* and *Q. variabilis* forest invade both the cooler *Quercus mongolica* and *Q. mongolica* var. *crispula* forest in China, Korea and Japan and the warmer evergreen broad-leaved forests in Japan and Korea. Potential natural sites of *Q. serrata* and *Q. variabilis* forest in East Asia are subject to laurophyllization, i.e. invasion by planted evergreen species, but laurophyllization from *Quercus serrata* forests to *Q. mongolica* forests does not occur in China. *Q. variabilis* forests occur in areas much drier than those of

---

K. Fujiwara (✉) • A. Harada
Yokohama City University, Yokohama 236-0027, Japan
e-mail: kazue@ynu.ac.jp

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*,
Geobotany Studies, DOI 10.1007/978-3-319-01261-2_3,

Q. mongolica and evergreen broad-leaved forests. Conclusions: (1) *Quercus serrata* and *Q. variabilis* forests are the main warm-temperate forests in East Asia; and (2) these species also invade as secondary elements into both temperate (deciduous) forests and warm-temperate evergreen broad-leaved forests in East Asia. Similar laurophyllization also occurs in western Mediterranean areas with good soil, where evergreen broad-leaved species invade *Quercus pubescens* forests, especially in Insubria (southern low slopes of the European Alps) and near the glacial lakes. (3) These warm-temperate forests can be characterized by values of the Warmth and Coldness Indices and an annual moisture index (Box and Fujiwara 2013 and herein).

Keywords

Coldness Index • Deciduous *Quercus* • Frost hardiness • Intermediate temperate forest • *Quercus serrata* • *Quercus variabilis* • Secondary deciduous *Quercus* forest • Warmth Index • Warm-temperate deciduous forest

1 Introduction

Deciduous broad-leaved forests are one of the main forest types of the Northern Hemisphere. In particular, *Fagus* and [deciduous] *Quercus* forests are considered to be temperate forests. In Japan, temperate forests were usually classified as cool-temperate or warm-temperate. The cool-temperate forests were mainly *Fagus* and *Quercus* forests (Kira 1949; Takahashi 1962), including forests of *Q. serrata, Fagus japonica, Abies sachalinensis-Q. mongolica* var. *crispula*, and even *Picea jezoensis-A. sachalinensis* (Numata 1974; Numata et al. 1972; Box 1995; Okitsu 2000; Box and Fujiwara 2004). Mixed forests with deciduous *Quercus* and *Abies* occur in the Russian Far East and Hokkaidō. Sakai and Larcher (1987) placed these mixed forests in the boreal zone. Tatewaki (1955, 1958) named them the pan-mixed forest zone, which Okitsu includes in cool-temperate forest. Nozaki and Okutomi (1990) classified these forests as temperate summergreen broad-leaved forest in northern Japan, subdivided into three types: (a) *Fagus crenata* forest, (b) intermediate-temperate forests (*Quercus mongolica* var. *crispula* forest on the Pacific side), and (c) upper temperate forest (mixed forest in Hokkaidō). Evergreen broad-leaved forests were generally understood as warm-temperate forest, which Kira (1991) called lucidophyll forest, perhaps not realizing that they had already been named laurel forest by Rübel (1930) when he visited the Canary Islands, based on the presence of Lauraceae such as *Ocotea foetens* and *Persea indica* in the canopy.

In order to relate forest types to climate, Kira introduced a Warmth Index and Coldness Index, representing sums of mean monthly temperatures (t) above and below a growth threshold of 5°C. The Warmth Index (WI) is defined as $\mathrm{WI} = \sum(t - 5)$, for months in which $t > 5°\mathrm{C}$; the Coldness Index (CI) is defined as $\mathrm{CI} = -\sum(t - 5)$, for months in which $t < 5°\mathrm{C}$. He then used these as the basis for bioclimatic zonation in Japan and eventually most of East Asia. The boundary between cool-temperate beech forests and warm-temperate lucidophyll forests was found to correspond approximately to a WI value of 85, based on a maritime climate (Kira 1945, 1949, 1976, 1977, 1991).

In Japan it is well-known that deciduous *Quercus* forests occur as secondary forests substituting for laurel forests after their disturbance. The canopy species of these substitute forests are *Quercus serrata, Q. acutissima, Q. variabilis* and *Q. aliena*. These species form natural (i.e. persisting) forests around Nagano and Ueda (Wada 1977; Shimada 1997), where precipitation is relatively low (for Japan) and the Coldness Index is under −10 (i.e. some months have mean monthly temperature below 5°C).

On the other hand, the idea of a mid-temperate zone was proposed quite early, by Tanaka (1887). This concept was rejected by Honda (1912), based on community succession, and Kira (1949) suggested that it belongs to the warm-temperate deciduous forest zone. An 'intermediate temperate' zone was re-proposed by Suzuki (1961), based on a *Tsuga* alliance (cf Takahashi 1962; Wada 1977; Nozaki and Okutomi 1990). This concept included an *Abies firma-Tsuga sieboldii* forest zone with *Fagus japonica* and *Quercus serrata* forest areas. Numata (1987) summarized these climate and forest zones as: (1) a cold-temperate zone or upper montane belt or evergreen conifer or mixed forest belt (*Abies sachalinensis-Picea jezoensis* forest or *A. sachalinensis-Q. mongolica* var. *crispula* mixed forest); (2) a cool-temperate forest zone or mid-montane forest belt or deciduous broad-leaved forest zone (*Fagus crenata* forest zone in Japan); and (3) a mid-temperate zone or lower forest or evergreen conifer zone (*Tsuga-Abies firma* zone in Japan) (only deciduous and mixed forest zones were quoted). Nakashizuka (2003) pointed out that intermediate or warm-temperate deciduous forests were common and distributed from the northern warm-temperate zone to drier areas of the cool-temperate zone. The occurrence of these forests is related to major disturbances such as wildfire or human activity beginning in the pre-historical period (Osumi 2003). Nakashizuka also pointed out that not only Kira's (1991) warm-temperate forests but also similar forest types would occur in areas with lower Warmth Index values and less winter precipitation. In Korea, Yim (1977) concluded finally, following Yim and Kira (1975-76), that forest vegetation in Korea could be classified into three main types: A. warm-temperate evergreen lucidophyll forest, with CI values above −10; B. warm-temperate broadleaf forest, with a Southern subzone (B1: WI 100–105) and Northern subzone (B2: WI < 99); and C. cool-temperate deciduous broadleaf forest, with CI values of −55 to −45**.** Type A is the *Camellia japonica* community (lucidophyll forest); B1 is *Carpinus tschonoskii* and *Pinus thunbergii* forests; B2 is forests with *Carpinus laxiflora, Quercus serrata, Q. variabilis*, and *Q. aliena*; and C is *Quercus mongolica* forest. There is also a further type D for Subarctic conifer forest (Yim 1995). For present purposes, data are omitted for type B1.

In China, the national zonation system is quite different from views in Japan and Korea, as discussed by Box and Fujiwara (2015, herein). Fang et al. (2002) presented a more suitable system for forest types, but this system still lacks one critical measure, namely the lowest extreme temperatures (cf Box 1995, 2002). The zonation presented earlier in this book (Box and Fujiwara, herein) identified forest types in East Asia with a more global view: cool-temperate, (typical) temperate and warm-temperate forests.

We have surveyed deciduous forests in China for a long time (e.g. Fujiwara et al. 2000; You et al. 2001; You 2001; Wang and Fujiwara 2003, 2005; Wang et al. 2006a, b; Zhi-Rong et al. 2010; Tang et al. 2009, 2015). As a result, we found a special deciduous *Quercus* zone in China similar to the warm-temperate forest zone near Ueda and Nagano in Japan.

Deciduous *Quercus* forests have wider geographic ranges than do *Fagus* forests, in Asia as well as other continents. Deciduous *Quercus* forests can tolerate lower temperatures, drier climates and human impact such as cutting for charcoal or firewood (Osumi 2003). The various deciduous *Quercus* species correspond to climate types: *Q. mongolica* and *Q. mongolica* var. *crispula* forests in the cool-temperate and typical temperate zones; and *Q. serrata, Q. acutissima, Q. variabilis, Q. dentata, Q. aliena* and others in the warm-temperate zone. Especially in China, about 20 species occur from the temperate zone well into the subtropical evergreen forest zone, sometimes due to human impact. Such species, similar to *Q. serrata, Q. acutissima, Q. variabilis, Q. dentata* and *Q. aliena*, occur at lower elevations, and *Q. mongolica* occurs at higher elevation and in northern China (due to their greater cold tolerance). All of these species may, however, be intermixed in many forests.

Descriptions of East Asian forests have been published in books and at least one large report (e.g. Box et al. 1995; Fujiwara 2008; Kolbek et al. 2003a; Box and Fujiwara 2012). Most of these books described the deciduous forests as cool-temperate forests. Here we would like to discuss forest types as corresponding to climatic forest types too, based on field data from many sites in China, Korea, the Russian Far East and Japan (see Fig. 1).

Sasaki (1991, 1993, 1996, 1998) proposed the concept of a 'deciduous oak culture' in Asia, based on agriculture and forest types. Sasaki recognized forest types similar to these deciduous *Quercus* forests in Japan, Korea, China and the Russian Far East, based partly on the *Vegetation of China* book by Wu (1980). Yasuda (1984) concurred, based on pollen analyses. In Asia, northeastern and middle China, Korea, the Russian Far East, Hokkaidō and northern Pacific parts of Japan are covered potentially by deciduous *Quercus* forests. These *Quercus* forests are not always natural (potentially stable over long periods), and more than half of their area involves secondary forest (see Fig. 2). Deciduous *Quercus* is very important for forestry and human life. In this paper we compared deciduous forests mixing natural and secondary forests together, which created much noise in the table work. It is very necessary to clarify the forest types and environmental factors.

Using phytosociological data, we discuss temperate deciduous *Quercus* forests in East Asia to try to clarify what kinds of *Quercus* forests can be classified as warm-temperate and which as other temperate forest. The main deciduous *Quercus* forests were compared phytosociologically, in order to address the following questions:

1. What is a warm-temperate deciduous forest (composition, ecology, etc.) in East Asia, and what types are the other forests?
2. What is the definition of warm-temperate deciduous forest?
3. Why do deciduous forests persist and evergreens not dominate if the climate really is warm enough for evergreens?
4. What will be the effects of global warming on warm-temperate forests in Japan?

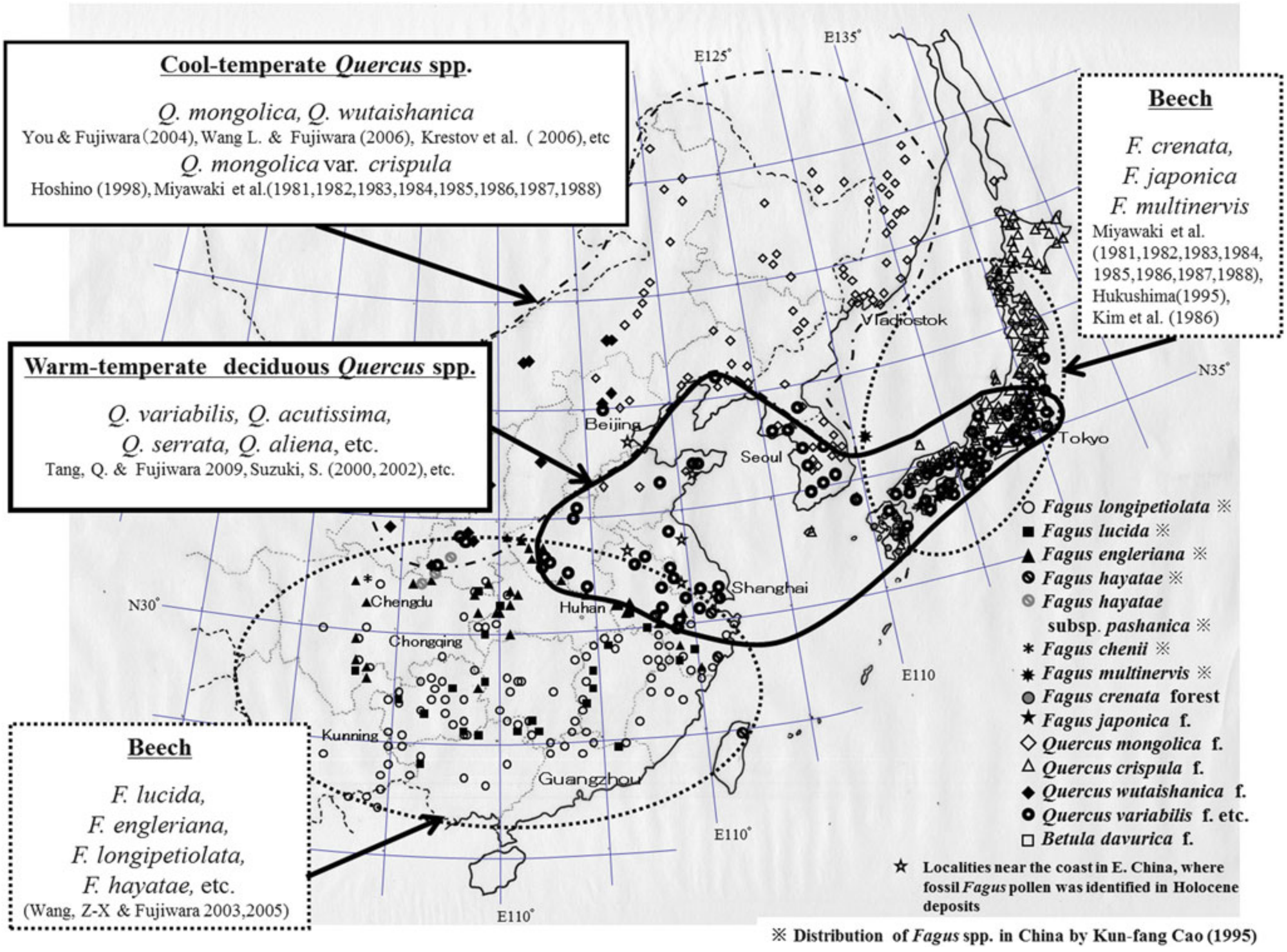


Fig. 1 Actual distribution of warm-temperate deciduous *Quercus* forests in East Asia, and of cool and typical temperate deciduous *Quercus* and *Fagus* forests

2 Field Surveys and Methodology

Deciduous *Quercus* forests were surveyed from 2002 to 2009, by phytosociological methods (Braun-Blanquet 1964; cf Fujiwara 1987), in China and the Russian Far East. All of the field data (relevés) and data from published papers were collected into a huge matrix (3,643 relevés) and compared in Excel. For this comparison, synoptic tables were constructed for forest types with similar compositions, based on the following averaging method:

1) Roman numerals in the synoptic table were changed to decimal Arabic numbers as follows:
   V: 5, IV: 4, III: 3, II: 2, I: 1, +: 0.5, r: 0.25, no number in cell: 0
2) Average values of the integrated synoptic columns were obtained as integers by the Excel function ROUND and then changed back to Roman numerals (as above).

The results are shown in Figs. 1 and 2, and summarized in Table 1 in the next section.

3 Results

All the available *Quercus* forest relevés from East Asia were compared in a large synoptic table (Table 1). The final result was also compared with *Fagus* forests. More details and a more definite syntaxonomy will be presented in a subsequent paper. This paper describes the forest types under the following seven headings:

1. *Quercus mongolica* var. *crispula* forest in Japan and Jeju-do island (temperate)
2. *Quercus serrata* forest in Japan and Korea (warm-temperate)
3. *Quercus variabilis-Q. serrata* var. *brevipetiolata* forest in China
4. *Quercus mongolica* forest in Korea, China and Far Eastern Russia (temperate and cool-temperate)
5. *Quercus mongolica* forest in the Da Xing An Ling and *Betula daurica* woodland in Russia

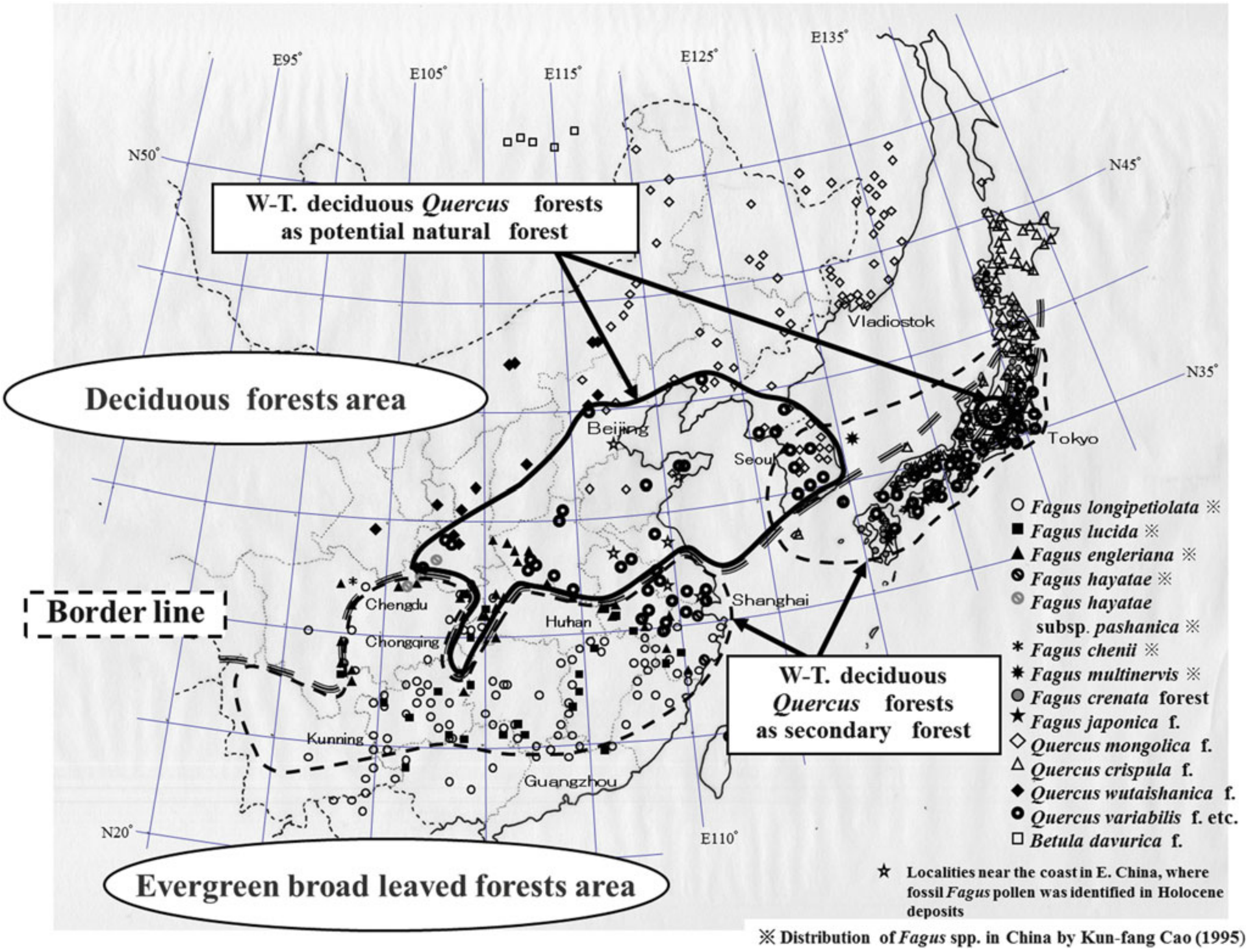


Fig. 2 Areas of potentially permanent and of secondary warm-temperate deciduous *Quercus* forests in East Asia

6. *Quercus mongolica* forest around Beijing and in Shandong (temperate)
7. *Quercus wutaishanica* forest in mid-western China (temperate).

1. *Quercus mongolica* var. *crispula* forest in Japan and Jeju-do

These are (intermediate or typical) temperate forests

Querco-Fagetea crenatae Miyawaki Ohba, Okuda, Nakayama et Fujiwara 1968

Synonyms: Saso-Fagetea Suz.-Tok. 1966, Fagetea crenatae Miyawaki, Ohba et Murase 1964

Diagnostic taxa: *Quercus mongolica* var. *crispula, Fraxinus lanuginosa, Acanthopanax sciadophylloides, Rhus ambigua, Schizophragma hydrangeoides, Viburnum furcatum, Magnolia obovata, Tilia japonica, Acer japonicum*

Holotype: Saso-Fagetalia crenatae Suz.-Tok 1966 ex Y. Sasaki 1970

Quercus mongolica var *crispula* has had many synonyms, including *Q*. *crispula* (more recently) and *Q*. *mongolica* var. *grosseserrata* (long used, especially in Japan). Many syntaxonomical names use *Q*. *mongolica* var. *crispula*, so it was decided to prefer it in this paper.

Quercus mongolica Fisch. ex Ledeb. var. *crispula* (Blume) H. Ohashi (1988)

Synonyms: *Q*. *mongolica* var. *grosseserrata* (Bl.) Rehd. et Wils.; *Q*. *crispula* Blume, Mus.; *Q*. *grosseserrata* Blume, Mus.; *Q*. *crispula* var. *grosseserrata* (Bl.) Miq.; *Q*. *crispula* var. *sachalinensis* Koidz.; *Q*. *grosseserrata* var. *crispula* (Bl.) Nakai; *Q*. *mongolica* subsp. *crispula* (Bl.) Menitskii**.**

Q. *mongolica* var. *crispula* forest occurs widely in the temperate zone of Japan, on Jeju-do island (= Cheju-do, south of the Korean peninsula), and on Sakhalin and the Kuril Islands. These forests are characterized by coverings of *Sasa* on the forest floor. For this paper all the available data were organized again and compared

Table 1 Synoptic Table of Deciduous *Quercus* Forests in East Asia

Running number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Country	**J**	**J**	**J**	**K**	**J**	**J**	**J**	**J**	**K**	**C**	**C**	**C**	**C**	**C**	**C**	**C**	**C**	**C**	**K**	**CR**	**R**	**C**	**C**	**C**	**R**	**R**	**R**	**RC**	**C**	**R**	**C**	**C**
Number of relevés	**345**	**163**	**317**	**57**	**118**	**138**	**589**	**191**	**259**	**13**	**4**	**36**	**10**	**10**	**10**	**26**	**13**	**13**	**121**	**97**	**118**	**94**	**115**	**31**	**24**	**96**	**104**	**116**	**58**	**159**	**18**	**71**
Fraxino-Quercion grosseserratae Ohba 1973																																
Lindera umbellata var. *membranacea*	III	·	·	·	r	+	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Ilex crenata* var. *paludosa*	III	·	I	·	r	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Cephalotaxus harringtonia* var. *nana*	III	·	I	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carex multifolia	II	·	·	·	·	·	r	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viola vaginata	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pruno-Quercion grosseserratae Wada 1982																																
Symplocos coreana	I	III	·	·	·	I	+	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer micranthum	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Abies homolepis	·	II	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Saso-Fagetalia crenatae Suz.-Tok. ex Y. Sasaki 1970																																
Acer sieboldianum	II	III	·	·	r	II	r	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Fagus crenata	II	II	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ligustrum tschonoskii	II	II	·	·	r	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carpino-Quercion grosseserratae Takeda, Uematsu et Nakanishi 1983, Carpino-Quercetalia grosseserratae Hoshino 1998																																
Tilia japonica	I	I	IV	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vitis coignetiae	I	I	IV	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cacalia hastata var. *orientalis*	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Abies sachalinensis	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Magnolia praecocissima var. *borealis*	I	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Hydrangea petiolaris	I	·	III	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cirsium kamtschaticum	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celastrus orbiculatus var. *papillosus*	I	I	III	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cimicifuga simplex	I	I	III	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	I	·	+	+	·	·	I	I	r	·	I	·	·
Fraxinus mandshurica var. *japonica*	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus ssiori	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Syringa reticulata	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ostrya japonica	·	·	II	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pachysandra terminalis	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Saso quelpaertensis-Quercion crispulae all. nov., Saso quelpaertensis-Quercetalia crispulae ord. nov.																																
Carpinus laxiflora	I	I	I	V	·	II	+	I	III	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·
Asarum maculatum	·	·	·	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sasa quelpaertensis	·	·	·	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Benthamidia japonica	II	I	·	IV	+	I	+	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Taxus cuspidata*	·	·	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	+	r	·	·	·	·
Carex ciliatomarginata	·	·	·	IV	r	+	·	·	·	·	·	·	·	·	·	I	·	·	r	·	·	·	r	·	·	·	·	·	·	·	·	·
Cacalia auriculata	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	r	+	·	·	II	II	I	·	·	·	·
Carpinus tschonoskii	I	I	·	III	r	II	II	+	II	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·
Asiasarum sieboldii	I	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Kadsura japonica*	·	·	·	III	r	·	I	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·
Viola hondoensis	·	·	·	III	·	·	I	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vaccinium koreanum	·	·	·	III	·	·	·	·	I	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Ligularia fischeri	·	·	·	III	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	·	I	+	r	·	·	+	I	r	I	II	·	·
Anemone asiatica	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lycopodium chinense	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	r	·	·	·	·	·
Querco-Fagetea crenatae Miyawaki, Ohba, Okuda, Nakayama et Fujiwara 1968																																
Quercus mongolica ssp. *crispula*	IV	V	V	III	I	II	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Schizophragma hydrangeoides	III	II	III	IV	·	I	r	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum furcatum	III	III	II	IV	r	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhus ambigua	III	II	IV	·	r	I	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Fraxinus lanuginosa	III	II	II	·	r	+	r	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer japonicum	III	I	III	·	r	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Magnolia obovata	III	I	III	·	+	II	I	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sasa senanensis	II	·	II	·	r	r	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicero gracilipedis-Quercion serratae Shimada, Fujiwara et A. Harada all. nov.																																
Prunus verecunda	II	I	·	·	V	II	r	II	·	·	·	r	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·
Lonicera gracilipes	·	I	·	·	V	II	I	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Smilax sieboldii	I	·	·	II	IV	II	r	r	+	·	·	I	IV	·	I	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Zelkova serrata	I	·	·	·	IV	I	II	+	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Atractylodes japonica	·	·	·	·	IV	II	I	+	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·
Dendranthema japonicum	·	·	·	·	III	r	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Smilax biflora var. *trinervula*	·	·	·	·	II	+	r	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Spiraea japonica	·	·	·	·	II	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dianthus superbus var. *longicalycinus*	·	·	·	·	II	·	r	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Kerria japonica	·	·	·	·	II	+	r	r	·	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburno phleobotrichi-Quercenion serratae suball. nov.																																
Viburnum phlebotrichum	I	I	·	·	I	III	r	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Abies firma	·	I	·	·	·	II	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Parabenzoin praecox	·	·	·	·	I	II	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer palmatum var. *amoenum*	I	I	II	·	r	II	r	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer rufinerve	II	II	·	·	+	II	r	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carpinus japonica	I	II	·	·	+	II	I	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Meliosma myriantha	·	·	·	I	+	II	+	+	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Moro australis-Quercenion serratae suball. nov.																																
Dioscorea tokoro	I	·	·	·	+	I	IV	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pleioblastus chino	·	·	·	·	r	I	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicera japonica	·	·	·	·	I	+	III	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Hedera rhombea*	·	·	·	I	r	r	III	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Neolitsea sericea*	I	·	·	·	·	+	III	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicera gracilipes var. *glabra*	·	·	·	·	·	+	III	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

Table 1 (continued)

Celtis sinensis var. *japonica*	·	·	·	·	I	·	III	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Smilax riparia var. *ussuriensis*	I	·	·	·	r	+	II	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aphananthe aspera	·	·	·	·	·	·	II	r	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Dryopteris varia* var. *setosa*	·	·	·	·	·	r	II	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carex lenta	·	·	·	·	·	r	II	r	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Athyrium niponicum	·	·	·	·	r	+	II	r	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Clematis japonica	·	I	·	·	+	+	II	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Magnolia praecocissima (*kobus*)	·	·	·	·	r	·	II	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Gynostemma pentaphyllum	·	·	·	·	·	·	II	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dumasia truncata	·	·	·	·	·	+	II	+	·	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ilici pedunculosae-Quercenion serratae suball. nov.																																
● *Ilex pedunculosa*	I	I	·	·	+	+	r	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lyonia ovalifolia var. *elliptica*	I	I	·	·	+	II	r	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhododendron macrosepalum	·	·	·	·	·	·	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Evodiopanax innovans	I	·	·	·	·	+	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhododendron reticulatum var. *ciliatum*	·	·	·	·	·	r	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Wisteria brachybotrys	·	·	·	·	·	+	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vaccinium smallii var. *glabrum*	·	I	·	·	·	r	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viola violacea	·	I	·	·	·	r	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda ex Fujiwara et A. Harada all. nov.																																
● *Eurya japonica*	I	·	·	·	·	+	IV	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Ardisia japonica*	II	·	·	I	·	II	III	III	·	·	·	·	·	·	·	I	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera umbellata	II	I	·	·	·	II	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pertya scandens	·	·	·	·	·	II	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus jamasakura	I	·	·	·	·	II	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Pieris japonica*	I	I	·	·	·	II	I	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·
● *Trachelospermum asiaticum* var. *intermedium*	·	·	·	I	·	I	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Aucuba japonica*	·	·	·	·	·	r	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Callicarpa mollis	·	·	·	II	·	I	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lilium auratum	·	·	·	·	·	II	II	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sorbus japonica	I	I	·	·	r	II	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Hydrangea hirta	I	I	·	·	·	II	+	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Ligustrum japonicum*	·	·	·	·	·	r	II	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Quercus glauca*	·	·	·	·	·	r	II	III	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhododendro kaempferi-Quercetalia serratae ord. nov.																																
Rhododendron obtusum var. *kaempferi*	I	II	·	·	IV	IV	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Akebia trifoliata	II	·	·	·	IV	III	IV	III	·	IV	·	I	I	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Wisteria floribunda	I	·	·	·	V	III	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Euonymus alatus var. *apterus* f. *ciliatodentatus*	III	·	II	·	IV	II	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Calamagrostis arundinacea var. *brachytricha*	·	I	·	·	IV	II	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pourthiaea villosa var. *laevis*	II	II	·	·	II	III	III	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viola grypoceras	I	I	·	·	III	II	III	I	r	·	·	·	·	·	·	·	II	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus grayana	III	I	·	·	III	III	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum erosum	I	I	·	III	IV	II	II	IV	I	·	·	·	·	·	·	·	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Akebia quinata	·	·	·	I	II	I	III	+	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Zanthoxylum piperitum	II	·	I	I	II	II	III	+	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Cymbidium goeringii*	I	·	·	·	I	II	II	III	·	·	·	·	·	·	II	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus acutissima	·	·	·	·	III	I	III	I	+	·	·	I	·	·	·	IV	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·
Abelia spathulata	·	I	·	·	III	II	I	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ligustrum obtusifolium	·	·	·	II	III	I	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Callicarpo japonicae-Quercion serratae Kim 1990, Aceri pseudosieboldiani-Quercetalia serratae ord. nov.																																
Acer pseudosieboldianum	·	·	·	V	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	V	I	+	+	·	II	I	·	r	II	·	·	·	·
Rhododendron schlippenbachii	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	IV	+	·	+	·	·	·	·	·	·	·	·	·	·
Weigela florida	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	I	·	·	II	I	·	·	·	·	·	·	·	·	·	·	II	·
Sasamorpha borealis	·	II	·	·	·	I	r	·	III	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Smilax nipponica	II	·	·	I	r	I	I	I	III	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Styrax obassia	II	·	I	·	·	II	r	·	III	·	·	·	I	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus levelliana	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·
Stewartia koreana	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburno dilatati-Quercetea serratae class. nov.																																
Quercus serrata	II	·	I	II	V	V	V	V	III	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum dilatatum	II	I	I	·	IV	IV	IV	II	II	·	·	+	+	·	+	I	·	II	+	·	·	·	·	·	·	·	·	·	·	·	·	·
Castanea crenata	III	I	·	·	III	IV	II	III	I	·	·	·	·	·	·	·	·	·	r	r	·	·	·	·	·	·	·	·	·	·	·	·
Callicarpa japonica	II	I	·	I	III	III	IV	II	II	·	·	·	·	·	·	·	I	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera (Benzoin) obtusiloba	I	I	·	I	V	II	r	I	V	·	·	II	·	·	+	+	·	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Fraxinus sieboldiana	I	I	·	·	III	III	I	II	III	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Stephanandra incisa	·	·	·	·	+	III	II	r	III	·	·	·	·	·	·	II	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Polygonatum falcatum	·	·	·	·	II	I	II	I	II	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicero standishii-Quercion variabilis Tang, Fujiwara et You all. nov in Box et Fujiwara 2014																																
Jasminum giraldii	·	·	·	·	·	·	·	·	·	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicera standishii	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Mahonia fortunei	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Elaeagnus umbellata	·	·	·	·	r	·	r	r	·	III	·	·	+	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cotinus coggygria	·	·	·	·	·	·	·	·	·	III	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus tabulaeformis	·	·	·	·	·	·	·	·	·	III	·	+	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	I
Bothriospermum secundum	·	·	·	·	·	·	·	·	·	III	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Roegneria kamoji	·	·	·	·	·	·	·	·	·	III	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum schensianum	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
Juniperus formosana	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sinarundinaria nitida	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
***Rhododendron mariesii-Quercus variabilis* community**																																
Spiraea dasyantha	·	·	·	·	·	·	·	·	·	·	4	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Deyeuxia sinelatior	·	·	·	·	·	·	·	·	·	·	4	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cotoneaster zabelii	·	·	·	·	·	·	·	·	·	II	3	+	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Atractylodes lancea	·	·	·	·	·	·	·	·	·	·	3	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	I

Table 1 (continued)

Thalictrum honanense	·	·	·	·	·	·	·	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Gnaphalium affine	·	·	·	·	·	·	·	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus thunbergii	·	·	·	·	·	·	r	+	·	·	2	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Galium kinuta	·	·	·	·	·	·	r	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Peucedanum terebinthaceum	·	·	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	I	·
Syringa oblata	·	·	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Association and communities																															
Rhus verniciflua	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cornus kousa var. *chinensis*	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Philadelphus incanus	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Styrax hemsleyana	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus armandii	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Litsea pungens*	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Adenophora petiolata	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Fragaria chinensis	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera trilobata	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Saussurea dutaillyana	·	·	·	·	·	·	·	·	·	·	·	II	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Saussurea sinuata	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	+	r	·	·	·	·	·	·	·	·
Association and community																															
Clematis florida	·	·	·	·	·	·	·	·	·	I	·	·	V	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Schisandra sphenanthera	·	·	·	·	·	·	·	·	·	·	·	·	V	·	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·
Crataegus cuneata	·	·	·	·	·	·	·	·	·	·	1	·	IV	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum mongolicum	·	·	·	·	·	·	·	·	·	·	1	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
Viola variegata	·	·	·	·	·	·	·	·	·	·	·	r	IV	II	·	·	·	·	·	r	·	r	II	·	·	·	·	·	I	·	·	I
Cotinus coggygria var. *pubescens*	·	·	·	·	·	·	·	·	·	·	·	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Indigofera bungeana	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
Allium anisopodium	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·
Atractylodes macrocephala	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus sibirica	·	·	·	·	·	·	·	·	·	·	2	+	III	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	I	·	·	II
Cephalanthera longifolia	·	·	·	·	·	·	·	·	·	·	1	·	III	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
Cynanchum versicolor	·	·	·	·	·	·	·	·	·	·	·	r	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Salvia multiorrhiza	·	·	·	·	·	·	·	·	·	·	·	r	III	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus davidiana	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	r	·	·	·	·	·	r	·	·	·	·	·	·	·	·	I
Rhododendron molle	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lespedeza pilosa	·	·	·	·	·	·	r	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Asparagus schoberioides	·	·	·	·	·	·	r	·	r	·	·	·	III	·	·	·	·	·	·	I	I	·	+	II	·	·	r	I	I	·	·	·
Sporobolus indicus	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vitex negundo	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Clematis obtusidentata	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Zelkova sinica	·	·	·	·	·	·	·	r	·	·	·	·	II	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Fraxinus bungeana	·	·	·	·	·	·	·	r	·	·	·	r	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhamnus rugulosa	·	·	·	·	·	·	·	r	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Syringa microphylla	·	·	·	·	·	·	r	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Spiraea hirsuta	·	·	·	·	·	·	r	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carpino turczaninovii-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2014																															
Carpinus turczaninovii	·	·	·	I	·	·	r	·	·	·	4	V	IV	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·
Forsythia suspensa	·	·	·	·	·	·	·	·	·	·	4	V	IV	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Adenophora polyantha	·	·	·	·	·	·	·	·	·	·	4	III	III	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	I
Adenophora trachelioides	·	·	·	·	·	·	·	·	·	·	3	I	V	I	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II
Rhus potaninii	·	·	·	·	·	·	·	·	·	·	3	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus aliena	·	·	·	·	·	·	·	r	I	·	·	IV	IV	I	I	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·
Carex subpediformis	·	·	·	·	·	·	·	·	·	·	·	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicera ferdinandii	·	·	·	·	·	·	·	·	·	·	·	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
Pteroceltido tatarinowii-Quercetum variabilis Tang, Fujiwara et You in Box et Fujiwara 2014																															
Rhamnus globosa	·	·	·	·	·	·	·	·	·	+	·	r	+	V	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
Aristolochia mollissima	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sinomenium acutum	·	·	·	·	·	·	·	r	·	+	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pteroceltis tatarinowii	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum macrocephalum	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aeluropus littoralis var. *sinensis*	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cornus walteri	·	·	·	·	·	·	r	·	·	·	·	·	·	II	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Morus alba	·	·	·	·	·	·	r	·	·	·	·	+	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Euphorbia helioscopia	·	·	·	·	·	·	r	·	·	·	·	r	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ixeris denticulata	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
Adenophora elata	·	·	·	·	·	·	r	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Association and community																															
● *Elaeagnus pungens*	·	·	·	·	·	r	+	II	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Alangium platanifolium	·	·	·	·	·	·	·	·	I	+	·	·	·	·	III	·	·	·	r	·	·	r	·	·	·	·	·	·	·	·	·
Ligustrum quihoui	·	·	·	·	·	·	·	·	·	I	·	r	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celastrus angulatus	·	·	·	·	·	·	·	·	·	+	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Solanum lyratum	·	·	·	·	·	·	r	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Alangium chinense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Parthenocissus heterophylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer oliverianum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Euonymus hamiltonianus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Exochorda racemosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celtis pubescens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera chienii	·	·	·	·	·	r	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Mallotus apelta	·	·	·	·	·	·	r	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhamnus bungeana	·	·	·	·	·	·	r	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Zelkova schneideriana	·	·	·	·	·	·	·	r	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Prunus conadenia	·	·	·	·	·	·	·	r	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Osmanthus cooperi	·	·	·	·	·	·	r	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acanthopanax divaricatus	·	·	·	·	·	·	r	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

Table 1 (continued)

Association and communities																																
Diospyros kaki var. *sylvestris*	·	·	·	·	·	·	r	r	·	·	·	r	·	·	·	III	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cocculus trilobus	·	·	·	·	·	·	·	·	r	·	·	r	·	·	+	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ulmus parvifolia	·	·	·	·	r	·	r	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Firmiana simplex	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Osmanthus fragrans	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vitex negundo var. *cannabiifolius*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Serissa foetida	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Trachelospermo jasminoidis-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2014																																
● *Trachelospermum jasminoides*	·	·	·	·	·	·	·	·	·	·	·	·	·	V	V	IV	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celtis sinensis	·	·	·	·	·	·	·	·	I	·	·	r	·	II	I	III	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·
Aleurites fordii	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer buergerianum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Smilax glauco-china*	·	·	·	·	·	·	·	·	·	·	·	+	·	·	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Ilex cornuta*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pistacio chinensis-Quercetalia variabilis Tang, Fujiwara et You in Box et Fujiwara 2014																																
Quercus variabilis	·	·	·	·	r	·	r	II	III	V	4	II	V	V	V	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pistacia chinensis	·	·	·	·	·	·	·	·	·	+	·	II	III	V	V	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Grewia biloba var. *parviflora*	·	·	·	·	·	·	·	·	·	V	·	+	II	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celtis koraiensis	·	·	·	·	·	·	·	·	·	·	·	IV	·	IV	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·
Liquidambaro formosanae-Quercion fabri all. nov.																																
Liquidambar formosana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus fabri	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus massoniana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Vaccinium bracteatum*	·	·	·	·	·	·	r	II	·	·	·	·	·	·	·	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cunninghamia lanceolata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Loropetalum chinense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Woodwardia japonica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Premna macrophylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Dryopteris fuscipes*	·	·	·	·	·	·	r	r	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Eurya muricata*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Castanopsis sclerophylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Symplocos sumuntia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Ilex rotunda*	·	·	·	·	·	·	r	r	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Myrica rubra*	·	·	·	·	·	·	r	r	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Gardenia jasminoides*	·	·	·	·	·	·	r	r	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus chenii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera aggregata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Schima superba*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sasamorpho sinicae-Quercion brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da ex Fujiwara et A. Harada all. nov.																																
Hydrangea angustipetala	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Castanea seguinii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	II	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Stephanandra chinensis	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pourthiaea villosa	·	·	·	·	·	r	·	r	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sasamorpha sinica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dendrobenthamia japonica var. *chinensis*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Corylus heterophylla var. *sutchuensis*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Quercus* (*Cyclobalanopsis*) *gracilis*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Castanea henryi	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pterostyrax corymbosus	·	·	·	·	·	r	·	r	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicera modesta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Veratrum schindleri	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Carpinus viminea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Hamamelis mollis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus stewardiana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
● *Litsea cubeba*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Callicarpa japonica var. *angustata*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Stewartia sinensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Magnolia cylindrica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sorbus amabilis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Fraxinus championii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da ex Fujiwara et A. Harada ord nov.																																
Rhododendron simsii	·	·	·	·	·	·	·	·	·	·	·	I	·	·	+	I	IV	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera reflexa	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	r	II	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum setigerum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercetea varliabili-brevipetiolatae Tang, Fujiwara et You class nov in Box et Fujiwara 2014																																
Dalbergia hupeana	·	·	·	·	·	·	·	·	·	III	·	·	·	III	IV	II	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aster ageratoides	·	·	·	·	·	·	r	·	r	·	3	IV	III	I	IV	IV	I	II	·	+	I	+	I	·	+	·	·	·	·	·	III	IV
Quercus serrata var. *brevipetiolata* (=*Q. glandulifera* var. *brevipetiolata*)	·	·	·	·	·	·	·	·	·	·	4	IV	·	·	III	II	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Platycarya strobilacea	·	·	·	·	·	·	r	II	I	·	1	II	·	·	IV	III	II	III	+	·	·	·	·	·	·	·	·	·	·	·	·	·
Symplocos paniculata	·	·	·	·	·	·	·	r	·	·	2	II	·	·	+	IV	II	V	·	·	·	r	·	·	·	·	·	·	·	·	·	·
Rhododendron mariesii	·	·	·	·	·	·	·	·	·	·	4	+	·	·	·	I	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lespedeza formosa	·	·	·	·	·	·	·	·	·	·	3	II	III	I	II	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Liriope spicata	·	·	·	·	·	·	·	·	·	·	·	II	·	I	II	IV	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rubus corchorifolius	·	·	·	·	·	·	·	·	·	·	·	I	·	·	III	III	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus aliena var. *acuteserrata*	·	·	·	·	·	·	·	·	·	·	3	I	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda, Nakanishi et Choe 1994, Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994																																
Symplocos chinensis	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	IV	I	·	·	·	·	·	·	·	·	·	·	·	·
Tripterygium regelii	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	IV	·	·	·	r	·	·	·	·	·	·	·	·	·
Ainsliaea acerifolia	·	·	·	·	·	r	·	·	III	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	·	·	·	·	·	·	·	·	·
Magnolia sieboldii	·	·	·	I	·	·	·	·	II	·	·	·	·	·	·	·	·	·	III	·	·	r	·	·	·	·	·	·	·	·	·	·
Astilbe chinensis	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	III	II	r	r	I	·	·	·	r	II	·	·	·	·
Pseudostellaria palibiniana	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·

Table 1 (continued)

Angelica gigas	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	III	·	·	r	r	·	·	·	·	·	·	·	·	·
Lespedeza maximowiczii	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	I	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Aconitum saxatile	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Cimicifuga heracleifolia	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	II	·	·	·	r	·	·	·	·	·	·	·	·	·
Acer pseudosieboldianum	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·
Lychnis cognata	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	II	·	·	r	·	·	·	·	·	·	·	·	·	·
Quercenion dentato-mongolicae suball. nov.																																
Quercus dentata	·	·	·	·	II	·	·	·	+	III	1	r	·	·	·	r	·	·	·	IV	II	·	·	·	·	·	·	·	·	·	·	·
Rubus crataegifolius	·	·	·	·	·	·	r	·	I	·	·	+	·	·	·	+	·	·	+	IV	II	I	r	·	·	·	I	+	·	·	II	·
Artemisia desertorum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	I	·	·	·	·	·	·	·	·	+	·	·
Clinopodium chinense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	r	r	r	·	·	·	·	·	·	·	·	·
Lycopus lucidus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	III	+	·	·	·	·	·	·	·	·	·	·	·
Veratrum maackii	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	III	+	+	·	·	·	·	·	·	·	·	·	·
Gentiana scabra	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	II	r	r	·	·	·	·	·	·	·	·	·	·
Platycodon grandiflorus	·	·	·	·	·	·	r	·	r	·	·	·	·	·	·	·	·	·	·	II	·	r	·	·	·	·	·	·	·	·	·	·
Sophora flavescens	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·
Dictamno dasycarpi-Quercenion mongolicae Kim ex Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada suball. nov.																																
Dictamnus dasycarpus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	IV	II	r	·	·	·	r	+	·	I	·	·
Vicia amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	·	·	·	·	·	·	·	·	r	·	·
Carex longerostrata	·	·	I	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	I	III	·	·	·	·	+	·	·	·	·	·	·
Vincetoxicum acuminatum	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	+	III	·	·	·	·	·	r	+	·	·	·	·
Veratrum ussuriense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·	·	·
Angelica cincta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	III	·	r	·	·	·	+	I	·	·	·	·
Geranium maximowiczii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	I	r	·	·	·	·	I	·	+	·	·
Pleurospermum uralense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	II	·	·	·	·	·	r	+	·	+	·	·
Galium platygalium	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	r	·	·	·	·	·
Carex subebracteata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	II	·	·	·	·	·	·	·	·	·	·	·
Viola brachyceras	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	II	·	·	·	·	·	·	·	·	·	·	·
Corylo heterophyllae-Quercion mongolicae Krestov, Song, Nakamura et Verkholat 2006																																
Atractylodes ovata	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	r	V	IV	·	·	·	·	·	·	·	·	·	·	·
Adenophora pereskiifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	IV	r	·	·	·	·	r	·	I	II	·	·
Hieracium umbellatum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	III	r	·	·	·	·	r	·	I	IV	·	·
Poa ochotensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	II	·	·	·	·	·	·	·	·	+	·	·
Galium maximowiczii	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	III	II	·	·	·	·	·	·	·	·	·	·	·
Serratula manshurica	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	II	III	·	·	·	·	·	r	·	·	r	·	·
Viola orientalis	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	II	III	·	·	·	·	·	·	r	·	·	·	·
Kitagawia eryngiifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	·	·	·	·	·	·	·	·	·	·	·
Vicia subrotunda	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	·	·	·	·	·	·	+	·	·	·	·
Amphicarpaea japonica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	·	·	·	·	·	·	+	·	·	·	·
Adenophoro tetraphyllae-Quercion mongolicae You, Fujiwara et A. Harada all. nov.																																
Adenophora tetraphylla	·	·	·	·	·	·	·	·	·	·	·	+	I	·	·	I	·	·	·	·	·	IV	II	·	·	·	·	·	·	·	·	·
Vicia pseudo-orobus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	+	·	·	·	·	·	III	III	·	·
Melampyrum roseum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·
Chrysanthemum zawadskii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·
Artemisia japonica	·	·	·	·	·	·	r	·	r	·	·	·	·	·	·	·	·	·	·	·	·	II	r	·	·	·	·	·	·	·	·	·
Iris tenuifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	r	·	·	·	·	·	·	·	·	·
Hieracium hololeion	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	r	·	·	·	·	·	·	·	·	·
Lespedezo bicoloris-Quercetalia mongolicae Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada ord. nov.																																
Lespedeza bicolor	·	·	I	·	II	I	+	+	II	IV	4	II	+	·	·	+	·	·	r	IV	V	V	I	II	+	·	·	I	IV	r	IV	IV
Potentilla fragarioides	·	·	·	·	·	·	·	·	I	·	3	r	·	·	II	r	·	·	+	IV	IV	III	I	II	·	·	r	I	II	IV	·	·
Sedum aizoon	·	·	·	·	·	·	·	·	·	·	4	III	·	·	·	·	·	·	·	IV	III	IV	+	I	·	·	·	·	III	IV	I	I
Corylus heterophylla	·	·	·	·	·	·	·	·	+	·	3	·	+	·	·	r	·	·	·	V	III	III	III	·	·	·	·	r	I	·	I	I
Spodiopogon sibiricus	·	·	·	·	I	·	r	+	II	I	3	II	·	I	·	I	I	·	+	V	III	II	r	·	·	·	·	·	I	·	I	I
Vicia unijuga	·	·	·	·	r	·	·	·	r	+	·	I	·	·	·	r	·	·	r	IV	III	III	II	·	·	·	r	+	III	III	I	·
Betula davurica	·	I	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	III	IV	III	r	+	+	·	r	I	III	III	I	I
Sanguisorba officinalis	·	·	·	·	r	·	r	·	·	II	·	·	II	·	·	II	·	·	·	IV	III	II	r	·	·	·	·	·	V	V	·	I
Patrinia scabiosifolia	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	r	·	·	II	IV	II	II	r	·	·	·	·	·	I	II	·	·
Viola collina	·	·	·	·	·	·	·	·	r	II	·	II	+	II	·	I	·	·	r	II	III	II	+	II	I	·	r	r	I	I	I	I
Viola acuminata	·	·	I	II	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	II	II	II	+	·	+	+	r	+	·	·	·	·
Lysimachia davurica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	I	r	·	·	·	·	·	·	·	·	·
Syringo amurensis-Pinenion koraiensis suball. nov.																																
Syringa amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	IV	·	·	·	·	·	·	·	·	·
Acanthopanax senticosus	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	IV	·	·	·	·	·	·	·	·	·
Philadelphus schrenkii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	IV	·	·	·	·	·	·	·	·	·
Aconitum raddeanum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	III	·	·	·	·	·	·	·	·	·
Diarrhena mandshurica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	III	·	·	·	·	·	·	·	·	·
Carex pilosa	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	·	·	·	·	·	·	·	·	·
Athyrium multidentatum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	·	·	·	·	·	·	·	·	·
Adenocaulon himalaicum	·	·	I	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	III	·	·	·	·	·	·	·	·	·
Allium ramosum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·	·	·	·	·	·
Viburnum burejaeticum	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	+	r	III	·	·	·	r	+	·	·	·	·
Urtica laetevirens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	III	·	·	·	+	I	·	·	·	·
Prunus padus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	II	·	·	·	·	·	I	·	·	·
Lonicero praeflorenti-Pinenion koraiensis suball. nov.																																
Lonicera praeflorens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	I	+	V	·	·	r	IV	·	·	·	·
Spiraea ussuriensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	II	IV	I	+	+	I	·	·	·	·
Pyrus ussuriensis	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	+	I	+	III	·	·	·	·	·	·	·	·
Galium mandshuricum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	r	III	·	·	·	·	·	·	·	·
Larix olgensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·
Patrinia intermedia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·
Tilio amurensis-Pinion koraiensis Kim ex Krestov, Song, Nakamura et Verkholat 2006																																
Deutzia glabrata	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	r	·	·	r	·	+	II	IV	IV	·	·	r	III	·	·	·	·
Aegopodium alpestre	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	III	IV	IV	·	·	·	I	·	I	·	·
Ulmus macrocarpa	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	II	III	III	·	·	·	·	I	·	I	I
Brachybotrys paridiformis	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	+	III	II	·	·	·	·	·	·	·	·

Table 1 (continued)

Rhamnus davurica	·	·	·	·	·	·	·	·	+	·	·	+	IV	·	·	·	·	·	·	r	I	I	II	III	·	+	I	I	·	·	III	·
Rhododendro daurici-Pinion koraiensis Krestov, Song, Nakamura et Verkholat 2006																																
Rhododendron dauricum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	IV	+	·	·	·	II	·	·
Gymnocarpium dryopteris	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	IV	I	I	+	·	·	·	·
Vaccinium vitis-idaea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·	·	·	II	·	·
Viola sacchalinensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	III	+	I	+	·	I	·	·
Rosa acicularis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	I	II	·	·	II	·	II
Polypodium vulgare	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	I	+	+	·	·	·	·
Orthilia secunda	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	+	+	·	·	I	·	·
Linnaea borealis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	+	+	·	·	·	·	·
Spiraea beauverdiana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	+	·	·	·	·	·
Euonymenion macropteri suball. nov.																																
Euonymus macropterus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	r	II	·	II	V	II	r	·	·	·	·
Thalictrum filamentosum	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	II	+	I	·	+	II	I	V	III	II	·	·	·	·
Carex xiphium	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	II	IV	I	+	·	·	·	·
Phegopteris connectilis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	III	I	II	·	·	·	·
Lycopodium annotinum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	II	+	·	·	·	·	·
Phrymo asiaticae-Pinenion koraiensis Krestov et al. ex Fujiwara et A. Harada suball. nov.																																
Sorbaria sorbifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	I	r	II	·	II	I	IV	II	·	I	·	·
Phryma asiatica	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	r	II	·	·	II	+	II	IV	II	·	·	·	·
Carex pallida	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	+	I	III	II	·	+	·	·
Trigonotis radicans	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	·	I	III	I	·	·	·	·
Aconitum volubile	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	r	·	·	·	II	+	·	·	·	·
Anemonoides amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	+	+	II	·	·	·	·	·
Carex falcata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	II	·	·	·	·	·
Galium triflorum	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	II	·	·	·	·	·
Abieti nephrolepidis-Pinion koraiensis Gumarova ex Krestov, Song, Nakamura et Verkholat 2006																																
Abies nephrolepis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	II	II	II	V	IV	II	·	·	·	·
Picea jezoensis (*P. ajanensis*)	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	IV	IV	+	·	·	·	·
Lonicera maximowiczii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	V	II	I	·	·	·	·
Leptorumohra amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	IV	II	+	·	·	·	·
Carex campylorhina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	I	III	IV	II	·	·	·	·
Paris quadrifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	III	III	+	·	·	·	·
Lycopodium juniperoideum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	II	·	·	·	·	·
Lilium distichum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	r	I	·	+	II	III	I	·	·	·	·
Athyrium filix-femina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	+	II	III	+	·	r	·	·
Stellaria bungeana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	II	III	+	·	·	·	·
Veratrum oxysepalum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	II	II	+	·	·	·	·
Jeffersonio-Quercion mongolicae Kim ex Krestov, Song, Nakamura et Verkholat 2006																																
Abies holophylla	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	II	·	r	·	·	·	·	·	·	V	·	·	·	·
Asarum sieboldii	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	II	+	+	·	·	·	·	·	r	IV	·	·	·	·
Acer barbinerve	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	r	·	·	·	·	·	IV	·	·	·	·
Kalopanax septemlobus	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	II	·	I	r	·	·	·	·	r	III	·	·	·	·
Polystichum subtripteron	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·	·
Euonymus maximowicziana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, Song, Nakamura et Verkholat 2006																																
Schisandra chinensis	·	·	II	·	·	·	r	·	r	·	·	III	·	·	+	·	·	·	r	+	II	II	IV	IV	II	III	III	V	·	·	·	·
Acer tegmentosum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	+	III	IV	IV	IV	IV	IV	·	·	·	·
Maianthemum bifolium	·	·	·	I	·	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	+	I	II	IV	IV	III	IV	II	·	I	·	·
Oxalis acetosella	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	III	II	IV	III	IV	·	·	·	·
Berberis amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	r	II	IV	I	III	III	I	·	·	·	I
Acer ukurunduense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	I	III	II	IV	IV	+	·	·	·	·
Viola selkirkii	·	·	·	·	·	r	·	·	r	·	·	III	·	·	·	·	·	·	·	·	I	I	III	III	II	III	III	II	·	·	II	I
Carex ussuriensis	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	I	II	I	IV	I	I	II	III	·	·	·	·
Fraxinus mandshurica	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	I	I	III	IV	·	III	IV	III	·	·	·	·
Betula costata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	r	II	·	IV	V	IV	II	·	·	·	·
Ribes manshuricum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	III	·	+	II	III	III	·	·	·	·
Lonicera chrysantha	·	·	·	·	·	·	·	·	·	·	·	II	+	·	·	·	·	·	·	r	·	I	IV	·	·	+	III	III	·	·	·	I
Ulmus laciniata	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	r	III	·	I	III	III	I	·	·	·	·
Philadelphus tenuifolius	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	+	·	III	·	·	IV	II	V	V	V	·	·	·	·
Eleutherococcus senticocus	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	·	I	·	·	IV	·	IV	V	V	·	·	·	·
Neomolinia mandshurica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	IV	II	III	III	III	·	·	·	·
Diplazium sibiricum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	IV	II	+	·	·	·	·
Mitella nuda	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	III	II	I	·	·	·	·
Sorbus amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	II	II	II	·	·	·	·	·
Circaea alpina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	II	+	III	III	I	·	·	·	·
Ligustrina amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	III	·	+	III	II	·	·	·	·
Waldsteinia ternata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	II	III	III	I	·	·	·	·
Quercetea mongolicae Song ex Krestov, Song, Nakamura et Verkholat 2006																																
Quercus mongolica	·	·	·	·	·	·	·	r	IV	·	·	II	·	·	·	·	·	·	V	V	V	V	IV	V	V	III	III	IV	V	+	IV	·
Maackia amurensis	·	·	·	I	·	·	·	·	II	·	·	·	·	·	·	·	·	·	II	III	III	II	II	III	II	I	II	II	·	·	·	·
Tilia amurensis	·	·	·	·	·	·	·	·	I	·	·	+	·	II	·	·	·	·	IV	I	III	IV	IV	V	IV	IV	IV	III	·	·	I	·
Vitis amurensis	·	·	·	·	·	·	·	·	I	·	·	I	IV	·	·	·	·	·	+	I	III	II	IV	III	+	I	I	III	·	·	I	·
Pinus koraiensis	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	·	III	·	II	II	II	IV	V	V	V	IV	·	·	·	·
Corylus mandshurica	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	II	r	II	II	III	V	III	IV	IV	II	·	·	I	II
Artemisia stolonifera	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	I	III	V	III	II	III	+	·	·	II	·	·	·	·
Convallaria keiskei	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	V	IV	IV	III	III	II	I	III	II	·	III	·	·
Tilia mandshurica	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	+	·	·	·	II	II	II	II	II	+	I	II	+	·	·	I	·
Cacalia hastata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	II	III	·	·	II	III	II	·	I	·	·
Euonymus pauciflorus	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	II	II	III	IV	II	III	II	III	·	·	·	·
Galium dahuricum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	III	II	II	·	II	II	IV	II	·	·	·	·
Polygonatum involucratum	·	·	·	·	·	·	r	·	r	·	·	II	·	·	·	·	·	·	r	I	IV	II	II	II	·	·	+	I	·	·	·	·
Viburnum sargentii	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	+	I	II	III	II	·	·	I	III	·	·	·	·
Poo nemoralis-Quercetalia mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010																																
Poa nemoralis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	II	I	r	·	·	·	r	·	IV	·	·	·

Table 1 (continued)

Dictamnus albus var. *dasycarpum*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·	·
Artemisia sacrorum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	III	·	·	·
Saussurea firma	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·
Adenophora gmelini var. *coronopifolia*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·
Elymus dahuricus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·
Hemerocallis citrina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·
Silene jenisensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	r	·	·	·	·	·	II	+	·	·
Artemisia sylvatica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	+	+	II	·	·	·
Saussurea recurvata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	+	·	·
Clematis hexapetala	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	II	·	·	·
Querco mongolicae-Betuletalia davuricae Ermakov et Ptelin in Ermakov 1997																																
Fragaria orientalis	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	r	III	II	r	·	·	·	·	+	I	V	·	I
Lathyrus humilis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	II	r	·	I	I	+	II	·	V	·	·
Lupinaster pentaphyllus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	r	·	·	·	·	·	·	·	·	V	·	·
Galium boreale	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	II	II	r	r	·	·	·	·	·	I	IV	·	I
Geranium eriostemon	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	+	·	·	·	·	·	·	I	IV	·	·
Dendranthema zawadskii	·	·	·	·	·	·	·	·	r	·	·	·	I	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	I	IV	·	·
Saussurea elongata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·
Carex amgunensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·
Pulsatilla patens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	·	·
Spiraea media	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	r	·	·	IV	·	·
Astragalus membranaceus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	IV	·	·
Adenophora triphylla	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	r	II	r	·	·	·	·	·	·	·	·	III	·	·
Rosa davurica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	I	·	·	·	·	·	·	III	·	·
Festuca ovina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	III	·	·
Lilium pensylvanicum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I	·	·	·	·	·	·	·	·	III	·	·
Valeriana alternifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	I	III	·	·
Rubus saxatilis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	r	·	·	·	·	·	·	III	·	·
Achnatherum sibiricum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	I	III	·	I
Adenophora tricuspidata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Scorzonera radiata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Pyrola rotundifolia	·	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Artemisia sericea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Poa botryoides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Thalictrum appendiculatum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Viola dactyloides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Elymus gmelinii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	·
Salix pyrolifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·
Pinus sylvestris	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	II	·	·
Salix abscondita	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·
Querco mongolicae-Betuletea davuricae Ermakov et Ptelin in Ermakov 1997																																
Artemisia tanacetifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	V	·	·
Betula platyphylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	II	+	II	·	III	I	II	I	II	V	·	II
Artemisia integrifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	·	r	·	·	·	·	·	·	II	III	·	·
Carex pediformis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	II	·	·
Spiraeo trilobatae-Quercion mongolicae Tang, Fujiwara et A. Harada all. nov. prov.																																
Spiraea trilobata	·	·	·	·	·	·	·	·	·	·	·	I	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	IV	I
Deutzia grandiflora	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	IV	·
Saussurea nivea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	r	·	r	·	·	·	·	·	·	I	·	III	I
Thalictrum thunbergii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	I
Calamagrostis arundinacea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	I	·	·	·	·	·	·	·	·	III	·
Myripnois dioica	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·
Andrachne chinensis	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·
Larix principis-rupprechtii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·
Carex onoei	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·
Leptodermis oblonga	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·
Quercetea wutaishanicae You, Fujiwara et A. Harada 2008 cl. prov.																																
Quercus wutaishanica (=*Q. liaotungensis*)	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	V
Agrimonia pilosa	·	·	·	I	·	·	·	·	·	·	·	I	·	·	+	r	·	·	·	I	I	r	I	·	·	·	r	·	I	+	·	III
Adenophora potaninii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II
Cotoneaster acutifolius	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II
Saposhnikovia divaricata	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	II
Crataegus kansuensis	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II
Other species																																
Carex lanceolata	I	I	I	·	III	II	II	II	II	·	4	II	+	II	+	IV	·	III	II	II	III	IV	IV	IV	II	+	+	+	III	III	II	IV
Pteridium aquilinum s.l.	II	I	I	·	II	I	+	II	I	+	1	III	·	·	I	I	III	I	·	IV	V	III	+	·	I	·	I	+	I	+	·	I
Acer mono	I	I	III	I	·	r	r	·	II	·	·	I	II	V	·	·	·	I	II	+	IV	IV	V	V	III	IV	IV	V	I	·	·	·
Carex siderosticta	I	I	I	·	I	II	r	r	III	·	·	II	·	·	·	r	·	I	V	IV	III	III	III	IV	IV	III	II	II	·	·	I	·
Aster scaber	I	·	·	·	I	II	II	II	III	·	3	+	I	·	·	I	II	II	II	V	IV	IV	I	·	+	·	+	+	·	·	·	·
Sorbus alnifolia	III	II	IV	II	III	II	r	I	III	·	·	II	·	·	·	I	·	III	II	·	I	I	II	I	·	·	·	I	·	·	·	·
Euonymus alatus	·	·	I	·	I	II	+	r	+	III	·	III	·	II	V	IV	·	II	r	II	·	II	III	III	·	·	·	·	·	·	·	I
Smilax china	II	I	·	V	II	III	IV	IV	+	V	·	II	III	V	III	IV	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Oplismenus undulatifolius s.l.	·	·	·	II	I	II	IV	II	II	III	·	III	III	V	V	IV	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lindera glauca	·	·	·	·	III	+	III	II	+	II	·	I	·	V	V	V	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Paederia scandens	·	·	·	·	r	I	III	II	r	III	1	II	·	·	III	III	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dioscorea nipponica	I	·	·	·	r	·	·	·	r	II	1	III	II	·	II	+	·	II	+	I	IV	III	III	II	·	+	I	I	·	·	IV	III
Rubia cordifolia	·	·	·	·	·	·	·	·	r	III	·	I	V	I	III	II	·	·	r	+	II	+	I	·	·	II	III	I	I	·	II	III
Polygonatum odoratum s.l.	·	·	III	·	r	·	r	·	I	·	4	IV	III	II	III	I	II	II	II	IV	I	III	III	·	·	·	·	·	IV	II	III	IV
Dryopteris crassirhizoma	I	I	IV	III	·	·	r	·	+	·	·	·	·	·	·	·	·	·	II	·	r	r	II	·	II	V	IV	IV	·	·	·	·
Pyrola japonica	I	·	I	II	II	I	I	II	II	·	·	·	·	·	·	·	·	·	I	r	+	·	·	·	+	+	+	r	·	·	·	·
Chloranthus japonicus	I	·	II	·	+	r	I	r	r	·	·	·	·	·	·	·	·	·	·	+	II	r	I	·	·	+	I	+	·	·	·	·
etc.																																

●: evergreen species

with other *Quercus* forests and Korean forests. Two groups of *Q. mongolica* var. *crispula* forests were apparent, the Japanese forests and the forests from Jeju-do. Japanese *Quercus mongolica* var. *crispula* forests are characterized by species combination and correspond to climatic zonal forests.

1. Cool and typical temperate *Q. mongolica* var. *crispula* forest in Hokkaidō and northern Tōhoku (northern Japan)
2. Typical temperate forest in Honshū (Japan)
3. Typical temperate forest on Jeju-do (Korea).

Q. mongolica var. *crispula* forests were classified as Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, Harada, Kusunoki et Okuda 1971 by Hoshino (1998). In this paper, though, it was decided that these forests belong to the Saso-Fagetalia Suz. Tok. 1966 ex Sasaki 1970, based on the results in Table 1. Character species are species of the Saso-Fagetalia Suz. Tok. 1966. Furthermore, Hoshino (1998) stated that the name Fagetea crenatae Miyawaki, Ohba et Murase 1964 was not approved because these authors named the class without naming an order. He proposed that Saso-Fagetea crenatae Suzuki T.1966 be used with Saso-Fagetalia crenatae, and this was accepted. This is right, based on early ideas of nomenclature by Dress (1953), stated before formalization by the Nomenclature Committee (1969). Miyawaki et al. (1968) renewed the class to include not only *Fagus* forests but also *Ulmus* forests (Ulmion davidianae Suz.-Tok. 1954). They also finally described associations, alliances, order and class as Querco-Fagetea crenatae, changing from Fagetea crenatae to Querco-Fagetea crenatae to correspond to the European system. Afterward, Miyawaki et al. (1972) realized that they should keep the naming priority and went back to Fagetea crenatae. Since then people have used Fagetea crenatae Miyawaki et al. 1964. In this sense, the name Querco-Fagetea crenatae Miyawaki, Ohba, Okuda, Nakayama et Fujiwara 1968 is valid. Hoshino (1998) also stated that Saso-Fagetea (T. Suzuki 1966) was correct, albeit with no supporting table. The first synoptic table was shown by Y. Sasaki (1970), with the order.

a. *Quercus mongolica* var. *crispula* forest in Japan

Saso-Fagetalia crenatae Suz. Tok 1966 ex Y. Sasaki1970

Synonyms: Saso-Fagetalia Suz.-Tok. 1966, Quercetalia serrato-mongolicae Miyawaki, Fujiwara, Harada, Kusunoki et Okuda 1971

Diagnostic taxa: *Rhus ambigua, Acer japonicum, A. sieboldianum, Magnolia obovata, Sasa senanensis, Fagus crenata, Schizophragma hydrangeoides, Ligustrum tschonoskii*

Holotype: Saso-Fagion crenatae Miyawaki, Ohba et Murase 1964

Early syntaxonomical studies were reported by Yoshioka (1935), Nakano (1942), and Murai (1950). Hoshino (1998) described the study history of *Q. mongolica* var. *crispula* forest and summarized all Japanese *Q. mongolica* var. *crispula* forests phytosociologically, describing 46 associations in: three alliances (only *Q. mongolica* var. *crispula* forest) (Fraxino-Quercion grosseserratae Ohba 1973; Pruno-Quercion grosseserratae Wada 1982a, b; Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983); one new order (Carpino-Quercetalia grosseserratae Hoshino 1998); and one class (Saso-Fagetea Suz.-Tok. 1966). These forests included mixed forests in Hokkaidō. S. Suzuki (2002a, b; 2006) compared these with *Q. serrata* forests and *Fagus japonica* forests, reporting 11 associations, four alliances (Tsugion sieboldii; Fraxino-Quercion grosseserratae Ohba 1973; Pruno-Quercion grosseserratae Wada 1982; and Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983), and one order (Quercetalia serrato-grosseserratae Miyawaki et al. 1971). We compared with *Q. mongolica* var. *crispula, Q. serrata* and other *Quercus* spp. in Asia in synoptic Table 1. As a result, *Quercus mongolica* var. *crispula* forests were summarized in two alliances belonging to the Saso-Fagetalia crenatae Suz. Tok 1966 ex Sasaki 1970 and one order representing *Q. mongolica* var. *crispula* forests in Hokkaidō. Then *Fagus crenata* and *F. japonica* were added in Table 1 (Fujwara et al. in preparation).

Okutomi and Hoshino (1983), Hoshino (1998), S. Suzuki (2002a, b), and Krestov et al. (2006) described *Q. mongolica* var. *crispula* forests as Quercetalia serrato-grosseserratae Miyawaki et al. 1971. We compared the species compositions and found that: (1) There are forests on hills or mountain mid-slopes that are transitional between *Q. serrata* forest and *Q. mongolica* var. *crispula* forest, but the *Q. serrata* forests have characteristic species; and (2) Species common with *Q. mongolica* var. *crispula* forest are species of Pacific-side *Quercus*-*Fagus* and *Fagus japonica* forests. We hope to discuss these species in the next paper (under the rubric *Fagus* vs. *Quercus*), with a table. We separated *Q. mongolica* var. *crispula* forest from Quercetalia serrato-grosseserratae Miyawaki et al. 1971 and moved it to the Saso-Fagetalia Suz. Tok. ex Sasaki 1970, except for the Carpino-Quercetalia grosseserratae Hoshino 1998.

(1) Japan Sea side of Honshū, excluding Chūbu (typical-temperate forest)

Fraxino-Quercion grosseserratae Ohba 1973

Diagnostic taxa: *Lindera umbellata* var. *membranacea, Ilex crenata* var. *paludosa, Cephalotaxus harringtonia* var. *nana*, *Viola vaginata, Carex multifolia,* excluding other species of the Saso kurilensis-Fagion crenatae

Holotype: Rhododendro-Quercetum grosseserratae Ohba 1973

Ohba (1973) described this type at the Kiyotsu Valley, and Hoshino (1998) extended it to eastern Honshū. The original diagnostic species were *Acer distylium*, *Ainsliaea acerifolia* var. *subapoda*, *Lilium auratum, Rhododendron albrechtii*, etc., which were determined by Hoshino. S. Suzuki (2002a, b) extracted indicator species of Japan Sea proximity, including *Magnolia salicifolia, Daphniphyllum macropodum* var. *humile* and *Sasa palmata*. In this paper, *Lindera umbellata* var. *membranacea, Ilex crenata* var. *paludosa* and *Cephalotaxus harringtonia* var. *nana* were found. These species occur under the Japan Sea climate with its heavy snow. We compared these data again, extracting *Lindera umbellata* var. *membranacea, Ilex crenata* var. *paludosa*, *Cephalotaxus harringtonia* var. *nana*, *Viola vaginata* and *Carex multifolia*, but missing were the main species of the Saso-Fagion crenatae (Japan Sea elements), such as *Sasa kurilensis, Ilex leucoclada, Mitchella undulata, Arachniodes mutica, Plagiogyria matsumureana, Magnolia salicifolia, Daphniphyllum macropodum* var. *humile* and *Aucuba japonica* var. *borealis.* When snow is deep enough, *Fagus crenata* produces coppice, as on mountains Chōkai-san and Hakkoda-san in northern Honshū, but *Q. mongolica* var. *crispula* makes secondary forests when snow or moisture is adequate. In this paper, four associations of the Fraxino-Quercion grosseserratae from S. Suzuki (2002a, b), three associations of the Carpino-Quercion grosseserratae from Hoshino (1998) and S. Suzuki (2002a, b), and one association of the Carpino-Quercion serratae from Hoshino (1998) were placed in the Fraxino-Quercion grosseserratae Ohba 1973, with the diagnostic species listed above (Table 1, cf Appendix 1). These two alliances do not have enough diagnostic species, including the order. Hoshino (1998) and Suzuki (2002a, b) described a new order Carpino-Quercetalia grosseserratae as an independent order because it did not have diagnostic taxa of the Quercetalia serrato-grosseratae, which are mostly warm-temperate species and taxa of temperate deciduous forests on the Pacific side. These units should be compared with *Fagus* forests.

(2) Western Honshū and Chūbu (temperate forest)

Pruno-Quercion grosseserratae Wada 1982

Diagnostic taxa: *Symplocos coreana, Acer micranthum, Abies homolepis.*

Holotype: Betulo-Quercetum grosseserratae

Wada (1982a, b) proposed Pruno-Quercion grosseserratae as *Quercus mongolica* var. *crispula* forest in Chūbu (literally ‘middle part’, i.e. middle Japan), based on the Betulo-Quercetum grosseserratae, and described it as mixed with *Abies homolepis.* The original diagnostic taxa were *Vitis coignetiae, Prunus maximowiczii* and *Schizandra chinensis.* Hoshino (1998) expanded the associations and proposed *Prunus maximowiczii, Betula ermanii, Euonymus sieboldianus* var. *sanguineus* and *Angelica edulis* as diagnostic taxa. Suzuki (2002a, b) expanded the set of diagnostic species to include *P. maximowiczii*, *Sasa nipponica*, *Betula tauschii*, *B. ermanii*, *Rhododendron wadanum*, *Abies homolepis,* and others. Chūbu is drier than the Japan Sea side of Honshū, so *Q. mongolica* var. *crispula* forest can find a suitable habitat more easily than can the *Fagus* species. In this paper, five associations of the Pruno-Quercion grosseserratae from Hoshino (1998) and S. Suzuki (2002a, b), and one association (Hoshino 1998) and two communities (S. Suzuki 2002a, b) of the Tsugion sieboldii are assigned to the Pruno-Quercion grosseserratae Wada 1982 (Table 1 and Appendix 1).

b. *Q. mongolica* var. *crispula* forest in Hokkaidō and northern Tōhoku (cool-temperate and typical temperate)

Carpino-Quercetalia grosseserratae Hoshino 1998

Diagnostic taxa: *Tilia japonica, Vitis coignetiae, Cacalia hastata* var. *orientalis, Abies sachalinensis, Magnolia praecocissima* var. *borealis, Hydrangea petiolaris, Cirsium kamtschaticum, Celastrus orbiculatus* var. *papillosus, Cimicifuga simplex, Fraxinus mandshurica* var. *japonica, Prunus ssiori, Syringa reticulata, Ostrya japonica, Pachysandra terminalis.*

Holotype: Carpino-Quercion grosseserratae Takeda, Uematsu et Nakanishi 1983

When Takeda et al. (1983) named the alliance Carpino-Quercion grosseserratae, they put it into the Quercetalia serrato-grosseserratae Miyawaki et al. 1971, since *Quercus serrata* and *Q. mongolica* var.

grosseserrata were usually present but *Fagus crenata* was missing. Hoshino (1998) established the Carpino-Quercetalia grosseserratae.

Quercus mongolica var. *crispula* forest occurs widely on the lowlands north of the Ōshima Peninsula of southern Hokkaidō. One subtype occurs around Tomakomai (in the south) and has *Q. mongolica* var. *crispula* as the dominant tree, plus occasional admixtures of *Quercus serrata*. Another subtype is mixed forest with *Abies sachalinensis*.

Takeda et al. (1994) proposed that the Carpino-Quercion grosseserratae belongs to the Saso-Fagetalia, based on diagnostic species. Afterward, Hoshino discussed this and established a new order Carpino-Quercetalia grosseserratae Hoshino 1998. In this paper, Carpino-Quercion grosseserratae was compared with other *Q. mongolica* var. *crispula* forests in Table 1. Then it was decided here that the Carpino-Quercion grosseserratae belongs to the Carpino-Quercetalia grosseserratae.

(1) Carpino-Quercion grosseserratae Takeda, Uematsu et Nakanishi 1983

Diagnostic taxa: same species as for the order

Holotype: Carpino-Quercetum grosseserratae Tohyama et Mochida ex Takeda, Uematsu et Nakanishi 1983

The *Quercus* forests in Hokkaidō and northern Honshū were summarized in the Carpino-Quercion grosseserratae, including two associations of mixed forest and two types of *Quercus* forest with elements from the Japan Sea side of Honshū, with six associations and two communities. The first was described as an association by Tohyama and Mochida (1978), and was upgraded subsequently to alliance status by Takeda et al. (1983). This alliance includes not only simple mixed forests with northern coniferous and deciduous trees but also involves so-called macro-mosaic phenomena (Tatewaki 1958; Walter 1973). Tatewaki (1955, 1958) proposed the term "pan-mixed forest" based on mixed forests with deciduous *Quercus* and conifers in northeast Asia and Scandinavia. The pan-mixed forest originated from relicts of *Abies sachalinensis* in Hokkaidō, with *Q. mongolica* var. *crispula* increasing from 8,000 years ago. *Picea jezoensis* and *Picea glehnii* disappeared and then recovered (Igarashi 1997).

c. *Quercus mongolica* var. *crispula* forest on Jeju-do (temperate forest)

Saso quelpaertensis-Quercetalia crispulae ord. nov.

Synonym: Acero-Quercetalia mongolicae Kim et Yim 1988

Diagnostic taxa: *Carpinus laxiflora*, *C. tschonoskii, Sasa quelpaertensis, Asarum maculatum, Carex ciliatomarginata, Cacalia auriculata, Benthamidia japonica* (*Cornus kousa*), *Taxus cuspidata, Asiasarum sieboldii, Viola hondoensis, Anemone asiatica, Kadsura japonica, Lycopodium chinense, Ligularia fischeri, Vaccinium koreanum.*

Holotype: Saso quelpaertensis-Quercion crispulae all. nov.

Quercus mongolica var. *crispula* forests on Jeju-do were grouped as Acero-Quercetalia mongolicae Kim et Yim 1988. *Quercus* on Jeju-do was changed from *Q. mongolica* to *Q. mongolica* var. *crispula*, but *Q. mongolica* var. *crispula* forest in Korea is treated separately in this paper. One new order and one alliance were established here.

(1) Saso quelpaertensis-Quercion crispulae all. nov.

Synonym: Rhododendro-Quercion mongolicae Kim et Yim 1988

Diagnostic taxa: Same as for the order.

Holotype: Hepatico-Quercetum grosseserratae Yim et al. 1990

Jeju-do is a volcanic island located just southwest of the Korean Peninsula, in the East China Sea. It is separated from the peninsula by about 90 km and is about 180 km from the Gōtō Islands of Japan. Mt. Halla (1,950 m) is the highest mountain on Jeju-do and of South Korea; the uppermost part of Mt. Halla has been a national park since 1970. The area from 600 to 1,400 m is covered by deciduous forests (Yim et al. 1990). The area below 400 m on the north face and 600 m on the south face is potentially evergreen broad-leaved forest; deciduous forest goes up to 1,500 m on the north face and 1,700 m on the south face (Kim and Choi 2012). Yim et al. (1990) reported *Abies koreana, Q. mongolica* var. *crispula, Q. serrata* and *Carpinus laxiflora* forest types. *Quercus* and *Carpinus* forests from Mt. Halla National Park were compared with Japanese *Quercus* forests.

Four forest types were reported by Yim et al. (1990), using the older name *Q. mongolica* var. *grosseserrata*. *Quercus mongolica* var. *crispula* forest occurs at about 1,200–1,400 m (Hepatico-Qurcetum grosseserratae Yim et al. 1990). This association is characterized by *Q. mongolica* var. *crispula, Lonicera maackii, and Majanthemum biflorum*, and belongs to the new alliance Acero-Quercion mongolicae. *Carpinus laxiflora* forest occurs at about 800–1,200 m (Saso-Carpinetum laxiflorae Yim et al. 1990); *Carpinus tschonoskii* forest occurs at 600–800 m (Daphniphyllo-Carpinetum tschonoskii Yim et al. 1990); and the *Q. serrata* forest occurs at 600–700 m (Asaro-Quercetum serratae Yim et al. 1990). These forest types are placed in different alliances by Kim and Choi (2012): Symploco-Quercion grosseserratae and Ilici-Quercion serratae. The authors, however, did not produce an original paper with a comprehensive table showing the species composition, so these alliances are still to be discussed further.

The *Quercus mongolica* var. *crispula* forest is classified as temperate forest, and the *Quercus serrata* and *Carpinus* forests are classified as warm-temperate forests. The *Quercus serrata* and *Carpinus* forests have mixed compositions involving species of the Querco-Fagetea crenatae and Viburno dilatati-Quercetea serratae, with more species from the Querco-Fagetea crenatae. *Q. mongolica* var. *crispula* forest on Jeju-do is represented by only seven of the total of 57 relevés. Mt. Halla is an isolated peak, which permits cold wind to affect the forest more. Lower elevations have species from the Viburno dilatati-Quercetea serratae of warmer areas. These species become mixed, especially on the forest floor.

2. ***Quercus serrata* forests in Japan and Korea** (warm-temperate)

Vibruno dilatati-Quercetea serratae class. nov.

Synonym: Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, Harada, Kusunoki et Okuda 1971

Diagnostic taxa: *Quercus serrata, Viburnum dilatatum, Castanea crenata, Lindera* (*Benzoin*) *obtusiloba, Fraxinus sieboldiana, Stephanandra incisa, Polygonatum falcatum, Callicarpa japonica.*

Holotype: Carpino-Quercetalia serratae Miyawaki et al. 1964 ex Fujiwara et A. Harada

Quercus serrata forest occurs commonly as secondary forest in the region of evergreen broad-leaved forests. The first concept of Quercetalia serrato-mongolicae Miyawaki et al. (1971) was that deciduous forest species invade the evergreen broad-leaved forest region due to human activity, such as cutting (often regular) for firewood or charcoal, and mowing of forest-floor grasses and herbs for compost before World War II. Thus the composition involved invasive species, fast-growing species and climbers mixed with natural species. These species also occur at elevations below the *Fagus* and *Q. mongolica* var. *crispula* forests. The typical natural habitat is in central Honshū (Nagano and Ueda) and in the Yamagata basin. These are areas where evergreen broad-leaved forests cannot occur due to low winter temperatures, as shown by Kira (1949, 1991). The climate of the potential habitat has Coldness Index (CI) values from −10 to −20, and an annual moisture index (P/PET) below 1.40–1.81 (Box and Fujiwara, herein). Natural *Q. serrata* forest occurs mainly in these areas. Hibino and Sasaki (1982) analyzed pollen in northwestern Nagano and reported that similar vegetation types without *Fagus* appeared after the last glacial period. It is difficult to think that *Fagus* forest came back into this area after the last glacial period. Nowadays since we cannot see natural forests, we also do not see temperate species such as *Q. mongolica* var. *crispula, Fagus crenata*, or *Viburnum furcatum* in the lowland *Quercus serrata* forests. On the other hand, very common forest-floor species are *Pleioblastus* (=*Arundinaria*) *chino* in eastern Japan and *P. pygmaea* in western Japan. Well managed, mowed areas have grassland species (*Miscanthus sinensis* grassland is a Miscanthetea), climbers from a mantle community (Rosetea multiflorae), and species of the potential natural vegetation. Such secondary forests are quite species-rich and sometimes become refugia for endangered species. Around 200 species were recorded in a secondary *Quercus serrata* forest in Chiba Prefecture, east of Tokyo. Usually only 80–120 species occur in such forests in Japan. The forests are not tall, only 10–18 m.

Miyawaki et al. (1971) named these secondary forests, including *Q. mongolica* var. *crispula* forests, the Quercetalia serrato-mongolicae, but the class was deferred for more comparison. Ohno (1977) decided that this order belongs to the Fagetea crenatae Miyawaki et al. 1964. He rejected inclusion of mid-temperate or warm-temperate deciduous forests, thinking that deciduous forests should belong to the Fagetea crenatae.

When we discuss *Quercus serrata* forests, we need to compare *Pinus densiflora* forests too. In western Japan, *Pinus* and *Quercus* make mixed forests, for which Nakanishi et al. (1977) proposed a Querco-Pinetea densiflorae. Tsuji (2001) supported this idea because *Quercus serrata* forest does not have species of the *Fagus crenata* forest.

On the other hand, Suzuki (2001) pointed out that natural *Pinus densiflora* forests have fewer species, with their own characteristic species on ridges and other rocky areas; that *Q. serrata* forests occur on sites with deeper soil; and that the species composition is different. Both forest types will belong to the Carpino-Quercion serratae. These need to be compared with *Fagus* forests, and the class needs to be discussed. Comparison of *Fagus* and *Quercus* forests throughout eastern Asia must wait for another paper, so what is shown here is the class Vibruno-Quercetea serratae class. nov.

Quercus forests were summarized in Table 1, comparing with many new data (original relevés in Chiba Prefecture by Fujiwara 1970–1985 and by Miyawaki 1970–1985, plus Miyawaki et al. 1994; Miyawaki and Ohno 1996; Fujiwara et al. 1997, 1999; Hayashi 2000; Hanazawa 2006). As a result, *Q. serrata* forests can be seen as independent and have been given a new class name in this paper. *Toxicodendron trichocarpum* is a very common shrub in *Fagus-Q. mongolica* var. *crispula* and *Q. serrata* forests, appearing in more disturbed areas. Common species, not of high frequency or dominant, are *Euonymus oxyphyllus* and *Prunus grayana*. *Sorbus alnifolia* and *Clethra barbinervis* occur sometimes. These species occur mostly at Pacific sites or in *Fagus japonica* forests and were authorized as diagnostic species of the Querco-Fagetea crenatae. *Sorbus alnifolia* and *Kalopanax* (*Acanthopanax*) *pictus* occur widely in *Quercus* forests of China and Korea. Many understorey species of *Q. serrata* forests are also common in *Quercus* forests of Korea and China. *Q. serrata* and *Q. variabilis* forests in Asia are mostly human-disturbed and have many common species, such as *Oplismenus undulatifolius* s.l., *Paederia scandens* and *Smilax china*. These species are indicators of human disturbance, are thus unstable, and cannot be diagnostic species of classes or orders. Here we propose woody species that are stable and not occasional.

Two types of *Quercus serrata* forest were identified, one in Japan and the other in Korea. Korean *Quercus serrata* forests occur in the southern part of the peninsula. These forests in lowland Korea have mostly diagnostic species of the new class (Viburno dilatati-Quercetea serratae). Two orders are established in this paper: a Rhododendro kaempferi-Quercetalia serratae ord. nov in Japan and an Acero-Quercetalia serratae ord. nov. in Korea.

a. *Quercus serrata* forests in Japan

Rhododendro kaempferi-Quercetalia serratae ord. nov

Synonym: Quercetalia serrato-mongolicae Miyawaki, Fujiwara, Harada, Kusunoki et Okuda 1971

Diagnostic taxa: *Rhododendron obtusum* var. *kaempferi, Pourthiaea villosa* var. *laevis, Akebia trifoliata, Euonymus alatus* var. *apterus* f. *ciliatodentatus, Calamagrostis arundinacea* var. *brachytricha, Viola grypoceras, Prunus grayana, Wisteria floribunda, Viburnum erosum, Akebia quinata, Zanthoxylum piperitum, Cymbidium goeringii, Quercus acutissima, Abelia spathulata, Ligustrum obtusifolium.*

Holotype: Carpino-Quercion serratae Miyawaki, Fujiwara, Harada, Kusunoki et Okuda 1971

This new order is established to correspond to the Korean order (Acero-Quercetalia serratae ord. nov.).

Miyawaki et al. (1971) proposed Quercetalia serrato-mongolicae for secondary deciduous forests in the evergreen broad-leaved forest region, thinking that secondary deciduous forests should have their own natural habitats, based on the theory of potential natural vegetation. The decision of the appropriate class should thus wait for comparison with all deciduous Fagaceae forests.

Here we compared deciduous secondary forests, mainly involving deciduous *Quercus*, *Fagus crenata* and *F. japonica*, with natural *Q. mongolica* var. *crispula* forests. The comparison showed that *Quercus serrata* forests have a significantly different species composition. Especially when these occur in lowland areas, they contain many herbaceous and some woody climbers, *Miscanthus* grassland species, evergreen forest species (from the Camelietea japonicae), and geophytes, as well as their own deciduous tree and shrub species. These forests do not have real species of the *Fagus* and *Quercus mongolica* var. *crispula* forests. The common species, such as *Clethra barbinervis, Rhus trichocarpa, Toxicodendron trichocarpum*, and *Carpinus japonica*, are not major species of *Fagus* or *Q. mongolica* var. *crispula* forests. The common species occur throughout lowland Asia. These woody species occur in the Fagion japonicae and are also companion species of the temperate forests on the Pacific side of Japan.

(1) *Q. serrata* forest in inland central Japan (Nagano)

Lindero gracilipedis-Quercion serratae Shimada, Fujiwara et A. Harada all. nov. (Table 1)

Diagnostic taxa: *Lonicera gracilipes, Smilax sieboldii, Prunus verecunda, Zelkova serrata, Atractylodes japonica, Dendranthema japonicum, Smilax biflora* var. *trinervula, Spiraea japonica, Dianthus superbus* var. *longicalycinus, Kerria japonica.*

Holotype: Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et A. Harada ass. nov. (Table 2).

Quercus serrata and *Q. acutissima* forests can be seen frequently in low mountains surrounding the Nagano basin, with *Q. serrata* forests mainly in the southern Nagano basin. *Q. mongolica* var. *crispula* forests are not seen.

The annual rainfall is less than 1,200 mm, and Nagano and Ueda have less rainfall. Each mountain around Nagano has a different vertical distribution pattern of *Q. serrata* forests (Shimada 1997). The *Carex stenostachys-Q. serrata* community occurs from 360–600 m to 950–1,020 m, and the Rhododendro japonici-Quercetum serratae can be seen above 950–1,020 m.

Table 2 Rhododendro japonici-Quercetum serratae in Interior Central Japan

Relevé reference number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Original relevé number (in field)	Uy18	Ut10	Ut8	Uy17	Uy4	Ut7	Ns15	Uy3	Uy2	Ns6	Uy5	Ut9	Uy1	Uy15
Date of relevé (2000)	10	10	10	10	10	10	10	10	10	10	10	10	10	10
	11	18	18	11	7	18	5	7	6	2	7	18	6	10
Relevé size (m^2)	500	600	400	500	375	500	400	400	300	300	375	375	375	375
Altitude (m)	1040	1150	1200	1140	1190	1240	1120	1320	1290	1170	1020	1180	1300	970
Aspect	SW	W	W	SW	W	SW	W	SW	E	SW	NW	W	SSW	W
Slope (°)	25	30	40	30	20	35	25	35	40	20	15	35	30	10
Height of Tree layer 1 (T1) (m)	14	15	18	17	17	14	14	13	16	12	12	15	14	17
Cover of Tree layer 1 (T1) (%)	95	90	90	90	90	95	85	85	90	85	95	90	85	95
Height of Tree layer 2 (T2) (m)	8	12	•	10	10	8	10	8	11	•	•	8	8	12
Cover of Tree layer 2 (T2) (%)	10	20	•	10	10	10	20	10	10	•	•	10	20	10
Height of Shrub layer S (m)	4	4	5	4	4	5	4	4	5	5	5	4	4	6
Cover of Shrub layer S (%)	30	75	60	40	60	50	50	50	60	50	60	80	40	50
Height of Herb layer H (m)	0.4	0.4	0.5	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.7	0.4	0.6	0.6
Cover of Herb layer H (%)	20	20	30	20	40	30	20	20	40	20	30	20	30	40
Number of species	54	51	54	58	67	65	56	47	54	55	62	37	54	48
Diagnostic species of Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et A. Harada ass. nov.														
Quercus mongolica var. *grosseserrata*	+	1•1	3•3	4•3	1•1	1•1	4•4	3•2	5•4	5•4	+•2	+•2	4•4	•
Symplocos chinensis var. *leucocarpa* f. *pilosa*	+	+	•	1•1	+	•	+	+	2•1	+	+•2	•	+•2	•
Acer crataegifolium	+	+	+	•	•	+	•	•	+	+	•	+	1•2	+
Rhododendron japonicum	+	1•1	+•2	1•1	•	•	•	•	+	•	•	+	+	1•2
Ilex macropoda	+	•	+	+	•	+	•	+	•	•	+	+	•	+
Chimaphila japonica	+	+	•	+	•	+	•	•	+	•	•	+	+•2	•
Prunus incisa	•	•	+	•	+	+	+	+	+	+	•	•	•	•
Adenophora triphylla var. *japonica*	+•2	•	•	+	•	•	•	+	+•2	•	+	•	•	+
Vitis coignetiae	+	•	•	•	+	•	+	+	•	+	+	•	•	•
Larix kaempferi	+	•	•	•	•	•	1•1	+	+	•	•	•	•	•
Rubus mesogaeus	•	•	•	•	+	+	+	•	•	•	•	•	•	•
Clematis stans	•	•	•	•	•	•	•	+	•	+	+	•	•	•
Diagnostic species of Lonicero gracilipedis-Quercion serratae Shimada, Fujiwara et A. Harada all. nov.														
Lindera obtusiloba	1•1	+	+	2•2	1•1	2•3	+	+•2	1•1	1•1	1•1	+	1•1	+•2
Lonicera gracilipes	+•2	+	1•1	+	1•1	1•1	+	+	+	+•2	+•2	•	+•2	+
Smilax sieboldii	+•2	+	+	+	+•2	+	1•1	+	+	+	+	•	+	+
Prunus verecunda	+•2	•	+•2	1•1	+	1•2	+	+	+	•	1•1	•	1•1	1•1
Pyrola japonica	+	+	+	+	•	+	+	+	•	•	•	+	+	+
Abelia spathulata	+•2	1•1	+	•	•	+•2	+	•	+	+	•	+•2	+•2	+
Atractylodes japonica	1•1	+	•	+•2	+	•	•	•	+	•	+	+	+•2	+
Smilax biflora var. *trinervula*	+•2	•	+	+	+	+	+•2	+	•	+	•	•	+	•
Eupatorium chinense var. *simplicifolium*	+	•	•	+	+	+	+	•	•	+	+	•	+	•
Artenmisia keiskeana	+•2	+	+	1•1	•	+•2	•	•	•	•	•	•	1•1	+•2
Vicia nipponica	+	+	+	•	+	+	•	+	•	+	•	•	•	•
Euphorbia pekinensis	+	•	•	+	1•1	•	•	+	+•2	•	•	•	•	+
Prunus apetala	+	•	•	•	•	•	+	•	•	+	+	•	•	+•2
Plectranthus inflexus	•	+	•	•	+	+•2	+	+	•	•	•	•	•	•
Spiraea japonica	+	•	+	•	•	•	•	+	•	•	•	•	•	+
Campanula puncutata var. *hondoensis*	+	•	•	•	+	•	•	•	•	+	•	•	+	•
Kerria japonica	•	•	+	•	•	+	•	•	+	•	1•1	•	•	•
Malus sieboldii	•	•	•	•	+	+•2	•	•	•	•	+	•	•	•
Diagnostic species of Rhododendro kaempferi-Quercetalia serratae Fujiwara et A. Harada ord nov.														
Euonymus alatus var. *apterus* f. *ciliatodentatus*	1•1	•	+	+	+	+	+	+	+	+	+	•	+	+
Solidago virga-aurea var. *asiatica*	+•2	+	+	+•2	+	+	•	•	1•1	+	+	•	+	+
Akebia trifoliata	+•2	•	+	+	+	+	+	+	•	+	+	•	+	+
Calamagrostis arundinacea var. *brachytricha*	1•1	+	1•2	+	+	+•2	+	+	•	•	+•2	•	+•2	•
Viola grypoceras	+•2	+	+	+	+	+•2	+	•	+•2	+•2	•	•	+	•
Pourthiaea villosa var. *laevis*	•	+•2	2•1	•	•	1•2	+	+	+	+	+	+•2	+	•
Prunus grayana	•	+	+	+	+	+	+	•	•	•	1•2	+	•	+
Rhododendron kaempferi	•	4•3	2•2	•	•	+	+	•	1•1	•	+	2•2	1•1	2•2
Zanthoxylum piperitum	•	•	+	+	+	•	+	+	•	+•2	+	•	+	•
Vaccinium oldhamii	+•2	1•1	•	+	•	•	+	•	•	•	+	1•2	•	+•2
Akebia quinata	+	•	•	+	+	+	•	•	•	+	+	•	•	•
Viburnum erosum	•	2•3	2•3	•	•	1•1	+	•	•	•	+	1•2	•	•
Wisteria floribunda	•	+	•	+	1•2	•	+	1•1	•	•	1•1	•	•	•
Diagnostic species of Viburno dilatati-Quercetea serratae Fujiwara et A. Harada 2013														
Viburnum dilatatum	1•1	+	+	+	+•2	1•1	1•1	+•2	1•1	1•1	2•2	+	+	+•2
Quercus serrata	5•4	5•5	4•3	3•3	5•4	4•4	+	+•2	+	•	4•3	5•4	1•1	5•5
Castanea crenata	1•1	•	•	+	1•1	+•2	1•1	4•3	+•2	+	2•2	1•1	1•1	+
Euonymus oxyphyllus	3•3	+	+	•	+•2	+	+	1•1	•	+	2•1	•	+•2	1•1
Fraxinus sieboldiana	1•1	•	•	1•1	•	•	1•2	1•2	2•2	+•2	1•1	+	1•1	+•2
Staphylea bumalda	•	•	•	+	1•1	+•2	+•2	+•2	•	+	+	•	•	•
Ligustrum obtusifolium	•	+	+	•	+	+•2	•	•	•	•	+•2	•	+	•
Polygonatum falcatum	+	•	•	+	•	•	+	•	•	+	•	•	•	•
Callicarpa japonica	•	+	+	•	•	•	+•2	•	•	•	•	•	•	•
Stephanandra incisa	•	•	+•2	•	•	•	•	•	•	•	•	•	•	•

Table 2 (continued)

Other species

Carex lanceolata	1·1	1·1	2·1	1·1	2·1	2·2	1·2	2·1	2·1	1·2	1·2	1·1	2·1	1·1
Corylus sieboldiana	+	•	+	+·2	+·2	1·1	+·2	+	+·2	+	+	+	+	+
Rhus trichocarpa	+	+	+	+	•	+	+	•	+	+	+·2	+	+·2	1·1
Sorbus alnifolia	+	1·1	+	+	•	•	+	2·2	+	+	1·1	•	+	1·1
Acer mono var. *mayrii*	+	+	+	•	+	+	+	1·1	+	•	•	+	1·1	+
Celastrus orbiculatus	+	•	+	+	+	+	+	+	+	•	+	•	+	+
Pteridium aquilinum var. *latiusculum*	•	+	+	+	+	+	+	•	•	+	•	+	+	+
Hosta montana	+	•	•	+	+	+	•	•	+	•	+	+	+	+
Clethra barbinervis	•	+·2	+	•	•	+	1·2	+	+·2	+	•	1·2	•	•
Viburnum wrightii	•	+	+·2	•	•	+	+·2	•	•	+	•	1·1	+	+
Viola keiskei f. *okuboi*	+	•	•	+	•	+	•	+	+	+	+	•	•	•
Aster scaber	+	•	•	+	+	•	•	+	+·2	•	+	•	•	•
Pinus densiflora	+	•	•	+	•	+	•	•	+	•	•	•	+	+
Carex siderosticta	•	2·1	+·2	•	+	1·2	•	•	•	•	+	1·1	•	•
Spodiopogon sibiricus	•	+·2	+·2	•	•	+·2	•	•	+	•	•	•	+	+
Lespedeza bicolor f. *acutifolia*	•	•	+	+	+	•	•	•	+	•	•	•	+	+
Lysimachia clethroides	•	+	+·2	•	+	+	•	•	+	•	•	•	•	•
Tripterospermum japonicum	•	+	+	•	+	+	•	•	•	•	•	+·2	•	•
Berchemia racemosa	•	•	•	+	+	•	+	+	•	•	+	•	•	•
Disporum smilacinum	•	•	•	•	+·2	•	•	•	+	1·2	2·1	•	+·2	•
Prunus maximowiczii	+	•	•	+	•	•	•	•	+	•	•	•	•	+
Senecio nemorensis	+	•	•	+	•	•	•	•	•	+	•	•	+	•
Viola rossii	+	•	•	•	+	•	•	+	+	•	•	•	•	•
Cornus kousa	+·2	•	•	•	•	•	+	+	•	+	•	•	•	•
Chrysanthemum makinoi	•	+	+	•	•	+	•	•	+	•	•	•	•	•
Viburnum phlebotrichum	•	2·1	+·2	•	•	+·2	•	•	•	•	•	2·3	•	•
Athyrium yokoscense	•	+	•	•	+	•	•	•	+	•	+	•	•	•
Metaplexis sp.	•	+	•	•	•	•	+·2	+	•	+·2	•	•	•	•
Hydrangea paniculata	•	+	•	•	•	•	•	•	•	•	+	+	•	+
Acer rufinerve	•	•	+	•	•	+·2	•	•	+·2	•	•	+	•	•
Berberis thunbergii	•	•	•	+	+	+	•	•	•	+	•	•	•	•
Chloranthus japonicus	•	•	•	•	+	•	•	+·2	+	•	+	•	•	•
Potentilla fragarioides var. *major*	+	•	•	+	•	•	•	•	+	•	•	•	•	•
Actinidia arguta	+	•	•	•	•	+	•	•	•	•	+	•	•	•
Meliosma myriantha	•	+	+	•	•	•	+	•	•	•	•	•	•	•
Lyonia ovalifolia var. *elliptica*	•	+·2	+	•	•	•	•	•	•	•	•	•	•	+
Ligustrum tschonoskii	•	•	•	+	•	•	+	•	•	+	•	•	•	•
Thalictrum kemense var. *hypoleucum*	•	•	•	•	+	+	•	•	•	•	•	•	+	•
Rubia akane	•	•	•	•	+	•	•	+	•	+	•	•	•	•
Acer palmatum var. *matsumurae*	•	•	•	•	•	•	2·1	•	+	+	•	•	•	•
Tilia japonica	•	•	•	•	•	•	•	+·2	+	+	•	•	•	•
Maackia amurensis var. *buergeri*	•	•	•	•	•	•	•	•	+	+	+	•	•	•
Cephalanthera longibracteata	•	+	•	•	+	•	•	•	•	•	•	•	•	•
Kalopanax pictus	•	+	•	•	•	+	•	•	•	•	•	•	•	•
Viola phalacrocarpa	•	+	•	•	•	+	•	•	•	•	•	•	•	•
Smilax china	•	+	•	•	•	•	•	•	•	•	•	+	•	•
Serratula insularis	•	•	•	+	•	+	•	•	•	•	•	•	•	•
Cephalanthera erecta	•	•	•	+	•	•	•	•	•	•	•	•	+	•
Patrinia villosa	•	•	•	+	•	•	•	•	•	•	•	•	•	+
Epimedium grandiflorum var. *thunbergianum*	•	•	•	•	+·2	•	•	•	•	•	+·2	•	•	•
Astilbe thunbergii	•	•	•	•	+·2	•	•	•	•	•	+	•	•	•
Rosa multiflora	•	•	•	•	+	•	•	•	•	•	+	•	•	•
Tulotis ussuriensis	•	•	•	•	+	•	•	•	•	•	•	•	1·1	•
Melampyrum roseum var. *japonicum*	•	•	•	•	+	•	•	•	•	•	•	•	+	•
Cirsium sp.	•	•	•	•	•	+	•	•	•	+	•	•	•	•
Ilex pedunculosa	•	•	•	•	•	+·2	•	•	•	•	•	+	•	•
Hamamelis japonica	•	•	•	•	•	•	+	•	•	2·3	•	•	•	•
Dioscorea nipponica	•	•	•	•	•	•	+	•	•	•	+	•	•	•
Deutzia crenata	•	•	•	•	•	•	•	•	+	•	•	•	•	+
Thalictrum sp.	•	•	•	•	•	•	•	•	•	+	+	•	•	•
Morus bombycis	•	•	•	•	•	•	•	•	•	•	+	•	•	+
Acer japonicum	•	•	•	•	•	•	•	•	•	•	•	+	+	•

Additional species occuring once in Running no.1: *Cocculus orbiculatus* +; no.3: *Quercus dentata* +, *Fraxinus lanuginosa* +; no.4: *Eularia quadrinervis* + ·2, *Acanthopanax spinosus* +, *Ixeris dentata* +, *Chloranthus serratus* +, *Dioscorea tokoro* +, *Paraixeris denticulata* +; no.5: *Viola eizanensis* + ·2, *Prunus sargentii* +, *Brachypodium sylvaticum* var. *miserum* +, *Actaea asiatica* +, *Cimicifuga acerina* +, *Vicia unijuga* +, *Thelypteris palustris* +, *Viola keiskei* +, *Viola* sp. +; no. 6: *Schisandra repanda* +, *Galium verum* var. *asiaticum* f. *nikkoense* +, *Rubus palmatus* var. *coptophyllus* +; no.7: *Magnolia obovata* +, *Helwingia japonica* +, *Parabenzoin praecox* +, *Kadsura japonica* +; no.8: *Carpinus tschonoskii* +, *Elaeagnus umbellata* +; no.9: *Viburnum wrightii* var. *stipellatum* +, *Alnus firma* +; no.10: *Acer sieboldianum* 1·1, *Aster ageratoides* var. *ovatus* +, *Dioscorea septemloba* +, *Clinopodium chinense* var. *parviflorum* +, *Vitis ficifolia* var. *lobata* +, *Torilis scabra* +; no.11: *Juglans ailanthifolia* +, *Impatiens nolitangere* +, *Cremastra appendiculata* +, *Smilax nipponica* +, *Calamagrostis hakonensis* +, *Potentilla freyniana* +; no.12: *Tripetaleia paniculata* + ·2, *Vaccinium japonicum* + ·2; no.13: *Sorbus commixta* 1·1, *Carpinus japonica* +, *Festuca ovina* var. *coreana* +, *Viola kusanoana* +; no.14: *Cornus brachypoda* +, *Amelanchier asiatica* +, *Juniperus rigida* +, *Fagara mantchurica* +.

Location of survey sites in Nagano Prefecture, Japan: in relevé reference no. 1, 4, 5, 8, 9, 11, 13, 14: Tomi City; no. 2, 3, 6: Sakaki-Machi, Hanishina-gun; no. 7, 10: Matsushiro-cho, Nagano City; 12: Sakaki-Machi, Hanishina-gun.

In this paper, the Lindero obtusilobae-Quercion serratae Shimada, Fujiwara et H. Harada is separated into a Quercetum dentatae-serratae Wada 1982 ex S. Suzuki 2002a; a Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et H. Harada (herein); and a *Carex stenostachys-Quercus serrata* community. The original diagnostic species of the Quercetum dentata-serratae were *Q. dentata, Dianthus superbus* and *Spiraea japonica*. S. Suzuki (2001) compared all *Q. serrata* forests in a synoptic table and added more diagnostic species for the Quercetum dentatae-serratae. The new association is defined here.

New association: Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et A. Harada ass. nov.

Synonym: *Clethra barvinervis-Quercus serrata* community, *Acer crataegifolium-Quercus serrata* community Wada 1982.

Diagnostic taxa: *Rhododendron japonicum, Quercus mongolica* var. *crispula, Betula platyphylla* var. *japonica, Chimaphila japonica, Vitis coignetiae, Ilex macropoda*, *Rubus mesogaeus, Clematis stans, Larix kaempferi.*

Holotype: Ut10 (Table 2, running no. 2), Nagano Prefecture.

The area surrounding the Nagano basin has a complicated climate, with deep snow (more than 50 cm) in the north and drier conditions in the south. Annual precipitation at Nagano is 918 mm, but Ueda, to the south, has only 880 mm. Mountains such as Tarō-zan (1,164 m) and Yunomaru-san to the south, as well as Ueda, are covered by deciduous *Quercus* forests. Mixed forests with *Quercus serrata* and *Q. mongolica* can be seen above 950–1,020 m. This kind of forest is characterized by *Rhododendron japonicum, Betula platyphylla* var. *japonica, Chimaphila japonica, Vitis coignetiae,* etc., and is defined as a Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et H. Harada ass. nov. Usually it has some species from the *Fagus-Quercus* forests, such as *Acer crataegifolium*, *Cornus kousa*, *Symplocos chinensis* var. *leucocarpa* f. *pilosa* and *Hosta sieboldiana*, but it does not have real species of the Saso-Fagetalia crenatae or Querco-Fagetea crenatae. It occurs until southern Nagano Prefecture and in the Mt. Kisō region (Wada 1982a).

(2) *Q. serrata* forest excluding Chūbu (central Japan)
Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1970 ex Fujiwara et A. Harada all. nov.

Diagnostic taxa: *Lindera umbellata, Pertya scandens, Prunus jamasakura, Callicarpa mollis, Lilium auratum, Sorbus japonica, Hydrangea hirta, Ligustrum japonicum*, and evergreen species (*Quercus glauca, Pieris japonica, Trachelospermum asiaticum* var. *intermedium, Eurya japonica, Ardisia japonica, Aucuba japonica*)

Holotype: Moroo-Quercenion serratae suball. nov.

This alliance summarizes the most typical secondary forests in Japan. It is divided into three suballiances.

i) *Quercus serrata* forests in the Kantō-Izu Region and coastal western Japan
Moro australis-Quercenion serratae suball. nov.

Diagnostic taxa: *Dioscorea tokoro*, *Morus australis*, *Pleioblastus chino*, *Lonicera japonica*, *L. gracilipes* var. *glabra*, *Smilax riparia* var. *ussuriensis*, *Celtis sinensis* var. *japonica*, *Rubus palmatus* var. *coptophyllus*, *Stachyurus praecox*, *Cephalotaxus harringtonia*, *Aphananthe aspera*, *Mallotus japonicus*, *Carex lenta*, *Athyrium niponicum*, *Clematis japonica*, *Magnolia praecocissima* (*kobus*), *Gynostemma pentaphyllum*, *Dumasia truncata*, *Aristolochia kaempferi*, *Dryopteris varia* var. *setosa*, *Castanopsis cuspidata* var. *sieboldii*, *Neolitsea sericea*, *Hedera rhombea.*

Holotype: Quercetum acutissimo-serratae Miyawaki et Fujiwara 1968

This suballiance involves two associations, a Daphno-Quercetum serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971; and a Quercetum acutissimo-serratae Miyawaki et Fujiwara 1968.

The most florest-floor species occur in this suballiance, especially in the Quercetum acutissimo-serratae. The soil is mainly black Kantō Loam, which has good moisture content when covered by forest. Many geophytes appear in spring. On steep slopes, evergreen shrubs such as *Eurya japonica, Pieris japonica* and *Aucuba japonica* become dominant in the shrub layer. A Daphno-Quercetum occurs on Tertiary layers, with more evergreen woody and herbaceous species.

ii) *Quercus serrata* forests in western Japan
Ilici pedunculosae-Quercenion serratae suball. nov.

Diagnostic taxa: *Ilex pedunculosa, Lyonia ovalifolia* var. *elliptica, Pieris japonica, Rhododendron macrosepalum*, *Quercus variabilis.*

Holotype: Pleioblasto pygmaeo-Quercetum serratae

This suballiance is divided into four associations and one community: Pygmaeo-Quercetum serratae Minamikawa et Yato 1962; Platycaryo-Quercetum serratae Itow 1981; Quercetum variabili-serratae Kobayashi, Muranaga, Takeda, Hasunuma 1976 em. S. Suzuki in Miyawaki 1983; and Lindero sericeae-Quercetum serratae, plus a *Symplocos myrtacea-Quercus serrata* community. The alliance is characterized by evergreen woody species such as *Ilex pedunculosa, Quercus glauca, Camellia japonica, Ligustrum japonica, Aucuba japonica, Eurya japonica*, and *Ilex crenata,* and occurs widely in Kansai, Chūgoku, Shikoku and Kyūshū. Mostly it occurs as substitute vegetation in the evergreen *Quercus* forest region. The soil is mostly shallow, and the substrate may be granite, limestone, fluvial terrace, or other.

iii) *Quercus serrata* forests at higher elevations

Viburno phleobotrichi-Quercenion serratae suball. nov.

Diagnostic taxa: *Viburnum phlebotrichum, Abies firma, Parabenzoin praecox, Acer palmatum* var. *amoenum, Acer rufinerve, Carpinus japonica, Meliosma myriantha*

Holotype: Castaneo-Quercetum serratae Tsuji et Kodaira 1976

Two associations are involved in this suballiance: a Castaneo-Quercetum serratae Okutomi, Tsuji et Kodaira 1976 in eastern Japan; and a Lindero sericeae-Quercetum serratae Ya. Sasaki ex S. Suzuki 2001 in Shikoku and Kyūshū. The Castaneo-Quercetum serratae occurs as secondary forest and as natural forest but with very few remnants.

Frequently the Castaneo-Quercetum serratae occurs next to the Quercetum acutissimo-serratae, but it grows until 1,000 m in Kantō and 1,400 m in Chūbu (S. Suzuki 2001). On the Bōsō Peninsula (east of Tokyo) it comes down to 100 m (Miyawaki and Fujiwara 1984).

The Lindero sericeae-Quercetum serratae occurs in Shikoku and Kyūshū, above 600 m. Hoshino (1998) ascribed this association to the *Quercus mongolica* var. *crispula* forest system, but S. Suzuki reorganized it and moved it to the *Quercus serrata* forest system.

b. *Quercus serrata* forest in Korea

Aceri pseudosieboldiani-Quercetalia serratae ord. nov.

Synonym: Aceri-Quercetalia mongolicae Song 1988

Diagnostic taxa: *Acer pseudosieboldianum, Rhododendron schlippenbachii, Weigela florida, Sasamorpha borealis, Styrax obassiai, Smilax nipponica, Prunus levelliana, Stewartia koreana.*

Holotype: Lespedezo-Quercion serratae Takeda, Nakanishi et D. Choe 1994

Takeda et al. (1994) placed *Quercus serrata* and *Q. mongolica* forests in the Acero-Quercetalia mongolicae Song 1988, which had been estiablished originally for mixed forests of *Quercus mongolica* (Song 1988). This order is characterized, according to Takeda et al. (1994), by *Acer pseudosieboldianum, Rhododendron schlippenbachii* (in common with the new order), *Astilbe chinensis, Pseudostellaria palibiniana*, and common species in *Quercus mongolica* forests throughout eastern Asia (*Corylus sieboldiana* var. *mandshurica*, etc.). Song (1988) criticized the fact that Nakanishi (1983) had suggested this order without providing a table involving *Quercus serrata* forests. Most *Quercus serrata* forests are secondary and have many species in common with Japanese *Q. serrata* forests, even *Fagus* forests. By comparing *Fagus* and *Quercus* forests in East Asia together in one table we could see some common species in Korea, but the *Quercus mongolica* and *Q. serrata* forests were seen to have different species compositions. In particular, *Quercus serrata* forests have many more species common to *Q. serrata* forests in Japan than do the *Quercus mongolica* forests in Korea, China and the Russian Far East. Therefore, in this paper, we establish a new order to separate the Lespedezo-Quercion serratae from the Quercetea mongolicae.

(1) Callicarpo japonicae-Quercion serratae Kim 1990

Synonym: Callicarpo japonicae-Quercion serratae Kim 1990, Lespedezo-Quercion serratae Takeda, Nakanishi et D. Choe 1994.

Diagnostic taxa: same species as in the order.

Holotype: Lespedezo-Quercetum serratae Takeda, Nakanishi et D. Choe 1994

The Callicarpo-Quercion serratae Kim 1990 represents communities at lower elevations in South Korea which are transitional to the Camellietea japonicae (Kim 1990). This alliance is typical warm-temperate forest in South Korea. It was a suballiance and belonged at one time to the Lindero obtusilobae-Quercion mongolicae, Aceri pseudosieboldiani-Quercetalia mongolicae, Quercetea mongolicae (Krestov et al. 2006).

Comparison of species compositions showed that this alliance had many species from the Viburno dilatati-Quercetea serratae. So we change the affiliation of this alliance from Quercetea mongolicae to Viburno dilatati-Quercetea serratae. The physiognomy of this alliance is very similar to that of the Carpino-Quercion serratae. This alliance has three associations and summarizes lowland forests in southern South Korea that are under human impact.

3. ***Quercus variabilis-Quercus serrata* var. *brevipetiolata* forest in China**

   Quercetea variabili-brevipetiolatae Tang, Fujiwara et You in Box et Fujiwara 2015

   Diagnostic taxa: *Quercus serrata* var. *brevipetiolata* (=*Q. glandulifera* var. *brevipetiolata*), *Aster ageratoides, Platycarya strobilacea, Symplocos paniculata, Rhododendron mariesii, Liriope spicata, Lespedeza formosa, Rubus corchorifolius, Dalbergia hupeana, Quercus aliena* var. *acuteserrata.*

   Holotype: Pistacio-Quercetalia variabilis Tang, Fujiwara et You 2015

   Quercus variabilis forests in middle China and *Q. brevipetiolata*-*Q. variabilis* forests of southern China were summarized as a class. The *Q. variabilis* forests are mostly natural and are protected in nature reserves around temples in middle and eastern China (Shaanxi, Henan, and Shandong). To the west, *Q. variabilis* forests remain commonly on lower hills. In southern China, *Q. variabilis* forests are secondary, especially in the evergreen broad-leaved forest region. Other deciduous *Quercus* species occur in the evergreen broad-leaved forest region more than in middle China (Quercetalia fabri-brevipetiolatae S. Suzuki et al. 2003 ex Fujiwara et A. Harada).

   The canopy of *Quercus variabilis* forests is always somewhat open, and the stands look like wooded savannas when the sites are very dry. *Q. variabilis* forests are relatively tall, as compared with other secondary *Quercus* forests, but the canopies of *Q. serrata* var. *brevipetiolata* and other deciduous *Quercus* forests are more closed. The other deciduous *Quercus* forests occur in the evergreen broad-leaved forest areas as secondary forests and also at high elevation, above the evergreen broad-leaved forests, such as *the Quercus stewardii* forest on the mountains Huang-Shan in Anhui or Tianmu-Shan in Zhejiang. Nowadays *Quercus serrata* var. *brevipetiolata* is treated as a synonym of *Quercus serrata* Murray (Kew Index, Wu and Raven 1999: Flora of China). This too still needs to be discussed further.

   a. *Quercus* forest in middle China (*Quercus variabilis* forest)

      Pistacio-Quercetalia variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

      Diagnostic taxa: *Quercus variabilis*, *Pistacia chinensis*, *Celtis koraiensis*, *Grewia biloba* var. *parviflora*.

      Holotype: Carpino turczaninovii – Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

      Quercus variabilis forests occur as preserved patches around temples in southern China, from the Qing-Lin Mountains and, in the east, from the Tai-Han Mountains. These forests were characterized by *Quercus variabilis*, *Pistacia chinensis*, *Celtis koraiensis*, etc. The sites are very dry, and most substrates are granite or limestone. In southern Jiangsu and Anhui, *Q. variabilis* forests have expanded as secondary forests in the evergreen broad-leaved forest region. Three alliances were included in this order.

      (1) *Quercus variabilis* forest in middle-western China

      Lonicero standishii-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

      Diagnostic taxa: *Jasminum giraldii, Lonicera standishii, Mahonia fortunei, Viburnum schensianum, Bothriospermum secundum, Roegneria kamoji, Cotinus coggygria, Juniperus formosana, Sinarundinaria nitida, Pinus tabulaeformis, Elaeagnus umbellata.*

      Holotype: Junipero formosanae-Quercetum variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

      This alliance summarizes *Quercus variabilis* forests in the Nanwutai and Louguantai Nature Preserves, on the northern slopes of the Qinling Mountains and also on the Dingjun-Shan (mountain) next to Sichuan in southern Shaanxi. The substrate is granite and very dry. The soil is poor and yellow, with sand and clay. This is quite different from eastern China. The Lonicero standishii-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015 involves two associations and one community.

      (2) Carpino turczaninovii-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

      Diagnostic taxa: *Forsythia suspensa*, *Carpinus turczaninovii*, *Adenophora polyantha*, *A. trachelioides*, *Rhus potaninii*, *Quercus aliena*, *Carex subpediformis*, *Lonicera ferdinandii*.

      Holotype: Viburno mongolicae-Quercetum alienae Tang, Fujiwara et You in Box et Fujiwara 2015

      This alliance summarizes *Quercus variabilis* forests mainly from the Yuntai-Shan mountains of northern Henan and the Baotianman Nature Preserve, in the Laojie-Ling and Shiren-Shan mountains in southwestern Henan, at elevations ranging from 832 to 1,320 m, mainly on south-facing aspects. The sites are drier, and the forest has other deciduous *Quercus* species admixed, such as *Q. aliena* and *Q. brevipetiolata*. This syntaxon consists of an association and two communities.

(3) Trachelospermo jasminoidis-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

Diagnostic taxa: *Trachelospermum jasminoides, Celtis sinensis, Aleurites fordii, Acer buergerianum, Ilex cornuta, Smilax glauco-china.*

Holotype: Pteroceltio tatarinowi-Quercetum variabilis Tang, Fujiwara et You in Box et Fujiwara 2015

This alliance combines most southern and eastern *Q. variabilis* forests, which occur on south-facing slopes, in limestone areas, at relatively lower elevations ranging from 100 to 568 m. The locations are in the Yuntai-Shan and Jigong-Shan mountains of Henan; the Huangcangyu Nature Preserve of Anhui; and the Maoshan hilly region of Jiangsu.

b. Montane deciduous *Quercus* forest in China

Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da ex Fujiwara et A. Harada ord. nov.

Diagnostic taxa: *Rhododendron simsii, Lindera reflexa, Viburnum setigerum.*

Holotype: Sasamorpho sinicae-Quercion brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da et al. 2003

The evergreen broad-leaved forest region has much more moisture than the northern *Q. variabilis* forests, and more deciduous *Quercus* species occur in this region. Two alliances were reported by S. Suzuki et al. (2003). The Quercion variabili-fabri S. Suzuki et al. 2003 is mostly secondary forest, but the Sasomorpho sinicae-Quercion brevipetiolatae is mainly natural forest on mountains. Unfortunately, *Quercus fabri* also occurs in *Quercus variabilis* forests (Pistacio-Quercetalia variabilis). This order name does not suggest southern deciduous *Quercus* forests but should be kept by right of prior naming.

(1) Southern deciduous *Quercus* forest

Liquidambaro formosanae-Quercion fabri all. nov.

Diagnostic taxa: *Liquidambar formosana, Quercus fabri, Pinus massoniana, Vaccinium bracteatum, Cunninghamia lanceolata, Loropetalum chinense, Woodwardia japonica, Premna macrophylla, Castanopsis sclerophylla, Symplocos sumuntia, Sassafras tzumu, Quercus chenii, Lindera aggregata, Schima superba.*

Holotype: Quercetum acutissimo-variabilis Suzuki, Nakamura, Kawano, X. Wang et Da 2003

Suzuki et al. (2003) used several portions of this alliance and the association name. The names are different in the description, tables and figures, but we use a unified name in the abstract and the first description. A new alliance for secondary forests was decided. *Liquidambar formosana* occurs in this alliance characteristically; it is a good indicator species of human impact and secondary forest. This alliance involves many evergreen species, such as *Vaccinium bracteatum, Eurya muricata, Dryopteris fuscipes, Woodwardia japonica* and *Castanopsis sclerophylla*. These species show that the potential natural forest is evergreen *Castanopsis-Quercus* forest. This alliance corresponds to the Carpino-Quercion serratae in Japan (Suzuki et al. 2003). One association and two communities are involved.

(2) Montane *Quercus* forest in China

Sasamorpho sinicae-Quercion brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da ex Fujiwara et A. Harada all. nov.

Diagnostic taxa: *Hydrangea angustipetala, Castanea seguinii, Stephanandra chinensis, Pourthiaea villosa, Sasamorpha sinica, Dendrobenthamia japonica* var. *chinensis, Corylus heterophylla* var. *sutchuensis, Quercus* (*Cyclobalanopsis*) *gracilis, Pterostyrax corymbosus, Lonicera modesta, Veratrum schindleri, Castanea henryi, Carpinus viminea, Hamamelis mollis, Q. stewardiana, Litsea cubeba, Callicarpa japonica* var. *angustata, Stewartia sinensis, Magnolia cylindrica, Sorbus amabilis, Fraxinus championii.*

Holotype: Quercetum brevipetiolati-acuteserratae Suzuki, Nakamura, Kawano, X. Wang et Da 2003

One association on Huang-Shan (Anhui) and another from Tianmu-Shan (Zhejiang) are described in this alliance. The physiognomy of forests in this alliance is similar to that of Saso quelpaertensis-Quercion crispulae in Korea. The canopy is closed by *Q. stewardiana, Q. fabri*, and *Q. aliena* var. *acuteserrata*, and the under storey is covered by *Sasamorpha sinica*. Suzuki et al. (2003) described *Quercus* forests on the top of Huang-Shan as substitutes for *Fagus engleriana* forest, but forest dominated by *F. engleriana* remains in wind-sheltered valleys on nearby mountains. *Quercus* occurs widely on the tops, and some *Fagus* individuals are mixed in. In this case, *Fagus engleriana* can make forests only in valleys, since it does not tolerate strong wind.

Usually *F. engleriana* occurs on valley slopes. *Fagus* and *Quercus* forests are segregated on Huang-Shan. Two associations are reported in this alliance.

4. ***Quercus mongolica*** **forest in Korea, China and the Russian Far East**

(temperate and cool-temperate)

Quercetea mongolicae Song ex Krestov, Song, Nakamura et Verkholat 2006

Synonyms: Quercetea mongolicae Kim 1992

Diagnostic taxa: *Quercus mongolica*, *Maackia amurensis*, *Pinus koraiensis*, *Tilia amurensis*, *T. mandshurica*, *Vitis amurensis*, *Corylus mandshurica*, *Artemisia stolonifera*, *Euonymus pauciflorus*, *Convallaria keiskei*, *Cacalia hastata*, *Viburnum sargentii*, *Polygonatum involucratum*, *Galium dahuricum*.

Holotype: Aceri-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994

Krestov et al. (2006) established this class for cool and cold-temperate forests in mainland regions and lower elevations of Hokkaidō, where there is no period of moisture deficit during the growing period. Actually, Hokkaidō has different species compositions (see Carpino-Quercetalia crispulae), so we separated the *Q. mongolica* var. *crispula* forests in Hokkaidō from this class. The Quercetalia mongolicae also involves both cool-temperate mixed forests and temperate forests. Krestov et al. included Quercetalia serrato-grosseserratae Miyawaki et al. 1971 in this class, but Quercetalia serrato-grosseserratae does not occur in Hokkaidō (Hoshino 1998). So we broke up this order because the main *Q. serrata* forests have warm-temperate and secondary species, and *Q. mongolica* var. *crispula* forests have temperate and cool-temperate species, and occur in the temperate and cool-temperate region.

Quercetea mongolicae involves three orders: Aceri pseudosieboldii-Quercetalia mongolicae Song ex Takeda, Nakanishi, et Choe 1994; Lespedezo bicoloris-Quercetalia monglicae Krestov, Song, Nakamura et Verkholat 2006, which was moved here from Querco mongolicae-Betuletea davuricae Ermakov 1997; and Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, Song, Nakamura et Verkholat 2006.

a. *Quercus mongolica* and mixed forests in the Korean Peninsula (temperate and cool-temperate)

Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe1994

Synonyms: Quercetalia serrato-mongolicae Nakanishi et al. 1983 prov., Rhododendro-Quercetalia mongolicae Kim 1992 nov. ined., Quercetalia serrato-mongolicae Kim et Yim 1986, Aceri-Quercetalia mongolicae Kim 1989.

Diagnostic taxa: *Symplocos chinensis*, *Tripterygium regelii*, *Ainsliaea acerifolia*, *Magnolia sieboldii*, *Astilbe chinensis*, *Pseudostellaria palibiniana*, *Angelica gigas*, *Lespedeza maximowiczii*, *Aconitum saxatile*, *Cimicifuga heracleifolia*, *Acer pseudosieboldianum*, *Lychnis cognata*.

Holotype: Vaccinio coreani-Quercion mongolicae Song ex Takeda, Nakanishi et Choe 1994

This order involves temperate and cool-temperate mixed forests with *Q. mongolica* occurring in the Korean Peninsula, which is the source of many descriptions of *Q. mongolica* forest (Song 1988; Kim 1990, 1992; Takeda et al. 1994; Kolbek et al. 2003b).

This order includes three alliances: a Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda, Nakanishi et Choe 1994; a Lindero obtusilobae-Quercion mongolicae Kim 1990; and a Rhododendro mucronulati-Pinion densiflorae Kim et Yim 1986, by Krestov et al. (2006). In this paper, the Rhododendro mucronulati-Pinion densiflorae Kim et Yim 1986 is omitted.

(1) *Quercus mongolica* and mixed forests in the Korean Peninsula (temperate and cool-temperate)

Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda, Nakanishi et Choe 1994

Synonyms: Lindero-Quercion mongolicae Kim 1992 nomen ined.

Diagnostic taxa: same as for the order.

Holotype: Lychno cognatae-Quercetum mongolicae Kim 1990

This alliance occurs at high elevation (1000–1500 m) on Mts. Sorak, Odae, Sobaek and Jiri in South Korea and on Mt. Paektu (= Changbai-Shan) in North Korea (500–1100 m) (Kim 1990; Krestov et al. 2006). Six associations are included in this alliance: Lychno cognatae-Quercetum mongolicae Kim 1990; Veronico coreani-Quercetum mongolicae Song et al. 1995; Vaccinio coreani-Quercetum mongolicae Song et al. 1995; Parthenocisso tricuspidati-Fraxinetum rhynchophyllae Kolbek et al. 2003b; Dryopterido crassirhizomae-Quercetum mongolicae Kim ex Krestov et al. 2006; and Ainsliaeo acerifoliae-Quercetum mongolicae Song et al. 1999.

b. Dry *Quercus mongolica* forests in Korea, China and Far Eastern Russia

Lespedezo bicoloris-Quercetalia mongolicae Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada ord. nov.

Diagnostic taxa: *Lespedeza bicolor*, *Potentilla fragarioides*, *Sedum aizoon*, *Corylus heterophylla*, *Spodiopogon sibiricus*, *Vicia unijuga*, *Betula davurica*, *Sanguisorba officinalis*, *Patrinia scabiosifolia*, *Viola collina*, *Viola acuminata*, *Lysimachia davurica*.

Holotype: Corylo heterophyllae-Quercion mongolicae Krestov et al. 2006

These *Quercus mongolica* forests have been burned frequently by humans, and the forest understorey is covered by *Lespedeza bicolor*. Afterward, many grassland species invade the forest floor, such as *Spodiopogon sibiricus, Potentilla fragarioides, Sedum aizoon, Sanguisorba officinalis, Viola collina, Vicia unijuga, Rubus crataegifolius, Carex nanella, Patrinia scabiosifolia, Lysimachia davurica* and *Viola acuminata*. The characteristic woody species are *Lespedeza bicolor, Betula davurica* and *Corylus heterophylla*. The soil is compact, gravelly or stony, and most of the topsoil has been washed away. In the Liangshui area in Heilongjiang there are areas of dry soil where natural forests occur on granite sites or poor dry sites. This kind of forest occurs widely in the Korean Peninsula, China and the Russian Far East.

This order belonged to the Querco mongolicae-Betuletea davuricae Ermakov et Ptelin in Ermakov 1997. Species comparison (Table 1), though, showed many species common to Quercetalia mongolicae in this order, plus species common in grassland and scrub. The common woody species are very important for the syntaxonomical system of the forests, while the herb species show micro-habitat conditions or human disturbance. So we moved this order from Querco mongolicae-Betuletea davuricae to Quercetalia mongolicae. This order had two alliances: Corylo heterophyllae-Quercion mongolicae Krestov et al. 2004 and Dictamno dasycarpi-Quercion mongolicae Kim ex Krestov 2006 (Krestov et al. 2006). These are combined now into one alliance: Corylo heterophyllae-Quercion mongolicae Krestov et al. 2006 ex Fujiwara et A. Harada. The two old alliances were downgraded to suballiances: Quercenion dentatae-mongolicae suball. nov. and Dictamno dasycarpi-Quercenion mongolicae Krestov et al. 2006 ex Fujiwara et A. Harada. Then another new alliance was established: an Adenophoro tetraphylla-Quercion mongolicae You, Fujiwara et A. Harada all. nov.

(1) China and Sikhote-Alin (Primorye) (temperate forest)

Corylo heterophyllae-Quercion mongolicae Krestov et al. 2006

Diagnostic taxa: *Atractylodes ovata, Adenophora pereskiifolia, Hieracium umbellatum, Galium maximowiczii, Kitagawia eryngiifolia, Serratula manshurica, Vicia subrotunda, Viola orientalis, Poa ochotensis, Amphicarpaea japonica.*

Holotype: Dictamno dasycarpi-Quercion mongolicae Kim ex Krestov et al. 2006

Two originally independent alliances were integrated by diagnostic spaces, and this alliance was divided into two suballiances: Quercenion dentatae-mongolicae suball. nov. and Dictamno dasycarpi-Quercenion mongolicae Krestov et al. 2006 ex Fujiwara et A. Harada.

a. Quercenion dentatae-mongolicae suball. nov.

Diagnostic taxa: *Quercus dentata, Rubus crataegifolius, Artemisia desertorum, Clinopodium chinense, Lycopus lucidus, Veratrum maackii, Gentiana scabra, Platycodon grandiflorus, Sophora flavescens.*

Holotype: Lycopi lucidi-Quercetum mongolicae Krestov et al. 2006.

Most of these forests are short: 6–8 m to 10–15 m, in different areas. These forests occur in Chinese Manchuria (Heilongjiang, Jilin, and Liaoning provinces) and in Far Eastern Russia, mostly in areas with dry summers. Frequent fire promotes the growth of *Quercus dentata*.

b. Dictamno dasycarpi-Quercenion mongolicae Kim ex Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada suball. nov.

Diagnostic taxa: *Dictamnus dasycarpus, Vicia amurensis, Carex longerostrata, Vincetoxicum acuminatum, Veratrum ussuriense, Angelica cincta, Geranium maximowiczii, Pleurospermum uralense, Galium platygalium, Carex subbracteata, Viola brachyceras.*

Holotype: Artemisio keiskeanae-Quercetum mongolicae Kim 1990

This suballiance occurs mainly in Far Eastern Russia and along the middle Amur River basin. Most associations are substitutes for *Quercus mongolica* mixed forests. The fire and drought-tolerant, mesic and xeromesic East Asian forest species are well adapted in this suballiance (Krestov et al. 2006).

(2) Adenophoro tetraphyllae-Quercion mongolicae You, Fujiwara et A. Harada all. nov.

Diagnostic taxa: *Adenophora tetraphylla, Vicia pseudo-orobus, Melampyrum roseum, Chrysanthemum zawadskii, Artemisia japonica, Iris tenuifolia, Hieracium hololeion, Ixeris sonchifolia.*

Holotype: Festuco-Quercetum mongolicae You, Fujiwara et A. Harada ass. nov. (Table 3)

Secondary forests in Heilongjiang, Jilin and Liaoning (which constitute Chinese Manchuria)

Table 3 Festuco-Quercetum mongolicae

Relevé reference number	1	2	3	4	5	6	7	8	9	10	11
Original relevé number (in field)	CHXY-3	CHXY-2	CHXY-6	CHXJ-3	CHXJ-4	CHXJ-5	CHXY-5	CHXJ-1	CHXJ-2	CHXY-1	CHXY-4
Date of relevé (2000)	8	8	8	9	9	9	8	9	9	8	8
	30	29	30	1	1	1	30	1	1	29	30
Relevé size (m²)	600	500	150	400	200	400	600	300	120	400	300
Altitude（m）	190	260	370	420	410	400	340	369	440	250	220
Aspect	S35W	S30W	S10W	S5W	S5W	S5W	S35E	N	N40W	E20S	N15W
Slope (°)	38	30	35	23	32	46	10	3	10	23	20
Height of Tree layer 1 (T1)(m)	15	14	15	12	9	11	16	16	16	17	22
Cover of Tree layer 1 (T1)(%)	80	70	75	70	40	40	85	70	70	85	80
Height of Tree layer 2 (T2)(m)	8	7	8	-	6	7	10	6	10	10	9
Cover of Tree layer 2 (T2) (%)	15	5	5	-	40	60	15	20	20	25	30
Height of Shrub layer (S)(m)	2.5	4	2	4	1.5	2	4	2	2	3	4
Cover of Shrub layer (S)(%)	5	15	1	30	50	25	20	3	25	60	25
Height of Herb layer (H)(m)	0.6	0.7	0.8	0.6	0.6	0.6	0.7	0.9	0.9	0.5	0.5
Cover of Herb layer (H)(%)	70	65	70	45	30	25	50	65	60	35	15
Number of Species	46	43	46	30	28	37	74	53	47	55	53
Diagnostic species of Festuco-Quercetum mongolicae You, Fujiwara et A. Harada ass. nov.											
Atractylodes chinensis	+	2·2	+	2·2	+	+·2	+	+	+	+	+
Bupleurum chinensis	1·1	1·1	+	·	·	·	1·1	·	+	·	·
Veronica sibirica	·	+	·	·	·	+	+·2	+·2	+	·	·
Aconitum volubile	·	+	·	·	·	·	+	+·2	+	·	1·1
Festuca mongolica	·	+	+	+	+	·	·	·	+	·	·
Festuco-Quercetum mongolicae, artemisietosum annuae You, Fujiwara et A. Harada subass. nov.											
Artemisia annua	2·2	2·2	1·1	2·2	+·2	+	·	·	·	·	·
Picea koraiensis	·	+	+	·	·	+	·	·	·	·	·
Rubia chinensis	+	·	+	·	·	+	·	·	·	·	·
Carex nanella	+·2	3·3	1·2	·	1·2	·	·	·	·	·	·
Saussurea sinuata	2·2	1·2	1·2	·	·	·	·	·	·	·	·
Allium senescens	·	1·1	·	+	+	·	·	·	·	·	·
Festuco-Quercetum mongolicae, anemonetosum sylvestris You, Fujiwara et A. Harada subass. nov.											
Anemone sylvestris	·	·	·	·	·	·	1·1	·	·	1·1	2·2
Polemonium liniflorum	·	+	·	·	·	·	+	+	+	·	·
Paris verticillata	·	·	·	·	·	·	+	+	·	1·1	+
Angelica anomala	·	·	·	·	·	·	2·1	+·2	+	·	+·2
Cimicifuga simplex	·	·	·	·	·	·	+	·	·	1·1	+
Aruncus dioicus var. *asiatica*	·	·	·	·	·	·	+·3	3·3	·	+	·
Cypripedium guttatum	·	·	·	·	·	·	+·2	+	·	+	·
Ligularia fischeri	·	·	·	·	·	·	+	+	+	·	·
Lysimachia davurica	·	·	·	·	·	·	+	+	+	·	+
Veratrum maackii	·	·	·	·	·	·	·	+	+	·	+
Hemerocallis minor	·	·	·	·	·	·	·	2·2	1·2	+	+
Athyrium acrostichoides	·	·	·	·	·	·	+·2	+	·	1·1	·
Saussurea serrata	·	·	·	·	·	·	1·1	·	+	·	+
Galium boreale	·	·	·	·	·	·	1·2	1·2	1·2	·	·
Rubus crataegifolius	·	·	·	·	·	·	+·2	+·2	+	·	·
Paeonia lactiflora	·	·	·	·	·	·	1·1	·	·	+·2	+
Viburnum sargenti	·	·	·	·	·	·	+	·	·	+	+
Aster scaber	·	·	·	·	·	·	+·2	·	+	+	·

Table 3 (continued)

Vitis amurensis	•	•	•	•	•	•	+•2	•	•	+	+•2
Adenophoro tetraphyllae-Quercion mongolicae You, Fujiwara et A. Harada all. nov.											
Artemisia japonica	1•1	2•2	1•2	1•2	1•2	+	1•1	+	+	+	+
Adenophora tetraphylla	1•1	1•1	1•1	•	+	1•2	1•1	1•1	1•1	+	+
Vicia pseudo-orobus	2•2	2•2	1•1	+	•	+	1•1	1•1	+	1•1	+
Melampyrum roseum	2•2	2•2	+	+•2	1•2	+•2	+	•	•	•	•
Chrysanthemum zawadzkii	•	1•1	+•2	•	•	•	•	•	•	•	•
Lespedezo bicoloris-Quercetalia mongolicae Krestov et al. 2006											
Lespedeza bicolor	3•3	2•2	+•2	1•2	2•2	1•2	+	1•2	+	+•2	+
Betula davurica	+	+	•	+	+	+	2•2	+	2•3	•	1•1
Spodiopogon sibiricus	1•2	1•2	1•2	1•2	+	+	•	•	+	•	•
Potentilla fragarioides	1•1	1•2	1•1	2•2	1•2	+•2	1•1	•	•	•	•
Sanguisorba officinalis	+	•	•	•	•	+	•	+•2	+	•	+
Vicia unijuga	•	•	+	•	•	•	+	1•1	•	•	+
Patrinia scabiosaefolia	1•1	1•2	1•2	•	•	•	•	•	•	•	+
Viola collina	+	•	+	•	•	•	•	•	•	•	•
Viola acuminata	•	•	•	•	•	•	1•1	•	•	•	+
Lysimachia barystachys	•	•	1•1	•	•	•	+•2	•	•	•	•
Quercetea mongolicae Song ex Krestov et al. 2006											
Quercus mongolica	5•4	4•4	4•4	4•4	4•3	4•4	5•4	3•4	4•3	5•4	5•4
Sedum aizoon	1•1	1•1	1•1	1•1	1•1	+	1•1	+	+	+	+
Corylus heterophylla	+	•	+	•	•	•	+•2	•	2•3	2•2	+
Polygonatum involucratum	1•2	1•3	•	+	•	+	+	+	•	•	•
Polygonatum humile	•	•	•	+	+	•	+	+	+•2	•	1•1
Tilia amurensis	•	•	+	•	•	•	+	•	+	+	+
Acer mono	•	+	+	•	•	•	2•2	•	•	2•2	3•3
Tilia mandshurica	•	•	+•2	•	•	•	+•2	+	2•2	+	•
Cacalia hastata	•	•	+	•	•	•	+•2	•	•	+	+
Rhamnus davurica	+	•	•	•	•	•	+	•	•	•	+
Pinus koraiensis	•	1•1	•	•	•	•	•	•	•	+	•
Euonymus pauciflorus	•	•	•	•	•	+	•	•	•	2•2	•
Rhamnus ussuriensis	•	•	+	•	•	•	•	•	•	•	+
Companion species											
Carex lanceolata	3•2	•	2•2	3•3	3•2	2•3	3•2	•	3•2	2•2	2•2
Convallaria keiskei	+	+	•	+	•	+	+	1•1	+•2	+•2	+
Polygonatum odoratum	1•1	1•1	+•2	+•2	•	•	+	+	+	•	+
Iris uniflora	1•1	1•1	1•1	•	•	•	1•1	+	•	+•2	1•2
Ixeris sonchifolia	+	+	•	1•1	+	+	•	•	+	•	•
Pteridium aquilinum	+	•	•	•	•	•	2•2	1•2	+•2	+	+
Lilium tenuifolia	+	+•2	•	+•2	+	+•2	•	•	•	1•2	•
Dioscorea nipponica	•	+	•	•	•	+	+•2	•	+	1•1	+
Clematis mandshurica	+	+	1•2	+	•	+	•	+	+	•	+
Dictamnus dasycarpus	•	•	+	•	•	•	+	•	+	+•2	+
Aegopodium alpestre	+	•	1•2	+	•	+	•	•	•	1•1	•
Plectranthus excisus	+	•	+	•	•	+	+	•	•	•	•
Deyeuxia angustifolia	2•2	•	2•2	•	•	+	•	•	+•2	•	•
Euphorbia esula	•	+	•	+•2	•	+	+	•	•	•	•
Synurus deltoides	•	•	•	•	+	•	+•2	+	•	+	•
Cyperus sp.	•	•	•	•	•	•	+	+•2	•	1•1	•
Silene jenisseensis	+	•	•	•	+	+	•	•	•	•	•
Thalictrum foetidum	•	+	•	•	•	•	•	+	•	•	+

Table 3 (continued)

Aconitum alboviolaceum	+	·	+	·	·	·	·	·	·	·	+
Geranium eriostemon	·	+	·	·	·	·	·	+	+	·	·
Desmodium oldhami	·	·	+	·	·	·	1·2	·	+	·	·
Carex duriuscula	·	+·2	·	·	·	·	·	+	1·2	·	·
Thalictrum contortum	·	·	+	·	·	·	+·2	·	·	·	+
Trifolium lupinaster	·	+·2	·	+	·	·	·	+	·	·	·
Silene repens var. *anguistifolia*	+	1·1	·	·	·	·	·	·	·	1·2	·
Artemisia mongolica	1·2	·	·	·	·	·	+	·	·	·	·
Allium macrostemon	·	·	1·1	+·2	·	·	·	·	·	·	·
Betula platyphylla	·	·	·	·	·	+·2	·	2·2	·	·	·
Polygonum perfoliatum	·	·	·	+	+	·	·	·	·	·	·
Veratrum nigrum	·	·	·	·	·	+	+	·	·	·	·
Viola diamantiaca	·	·	·	·	·	·	+	·	·	·	+
Bupleurum scorzoneraefolium	·	1·1	+	·	·	·	·	·	·	·	·
Athyrium spinulosum	·	·	·	·	·	·	·	+·3	·	+	·
Erodium stephanianum	+	·	·	·	·	·	+	·	·	·	·
Iris monoflora	·	·	·	+	·	·	·	·	+·2	·	·
Pseudostellaria heterophylla	·	·	·	·	·	·	·	·	+	·	+
Solidago virga-aurea	·	·	·	·	·	·	·	+	+	·	·
Euphorbia fisheriana	+	·	·	·	·	·	·	·	·	+	·
Asparagus gilbus	+	·	·	·	·	·	+	·	·	·	·
Plectranthus glaucocalyx	·	·	·	·	·	·	+	·	·	·	+
Rosa davurica	·	·	·	·	·	·	·	+·2	·	+	·
Adenophora stenophylla	·	·	·	·	·	·	1·1	+	·	·	·
Carex siderosticta	·	·	·	·	·	·	+·2	·	·	+·2	·
Galium spurium	·	·	·	·	+	·	·	·	+	·	·
Glycina soja	·	·	·	·	·	·	+	·	·	·	+
Phryma leptostachya var.*asiatica*	·	·	+	·	·	+	·	·	·	·	·
Fraxinus mandshurica	·	·	·	·	·	·	·	·	·	+	+
Lonicera chrysantha	·	·	·	·	·	·	·	·	·	2·3	+
Adiantum pedatum	·	·	·	·	·	·	·	·	·	+	+
Athyrium multidentatum	·	·	·	·	·	·	·	·	·	2·2	+

Additional species occurring once in relevé reference no. 1: *Sedum telephium* +, *Celastrus orbiculatus* +, *Leibnitzia anandria* +, *Ixeris denticulata* 1·2, *Allium tenuissimum* +·2, *Melica nutans* +; no. 2: *Rhododendron amurensis* 1·2, *Artemisia integrifolia* 1·2; no. 3: *Chenopodium album* +, *Artemisia stolonifera* 2·3, *Aster tataricus* 1·2, *Ulmus japonica* f. *saberosa* +; no.4 : *Lactuca indica* +, *Potentilla freyniana* +·2, *Scutellaria indica* +; no. 5: *Lactuca raddeana* +, *Dianthus cinensis* +, *Bupleurum longiradiatum* +, *Peucedanum senticosus* +; no. 6: *Epilobium* sp. +, *Dimnotamnus* sp. +, *Galium verum* +, *Spiraea pubesceus* 1·1, *Calamagrostis arundinacea* +, *Ulmus macrocarpa* +, *Brachypodium sylvaticum* +, *Rhamnus diamantiaca* +, *Clintonia udensis* +, *Lychnis coznata* +, *Thelypteris* sp. +; no. 7: *Impatiens nolitangere* +, *Cirsium segetium* +, *Euphorbia lunulasta* +, *Thalictrum baicalensis* +, *Rhododendron dahuricum* 2·3; no. 8: *Salix flavida* var. *metaformosa* +, *Orthilia secunda* +·2, *Trientalis europaea* +, *Pyrola dahurica* +, *Carex ussuriensis* 3·3, *Maackia amurensis* 2·2, *Carex quadriflora* 2·2, *Maianthemum bifolium* +, *Valeriana amurensis* +, *Stellaria jaluana* +, *Deyeuxia sylvatica* +; no. 9: *Vicia amoena* +, *Angelica davurica* +, *Calamagrostis epigeios* +, *Smilacina davurica* +; no. 10: *Acer tegmentosum* +, *Acanthopanax senticosus* +, *Schisandra chinensis* +·2, *Chloranthus japonicus* +, *Philadelphus schrenkii* +, *Angelica gigas* +, *Thalictrum tuberiferum* +, *Larix gmelinii* +·2, *Rubus arcticus* +·2, *Saussurea amurensis* +; no. 11: *Euonymus alatus* +·2, *Malus baccata* +.

Location in relevé reference no. 1- 3, 7- 9: Liangshui Nature Reserve in Yichun City, no.4- 6, 10- 11: Jiayin County (Heilongjiang Province, China) were summarized in this alliance. The southern part of Chinese Manchuria is warmer and drier than Heilongjiang, and the secondary forests are influenced by cutting, fire and acorn collecting. The soil has become hard and drier after human impact. *Melampyrum roseum* is a good indicator for compact, hard soil. These forests are shorter, at 6–15 m. This alliance also includes natural forests. Natural forests in the Liangshui Nature Reserve in Heilongjiang occur as patches in plantations of *Larix gmelinii* and *Pinus koraiensis*. The height of these forests is 17–22 m, and the canopy cover is 80–85% (You 2001).

(2)1 Festuco-Quercetum mongolicae You, Fujiwara et A. Harada ass. nov. (Table 3)

Diagnostic taxa: *Atractylodes chinensis*, *Artemisia annua*, *Bupleurum chinensis*, *Veronica sibirica*, *Aconitum volubile*, *Festuca mongolica*.

Holotype: Table 3, relevé reference no. 11 (original relevé CHXY-4), Forestry office of Jia Yin Xian in Heilongjiang.

This association occurs in Liangshui and Jia Yin Xian in Heilongjiang province. Mixed forests are common in Liangshui and Jia Yin Xian, but *Quercus mongolica*-dominated forests occur on concave areas and following human disturbance, such as by burning, cutting or planting other species. *Quercus*-dominated forests occur mainly on the lower hills (190–440 m). This association is divided into two subassociations.

(2)1-i. Artemisietosum annuae You, Fujiwara et A. Harada subass. nov.

Diagnostic taxa: *Picea koraiensis*, *Rubia chinensis*, *Artemisia annua*, *Carex nanella*, *Saussurea sinuata*, *Allium senescens*.

Holotype: Table 3, relevé ref. no. 2 (original relevé CHXY-2), Liangshui Nature Reserve, Heilongjiang

Ths subassociation was defined as forests on steep south-facing slopes and where rocks and stones are exposed by rain-induced erosion. Forest height is 9–15 m, and canopy cover is 70–80%, but some forests have only 40% canopy coverage. The forest floor is dry and covered by herbs, Gramineae and sedges, with 25–70% cover. The forest floor especially has indicators of dry sites with shallow soil, such as *Spodiopogon sibiricus*, *Lespedeza bicolor*, *Melampyrum roseum* and *Carex nanella*.

(2)1-ii. Anemonetosum sylvestris You, Fujiwara et A. Harada subass. nov.

Diagnostic taxa: *Anemone sylvestris*, *Polemonium linifolius*, *Paris verticillata*, *Angelica anomala*, *Cimicifuga simplex*, *Aruncus dioicus* var. *asiatica*, *Cypredium guttatum*, *Ligularia fischeri*, *Lysimachia davurica*, *Veratrum maackii*, *Hemerocallis minor*, *Athyrium acrostichoides*, *Saussurea serrata*, *Galium boreale*, *Adenophylla stenophylla*, etc.

Holotype: Festuco-Quercetum mongolicae You, Fujiwara et A. Harada ass. nov.

Thus subassociation occurs on deep soil and gentle slopes of 3–23°. The forests are relatively tall at 16–22 m. Canopy cover is also good at 70–85%, with *Q. mongolica* (dominant), *Betula davurica*, *Acer mono*, and *Tilia mandshurica*. Forest-floor cover varies widely at 15–65%, but most diagnostic species indicate good soil and a mesic to rather moist environment. The number of species is high, with 47–74 species in plots of 220–440 m^2.

c. Mixed forests in China and Far Eastern Russia (temperate and cool-temperate)

Tilio amurensis-Pinetalia koraiensis Kim ex Krestov Song, Nakamura et Verkholat 2006

Diagnostic taxa: *Schisandra chinensis*, *Acer tegmentosum*, *Maianthemum bifolium*, *Oxalis acetosella*, *Berberis amurensis*, *Acer ukurunduense*, *Viola selkirkii*, *Carex ussuriensis*, *Fraxinus mandshurica*, *Betula costata*, *Ribes manshuricum*, *Lonicera chrysantha*, *Ulmus laciniata*, *Philadelphus tenuifolius*, *Eleutherococcus senticocus*, *Neomolinia mandshurica*, *Diplazium sibiricum*, *Mitella nuda*, *Sorbus amurensis*, *Circaea alpina*, *Ligustrina amurensis*, *Waldsteinia ternata*.

Holotype: Tilio amurense-Pinion koraiensis Kim ex Krestov et al. 2006

This order represents cool-temperate mixed forests with *Quercus mongolica, Pinus koraiensis, Abies homolepis* and *A. nephrolepis*, as occur in northern China, the Russian Far East and higher elevations of North Korea. These mixed forests develop under humid conditions and no moisture deficit or drought (Krestov et al. 2006). This order includes both natural and disturbed forests.

Table 4 Lonicero ruprechtianae-Quercetum mongolicae

Running number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Original relevé number (in field)	BXc7	BXc8	BXc9	BXc10	BXc11	BXc12	BXc13	BXc14	BXc15	BXc16	BXc17	BXc18	BXc19	BXc20	BXc21	BXc26
Date of relevé (2002)	8	8	8	9	9	9	9	9	9	9	9	9	9	9	9	9
	29	29	29	1	1	2	2	4	4	4	6	7	7	8	8	13
Relevé size (m²)	300	375	300	375	240	375	400	300	600	450	400	450	375	750	375	300
Altitude (m)	279	369	306	419	327	435	330	310	320	350	433	323	311	338	346	340
Aspect	S23W	S4E	N64W	S55W	N32W	S30W	S10W	S32E	N65W	S60W	S78W	N75W	N58W	N60W	N80W	S65E
Slope (º)	7	23	23	23	18	7	15	16	22	18	23	24	18	24	24	13
Height of Tree layer 1 (T1)(m)	15	16	17	18	17	18	22	16	18	20	15	20	22	20	22	20
Cover of Tree layer 1 (T1)(%)	75	75	75	75	75	80	80	75	80	80	75	75	75	75	75	75
Height of Tree layer 2 (T2)(m)	4	9	12	12	16	10	12	10	12	14	9	13	12	13	15	13
Cover of Tree layer 2 (T2)(%)	20	20	30	30	20	35	20	35	35	30	30	40	20	30	20	25
Height of Shrub layer (S)(m)	2	2.5	2.5	6	3	3	4	4	4	6	4	3	6	4	4	4
Cover of Shrub layer (S)(%)	45	10	60	45	60	50	50	40	40	40	40	20	70	35	25	60
Height of Herb (H)(m)	0.5	0.8	0.6	0.9	0.5	0.5	0.5	0.8	0.9	1	0.5	0.5	0.5	0.9	0.5	0.9
Cover of Herb (H)(%)	20	20	25	50	15	40	50	40	20	50	20	50	15	60	60	50
Number of Species	56	34	52	55	50	40	60	52	54	53	37	49	52	70	49	53
Diagnostic species of Lonicero ruprechtianae-Quercetum mongolicae																
Crataegus pinnatifida	+	+·2	+·2	+·2	+·2	·	+·2	2·2	+	+·2	·	+	+	·	+	+
Glechoma hederacea var. *longituba*	·	+	+	+	·	·	+	+	+	+	+	+	+	+	·	+
Dendranthema chanetii	+	+	+	·	+	+	+·2	+·2	·	+	+·2	·	·	·	+·2	·
Lonicera ruprechtiana	·	·	·	·	+	+·2	+·2	+	·	+	·	+	+·2	+·2	+·2	+·2
Elsholtzia ciliata	·	+	+	·	·	·	·	+	+	·	+	+	+	+	+·2	·
Veratrum nigrum	+	·	+	+	·	·	·	·	+	+	+	+	·	·	·	·
Diagnostic species of higher units																
Quercus mongolica	5·4	4·4	4·3	3·3	5·4	4·4	4·4	4·4	5·4	5·4	5·4	4·3	3·3	4·3	3·3	4·4
Acer mono	+	+·2	+	1·2	2·2	1·1	+	+	+·2	1·1	+	2·2	2·2	2·2	2·2	3·3
Carex lanceolata	2·2	1·2	3·3	3·4	3·3	3·2	2·2	3·3	3·3	2·2	2·2	3·2	3·2	2·2	2·2	3·2
Tilia amurensis	+	2·2	1·2	2·2	+·2	+·2	+	+·2	1·1	1·1	3·3	1·1	3·3	1·1	+·2	·
Tilia mandshurica	+	+	3·3	1·2	2·2	1·1	+·2	+·2	2·2	2·2	+	3·2	1·1	+·2	+	·
Polygonatum involucratum	+	+	·	+·2	+	+	+	+	+·2	+	+	+	+·2	+	+	+
Convallaria keiskei	+	·	1·2	+·2	+·2	+·2	+·2	+	+·2	+·2	+	+·2	+	+	+	+·2
Dioscorea nipponica	+·2	1·2	+·2	1·1	+·2	+·2	+·2	+	+·2	+·2	1·1	1·1	·	·	+·2	+
Ulmus macrocarpa	+	+	·	+·2	+	·	+·2	1·1	+·2	+	+	1·1	+	+	+·2	+
Lonicera chrysantha	1·2	+·2	+	+	+·2	+·2	+·2	·	2·2	1·1	·	·	1·1	1·1	+	+·2
Adenocaulon himalaicum	+	+	+	+	+	·	+	+·2	+	+	·	+	+	+	·	+
Asparagus dauricus	+	+	+	+	·	·	+	+	+	+	+	+	+	+	+	·
Acanthopanax senticosus	+	·	+·2	+·2	+·2	+·2	+·2	+	·	+	·	+·2	+·2	+·2	+	1·1
Aster scaber	+	+	+	+	+	+	+	+	·	·	·	+	+	+	+	·
Aegopoduim alpestre	+·2	·	·	+	+	·	+	+	+	+·2	·	+	+	+	+	+
Polygonatum himalaicum	·	+	+	+	+	·	+	+·2	+	+	+	+	·	+	·	+
Corylus mandshurica	1·2	+	·	1·2	1·1	+·2	·	·	+·2	1·1	·	·	1·1	1·2	+·2	+·2
Ulmus japonica	+	·	+	+	+	+	+	+	+	+·2	·	·	·	+	·	+
Juglans mandshurica	+	·	+	+	+	·	+·2	+	·	+	·	+	·	3·3	+	+
Euonymus pauciflorus	·	·	+	·	+	1·1	2·3	+	+·2	+·2	+·2	·	1·1	+·2	·	+
Euonymus alatus	1·2	+	+·2	·	+	·	3·3	+·2	·	+	·	+	+	·	+	·
Philadelphus schrenkii	·	·	+	+·2	+	+	·	·	+·2	·	+	·	+·2	+·2	+·2	+
Adenophora tetraphylla	·	·	·	·	+	·	+	·	+·2	+	+	+	+	+	+	·
Aconitum raddeanum	+	·	+·2	1·2	·	·	·	+·2	+	1·1	+	+	·	·	·	·
Acer ginnala	+·2	·	+	·	·	·	+	2·2	+	+	+	·	·	+	·	·
Cacalia hastata	·	·	+	+	+	1·1	+	·	·	·	·	+	·	+	·	+
Carex pilosa	·	·	1·2	2·2	2·2	·	3·3	·	·	1·1	·	1·1	1·1	·	·	3·3
Viburnum burejaeticum	+	·	+	·	+	·	+	·	+	+	·	·	·	+	·	·
Ribes mandshuricum	+	·	·	+	·	·	+	·	+	·	·	·	·	+·2	+	+·2
Spiraea pubescens	·	·	4·3	·	4·3	4·3	·	·	·	·	3·3	·	+	+·2	3·3	·
Viburnum sargenti	·	·	+	·	·	·	+	·	+	+	·	·	+	+	·	+
Carex siderosticta	·	·	1·2	·	·	·	·	·	1·1	+	+·2	·	+·2	+·2	1·1	·
Brachybotrys paridiformis	·	·	·	·	+·2	+	+·2	·	·	·	·	+	+·2	1·1	·	+·2
Cardamine leucantha	·	·	·	+	·	+	+	·	·	+	·	·	+	+	·	·
Prunus padus	+	+·2	·	+	·	·	+	·	·	·	·	·	·	·	+	·
Corylus heterophylla	2·2	·	·	3·3	1·1	·	1·1	·	·	·	·	·	·	+·2	·	·
Urtica angustifolia	+	·	·	+	+	·	·	·	·	·	·	·	+	·	+	·
Rubia sylvatica	+	·	·	·	·	+	·	+	·	·	·	·	·	+	·	+
Maackia amurensis	·	·	·	+	·	+	+	+	·	·	·	·	·	·	·	·
Fraxinus mandshurica	·	·	·	+·2	·	·	·	·	·	+	·	·	·	·	+	+·2
Artemisia stolonifera	·	·	·	·	+	+	+	·	·	+	·	·	·	·	·	·
Schizandra chinensis	·	·	·	·	·	·	+·2	·	·	·	·	·	+·2	1·1	·	+·2
Sorbaria sorbifolia	·	·	·	·	·	·	·	·	·	+	·	·	·	+	+	+

Table 4 (continued)

Carex quadriflora	·	+·2	·	·	·	·	·	·	·	·	·	2·2	·	+	·	·
Maianthemum bifolium	+·2	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·
Chelidonium majus	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+
Athyrium multidentatum	·	·	·	+·2	·	·	·	·	·	·	·	·	+	·	·	·
Vitis amurensis	·	·	·	·	+	+·2	·	·	·	·	·	·	·	·	·	·
Bupleurum longiradiatum	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·
Urtica laetevirens	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·
Viola selkirkii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+
Companion species																
Diarrhena mandshurica	+	·	+	+	+	+·2	+	+	+	+	·	1·1	+	+·2	·	1·1
Woodsia ilvensis	·	·	+	+	+	+·2	+	+	+·2	+	+	+	+	+·2	·	+·2
Potentilla fragarioides	+·2	+	+	+	·	+	+	+·2	+	·	+	+	+	·	·	+
Malus baccata	+·2	+	+	·	·	+·2	+	+·2	·	+·2	+	+	+	+	·	+
Viola dactyloides	+	+	+·2	·	·	·	+	+	+·2	+·2	+	+·2	·	+	+·2	+
Rhamnus diamantiaca	+·2	+	+·2	+·2	·	·	+·2	+·2	·	+·2	+	1·1	1·2	+·2	·	·
Syringa amurensis	1·1	·	·	+·2	+	·	1·1	1·1	2·2	1·1	·	+·2	2·2	1·1	+·2	·
Schizopepon bryoniaefolius	+	·	+	·	+·2	·	·	+	+	·	+	·	+·2	1·1	+	+·2
Plectranthus japonicus	+	·	+	·	·	+	·	+	·	+	·	+	+	+	+·2	+
Lespedeza bicolor	2·2	+·2	1·2	·	·	·	·	+·2	+	1·2	+	·	·	+	1·1	·
Viola variegata	+	·	+	·	·	·	+	+	·	·	+	·	+	+	+	+
Amphicarpaea trisperma	+	·	·	+·2	+·2	+	+	·	·	+	+	+·2	·	+	·	·
Deutzia amurensis	+	·	·	1·1	+	+	·	·	+·2	+	·	·	·	+	+	·
Pteridium aquilinum	+	·	·	+	·	+	·	·	+	·	+	·	+	+	·	+
Ulmus laciniata	·	1·2	+	·	·	+	·	·	+	+	·	+·2	·	+	·	+
Selaginella tamariscina	·	+·2	+	·	·	·	+	·	·	+	·	+	1·1	+	+	·
Actaea leptostachya var. *asiatica*	·	·	·	+	+	+	·	·	+	+	·	·	+	+	·	+
Ostericum maximowiczii	+	·	+	+	+	·	+	·	+	·	·	·	+	·	·	·
Betula platyphylla	+	·	·	·	+	·	1·1	+	·	+	·	·	·	+·2	3·3	·
Trientalis europaea	·	+	·	+	·	·	+	+	+	·	·	·	+	·	·	+·2
Artemisia mongolica	·	+	·	·	·	·	+	·	·	·	+	·	+	+	+·2	+
Euonymus macropterus	·	·	+·2	·	+	·	3·3	+·2	+	·	+	·	·	+	·	·
Synurus deltoides	·	·	·	·	·	+	+	·	+	·	·	·	+	+	+·2	+·2
Viola collina	+	·	+	·	·	·	·	+	+	+	·	·	·	·	·	+
Vicia ramuliflora	·	·	·	+	+	+	·	·	+	·	·	·	·	·	+	+
Carex callitrichos	3·3	3·3	·	·	·	2·2	·	·	·	3·2	+·2	·	·	·	·	·
Vicia amurensis	+	·	·	·	+	·	·	+	+·2	·	+	·	·	·	·	·
Artemisia latifolia	·	·	+·2	+	+	·	·	·	·	·	+	·	+	·	·	·
Sorbus alnifolia	·	·	·	·	·	·	+	·	·	+	·	+	·	+	·	+
Phellodendron amurensis	+	·	·	·	+·2	·	·	·	·	·	·	·	+	+	·	·
Populus davidiana	2·2	·	·	·	·	·	+	3·3	·	·	·	·	2·1	·	·	·
Aster ageratoides	+	·	·	·	·	·	·	·	+	·	·	·	·	+·2	+·2	·
Rubus kanayamensis	+	·	·	·	·	·	·	+	·	·	·	·	·	+	·	·
Filipendula palmata var. *amurensis*	·	·	·	+	·	·	+	·	·	+	·	·	·	·	·	·
Thalictrum filamentosum	·	·	·	+	·	·	·	+	·	+	·	·	·	·	·	·
Saussurea umbrosa	·	·	·	·	+·2	·	·	·	+	·	·	·	·	·	·	+
Polygonatum odoratum	+	·	·	·	·	·	·	·	·	·	·	1·1	·	·	·	·
Plectranthus excisa	+	·	·	·	·	·	·	·	·	·	·	·	·	+·2	·	·
Moehringia lateriflora	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·
Aconitum albo-violaceum	·	·	·	+	·	·	·	·	·	·	·	+·2	·	·	·	·
Rubia cordifolia	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·
Vaccinium uliginosum	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	+
Thalictrum simplex	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·
Angelica anomala	·	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·
Circaea quadrisulcata	·	·	·	·	·	·	·	·	+	·	·	·	·	+	·	·
Saussurea mandshurica	·	·	·	·	·	·	·	·	·	+	·	+·2	·	·	·	·
Adenophora divaricata	·	·	·	·	·	·	·	·	·	+	·	·	·	+	·	·
Smilacina japonica	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·
Carex ussuriensis	·	·	·	·	·	·	·	·	·	·	·	·	·	3·3	3·3	·

Additional species occurring once in Running no. 1: *Erigeron annuus* +, *Sambucus mandshurica* +; no. 2: *Axyris hybrida* +, *Lathyrus palustris* +; no. 3: *Dryopteris geringiana* 1·2, *Metaplexis japonica* +; no. 4: *Aconitum fischeri* +, *Rhamnus davurica* +·2, *Fragaria orientalis* +; no. 5: *Artemisia sylvatica* +, *Galeopsis bifida* +, *Lonicera edulis* +; no. 6: *Aconitum koreanum* +, *Lamium album* +, *Lilium distichum* +; no. 7: *Salix rosmarinifolia* +, *Syneilesis aconitifolia* +; no. 8: *Artemisia argyi* +, *Hypericum attenuatum* +, *Prinsepia sinensis* +; no. 9: *Artemisia keiskeana* +, *Galium mandshuricum* +, *Liparis japonica* +; no. 11: *Solidago virgaurea* +; no. 12: *Arabis pendula* +, *Caltha palustris* +, *Elsholtzia pseudo-cristata* +, *Paris verticillata* +; no. 13: *Caulophyllum robustum* +, *Heracleum moellendorffii* +; no. 14: *Clematis macropetala* +, *Deyeuxia langsdorffii* +·2, *Heracleum barbatum* +, *Aruncus sylvester* +, *Acer mandshuricum* +; no. 15: *Osmanda cinnamomea* +, *Peucedanum elegans* +, *Peucedanum terebinthaceum* +, *Smilacina davurica* +; no. 16: *Aralia elata* +·2, *Artemisia selengensis* +, *Saussurea odontolepis* +.

Location: Eastern mountains in Binxian, Harbin City (Heilongjiang Province, China).

Five alliances were described by Krestov et al. (2006): Tilio amurense-Pinion koraiensis Kim ex Krestov et al. 2006; Rhododendron dauricii-Pinion koraiensis Krestov et al. 2006; Abieti nephrolepidis-Pinion koraiensis Gumarova ex Krestov 2006; Phrymo asiaticae-Pinion koraiensis Krestov et al. 2006; and Jeffersonio-Quercion mongolicae Kim ex Krestov et al. 2006. This paper retains four of these alliances, but the Phrymo asiaticae-Pinion koraiensis was downgraded to a suballiance of the Abieti nephrolepidis-Pinion koraiensis: Phrymo asiaticae-Pineion koraiensis Krestov et al. ex Fujiwara et A. Harada.

1. Tilio amurensis-Pinion koraiensis Kim ex Krestov et al. 2006

   Diagnostic taxa: *Deutzia glabrata, Aegopodium alpestre, Ulmus macrocarpa, Rhamnus davurica, Brachybotrys paridiformis.*

   Holotype: Athyrio-Pinetum koraiensis Kim ex Krestov et al. 2006

   This alliance occurs in Heilongjiang and the Russian Far East, especially the southern part. It is mostly mixed forests with *Q. mongolica*, *Pinus koraiensis, Abies holophylla, A. nephrolepis* and *Picea jezoensis* (*P. ajanensis*).

   Acording to Krestov et al. (2006), diagnostic taxa of the Tilio amurense-Pinion koraiensis Kim ex Krestov et al. 2006 are *Deutzia glabrata, Aegopodium alpestre, Carex ussuriensis, Fraxinus mandshurica, Sorbus amurensis* and *Ulmus macrocarpa*. Three of these species, *Deutzia glabrata, Aegopodium alpestre* and *Ulmus macrocarpa,* were grouped with *Rhamnus davurica* and *Brachybotrys paridiformis* as the Tilio amurense-Pinion koraiensis. Then a Syringo amurense-Pineion koraiensis suball. nov. and a Lonicero praeflorenti-Pineion koraiensis suball. nov. were recognized here (Table 1). Krestov described the associations from the Tilio amurense-Pinion koraiensis Kim ex Krestov et al. 2006 as mostly secondary forests. Of the two suballiances, the Syringo amurense-Pineion koraiensis involves mostly natural *Q. mongolica* forests. The Lonicero praeflorenti-Pineion koraiensis, is for secondary forests.

   a. Syringo amurensis-Pinenion koraiensis suball. nov.

      Diagnostic taxa: *Syringa amurensis, Acanthopanax senticosus, Philadelphus schrenkii, Carex pilosa, Athyrium multidentatum, Aconitum raddeanum, Adenocaulon himalaicum, Diarrhena mandshurica*, *Allium ramosum*, *Viburnum burejaeticum*, *Urtica laetevirens*, *Prunus padus.*

      Holotype: Lonicero ruprechtianae-Quercetum mongolicae L. Wang, Fujiwara et A. Harada ass. nov.

      This suballiance involves mostly natural forests in Heilongjiang, mainly some small patches in the Zhǎngshòu Nature Reserve in Bīn Xiàn. Even so, the forest height is 20 m and the DBH of *Q. mongolica* reaches 32 cm. This suballiance also occurs in the Maoer-Shan mountains at Shangzhi near Harbin, the Fuyuan Xian Da Liangzi He Nature Reserve in the Xiao Hìnggan range, and the Xiao Beihu Nature Reserve in the Laoye Mts. The old secondary *Populus* forest (37 years old), with a height of 20 m and DBH to 20 m, is also included in this suballiance. *Acer mandshuricum-Acer mono* forest is a very rare remnant forest type on alluvial areas in China. It is also included in this suballiance and occurs at the Forestry station of the Zhangguangcai-Ling and Wanda-Shan mountains.

      (a1) Lonicero ruprechtianae-Quercetum mongolicae L. Wang, Fujiwara et A. Harada ass. nov.

      Diagnostic taxa: *Lonicera ruprechtiana, Crataegus pinnatifida, Dendranthema chanetii, Glechoma longituba, Elsholtzia ciliata, Veratrum nigrum.*

      Holotype: Table 5, relevé 10, Zhangshou Forest Park in Bin Xian, Heilongjiang.

      This association occurs in the Zhangshou Nature Reserve in the eastern mountains of Heilongjiang. Forest height is 15–22 m, with a mean height of 19 m. It is composed of four strata, with canopy layer of 80%. The herb layer also has a relatively high cover (mean 37%). The soil is deep, with an A layer of about 30–50 cm, and the soil moisture was 41.6% (Wang L. 2007; Wang L., Fujiwara and You 2006).

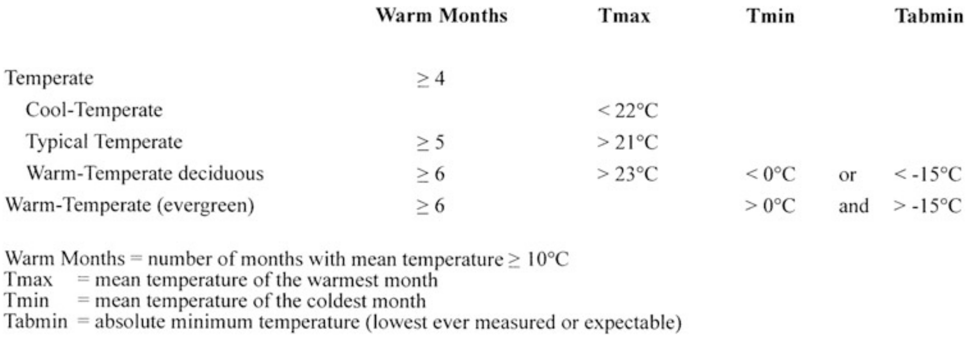
   b. Lonicero praeflorenti-Pinenion koraiensis sub all. nov.

      Diagnostic taxa: *Lonicera praeflorens*, *Galium mandshuricum*, *Pyrus ussuriensis*, *Larix olgensis*, *Patrinia intermedia.*

      Holotype: Athyrio crenati-Pinetum koraiensis Kim ex Krestov et al. 2006

      Associations from this suballiance are mostly secondary forests and were reported from the Maoer-Shan at Shangzhi (Heilongjiang) and the Changbai-Shan by Kim (1992) and from the Russian Far East by Krestov et al. (2006). Two associations are involved: Athyrio crenati-Pinetum koraiensis Kim ex Krestov et al. 2006

Table 5 Quantitative delimitation of temperate and adjacent climates in East Asia (after Box 2013, edited)



	Warm Months	Tmax	Tmin		Tabmin
Temperate	≥ 4				
Cool-Temperate		< 22°C			
Typical Temperate	≥ 5	> 21°C			
Warm-Temperate deciduous	≥ 6	> 23°C	< 0°C	or	< -15°C
Warm-Temperate (evergreen)	≥ 6		> 0°C	and	> -15°C

Warm Months = number of months with mean temperature ≥ 10°C
Tmax = mean temperature of the warmest month
Tmin = mean temperature of the coldest month
Tabmin = absolute minimum temperature (lowest ever measured or expectable)

and Tilio amurensis-Betuletum platyphyllae Kim ex Krestov et al. 2006.

2. Rhododendro daurici-Pinion koraiensis Krestov, Song, Nakamura et Verkholat 2006

   Diagnostic taxa: *Rhododendron dauricum*, *Gymnocarpium dryopteris*, *Vaccinium vitis-idaea*, *Rosa acicularis*, *Viola sachalinensis*, *Polypodium vulgare*, *Orthilia secunda*, *Linnaea borealis*, *Spiraea beauverdiana*.

   Holotype: Vaccinio vitis-idaeae-Pinetum koraiensis Krestov et al. 2006.

   This alliance occurs in the northwestern, coldest, most continental areas of the Tilio amurensis-Pinetalia koraiensis (Krestov et al. 2006), on drier, well-drained, nutrient-poor sites of the cool-temperate zone. The forests occur on south slopes or different slope aspects, steep slopes or near ridges. The canopy layer has *Pinus koraiensis* and *Q. mongolica* as dominants. Two associations are involved in this alliance: Carici callitrichoi-Pinetum koraiensis Krestov et al. 2006 and Vaccinio vitis-idaea-Pinetum koraiensis Krestov et al. 2006.

3. Abieti nephrolepidis-Pinion koraiensis Gumarova ex Krestov, Song, Nakamura et Verkholat 2006

   Diagnostic taxa: *Abies nephrolepis*, *Picea jezoensis*, *Leptorumohra amurensis*, *Carex campylorhina*, *Paris quadrifolia*, *Lycopodium juniperoideum*, *Lilium distichum*, *Athyrium filix-femina*, *Stellaria bungeana*, *Veratrum oxysepalum***.**

   Holotype: Phrymo asiaticae-Pineion koraiensis Krestov et al. 2006 ex Fujiwara et A. Harada

   This alliance was described by Gumarova (1993) and validated by Krestov et al. (2006). It has *Picea jezoensis* and *Pinus koraiensis* in the canopy layer as well as the shrub and sub-canopy layers. Two suballiances are recognized in this paper.

   a. Euonymenion macropterus suball. nov.

      Diagnostic taxa: *Euonymus macropterus*, *Thalictrum filamentosum*, *Carex xiphium*, *Phegopteris connectilis*, *Lycopodium annotinum*.

      Holotype: Diplazio sibirici-Abietetum nephrolepidis Gumarova ex Krestov et al. 2006

      This suballiance occurs in the northern and southern Sikhote-Alin, at elevations of 100–700 m, on various slope aspects. Dominant species in the canopy are *Betula costata, Picea jezoensis, Pinus koraienis* and *Tilia amurensis* plus *Q. mongolica* sometimes. *Acer mono* and *A. ukurunduense* are mixed in the sub-canopy or canopy layer. Two associations are involved in this suballiance: Diplazio sibirici-Abietetum nephrolepidis and Lycopodio annotini-Abietetum nephrolepidis Gumarova ex Krestov et al. 2006.

   b. Phrymo asiaticae-Pinenion koraiensis Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada suball. nov.

      Diagnostic taxa: *Sorbaria sorbifolia*, *Trigonotis radicans*, *Anemonoides extremiorientalis*, *Juglans mandshurica*, *Carex pallida*, *Scutellaria ussuriensis*.

      Holotype: Arisaemo asiaticae-Pinion koraiensis Krestov et al. 2006.

      This suballiance was established by Krestov et al. (2006) as an alliance, but it is demoted here to suballiance (Table 1). The distribution area is in the Sikhote-Alin, at elevations of 50–600 m, and north of the Amur River basin near Birobidzhan. The canopy is co-dominated by *Betula costata*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Phellodendron amurense*, *Pinus koraiensis*, *Tilia amurensis*, *T. mandshurica* and *Q. mongolica*. The sub-canopy and shrub layers commonly have *Acer mono*, *A. tegmentosum*, *A. ukurunduense* and *Abies nephrolepis*. The herb layer is covered to 50–80%. The species differ, but *Carex campylorhina, C. falcata, C. armellii, C. egena, C. jaluensis, C. pallida, C. siderosticta, C. reventa* and many other sedges may occur, depending on the location. Ferns are also diverse, depending on location, including *Athyrium filix-femina, Cornopteris crenulatoserrulata, Matteuccia truthiopteris, Osmundastrum asiaticum, Dryopteris classirrhizoma* and *Pseudocystopteris spinulosa*. Four sssociations are included in this auballiance: Carici falcata-Pinetum koraiensis Krestov et al. 2006; Ulmo japonicae-Pinetum koraiensis Krestov et al. 2006; Arisaemo amurensi-Pinetum koraiensis Krestov et al. 2006; and Riberi maximowicziani-Pinetum koraiensis Krestov et al. 2006.

4. Jeffersonio-Quercion mongolicae Kim ex Krestov, Song, Nakamura et Verkholat 2006

   Diagnostic taxa: *Abies holophylla*, *Asarum sieboldii*, *Acer barbinerve*, *Kalopanax septemlobus*, *Polystichum subtripteron*, *Euonymus maximowicziana*.

   Holotype: Abieti holophyllae-Quercetum mongolicae Kim ex Krestov et al. 2006

   This alliance was established by Kim (1992) and validated by Krestov et al. (2006). It occurs on southern spurs of the Shikhote-Alin range, in the Lao-ye mountain system, and on the Changbai-Shan (Kim 1992; Qian et al. 2003; Kolbek et al. 2003b; cf Krestov et al. 2006). Four associations were reported from the Shikhote-Alin, Mukraviov-Amursky peninsula (Vladivostok suburbs) and the Borisovka plateau, and it likely occurs also in northeastern China and North Korea. It was curious that we surveyed north China widely but never encountered any forest type of this alliance. Three associations and one community are described in this alliance: an Abieti holophyllae-Quercetum mongolicae Kim ex Krestov et al. 2006; a Polysticho subtripteron-Pinetum koraiensis Gumarova et al. ex Krestov et al. 2006; a Fraxino mandshurici-Abietetum holophyllae Gumarova et al. ex Krestov et al. 2006; as well as a *Taxus cuspidata*-*Carpinus cordata* community. Three associations have canopies dominated by the conifers *Abies holophylla* or *Pinus koraiensis*. Forest height is 30–35 m in the Abieti holophyllae-Quercetum mongolicae, and the Polysticho subtripteron-Pinetum koraiensis can reach 40–45 m.

5. ***Quercus mongolica* forest in the Greater Hinggan Mountains (Da Xing An Ling) and *Betula daurica* woodland in Russia**

   Querco mongolicae-Betuletea davuricae Ermakov et Ptelin in Ermakov 1997

   Diagnostic taxa: *Betula platyphylla, Artemisia tanacetifolia, A. integrifolia, Carex pediformis.*

   Holotype: Querco mongolicae-Betuletalia davuricae Ermakov et Ptelin in Ermakov 1997

   Ermakov (1997) and Ermakov et al. (2000) described the Querco mongolicae-Betuletea davuricae as constituting the western limit of forests toward the drier continental interior. Krestov et al. (2006) stated that many constituent species also belong to a larger South Siberian-Manchurian chrological group and occur in disjunct distributions in the forest-steppe zone of southern Siberia. Two orders were described as belonging to the Querco mongolicae-Betuletea davuricae. The Lespedezo bicoloris-Quercetalia mongolicae Krestov et al. 2006 was moved to Quercetalia mongolicae because the species combination is closer to that of the Quercetea mongolicae than to the Querco mongolicae-Betuletea davuricae. As a result, a new order from the Hinggan region is added as Poo nemoralis-Quercetalia mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010.

   a. *Quercus mongolica* forests in the Greater Hinggan Range

      Poo nemoralis-Quercetalia mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010

      Diagnostic taxa: *Poa nemoralis*, *Dictamnus dasycarpus*, *Artemisia sacrorum*, *Saussurea firma*, *Adenophora gmelini* var. *coronopifolia*, *Elymus dahuricus*, *Hemerocallis citrine*, *Silene jenisensis*, *Artemisia sylvatica*, *Saussurea recurvata*, *Clematis hexapetala*.

      Holotype: Poo nemoralis-Quercion mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010

      The Da Hinggan (Manchu, = Greater Khingan; Chinese: Da Xing An Ling) mountain range separates the Inner Mongolian steppe to the west and Heilongjiang to the east. The mountains reach the Amur River in the north and the Xilamulun River in the south, over a distance of 1,200 km from north to south. The geological substrate is mainly granite, and soils are mostly very shallow. Annual precipitation is around 300–400 mm in the south and 370–460 mm in the north. *Quercus mongolica* forests in the southern Da Hinggan region are mostly secondary and only 5–15 m tall, mostly with only three layers. Northern forests are relatively natural, and sometimes thickets 200 years old can be found. These may have four layers. There are effects of wildlife (deer and boar), and fire, in particular, impoverishes the understorey, leaving exposed gravel and pebbles (Zhi-Rong, Fujiwara, Ohno et Zhao 2010). The Poo nemoralis-Quercetalia mongolicae involves one alliance and four associations.

b. Siberian forest-steppe

Querco mongolicae-Betuletalia davuricae Ermakov et Ptelin in Ermakov 1997

Diagnostic taxa: *Fragaria orientalis*, *Lathyrus humilis*, *Lupinaster pentaphyllus*, *Galium boreale*, *Geranium eriostemon*, *Dendranthema zawadskii*, *Saussurea elongata*, *Carex amgunensis*, *Pulsatilla patens*, *Spiraea media*, *Astragalus membranaceus*, *Adenophora triphylla*, *Rosa davurica*, *Festuca ovina*, *Lilium pensylvanicum*, *Valeriana alternifolia*, *Rubus saxatilis*, *Achnatherum sibiricum*, *Adenophora tricuspidata*, *Scorzonera radiata*, *Pyrola rotundifolia*, *Artemisia sericea*, *Poa botryoides*, *Thalictrum appendiculatum*, *Viola dactyloides*, *Elymus gmelinii*, *Salix pyrolifolia*, *Pinus sylvestris*, *Salix abscondita*.

Holotype: Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997

This order includes continental and ultra-continental deciduous forests and mixed forests with *Betula davurica, B. platyphylla, Larix gmelinii* and *Pinus sylvestris*. These forests occur as azonal vegetation types near and on the forest-steppe ecotone in the uppermost part of the Amur River basin and as zonal vegetation in the middle Amur basin (Zea plain) (Krestov et al. 2006). The upper-Amur distribution area is characterized by mean annual temperatures as low as −3°C and by very low precipitation, from 250 to 310 mm annually. This order involves two alliances, two suballiances and nine associations (Ermakov 1997).

6. ***Quercus mongolica* forest around Beijing and Shandong** (mid-temperate)

Spiraeo trilobatae-Quercion mongolicae Tang, Fujiwara et A. Harada all. nov. prov.

Diagnostic taxa: *Spiraea trilobata, Deutzia grandiflora, Myripnois dioica, Calamagrostis arundinacea, Thalictrum thunbergii, Saussurea nivea, Larix principis-rupprechtii, Andrachne chinensis, Carex onoei, Leptodermis oblonga.*

Holotype: Rhododendro micrantho-Quercetum mongolicae Tang, Fujiwara et A. Harada ass. nov. prov.

Quercus mongolica forests around Beijing and Shandong, where it is warmer and drier, are quite different from others in northern China, the Russian Far East and the Korean peninsula (Quercetea mongolicae) (Table 1). The Coldness Index at Bejing is only −21.3 and annual precipitation is 539 mm (climate data from 1978 to 2008), whereas the Coldness Index of Quercetea mongolicae forest areas is mostly below −80 (with annual precipitation 440–600 mm). Very dry *Quercus mongolica* forests occur in mountains of the Chinese warm-temperate zone. This alliance includes the forests in the Yunmeng-Shan mountains north of Beijing, the Songshan Preserve in Beijing, and the Yantian-Shan Forest Park of Shandong. The forests are mostly 8–15 m tall, but only 5–8 m in the Songshan Preserve. Canopy cover is about 75–80%, and the cover of the shrub layer is relatively high, around 40%. Herb-layer cover is usually about 5–10% but can reach 40–45%, especially in Shandong.

7. ***Quercus wutaishanica* forest in mid-western China** (mid-temperate)

Quercetea wutaishanicae You, Fujiwara et Tang 2008 cl. prov.

Diagnostic taxa: *Quercus wutaishanica, Agrimonia pilosa, Adenophora potaninii*, *Cotoneaster acutifolius*, *Saposhnikovia divaricata*, *Crataegus kansuensis*.

Holotype: Aceri ginnarae-Quercetum liaotungensis You, Fujiwaraet Tang 2008 prov.

Zhao and Tian (2001) described *Quercus liaotungensis* as a synonym of *Q. wutaishanica*, and Wu and Raven (1999) have even included it now as a synonym of *Q. mongolica*. In the field, however, these two species are quite different, with different typical leaf shapes. The leaves of *Q. mongolica* are toothed and those of *Q. wutaishanica* are lobed; the leaves of *Q. wutaishanica* are shorter ((5)7–10 (12) cm) and narrower (3–6 cm) than leaves of *Q. mongolica* ((8)12–25 cm by (5)7–10 cm), and the lobes are slightly different. *Q. mongolica* has 8–12 pairs of lateral veins and *Q. wutaishanica* has 6–9 pairs of lateral veins, sometimes intercalary veins. Some *Q. mongolica* on sites with poor nutrient status or bad drainage has fewer lobes than normal *Q. mongolica* (Menitsky 2005). It is difficult to identify the exact species in the southern Da Hinggan region. You et al. (2008) described this class with two orders, four alliances and 13 communities, but details must wait for another paper.

4 Discussion

1. What is a warm-temperate deciduous forest in East Asia, and what types are the other forests?

Syntaxnomically speaking, we found two types of warm-temperate deciduous forest, namely the *Quercus serrata* forests in Japan and Korea, and the *Quercus variabilis* forests in China. The *Q. serrata* forests in Japan are mostly secondary forests following cutting and mowing before

World War II. After the war, the basis of people's life changed from firewood and charcoal to oil and gas. The *Quercus* forests then changed very much, but some people continue the practice of mowing the floor of *Q. serrata* forests, in order to keep species richness high. These forests have four layers, with canopy height usually 10–20 m. The canopy layer is dominated by *Q. serrata*, with *Prunus grayana*, *Styrax japonica*, *Pourthiaea villosa* var. *laevis*, *Q. acutissima*, *Celtis sinensis* var. *japonica*, *Castanea crenata*, etc. The shrub layers have *Viburnum erosum*, *Zanthoxylum piperitum*, *Vaccinium oldhamii*, *Ligustrum obtusifolium*, etc. Many species are common to both Korea and Japan, such as *Q. serrata*, *Q. acutissima*, *Castanea crenata*, and *Fraxinus sieboldiana* in the canopy layer and *Viburnum dilatatum*, *Callicarpa japonica*, *Lindera obtusiloba*, and *Stephanandra incisa* in the understorey. Some species have flowers and fruit from spring to autumn. In particular, in the *Q. serrata* forest in central Japan, trees and herbaceous plants on the forest floor bloom one after the other from spring to summer. The herb layer is very species-rich. Many species, including small bamboos (*Pleioblastus* spp.), occur on the forest floor, along with *Cephalanthera falcata*, *Cymbidium goeringii*, *Aster scaber*, *Pertya scandens*, *Viola grypoceras*, *Lilium auratum*, *Polygonatum falcatum*, *Miscanthus sinensis*, *Calamagrostis arundinacea* and *Carex lanceolata*, and climbers like *Wisteria floribunda*, *Akebia quinata*, *Cocculus orbiculatus*, *Lonicera japonica*, and *Parthenocissus tricuspidata*. This species richness shows the combined results of dry forest conditions and disturbance by humans. The secondary forests preceding evergreen broad-leaved forests in central Japan have many species. On the other hand, *Q. variabilis* forests in China are simpler and have fewer species. The forest flora is similar, but there is less herbaceous cover than in Japanese *Q. serrata* forests.

The other type of warm-temperate *Q. serrata* forest in Japan is further inland, where it is drier and warmer in summer than in the *Fagus*-*Q. mongolica* var. *crispula* forest region. In the areas of these *Q. serrata* and *Q. variabilis* forests the Coldness Index is generally not below about −10. The area of warm-temperate deciduous forests is in lowlands or on low hills. Settlements and cultivation are common, including utilization for firewood and tree plantations.

Most areas are secondary forest, but temple forests and nature reserves still preserve relatively natural forests in China. The forest height is 10–20 m.

The temperate deciduous forests in East Asia can be classified into three basic forest types: (1) Warm-temperate deciduous forest, with *Q. serrata*, *Q. brevipetiolata, Q. variabilis, Q. acutissima* and *Q. aliena*; (2) Temperate forest, with *Q. mongolica* var. *crispula* and *Q. dentata* in Japan, *Q. mongolica* in the Beijing area and southern Chinese Manchuria, and *Q. wutaishanica* in drier southern Inner Mongolia and the northern Qinling Mts.; and (3) Cool-temperate forest, with mixed forests of *Q. mongolica* and conifers (*Pinus koraiensis*, *Abies holophylla* and *A. homolepis*) on the Asian mainland (China, Korea and Russia), plus *Q. mongolica* var. *crispula* and *Abies sachalinensis* in Japan.

2. Definition of warm-temperate deciduous forests

Kira (1949) recognized that deciduous forests may also occur as stable forests in warm-temperate areas, if winter temperatures are too low for evergreens (e.g. interior Japan, as around Nagano and in northern Kantō and Yamagata). Warm-temperate deciduous forests occur where winter is too cold (and dry) for evergreens but too warm (and summer too dry) for beech. The Coldness Index (CI) of the warm-temperate deciduous forest would be below −10 and the Warmth Index above 85. Warm-temperate forests are usually evergreen broad-leaved forest (Honda 1912; T. Suzuki 1966), but Hämet-Ahti et al. (1974) and Nozaki and Okutomi (1990) assigned warm-temperate deciduous forests to an Intermediate (or lower) temperate forest zone. Hämet-Ahti et al. (1974) also designated the forests in Hokkaidō as cool-temperate or cold-temperate, and designated the *Fagus* forests as temperate (incl. oro-temperate) forest or upper temperate.

Nozaki and Okutomi (1990) called Hokkaidō the upper temperate zone, based on *Fagus crenata* forest. The warm-temperate deciduous forests (Kira 1949, 1991) have been discussed as intermediate between cool-temperate and the warm-temperate evergreen broad-leaved forest zone (Yoshioka 1954a, b; T. Suzuki 1961; Yamanaka 1969; Hämet-Ahti et al. 1974; Hotta 1974) and not as part of an independent zonation (Honda 1912, Miyawaki et al. 1980). Chen (1995) showed the climatic characteristics of the various temperate *Quercus* forests in China (cf Table 1). *Q. wutaishanica* (=*Q. liaotungensis*) has the lowest mean temperature in January (−6.2°C to −14.6°C) and in July (17.5–22.2°C). These values are lower than for *Q. variabilis* forest (−1.9°C to −10.3°C in January and 20.6 to 24.5°C in July).

Forests of *Q. aliena* var. *acuteserrata* occur where mean temperatures are −4.4°C to −5°C in January and 17.7 to 21.6°C in July, i.e. where summer mean temperatures are above 20°C and winter means above −10°C. Based on the climatic summary of temperate forests in Asia by Box and Fujiwara (2015, herein), the warm-month mean temperature (Tmax) of typical temperate forest should be above 21°C and that for

Table 6 Frost hardness of organs of some main deciduous tree species in East Asia (°C, after Sakai and Larcher 1987)

	species name	buds	cortex	xylem	remarks
Temperate	*Quercus crispula*	-30 to -50	-70	-35	need moisture
	Fagus crenata	-27	-30	-27	
	Acer mono	-30 to -40	-70	-35	
Temperate to boreal	*Betula platyphylla*	-70	-70	-70	
Warm-temperate deciduous	*Q. aliena*	-30	-30	-30	dry
	Q. acutissima	-27	-40	-25	
	Q. serrata	-25	-30	-27	
Warm-temp. evergreen	*Q. glauca*	-15	-15	-18	need moisture
	Q. myrsinaefolia	-15	-15	-15 to -17	

All numbers represent temperature limits, below freezing, in ºC.

warm-temperate forest above 25°C (see Table 6). The Warmth Index of temperate forests is above 60, and that of warm-temperate forests is above 90. Typical temperate forests should occur where there are at least five warm months (mean temperature above 10°C) and warm-temperate forests where there are at least six warm months. For the coldest month (Tmin), warm-temperate deciduous forests may have means as low as −5°C (Box and Fujiwara, herein: Table 2). Warm-temperate forests are warmer in winter and in summer than are temperate forests.

3. Why do deciduous forests persist and evergreens not dominate if the climate really is warm enough for evergreens?
   The main differences between warm-temperate evergreen broad-leaved (WT-EG-BL) and deciduous forest (WT-D) can be summarized as follow, based partly on mean temperatures of the warmest (Tmax) and coldest (Tmin) months and the absolute minimum temperature (Tabmin):
   1. WT-EG-BL forests require moisture and mild winters (Tabmin above −15°C).
   2. WT-D forests can tolerate dryness and coldness more than can EG-BL species (Table 6; cf Box 2013).
   3. Evergreen broad-leaved forest is zonal vegetation (e.g. “laurel forests” of East Asia), but deciduous forest is locally patchy and spread within the WT-EG-BL forest region as secondary forest in Japan.
   4. The Tmax of WT-D forest is more than 25°C but that of EG-BL forest can be as low as 19°C (in the Southern Hemisphere). The Tmin of WT-D forest can be $<$ 0°C but that of EG-BL forest is $>$ 0°C. Tabmin is important since it can be below −15°C for WT-D forest but not for EG-BL forest. These temperature levels delimit WT-EG-BL versus WT-D forest.
   5. WT-D forest occurs where the climate is drier: the annual moisture index (P/PET) can be below 0.60 (open woodlands); in China the mean annual temperature can be more than 12°C.
   6. The temperature limits above are for the frost hardiness of the main species of the warm-temperate evergreen and deciduous forests. According to Sakai and Larcher (1987) (see Table 7), EG-BL species such as *Q. glauca* and *Q. myrsinaefolia* have higher temperatures in their buds, cortex and xylem than do WT-D species such as *Q. serrata* and *Q. aliena*. WT-D forest species have higher temperatures in their cortex and xylem than do temperate species such as *Q. mongolica* var. *crispula*, *Fagus crenata* and *Acer mono*. *Betula platyphylla* can go further north, well into the boreal region, because it can tolerate extreme temperatures as low as −70°C.
   7. WT-D forest species (e.g. *Q. serrata*) invade and form forests in the WT-EG-BL forest region, mainly as secondary forests. Some subtropical species occur in EG-BL forests, and *Q. serrata* forests do not occur as secondary forest (in Japan) in the subtropical region. Secondary forests of these subtropical EG-BL forests are young generations of the EG-BL forests themselves or deciduous *Ficus-Mallotus* forests (Fico-Mallotetalia S. Suzuki et Miyawaki 1986).

4. Effects of global warming on warm-temperate forests in Japan.
   Weedy and other highly mobile species from warmer areas can be expected to invade poleward under global warming (e.g. Fujiwara and Box 1999a, b). In East Asia, we can see evergreen broad-leaved species invading warm-temperate deciduous forests, especially the inland *Quercus serrata* forests (Lonicero gracilipedi-Quercion serratae Shimada, Fujiwara et A. Harada all. nov.). *Q. myrsinaefolia* can tolerate −17°C in its xylem, so if the lowest winter temperatures are above −17°C, then recently germinated acorns may survive in winter under

Table 7 Syntaxonomical summary of deciduous *Quercus* forests in East Asia, based on phytosociological comparison

Syntaxonomic units	Climatic zones
Querco-Fagetea crenatae Miyawaki, Ohba, Okuda, Nakayama et Fujiwara 1968	Cool and typical temperate
Saso-Fagetalia crenatae Suz.-Tok. ex Y. Sasaki 1970	
Fraxino-Quercion grosseserratae Ohba 1973	Temperate forests
Pruno-Quercion grosseserratae Wada 1982	Temperate forests
Carpino-Quercetalia grosseserratae Hoshino 1998	
Carpino-Quercion grosseserratae Takeda, Uematsu et Nakanishi 1983	Cool and typical temperate
Saso quelpaertensis-Quercetalia crispulae ord. nov.	Temperate forests
Saso quelpaertensis-Quercion crispulae all. nov.	Temperate forests
Viburno dilatati-Quercetea serratae class. nov.	Warm-temperate forest
	(Japan & Korea)
Rhododendro kaempferi-Quercetalia serratae ord. nov.	
Lonicero gracilipedis-Quercion serratae Shimada, Fujiwara et A. Harada all. nov.	
(Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et A. Harada ass. nov.)	
Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda ex Fujiwara et A. Harada all. nov.	
Moro australis-Quercenion serratae suball. nov.	
Ilici pedunculosae-Quercenion serratae suball. nov.	
Viburno phleobotrichi-Quercenion serratae suball. nov.	
Aceri pseudosieboldiani-Quercetalia serratae ord nov.	
Callicarpo japonicae-Quercion serratae Kim 1990	
Quercetea variabili-brevipetiolatae Tang, Fujiwara et You in Box et Fujiwara 2015	Warm-temperate forests (China)
Pistacio chinensis-Quercetalia variabilis Tang, Fujiwara et You in Box et Fujiwara 2015	
Lonicero standishii-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015	
Carpino turczaninovii-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015	
Trachelospermo jasminoidis-Quercion variabilis Tang, Fujiwara et You in Box et Fujiwara 2015	
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da ex Fujiwara et A. Harada ord. nov.	
Liquidambaro formosanae-Quercion fabri all. nov.	
Sasamorpho sinicae-Quercion brevipetiolatae S.Suzuki, Nakamura, Kawano, X. Wang et Da ex Fujiwara et A. Harada all. nov.	
Quercetea mongolicae Song ex Krestov, Song, Nakamura et Verkholat 2006	Cool and typical temperate
	(China, Korea, Russia)
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Cool and typical temperate
Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda, Nakanishi et Choe 1994	(Korea)
Lespedezo bicoloris-Quercetalia mongolicae Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada ord. nov.	Temperate forests (China & Russia)
Corylo heterophyllae-Quercion mongolicae Krestov, Song, Nakamura et Verkholat 2006	
Quercenion dentato-mongolicae suball. nov.	
Dictamno dasycarpi-Quercenion mongolicae Kim ex Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada suball. nov.	
Adenophoro tetraphyllae-Quercion mongolicae You, Fujiwara et A. Harada all. nov.	
(Festuco-Quercetum mongolicae You, Fujiwara et A. Harada ass. nov.)	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, Song, Nakamura et Verkholat 2006	Cool and typical temperate
	(China and Russia)
Tilio amurensis-Pinion koraiensis Kim ex Krestov et al. 2006	Cool-temperate (China & Russia)
Syringo amurensis-Pinenion koraiensis suball. nov.	
(Lonicero ruprechtianae-Quercetum mongolicae L. Wang, Fujiwara, et A. Harada ass. Nov.)	
Lonicero praeflorenti-Pinenion koraiensis suball. nov.	
Rhododendro daurici-Pinion koraiensis Krestov, Song, Nakamura et Verkholat 2006	
Abieti nephrolepidis-Pinion koraiensis Gumarova ex Krestov, Song, Nakamura et Verkholat 2006	Cool-temperate forest (Russia)

(*continued*)

Table 7 (continued)

Syntaxonomic units	Climatic zones
Euonymenion macropteri suball. nov.	
Phrymo asiaticae-Pinenion koraiensis Krestov, Song, Nakamura et Verkholat ex Fujiwara et A. Harada suball. nov.	
Jeffersonio-Quercion mongolicae Kim ex Krestov, Song, Nakamura et Verkholat 2006	Cool and typical temperate (Korea)
Querco mongolicae-Betuletea davuricae Ermakov et Ptelin in Ermakov 1997	
Poo nemoralis-Quercetalia mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010	Cool-temperate forest
Querco mongolicae-Betuletalia davuricae Ermakov et Ptelin in Ermakov 1997	
Higher-level unit not yet decided:	
Spiraeo trilobatae-Quercion mongolicae Tang, Fujiwara et A. Harada all. nov. prov.	Temperate forest (China)
Quercetea wutaishanicae You, Fujiwara et Tang 2008 cl. prov.	Temperate forest (China)

The syntaxa, which involve six classes and two extra alliances, correspond to zonal climatic forest types, as shown in the last column. The seven leftmost lines (classes) correspond to subsections 1–7 under 'Results' in the main text.

the *Q. serrata* forests. Even shrub species such as *Aucuba japonica* can survive after germination and spread vegetatively in the understorey of *Q. serrata* forests. We recorded *Q. myrsinaefolia* growing up to 10 m, which means that winter temperatures had not been below −17°C over the past 50 years. *Q. myrsinaefolia* was planted around temples in Nagano and Ueda, in inland middle Japan (Fujiwara 1998; Fujiwara and Yoshino 2005), and *Aucuba japonica* has been planted widely in residence areas as a garden plant.

This phenomenon is reported also from Switzerland by Klötzli and Walther (1999). We also investigated in southern Switzerland and around Arco in Italy (unpublished material). As results it appears that: (1) Laurophyll species will go north along coastlines, and evergreen Fagaceae species will go inland in the warm-temperate deciduous forests on south slopes, especially along lakes and foothills in basins; (2) Understorey species such as *Aucuba japonica* can survive through vegetative reproduction; (3) Tropical and subtropical weed and secondary deciduous tree species and communities can spread into warm-temperate forests; and (4) Mid-successional evergreen species can spread into warm-temperate deciduous forests (Fujiwara and Box 1999a, b; Fujiwara and Yoshino 2005).

Conclusion

It appears that *Quercus* forests can be classified into ten forest types: (1) *Quercus mongolica* var. *crispula* forests in Japan (cool-temperate and temperate types); (2) *Carpinus laxiflora-Q. crispula* forest on Jeju-do island off southwestern Korea (temperate); (3) *Viburnum dilatata-Q. serrata* forests in Japan and Korea (warm-temperate); (4) Q. *brevipetiolata-Q. variabilis* forests in China (warm-temperate); (5) *Acer pseudosieboldii-Q. mongolica* forests in Korea (temperate); (6) *Lespedeza bicolor-Q. mongolica* forests (temperate) in Chinese Manchuria and the Russian Far East; (7) *Tilia amurensis-Pinus koraiensis* forests in northern China, North Korea and the Russian Far East (cool-temperate); (8) *Artemisia integrifolia-Quercus mongolica* forest in the Manchurian Da Hinggan mountains and *Betula daurica* woodland in Trans-Baikal Russia (cool-temperate); (9) *Quercus wutaishanica* (*liaotungensis*) forests in middle western China (temperate); and (10) *Spiraea trilobata-Quercus variabilis* forests around Bejing and Shandong (warm-temperate).

The phytosociological comparison of deciduous *Quercus* forests in eastern Asia yielded the syntaxonomical summary shown in Table 7, with six classes and two extra alliances. These correspond to climatic forest types.

Other conclusions include the following:

1. Species of the warm-temperate deciduous forest (Viburno dilatati-Quercetea serratae and Quercetea variabili-brevipetiolatae) are more frost-hardy and can tolerate greater dryness, coldness and human impact than can species of evergreen broad-leaved forests.
2. Warm-temperate deciduous forests will occur next to warm-temperate evergreen broad-leaved forests and will invade evergreen broad-leaved forest areas as secondary forests under human disturbance, such as cutting for firewood and charcoal and mowing for compost.
3. Warm-temperate deciduous forests may undergo laurophyllization in moist environments. This indicates environmental disturbance.

Acknowledgements We like to express gratitude to Dr. Pavel Krestov, Institute of Biology and Soil Science, Vladivostok, for providing original tables after publishing his paper. It was great work and helped our work very much. We also thank Prof. Shinichi Suzuki, Tokyo University of Agriculture, for providing his synoptic table. He worked hard on the syntaxonomy of *Quercus serrata* and *Q. mongolica* forest. We sincerely thank them for their goodwill. We also express our thanks to Dr. Jean-Paul Theurillat, Centre Alpien de Phytogéographie, Champex-Lac, for giving syntaxonomical advice. We also thank greatly Dr. You Hai-Mei, Dr. Wang Lin, Dr. Zhi Rong and Dr. Zhao, in China, who have worked in the field together with us since 1999. We also thank Prof. Elgene Box (University of Georgia) for English editing.

References

Box, E. O. 1995. Climatic Relations of the Forests of East and South-East Asia. In: *Vegetation Science in Forestry: Global Perspective based on Forest Ecosystems of East and Southeast Asia*. (E. O. Box et al., eds.), pp 23–55. Kluwer.

Box, E. O. 2002. Vegetation analogs and differences in the Northern and Southern Hemispheres: a global comparison. *Plant Ecology*, 163:139–154 (appendix missing – request from author).

Box, E. O. 2013 (herein). Quantitative Delimitation of Warm-Temperate Deciduous Forest Areas.In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O. and K. Fujiwara 2004 (2nd ed. 2013). Vegetation Types and their Broad-Scale Distribution. In: *Vegetation Ecology* (E. van der Maarel, ed.), pp. 106–128. Blackwell, Oxford.

Box, E. O. and K. Fujiwara 2012. A comparative look at bioclimatic zonation, vegetation types, tree taxa and species richness in Northeast Asia. *Botanica Pacifica* (Vladivostok), 1:5–12.

Box, E. O. and K. Fujiwara 2015 (herein). Warm-Temperate Deciduous Forests: Concept and Global overview. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O. (ed.), R. K. Peet, T. Masuzawa, I. Yamada, K. Fujiwara and P. F. Maycock (co-eds.) 1995. *Vegetation Science in Forestry: Global Perspective based on Forest Ecosystems of East and Southeast Asia*. Handbook Vegetation Science, vol. 12/1. Dordrecht: Kluwer. 663 pp.

Braun-Blanquet, J. 1964. *Pflanzensoziologie, Grundzüge der Vegetationskunde*. 3rd ed.Springer-Verlag, Vienna. 613pp.

Cao K.-F. 1995. *Fagus* Dominance in Chinese Montane Forests: Natural regeneration of *Fagus lucida* and *Fagus hayatae* var. *pashanica*. Doctoral thesis, Wageningen Agricultural University. 116pp.

Chen W.-L. 1995. Subtropical Montane Deciduous Forests in Southern China. In: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 317-323. Kluwer, Dordrecht.

Dress, M. 1953. Rules of phytosociological nomenclature tentatively proposed. *Vegetatio*, Fasc. 4:205-214 (Japanese translation by Y. Sasaki 1961: *Hikobia*, 2(2):135–233).

Ermakov, N. B. 1997. Forest of Daurian birch (*Betula davurica*) – an element of Manchurian forest-steppe in the vegetation of Siberia. *Siberian J. Ecol*., 1:57–66.

Ermakov, N., J. Dring, and J. Rodwell 2000. Classification of continental hemi-boreal forests of North Asia. *Braun-Blanquetia*, 28:1–131.

Fang J.-Y., Song Y.-Ch., Liu H.-Y. and Piao Sh.-L. 2002. Vegetation-climate relationship and its application in the division of vegetation zones in China. *Acta Botanica Sinica*, 44(9): 1105–1122.

Fujiwara, K. 1987. Aims and methods of phytosociology or "vegetation science". In: *Plant Ecology and Taxonomy to the memory of Dr. Satoshi Nakanishi*, pp. 607–628. Kōbe Geobotanical Society, Kōbe.

Fujiwara, K. 1998.Vegetation shift in Japan and overview in warming. In: Abstracts, VII International Congress of Ecology, Firenze (A Farina et al., eds.), p. 147.

Fujiwara, K. (project leader) 2008. Integrated Vegetation Mapping of Asia. Report to Japan Society for Promotion of Science, project #16255003. 189pp.

Fujiwara, K. and E. O. Box 1999a. Evergreen broad-leaved forests in Japan and eastern North America. In: Recent Shifts in Vegetation Boundaries of Deciduous Forests (F. Klötzli & G.-R. Walther, eds.), pp 273–300. Birkhauser.

Fujiwara, K. and E. O. Box 1999b. Climate change and vegetation shift. In: Perspectives in Ecology: A glance at the VII International Congress of Ecology (Florence, July 1998) (A. Farina, ed.), pp 121–126. Blackhuys, Leiden.

Fujiwara, K., H. Fukutome, H. Tohma, N. Shimada, M. Watanabe and H. Saito 1997. [Vegetation in Iruma City: study for green environmental planning with symbiosis between humans and nature]. Bull. Kanagawa Vegetation Soc., vol. 2. 143pp (in Japanese, with English summary).

Fujiwara, K., Y. Kusumoto, T. Enomoto and H. Tojima 1999. [Vegetation in Hisai City]. Bull. Kanagawa Vegetation Society, vol. 4. 140pp (in Japanese with English summary).

Fujiwara, K. and T. Yoshino 2005. Does global change contribute to diversity in broad-leaved forests or is it only a "disturbance"? XVII International Botanical Congress, p.19.

Fujiwara, K., You H-M., A. Miyawaki, N. Shimada, K. Futami, N. Tsuge and R. Tanaka 2000.[Potential natural vegetation and proposals for restoration of green environments in Xuzhou City, China]. Handa City and Handa International Association. 81 pp (in Chinese, with English summary).

Gumarova, R. R. 1993. [Syntaxonomy of montane Korean pine-broad-leaved forests of the southern Sikhote Alin]. All-Union Inst. Scient. Techn. Information (VINITI), vol. 93, ms. N502. Vladivostok. 61pp (in Russian).

Hämet-Ahti, L. T. Ahti and T. Koponen 1974. A scheme of vegetation zones for Japan and adjacent regions. *Ann. Bot. Fenn*., 11:59–88.

Hanazawa, M. 2006. [Vegetation ecology of secondary *Quercus serrata* forests in southern Kantō (eastern Japan): species composition and vegetation distribution in the Tama and Miura Hills]. Masters Thesis, Yokohama National University. 39pp plus tables and figures (in Japanese).

Hayashi, A. 2000. [Species composition and maintenance mechanism of coppice forest of *Quercus acutissima* and *Quercus serrata* secondary forest]. Masters Thesis, Yokohama National University. 16pp plus tables and figures (in Japanese).

Hibino, K. and A. Sasaki 1982. [Pollen analysis in northwest Nagano Prefecture]. *Bull Agric. College Miyagi Prefecture*, 30:93–101 (in Japanese).

Honda, S. 1912. [*Forest Zones of Japan*]. Miura-Shōten, Tokyo. 400 pp (in Japanese).

Hoshino, Y. 1998. [Phytosociological studies of *Quercus mongolica* var. *grosseserrata* forest in Japan]. *Bull. Faculty Agriculture*, Tokyo University of Agriculture and Technology, 32:1–99 (in Japanese).

Hotta, M. 1974. [*History and Geography of Plants*]. Sanseidō. 400 pp (in Japanese).

Hukusima (Fukushima), T., H. Takasuna, T. Matsui, T. Nishio, Y. Kyan and Y. Tsunetomi 1995. Nihon-no buna-rin gunraku-no shokubutsu-shakai-teki shintaikei [New phytosociological classification of beech forests in Japan]. *Japanese. J. Ecology*, 45:79–98.

Igarashi, Y. 1997. [Development of Mixed Forest]. In: *Natural History of Hokkaidō* (Y. Ono and Y. Igarashi, eds.), pp 202–203. Hokkaidō University (in Japanese).

Kim J.-U. and Yim Y.-J. 1986. Classification of forest vegetation of Seonun-san area, southwestern Korea. *Korean J. Ecology*, 9(4): 209–223.

Kim J.-W. 1990. A syntaxonomic scheme for the deciduous oak forest of South Korea. *Abstracta Botanica*, 14:51–81.

Kim J.-W. 1992. Vegetation of northeast Asia, on the syntaxonomy and syngeography of the oak and beech forest. Ph. D. Thesis. University of Vienna. 314pp.

Kim J.-W. and Choi B.-K. 2012. Discovering the essence of the Korean vegetation for field excursion – The spirit of place, Korea. World science Publishing, Seoul. 163pp.

Kim S.-D., M. Kimura and Yim Y.-J. 1986. Phytosociological studies on the beech (*Fagus multinervis* Nakai) forest and the pine (*Pinus parviflora* S. et Z.) forest of Ulreung Island, Korea. *Korean J. Botany*, 29(1):53–65.

Kira, T. 1945. *Nōgyō Chirigaku-no Kisō to shite no Tō-A no Shin Kikō Kubun* (A new classification of climate in eastern Asia, as a basis for agricultural geography.) Horticult. Inst., Kyoto University. 23 pp (in Japanese).

Kira, T. 1949. Nippon-no shinrin-tai [Forest zones in Japan]. *Ringyō Kaisetsu*, 17:105-141. Nippon Ringyō Gijutsu Kyōkai,Tokyo; reprinted in Kira 1971, pp 105–141 (in Japanese).

Kira, T. 1976. [*Terrestrial Ecosystems – a General Survey*]. Kyōritsu-Shuppan, Tokyo. 166 pp (in Japanese).

Kira, T. 1977. A Climatological Interpretation of Japanese Vegetation Zones. In: *Vegetation Science and Environmental Protection* (A. Miyawaki, ed.), pp. 21–30. Maruzen, Tokyo

Kira, T. 1991. Forest ecosystems of East and Southeast Asia in a global perspective. *Ecol. Research* (Japan), 6:185-200. Reprinted in: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 1-21. Kluwer, Dordrecht.

Kira, T. 2011. [Vegetation of Japan: Position of Japanese vegetation distribution in the world]. In: Collected Works of Tatsuō Kira, vol. 1: Forest and Culture, pp 229–263. Shinju-sha (in Japanese).

Klötzli, F. and G.-R. Walther 1999. Recent Vegetation Shifts in Switzerland. In: Conference on Recent Shifts in Vegetation Boundaries of Deciduous Forests (F. Klötzli & G.-R. Walther, eds.), pp 15–29. Birkhäuser, Basel.

Kobayashi, K., A. Muranaga, M. Takeda and O. Hasunuma 1976. [Vegetation around Takehara City]. Chūbu Electric Power and Urban Greenery Institute, Hiroshima. (In Japanese)

Kolbek, J., M. Srůtek and E. O. Box (eds.) 2003a. *Forest Vegetation of Northeast Asia*. Kluwer. 462pp.

Kolbek, J., I. Jarolímek and M. Valachovič 2003b. Forest vegetation of the northern Korean Peninsula. In: *Forest Vegetation of Northeast Asia* (J. Kolbek et al., eds.), pp 263–361. Kluwer. Academic Publisher.

Krestov, P. V., Song J.-S., Y. Nakamura and V. P. Verkholat 2006. A phytosociological survey of the deciduous temperate forests of mainland Northeast Asia. *Phytocoenologia*, 36(1):77–150.

Menitsky, Yu. L. 2005. *Oaks of Asia*. Science Publishers, Inc. (Enfield, NH, and Plymouth, UK). 549pp (translated from Russian, originally published 1984 by Komarov Botanical Institute, Leningrad).

Miyawaki, A. (ed.) et al. 1980. [*Vegetation of Kyūshū*]. Vol 1 of *Nippon Shokusei Shi* [Vegetation of Japan]. Shibundō, Tokyo. 484 pp + 30 phytosociological tables + 4 maps (in Japanese, with German summary).

Miyawaki, A. (ed.) et al. 1981-88. Volumes 2-9 of *Nippon Shokusei Shi* [Vegetation of Japan]. Each volume 400-700pp plus vegetation tables and color maps (in Japanese, with German or English summary). Shibundō, Tokyo.

Miyawaki, A. and 27 co-authors 1972. [Reale Vegetation der Präfektur Kanagawa]. Board of Education of Kanagawa Prefecture. 788pp (in Japanese, with German summary).

Miyawaki, A. and K. Fujiwara 1968. [Pflanzensoziologische Studien im "Neugestaltungsbezirk" westlich Fujisawa bei Yokohama]. [Fujisawa Western Development Secretariat]. 44pp (in Japanese, with German summary).

Miyawaki, A. and K. Fujiwara 1984. Evergreen broad-leaved forests and secondary forests in the Bōsō Peninsula (SE parts of the Kantō region). *Bull. Inst. Envr. Sci. Tech.*, Yokohama Nat. Univ., 9:63–76.

Miyawaki, A., K. Fujiwara, H. Harada, T. Kusunoki and Sh. Okuda 1971. [Vegetation of Zushi City – Evergreen broad-leaved forests in Japan]. Zushi City Board of Education. 151pp (in Japanese, with German summary).

Miyawaki, A., K. Fujiwara and S. Ishii 1994. [Vegetation of Haramachi City, Fukushima Prefecture, Japan: Vegetation-ecological study for conservation and restoration of green environment near the northern limit of evergreen broad-leaved forest]. 89pp (in Japanese with English summary).

Miyawaki, A., T. Ohba, Sh. Okuda, K. Nakayama and K. Fujiwara 1968. [Phytosociological study of Echigo Sanzan and Okutadami, Niigata Pref. and Fukusima Pref., Japan]. In: [Scientific report on Echigo-Sanzan, Okutadami and their vicinity, Niigata and Fukushima Prefectures], pp 57–152. Nature Conservation Society of Japan, Tokyo (in Japanese).

Miyawaki, A. and K. Ohno 1996. [Vegetation of Kani City]. Kani City (in Japanese).

Murai, S. 1950. [Overview of forest vegetation in Aomori]. Regional Forestry Office. Aomori-Rinyū, 25:7–21 (in Japanese).

Nakanishi, S. 1983. [Vegetation and plants in *Fagus* and *Quercus mongolica* var. *crispula* forests]. In: Illustrated Book of the Vegetation of Japan (S. Nakanishi, ed.): I. Forests, pp 66–210. Shokokusha. (In Japanese)

Nakanishi, S., Y. Takeda and T. Hattori 1977. [Vegetation of the western part of Harima Province, Hyōgo Prefecture]. In: Soil, flora and vegetation of the western part of Harima Province, Hyōgo Prefecture (S. Nakanishi, ed.), pp 70–144. Society for Study of Vegetation in the western part of Harima Province. (In Japanese)

Nakanishi, Sawako 2004. [Species composition and environmental factors of the secondary forests in the southern Kantō region, Japan]. Master Thesis of Yokohama National University. 39pp (in Japanese).

Nakano, H. 1942. [The forest community composition of the deciduous forest zone in Honshū]. *Shokubutsu-Seitai-Gakuhō* [*Annals of Phytoecology*], 2:57–72.

Nakashizuka, T. 2003. [Reconsideration of cool-temperate deciduous forest types in northern Japan]. *Jap. J. Histor. Botany*, 11(2):39–43 (in Japanese, with English abstract).

Nomenclature Committee 1969. International Code of Phytosociological Nomenclature, I. *Vegetatio*, 32:131–185.

Nozaki, R. and K. Okutomi 1990. [Geographical distribution and zonal interpretation of intermediate-temperate forests in eastern Japan]. *Japan. J. Ecology*, 40:57–69 (in Japanese with English synopsis).

Numata, M. (ed.) 1974. *The Flora and Vegetation of Japan*. Kodansha (Tokyo), Elsevier (Amsterdam). 294 pp.

Numata, M. 1987. *Shokubutsu-Seitaigaku-Ronkō* [Discourse on Plant Ecology]. Tokai Univ. Press. 918pp (in Japanese).

Numata, M., A. Miyawaki and D. Itow 1972. Natural and semi-natural vegetation in Japan. *Blumea*, 20:435-481 (with 26 photos, veg. maps, and altitudinal profile).

Ohba, T. 1973. [Über die Vegetation des Kiyutsu-Tales, Zentral-Japan]. [*Nature Conservation Society*], 43:57–128 (in Japanese, with German summary).

Ohashi, H. 1988. The new name instead of *Quercus mongolica* Fisch. var. *grosseserrata* (BL.) Rhd. & Wills. (Fagaceae). *Japanese J. Bot*., 63(1):13–14.

Ohno, K. 1977. [Temperate Forests (Cold-temperate forests)]. In: [Vegetation of Tōyama Prefecture] (A. Miyawaki, ed.), pp 230–233. Contrib. Dept. Vegetation Sci., Inst. Env. Sci. Tech., Yokohama Nat. Univ., 36 (in Japanese).

Okitsu, S. 2000. [Phytogeography of the major forests of northern Japan in northeastern Asia]. *Bull. Geogr. Kokushikan Univ*., 9:7–11 (in Japanese, with English abstract).

Okutomi, K. and Y. Hoshino 1983. [Phytosociological studies of the *Quercus mongolica* var. *grosseserrata* forests in Kantō and the Tōhoku region, Japan]. *J. Phytogeog. & Taxon*., 31:34–45 (in Japanese, with English summary).

Osumi, K. 2003. [Anthropogenic disturbances and the development of present cool-temperate forests in the Kitakami mountain Range]. *Japan. J. Histor. Bot*., 11(2):53–59 (in Japanese, with English abstract).

Qian H., P. V. Krestov, Fu P.-Y., Wang Q.-Li., Song J.-S. and Ch. Chourmouzis 2003. Phytogeography of Northeast Asia. In: *Forest Vegetation of Northeast Asia* (J. Kolbek, M. Šrůtek, and E. O. Box, eds.), pp 51–91. Kluwer.

Rübel, E. 1930. *Pflanzengesellschaften der Erde*. Verlag Hans Huber, Berlin.

Sakai, A. and W. Larcher 1987. *Frost Survival of Plants: Responses and Adaptation to Freezing Stress*. Springer-Verlag, Berlin. 321pp.

Sasaki, K. 1991. [*Birth of Japanese History*]. Shuei-sha. 366pp (in Japanese).

Sasaki, K. 1993. [*Exploring the Substrate of Japanese Culture: Deciduous-Oak Culture and Laurel-Forest Culture*]. NHK Books. 253pp (in Japanese).

Sasaki, K. 1996. [Two Deciduous Oak zones in East Asia and Deciduous Oak Culture]. In: Proceedings, 88-year Memorial for Dr. N. Kokubu. 'Anthropology of People, Goods and Words' (M. Ryu, ed.), pp 317–330. Keiyu-sha (in Japanese).

Sasaki, K. 1998. [Deciduous oak forest culture considered: Cultural ecology in the cultural substrate of Northeast Asia]. In: [*Region, Culture and Farming Community*] (K. Sasaki, ed.), pp 311–348. Taimei-do (in Japanese).

Sasaki, Y. 1970. Versuch zur systematischen und geographischen Gliederung der japanischen Buchenwald-Gesellschaften. *Vegatatio*, 20:214–249.

Sasaki, Ya. 1984. [Phytosociological study of vegetation of Fagetea crenatae in western Japan. I. Phytosociological vegetation units]. *Social Science Review* (Saitama University Economics Laboratory), 53:129–181 (in Japanese).

Shimada, N. 1997. [A study of distribution of the summergreen secondary forests and their environmental factors in the northern Chūbu region, based on vegetation science]. Master Thesis, Yokohama National University. 16pp + figures and tables (in Japanese).

Song J.-S. 1988. [Phytosociological study of the mixed conifer and deciduous broad-leaved forests in South Korea]. *Hikobia*, 10: 145–156 (in Japanese).

Song J.-S., Roh K.-S., Chung H.-S., Song S.-D., K. Ohno and Y. Mochida 1999. [Phytosociology of the *Quercus* forests on Mts. Palgong, Kumo, and Hwangak in the city areas of Taegu, Kumi and Kimchon, Kyongpook province, Korea]. *Korean J. Environm. Ecology*, 13:220–233 (in Korean, with English abstract).

Song J.-S., Song S.-D., Park J.-H., Seo B.-B., Chung H.-S., Roh K.-S. and Kim I.-S. 1995. [A phytosociological study of *Quercus mongolica* forests on Mt. Sobaek by ordination and classification techniques]. *Korean J. Ecology*, 18:63–87 (in Korean, with English abstract).

Suzuki, S. 2001. [Phytosociological classification system of the *Quercus serrata* forests in Japan]. *Shokusei-gaku* [Vegetation Science],18:61–74 (in Japanese, with English synopsis).

Suzuki, S. 2002a. [Phytosociological study of summergreen broad-leaved forests in Japan]. Doctoral thesis, Yokohama National University. 139pp (in Japanese).

Suzuki, S. 2002b. [Phytosociological studies on the *Quercus mongolica* var. *grosseserrata* forests in comparison with *Quercus serrata* forests in Japan]. *Eco-Habitat*, 9(1):1–23 (in Japanese, with English synopsis).

Suzuki, S. 2006. [Review of the phytosociological vegetation units in the *Fagus japonica* forest in Japan, based on comparison of the related forest vegetation]. *Eco-Habitat*, 13(1):33–42 (in Japanese with English synopsis).

Suzuki, S., Y. Nakamura, K. Kawano, Wang X. and Da L. 2003. [Phytosociological study on the deciduous oak forests in eastern China]. *Eco-Habitat*, 10(1):85–103 (in Japanese, with English synopsis).

Suzuki, T. 1961. [Forest zones of Japan]. *Chiri* [Geography], 6: 1036–1043 (in Japanese).

Suzuki, T. 1966. [Preliminary system of Japanese natural communities]. *Jap. Soc. Forest Environm.*, 8(1):1–12 (in Japanese, with English abstract).

Takahashi, K. 1962. [Studies on vertical distribution of forest in middle Honshū]. *Bull. Forest Exp. Sta.*, 142:1–71 (in Japanese).

Takeda, Y., S. Uemura and S. Nakanishi 1983. [Phytosociological study of *Quercus mongolica* var. *grosseserrata* forests in Hokkaidō]. Acquisition of the Faculty of Education, Kōbe University 71:105–122 (in Japanese).

Takeda, Y., S. Nakanishi and Choe D. 1994. Phytosociological study on natural summergreen forests in Korea. *Ecological Research*, 9: 21–32.

Tanaka, J. 1887. [*Report on the Forest Zones of Japan*]. Ministry of Home Affairs, Tokyo. 176pp (in Japanese).

Tang Q. 2010. Phytosociological study of deciduous *Quercus* forest in the warm-temperate zone of China. Doctoral Thesis, Yokohama National University. 52pp.

Tang Q., K. Fujiwara and You H.-M. 2008. Warm-Temperate Deciduous *Quercus* Forest in China.In: Integrated Vegetation Mapping of Asia (K. Fujiwara, project leader), pp 114–123. Grant Report (see Fujiwara 2008).

Tang Q., K. Fujiwara and You H.-M. 2009. Phytosociological study of deciduous *Quercus* forest in the warm-temperate zone of China: Primary study of different kinds of *Quercus* communities. *Hikobia*, 15(3):311–322.

Tang Q., K. Fujiwara and You H.-M. 2015 (herein). Phytosociological study of *Quercus variabilis* forest in warm-temperate China. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Tatewaki, M. 1955. [Pan-mixed zone]. *Hoppō Ringyō* (Northern Forestry), 7(11):8–11 (in Japanese).

Tatewaki, M. 1958. [Forest ecology of the islands of the north Pacific Ocean]. *J. Facul. Agricul., Hokkaidō Univ.*, 50:371–486 + 50 plates (in Japanese).

Tohyama, M. and Y. Mochida 1978. [Vegetation of the deciduous broad-leaved forest of the eastern Iburi district in Hokkaidō, Japan]. In: Papers on Plant Ecology to the Memory of Dr. Kuniji Yoshioka, pp 134–149 (in Japanese).

Tsuji, S. 2001. [Vegetation-ecological study of *Quercus serrata* secondary forests in Japan]. Tokyo Vegetation Research Association (in Japanese).

Ushijima, S., 2007. [A phytosociological study on forest vegetation in Atami and its vicinity]. Master Thesis, Yokohama National University. 18pp plus tables and figures (in Japanese).

Wada, K. 1977. [Forest vegetation in the montane belt in Nagano Prefecture, central Japan, with special reference to the 'temperierter Ekoton']. *Bull. Bot. Soc. Nagano*, 10:90–96 (in Japanese).

Wada, K. 1982a. [Phytosociological studies on the summergreen forests in inland central Japan: I]. *J. Facult. Educ., Shinshū Univ.*, 20:1–39 (in Japanese, with English synopsis).

Wada, K. 1982b. [Phytosociological studies on the summergreen forests in inland central Japan: II]. *J. Facult. Educ. Shinshū Univ.*, 48:221–254 (in Japanese).

Walter, H. 1973. *Die Vegetation der Erde, in öko-physiologischer Betrachtung*. Vol. I: Die tropischen und subtropischen Zonen. 3rd ed. Gustav-Fischer-Verlag, Jena-Stuttgart. 744 pp.

Wang L. 2007. [Vegetation-ecological study of deciduous broad leaved forests in Heilongjiang Province, China]. Doctoral Thesis, Yokohama National University. 68pp (in Japanese).

Wang L., K. Fujiwara and You H.-M. 2006. A vegetation-ecological study of deciduous broad-leaved forests in Heilongjiang province, China: species composition, structure, distribution and phytosociological scheme. *Hikobia*, 14:431–457.

Wang Z.-X. and K. Fujiwara 2003. A preliminary vegetation study of *Fagus* forests in central China: species composition, structure and ecotypes. *J. Phytogeogr. Taxon.*, 51:137–157.

Wang Z.-X., K. Fujiwara and Lei Y. 2005. [Phytosociological study of the *Fagus lucida* forests and *Fagus engleriana* forests in China]. *J. Phytogeogr. Taxon.*, 53:43–65 (in Japanese, with English abstract).

Wang Z.-X., Lei Y. and K. Fujiwara 2006. Community classification, species composition, and regeneration of *Fagus lucida* forests in subtropical mountains, China. *Biodiversity Science*, 14:29–40.

Wu Zh.-Yi and committee (eds.) 1980, 1995. *Zhongguo Zhibei* [Vegetation of China]. Science Press, Beijing. 1375 pp + 339 B/W photos; 1382 pp + photos (in Chinese; Latin-Chinese species lists).

Wu Zh.-Yi and P. H. Raven (eds.) 1999. *Flora of China*. 4 vols. Science Press, Beijing. 374pp.

Yamanaka, T. 1969. [Study of secondary forest in southern Shikoku]. *Bull. Educ., Kōchi Univ*., 12:57–59 (in Japanese).

Yasuda, Y. 1984. [The Sea of Japan: Influences on the evolution of Japanese civilization and environment]. *Bull. Natnl. Museum of Ethnology*, 9(4):761–798 (in Japanese).

Yim Y.-J. 1977. Distribution of forest vegetation and climate in the Korean Peninsula. *Jap. J. Ecol*., 27:177-189, 269-278.

Yim Y.-J. 1995. Composition and Distribution of Deciduous Broad-Leaved Forests in Korea. In: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 273–298. Kluwer, Dordrecht.

Yim Y.-J. and T. Kira 1975-76. Distribution of forest vegetation and climate in the Korean Peninsula. Parts 1 and 2. *Jap. J. Ecol*., 25: 77-88, 26:157-164.

Yim Y.-J., Kim J.-U., Lee N.-J., Kim Y.-B. and Paek K.-S. 1990. Phytosogiological classification of plant communities on Mt. Halla National Park, Korea. *Korean J. Ecol*., 13(2):101–130.

Yoshioka, K. 1935. [Study of vegetation on Mt. Zao]. *Ecol. Research*, 1:107–116, 212–224, 327–338 (in Japanese).

Yoshioka, K. 1954a. [Forest community study, 4th report: Forests at the northern limit of *Castanopsis cuspidata* var. *sieboldii* forest]. *Seitai-Gakkai-Hō* [Ecological Research], 3:219–229 (in Japanese).

Yoshioka, K. 1954b. [Forest community study, 5th report: Forests at the northern limit of evergreen *Quercus* forests]. *Bull. Science, Fukushima University*, 12:57–59 (in Japanese).

You H.-M. 2001. [Vegetation-ecological Study of *Quercus mongolica* Forests in China]. Doctoral Thesis, Yokohama National University. 67pp (in Japanese).

You H.-M., K. Fujiwara and Tang Q. 2008. *Quercus liaotungensis* forest in China. In: Integrated Vegetation Mapping of Asia (K. Fujiwara, project leader), pp. 91–101. Report for Research Grant-In-Aid #16255003.

You H.-M., K. Fujiwara, Wu S.-J. and Wang X.-L. 2001. A preliminary vegetation-ecological study of *Quercus mongolica* forests in China. *J. Phytogeogr. Taxon*., 49:31–51.

Zhao Y.-Zh. and Tian H. 2001. [Taxonomic revision and floristic analysis of *Quercus* in Inner Mongolia]. *Inner Mongolia University Study Reports*, 32(4):470–472 (in Chinese).

Zhi-Rong, K. Fujiwara, K. Ohno and Zhao Y. 2010. [Phytosociological study of the *Quercus mongolica* forests in the Da Xing'an Ling, China]. *Eco-Habitat*, 17(1):59–79 (in Japanese with English synopsis).

Appendix 1. References of Table 1 and original syntaxonomical name.

No.	No. of relevés	References	Association/community	Original upper	
				suballiance	alliance
1	345	S. Suzuki 2002 (Table 8:8)	Castaneo-Quercetum crispulae Horikawa et Sasaki 1959		Fraxino-Quercion grosseserratae Ohba ex Wada 1982
		S. Suzuki 2002 (Table 8:9)	Pruno kinkiensis-Quercetum grosseserratae S. Suzuki 2002		Fraxino-Quercion grosseserratae Ohba ex Wada 1982
		S. Suzuki 2002 (Table 8:10)	Pruno pilosae-Quercetum serratae S. Suzuki in Miyawaki 1985		Fraxino-Quercion grosseserratae Ohba ex Wada 1982
		S. Suzuki 2002 (Table 8:11)	Lindero membranaceae-Quercetum mongolicae grosseserratae Ohba 1973		Fraxino-Quercion grosseserratae Ohba ex Wada 1982
		S. Suzuki 2002 (Table 8:12)	Magnolio borealis-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		S. Suzuki 2002 (Table 8:13)	Symploco pilosae-Quercetum grosseserratae S. Suzuki in Miyawaki 1987		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Hoshino 1998 (Table 14)	Cimicifugo acerinae-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Hoshino 1998 (Table 16)	Magnolio borealis-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Hoshino 1998 (Table 20)	Lonicero vidalii-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
2	163	S. Suzuki 2002 (Table 8:1)	Enkiantho sikokiani-Quercetum grosseserratae S. Suzuki 2002		Tsugion sieboldii Suz.-Tok. 1952
		S. Suzuki 2002 (Table 8:2)	Clethro-Quercetum crispulae Suz.-Tok., Arakane, Yamanaka, et Shono et al.		Tsugion sieboldii Suz.-Tok. 1952
		S. Suzuki 2002 (Table 8:3)	*Stewartia monadelpha-Quercus mongolica* var. *grosseserrata* community (S. Suzuki 2002)		Tsugion sieboldii Suz.-Tok. 1952
		S. Suzuki 2002 (Table 8:4)	Saso nipponicae-Quercetum grosseserratae A. Yamazaki in Miyawaki 1979		Pruno-Quercion mongolicae grosseseratae Wada 1982
		S. Suzuki 2002 (Table 8:5)	Aceri mono savatieri-Quercetum grosseserratae Hoshino 1998		Pruno-Quercion mongolicae grosseseratae Wada 1982
		S. Suzuki 2002 (Table 8:6)	Betulo-Quercetum grosseserratae Wada ex Hoshino 1998		Pruno-Quercion mongolicae grosseseratae Wada 1982
		S. Suzuki 2002 (Table 8:7)	Plenantho acerifoliae-Quercetum crispulae Maeda 1952		Pruno-Quercion mongolicae grosseseratae Wada 1982
		Hoshino 1998 (Table 18)	Aceri mono savatieri-Quercetum grosseserratae Hoshino 1998		Pruno-Quercion mongolicae grosseseratae Wada 1982
3	317	Hoshino 1998 (Table 8)	Carici longerostratae-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Hoshino 1998 (Table 10)	Sambucuso miquelii-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Hoshino 1998 (Table 12)	Astilbo congestae-Quercetum grosseserratae Hoshino 1998		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Takeda, Uemura and Nakanishi 1983 (Table 5)	Carpino-Quercetum grosseserratae Tohyama et Mochida 1978		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Takeda, Uemura and Nakanishi 1983 (Table 6)	Pachysandro-Quercetum grosseserratae Takeda, Uemura et Nakanishi 1983		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
		Takeda, Uemura and Nakanishi 1983 (Table 7)	Skimmio-Quercetum grosseserratae Takeda, Uemura et Nakanishi 1983		Carpino-Quercion grosseserratae Takeda, Uemura et Nakanishi 1983
4	57	Yim, Kim J.-W., Lee N.-J., Kim Y.-B. and Paek 1990 (Table 3)	Hepatico-Quercetum grosseserratae Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990		Acero-Quercion mongolicae Kim et Yim 1988
		Yim, Kim J.-W., Lee N.-J., Kim Y.-B. and Paek 1990 (Table 4)	Saso-Carpinetum laxiflorae Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990		Saso-Carpinion laxiflorae Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990
		Yim, Kim J.-W., Lee N.-J., Kim Y.-B. and Paek 1990 (Table 5)	Daphniphyllo-Carpinetum tschonoskii Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990		Saso-Carpinion laxiflorae Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990
		Yim, Kim J.-W., Lee N.-J., Kim Y.-B. and Paek 1990 (Table 6)	Asaro-Quercetum serratae Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990		Saso-Carpinion laxiflorae Yim, J.-W. Kim, N.-J. Lee, Y.-B. Kim et Paek 1990
5	118	S. Suzuki 2002 (Table 6: 8)	Quercetum dentato-serratae Wada 1982		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		Shimada 1997 (Table 3: 1-50)	Rhododendro japonici-Quercetum serratae Shimada, Fujiwara et A. Harada ass. nov		

Symbol of country: J: Japan, K: Korea, C: China, R: Russia

Phytosociological units		**Location**	**Country**
order	**class**		
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Japan Sea side of western Japan (Chugoku Region)	Japan
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Japan Sea side of western Japan (Kinki Region)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Japan Sea side of eastern Japan (Chubu, Kanto, Tohoku Regions)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Japan Sea side of eastern Japan (Chubu, Kanto, Tohoku Regions)	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Fagetea crenatae Miyawaki, Ohba et Murase 1964	northern Honshu (Tohoku Region)	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Fagetea crenatae Miyawaki, Ohba et Murase 1964	northern Honshu (Tohoku Region)	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Saso-Fagetea Suz.-Tok. 1966	north Honshu (Aomori, Iwate, Akita, Yamagata Prefectures)	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Saso-Fagetea Suz.-Tok. 1966	northern Honshu (Iwate Prefecture)	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Saso-Fagetea Suz.-Tok. 1966	Oki Island (Shimane Prefecture, Japan Sea side of western Japan)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	western central Japan (Kinki Region)	Japan
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Kyushu (southwestern Japan)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	western central Japan (Kinki Region)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	central Japan (Chubu Region)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	eastern central Japan (Kanto Region)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	central Japan (Kanto Region)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	central Japan (Chubu Region)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Saso-Fagetea Suz.-Tok. 1966	inland central Japan (Nagano, Yamanashi, Gunma, Tochigi, Fukushima Prefectures,	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Saso-Fagetea Suz.-Tok. 1966	Hokkaido (northern Japan)	Japan
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Saso-Fagetea Suz.-Tok. 1966	Hokkaido (northern Japan)	
Carpino cordatae-Quercetalia grosseserratae Hoshino 1998	Saso-Fagetea Suz.-Tok. 1966	Hokkaido (northern Japan)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Hokkaido (northern Japan)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Hokkaido (northern Japan)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Hokkaido (northern Japan)	
-	-	Mt. Halla, Cheju Island (southern Korea)	Korea
-	-	Mt. Halla, Cheju Island (southern Korea)	
-	-	Mt. Halla, Cheju Island (southern Korea)	
-	-	Mt. Halla, Cheju Island (southern Korea)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	inland central Japan (Nagano Prefecture)	Japan
		inland central Japan (Nagano Prefecture)	

Appendix 1 (continued)

No.	No. of relevés	References	Association/community	Original upper	
				suballiance	alliance
6	138	S. Suzuki 2002 (Table 6: 9)	Castaneo-Quercetum serratae Okutomi, Tsujii et Kodaira 1976		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		S. Suzuki 2002 (Table 6: 6)	Lindero sericeae-Quercetum serratae Ya. Sasaki 1984 in Miyawaki ex S. Suzuki 2001		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		Miyawaki, Fujiwara and Ishii 1994 (Table 16)	Castaneo-Quercetum serratae Okutomi, Tsujii et Kodaira 1976		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
7	589	S. Suzuki 2002 (Table 6: 1)	Daphno pseudomezerei-Quercetum serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		S. Suzuki 2002 (Table 6: 2)	Platycaryo-Quercetum serratae Itow 1981		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		S. Suzuki 2002 (Table 6: 7)	Quercetum acutissimo-serratae Miyawaki 1967		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		Fujiwara et al. 1997 (Table 12)	Quercetum acutissimo-serratae Miyawaki 1967		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		Hayashi 2000 (original data)			
		Ushijima 2007 (Table 3)	Daphno pseudomezerei-Quercetum serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971		
		Nakanishi 2004 (Table 4: A-E)	Quercetum acutissimo-serratae Miyawaki 1967		
		Nakanishi 2004 (Table 4: F,G)	Daphno pseudomezerei-Quercetum serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971		
		Hanazawa 2006 (original data)			
		Miyawaki et al. (original data)	-		-
8	191	S. Suzuki 2002 (Table 6: 3)	Quercetum variabilii-serratae Kobayashi, Muranaga et Takeda em. S. Suzuki in Miyawaki 1983		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		S. Suzuki 2002 (Table 6: 4)	Arundinario pygmaeae-Quercetum serratae Minamikawa et Yato 1962		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		Miyawaki et Ohno 1996 (Table 15: 5-16)	Arundinario pygmaeae-Quercetum serratae Minamikawa et Yato 1962		-
		Fujiwara et al. 1999 (Table 11)	Arundinario pygmaeae-Quercetum serratae Minamikawa et Yato 1962		Carpino-Quercion serratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971
		Ochiai 2006 (original data)	-		-
9	259	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 24)	Artemisio keiskeanae-Quercetum mongolicae Kim 1990	Lindero obtusilobae-Quercenion mongolicae Kim ex Krestov et al. 2006	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 25)	Saso borealis-Quercetum mongolicae Kim 1990	Lindero obtusilobae-Quercenion mongolicae Kim ex Krestov et al. 2006	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 27)	Lindero obtusilobae-Quercetum mongolicae Song et al. 1995	Lindero obtusilobae-Quercenion mongolicae Kim ex Krestov et al. 2006	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 28)	Staphylleo bumaldae-Quercetum serratae Kim 1990	Callicarpo japonicae-Quercenion serratae Kim 1990	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 29)	Meliosmo myrianthae-Quercetum serratae Kim 1990	Callicarpo japonicae-Quercenion serratae Kim 1990	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 30)	Lespedezo maximowiczii-Quercetum serratae Takeda et al. 1994	Callicarpo japonicae-Quercenion serratae Kim 1990	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 31)	Syneilesio palmatae-Quercetum serratae Song et al. 1999	Carpinenion laxiflorae-tschonoskii Kim ex Krestov et al. 2006	Lindero obtusilobae-Quercion mongolicae Kim 1990
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 32)	Carpinetum laxiflorae Kim et Yim 1986	Carpinenion laxiflorae-tschonoskii Kim ex Krestov et al. 2006	Lindero obtusilobae-Quercion mongolicae Kim 1990

Phytosociological units		**Location**	**Country**
order	**class**		
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	eastern Japan (Chubu, Kanto, Tohoku Regions)	Japan
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	southwestern Japan (Kyushu and Shikoku)	
Quercetalia serrata-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	northeastern Japan (Haramachi City in Fukushima Prefecture)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	coastal western half of Japan (Shikoku, Chugoku, Kinki, Kanto Regions)	Japan
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Kyushu (southwestern Japan)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Pacific side of western half of Japan (Kyushu, Shikoku, Chugoku, Kanto Regions)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Pacific side of east-central Japan (Iruma City in Saitama Prefecture)	
		Pacific side of east-central Japan (Izu Peninsula in Shizuoka Prefecture)	
		Pacific side of east-central Japan (Atami City in Shizuoka Prefecture)	
		Pacific side of east-central Japan (Kanagawa Prefecture)	
		Pacific side of east-central Japan (Kanagawa Prefecture)	
		Pacific side of east-central Japan (Kanagawa Prefecture)	
-	-	Pacific side of east-central Japan (Boso Peninsula in Chiba Prefecture)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	western half of Japan (Shikoku, Chugoku, Kinki, Chubu Regions)	Japan
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	central Japan (Kinki and Chubu Regions)	
-	-	Pacific central Japan (Kani City in Gifu Prefecture)	
Quercetalia serrato-grosseserratae Miyawaki, Fujiwara, H. Harada, Kusunoki et Okuda 1971	Fagetea crenatae Miyawaki, Ohba et Murase 1964	Pacific central Japan (Hisai City in Mie Prefecture)	
-	-	Pacific central Japan (Aichi, Gifu, Mie Prefectures)	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea, northern Korea	Korea
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea, northern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov et al. 2007	southern Korea	

Appendix 1 (continued)

No.	No. of relevés	References	Association/community	Original upper	
				suballiance	alliance
10	13	Tang 2010 (Table 9: C1-2-2)	Junipero formosanae-Quercetum variabilis ass. nov. Tang 2010		Lonicero standishii-Quercion variabilis all. nov. Tang 2010
		Tang 2010 (Table 9: C1-2-3)	Vitici negundo heterophyllae-Quercetum variabilis ass. nov. Tang 2010		Lonicero standishii-Quercion variabilis all. nov. Tang 2010
11	4	Tang 2010 (Table 9: C1-1-3)	*Rhododendron mariesii-Quercus variabilis* community Tang 2010		Carpino turczaninowii-Quercion variabilis all. nov. Tang 2010
12	36	Tang 2010 (Table 9: A-3)	*Quercus aliena-Quercus mongolica* community Tang 2010		-
		Tang 2010 (Table 9: C1-1-1)	Corno kousa chinensis-Quercetum variabilis Tang 2010		Carpino turczaninowii-Quercion variabilis all. nov. Tang 2010
		Tang 2010 (Table 9: C1-1-2)	*Quercus aliena* var. *acuteserrata* community Tang 2010		Carpino turczaninowii-Quercion variabilis all. nov. Tang 2010
		Tang 2010 (Table 9: C1-1-4)	*Melica radula-Quercus variabilis* community Tang 2010		Carpino turczaninowii-Quercion variabilis all. nov. Tang 2010
		You 2001 (Table 11: L)	*Quercus aliena-Quercus mongolica* community You 2001		Celtido koraiensis-Quercion mongolicae all. nov. You 2001
13	10	Tang 2010 (Table 9: C1-1-5)	Quercetum alienae-variabilis ass. nov. Tang 2010		Carpino turczaninowii-Quercion variabilis all. nov. Tang 2010
		Tang 2010 (Table 9: C1-3-2)	*Vitex negundo-Quercus variabilis* community Tang 2010		Pistacio chinensis-Quercion variabilis all. nov. Tang 2010
14	10	Tang 2010 (Table 9: C1-3-1)	Pteroceltio tatarinowii-Quercetum variabilis ass. nov. Tang 2010		Pistacio chinensis-Quercion variabilis all. nov. Tang 2010
15	10	Tang 2010 (Table 9: C1-3-3)	*Zelkova schneideriana-Quercus variabilis* community Tang 2010		Pistacio chinensis-Quercion variabilis all. nov. Tang 2010
		Tang 2010 (Table 9: C1-3-4)	Alangio chinense- Quercetum variabilis ass. nov. Tang 2010		Pistacio chinensis-Quercion variabilis all. nov. Tang 2010
16	26	S. Suzuki , Nakamura, Kawano, Wang X. and Da 2003 (Table 2: 10-23)	Quercetum variabili-fabri S. Suzuki , Nakamura, Kawano, X. Wang et Da. 2003		Quercion variabili-fabri S. Suzuki , Nakamura, Kawano, X. Wang et Da 2003
		You 2001 (Table 11: O)	*Stephanandra incisa-Quercus serrata* var. *brevipetiolata* community You 2001		-
		You 2001 (Table 11: P)	*Quercus fabri-Quercus acutissima* community You 2001		-
17	13	S. Suzuki, Nakamura, Kawano, Wang X. and Da 2003 (Table 2: 1-3)	*Syneilaris aconitifolia-Quercus glandulifera* var. *brevipetiolata* community S. Suzuki, et al. 2003		Quercion variabili-fabri S. Suzuki , Nakamura, Kawano, X. Wang et Da 2003
		S. Suzuki, Nakamura, Kawano, Wang X. and Da 2003 (Table 2: 4-9)	*Quercus chenii-Quercus fabri* community S. Suzuki, et al. 2003		Quercion variabili-fabri S. Suzuki , Nakamura, Kawano, X. Wang et Da 2003
		S. Suzuki , Nakamura, Kawano, Wang X. and Da 2003 (Table 3: 12)	*Dicranopteris dichotoma-Pinus massoniana* community		Quercion variabili-fabri S. Suzuki , Nakamura, Kawano, X. Wang et Da 2003
18	13	S. Suzuki , Nakamura, Kawano, Wang X. and Da 2003 (Table 1: 1-4)	Sasomorpho sinicae-Quercetum stewardii S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003		Sasamorpho sinicae-Quercion brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003
		S. Suzuki , Nakamura, Kawano, Wang X. and Da 2003 (Table 1: 5-13)	Quercetum brevipetiolata-acuteserratae S. Suzuki , Nakamura, Kawano, X. Wang et Da 2003		Sasamorpho sinicae-Quercion brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003
19	121	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 16)	Lychno cognatae-Quercetum mongolicae Kim 1990		Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda et al. 1994
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 17)	Veronico coreani-Quercetum mongolicae J.S. Song, S.D. Song, Park, Seo, Chung, Roh et I.S. Kim 1995		Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda et al. 1994
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 18)	Vaccinio koreani-Quercetum mongolicae Kim 1990		Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda et al. 1994
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 20)	Dryopterido crassirhizomae-Quercetum mongolicae Kim ex Krestov, J.-S. Song., Nakamura et Verkholat 2006		Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda et al. 1994
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 21)	Ainsliaeo acerifoliae-Quercetum mongolicae J.S. Song, S.D. Song, Park, Seo, Chung, Roh et I.S. Kim 1995		Rhododendro schlippenbachii-Quercion mongolicae Song ex Takeda et al. 1994

Phytosociological units		Location	Country
order	class		
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	southern Shaanxi	China
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	southern Shaanxi	
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	Henan	China
-	Quercetea mongolicae Song ex Krestov, J.-S. Song., Nakamura et Verkholat 2006	Shandong	China
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	Henan	
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	Henan	
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	Henan	
Tilio mandshuricae-Quercetalia mongolicae ord. nov. You 2001	Fraxino-Quercetae mongolicae class nov. You 2001	Shandong	
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	Henan	China
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	northern Henan	
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	Anhui	China
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	southern Jiangsu	China
Quercetalia variabilis ord. nov. Tang 2010	Quercetea variabilis class nov. Tang 2010	southeastern Henan	
Quercetalia fabri-brevipetiolatae S. Suzuki , Nakamura, Kawano, X. Wang et Da 2003	-	Anhui, Zhejiang, Jiangsu	China
-	-	Shandong	
-	-	Jiangsu	
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003	-	Anhui (Mt. Huangshan), Zhejiang (Mt. Tianmushan, Mt. Longwangshan)	China
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003	-	Anhui, Zhejiang	
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003	'-	-	
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003	'-	Anhui (Mt. Huangshan)	China
Quercetalia fabri-brevipetiolatae S. Suzuki, Nakamura, Kawano, X. Wang et Da 2003	'-	Zhejiang (Mt. Tianmushan)	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Korea, northern Korea	Korea
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Korea, northern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Korea	
Aceri pseudosieboldiani-Quercetalia mongolicae Song ex Takeda, Nakanishi et Choe 1994	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Korea	

Appendix 1 (continued)

No.	No. of relevés	References	Association/community	Original upper	
				suballiance	alliance
20	97	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 42)	Indigofero kirilowii-Quercetum mongolicae Ban, Takeda, Song, Nakagawa et Tan in Krestov, J.-S. Song, Nakamura et Verkholat 2006		Corylo heterophyllae-Quercion mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 44)	Gypsophyllo pacificae-Quercetum mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006		Corylo heterophyllae-Quercion mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 45)	Sophoro flavescentis-Quercetum mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006		Corylo heterophyllae-Quercion mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 46)	Lycopi lucidi-Quercetum mongolicum Krestov, J.-S. Song, Nakamura et Verkholat 2006		Corylo heterophyllae-Quercion mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006
21	118	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 47)	Campanulo glomeratae-Quercetum mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006		Dictamno dasycarpi-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 48)	Melico nutansi-Quercetum mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006		Dictamno dasycarpi-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 49)	Melampyroso setacei-Quercetum mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006		Dictamno dasycarpi-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 50)	Lespedezo bicoloris-Quercetum mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006		Dictamno dasycarpi-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
22	94	You 2001 (Table 11: B)	Festuco-Quercetum mongolicae You 2001 prov		Pino koraiensis-Quercion mongolicae Kim 1990
		You 2001 (Table 11: D)	Ulmo propinquae-Quercetum mongolicae You 2001 prov		Pino koraiensis-Quercion mongolicae Kim 1990
		You 2001 (Table 11: F)	*Aconitum raddeana-Quercus mongolica* community You 2001	Betulo-Quercenion mongolicae suball. nov. You 2001	Pino koraiensis-Quercion mongolicae Kim 1990
		You 2001 (Table 11: H)	*Weigela praecox-Quercus mongolica* community You 2001		Pino koraiensis-Quercion mongolicae Kim 1990
22	94	You 2001 (Table 11: I)	*Prunus mandshurica-Quercus mongolica* community		Celtido koraiensis-Quercion mongolicaeall. nov. You 2001
		Wang L., Fujiwara and You 2007 (Table 6)	*Carex callitrichos-Quercus mongolica* community Wang L., Fujiwara and You 2007		Corylo heterophyllae-Quercion mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006
23	115	You 2001 (Table 11: C)	*Fraxinus mandshurica-Quercus mongolica* community You 2001		Pino koraiensis-Quercion mongolicae Kim 1990
		Wang L., Fujiwara and You 2007 (Table 2)	*Berberis amurensis-Pinus koraiensis* community Wang L., Fujiwara and You 2007	Abieti nephrolepidis-Pinenon koraiensis all. Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat ex suball. nov. prov. Wang L., Fujiwara and You 2007	Tilio amurensis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Wang L., Fujiwara and You 2007 (Table 3)	*Acer mandshuricum-Acer mono* community Wang L., Fujiwara and You 2007	Brachybotryo-Acerenon mono suball. nov. prov. Wang L., Fujiwara and You 2007	Tilio amurensis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Wang L., Fujiwara and You 2007 (Table 4: 1-16)	*Lonicera ruprechtiana-Quercus mongolica* community Wang L., Fujiwara and You 2007	Brachybotryo-Acerenon mono suball. nov. prov. Wang L., Fujiwara and You 2007	Tilio amurensis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Wang L., Fujiwara and You 2007 (Table 4: 17-24)	*Spiraea ussuriensis-Quercus mongolica* community Wang L., Fujiwara and You 2007	Brachybotryo-Acerenon mono suball. nov. prov. Wang L., Fujiwara and You 2007	Tilio amurensis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Wang L., Fujiwara and You 2007 (Table 5: 1-7)	*Agrimonia pilosa-Populus davidiana* community Wang L., Fujiwara and You 2007	Brachybotryo-Acerenon mono suball. nov. prov. Wang L., Fujiwara and You 2007	Tilio amurensis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
24	31	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 5)	Spiraeo ussuriensis-Quercetum mongolicae Kim ex Krestov, J.-S. Song., Nakamura et Verkholat 2006		Tilio amurensis-Pinion koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 6)	Athyrio crenati-Pinetum koraiensis Kim ex Krestov, J.-S. Song., Nakamura et Verkholat 2006		Tilio amurensis-Pinion koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 7)	Tilio amurensis-Betuletum platyphyllae Kim ex Krestov, J.-S. Song., Nakamura et Verkholat 2006		Tilio amurensis-Pinion koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
25	24	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 1)	Carici callitrichoi-Pinetum koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006		Rhododendro daurici-Pinion koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 2)	Vaccinio vitis-idaeae-Pinetum koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006		Rhododendro daurici-Pinion koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006

Phytosociological units		**Location**	**Country**
order	**class**		
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	Liaoning	China & Russia
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	Hasan area	
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	Hanka, southern Sikhote-Alin	
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	southern Sikhote-Alin	
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	southern Sikhote-Alin	Russia
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	middle and southern Sikhote-Alin	
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	middle and southern Sikhote-Alin	
Lespedezo bicoloris-Quercetalia mongolicae Krestov, J.-S. Song, Nakamura et Verkholat 2006	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 2000	middle and southern Sikhote-Alin	
Tilio mandshuricae-Quercetalia mongolicae ord. nov. You 2001	Fraxino-Quercetae mongolicae class nov. You 2001	Heilongjiang (Xiao Xing'an Ling)	China
Tilio mandshuricae-Quercetalia mongolicae ord. nov. You 2001	Fraxino-Quercetae mongolicaeclass nov. You 2001	Heilongjiang (Jingbohu)	
Tilio mandshuricae-Quercetalia mongolicae ord. nov. You 2001	Fraxino-Quercetae mongolicaeclass nov. You 2001	Jilin	
Tilio mandshuricae-Quercetalia mongolicae ord. nov. You 2001	Fraxino-Quercetae mongolicaeclass nov. You 2001	Liaoning (Baishilazi natural reserve)	
Tilio mandshuricae-Quercetalia mongolicae ord. nov. You 2001	Fraxino-Quercetae mongolicae class nov. You 2001	Liaoning (Qianshan natural reserve)	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Heilongjiang, Jilin	
Tilio mandshuricae-Quercetalia mongolicae	Fraxino-Quercetae mongolicae class nov. You 2001	Heilongjiang (Maoershan forest station)	China
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Heilongjiang	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Heilongjiang	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Heilongjiang	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Heilongjiang	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Heilongjiang	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Changbai-Shan	China
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Changbai-Shan	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Changbai-Shan	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	middle and northern Sikhote-Alin	Russia
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	middle and northern Sikhote-Alin, south of Bureya highland	

Appendix 1 (continued)

No.	No. of relevés	References	Association/community	Original upper	
				suballiance	alliance
26	96	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 3)	Diplazio sibirici-Abietetum nephrolepidis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006		Abieti nephrolepidis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 4)	Lycopodio annotini-Abietum nephrolepidis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006		Abieti nephrolepidis-Pinion koraiensis Gumarova ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
27	104	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 8)	Carici falcatae-Pinetum koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006		Phrymo asiaticae-Pinion koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 9)	Ulmo japonicae-Pinetum koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006		Phrymo asiaticae-Pinion koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 10)	Arisaemo amurensae-Pinetum koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006		Phrymo asiaticae-Pinion koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 11)	Ribesi maximowicziani-Pinetum koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006		Phrymo asiaticae-Pinion koraiensis Krestov, J.-S. Song, Nakamura et Verkholat 2006
28	116	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 12)	Abieti holophyllae-Quercetum mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006		Jeffersonio-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 13)	Polysticho subtripteron-Pinetum koraiensis Gumarova et al. ex Krestov, J.-S. Song, Nakamura et Verkholat 2006		Jeffersonio-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 14)	Fraxino mandshurici-Abietetum holophyllae Gumarova et al. ex Krestov, J.-S. Song, Nakamura et Verkholat 2006		Jeffersonio-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 15)	*Taxus cuspidata -Carpinus cordata* community Krestov, Song J.-S., Nakamura and Verkholat 2006		Jeffersonio-Quercion mongolicae Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006
29	58	Zhi-Rong, Fujiwara, Ohno and Zhao 2010 (Table 2:A)	Aconito kusnezoffii-Quercetum mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010		Poo nemoralis-Quercion mongolicae Zhi-Rong et al. 2010
		Zhi-Rong, Fujiwara, Ohno and Zhao 2010 (Table 2:B)	Aconito umbrosi-Quercetum mongolicae Zhi-Rong, Fujiwara, Ohno		Poo nemoralis-Quercion mongolicae Zhi-Rong et al. 2010
		Zhi-Rong, Fujiwara, Ohno and Zhao 2010 (Table 2:C)	Artemisio vestitae-Quercetum mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010		Poo nemoralis-Quercion mongolicae Zhi-Rong et al. 2010
		Zhi-Rong, Fujiwara, Ohno and Zhao 2010 (Table 2:D)	Larici gmelinii-Quercetum mongolicae Zhi-Rong, Fujiwara, Ohno et Zhao 2010		Poo nemoralis-Quercion mongolicae Zhi-Rong et al. 2010
30	159	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 33)	Artemisio desertori-Betuletum davuricae Ermakov 1997	Paeonio lactiflorae-Betulenion davuricae Ermakov 1997	Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 34)	Geranio davuricae-Betuletum davuricae Ermakov 1997	Paeonio lactiflorae-Betulenion davuricae Ermakov 1997	Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 35)	Carici vanheurckii-Betuletum davuricae Ermakov et Petelin in Ermakov 1997	Paeonio lactiflorae-Betulenion davuricae Ermakov 1997	Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 36)	Galatello dahuricae-Betuletum platyphyllae Ermakov in Ermakov, Dring, et Rodwell 2000	Calamagrostio epigei-Pinenion sylvestris Ermakov in Ermakov, Dring, et Rodwell 2000	Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 37)	Oxytropido myriophyllae-Pinetum sylvestris Ermakov, Dring, et Rodwell 2000	Calamagrostio epigei-Pinenion sylvestris Ermakov in Ermakov, Dring, et Rodwell 2000	Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997
30	159	Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 38)	Bromopsido pumpellianae-Pinetum sylvestris Ermakov in Ermakov, Dring, et Rodwell 2000	Calamagrostio epigei-Pinenion sylvestris Ermakov in Ermakov, Dring, et Rodwell 2000	Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 39)	Veronicastro sibirici-Betuletum davuricae Ermakov 1997		Ligulario fischeri-Betulion davuricae Ermakov & Petelin in Ermakov, Dring, et Rodwell 2000
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 40)	Geranio vlassowiani-Laricetum gmelinii Ermakov 1997		Ligulario fischeri-Betulion davuricae Ermakov & Petelin in Ermakov, Dring, et Rodwell 2000
		Krestov, Song J.-S., Nakamura and Verkholat 2006 (Table 3: 41)	Aquilegio parviflorae-Quercetum mongolicae Ermakov et Petelin in Ermakov 1997		Ligulario fischeri-Betulion davuricae Ermakov & Petelin in Ermakov, Dring, et Rodwell 2000
31	18	Tang 2010 (Table 9: A1)	*Rhododendron micranthum-Quercus mongolica* community		-
		Tang 2010 (Table 9: A2)	*Fraxinus chinensis-Quercus mongolica* community		-
		You 2001 (Table 11:K)	*Myripnois dioica-Quercus mongolica* community You 2001		Typical alliance all. nov. You 2001

Phytosociological units		Location	Country
order	class		
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Sikhote-Alin	Russia
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Sikhote-Alin	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	northern Sikhote-Alin	Russia
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	middle Sikhote-Alin	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Sikhote-Alin	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Sikhote-Alin	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Sikhote-Alin, Changbai-Shan	Russia & China
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Sikhote-Alin	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	southern Sikhote-Alin	
Tilio amurensis-Pinetalia koraiensis Kim ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	islands of Peter the Great Bay	
Poo nemoralis-Quercetalia mongolicae Zhi-Rong et al. 2010	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Inner Mongolia (Da Xing'an Ling)	China
Poo nemoralis-Quercetalia mongolicae Zhi-Rong et al. 2010	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Inner Mongolia (Da Xing'an Ling)	
Poo nemoralis-Quercetalia mongolicae Zhi-Rong et al. 2010	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Inner Mongolia (Da Xing'an Ling)	
Poo nemoralis-Quercetalia mongolicae Zhi-Rong et al. 2010	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Inner Mongolia (Da Xing'an Ling)	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	Russia
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
Querco mongolicae-Betuletalia davuricae Ermakov 1997	Querco mongolicae-Betuletea davuricae Ermakov et Petelin in Ermakov 1997	Transbaikalia	
-	Quercetea mongolicae Song ex Krestov, J.-S. Song, Nakamura et Verkholat 2006	Beijing	China
-	Quercetea mongolicae Song ex Krestov, J.-S. Song., Nakamura et Verkholat 2006	Beijing	
Tilio mandshuricae-Quercetalia mongolicae	Fraxino-Quercetae mongolicae class nov. You 2001	Beijing	

Appendix 1 (continued)

No.	No. of relevés	References	Association/community	Original upper phytosociological units				Location	Country
				suballiance	alliance	order	class		
32	71	Tang 2010 (Table 9: B1-1-1)	Stephanandro incisa-Quercetum liaotungensis You et Fujiwara 2008 ex Tang 2010		Viburno schensiano-Quercion liaotungensis prov. You et al. 2008	Aceri ginnalae-Quercetalia liaotungensis prov. You et al. 2008	Quercetea liaotogensis prov. You et al. 2008	Gansu	China
		Tang 2010 (Table 9: B1-1-2)	Ajugo ciliatae-Quercetum liaotungensis Tang 2010		Viburno schensiano-Quercion liaotungensis prov. You et al. 2008	Aceri ginnalae-Quercetalia liaotungensis prov. You et al. 2008	Quercetea liaotogensis prov. You et al. 2008	Shaanxi	
		Tang 2010 (Table 9: B1-1-3)	Rubo parvifolius-Quercetum liaotungensis ass. nov. Tang 2010		Viburno schensiano-Quercion liaotungensis prov. You et al. 2008	Aceri ginnalae-Quercetalia liaotungensis prov. You et al. 2008	Quercetea liaotogensis prov. You et al. 2008	Shaanxi	
		Tang 2010 (Table 9: B1-1-4)	Ribes burejense-Quercetun liaotungensis You et Fujiwara 2008 ex		Viburno schensiano- Quercion liaotungensis prov. You et al. 2008	Aceri ginnalae- Quercetalia liaotungensis prov. You et al. 2008	Quercetea liaotogensis prov. You et al. 2008	Shanxi	
		Tang 2010 (Table 9: B2-1-1)	Aceri truncatum-Quercetum liaotungensis You et Fujiwara 2008 ex Tang 2010		Deutzio-Quercion liaotungensis prov. You et al. 2008	Deutzio parviflora-Quercetalia liaotungensis prov. You et al. 2008	Quercetea liaotogensis prov. You et al. 2008	Beijing	
		Tang 2010 (Table 9: B2-1-2)	*Artemisia gmelinii-Quercus liaotungensis* community Tang 2001		Deutzio-Quercion liaotungensis prov. You et al. 2008	Deutzio parviflora-Quercetalia liaotungensis prov. You et al. 2008	Quercetea liaotogensis prov. You et al. 2008	Beijing	
		You 2001 (Table 11: M)	*Mazus japonica-Quercus liaotungensis* community You 2001		-	'-	'-	Beijing	

Phytosociological Study of *Quercus variabilis* Forest in Warm-Temperate China

Tang Qian, Kazue Fujiwara, and You Hai-Mei

Abstract

Deciduous *Quercus* forest is a typical forest type in the warm-temperate zone of China (*sensu sinico*). Among different kinds of deciduous *Quercus* forest, *Quercus variabilis* forest is the important, major forest type in the southern part of this area. In order to clarify the phytosociological characteristics of *Q*. *variabilis* forest in warm-temperate China, this study surveyed 12 sites and recorded 54 relevés, using the Braun-Blanquet (1964) methodology (Fujiwara 1987, 1997); a syntaxonomical scheme for *Q*. *variabilis* forest was also made. The classification result showed that there were five communities, five associations grouped into three alliances, an order Quercetalia variabilis ord. nov. and the class Quercetea variabilis class. nov. This can be subdivided into: (1) a Lonicero standishii-Quercion variabilis all. nov., consisting of an *Acer grosseri*-*Quercus variabilis* comm. nov., a Junipero formosanae-Quercetum variabilis ass. nov., and a Vitici negundo heterophyllae-Quercetum variabilis ass. nov., on very poor soil over granite; (2) a Carpino turczaninowii-Quercion variabilis all. nov., composed of *Rhododendron mariesii* and *Melica radula* communities, and a Viburno mongolicae-Quercetum variabilis ass. nov., which can always be found at higher elevation on south-facing aspects; and (3) a Pistacio chinensis-Quercion variabilis all. nov., which includes a Pteroceltio tatarinowii-Quercetum variabilis ass. nov., an Alangio chinensis-Quercetum variabilis ass. nov., and *Vitex negundo* and *Zelkova schneideriana* communities, usually occurring on limestone at relatively low elevation. De-trended correspondence analysis (DCA) was performed to distinguish the spatial distribution characteristics of the different communities. The result showed that the communities classified are mostly related to elevation and climatic variables such as mean annual temperature, mean annual precipitation, and mean temperature of the warmest and coldest months. This indicates that, even within the same forest type, *Quercus variabilis* forest shows very different floristic composition and environmental characteristics across the warm-temperate zone of China.

T. Qian
College of Environment and Planning, Henan University, Kaifeng City,
Henan 475004, China

K. Fujiwara (✉)
Yokohama City University, Yokohama 236-0027, Japan
e-mail: kazue@ynu.ac.jp

Y. Hai-Mei
Institute of City and Environment, Jiangsu Normal University,
Shanghai Road 29, Tongshan County, Xuzhou City, Jiangsu 221116,
China

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*,
Geobotany Studies, DOI 10.1007/978-3-319-01261-2_4,

Keywords
Phytosociology • Ordination, Pistacio-Quercetalia variabilis • Quercetea brevipetiolatae-variabilis • Warm-temperate deciduous forests of China

1 Introduction

A deciduous broad-leaved forest, also called summergreen forest in the temperate zone, has very obvious physiognomy changes over the different seasons. Its annual cycle involves resuming growth in spring and summer, dropping leaves in autumn, and dormancy in winter. Deciduous genera such as oak, elm, maple and beech are representative trees in this kind of forest. Deciduous broad-leaved forests are widely developed in mid-latitude regions of the Northern Hemisphere, especially in eastern North America, western and central Europe, and in eastern Asia (Archibold 1994).

Menitsky (2005) suggests that 400–500 species of *Quercus* may be important forest-forming trees of the temperate latitudes of the Northern Hemisphere. Characteristic *Quercus* forest also occurs widely in eastern and northeastern China, especially in the climatic zone called *nuǎn wên* (暖温, = warm-warm), which the Chinese translate as warm-temperate but which ranges from 32°30’ up to 42°30′N latitude. Some *Quercus* species in this region are common to Korea and Japan. Moreover, deciduous *Quercus* forest is thought to be the representative, typical forest type of this climatic region (Wang 1935; Wu 1980).

Studies on vegetation-climate relationships in China can be traced back to the eleventh century BC (Fang et al. 2002), but vegetation-climatic zonation and regionalization have been a major focus of research mainly since World War II (Box 1995; Fang et al. 2002). Especially from the 1980s to the present, studies on vegetation-climatic zonation and regionalization in China have always been a hot issue and discussed by many scholars. Widely used climate classification systems, such as the Köppen climates (1936), the life zones of Holdridge (1947, 1967), the Thornthwaite classification (1948), and the eco-climate classification of Kira (1945), have been applied to discuss Chinese vegetation-climatic zonation and regionalization (Chang 1989; Fang and Yoda 1989; Fang 1991; Wang and Xiao 1993; Zhou and Zhang 1996). Some studies have also tried to find suitable climate indices for dividing vegetation-climate zones by themselves (Chen 1982; Zhu et al. 1984; Song 1999).

Zhu et al. (1984) classified the climate zones of China systematically and established the currently used classification, which was published as the ‘Climate’ volume in the series “Physical Geography of China”. Since then this system has been widely accepted by Chinese scholars. The Chinese climate system, however, is quite different from other widely used climate classification systems, such as those by Köppen (1936), Walter (1977) or Holdridge (1947, 1967). The largest difference versus these other systems is that the thermal zonation is not based on the climate of the full year but rather on the number of days with average daily temperature ≥10°C during the year. This $T \geq 10°$ index for daily temperature represents the threshold temperature for plant sprouting and is an important climate variable for forestry and agriculture, widely adopted by Chinese meteorologists (Zhu et al. 1984). Some other indices in this system include average temperature of the coldest and warmest months of the year; vegetation types were also considered. Synthesizing these indicators, Zhu et al. (1984) identified nine different climate zones in the climate classification system of China, recognizing ‘warm-temperate’ as one zone.

In China, the genus *Quercus* has about 53 species, including deciduous and evergreen (Peng et al. 2007), and they can be found in the temperate, warm-temperate and subtropical zones (*sensu sinico*). The warm-temperate zone is the best region for investigating and studying deciduous *Quercus* species and their forests because most of the major deciduous *Quercus* species of China can be found in this area, for example, *Q. liaotungensis, Q. mongolica, Q. dentata, Q. variabilis, Q. acutissima, Q. serrata* and its variant species *Q. serrata* var. *brevipetiolata* (= *Q. glandulifera* var. *brevipetiolata*), and *Q. aliena*, including its variant species *Q. aliena* var. *acuteserrata*.

Quercus variabilis (Chinese cork oak) is a major native deciduous oak species occurring widely in China, Japan, and Korea (Wu and Raven 1999). It can be recognized easily by its thick corky bark with deep fissures. Because of this characteristic and its good timber quality, *Q. variabilis* is always peeled for making cork or cut for use as building timber. This leads directly to wide areas of *Q. variabilis* forest being seriously damaged or lost completely, especially at lower elevation (Wu 1980; Li et al. 2006).

Q. variabilis forest is one of the stable, major forest types in the warm-temperate zone, occurring for example in Henan, Shaanxi, and Shandong provinces (Wu 1980). Of these areas, Henan is thought to be the center of distribution of *Q. variabilis* forest (Ye et al. 1993). *Q. variabilis* forest always occurs at elevations of 400–1,600 m but can also be found at higher elevation in the subtropical zone, even at 2,500 m in the southwestern subtropical area of China. In the subtropical zone, *Q. variabilis* grows mixed with evergreen species to form deciduous-evergreen mixed broad-leaved

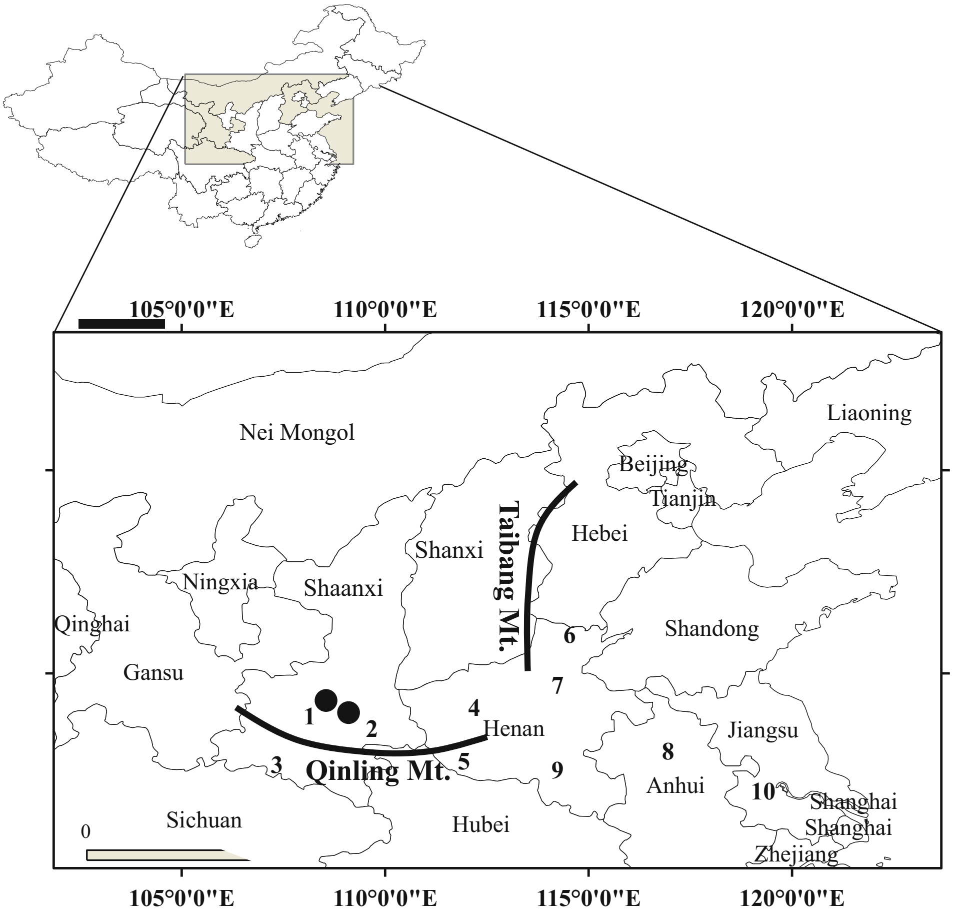


Fig. 1 Locations of study sites in warm-temperate China. *Solid circles* represent sites surveyed: 1 Louguantai NR, 2 Nanwutai NR, 3 Dingjun-shan NR, 4 Mt. Shirenshan, 5 Mt. Laojieling, 6–7 Mt. Yuntaishan, 8 Huangcangyu NR, 9 Mt. Jigongshan, 10 Mt. Maoshan (NR = nature reserve)

forest. This kind of forest, however, is thought to be a secondary forest type that developed after evergreen broad-leaved forests were destroyed (Wu 1980).

There have long been arguments about whether deciduous-evergreen mixed forest and evergreen broad-leaved forest in the northern subtropical zone of China should actually belong to the warm-temperate zone (Fang1991, 2001; Song 1999). The same arguments also exist in other East Asian countries. Kira (1945) pointed out that the warm-temperate zone (defined more globally) is also one of the basic climate zones in Japan. Although it is commonly believed that evergreen broad-leaved forest is the predominant, zonal forest type in the warm-temperate zone of Japan and other countries (Walter 1977; Greller 1989; Box 1995; Iwasa et al. 2003), deciduous broad-leaved forest can also be an important forest type in some parts of warm-temperate Japan (Kira 1971, 1977). *Q. variabilis* forest of China occurs in zones called warm-temperate and northern subtropical, and can also form deciduous-evergreen mixed forest in subtropical areas. Therefore, phytosociological study of *Q. variabilis* forest in the warm-temperate zone may provide a basis for resolving these arguments and understanding the division of vegetation zones of China.

Ecological study of *Q. variabilis* forest, a main type of deciduous *Quercus* forest in warm-temperate China, is very necessary and important. There have been a few studies on different aspects of *Q. variabilis* forest, for example, the spatial distribution pattern of *Q. variabilis* forest (Zhang et al. 2002; Han et al. 2005) and community structure and species composition or species diversity of *Q. variabilis* forest (Ye et al. 1993; Wu et al. 2004; Li et al. 2006). These studies, however, are all limited to small regions, and study of *Q. variabilis* forest over its whole range is rarely seen. Moreover, *Q. variabilis* forest also occurs in Japan and Korea. So understanding the different characteristics of *Q. variabilis* forest, in order to compare China with Japan and Korea, requires phytosociological study, a kind of study that has not been seen until now. Therefore, this chapter aims: (1) to classify plant community types of warm-temperate *Q. variabilis* forest by the Braun-Blanquet methodology and to describe the floristic composition of the communities classified; (2) to recognize the environmental limiting factors of different *Q. variabilis* communities by analyzing the relationships between plant communities and environmental variables; and (3) to compare with the *Q. variabilis* forest in subtropical China, to find the

Table 1 Climate data from some main weather stations in Eastern to Northern China

Location	Lat	Elev	Tmax	Tmin	Tabmin	Ty	WI	CI	MIy	Py
Nanjing	32.00	7	27.8	2.4	−13.1	15.8	129.4	−3.9	1.15	1050
Xinyang	32.08	115	27.4	2.2	−16.6	15.5	127.6	−3.9	1.24	1118
Hanzhong	33.04	510	25.2	2.4	−7.0	14.6	116.1	−4.1	0.99	835
Lushi	34.03	57	25.0	−0.9	−17.9	12.6	103.6	−13.5	0.86	639
Zhengzhou	34.43	110	27.0	0.1	−16.3	14.7	122.1	−9.9	0.75	634
Xuzhou	34.17	41	27.1	0.4	−12.8	14.8	123.1	−9.3	1.00	850
Xi'an	34.18	398	26.6	−0.1	−16.0	14.1	115.1	−11.9	0.69	560
Pingliang	35.33	1347	22.4	−5.3	−17.7	9.2	74.4	−28.3	0.85	480
Ji'nan	36.41	52	27.5	−0.4	−14.5	14.8	127.8	−11.4	0.80	691
Yan'an	36.36	959	23.1	−5.5	−21.4	10.3	87.3	−28.5	0.81	514
Taiyuan	37.47	778	23.4	−5.5	−22.7	10.0	89.0	−29.5	0.65	419
Beijing	39.48	31	26.2	−3.7	−18.3	12.7	108.5	−21.3	0.72	539

Lat latitude (°N), *Elev* elevation (m), *Tmax (Tmin)* mean temperature of warmest (coldest) month (°C), *Tabmin* absolute minimum temperature (°C, for 1978–2008), *Ty* mean annual temperature (°C), *WI (CI)* Kira's Warmth (Coldness) Index (°C · month), *MIy* annual moisture index (precipitation/potential evapotranspiration), *Py* mean annual precipitation (mm)

different characteristics of *Q. variabilis* forest in these two climatic zones.

2 Study Area

The study area ranges from 32°30′ to 42°30′N and from 103°30′ to 124°10′E (see Fig. 1). The Yellow Sea and Bohai Sea (inland sea of China) lie east of this study area, while mainland lies to the north, west and south. Temperate grassland approaches the northern part of this area, and the area of evergreen broad-leaved forest is to the south.

The climate of the study area is a temperate monsoon climate, which is hot and rainy in summer, but cold and dry in winter (see Table 1). Mean annual temperature is 8–14°C and the mean temperature of the coldest month (January) is −3 to −22°C, both of which are similar to ranges in the northeastern USA and in central to eastern Europe. The mean temperature of the warmest month (July) is much higher, though, at 24–28°C. The average annual precipitation ranges from 500 to 1,000 mm, increasing from west to east throughout the study area. The study sites further south are mainly under the influence of the subtropical monsoon climate. The mean annual temperature there is 13.5–16.5°C, the mean temperature of the coldest month (January) is 0–5°C, and the average annual precipitation ranges from 800 to 1,200 mm (Wu 1980). These values are similar to those in the interior southeastern USA (see climate data in the book Appendix).

Over the whole study area, topography varies from high mountains in the north and northwest to eastern hills and plains. The average elevation of the mountains in the north and northwest is over 1,500 m, and some high mountains can reach 3,000 m (e.g., Taibai-Shan, in Shaanxi). The Loess Plateau is also located in this study area, which has a mean elevation of 1,000–1,500 m. These highlands are the main locations for deciduous broad-leaved forest. In the east are mainly hills, including the Liaodong hills and Shandong hills, with mean altitudes less than 500 m. Deciduous forest can also be found in these hills, but most of these forests have been destroyed by human activities. Between the high mountains and eastern hills is the North China Plain (Huabei Plain), the second largest plain in China. The average altitude of this plain is less than 50 m. Some deciduous tree species can be found scattered on the plain.

Geographic conditions are complicated in this study area. Rock types differ in the major mountain areas, and soil conditions change with different rock types. In the southwest (Fig. 1), the Qinling Mountains trend east-west across Shaanxi and Henan; granite is the main rock type here, and the corresponding soil type is brown forest soil. In the limestone area of Anhui Province, however, under the influence of this substrate, limy soil is the major soil type. Yellow-brown soil is the typical soil type further south (southern part of Henan and Jiangsu).

3 Methods

The vegetation survey in the study area was performed from May to August in 2008 and 2009. Twelve study sites were surveyed and 54 relevés were recorded, by Braun-Blanquet methodology (Fujiwara 1987, 1997), within the area of the four provinces Shaanxi, Henan, Anhui and Jiangsu (Fig.1).

Table 2 Phytosociological table of *Quercus variabilis* forest in warm-temperate China

Group number	1															2													3																								4		
	1-1		1-2								1-3					2-1			2-2					2-3					3-1												3-3				3-4									
Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	48	46	47	48	49	50	51	52	53	54
Relevé (field number)	SCNW1	SCNW2	SZL1	SZL2	SZL3	SZL4	SZLX1	SZLX2	SZLX3	SZLX4	SMD1	SMD2	SMD3	SMD4	SMD5	HNN12	HNL1	HNL2	HNS5	HNS6	HNS7	HNS8	HNS9	HNJ2	HNJ3	HNJ5	HNJ6	HNJ7	AH1	AH2	AH3	AH4	AH5	AH6	AH7	AH8	CH5	CH9	CH10	CH11	JJM1	JJM2	JJM3	JJM4	HNXJ2	HNXJ3	HNXJ4	HNXJ5	HNXJ6	HNXJ7	HNXJ8	HNJ8	HNJ9	HNJ10
Altidude (m)	1210	1190	731	703	685	676	592	595	620	662	682	704	719	728	763	1320	975	1000	832	900	920	910	900	1000	1140	1130	997	982	276	221	182	192	215	203	133	100	55	110	150	180	125	122	150	149	333	346	362	354	568	482	450	468	488	451
Relevé size (m×m)	15×20	10×20	15×15	15×15	20×20	15×15	20×10	20×30	15×15	10×20	10×15	10×15	10×10	10×10	10×10	15×30	25×15	8×15	15×12	15×20	40×8	25×25	30×20	30×20	10×15	20×25	10×30	10×30	20×20	15×30	20×8	20×20	20×21	10×60	10×40	20×40	20×20	15×40	20×20	17×20	15×20	12×25	15×25	15×20	15×20	15×20	15×20	10×20	20×15	20×20	15×10	15×20	15×25	15×15
Aspect	SW	SW	N	NW	NW	NW	SE	NE	NW	NW	NE	NW	NW	NW	NW	SW	SW	NW	SE	SE	SW	SW	SE	SW	SE	SW	SE	SE	SE	W	NW	SE	SE	S	W	NW	NW	NE	SE	SE	SW	SW	NW	NW	SW	E	SE	SW	SE	SW	SW	SW	SW	SW
Slope (°)	40	40	34	29	32	28	15	15	25	30	23	19	24	20	26	25	35	30	0	36	36	60	37	18	20	25	18	20	25	20	10	10	15	25	25	15	7	3	24	34	21	22	28	36	28	35	20	30	22	23	23	30	32	30
Height of Tree layer T1 (m)	24	22	13	18	18	19	14	16	15	15	18	19	20	20	20	15	16	15	12	16	15	14	17	16	9	14	13	10	22	17	14	18	16	15	17	18	22	16	25	12	13	15	14	14	17	20	18	20	20	20	17	14	16	17
Cover of Tree layer T1 (%)	80	75	75	75	75	70	75	70	70	70	70	70	75	70	70	85	70	50	70	65	85	75	65	80	65	75	85	80	85	15	85	70	80	80	80	90	80	85	90	75	80	75	80	75	85	80	75	80	80	70	80	85	80	80
Height of Tree layer T2 (m)	14	12	8	8.5	10	10	7	8	8	8	10	12	10	13	12	9	9	8	7	6	7	8	9	8	-	8	5	7	14	10	10	10	10	9	12	10	8	10	12	7	7	10	10	6	11	13	12	11	12	12	10	9	10	8
Cover of Treelayer T2 (%)	20	10	5	15	10	15	10	15	15	30	8	8	15	20	15	25	25	70	25	40	15	20	40	15	-	25	20	30	20	20	25	30	30	25	8	20	5	3	10	20	25	15	10	15	25	10	30	20	10	30	30	15	5	10
Height of Shrub layer S (m)	6	7	3.5	3	4	4	3.5	3	4	3.5	4	4.5	4.5	4.5	5	3	3	1.5	2	1.5	2	2	2	3	4	3	2.5	2.5	5	4	4	2	3	2.5	2	2.5	4	2.5	5	3	2.5	4	4	1.5	4	6	4	5	6	5	4	3	3	2
Cover of Shrub layer S (%)	50	40	60	30	50	50	20	40	30	50	50	50	50	30	45	15	25	30	20	10	30	20	20	50	60	30	50	45	50	30	40	50	45	30	15	30	70	20	15	50	30	50	50	45	35	50	25	35	50	45	50	50	40	40
Height of Herb layer H (m)	0.8	0.8	0.6	0.6	0.4	0.8	0.8	0.8	0.6	0.8	0.6	0.8	0.9	0.8	0.8	0.5	0.4	0.5	0.8	0.6	0.4	0.4	0.5	0.6	0.3	0.6	0.4	0.3	0.3	0.4	0.6	0.5	0.5	0.3	0.3	0.4	0.5	0.6	0.5	0.4	0.4	0.6	0.6	0.4	0.8	0.8	0.6	0.6	0.6	0.7	0.8	0.6	0.5	0.5
Cover of Herb layer H (%)	15	20	10	15	10	10	15	15	20	8	25	30	35	20	25	10	20	15	20	20	10	10	15	20	10	30	20	15	5	30	50	25	25	10	85	45	10	75	15	25	50	50	35	75	20	15	30	10	30	20	60	10	10	5
Number of species	34	52	24	35	27	32	23	28	27	17	35	38	34	32	32	44	47	37	47	53	41	19	40	58	31	47	59	45	32	35	35	29	29	30	29	35	45	57	31	49	54	57	37	45	51	64	57	46	52	63	54	51	48	40
Differential species of *Acer grosseri-Quercus variabilis* community																																																						
Acer grosseri	+	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·
Rosa moyesii	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rubus parvifolius	+	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Rhododendron micranthum	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Hypericum przewalskii	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Diagnostic species of Junipero formosanae-Quercetum variabilis ass. nov.																																																						
Juniperus formosana	·	·	+	+	+	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viburnum schensianum	·	·	+	·	1	1	+	+	+	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cotoneaster zabelii	·	·	1	1	·	1	·	·	+	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sinarundinaria nitida	·	·	·	1	2	2	1	1	+	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Roegneria kamoji	·	·	·	+	1	+	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·
Picrasma quassioides	·	+	·	·	+	·	2	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Bothriospermum secundum	·	·	·	+	+	+	1	1	+	·	·	·	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
Cudrania tricuspidata	·	·	·	·	·	1	1	2	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	·	+	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·
Diagnostic species of Vitici negundo heterophyllae-Quercetum variabilis ass. nov.																																																						
Vitex negundo var. *heterophylla*	·	·	·	·	·	·	·	·	·	·	2	3	2	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhynchosia dielsii	·	·	·	·	·	·	·	·	·	·	1	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pyracantha fortuneana	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ficus heteromorpha	·	·	·	·	·	·	·	·	·	·	+	+	·	2	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
Zanthoxylum armatum	·	·	·	·	·	·	·	·	·	·	+	+	·	+	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rosa giraldii	·	·	·	·	·	·	·	·	·	·	+	+	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Epimedium grandiflorum	·	·	·	·	·	·	·	·	·	·	2	·	+	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Thalictrum shensiense	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cleistogenes chinensis	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cacalia ambigua	·	·	·	·	·	·	·	·	·	·	+	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Menispermum dauricum	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Diagnostic species of Lonicero standishii-Quercion variabilis all. nov.																																																						
Lonicera standishii	+	+	·	2	1	+	1	1	1	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus dentata	+	1	1	2	2	1	·	·	1	3	·	·	·	·	·	·	2	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Jasminum giraldii	·	·	·	·	+	·	2	1	+	+	1	+	+	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Mahonia fortunei	·	·	+	·	+	+	·	+	·	·	2	+	+	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vitis ficifolia	+	+	+	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus tabulaeformis	·	·	+	·	·	·	·	·	+	·	+	·	+	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Elaeagnus umbellata	·	·	·	·	·	·	+	+	·	·	+	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·
Differential species of *Rhododendron mariesii-Quercus variabilis* comm.																																																						
Rhododendron mariesii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Spiraea dasyantha	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus thunbergii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Differential species of *Melica radula-Quercus variabilis* comm.																																																						
Melica radula	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Deutzia parviflora	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Acer henryi	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·
Cercidiphyllum japonicum var. *sinense*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Meliosma cuneifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Diagnostic species of Viburno mongolicae-Quercetum alienae ass. nov.																																																						
Quercus aliena	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	3	1	1	3	1	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	1	+	·	+	·	·	·	·	·	·
Viburnum mongolicum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	+	+	1	1	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Crataegus cuneata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	+	·	+	·	·	·	·	·	·	·
Carex subpediformis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	2	2	3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Allium anisopodium	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Atractylodes macrocephala	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lespedeza pilosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Phyllanthus glaucus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
Rhamnus davurica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Clematis obtusidentata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·
Fraxinus bungeana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Zelkova sinica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·
Lonicera ferdinandii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	+	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhododendron molle	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	+	+	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Clematis obscura	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Sporobolus indicus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lilium concolor	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhamnus rugulosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Spiraea hirsuta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Syringa microphylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Diagnostic species of Carpino turczaninowii-Quercion variabilis all. nov.																																																						
Carpinus turczaninowii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	2	1	+	1	+	3	4	2	3	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Forsythia suspensa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	1	+	+	+	+	+	2	1	1	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+
Spiraea pubescens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	+	+	·	+	1	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·
Adenophora polyantha	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	+	+	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Quercus glandulifera var. *brevipetiolata*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	2	3	1	+	1	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	1	+	+	+	+	·	·	·
Symplocos paniculata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	+	·	2	+	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·
Sedum aizoon	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rubus phoenicolasius	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhus verniciflua	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Diagnostic species of Pteroceltido tatarinowii-Quercetum variabilis ass. nov.																																																						
Acer mono	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	1	·	+	·	·	·	·	·	+	+	1	1	1	3	1	1	2	2	·	+	+	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pteroceltis tatarinowii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	2	3	1	2	·	·	·	·	5	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celtis koraiensis	1	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	+	+	1	+	+	·	+	·	·	+	1	+	·	·	·	·	+	·	·	·	·	·	·	·	·	·
Viburnum macrocephalum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	+	+	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vitex negundo var. *cannabifolia*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	·	+	+	·	+	+	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·
Sinomenium acutum	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aristolochia mollissima	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	+	·	+	+	1	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aeluropus littoralis var. *sinensis*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Liriope platyphylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	·	·	·	·	+	·	·	+	1	·	·	·	·	·	·	·	·	·	·	·	·

(*continued*)

Table 2 (continued)

Differential species of *Zelkova schneideriana-Quercus variabilis* comm.																																																						
Zelkova schneideriana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	1	1	·	·	·	·	·	·	·	·	·	·
Phyllostachys bambusoides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	1	1	2	·	·	·	·	·	·	·	·	·	·
Parthenocissus tricuspidata	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	·	+	+	1	2	·	·	+	·	·	·	·	·	·	·
Celastrus angulatus	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	1	·	·	·	+	·	·	·	·	·	·
Berchemia floribunda	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	·	+	·	+	·	·	·	·	·	·	·	·
Punica granatum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·
Rubus lambertianus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·
Viburnum ichangense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·
Osmanthus cooperi	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·
Lygodium japonicum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	+	·	·	·	·	·	·	·	·	·	·
Acanthopanax divaricatus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·
Desmodium pedocarpum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·
Vitis romanetii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·
Pteris dispar	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	·	·	·	·	·	·	·	·	·	·	·	·
Rhynchosia volubilis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·
Serissa serissoides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·
Rubus coreanus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	·	·	·	·	·	·	·	·	·	·	·
Setaria plicata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·
Cryptotaenia japonica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·
Calystegia pellita	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·	·	·	·	·	·
Quercus gracilis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·
Diagnostic species of *Alangio chinensis-Quercetum variabilis* ass. nov.																																																						
Alangium chinense	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	1	+	2	·	·	·
Celtis pubescens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	+	+	1	2	1	·	·	·
Rhus sylvestris	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	1	1	+	+	·	·	·
Euonymus hamiltonianus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	+	+	+	·	·	·
Exochrda racemosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	+	+	+	+	·	·	·
Acer oliverianum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	1	+	1	2	·	·	·
Rubus corchorifolius	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	1	1	1	·	·	·
Parthenocissus heterophylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	+	3	1	2	·	·	·
Lindera chienii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	1	+	+	·	·	·
Malotus apelta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	+	+	+	·	·	·	·
Liliope platyphylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	+	·	·	·	·
Commelina communis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	·	+	·	·	·	·
Trachelospermum axillare	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·
Achyranthes bidentata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	+	+	·	·	+	·	·	·	·
Diospyros kaki	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	+	·	·	·
Pyrus serrulata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	·	·	·	·	·	·
Sorbus folgneri	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	+	·	·	·	·
Prunus serrulata var. *pubescens*	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	+	·	·	·	·
Pinus massoniana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	+	·	1	1	·	·	·	·	·
Castanea seguinii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	·	·
Prunus conadenia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	+	+	·	·	·
Camellia fraterna	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	+	·	·	·
Diagnostic species of *Trachelospermo jasminoidis-Quercion variabilis* all. nov.																																																						
Trachelospermum jasminoides	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	1	2	2	1	·	1	+	+	+	+	3	+	1	4	+	+	+	·	+	+	+	·	·	·
Aleurites fordii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	+	+	2	·	·	+	·	·	·	·	·	·	·	·	2	2	2	2	+	+	·	·	·	·
Rhamnus globosa	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	1	1	1	1	2	+	+	·	·	·	+	+	·	·	·	+	+	+	·	·	·	·	·	·	·
Celtis sinensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	+	·	·	2	·	·	·	·	+	+	·	·	·	·	·	·	·	·	+	·	·	·	+	·	·	·
Acer buergerianum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	+	1	+	·	·	·	·	+	1	1	·	·	·
Alangium platanifolium	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	1	2	1	·	·	·	·	·	+	·	·	·	·
Liriope spicata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	1	+	+	·	1	+	+	+	·	·	·	·	·	·	·	·	·	·
Smilax glauco-china	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	+	+	1	+	·	·	·
Liquidambar formosana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	3	·	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·	·
Ilex cornuta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	1	+	·	·	·	·	·	·	·	·	·	·	·
Differential species of *Vitex negundo-Quercus variabilis* comm.																																																						
Vitex negundo	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	3	2	1
Aconitum henryi	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	+
Diospyros lotus	+	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	2	1	·	2	2	1
Parthenocissus himalayana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	+
Vitis amurensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Artemisia shangnanensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	+	+	+
Rabdosia inflexa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Asparagus schoberioides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Thalictrum przewalskii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Thalictrum przewalskii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Gleditsia heterophylla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·
Stephania tetrandra	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Rhamnus parvifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+
Liliope minor	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Amorpha fruticosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+
Juglans regia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+
Diagnostic species of *Pistacio chinensis-Quercetalia variabilis* ord. nov. and *Quercetea variabilii-brevipetiolatae* class. nov.																																																						
Quercus variabilis	5	5	4	4	4	5	5	5	5	4	4	4	5	4	4	4	3	3	4	4	5	5	4	3	3	4	3	4	4	3	3	3	3	3	4	4	5	5	+	1	4	3	4	4	4	4	4	4	5	4	5	5	5	5
Grewia biloba var. *parviflora*	+	+	2	2	1	1	+	3	2	1	+	+	+	+	1	·	·	·	·	+	+	·	·	+	·	·	·	·	+	+	2	+	+	·	·	·	·	2	·	1	+	·	+	+	+	+	+	+	+	·	·	1	1	1
Dalbergia hupeana	·	·	·	·	·	·	+	+	·	+	1	·	2	+	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	+	+	1	·	·	1	·	+	·	·	·	+	1	+	+	+	1	·	·	·
Platycarya strobilacea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	+	·	·	+	+	+	+	+	1	2	·	·	·
Pistacia chinensis	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	+	·	·	·	+	·	·	·	·	1	1	1	2	1	2	2	2	+	·	·	2	1	+	1	+	2	3	2	2	+	2	+	2	2	1
Aster ageratoides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	1	+	·	·	+	+	+	+	1	·	+	+	·	·	·	·	·	·	+	+	·	1	·	+	+	·	·	1	+	·	+	+	+	·	+	·
Lindera glauca	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·	·	3	2	1	+	2	2	·	3	+	+	·	2	2	2	3	1	1	1	1	2	2	2	+	·	·	·
Cotinus coggygria var. *pubescens*	2	+	2	+	1	2	·	+	+	2	·	·	·	·	·	·	·	·	+	+	+	+	+	+	1	+	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Ligustrum quihoui	·	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	+	·	·	·	·	+	1	1	+	·	+	+	·	·	·
Rhus chinensis	+	+	·	·	·	+	·	·	·	·	·	+	1	·	·	+	+	+	·	+	+	+	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·
Koelreuteria paniculata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	+	+	+	·	2	·	·	·	·	·	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	+	·	1
Quercus acutissima	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Celtis biondii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	+	1	+	·	·	·	·	·	·	·	·	+	+
Other species																																																						
Oplismenus undulatifolius	·	+	·	2	·	1	·	+	·	·	+	+	+	+	2	·	·	·	+	1	+	·	+	+	·	·	·	·	+	+	1	+	+	1	4	3	+	1	2	1	1	2	1	1	+	+	1	+	+	+	+	+	+	+
Euonymus alatus	1	+	1	+	·	+	+	+	1	1	·	·	·	·	·	·	·	·	+	+	2	2	+	·	·	·	·	·	+	+	·	·	+	·	+	·	+	·	·	+	+	1	+	+	1	+	1	+	·	+	+	·	·	·
Smilax china	·	·	+	+	+	+	+	·	·	·	+	+	+	+	+	·	·	·	·	·	·	·	+	+	+	+	·	·	+	1	2	+	+	+	2	2	·	1	+	+	+	+	1	+	·	+	·	·	·	·	·	·	·	+
Polygonatum odoratum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	·	+	+	+	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	+	·	+	·
Lespedeza bicolor	1	+	+	·	+	+	·	·	+	1	·	+	+	+	·	·	+	+	+	·	+	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rubia cordifolia	+	·	·	+	+	·	·	·	·	·	·	+	·	+	+	·	·	·	·	·	·	·	·	+	+	+	+	+	·	·	·	·	·	·	·	·	·	+	·	+	1	·	·	+	+	+	+	+	·	+	·	+	+	+
Akebia trifoliata	+	·	+	+	+	+	+	+	+	·	·	·	·	+	·	·	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	2	+	+	+	+	+	+	·	+
Solanum lyratum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	+	·	+	·	·	·	·	·	·
Elaeagnus pungens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	+	+	+	+	+	+	·	·	·	·	·	·
Carex lanceolata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	2	·	+	1	·	+	·	·	·	·	·	·	·	·	·	+	·	2	+	+	4	·	1	·	·	·	·	·	+	·	·	·	·	·	·	·	·
Polygonatum sibiricum	·	+	+	+	·	+	·	·	·	·	·	·	·	·	·	+	+	·	+	+	·	·	·	+	·	+	+	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	+	+	+	+	·
Viburnum betulifolium	1	+	1	+	·	+	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ligustrum guihoui	1	·	1	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·
Corylus sieboldiana var. *mandshurica*	1	+	·	·	·	·	·	·	·	·	·	1	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Viola collina	·	·	·	·	·	·	·	·	·	·	+	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dioscorea nipponica	+	·	·	+	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	+	·	·	+	+	·	·	·	·	·	·	·	+	·	·	·	·	·	+	·	·	·	+	+	+	·	·	·	·	·	·
Rubus swinhoei	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dendranthema indicum	+	+	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	·	·	+	+	+	+	·	·	·	·	·	·	+	+	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ophiopogon japonicus	·	·	·	·	·	·	+	+	+	+	+	+	+	+	+	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	·	·	+
Spodiopogon sibiricus	+	1	·	·	·	·	·	·	·	·	·	1	·	2	·	1	+	·	·	+	+	+	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Paederia scandens	·	+	·	·	+	+	·	·	·	·	+	+	+	·	·	·	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	1	+	·	1	+	·	·	+	1	+	·	·	·	·
Deyeuxia arundinacea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	+	+	+	·	+	+	1	1	·	·	+	1	·	·	·	·	+	·	·	·	·	·	·	·	·	1	·	·	·	·	·	+	+	·	·
Clematis florida	·	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	1	+	+	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+
Adenophora trachelioides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	·	+	·	·	+	+	+	+	+	+	·	·	·	·	·	·	+	·	·	1	·	+	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Lespedeza formosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	1	+	·	·	·	·	·	·	·	·	+	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	·
Celastrus orbiculatus	·	+	·	·	·	+	·	+	+	·	·	·	·	+	·	+	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·
Viola variegata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	+	·	+	1	+	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Cyrtomium fortunei	·	·	·	·	·	·	·	·	·	·	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	+	+	·	+	·	·	+	·	·	·	·
Pteridium aquilinum var. *latiusculum*	+	+	·	+	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·	·	·	·	·	·

(*continued*)

Table 2 (continued)

Smilax sieboldii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	+	.	.	.	.	+	+	+
Syneilesis aconitifolia	.	+	.	+	+	+	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster tataricus	.	.	.	+	.	.	+	+	+	.	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Smilax stans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	+	+	.	.
Fraxinus chinensis var. *rhynchophylla*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+	.	+	.
Aristolochia debilis	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dioscorea bulbifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.	.	.	.	.
Indigofera bungeana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+
Morus alba	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	1	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salvia miltiorrhiza	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	+	.	.
Schisandra chinensis	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Schisandra sphenanthera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Vitis adstricta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	.	.
Adenophora elata	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ajuga ciliata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.
Broussonetia papyrifera	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Cephalanthera longifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.
Cynanchum versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Kalopanax pictus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	.	.	.	.	.	.	.	.	.	.
Leibnitzia anandria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla fragarioides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.	.
Wisteria sinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	.	+	+	.	.	.	.
Acer ginnala	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	2	.	+	.	.	.	.	.	.
Albizzia kalkora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	1	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.
Cornus walteri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Prunus sibirica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Sanguisorba officinalis	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antenoron filiforme	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	+	.	.	+	.	.	.	.
Asparagus cochinchinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Berchemia giraldiana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Carpesium cernuum	.	+	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Celtis bungeana	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dioscorea opposita	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Patrinia heterophylla	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunus davidiana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Firmiana simplex	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhus potaninii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Asparagus filicinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.
Berberis henryana	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Boehmeria nivea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	+	.	.	.
Carex sp1.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clematis kirilowii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crataegus pinnatifida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynanchum mooreanum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Discocleidion rufescens	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Disporum sessile	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Euphorbia helioscopia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gynostemma pentaphyllum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.	.	.
Humulus scandens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Melia azedarach	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Morus cathayana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.
Muhlenbergia hugelii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Peucedanum terebinthaceum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonatum verticillatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pueraria lobata	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Pyrrosia petiolosa	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrus betulaefolia	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhamnus bungeana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	+	.	.	.
Rhamnus utilis	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Speranskia tuberculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Spergularia marina	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viburnum dilatatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.
Tilia amurensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia unijuga	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola acuminata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.
Zanthoxylum planispinum	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Ixeris denticulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Liriope spicata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	+	.	.	.	.	.	.
Tilia miqueliana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cymbidium goeringii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.

Quercetalia variabilis ord. nov. & Quercetea variabilis class. nov.
1: Lonicero standishii-Quercion variabilis all. nov.3: Pistacio chinensis-Quercion variabilis all. nov.
1-1: *Acer grosseri-Quercus variabilis* community
1-2: Junipero formosanae-Quercetum variabilis ass. nov.
1-3: Vitici negundo heterophyllae-Quercetum variabilis ass. nov.
2: Carpino turczaninowii-Quercion variabilis all. nov.
2-1: *Rhododendron mariesii-Quercus variabilis* comm.
2-2: *Melica radula-Quercus variabilis* comm.
2-3: Viburno mongolicae-Quercetum alienae ass. nov.
3-1: Pteroceltino tatarinowii-Quercetum variabilis ass. nov.
3-2: *Zelkova schneideriana-Quercus variabilis* comm.
3-3: Alangio chinensis-Quercetum variabilis ass. nov.
4: *Vitex negundo-Quercus variabilis* comm.

Additional species occurring two times: *Atractylodeschinensis* in relevé reference no. 1−+, no. 2−+; *Cynanchumwilfordii* no. 1−+, no. 8−+; *Benthamidia japonica* var. *chinensis* no. 2−+, no. 16-1; *Cunninghamialanceolata* no. 2−+, no. 43-1; *Eupatorium japonicum* no. 2−+, no. 4−+; *Indigoferaamblyantha* no. 2−+, no. 5−+; *Thladianthaoliveri* no. 2−+, no. 6−+; *Pinusarmandii* no. 2−+, no. 16−+; *Vitispiasezkii* no. 2−+, no. 26−+; *Juglanscathayensis* no.2−+, no. 48−+; *Prunustomentosa* no.2−+, no. 40−+; *Neilliathyrsiflora* no. 3-2, no. 4−+; *Cynanchumauriculatum* no. 3−+, no. 14−+; *Spiraeafritschiana* no. 4−+, no. 13−+; *Zizyphusjujuba var. spinosa* no. 7−+, no. 9−+; *Adenophorawawreana* no. 8−+, no. 28−+; *Calamagrostisepigejos* no. 8-2, no. 9-2; *Rubuspalmatus*no.9−+, no. 16−+; *Lespedeza cyrtobotrya* no. 9−+, no. 25−+; *Elatostemainvolucrata* no. 11−+, no. 12−+; *Viola phalacrocarpa* no. 11−+, no. 12−+; *Polystichumtsus-simense* no. 11−+, no. 15−+; *Caesalpiniasepiaria*no. 12-1, no. 13-1; *Sageretiasubcaudata* no. 14−+, no. 15; *Cephalantheraerecta* no. 16−+, no. 20−+; *Artemisia annua* no.17−+, no. 18−+, *Chimaphila japonica* no. 17−+, no. 18−+; *Deyeuxiasinelatior* no. 17−+, no. 18−+; *Pyrolaincarnata* no. 17−+, no. 18−+; *Melampyrumroseum*no.17−+, no. 19−+; *Corylusheterophylla* no.17−+, no. 36-2; *Doellingeriascaber* no. 17−+, no. 27−+; 24−+, no. 26−+; *Andrachnechinensis* no. 19−+, no. 20−+; *Artemisia apiacea* no. 19−+, no. 20−+; *Athyriumyokoscense* no.19−+, no. 23−+; *Smilax discotis* no. 19−+, no. 21−+; *Cleistogeneshackelii* no.19−+, no. 40−+, *Potentillafreyniana* no. 20-1, no. 23−+; *Fragariaorientalis* no. 21−+, no. 22−+; *Cocculustrilobus* no. 23−+, no. 50−+,*Carpesium* sp. no. *Euphorbia pekinensis* no. 24−+, no. 27-1; *Pertyasinensis* no. 24−+, no. 28−+; *Lespedeza chinensis* no. 24−+, no. 38−+; *Styraxobassia* no. 24−+, 53−+; *Adenophoratetraphylla* no. 24−+, no. 28−+; *Galiumbungei* no. 24−+, no. 53−+; *Bupleurumscorzonerifolium* no. 25−+, no. 26−+; *Platycladusorientalis* no. 25−+, no. 28−+; *Bupleurumchinensis* no. 26−+, no. 29−+; *Iris ruthenica* no. 27−+, no. 28−+; *Hemerocallisfulva* no. 27−+, no. 37−+; *Spiraeatrilobata* no. 27−+, no. 54−+; *Maianthemumbifolium* no. 29−+, no. 30−+; *Morusaustralis* no. 29−+, no. 34-1; *Geranium wilfordii*no. 30−+, no. 39−+; *Albiziajulibrissin* no.31−+, no. 53−+; *Kalimerisindica* no. 33−+,no. 36−+; *Diospyros kaki* var. *sylvestris* no. 37−+, no. 40−+; *Carex*sp. 3: no. 38−+, no. 40−+; *Ixerisdentata* no. 38−+, no. 40−+; *Microstegiumvimineum* no. 38−+, no.40−+; *Chrysanthemum indicum* no. 38−+, no. 40−+; *Ajugadecumbens* no.39−+, no. 40−+; *Viola betonicifolia* ssp. *nepalensis* no. 39−+, no. 40−+; *Roegneriahybrida* no. 39-1,no. 40−+; *Lonicerafragrantissima* no. 39−+, no. 45−+; *Thladianthaclubia*no. 45−+, no. 47−+; *Fortunneariasinensis* no.46−+, no. 48−+; *Gynostemmapentaphylla* no. 46−+, no.47−+; *Albiziakolkara* no. 47−+, no. 49−+; *Paederiascandens* no. 47−+, no. 51; *Cyclobalanopsisglauca* no.48−+, no 49−+; *Lactucatriangulata* no. 49−+,no.50−+; *Rosa cymosa* no. 49−+, no. 51−+; *Styraxdasyantha* no. 50−+, no.51−+; *Prunus japonica* no.50−+, no. 51-1; *Dryopterischinensis* no. 50−+, no. 49−+

Additional species occurring once in relevé no. 1: *Litseaszechuanica*+, Carpinuscordata +, *Ailanthus altissima*+, *Spiraeawilsonii*+, *Rubusbiflorus* +, *Populusdavidiana* +; in no. 2: *Leontopodiumleontopodioides*+, *Litseapungens*+, *Sedum erythrostictum*+, *Rubiaovatifolia* +, *Sambucuswilliamsii*+, *Aesculuschinensis* +; in no. 3: *Rosa xanthina* +, *Cercischinensis*+; *Acer truncatum*1; in 4: *Spiraeasericea* +, *Saussureaamara* +, *Dictamnusdasycarpus*+; in no. 8: D*esmodiumracemosum* +, in no. 11: *Coriariasinica*1, *Robiniapseudoacacia*+, *Pterisvittata* +, *Selaginellatamariscina* +, *Viciagigantea*+; in 12: in no. Sa*lix caprea*+; in no. 13: *Elsholtziaciliata* +, *Dryopterisshensicola*+; in no. 14: *Elaeagnuslanceolata* +, *Parthenocissushenryana*+; in no. 15: *Athyriumpachyphlebium* +, *Abeliaengleriana*+; in no. 16: *Acer griseum*+, *Adenophorapetiolata* +, *Broussonetiakazinoki*+,*Malusbaccata*+, *Malusprunifolia*+, *Lespedeza buergeri*+, *Fragariachinensis*+, *Styraxhemsleyana*+, *Pyrolarotundifolia*+, *Pterocaryahupehensis*+, *Styraxjaponicus*+; in no. 17: *Saussureacordifolia*+, G*naphalium affine* +, *Liriope minor* +, *Lysimachiaclethroides* +; in no. 18: '*Atractylodeslancea*'+, *Carexbreviaristata* +, *Prunuscanescens*+,*Thalictrumhonanense* +, *Quercus aliena*var. *acuteserrata*1; in 19: *Bothriospermumchinens*+,*Caryacathayensis*1, *Chenopodiumglaucum*+, *Thalictrumaquilegifolium* var. *sibiricum*+, *Viola selkirki*+, *Periplocasepium*+, *Daphne genkwa*+, *Clematis heracleifolia* +, C*orydalis pallida*1, *Cotoneaster submultiflorus*+; in no. 20: *Clematis lasiandra* +, *Fraxinuschinensis*+; in no. 21: *Sorbuspohuashanensis*+, *Patriniascabiosaefolia* +, *Viola verecunda*+, *Dracocephalumrupestre*+; in no. 23: *Catalpa bungei*+, *Celosia argentea*+, *Deutzia discolor* +; in no. 24: *Celtis* sp. +, *Deyeuxia* sp. 1, *Saussureadeltoidea*+, *Peucedanumpraeruptorum* +, *Syneilesis* sp. +,*Potentilla* sp. +, *Viola patrinii*+, *Viola patrinii*+; in no. 26: *Asparagus trichophyllus*+, *Saposhnikoviadivaricata* +, *Zelkovaserrata* +, *Cynanchuminamoenum*+, *Dendranthemazawadskii*+; in no. 27: *Clematis peterae*+,*Crataeguswilsonii*+, *Dendranthemagrandiflorum*+, *Synurusdeltoides*+, *Viola mandshurica*+, *Vitisbryoniaefolia* +, *Lonicerachrysantha* +, *Euonymus porphyreus*+; in no. 28: *Deutzia grandiflora*+, *Ribesgiraldii*+, *Saussureadutaillyana*+; in no. 29: *Arisaemaconsanguineum*+, *Equisetum arvense* +; in no. 30: *Bidensbipinnata*+, *Osmorhizaaristata* +, *Taraxacummongolicum*+, *Changnieniaamoena*+; in no. 33: A*rtemisia lavandulaefolia*+, *Patriniasinensis*+,*Desmodiumheterocarpum*+,*Hemerocallislilioasphodelus*+, *Indigoferakirilowii*+; in no. 35: *Metaplexis japonica* +; in no. 36: *Plectranthusmacrocalyx*2, *Potentillacentigrana* 2, *Prunusverecunda*+, *Euonymus bungeanus*+, *Sorbusalnifolia*+, *Spiranthessinensis*+; in no. 37: *Serissafoetida*1,*Deyeuxiasylvatica*1, *Kalopanaxseptemlobus*+,*Osmanthusfragrans*+, *Photiniaserrulata*+, *Ehretiathyrsiflosa*+, *Eupatorium lindeyanum* +, *Ulmuspumila* +, *Carexsendaica*+, *Aphanantheaspera*+, *Ampelopsis* sp. +, *Quercus fabri*+, *Desmodiumcandatum*+; in no. 38: *Cleistogenes 'hancei*3, *Artemisia anomala*1, *Scutellariaindica*+, *Desmodiumsinuatum*+, *Aster fastigiatus*+, *Carex* sp. 2 +, P*eucedanumwawrii*+, *Ixerisgraminea*+, *Loniceramaackii* +, *Lactuca*sp. 1 +, *Artemisia mongolia*+, *Themedatriandra*var. *japonica* +,*Seneciokirilowii* +,*Lithospermumzollingeri*+, *Smilax glabra*+, *Chrysanthemum boreale* +, *Eccoilopuscotulifer*+; in no. 39: *Ulmusparvifolia* +, *Clematis ganpiniana*+, *Chenopodiumganpiniana* +, *Phrymaleptostachya* var.*asiatica*+,*Gramineae* sp. +; in no. 40: *Carexhumilis*3, *Polygonatumofficinalis*1, *Lonicera* sp. 1 +, *Cornus* sp. +, *Artemisia princeps* +, *Scillascilloides*+, *Orchidaceae* sp. +, *Allium tenuissimum*+; in no. 41: *Cayratis japonica* 1, *Liliumspeciosum var. gloriosoides*+, *Linderaobtusiloba*+, *Phytolaccaacinosa*+, *Pterismultifida* +, *Sapiumsebiferum*+, *Saussureanivea* +, *Asarumforbesii*+, in no. 42: *Pileanotata*+, *Clematis cadmia*+, *Isodoninflexus*+, *Ribesfasciculatum*var. *chinense*+, *Clematis finetiana*+,*Cornuscontroversa*1; in no. 43: *Microlepiamarginata* +; in no. 44: *Lyciumchinense*+, *Clematis apiifolia*+; in no. 45: *Euonymus multiflora* +, *Euphorbia esula*+, *Morusmongolica*+, *Ophiopogonbodinieri* +, *Parthenopsisthomsonii*2, *Desmodiumfallax*+, *Salvia honania*+, *Symplocossumuntia*+; in no. 46: *Symplocoscaudata* 1, *Viburnum melanocarpum* +, *Rosa 'odorata*+, *Rhododendron simsii*+, *Carpesiumabrotanoides*+, *Goodyerarepens*+, *Platycodongrandiflorum*+; in no. 47: *Aspleniumincisum* +, *Ligustrumacutissimum*+, *Lysimachiapentapetala* +, *Camellia oleifera*+, *Agrimoniapilosa*+, *Rhamnushypochyrysus*+; in no. 48: *Pseudosasamaculifera*+; in no.49: *Prunusdielsiana*1, *Linderaerythrocarpa* +, *Magnolia biondii*+, *Rubusamabilis*+, *Magnolia denudata*+; in no. 50: *Cephalotaxusfortunei*+, *Bolbostemmapaniculatum*+, *Aristolochiacontorta*+, *Ribesfasciculatum* +, *Vitisdavidii*+; in no. 51: *Philadelphusincanus* +, *Ficussarmentosa*var. *henryi*+, *Stephanandrachinensis*+; in no. 52: *Toxicodendron succedaneum* +, *Carpesiummacrocephalum*+, *Dioscoreacollettii*var. *hypoglauca*+, *Cephalantherafalcata*+; in no. 53: *Zanthoxylumbungeanum*+; in no. 54: *Ribesemodens*+, *Catalpa ovata*+, *Nepetacataria*+, *Boehmeriaplatanifolia*+

Locations of sites surveyed: Relevés 1–2: Nanwutai Nature Preservation Zone, Shaanxi; 3–10: Louguantai Nature Preservation Zone, Shaanxi; 11–15: Dingjunshan Mountains, Shaanxi; 16: Baotianman Nature Preservation Zone, Henan; 17–18: Laojieling Mountains, Henan; 19–23: Shirenshan Mountains, Henan; 24–28 Henan; 29–40: Huangcangyu Nature Preservation Zone, Anhui; 41–44: Maoshan Mountains, Jiangsu; 45–51: Jigongshan Mountains, Henan; 52–54: Yuntaishan Mountains

In addition to recording the species composition, cover, and occurrence frequency of the species, we also recorded environmental variables for every relevé, including elevation, slope aspect, slope inclination, and soil moisture.

The plant communities were classified by Braun-Blanquet methodology. De-trended Correspondence Analysis (DCA, PC-ORD Version 4.25) was also used, in order to analyze the relationship between plant communities and environmental variables, using the middle values of cover-abundance on the Braun-Blanquet scale. Elevation, slope, mean annual precipitation, mean annual temperature, mean temperature of the warmest and coldest months, mean absolute maximum and minimum temperature and an annual moisture index were selected as the main variables to represent environmental conditions. For climate data, the weather station closest to each vegetation survey plot was chosen (Table 2) and the 30-year climate data-set (1978–2008) was downloaded from the "China Meteorological Data Sharing Service System". Temperature data for each study site were modified following a vertical lapse rate of 0.6°C decrease for each 100 m increase in elevation.

4 Results

4.1 Classification and Description of the Vegetation

Quercus variabilis forest is the representative forest type in part of the Chinese zone called warm-temperate. It occurs usually at relatively lower elevation and can be found in Henan, Shaanxi, Shanxi and other provinces. According to the data from the 54 relevés, and based on Braun-Blanquet procedures, the *Quercus variabilis* forests can be classified provisionally into one class and one order, with three alliances, five associations, five communities (Table 2).

Pistacio-Quercetalia variabilis ord. nov. and **Quercetea variabilii-brevipetiolatae class. nov.** (Table 2)

Diagnostic species: *Quercus variabilis*, *Grewia biloba* var. *parviflora*, *Dalbergia hupeana*, *Platycarya strobilacea, Pistacia chinensis, Aster ageratoides, Lindera glauca, Cotinus coggygria* var. *pubescens*, *Ligustrum quihoui, Rhus chinensis, Koelreuteria paniculata, Quercus acutissima, Celtis biondii*.

Holotype: Carpino turczaninovii-Quercion variabilis all. nov.

Ecology and distribution: This new syntaxon occurs mainly in the southern part of temperate China. Due to different geologic and topographic conditions, this syntaxon can occur at very different elevations. In the limestone area (i.e., Anhui), it usually occurs at altitudes ranging from 100 to 276 m. In the Qinling mountain area (i.e., Shaanxi and Henan) granite is the main rock type, and *Q. variabilis* forest always occurs at much higher elevations, at 592–1,210 m in Shaanxi and 451–1,320 min Henan.

Physiognomy and composition: The community structure of this syntaxon is not very complicated. In general it consists of four layers and does not have very many species. The height of the tree layer is usually more than 10 m, and the tallest trees can reach 24 m (in Nanwutai Nature Preservation Zone of Shaanxi). The cover generally reaches 70–80%.

In the Qinling mountain area, under the influence of elevation, *Quercus variabilis* forest shows very different floristic composition at different altitudes. At lower elevation, *Quercus variabilis* usually takes a dominant position in the tree layer, while at higher elevation it often grows mixed with other tree species in the upper layer. For example, at elevation 997–1,140 m in the Yuntaishan Mountains of Henan, *Quercus variabilis* often grows mixed with *Carpinus turczaninowii* and *Quercus aliena,* while in the Laojieling Mountains of southwestern Henan it can always be found mixed with *Quercus glandulifera* var. *brevipetiolata* and *Pinus thunbergii*, at an altitude of 975–1,000 m (Table: Rel. 17, 18). In hilly regions of the limestone area (northern Anhui), *Q. variabilis* can be found growing mixed with *Pistacia chinensis*, *Aleurites fordii*, *Acer mono*, and *Dalbergia hupeana*, and forms a unique community type of this area (Table: Rel. 32–39). This may be because of different geological conditions, due to which *Q. variabilis* forest shows a complicated floristic composition in the tree layer, even at lower altitude. This area is quite different from the other study sites.

The plant communities in the transition southward show much different floristic compositions (Table 2: Rel. 40–50). Evergreen species, such as *Camellia fraterna*, *Ilex cornuta*, and *Osmanthus cooperi*, increase obviously in the upper layer of the community.

Syntaxonomy: The Pistacio-Quercetalia variabilis ord. nov. can be subdivided into three alliances: Lonicero standishii-Quercion variabilis, Carpino turczaninowii-Quercion variabilis, and Pistacio chinensis-Quercion variabilis. Quercetea variabilii-brevipetiolatae S. Suzuki et al. 2003 ex Fujiwara et A. Harada was reported by S. Suzuki et al. 2003 as Quercetalia variabilii-brevipetiolatae. We compared *Quercus variabilis* forests with this system and promoted it to class status.

1. **Lonicero standishii-Quercion variabilis all. nov.** (Table 2, A)

Diagnostic species: *Lonicera standishii*, *Quercus dentata*, *Jasminum giraldii*, *Mahonia fortunei, Vitis ficifolia, Pinus tabulaeformis, Elaeagnus umbellata*.

Holotype: Junipero formosanae-Quercetum variabilis Tang, Fujiwara et You 2013

Ecology and distribution: Lonicero standishii-Quercion variabilis can be found in southern Shaanxi (Fig. 1), in the

Nanwutai and Louguantai Nature Preservation Zones on northern slopes of the Qinling Mountains and also on Dingjun-Shan mountain. In fact, the Dingjun-Shan is near Sichuan and belongs to the Qinba mountain area (southern slope of the Qinling Mtns. and Mt. Bashan), which is in the transition between the deciduous and evergreen broad-leaved forest zones. Therefore, some evergreen species occur in this syntaxonomical unit, and it has both temperate and subtropical characteristics. This alliance usually occurs at mean altitude of about 750 m, but in the Nanwutai Nature Preservation Zone it always occurs at much higher elevation, around 1,200 m. The soil under this alliance is poor, yellow in colour, with sand and clay. On some sites the slope can reach 40°, with very much bare rock.

Physiognomy and composition: The average tree height in this syntaxon can reach 18 m, with mean cover about 73%. The average number of species is about 31. *Quercus dentata* and *Cotinus coggygria* var. *pubescens* can usually be found growing mixed with *Quercus variabilis*; *Dalbergia hupeana* also occurs commonly in the tree layer at some sites. In the shrub layer, *Grewia biloba* var. *parviflora* is the dominant species, usually along with species such as *Lonicera standishii*, *Jasminum giraldii* and *Mahonia fortunei*. Some evergreen species also occur in this syntaxon, such as: *Zanthoxylum armatum*, *Mahonia fortunei*, *Hedera nepalensis* var. *sinensis*, and *Pyracantha fortuneana*.

Syntaxonomy: Lonicero standishii-Quercion variabilis consists of *Acer grosseri-Quercus variabilis* community, Junipero formosanae-Quercetum variabilis ass. nov., and Vitici negundo heterophyllae-Quercetum variabilis ass. nov.

. 1-1. ***Acer grosseri-Quercus variabilis* Community** (Table 2, 1-1)

Differential species: *Acer grosseri*, *Rosa moyesii*, *Rubus parvifolius*, *Rhododendron micranthum*, *Hypericum przewalskii*.

Ecology and distribution: This kind of community occurs mainly in the Nanwutai Nature Preservation Zone, near Xi'an (Shaanxi, Fig. 1), at higher elevation (around 1,200 m), on steep (40°) southwest-facing slopes.

Physiognomy and composition: The mean number of species reaches 43, in communities consisting of four layers. The height of the tree layer is 22–24 m, the understorey tree layer can reach 12–14 m, and the cover of the whole community ranges from 75% to 80%. *Quercus variabilis* takes a predominant position in the canopy and understorey tree layers; *Quercus aliena* can also be found in this layer but in small quantities. The shrub-layer cover can reach 40–50%, with an average height of 6.5 m. The main species in this layer include *Quercus dentata*, *Viburnum betulifolium*, *Rhus chinensis*, *Cotinus coggygria*, *Celtis koraiensis*, *Rhododendron micranthum*, and *Ligustrum guihoui*. The mean cover of the herb layer is only 15–20%, but the height can reach 0.8 m, with dominant species *Spodiopogon sibiricus*, *Eriophorum comosum*, *Cotinus coggygria* and others.

. 1-2. **Junipero formosanae-Quercetum variabilis ass. nov.** (Table 2, 1-2)

Diagnostic species: *Juniperus formosana, Viburnum schensianum, Cotoneaster zabelii, Sinarundinaria nitida, Roegneria kamoji, Picrasma quassioides, Bothriospermum secundum, Cudrania tricuspidata.*

Holotype: Table 2: running number 6, Zhouzhi county of Shaanxi.

Ecology and distribution: This association can be found in the Louguantai Nature Preservation Zone in Zhouzhi county of Shaanxi, at elevations between 592 and 731 m, usually on north-facing slopes.

Physiognomy and composition: This association has not so many species, the mean being just 27, mainly in the herb layer. At one study site the herb layer had only 14 species, and most were not herbs. The height of this community ranges from 13 to 19 m, with mean cover about 73%. *Quercus variabilis* is predominant in the tree layer; sometimes *Quercus dentata* also occurs in the tree layer but much less than *Quercus variabilis.* In the understorey tree layer, *Quercus dentata*, *Juniperus formosana*, *Pinus tabulaeformis*, *Sinarundinaria nitida* and *Picrasma quassioides* can also be found. The height of the shrub layer can reach 3–4 m, and cover can sometimes reach 60%. The dominant species in this layer include *Viburnum schensianum*, *Cotinus coggygria*, *Viburnum betulifolium*, *Neillia thyrsiflora*, *Lonicera standishii*, *Jasminum giraldii*, and *Cudrania tricuspidata*. Herb-layer height ranges from 0.4 to 0.8 m and average cover reaches about 13%. Within this layer, *Oplismenus undulatifolius*, *Bothriospermum secundum*, *Aster tataricus*, and *Roegneria kamoji* are some of the main species.

. 1-3. **Vitici negundo heterophyllae-Quercetum variabilis ass. nov.** (Table 2, 1-3)

Diagnostic species: *Vitex negundo* var. *heterophylla*, *Rhynchosia dielsii*, *Pyracantha fortuneana*, *Ficus heteromorpha*, *Zanthoxylum armatum*, *Rosa giraldii*, *Epimedium grandiflorum*, *Hedera nepalensis* var. *sinensis*, *Thalictrum shensiense, Cleistogenes chinensis, Cacalia ambigua, Menispermum dauricum.*

Holotype: Table 2: running number 11, at 682 m of Dingjun-Shan mountain in Hanzhong (Shaanxi).

Ecology and distribution: This association is found on Dingjun-Shan in Hanzhong, at elevations of 682–763 m, usually on north-facing aspects.

Physiognomy and composition: The height of this association can reach 20 m, with average community cover about 70%. The average number of species is 34. *Quercus variabilis* takes an absolutely predominant position in the canopy and understorey layers. No other tree species appears in the canopy layer, but some others can be found in the understorey layer, for example *Pinus tabulaeformis* and *Ficus heteromorpha*. Shrub-layer mean height is 4.5 m and average cover is 45%. Species such as *Vitex negundo* var. *heterophylla*, *Mahonia fortunei*, *Pyracantha fortuneana*, *Zanthoxylum armatum*, *Corylus sieboldiana* var. *mandshurica* and *Elaeagnus umbellata* are dominant in this layer. The herb layer can reach 0.8 m and has a mean cover of 27%. Major species in this layer are *Epimedium grandiflorum, Hedera nepalensis* var. *sinensis, Thalictrum shensiense,* and *Bothriospermum secundum*.

2. **Carpino turczaninowii-Quercion variabilis all. nov.** (Table 2, 2)

Diagnostic species: *Carpinus turczaninowii*, *Forsythia suspensa*, *Spiraea pubescens, Adenophora polyantha, Quercus glandulifera* var. *brevipetiolata, Symplocos paniculata, Sedum aizoon, Rubus phoenicolasius, Rhus verniciflua*.

Holotype: Viburno mongolicae-Quercetum alienae ass. nov.

Ecology and distribution: This alliance occurs mainly on Yuntaishan Mountain of northern Henan and in the Baotianman Nature Preservation Zone, Laojieling Mountains and Shirenshan Mountains in southwestern Henan. This syntaxon can usually be found at elevations ranging from 832 to 1,320 m, mainly on south-facing aspects.

Physiognomy and composition: The mean tree height of this unit can reach about 14 m, with cover 73%. The average number of species reaches 44. *Carpinus turczaninowii* usually occurs with *Quercus variabilis* in the tree layer, while species such as *Quercus aliena* and *Quercus glandulifera* var. *brevipetiolata* occur commonly with *Quercus variabilis* on different sites. In the shrub layer, *Forsythia suspensa* and *Spiraea pubescens* are dominant species, but *Viburnum mongolicum*, *Rubus phoenicolasius*, and *Symplocos paniculata* can also be found commonly.

Syntaxonomy: This syntaxon consists of two communities and an association: *Rhododendron mariesii-Quercus variabilis* and *Melica radula-Quercus variabilis* communities, and Viburno mongolicae-Quercetum variabilis ass. nov.

. 2-1. ***Rhododendron mariesii-Quercus variabilis* community** (Table 2, 2-1)

Differential species: *Rhododendron mariesii*, *Spiraea dasyantha*, *Pinus thunbergii*

Ecology and distribution: This community is located mainly in the Baotianman Nature Preservation Zone and the Laojieling Mountains in southwestern Henan, at relatively higher elevation (975–1,320 m) mainly on south-facing aspects.

Physiognomy and composition: The average number of species in this community is about 43. The height of this forest is about 15–16 m, and its average cover is about 68%, but at some sites the community cover was only 50%. Dominant tree-layer species are *Quercus variabilis*, *Quercus glandulifera* var. *brevipetiolata*, and *Symplocos paniculata*. In some places, *Platycarya strobilacea*, *Carpinus turczaninowii*, *Rhus verniciflua* and *Rhus chinensis* can also be found in the tree layer. Mean shrub-layer height is 2.5 m, and cover of this layer is 15–30%, with *Forsythia suspensa*, *Rhododendron mariesii* and *Spiraea dasyantha* as dominant species. The mean height of the herb layer is about 0.5 m, with cover of 10–20%. The dominant species of this layer are *Sedum aizoön*, *Carex lanceolata*, *Polygonatum odoratum* and others.

. 2-2. ***Melica radula-Quercus variabilis* community** (Table 2, 2-2)

Differential species: *Melica radula, Deutzia parviflora, Acer henryi, Cercidiphyllum japonicum* var. *sinense, Meliosma cuneifolia*

Ecology and distribution: This community can be found on Shirenshan Mountain in Nanyang city of Henan, usually at altitudes ranging from 832 to 920 m and on southern aspects. The soil is poor, with much exposed bare rock.

Physiognomy and composition: The average height of this community is about 16 m, with cover of 65–85%. Dominant tree-layer species are *Quercus variabilis, Carpinus turczaninowii*, *Quercus glandulifera* var. *brevipetiolata*, and *Symplocos paniculata*, but *Cercidiphyllum japonicum* var. *sinense* and *Meliosma cuneifolia* also occur in this layer. *Spiraea pubescens* and *Euonymus alatus* are dominant species in the shrub layer, but *Cotinus coggygria* var. *pubescens* and *Lespedeza bicolor* usually occur also. The cover of the shrub layer reaches only 20%, with a height of about 2 m. The herb layer has a mean cover of about 15%, with average height 0.5 m. *Melica radula*, *Oplismenus undulatifolius*, *Aster ageratoides*, *Polygonatum odoratum* and others are the dominants in this layer.

. 2-3. **Viburno mongolicae-Quercetum alienae ass. nov.** (Table 2, 2-3)

Diagnostic species: *Quercus aliena*, *Viburnum mongolicum*, *Crataegus cuneata*, *Carex subpediformis, Allium anisopodium, Atractylodes macrocephala, Lespedeza pilosa, Phyllanthus glaucus, Rhamnus davurica, Clematis obtusidentata, Fraxinus bungeana, Zelkova sinica, Lonicera ferdinandii, Rhododendron molle, Clematis obscura, Sporobolus indicus, Lilium concolor, Rhamnus rugulosa, Spiraea hirsuta, Syringa microphylla.*

Holotype: Table 2: running number 28, at 982 m on gentle southeast-facing slopes of the Yuntai-Shan mountains of Jiaozuo city in northern Henan.

Ecology and distribution: This association occurs mainly on the Yuntai-Shan of Jiaozuo (northern Henan), usually at elevation of 982–1,140 m, on south-facing aspects with slope of 18–25°.

Physiognomy and composition: This association can reach 16 m in height, with average cover of about 77%. The average number of species is 48. *Quercus aliena* and *Carpinus turczaninowii* grow in the tree layer, mixed with *Quercus variabilis*. In the understorey layer, species such as

Forsythia suspensa, *Carpinus turczaninowii* and *Cotinus coggygria* var. *pubescens* are dominant. Mean shrub-layer height is 3 m and average cover is 47%. Species such as *Spiraea pubescens*, *Viburnum mongolicum*, *Crataegus cuneata*, and *Cotinus coggygria* var. *pubescens* are dominant in this layer. The herb layer can reach 0.6 m and has a mean cover of 19%. In this layer, *Carex subpediformis*, *Aster ageratoides*, *Clematis florida*, and *Deyeuxia arundinacea* are dominant species.

3. **Trachelospermo jasminoidies-Quercion variabilis all. nov.** (Table 2, 3)

Diagnostic species: *Trachelospermum jasminoides, Aleurites fordii, Rhamnus globosa, Celtis sinensis, Acer buergerianum, Alangium platanifolium, Liriope spicata, Smilax glauco-china, Liquidambar formosana, Ilex cornuta.*

Holotype: Pteroceltio tatarinowii-Quercetum variabilis ass. nov.

Ecology and distribution: This alliance occurs in the Yuntai-Shan and Jigong-Shan mountains of Henan, in the Huangcangyu Nature Preservation Zone of Anhui, and in the Maoshan hilly region of Jiangsu. It can usually be found on south-facing slopes, at relatively lower elevations in limestone areas, ranging from 100 m to 568 m.

Physiognomy and composition: The mean height of this forest is about 17 m, with average cover about 77%. The average number of species in this alliance is about 44. Dominant tree-layer species are *Quercus variabilis, Pistacia chinensis,* and *Aleurites fordii*. Mean shrub-layer height is 3.6 m, and average cover of this layer is about 40%, with *Vitex negundo*, *Amorpha fruticosa*, and *Grewia biloba* var. *parviflora* as dominant species in this layer. The mean height of the herb layer is about 0.5 m, with average cover of 32%. The dominant species of this layer are *Artemisia shangnanensis*, *Rabdosia inflexa*, *Asparagus schoberioides*, *Oplismenus undulatifolius*, *Akebia trifoliata* and others.

Syntaxonomy: Pistacio-Quercion variabilis has two associations and two communities: Pteroceltio tatarinowii-Quercetum variabilis ass. nov. and Alangio chinense-Quercetum variabilis ass. nov., plus a *Vitex negundo-Q. variabilis* community and a *Zelkova schneideriana-Quercus variabilis* community.

. 3-1. **Pteroceltio tatarinowii-Quercetum variabilis ass. nov.** (Table 2, 3-1)

Diagnostic species: *Pteroceltis tatarinowii*, *Acer mono, Celtis koraiensis, Viburnum macrocephalum, Vitex negundo* var. *cannabifolia*, *Sinomenium acutum, Aristolochia mollissima, Aeluropus littoralis* var. *sinensis, Liriope platyphylla.*

Holotype: Table 2: running number 32, at the 192 m in Huangcangyu Nature Preservation Zone of Xiao County in Anhui.

Ecology and distribution: This association can be found in Huangcangyu Nature Preservation Zone of Xiao County in Anhui, where it appears at lower elevations and can be found everywhere at elevations of 100–276 m, without special distribution characteristics. It occurs mainly on poor soils, with much exposed bare rock.

Physiognomy and composition: The mean number of species in this association is about 36, and the average height of the tree layer is 17 m, with mean cover about 75%. In the tree layer, *Quercus variabilis* is predominant but always growing mixed with other species. These species include *Aleurites fordii*, *Quercus aliena*, *Pistacia chinensis*, *Quercus glandulifera* var. *brevipetiolata*, *Acer mono*, *Morus alba* and others. The understorey layer also has relatively higher cover (20%), and the mean height can reach 11 m. *Quercus variabilis*, *Pistacia chinensis*, *Aleurites fordii* and *Tilia amurensis* are the dominant species in this layer. For the shrub layer, height ranges from 2 to 5 m and cover from 15% to 50%. The dominant species of this layer are *Aleurites fordii*, *Rhamnus globosa*, *Pteroceltis tatarinowii*, *Viburnum macrocephalum*, *Celtis sinensis*, *Celtis koraiensis* and others. Herb-layer height ranges from 0.3 to 0.8 m and average cover reaches about 37%. *Grewia biloba* var. *parviflora*, *Viola collina*, *Aristolochia mollissima*, *Aeluropus littoralis* var. *sinensis* and *Carex lanceolata* are some of the dominant species in the herb layer.

. 3-2. ***Zelkova schneideriana-Quercus variabilis* community** (Table 2, 3-2)

Differential species: *Zelkova schneideriana*, *Phyllostachys bambusoides, Parthenocissus tricuspidata Celastrus angulatus, Berchemia floribunda, Punica granatum, Rubus lambertianus, Viburnum ichangense, Osmanthus cooperi, Lygodium japonicum, Acanthopanax divaricatus, Desmodium pedocarpum, Vitis romanetii, Pteris dispar, Rhynchosia volubilis, Serissa serissoides, Rubus coreanus, Setaria plicata, Cryptotaenia japonica, Calystegia pellita, Quercus gracilis.*

Ecology and distribution: This kind of community is located in the Maoshan hilly region in Zhulin County of Jiangsu. The *Zelkova schneideriana-Quercus variabilis* community occurs at very low elevations (122–150 m), normal throughout Jiangsu, and usually can be found everywhere in this area except on eastern aspects.

Physiognomy and composition: The mean number of species in this community is 48; its tree layer reaches about 14 m and its mean canopy cover is 78%. In the tree layer the dominant species is *Quercus variabilis,* but on some sites *Zelkova schneideriana* and *Pistacia chinensis* can also be found mixed with *Quercus variabilis*, with a cover of 10%. In the understorey layer, many more tree species appear, such as *Celtis biondii*, *Alangium platanifolium*, *Berchemia floribunda*, *Acer buergerianum*, and *Lindera glauca*. Shrub-layer cover can reach 44%, with a height of about 3 m. *Phyllostachys bambusoides*, *Lindera glauca, Acer buergerianum*, *Euonymus alatus* and *Elaeagnus pungens* are dominant species in this layer. The herb layer has very high cover at 53%, and its mean height is 0.5 m. In this layer, *Liriope spicata*, *Desmodium pedocarpum*, *Oplismenus undulatifolius*, *Trachelospermum jasminoides*, *Lygodium japonicum* and *Antenoron filiforme* are the dominant species. In this community, there are more evergreen species, not only herb species but also some tree species, such as *Elaeagnus pungens* and *Osmanthus cooperi*.

. 3-3. **Alangio chinensis-Quercetum variabilis ass. nov.** (Table 2, 3-3)

Diagnostic species: *Alangium chinense, Celtis pubescens, Rhus sylvestris, Euonymus hamiltonianus, Exochorda racemosa, Acer oliverianum, Rubus corchorifolius, Parthenocissus heterophylla, Lindera chienii, Mallotus apelta, Liliope platyphylla, Commelina communis, Trachelospermum axillare, Achyranthes bidentata, Diospyros kaki, Pyrus serrulata, Sorbus folgneri, Prunus serrulata* var. *pubescens, Pinus massoniana, Castanea seguinii, Prunus conadenia, Camellia fraterna.*

Holotype: Table 2: running number 53, at 482 m on south-facing slope, Jigong-Shan mountain of Xinyang city in Henan.

Ecology and distribution: The association is located on the Jigong-Shan mountain of Xinyang (Henan), at elevations of 346–568 m, always on south-facing slopes.

Physiognomy and composition: The average number of species in this association is 56. The tree layer ranges from 17 to 20 m and has an average cover of 78%. *Quercus variabilis* and *Pistacia chinensis* are the dominant species in the tree layer, but other species can also be found in this layer, such as *Quercus glandulifera* var. *brevipetiolata*, *Quercus aliena*, *Pinus massoniana*, *Platycarya strobilacea*, *Liquidambar formosana* and *Dalbergia hupeana*. The shrub layer has a mean height of 5 m, with average cover of 43%. *Acer oliverianum*, *Ligustrum quihoui*, *Mallotus apelta*, *Lindera chienii*, *Camellia fraterna*, *Lindera glauca*, *Platycarya strobilacea* and others are dominant species in the shrub layer. The herb layer has average height of 0.7 m and its mean cover is 28%. In this layer the dominant species are *Oplismenus undulatifolius*, *Aster ageratoides*, *Aleurites fordii*, *Akebia trifoliata* and others.

4. **Alliance not yet decided**

. 4-1. ***Vitex negundo-Quercus variabilis* community** (Table 2, C2)

Differential species: *Vitex negundo*, *Prunus sibirica*, *Gleditsia heterophylla*

Ecology and distribution: The *Vitex negundo-Quercus variabilis* community occurs on Yuntaishan Mountain in Jiaozuo city of Henan, usually on southwest-facing slopes and was found in a relatively narrow elevation range of 468–488 m. The soil of this community is poor, with much exposed bare rock.

Physiognomy and composition: The average number of species in this community is about 46. The height of this forest is about 14–17 m, and its average cover is about 80%. Dominant tree-layer species are *Quercus variabilis, Pistacia chinensis,* and *Koelreuteria paniculata*. Mean shrub-layer height is 2.7 m, and cover of this layer is 40–50%, with *Vitex negundo*, *Amorpha fruticosa*, and *Grewia biloba* var. *parviflora* as dominant species. The mean height of the herb layer is about 0.5 m, with cover of 5–10%. The dominant species of this layer are *Artemisia shangnanensis*, *Rabdosia inflexa*, *Asparagus schoberioides*, *Oplismenus undulatifolius*, *Akebia trifoliata* and others.

4.2 Ordination

In the DCA analysis of *Quercus variabilis* forest, the eigenvalue of axis 1 is 0.780, the eigenvalue of axis 2 is 0.2780 and the eigenvalue of axis 3 is 0.2503. Different syntaxonomical units of *Q. variabilis* forest can be distinguished clearly by six environmental factors: elevation, average annual precipitation, mean annual temperature, mean temperature of the coldest month, and mean absolute maximum and minimum temperature (Fig.2).

The result shows that Pistacio chinensis-Quercion variabilis is quite different from both the Lonicero standishii-Quercion variabilis and the Carpino turczaninowii-Quercion variabilis. The Pistacio chinensis-Quercion variabilis occurs at lower elevation in warmer, more humid regions, while the other two units occur usually in much higher, colder, drier areas.

The *Zelkova schneideriana-Q. variabilis* community and the Alangio chinensis-Quercetum variabilis, which are located in the transition between the Chinese warm-temperate and subtropical zones, were not distinguished clearly by the DCA ordination from the warm-temperate type Pteroceltio tatarinowii-Quercetum variabilis. This may be because of the similar topographic and climatic conditions in these regions.

5 Discussion

Classification of the deciduous *Quercus* forests in temperate China showed three different classes existing in this climatic area (Tang 2010): Quercetea mongolicae, Quercetea liaotungensis, and Quercetea variabilis. The fact that Quercetea mongolicae in northern China belongs to the Quercetea mongolicae Krestov et al. 2006 indicates in fact that the classes Quercetea liaotungensis and Quercetea variabilis are the two highest representative syntaxonomical units in the warmer parts of temperate China.

It has been widely accepted that different vegetation types are usually distinguished according to different climatic zones, especially temperature zones. Fang (2001), however, suggested that not only thermal conditions but

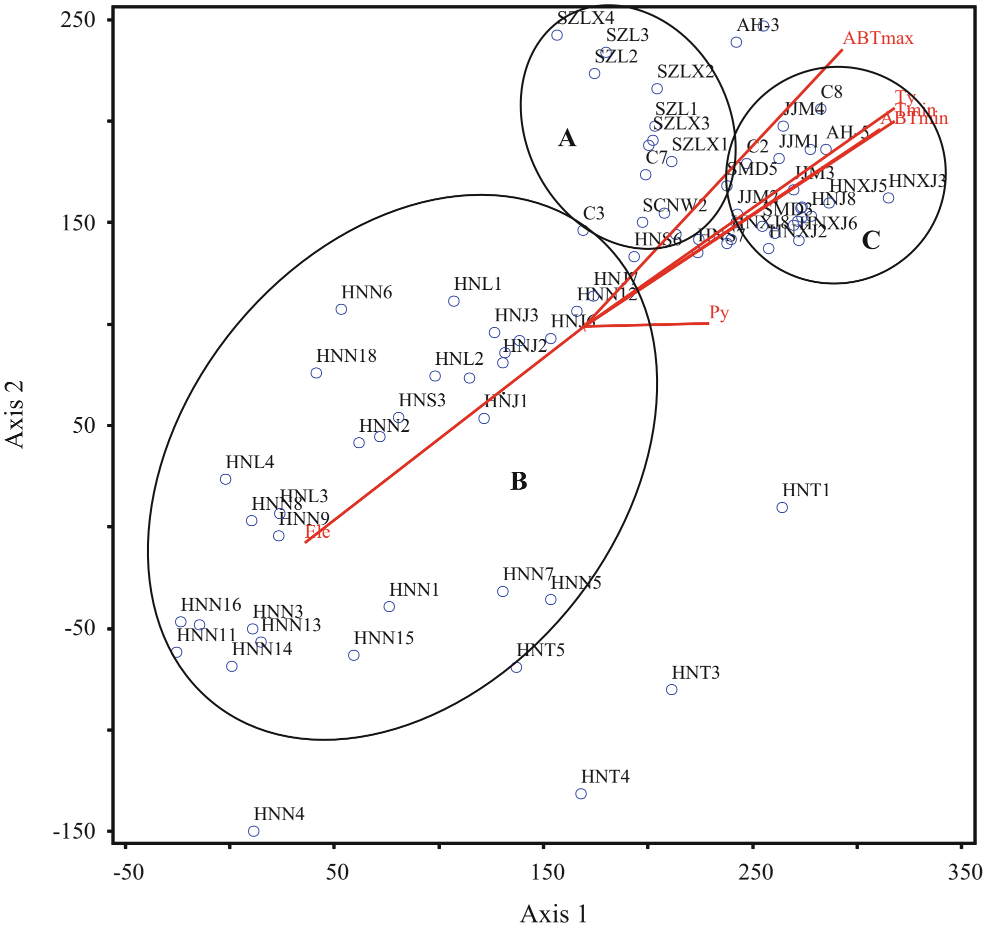


Fig. 2 DCA ordination of *Quercus variabilis* forests in warm-temperate China. Abbreviations: *Ele* elevation, *Ty* mean annual temperature, *ABTmax* mean absolute maximum temperature, *ABTmin* mean absolute minimum temperature, *Tmin* mean temperature of the coldest month, *Py* average annual precipitation. (**a**): Lonicero standishii-Quercion variabilis all. nov. (**b**): Carpino turczaninowii-Quercion variabilis all. nov. (**c**): Pistacio chinensis-Quercion variabilis all. nov.

Table 3 Climatic Indices of different deciduous *Quercus* forests in warm-temperate China

	Forest type	WI	CI	MI
Warm-temperate	*Quercus liaotungensis*	74.4–115.1	−10.9 to−29.5	0.65–0.85
	Quercus mongolica	108.5	−21.3	0.72
	Quercus variabilis	103.6–129.4	−13.5 to−3.9	0.75−1.24

Warmth index (WI) and Coldness index (CI) values are temperature sums in degrees Celsius; MI is the simple annual moisture index defined as P/PET, where P is precipitation and PET is potential evapotranspiration (cf. Box 1995).

also other environmental factors should be considered when classifying vegetation zones, in particular moisture and humidity conditions. That two or more vegetation types can exist in the same temperature zone is an objective fact. Therefore, the idea that one vegetation type must correspond to one temperature zone is not right.

Because of the very wide range of the Chinese zone called warm-temperate, the thermal and humidity conditions are very different, especially from south to north, west to east (Table 1). Although the typical vegetation type in this climatic zone is deciduous broad-leaved forest, the difficult environmental conditions lead to different kinds of *Quercus* forest in this area (Table 3). Wu (1980) suggested that it is better to divide this zone into two sub-zones according to different forest types: (1) deciduous *Quercus* forest of the northern sub-zone, with the representative forest of *Q. liaotungensis*; and (2) deciduous *Quercus* forest of the southern sub-zone, in which *Q. variabilis* forest is the dominant forest type.

Arguments about whether the evergreen broad-leaved forest to the south should or should not belong to the warm-temperate zone have lasted a long time (Xu 1986; Fang 1991; Song 1999; Fang 2001). The viewpoint of placing the boundary between warm-temperate and subtropical at the Qingling Mountain-Huaihe River line has always been adopted. Some research, however, suggested that the southern boundary of the warm-temperate zone should be much further south than at present (Fang 1991). In fact, the key to this question is to ascertain to which climatic zones the deciduous and evergreen broad-leaved mixed forests belong, the temperate, warm-temperate or subtropical.

According to Wu (1980), the southernmost boundary of the warm-temperate zone is at latitude 32°30’N, which is

Table 4 Vegetation Zones in Eastern China (After Fang 2001)

Thermal zone	Vegetation	Climatic indices
Cold-temperate	Coniferous forest	WI < 50, Im > 0
Mid-temperate	Mixed coniferous and deciduous forest	$50 <$ WI < 90, Im > 0
Warm-temperate	Deciduous broadleaf forest	$90 <$ WI < 120, CI < -10, $-20 <$ Im < 0
	Mixed deciduous and evergreen broadleaf forest	$120 <$ WI < 135, CI > -10, $0 <$ Im < 60
Subtropical	Evergreen broadleaf forest	$135 <$ WI < 240, Im > 60
Tropical	Rainforest and monsoon forest	WI > 240

Warmth index (WI) and Coldness index (CI) values are temperature sums in degrees Celsius, normally written without a degree symbol; Im is Thornthwaite's (1948) moisture index (integerized by multiplying by 100)

also the northern limit of the subtropical zone. In this study, however, deciduous *Quercus* forests were also found at latitude of 31°46′~32°22′N, in the Tongbai and Jigong Mountains (Henan), and the Maoshan hilly region of Jiangsu. In fact, the deciduous *Quercus* forests in these regions are in the transition southward to the evergreen broad-leaved forest zones. The largest difference between the deciduous *Quercus* forests in the typical warm-temperate zone and in the transitional area is the number of evergreen species occurring. The floristic composition is quite different. In the deciduous *Quercus* forests of the transitional area, evergreen species increase not only in the herb layer but also in the upper layers of the communities. For example, species such as *Camellia fraterna*, *Ilex cornuta*, and *Osmanthus cooperi* can usually be found in the understorey and shrub layers of this kind of forest.

It is commonly accepted that forest types are judged mainly according to the dominant species occurring in the tree layer. Even if some evergreen species can be found in the deciduous *Quercus* forests further south, beyond the southern limit of the current Chinese zone called 'warm-temperate', these *Quercus* forests are also considered as forest types of the warm-temperate zone, because the dominant species in the tree layer are *Q. variabilis* and other deciduous species. Fang (2001) suggested calling this transitional region the 'deciduous and evergreen broad-leaved mixed forest region' and treating it as belonging to the warm-temperate zone and not the subtropical zone (Table 4). Therefore, according to real investigation results and considering other studies (Song 1999; Fang 2001), we agreed to shift the southern boundary of the Chinese warm-temperate zone much further south. Where the exact southern limit of the warm-temperate zone actually is, however, has not been clarified. It needs much more vegetation investigation in the future.

Table 5 Major tree families and genera in *Q. variabilis* forest in warm-temperate China

Family	Genera	Spp.	Genera	Spp.
Oleaceae	6	11	*Quercus*	7
Ulmaceae	3	10	*Celtis*	6
Moraceae	6	10	*Rhus*	4
Fagaceae	2	8	*Fraxinus*	4
Aceraceae	1	8	*Carpinus*	2
Anacardiaceae	3	6	*Ficus*	2
Pinaceae	1	4		
Betulaceae	1	4		
Elaegnaceae	1	3		
Symplocaceae	1	3		

According to the current investigation, *Quercus variabilis* forest occurs mainly in the southernmost part of temperate China (cf Fig. 1), generally presenting scattered, small distributions in most parts of the study area. Some *Q. variabilis* forests have been well protected, such as in the Nanwutai Nature Preservation Zone of Shaanxi, where there is a huge area of tall *Q. variabilis* forest with high cover.

There are many tree families, genera and species in *Q. variabilis* forest (Table 5). In this study, the seven *Quercus* species occurring in *Q. variabilis* forest are rarely seen in other kinds of *Quercus* forest (Tang et al. 2009).

The biggest difference over the north-south range of *Quercus variabilis* forests is that evergreen species increase obviously toward the south (Table 2) and the community structure and species composition become more complicated. In the association Alangio chinensis-Quercetum variabilis (Table 2: C4), which is assigned in Chinese literature to the Chinese northern subtropical zone, evergreen species, both the same and different from those of temperate *Q. variabilis* communities, occur in both the shrub and herb layers; and bamboo appears with a certain quantity. Moreover, the Junipero formosanae-Quercetum variabilis of Shaanxi (Table 2: A2) also has a certain cover of bamboo (*Sinarundinaria nitida*). Although this kind of community is considered warm-temperate, it presents transitional characteristics representing the change from warm-temperate to subtropical. This indicates that *Quercus variabilis* forest in the warm-temperate zone, especially in the transition area, has very complicated community characteristics and floristic composition.

Acknowledgements We wish to express our thanks to Prof. Ding S. Y. (Henan University), Associate Prof. Liu Z. C. (Nanyang Normal University), and Associate Prof. Guo X. S. (Northwest Agriculture and Forestry University) for helping us to do the vegetation survey in Henan and Shaanxi Provinces. We are grateful to Prof. E. O. Box (University of Georgia) for revising this manuscript. This survey grant was funded by Yamada Honey Bee Co. Ltd. for restoration of natural forest in China.

References

Archibold, O.W. 1994. *Ecology of World Vegetation*. Chapman & Hall Press, London. 510 pp

Braun-Blanquet, J. 1964. *Pflanzensoziologie, Grundzüge der Vegetationskunde*. 3rd edition. Springer-Verlag, Wien. 631 pp

Box, E.O. 1995. Climatic Relations of the Forests of East and South-East Asia. In: *Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and Southeast Asia* (E. O. Box et al., eds.), pp. 23-55. Kluwer Academic Publishers, Dordrecht

Chang X. S. 1989. [The potential evapotranspiration (PE) index for vegetation and vegetation-climatic classification (2): an introduction to main methods and the PEP program]. *Acta Phytoecol. Geobot. Sin.*, 13:197-207 (in Chinese, with English synopsis)

Chen X. J. 1982. [A new approach on climatic division of China]. *Acta Meteorologica Sinica*, 40:35-47 (in Chinese, with English synopsis)

Fang J. Y. 1991. [Ecoclimatological analysis of the forest zones in China]. *Acta Ecologica Sinica*, 4:377-387 (in Chinese, with English synopsis)

Fang J. Y. 2001. [Re-discussion about the forest vegetation zonation in eastern China]. *Acta Botanica Sinica*,5:522-533 (in Chinese, with English synopsis)

Fang J. Y., Song Y. Ch., Liu H. Y. and Piao S. L. 2002. Vegetation-climate relationship and its application in the division of vegetation zone in China. *Acta Botanica Sinica*, 44(9):1105-1122

Fang J. Y. and K. Yoda 1989. Climate and vegetation in China (II). Distribution of main vegetation types and thermal climate. *Ecol. Research*, 4:71-83

Fujiwara, K. 1987. Aims and methods of phytosociology or "vegetation science". Plant Ecology and Taxonomy, Special issue to the memory of Dr. Satoshi Nakanishi, pp. 607-628. Kōbe Geobotanical Society, Kōbe

Fujiwara, K. 1997. [Methodology of vegetation analysis and mapping based on phytosociology and vegetation science]. *Bull. Inst. Environ. Sci. Technol. Yokohama Natn. Univ.*, 23(1):13-46(in Japanese, with English synopsis)

Greller, A. M. 1989. Correlation of warmth and temperateness with the distributional limits of zonal forests in eastern North America. *Bull. Torrey Botan. Club* (New York), 116:145-163

Han Z. X., Zhu H. J., Zhang W. H., and Shan L. 2005. [Spatial distribution patterns of *Quercus variabilis*populations in different regions by different measurement yardsticks]. *Acta Bot. Boreal-Occident. Sin..*, 25:1216-1221 (in Chinese,with English synopsis)

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science*, 105: 367-368

Holdridge, L. R. 1967. Life Zone Ecology. Tropical Science Center, San José. 206pp

Iwasa, Y., T. Matsumoto, K. Kikuzawa, and Ecological Society of Japan 2003. In: [Encyclopedia of Ecology], pp. 384-385. Kyōritsu Shuppan, Tokyo (in Japanese)

Kira, T. 1945. [A new classification of climate in eastern Asia as the basis for agricultural geography]. Horticulral Institute, Kyōto Univ., Kyōto. 23pp (in Japanese)

Kira, T. 1971. [A look at nature from the ecological view point]. Kawade Shobō Shinsha, Tokyo. 295pp (in Japanese)

Kira, T. 1977. A Climatological Interpretation of Japanese Vegetation Zones. In: Vegetation Science and Environmental Protection (A. Miyawaki &R. Tüxen, eds.), pp. 21-30. Maruzen, Tokyo

Köppen, W. 1936. Das geographische System der Klimate. In: *Handbuch der Klimatologie* (W. Köppen and R. Geiger, eds.), pp C1-C44. Gebr. Bornträger, Berlin

Li L., Huang Z. L., Zhang H.R. Z., Wei S. G., and Zhang W. H. 2006. [Spatial heterogeneity on species diversity of *Quercus variabilis* community in Shanxi Province]. *J. Fujian Coll. Forestry*, 26:63-68 (in Chinese,with English synopsis)

Menitsky, Y. L. 2005. *Oaks of Asia*. Science Publishers, Enfield, New Hampshire. 549pp

Peng Y. S., Chen, L., and Li J. Q. 2007. [Study on numerical taxonomy of *Quercus* L. (Fagaceae) in China]. *J. Wuhan Bot. Res.*, 25(2): 149-157 (in Chinese, with English synopsis)

Song Y. Ch. 1999. [Perspective of the vegetation zonation of forest regions in eastern China]. *Acta Bot. Sinica*, 5:92-103 (in Chinese, with English synopsis)

Suzuki, S., Y. Nakamura, K. Kawano,Wang X.H., and Da L.J. 2003. A phytosociological study on the deciduous oak forests in eastern China. *Eco-Habitat*, 10(1):85-103

Suzuki, S., and A. Miyawaki 2006. Comparison of *Quercus* forests in western Japan and eastern China. *Polish Bot. Studies*, 22:487-501

Tang Q. 2010. Phytosociological study of deciduous *Quercus* forest in the warm-temperate zone of China. Doctoral thesis. Yokohama National University, Japan

Tang Q., K. Fujiwara, and You H. M. 2009. Phytosociological study of deciduous *Quercus* forest in the warm-temperate zone of China: Primary study of different kinds of *Quercus* communities. *Hikobia*, 15:255-267

Thornthwaite, C. W. 1948. An approach toward a rational classification of Climate. *Geogr. Review*, 38:55-94

Walter, H. 1977. *Vegetation und Klimazonen*. 3rd ed. Verlag Eugen Ulmer, Stuttgart. 309pp

Wang Y. F. and Xiao X. M. 1993. [Distribution of major vegetation types along climatic gradients on the Loess Plateau]. *Acta Bot. Sinica*, 35:291-299 (in Chinese, with English synopsis)

Wang Z. 1935. [Forest zones of China]. [*Agronomy*] 1:41-66 (in Chinese)

Wu Z.Y. and P. H. Raven 1999. *Flora of China*, Vol. 4. Science Press, Beijing, and MissouriBotanical Garden Press, St. Louis. 453pp

Wu Z. Y. and committee 1980. *Zhongguo Zhibei* [Vegetation of China]. Science Press, Beijing. 1375pp (in Chinese)

Wu X. P., Wang Z. H., Cui H. T. and Fang J.Y. 2004. [Community structure and species composition of oak forests in the mountainous area of Beijing]. *Biodiversity Science*, 12:155-163 (in Chinese,with English synopsis)

Ye Y. Z., Wang S. Y., Tian C. Y. and Fan Z. B. 1993. [Study on oak forests in Henan province]. *J. Henan Agr. Univ.*, 27:187-195 (in Chinese,with English synopsis)

Zhang X. L. 2007. [Studies on the plant communities in mountainous areas in southern Hebei province]. *J. Hebei Normal Univ. Nat. Scie. Edit.*, 31:99-103 (in Chinese, with English synopsis)

Zhou G. S. and Zhang X. S. 1996. [Study on Chinese climate-vegetation relationships]. *Acta Phytoecol. Sinica*, 20:113-119 (in Chinese, with English synopsis)

Zhu K. Z. and Committee (ed.) 1984. [*Physical Geography of China*]. Science Press, Beijing. 161pp (in Chinese)

Warm-Temperate Forests of Central Portugal: A Mosaic of Syntaxa

José Carlos Costa, Tiago Monteiro-Henriques, Pedro Bingre, and Dalila Espírito-Santo

Abstract

Despite extensive afforestations with allochthonous tree species, the Atlantic façade of the mountain chain that extends through central Portugal still presents several examples of autochthonous forests that show significant floristic and ecophysiological diversity. Along a N-S transect of no more than 100 km along this range, zonal forest types may vary from semi-deciduous *Quercus robur* formations with evergreen understory (*Viburnum tinus* or *Arbutus unedo*) to marcescent *Quercus broteroi* forests and sclerophyllous forests of *Quercus suber*. Adding further diversity to the vegetated landscape are extrazonal groves of non-sclerophyllous evergreens like *Prunus lusitanica, Ilex aquifolium, Rhododendron ponticum*, *Laurus nobilis* and *Myrica faya*, relicts of the Tertiary laurisilva. While data suggest that a macrobioclimatic gradient (from temperate to mediterranean) may be responsible for such a variety of forest formations, a convoluted set of orographic, edaphic, hydrologic, microclimatic and paleohistorical factors certainly contributes to explain the variation in this peculiar region. This study compares these plant communities of central Portugal, classified according to Braun-Blanquet methodology. We studied the number of relict species present in each community, as well as the laurophyllous taxa that had become adapted to the present climatic conditions. Extrazonal groves showed the greatest percentage cover by relict species, while zonal forests contained more newly adapted laurophyll species. Among the zonal forests, those dominated by *Quercus robur* in warmer areas had the highest percentage covers of relict species. Finally, we propose the new syntaxon *Asparago aphylli-Quercetum suberis lauretosum nobilis*.

Keywords

Laurophyllous • Relict flora • Arcto-tertiary flora • Vegetation • Phytosociology • Constrained Correspondence Analysis (CCA)

1 Introduction

The changes in climatic patterns that occurred in Western Europe since the late Tertiary have been partially dampened, in western Portugal, by the thermal inertia of the Atlantic Ocean, enabling ancient laurel-forest (laurisilva) taxa to survive. Especially during the Pleistocene glaciations, a large number of meso-thermophilous species became extinct or confined, within Europe, to rather isolated positions in southern areas (Muñoz et al. 1996; Ramil-Rego et al. 1996), mostly in the current Mediterranean region (Svenning et al.

J.C. Costa (✉) • T. Monteiro-Henriques • D. Espírito-Santo
Centro de Botânica Aplicada à Agricultura, Instituto Superior de Agronomia, University of Lisbon (ULisboa), Tapada da Ajuda, 1349-017 Lisboa, Portugal
e-mail: jccosta@isa.ulisboa.pt

P. Bingre
Escola Superior Agrária, Instituto Politécnico de Coimbra, Coimbra, Portugal

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_5, © Springer International Publishing Switzerland 2015

2008; Médail and Diadema 2009). Plant families that were diverse and widespread (*Palmae, Lauraceae, Myrtaceae*) became represented in Europe by only a few species (Honrado et al. 2007). Phylogeographic studies using both palynological and molecular data (Bennet et al. 1991; Ferris et al. 1993, 1995, 1998; Dumolin-Lapegue et al. 1997) have repeatedly identified the southern peninsulas (Iberian, Italian and Balkan) as major refuges for the flora during glacial periods.

In some locations of central Portugal, where frost does not occur frequently, there are relict subtropical laurophyll formations co-dominated by *Laurus nobilis*, *Prunus lusitanica, Ilex aquifolium, Myrica faya* and *Rhododendron ponticum* ssp. *baeticum*, along with other relicts such as *Dryopteris guanchica* and *Woodwardia radicans* present in the undergrowth (Honrado et al. 2007). There is also another group of laurophyll taxa which became adapted to submediterranean climatic conditions and cannot, therefore, be considered true relicts: *Viburnum tinus*, *Arbutus unedo*, *Myrtus communis*, *Phillyrea latifolia*, *Phillyrea media, Rubia peregrina*, *Vinca difformis* and others.

Most tropical and subtropical Tertiary vegetation was eliminated from the area by the Pleistocene glaciations (Honrado et al. 2001). Several kinds of evidence, however, suggest that some remaining forest survived in topographically sheltered valleys. In fact, paleo-subtropical Arcto-Tertiary taxa existing in continental Europe and in the Atlantic islands survived not only the Pleistocene glacial episodes but also the environmental changes initiated during the Cenozoic: the development of the Mediterranean climate (with lack of precipitation in summer) and the Alpine tectonic events with their severe disruption of the Arcto-Tertiary flora (the Messinian salinity crisis) (Costa et al. 2000). The forest climaxes that replaced the Arcto-Tertiary vegetation involved both the deciduous forests of paleo-boreal origin (*Querco-Fagetea*) and the sclerophyllous evergreen forests of paleo-Mediterranean origin (*Quercetea ilicis*) (Coudé-Gaussen 1981; Costa et al. 2000).

The Atlantic façade of the mountains in central Portugal presents several examples of autochthonous forest that show significant diversity both floristically and ecophysiologically. Along a N-S transect of about 100 km along the range, between the 41° 00′ and the 39° 50′ N latitude, different zonal forest types form an intricate mosaic of: (a) deciduous to semi-deciduous *Quercus robur* ssp. *broteroana* formations with an evergreen understory (*Viburnum tinus* or *Arbutus unedo*); (b) marcescent *Quercus faginea* ssp. *broteroi* forests; (c) sclerophyllous forests of *Quercus suber*; and (d) groves of extrazonal non-sclerophyllous evergreens like *Prunus lusitanica, Rhododendron ponticum* ssp. *baeticum*, *Laurus nobilis* and *Myrica faya*, relicts of the Tertiary laurisilva, which are found in valley bottoms on damp soils.

The occurrence of deciduous to semi-deciduous forests of *Quercus robur* ssp. *broteroana* covering the northern half of this region reflects proximity to the Euro-Siberian Region; the occurrence of sclerophyllous forests of *Quercus suber* in the southern half of this *region* is explained by the transition to the Mediterranean climate. The occurrence of semi-deciduous forests of *Quercus faginea* ssp. *broteroi* along the ecotone between the two regions suggests that this ecophysiological trait represents an adaptation to submediterranean climatic conditions.

In this work we described and analysed the low-altitude (<1,000 m) vegetation consisting of: zonal deciduous forests of *Rusco aculeati-Quercetum roboris* (Rus), zonal semi-deciduous forests of *Viburno tini-Quercetum roboris* (Vib), zonal marcescent forests of *Arisaro-Quercetum broteroi* (Bro), zonal evergreen forests of *Asparago aphylli-Quercetum suberis* (Sub), and extrazonal laurophyll forests and thickets (also azonal) of *Vinco difformis-Lauretum nobilis* (Lau), *Frangulo alni-Prunetum lusitanicae* (Pru), *Myrico fayae-Arbutetum unedonis* (Myr) and *Calluno vulgaris-Rhododendretum pontici* (Rho).

2 Material and Methods

2.1 The Research Area

Field research covered an area between the rivers Douro (south of Oporto) and Liz (north of Leiria), at altitudes below 1,000 m, including the river basins of the Vouga and Mondego (Fig. 1). The macrobioclimate (Rivas-Martínez 2005b) is temperate to mediterranean (Fig. 2), and the ombrotype is lower hyperhumid to upper subhumid (Fig. 3). Granitic rocks, meta-sediments, sandstones, limestones and sands are the substrate types found in the study area (Fig. 4).

2.2 Sampling Design and Data Collection

Phytosociological relevés were made according to the principles of the Zürich-Montpellier landscape and 'sigmatist' schools (Braun-Blanquet 1965; Müller-Dombois and Ellenberg 1974; Géhu and Rivas-Martínez 1981; Rivas-Martínez 2005a). The biogeographical and bioclimatological typologies used in the description of syntaxa followed Costa et al. (1999), Rivas-Martínez et al. (2001, 2002a) and Rivas-Martínez (2005b, 2007), while the syntaxonomic nomenclature followed the International Code of Phytosociological Nomenclature (Weber et al. 2000).

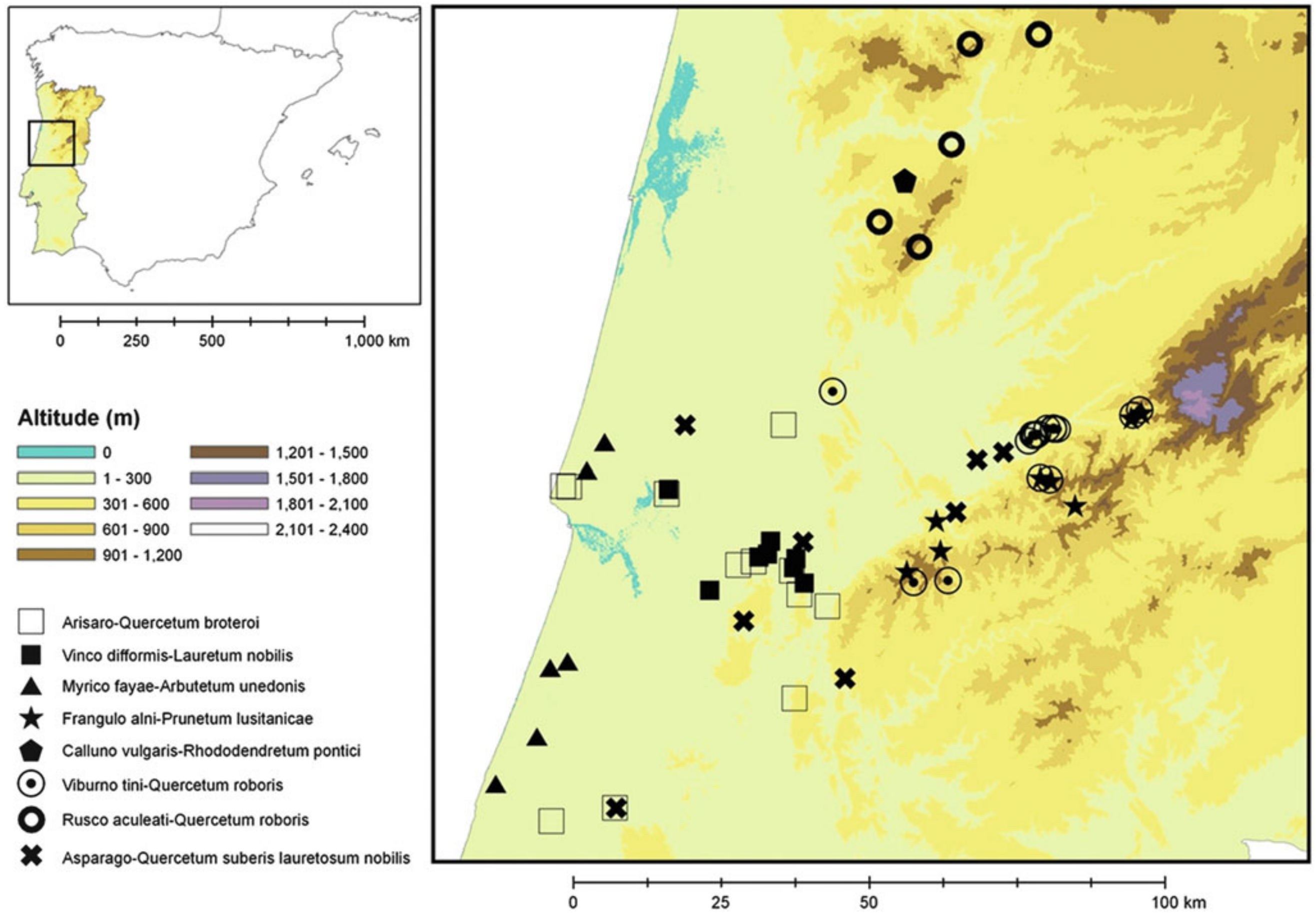


Fig. 1 Altitude of the study area (Consultative Group on International Agricultural Research 2008)

2.3 Data Analysis

The following environmental data were used for the study area:

i. A digital elevation model (DEM) based on the Shuttle Radar Topography Mission (SRTMv4) (Consultative Group on International Agricultural Research 2008);

ii. A set of bioclimatological indices proposed by Rivas-Martínez (2005b), released by Monteiro-Henriques (2010) for continental Portugal: Ombrothermic Index (Io), Compensated Thermicity Index (Itc), Continentality Index (Ic), Ombrothermic index of the warmest bimonth of the summer quarter (Ios2), Ombrothermic index of the summer quarter (Ios3), Ombrothermic index of the summer quarter plus the previous month (Ios4), Equivalent ombrothermic index for dry years, Equivalent ombrothermic index for humid years, Mean temperature of the coldest month of the year, and Mean temperature of the warmest month;

iii. The substrate type at each relevé site, which was included in the model as a dummy variable: granitic, meta-sediment (meatsedmnt), sandstone (sandst), limestone (limest) or sand; and

iv. A set of DEM-derived variables calculated using software from the SAGA 2.0.7 geographical information system: slope, aspect, surface curvature, and the topographic wetness index (Saga User Group Association 2011).

A matrix of 70 relevés by 168 species was built, with some of the relevés taken from Braun-Blanquet et al. (1956), Costa et al. (2002a) and Honrado et al. (2007). Braun-Blanquet cover-abundance values were transformed to central percentage values, as proposed by Monteiro- Henriques (2010), in order to perform the analysis: 5–87.5%; 4–62.5%; 3–37.5%; 2–15%; 1–3%; and +to 0.5%.

A constrained correspondence analysis (CCA) model with all the environmental variables was prepared and submitted to the function “step()” of the R statistical software (R Development Core Team 2010) in order to select, using a backward stepwise algorithm, the group of variables that minimizes the Akaike Information Criterion (AIC) associated with each model. The functions “cca()” and “anova.cca()” were used, respectively, for the constrained correspondence analysis (CCA) and the permutation test, all from the “vegan” package (Oksanen et al. 2008).

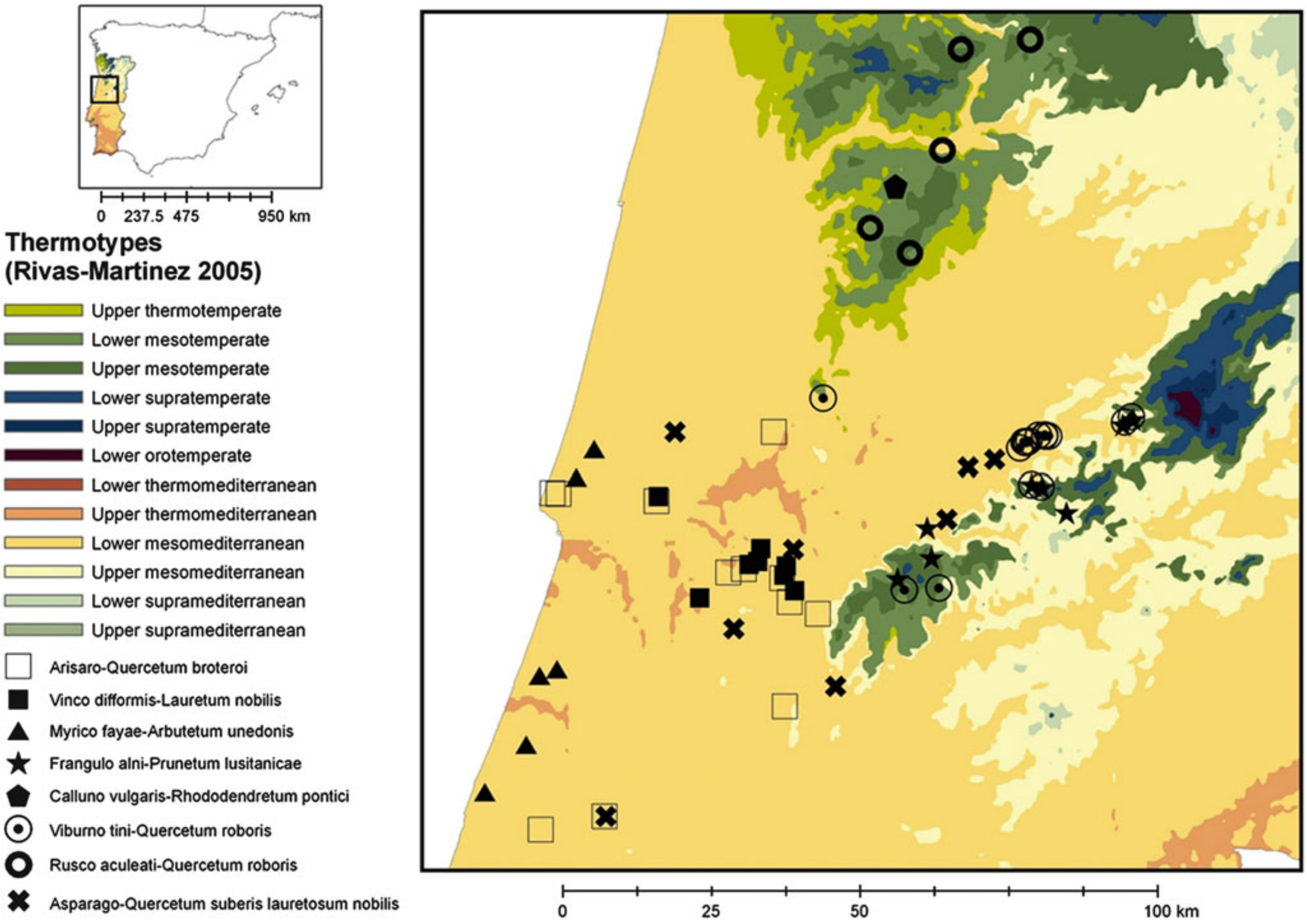


Fig. 2 Thermotypes present in the study area, according to Rivas-Martínez (2005b)

Finally, an analysis of the total percentage cover of relict species (*Prunus lusitanica, Ilex aquifolium, Laurus nobilis, Rhododendron ponticum* ssp. *baeticum* and *Myrica faya*) and of newly adapted laurophyll taxa, i.e. that became adapted to present climatic conditions (*Ruscus aculeatus, Rubia peregrina, Arbutus unedo, Phillyrea latifolia, Ph. media, Smilax aspera, Rhamnus alaternus, Myrtus communis, Hedera maderensis* ssp. *iberica, H. hibernica, Viburnum tinus* and *Hypericum androsaemum*) was performed for each association treated. The total percentage cover was calculated by merging the cover of each species under the independence assumption, as in Tichý and Holt (2006).

3 Results and Discussion

The variables selected by the backward stepwise algorithm were Io, Itc and the dummy substrate variables, which were used as constraining variables in the CCA presented in Fig. 5. The factors represented by these variables are expected to have a strong physiologic influence on the species, and these variables produced a significant result ($p < 0.001$) in the permutation test. The CCA supports strongly the ecological description of the communities studied.

1. ***Viburno tini-Quercetum roboris***

   Quercus robur ssp. *broteroana* zonal meso-macroforest, growing on deep mesic soils from meta-sediments and granitic rocks. *Quercus robur* ssp. *broteroana* is endemic to the northwestern Iberian Peninsula. It is characterized by having simple hairs on young branches; a late-deciduous or semi-deciduous habit, sometimes marcescent; leathery leaves with a shiny underside; and a large cupule of more than 16 mm, with acute, brown scales (Rivas-Martínez and Sáenz Laín 1991). This oak dominates communities thriving in lower meso-mediterranean or thermotemperate submediterranean humid hyperoceanic bioclimates of the Littoral Beirensean and Miniensien districts. The characteristic combination of species is composed by *Quercus broteroana, Viburnum tinus, Prunus lusitanica, Laurus nobilis, Ilex aquifolium, Hedera hibernica, Ruscus aculeatus, Castanea sativa, Polystichum setiferum, Teucrium scorodonia, Crataegus monogyna* ssp. *brevispina, Luzula forsteri, Lonicera periclymenum* ssp.

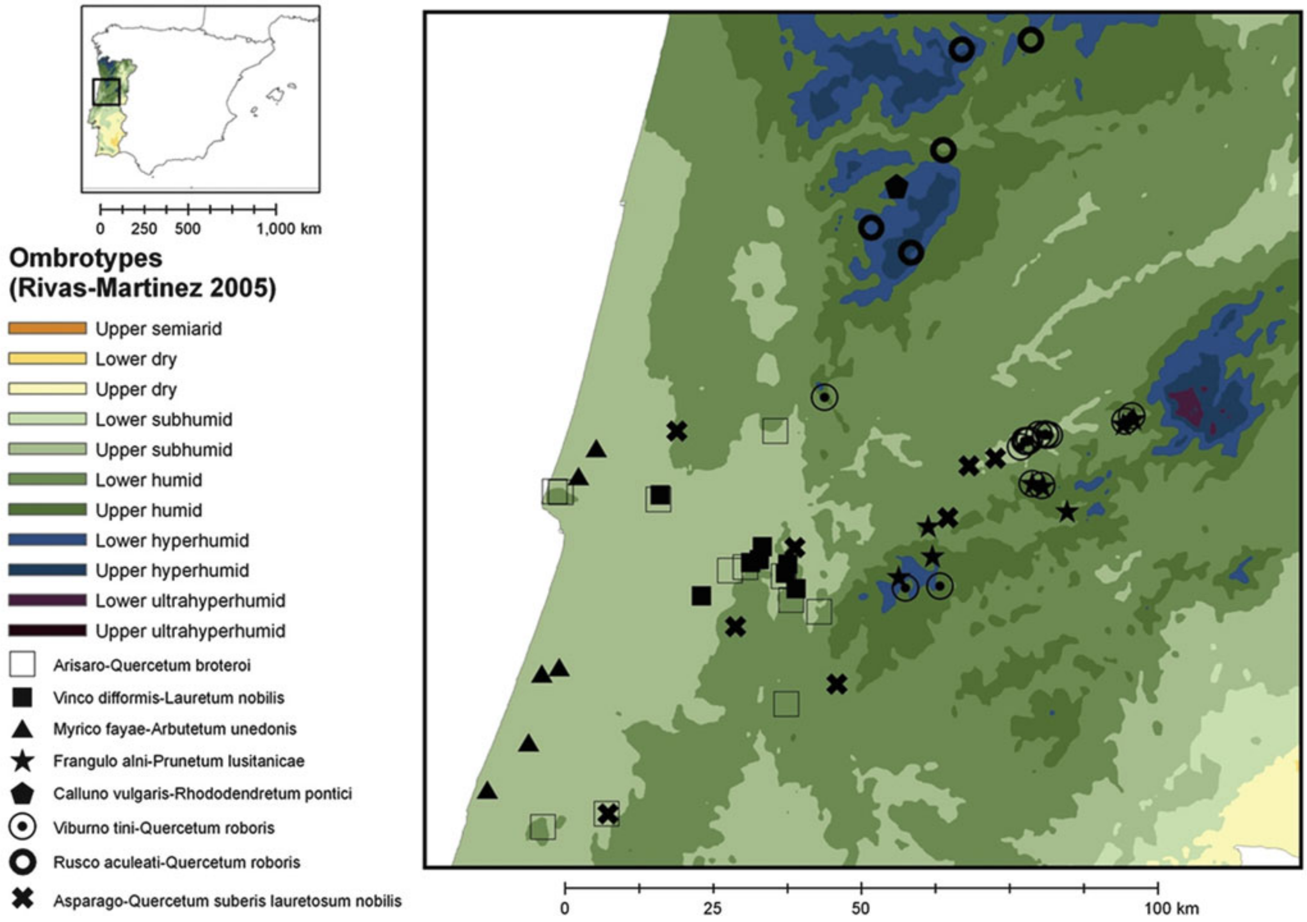


Fig. 3 Ombrotypes present in the study area, according to Rivas-Martínez (2005b)

hispanica, Acer monspessulanum, Viola riviniana, Asplenium onopteris, Vinca difformis, Linaria triornithophora, Blechnum spicant, and thermophilous species such as *Rubia peregrina, Arbutus unedo, Phillyrea latifolia, Smilax aspera* var. *altissima, Olea sylvestris, Asparagus aphyllus*, and *Phillyrea media* (Table 1). This community belongs to the *Querco-Fagetea, Quercetalia roboris, Quercion pyrenaicae, Quercenion robori-pyrenaicae*.

2. ***Rusco aculeati-Quercetum roboris***

   Quercus robur zonal deciduous meso-macroforest, growing on deep mesic soils derived from granitic rocks or meta-sediments. The thermophilous species disappear, as well as *Prunus lusitanica, Acer monspessulanum* and *Vinca difformis* (Table 1). This type occurs in the mesotemperate submediterranean humid to hyperhumid hyperoceanic Galician-Portuguese Sector. It has the same syntaxonomic position as the previous association.

3. ***Frangulo alni-Prunetum lusitanicae***

   Prunus lusitanica tempori-hygrophilous (azonal) mesoforest, growing on meta-sediments of rocky places, on steep slopes near valley bottoms, under meso-mediterranean humid hyperoceanic bioclimates, in the Littoral Beirensean mountains. This is constituted by laurophyll evergreen groves characterized by *Prunus lusitanica, Frangula alnus, Hedera hibernica, Polystichum setiferum, Ilex aquifolium, Viburnum tinus, Ruscus aculeatus, Asplenium onopteris, Lonicera periclymenum* ssp. *hispanica, Brachypodium sylvaticum, Salix atrocinerea, Blechnum spicant, Viola riviniana, Athyrium filix-femina, Saxifraga spathularis, Teucrium scorodonia, Laurus nobilis*, and *Dryopteris affinis* (Table 2). For now we place it in the class *Salici purpurea-Populetea nigrae*, order *Populetalia albae*, *Populion albae* alliance and *Fraxino angustifoliae-Ulmenion minoris* suballiance, due to its ecology (riparian-related vegetation) and the presence of *Frangula alnus, Hedera hibernica, Polystichum setiferum, Salix atrocinerea*, *Brachypodium sylvaticum, Vitis vinifera, Carex pendula, Scrophularia scorodonia, Oenanthe crocata, Alnus glutinosa, Fraxinus angustifolia, Osmunda regalis, Arum italicum, Ranunculus ficaria, Elymus caninus, Iris foetidissima* and *Angelica sylvestris*.

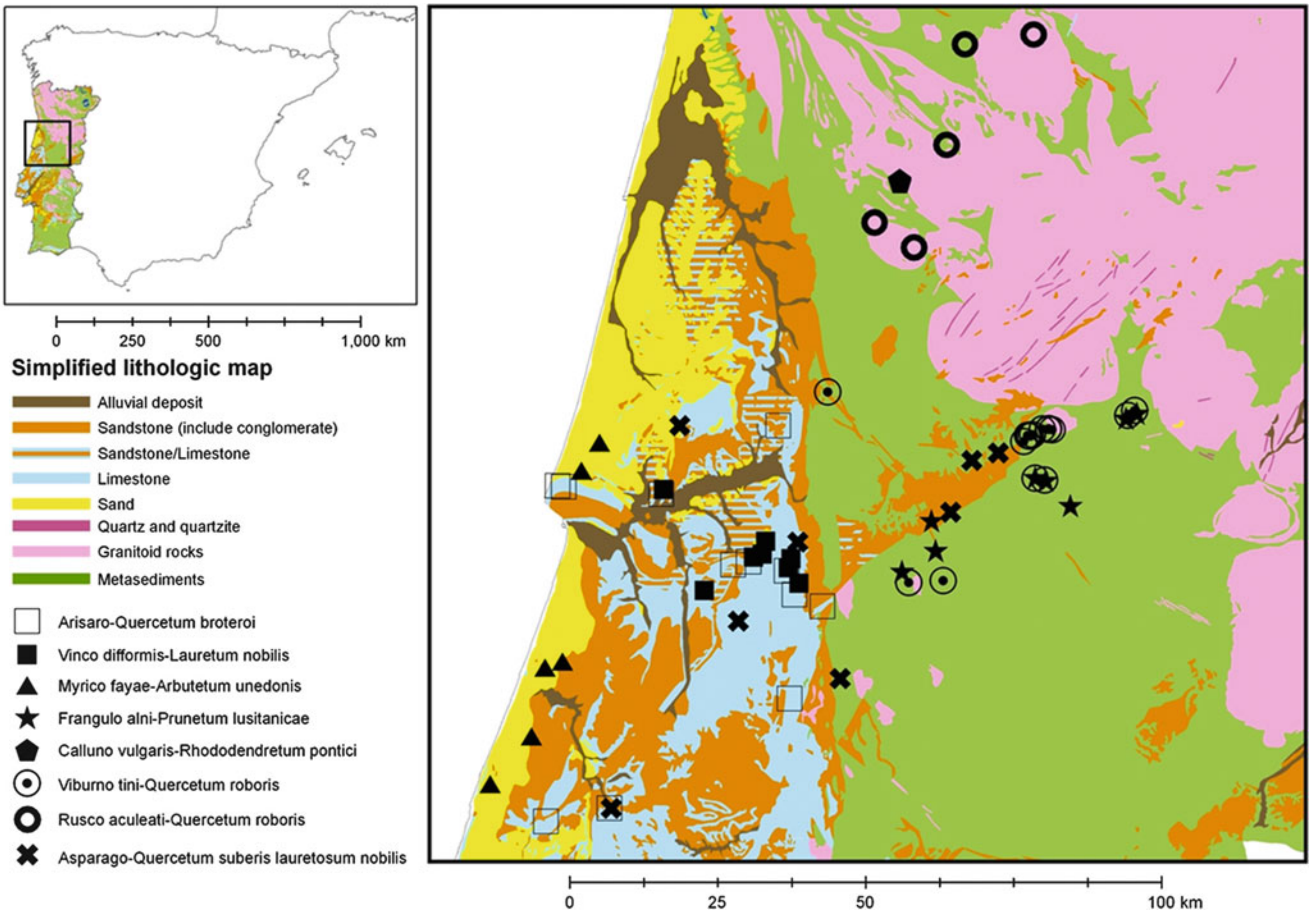


Fig. 4 Lithologic types present in the study area, adapted from the *Carta Geológica de Portugal 1/500,000* (Instituto Nacional de Engenharia, Tecnologia e inovação 2007)

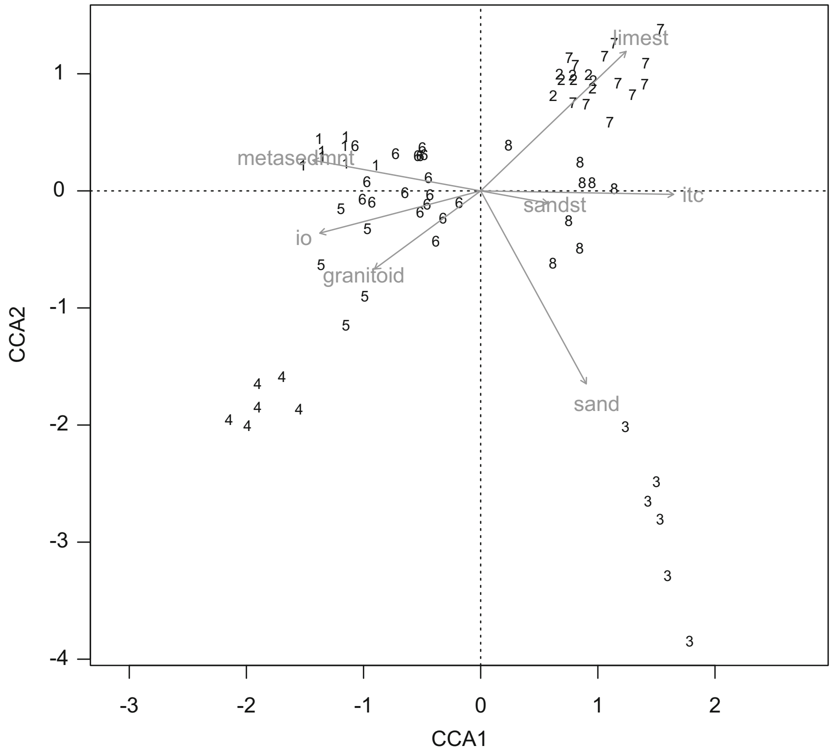


Fig. 5 CCA for relevé data and environmental data (Io, Itc and lithologic types). Total inertia 5.382; Constrained inertia 1.686 (31.34%); Unconstrained inertia 3.695 (68.66%). Legend: *1* Pru; *2* Lau; *3* Myr; *4* Rho; *5* Rus; *6* Vib; *7* Bro; *8* Sub

Table 1 *Viburno tini-Quercetum roboris* (1–17) *Rusco-Quercetum roboris* (18–22)

# releve	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Altitude (m)	230	250	245	240	295	200	250	430	610	425	700	650	300	270	470	235	505	790	520	250	833	670
Minimum surface (m^2)	150	100	200	100	50	100	400	200	200	100	200	200	200	200	100	200	200	100	200	100	100	100
Aspect	N	N	NW	N	NW	N	N	N	N	SW	S	SW	NW	N	SW	NW	SW	SW	NW	N	Pl	Pl
N° de espécies/*N° of releves*	35	29	42	26	40	38	40	48	37	41	32	36	35	41	25	37	26	33	37	27	11	18
Characteristics																						
Quercus broteroana	3	3	3	3	3	3	3	4	2	3	4	4	4	3	3	3	3	3	4	5	5	5
Lonicera hispanica	+	+	2	1	3	1	+	1	3	2	1	1	2	1	1	1		2	2	1	+	+
Hedera hibernica	4	2	1	3	1	1	1	3	3	2	2	1	1	1	2	2		+	4		1	+
Teucrium scorodonia		+	+	+	+	+	1	+	1	+	2	+	+	1	+	+	2	2	+			
Castanea sativa	+	1	1	+	2		+	2	4	2	2	2					3	2	2	1		
Polystichum setiferum	+	1	1	1	2	2	+	1	2	+	1			1			1	2	2	1		
Prunus lusitanica	1	1	+	1	+	1	+	1	2	2	+	1	1	1								
Crataegus brevispina	1	+	+	1			1		2	+			1	1		+			2			
Tamus communis	+	1	1	2	+	2							+	+	+	2			1			
Linaria triornithophora	+	+	1	+	+	+		+	+			+	+					+				
Clinopodium arundanum	+		+			+		+	+	+	2	1						+	+			
Sedum forsterianum	+	+	+	+				+		+			+			+		+	+			
Ilex aquifolium		+				+		2	+	1			1	+	2			1				
Luzula forsteri			+		+	+	+		2	+				+	+				+			+
Laurus nobilis	3	3	4	1	+	5		1							+				1			
Viola riviniana								+	+	1		2	1	+	2			+	+			+
Brachypodium sylvaticum	+		1		1	+		+	2		+					+						
Sambucus nigra	+	+	+	+	2	+			+										+			
Acer monspessulanum	3	2	3	4	3	1	+															
Bryonia dioica	+		+		1	1			1	+						1						
Holcus mollis											+	+	+					+	1	+	1	1
Arenaria montana										+			+	+		+		+	+	+		+
Pyrus cordata							+				1	2		+	+							
Frangula alnus							+				+	1					1			1		
Vinca difformis			1		+						1	1	+									
Quercus pyrenaica	+					1	+					1				1						
Quercus robur (frut.)					+			+	1									+			+	1
Prunus avium		+		+			+		+										3			
Crepis lampsanoides		+	+	1	+													+				
Polygonatum odoratum		+		+				+							1							
Blechnum spicant							+		+	+			+									
Silene latifolia						+						+						+		+		
Aristolochia paucinervis										+	+	+					+					
Corylus avellana	1						+							+								

(*continued*)

Table 1 (continued)

# releve	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Athyrium filix-femina	+				+						1											
Primula vulgaris									+	1										+		
Physospermum cornubiense										+				+	+							
Aquilegia dichroae							+		+										+			
Omphalodes nitida							+												3			
Acer pseudoplatanus			1									1										+
Luzula henriquesii							+		1													
Dryopteris borreri							1									+						
Melica uniflora	+		+																			
Saxifraga spathularis									+	+												
Rosa canina							+												+			
Stellaria holostea																		+	+			
More: 2*Ulmus glabra*,1*Cephalanthera longifolia*, +*Hypericum androsaemum* in 9; 1*Quercus* x *coutinhoi* in 12; 1*Euphorbia amygdaloides* in 19; +*Silene nutans*, +*Anemone albida* in 21																						
Characteristics of *Quercetea ilicis*																						
Ruscus aculeatus	+	2	2	+	1	2	1	2	1	1	.	1	2	1	2	1		1	1			
Asplenium onopteris	+	1	1	+	+	+	1	2	1	1	1	.	1	1	1	+		+	+			
Erica arborea	+		+		1			1	+	+	+	+	1	+		+	+	1	+	1	3	+
Viburnum tinus	4	2	2		+	+	1	3	2	2		+	1	2	+	+	1					
Rubia peregrina	+	1	1	+	1	+	+	+		1			+	+	+	2	+	+				
Arbutus unedo	+	+	+		1			3		1	+		1	1	2	2	1					
Daphne gnidium	+				+	+	+			+			1			1	+		+			
Carex distachya		+		+		+		+	+			+		+					+			
Quercus suber			1			+		+				2					2	2		+		
Phillyrea latifolia	2	1	+					+					+	1	+							
Olea sylvestris								+			2		+	1		+	+					
Smilax aspera var. *altissima*	+				+								+	1	+	1						
Phillyrea angustifolia								+		+				2		1	+					
Osyris alba		+	+			+										+	+					
Phillyrea media			1				+	2														
Asparagus aphyllus								+					+	+								
Scilla monophyllus								+						+	+							
Rhamnus alaternus								2						+								
Melica arrecta						+		+														
More: +*Lonicera etrusca* in 11; +*Hyancinthoides hispanica* in 15																						
Companions																						
Rubus ulmifolius	3	+	1	2	4	2		+	+	1	3	2	+	+		2	2	1	+	1		1
Pteridium aquilinum	+		+	1	1	1	1	+		1	1		1	1		1	1	2	2	3	3	2
Dactylis lusitanica		+	+	1	+	+		+			2	2	+	+		+	+	+	+	1		+
Digitalis purpurea					+	+	+	+	+			+		+			+	+	+	+	+	+

Pinus pinaster					1		+			3		1				1	3	2		2		
Polypodium australe							+	+		+	+	+		+	+			+		+		
Pseudarrhenatherum longifolium					+			+			+	1				+			+	1		2
Fraxinus angustifolia	1	1	1	1	1										+							+
Cytisus striatus					1			+						+			+	+		2		
Rumex acetosa	+		+		+		+	+	+							+				+		
Asplenium trichomanes	+		+			+		+		+	+											
Geranium purpureum	+			+		+			+	+									+			
Ulex minor							+				+	+	+	+				+				+
Genista falcata			+				2		+	1								+				
Agrostis castellana							+				+	1	+	+								
Scrophularia scorodonia											+					+	+		+	+		
Chelidonium majus			+			+			+		+											
Cytisus grandiflorus					+		+	+		+												
Calluna vulgaris										+		+	+				+					
Ailanthus altissima					1	+										1						
Erica scoparia										+			1	+								
Lavandula luisieri										+						+	1					
Lithodora prostrata														+				1				+
Vitis vinifera						+	+				+											
Carex depressa							+							+	+							
Calamintha baetica										+	+	+										
Simethis mattiazzi												+			+						+	

More: 1*Robinia pseudacacia* in 5 and 16; +*Urtica dioica* in 6 and 8; +*Origanum virens* in 6 and 17; +*Lamium maculatum* in 8 and 16; +*Galium mollugo* in 10 and 16; +*Pterospartum tridentatum* in 11 and 12; +*Thalictrum speciosissimum* in 3; +*Erica lusitanica*, +*Ajuga reptans* in 7; 1*Tradescantia fluminensis*, +*Sellaginella denticulata*, +*Antirrhinum meonanthum*, +*Coincya pseudoerucastrum* in 8; +*Agrostis curtisii* in 12; +*Erica umbellata* in 13; 1*Acacia melanoxylon*, +*Thapsia villosa* in 16; +*Cistus salviifolius* in 17; +*Erica cinerea*, +*Hypericum perforatum* in 18; +*Cistus psilosepalus*, +*Anthoxanthum odoratum* in 19; 1*Ulex latebracteatus*, 1*Adenocarpus lainzii*, 1*Agrostis stolonifera*, +*Poa sylvicola* in 20; 2*Genista polygaliphylla* in 21

Places: 1, 2, 3, 4, 6 Vila Cova de Alva, 5 Quinta do Casal, Vila Cova de Alva (Arganil), 7 Avô (Braun-Blanquet et al. 1956), 8 Fraga da Pena (Arganil), 9 Mata da Margaraça (Arganil), 10 Casal do Rei (Seia), 11 Ribeira de Pena, Coentral (Castanheira de Pêra), 12 Coentral Grande (Castanheira de Pêra), 13 Serra do Buçaco (Penacova, Braun-Blanquet et al. 1956), 14 Avô (Costa et al. 2002), 15, 16 Avô (Oliveira do Hospital), 17 Cabeça (Seia), 18 Pena (S. Pedro do Sul), 19 Castro Daire, 20 Paço, Vilharigues (Vouzela), 21 Serra do Caramulo (Tondela), 22 Paranhos de Arca (Oliveira de Frades)

Table 2 *Frangulo alni-Prunetum lusitanicae*

# releve	1	2	3	4	5	6	7	8	9
altitude (m)	595	378	440	410	350	700	610	730	
Minimum surface (m^2)	50	60	70	100	40	50	50	40	
Aspect	N	N	N	N	NE	N	N	W	
N° of species/*N° of releves*	26	45	38	41	29	31	30	21	*19*
Characteristics									
Prunus lusitanica	4	4	4	4	4	3	3	4	V
Frangula alnus	+	2	1	2	2	3	3	4	IV
Hedera hibernica	3	2	2	3	2	+	2	1	IV
Polystichum setiferum	3	3	2	2	1	2	3	1	III
Ilex aquifolium	1	1	+	+	+	2	1	2	III
Lonicera hispanica	2	1	1	3	1	+	1		IV
Brachypodium sylvaticum		1	1	1	1	+	1	1	III
Rubus ulmifolius	+	1	1	2	+		2	1	II
Salix atrocinerea	2	1	2	1	1	+			+
Blechnum spicant	+	1	2			+	1	1	III
Viola riviniana	+	+		+	1	2	+		III
Vitis vinifera		+	+	+	+	1		1	I
Athyrium filix-femina		1	+			1	+	1	II
Saxifraga spathularis	+	+	+			+		1	III
Teucrium scorodonia		+	+	+	+		+	+	II
Laurus nobilis			1	+		1		1	I
Scrophularia scorodonia		1	+	2	+			+	
Oenanthe crocata		1	+	+	+		+		
Dryopteris affinis			+	1		1	1		II
Carex pendula	3			1		1			+
Sambucus nigra	1	2	+	1					
Alnus glutinosa		1				1		1	I
Osmunda regalis			2	1		+			+
Castanea sativa	2	1			1				III
Hypericum androsaemum	+	1		+					+
Quercus robur		+	+	+					I
Crataegus monogyna ssp. *brevispina*			+		1	2			II
Sedum forsterianum				+	+	+			II
Luzula forsteri	+						+		II
Primula vulgaris	+	+							I
Prunus lusitanica (frut.)		+	+						I
Fragaria vesca		+	+						+
Fraxinus angustifolia		1	2						
Arum italicum	+	+							
Ranunculus ficaria			+	+					
Elymus caninus								1	+
Tamus communis		+							I
Prunus avium							+		I
More: 2*Ulmus glabra* in 1; 1*Prunus spinosa,* 1*Omphalodes nitida* in 2; +*Corylus avellana* in 3; +*Iris foetidissima,* +*Linaria triornithophora* in 4; I *Geum sylvaticum* I *Arenaria montana*, +*Aristolochia paucinervis*, +*Calamintha baetica,* +*Quercus pyrenaica*, +*Clinopodium vulgare* in 9;									
Characteristics *Quercetea ilicis*									
Viburnum tinus	1	1	1	2	2	+	2		IV
Asplenium onopteris	+		+	+	+	+	1		IV
Ruscus aculeatus	+	+	+	+		+	1		IV
Erica arborea			+		1	+	+	3	III
Rubia peregrina		+	+	+			+		III
Phillyrea angustifolia					+	1	+		III
Arbutus unedo				1	1				III

(*continued*)

Table 2 (continued)

# releve	1	2	3	4	5	6	7	8	9
Phillyrea latifolia				2	1				+
Osyris alba							+		II
Daphne gnidium					+				I
Phillyrea media				3					
More: +*Rhamnus alaternus* in 3, I *Scilla monophyllus*, +*Quercus suber*, +*Quercus rotundifolia* in 9;									
Companions									
Hypericum undulatum		+	+	+		+	+	+	II
Sellaginella denticulata		1	1	2			1		I
Rumex angiocarpus	+	+		+			+		II
Prunella vulgaris		+	+	+	+				I
Geranium purpureum	+		+	+		+			+
Galium broterianum		+				1		1	I
Carex acuta		+			+		1		II
Pteridium aquilinum	+	1	1						
Dactylis lusitanica				+		+		1	I
Lotus pedunculatus		+				+			II
Cytisus scoparius					+		+		II
Lithodora prostrata					+		+		II
Urtica dioica	1			+					
Lycopus europaeus	+	+							
Mentha suaveolens		+	+						
Digitalis purpurea	+				+				I
Wahlenbergia hederacea		+				+			I
Holcus lanatus		+							I
Potentilla erecta								+	II
Ulex minor								+	I

More: +*Angelica sylvestris* in 2; 2*Tradescantia fluminensis*, +*Chelidonium majus*, +*Lamium maculatum* in 4; II *Cytisus striatus*, II *Lavandula luisieri*, II *Polypodium vulgare*, I *Cistus psilosepalus*, I *Cytisus grandiflorus*, I *Pterospartum tridentatum*, I *Ranunculus flammula* in 9

Places: 1 Mata da Margaraça (Arganil), 2 Ribeira da Loriga, Casal do Rei (Seia) 3 Ribeira da Loriga, Cabeça (Seia), 4 Fraga da Pena (Arganil), 5 Aldeia de Sotão (Góis), 6 Ribeira da Pena (Serra da Lousã, Góis), 7 Rio Ceira, Camba (Serra do Açor, Pampilhosa da Serra), 8 Serra da Lousã, 9 Costa et al. (2000a)

4. ***Asparago aphylli-Quercetum suberis***

   Quercus suber zonal mesoforest, growing on deep mesic soils, predominantly over sandstones (rarely over metasediments). This is constituted by evergreen woods, under a meso-mediterranean subhumid to humid hyperoceanic bioclimate, mainly in the Sadensean Subprovince of the Portuguese Dividing Province. *Quercus suber, Asparagus aphyllus, Arbutus unedo, Rubia peregrina, Smilax aspera* var. *altissima, Quercus broteroi, Quercus lusitanica, Ruscus aculeatus, Rhamnus alaternus, Hedera maderensis* ssp. *iberica, Phillyrea latifolia, Viburnum tinus, Myrtus communis, Pistacia lentiscus, Quercus coccifera, Scilla monophyllus,* etc. (Table 3) are the characteristics species.

   For the Littoral Beirensean district we propose the new subassociation ***lauretosum nobilis*** subass. nova hoc loco (*typus* relevé 2, Table 3), the differential species of which are *Laurus nobilis, Quercus robur* ssp. *broteroana, Ranunculus bupleuroides, Viola riviniana* and missing *Deschampsia stricta, Euphorbia characias, Lonicera implexa, Biarum arundanum* (Table 3). Its syntaxonomic position is in *Quercetea ilicis, Quercetalia ilicis* and *Querco rotundifoliae-Oleion sylvestris.*

5. ***Arisaro-Quercetum broteroi***

   Quercus broteroi zonal mesoforest, growing on deep mesic soils derived from calcareous marls and limestones of the Portuguese Dividing Sector and Serra da Arrábida (mountain), under a meso-mediterranean subhumid to humid hyperoceanic bioclimate. It constitutes marcescent woods formed by *Quercus broteroi, Smilax aspera* var. *altissima, Ruscus aculeatus, Rubia peregrina, Arisarum simorrhinum, Laurus nobilis, Asparagus aphyllus, Rosa sempervirens, Rhamnus alaternus, Hedera hibernica, Quercus coccifera, Arbutus unedo, Vinca difformis, Euphorbia characias, Pistacia lentiscus, Coronilla glauca, Phillyrea latifolia, Genista tournefortii, Viburnum tinus, Lonicera etrusca, Crataegus monogyna* ssp. *brevispina*, *Cheirolophus sempervirens,* etc. (Table 4). It

Table 3 *Asparago aphylli-Quercetum suberis*

# releve	1	2	3	4	5	6	7	8	9
Altitude (m)	235	265	240	275	125	230	100	210	
Minimum surface (m^2)	50	200	100	150	200	200	95	210	
Aspect	W	SE	S	NW	NW	SW	SW	W	
N° of species/*N° of releves*	29	31	35	32	38	37	30	31	*30*
Characteristics									
Quercus suber	2	5	5	4	4	3	4	3	V
Rubia peregrina	+	2	+	1	1	1	1	+	V
Asparagus aphyllus	+	+	+	+	1	1	+	+	V
Arbutus unedo	3		1	1	2	3	1	2	III
Smilax aspera var. *altissima*	1	3	+	1	1	1	1		V
Ruscus aculeatus	3		1	1	2	3	+	2	III
Quercus lusitanica	1	+		2	+	2		2	III
Rhamnus alaternus	+	1	+	1		1		+	IV
Erica arborea	2	+	1			1	+	2	II
Daphne gnidium	1	+		+		1	1	+	IV
Pistacia lentiscus	+			1	+	+	1	+	III
Pulicaria odora	+		+	+		+	+	+	II
Quercus broteroi		1	1	+	1		1		IV
Scilla monophyllus			+	+	+	+		+	II
Quercus coccifera				1	1	+	1	+	III
Hedera maderensis ssp. *iberica*		2	+		1	+			IV
Osyris alba	1	3		1		+			III
Quercus suber (frut.)		1			1	+		+	III
Phillyrea latifolia	+	+	+		2				II
Carex hallerana			1	1	+	+			r
Viburnum tinus			1		2			+	II
Asplenium onopteris		3			+	+			II
Myrtus communis			+		2	+			III
Luzula forsteri		2			+	+			I
Carex distachya		2			+	+			II
Olea sylvestris	+	+						+	III
Phillyrea angustifolia	1				+				II
Vinca difformis	+				1				III
Arisarum simorrhinum			+		+				III
Rosa sempervirens			1						III

More: III L*onicera etrusca,* III *Euphorbia characias,* II *Deschampsia stricta*, II *Epipactis tremolsii*, I *Lonicera implexa,* I *Cephalanthera longifolia,* I *Asparagus acutifolius,* I *Biarum arundanum, +Rhamnus oleoides, +Genista tournefortii, +Hyacinthoides hispanica, +Quercus* x *airensis*, *+Anemone palmata, +Melica arrecta, +Sanguisorba hybrida,* r *Coronilla glauca,* r *Paeonia broteroi* in 9

Differentials of subassociation *lauretosum nobilis*									
Laurus nobilis	+	+	1	+	1	1	1	+	
Quercus robur ssp. *broteriana*	+	+				+			
Ranunculus bupleuroides	+					+		+	
Viola riviniana		+				+			
Companions									
Lonicera hispanica		1	+	+	+	+	+	+	III
Dactylis lusitanica	+		+	+	+	+		+	II
Tamus communis		2	+	.	+	+	+		IV
Cistus salviifolius			+	+	+		1	1	IV
Lavandula luisieri			+	+		+	1	1	II
Ulex jussiaei			+	+	+	+		+	IV
Origanum virens	+			+	+		+	+	III
Rubus ulmifolius	1				3		2	1	V
Urginea maritima		+		+		+		+	II

(*continued*)

Table 3 (continued)

# releve	1	2	3	4	5	6	7	8	9
Pteridium aquilinum	2					1		1	II
Aristolochia paucinervis		+				+	1	+	II
Crataegus monogyna ssp. *brevispina*	+			+	+				II
Erica cinerea			+	+	+		+		II
Genista triacanthos			1			+	+		II
Brachypodium sylvaticum		1		+		+			+
Erica scoparia				+		+		+	II
Teucrium scorodonia					+	+	+		III
Brachypodium phoenicoides				+	+		+		III
Agrostis curtisii	+		+					+	r
Pinus pinaster	3					2		2	
Cytisus striatus	1		+						+
Polypodium cambricum		1				+			I
Geranium purpureum					+		+		II
Digitalis purpurea	+	+	+						
Calluna vulgaris			+	+					I
Erica australis	+		+						
Sanguisorba spachiana			+	+					
Calamintha baetica					+				III
Cistus crispus							1		II
Iris foetidissima					+				II
Lithodora prostrata							+		II
Thapsia villosa							+		II
Agrimonia eupatoria							+		I
Clinopodium arundanum							+		I

More: 2*Acacia melanoxylon* in 1; 1*Selaginella denticulata, +Agrostis castellana* in 2; 1*Asphodelus lusitanicus,*1*Agrostis truncatula, +Genista falcata* in 3; III *Prunus insititioides,* I *Quercus pyrenaica* in 9;

Places: 1 Góis, 2 Casal de S. Simão (Figueiró dos Vinhos), 3 Condeixa, 4 Degracias (Soure), 5 Curvachia (Leiria), 6 Sarzedo (Arganil), 7 Cabeço da Arroteia, 8 Arazede (Montemor-o-Velho), 8 Secarias (Arganil), 9 Costa et al. (2002a, b)

stands in the *Quercetea ilicis, Quercetalia ilicis* and *Quercion broteroi.*

6. ***Vinco difformis-Lauretum nobilis***

   Laurus nobilis tall scrub or thicket growing on limestone, usually found along the edges of *Arisaro-Quercetum broteroi* woods, especially in the contacts with damp soils (azonal). It occurs in the Portuguese Dividing Sector, under a meso-mediterranean subhumid to humid hyperoceanic bioclimate. These laurophyll thickets are characterized by *Laurus nobilis, Vinca difformis, Smilax aspera* var. *altissima, Ruscus aculeatus, Hedera hibernica, Rubia peregrina, Cornus sanguinea, Asparagus aphyllus, Rosa sempervirens, Crataegus monogyna* ssp. *brevispina, Quercus broteroi, Tamus communis, Arbutus unedo, Fraxinus angustifolia, Prunus spinosa* ssp. *insititioides, Phillyrea latifolia, Brachypodium sylvaticum, Viburnum tinus, Ulmus minor, Rhamnus alaternus, Teucrium scorodonia,* etc. (Table 5). Its syntaxonomic position is in the *Quercetea ilicis, Pistacio lentisci-Rhamnetalia alaterni, Arbuto unedonis-Laurion nobilis* and *Arbuto unedonis-Laurenion nobilis.*

7. ***Myrico fayae-Arbutetum unedonis***

   Myrica faya and *Arbutus unedo* tall scrub, found regenerating underneath the coppice of *Pinus pinaster* plantations, growing in depressions with a relatively high water table (azonal), on old fixed dunes of the Portuguese Dividing Sector. It is a meso to thermo-mediterranean subhumid hyperoceanic community, formed by *Myrica faya, Arbutus unedo, Phillyrea angustifolia, Erica arborea, Cytisus grandiflorus, Corema album, Ulex latebracteatus, Hedera iberica, Rubia peregrina, Ruscus aculeatus, Viburnum tinus, Quercus coccifera, Laurus nobilis, Smilax aspera, Pistacia lentiscus, Rhamnus alaternus, Asparagus aphyllus, Pteridium aquilinum, Pinus pinaster* ssp. *atlantica, Halimium halimifolium* ssp. *multiflorum*, etc. (Table 6). It has the same syntaxonomic position as the previous association.

8. ***Calluno vulgaris-Rhododendretum baeticae***

   Meso-temperate submediterranean humid to hyperhumid silicicolous low scrub, dominated by *Rhododendron ponticum* ssp. *baeticum*, colonising the heads of small,

Table 4 *Arisaro-Quercetum broteroi*

# releve	1	2	3	4	5	6	7	8	9	10	11	12
Altitude (m)	80	160	100	120	250	280	345	90	120	168	300	70
Aspect	P	SW	NE	NW	W	N	N	N	Pl	NW	W	N
Minimum surface (m^2)	600	800	200	200	100	200	100	100	100	200	100	100
N° of species	31	35	23	51	24	32	25	25	28	32	18	23
Characteristics												
Quercus broteroi	5	5	4	4	4	5	5	4	4	4	4	4
Smilax aspera var. *altissima*		4	+	3	+	2	2	1	1	1	1	+
Ruscus aculeatus	2	2	+	+	+	2	3	2	1	2	2	
Rubia longifolia	+	2	1	2	1	1	+		+	+	1	+
Crataegus brevispina	2	1	1	2	1		+	1	2	1		1
Arisarum simorrhinum	+	+	+	+	1	1	+	+	1	+		+
Asparagus aphyllus		1	+	+	+	+	+	+	+		+	
Laurus nobilis	+	1	2	1	+	+	2	2	1			
Rhamnus alaternus	+	2		1		1	+		2	1	2	
Quercus coccifera		1	1	2	+	1			1	1	+	
Euphorbia characias	+			+	1		2	1	1	+	+	
Hedera hibernica	2	4		2		+	3	1		3		1
Rosa sempervirens	+	3		2	+	1		1	1	2		
Arbutus unedo	2	1		2	+	+			1		+	
Vinca difformis			1	1		+	2	1		2	1	
Pistacia lentiscus	1	1		1		1			+	+		
Quercus x *coutinhoi*			2	+			+	+		1		1
Genista tournefortii		+		2	+	+				1		+
Daphne gnidium		+		+		+			1	+		1
Quercus robur ssp. *broteroana*			2				1	2		+		1
Asplenium onopteris	1			+			3	1	1			
Coronilla glauca	1		+	2					+	1		
Scilla monophyllus		+	+	+						+		+
Phillyrea latifolia	2						2	1		2		
Viburnum tinus	3	2		+						1		
Lonicera etrusca				+					1	+	1	
Myrtus communis	1								+	2		1
Cephalanthera longifolia		+			1				+	+		
Melica arrecta						1	+	+	+			
Osyris alba		2		+					1			
Quercus suber	+								1			1
Erica arborea	+			+								2
Luzula baetica	1						+	1				
Olea sylvestris		1		+		+						
Carex distachya	+	+								+		
Quercus lusitanica										1		1
Hyacinthoides hispanica		+	+									
Epipactis tremolsii		+				+						
Pulicaria odora				+								+
More: 1*Cheirolophus sempervirens* in 4; +*Biarum arundanum*, +*Carex hallerana* in 5; +*Lonicera implexa* in 6; +*Phillyrea angustifolia* in 9; +*Jasminum fruticans*, +*Paeonia broteroi* in 11												
Companions												
Rubus ulmifolius	+	3	1	1				1	+	1		1
Tamus communis	+	1		+			2	1		1	+	
Dactylis hispanica			+	+	+	1				+		+
Brachypodium phoenicoides			1	1	+	1						1
Brachypodium sylvaticum		1	1				+	1		+		
Arum italicum	1	+				1	+				+	

(*continued*)

Table 4 (continued)

# releve	1	2	3	4	5	6	7	8	9	10	11	12
Geranium purpureum		+	1	+						+		+
Polypodium australe		+		+			+	1				
Lavandula luisieri				+	+	+		1				
Iris foetidissima	+		+	+			+					
Sanguisorba spachiana					+	+			+		+	
Cistus salviifolius					+	+						2
Pinus pinaster		1				1		+				
Aristolochia paucinervis	+	1		+								
Prunus spinosa ssp. *insititioides*			1			+	+					
Ulex jussiaei								+	1		+	
Urginea maritima				+		+						+
Lonicera hispanica	1			+								
Origanum virens				+		1						
Geum sylvaticum				+						1		
Asplenium quadrivalens	+			+								
Teucrium scorodonia			+	+								
Agrimonia eupatoria			+	+								
Thapsia villosa				+	+							
Lathyrus sylvestris				+	+							
Sedum forsterianum				+		+						
Cistus crispus					1							

More: +*Polygonatum odoratum*, +*Ficus carica* in 2; +*Silene longicilia,* +*Antirrhinum linkianum* in 4; +*Carex flacca* in 6; +*Ulex minor* in 7; +*Calamintha baetica* in 8; +*Erica scoparia* in 9; +*Fraxinus angustifolia,* +*Carex divulsa* in 11; +*Holcus lanatus* in 12

Places: 1 Mata da Curvachia (Leiria), 2 Maceira de Leiria, 3 Quintas (Mealhada), 4, 10 Serra da Boa Viagem (Figueira da Foz), 5 Traveira (Condeixa), 6, 11 Condeixa, 7 Casal Soeiro (Ansião), 8 Montemor-o-Velho, 9 Ameixeira (Condeixa), 12 Ega (Condeixa)

seasonally flowing streams (azonal) of the Caramulo mountain. This laurophyll species occurs as a paleo-endemic element with a disjunct distribution in the south-western Iberian Peninsula (Algibe and Monchique mountains). *Rhododendron ponticum* ssp. *baeticum*, *Quercus robur, Lonicera periclymenum, Erica arborea, Rubus ulmifolius, Salix atrocinerea, Calluna vulgaris, Blechnum spicant, Tamus communis, Teucrium scorodonia, Osmunda regalis, Agrostis x fouilladei, Dactylis lusitanica, Calluna vulgaris* are the common species (Table 7). We position it in the *Salici purpurea-Populetea nigrae*, *Populetalia albae* and *Osmundo-Alnion*, due to its ecology (riparian vegetation) and floristic composition (*Salix atrocinerea, Osmunda regalis*).

Syntaxonomic scheme:

QUERCO-FAGETEA Br.-Bl. & Vlieger in Vlieger 1937

Quercetalia roboris Tüxen 1931

Quercion pyrenaicae Rivas-Goday ex Rivas-Martínez 1975

Quercenion robori-pyrenaicae (Br.-Bl., P. Silva & Rozeira 1956) Rivas-Martínez 1975

Rusco aculeati-Quercetum roboris Br.-Bl., P. Silva & Rozeira 1956 em. Amigo, Izco, J. Guitián & Romero 1998

Viburno tini-Quercetum roboris (Br.-Bl., P. Silva & Rozeira 1956) J.C. Costa, Capelo, Honrado, Aguiar & Lousã 2002

QUERCETEA ILICIS Br.-Bl. ex A. & O. Bolòs 1950

Quercetalia ilicis Br.-Bl. ex Molinier 1934 em. Rivas-Martínez 1975

Quercion broteroi Br.-Bl., P. Silva & Rozeira 1956 em. Rivas-Martínez 1975 corr. V. Fuente 1986

Quercenion broteroi

Arisaro-Quercetum broteroi Br.-Bl., P. Silva & Rozeira 1956 corr. Rivas-Martínez 1975

Querco rotundifoliae-Oleion sylvestris Barbéro, Quézel & Rivas-Martínez in Rivas-Martínez, Costa & Izco 1986

Asparago aphylli-Quercetum suberis J.C. Costa, Capelo, Lousã & Espírito Santo 1996

lauretosum nobilis J.C. Costa, Monteiro-Henriques, P. Bingre & Espírito Santo subass. nova hoc loco

Pistacio lentisci-Rhamnetalia alaterni Rivas-Martínez 1975

Arbuto unedonis-Laurion nobilis Rivas-Martínez, Fernández-González & Loidi 1999

Arbuto unedonis-Laurenion nobilis Rivas-Martínez & Sánchez-Mata 2001

Table 5 *Vinco difformis-Lauretum nobilis*

# releve	1	2	3	4	5	6	7	8	9
altitude (m)	110	50	200	205	160	130	100	250	
Aspect	N	NW	NE	N	N	N	NW	N	
Minimum surface (m^2)	50	20	20	50	50	50	100	30	
N° of species/*N° of releves*	19	27	21	18	29	31	38	20	*10*
Characteristics									
Laurus nobilis	4	4	4	4	4	5	5	5	V
Hedera hibernica	2	2	+	3	4	4	3	1	V
Smilax aspera	+	1	+	2	1	2	3		V
Vinca difformis		2	1	3	3	3	3	+	V
Rosa sempervirens	2	1	+		+		2	+	V
Rubia peregrina		+	1	+		+	1	+	IV
Ruscus aculeatus		1		3	3	1	+		IV
Quercus broteroi		1		1	1	+	+		IV
Viburnum tinus	+	1				+	2	+	III
Erica arborea	+		1			+	1	+	
Rhamnus alaternus		+	+		+		+		III
Asparagus aphyllus		+		+	+	+			II
Phillyrea latifolia				1	2	1			II
Arbutus unedo		1					2	+	III
Prunus spinosa ssp. *insititioides*		1					+	+	V
Euphorbia characias				+	1	+			III
Asplenium onopteris				1	2	+			II
Olea sylvestris				1	1	+			II
Quercus coccifera	+						1		V
Lonicera etrusca		+					+		I
Phillyrea angustifolia							1		II
Osyris alba		+							III
Pistacia lentiscus		+							II
Arisarum simorrhinum					+				II
Luzula forsteri					+				II
Melica arrecta					+				I
Daphne gnidium			+						
More: +*Daphne gnidium* in 3; I *Bupleurum fruticosum*, I *Prunus lusitanica*, I *Hyacinthoides hispanica* in 9									
Characteristics of *Querco-Fagetea, Pruno-Rhamnetea, Trifolio-Geranietea*									
Rubus ulmifolius	+	2	+	+	1	2	2	+	V
Crataegus monogyna ssp. *brevispina*	+	2	+	+	1	2	2	+	III
Tamus communis	+		+	2	1	2	2	+	IV
Lonicera hispanica	1	1	+			1	2	+	III
Cornus sanguinea	1	2	2			+	+	+	
Brachypodium sylvaticum	1	+	+		1	+			III
Fraxinus angustifolia	+	1	+				+	+	II
Ulmus minor			+	+	+	+	1		III
Arum italicum		+	+		+	+	+	+	
Quercus robur				1	1	+		1	I
Iris foetidissima	+	+		+			+		III
Teucrium scorodonia		+				+	+	+	IV
Bryonia dioica		+				+	+		III
Origanum virens						+	+		III
Calamintha baetica					+		+		II
Cheirolophus sempervirens		+							IV
Salix atrocinerea	1								II
Corylus avellana								+	II
Primula vulgaris	+				+				

(*continued*)

Table 5 (continued)

# releve	1	2	3	4	5	6	7	8	9
More: +*Vitis vinifera* in 3; +*Thalictrum speciosissimum* in 9; II *Castanea sativa*, II *Prunus avium* I *Clematis vitalba,* I *Rosa canina,* I *Leucanthemum sylvaticum* in 9									
Companions									
Equisetum ramosissimum	+		+			+	+		
Cistus salviifolius					+	+	+		I
Geranium purpureum						+	+		IV
Dactylis hispanica						+	+		I
Brachypodium phoenicoides							1		I
Pteridium aquilinum							+		III
Silene longicilia							+		III
Piptatherum miliaceum							+		III
Lathyrus clymenum							+		II
Urginea maritima						+			II
More: +*Holcus lanatus* in 1; +*Ulex minor* in 3; +*Scrophularia grandiflora,* +*Agrostis stolonifera*, +*Ulex jussiaei* in 5; I *Rosmarinus officinalis* in 9									

Places: 1 Ereiras (Condeixa), 2 Paleão (Soure), 3 Bruscos (Condeixa), 4 Traveira (Condeixa), 5 Condeixa, 6 Montemor-o-Velho, 7 Conimbriga (Condeixa), 8 Eira da Lagoa (Penela), 9 Costa et al. (2000)

Myrico fayae-Arbutetum unedonis Capelo & Mesquita 1998

Vinco difformis-Lauretum nobilis Capelo & J.C. Costa in J.C. Costa, C. Lopes, Capelo & Lousã 2000

SALICI PURPUREAE-POPULETEA NIGRAE (Rivas-Martínez & Cantó ex Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González & Loidi) Rivas-Martínez & Cantó 2002

Populetalia albae Br.-Bl. ex Tchou 1948

Populion albae Br.-Bl. ex Tchou 1948

Fraxino angustifoliae-Ulmenion minoris Rivas-Martínez 1975

Frangulo alni-Prunetum lusitanicae C. Lopes, J.C. Costa, Lousã & Capelo in J.C. Costa, C. Lopes, Capelo & Lousã 2000

Osmundo-Alnion (Br.-Bl., P. Silva & Rozeira 1956) Dierschke & Rivas-Martínez in Rivas-Martínez 1975

Calluno vulgaris-Rhododendretum baetici Honrado, P. Alves, Lomba, Torres & B. Caldas 2007

Analysis of the cover percentage of relict species and of newly adapted laurophyll species revealed, as expected, that the relict species dominate in the extrazonal groves and the newer, laurophyll species have high total cover in the zonal communities (Figs. 6 and 7). The *Calluno vulgaris-Rhododendretum baetici* and the *Rusco aculeati-Quercetum roboris* associations show the lowest cover values by the newly adapted species (Fig. 7). This can be explained by the fact that these communities occur in a meso-temperate bioclimate and the newly adapted species are frequently thermophilous.

Figure 6 also shows that, among zonal forests, the *Viburno tini-Quercetum roboris* and *Arisaro-Quercetum broteroi* show the highest values of true relict elements, leading us to the conclusion that these two forests (especially the *Viburno-Quercetum*) may occupy areas with climatic conditions closer to those of their ancient tropical/subtropical habitats.

The communities studied respond to a complex gradient of temperature and water availability, as was confirmed by the CCA. Temperature decreases towards the higher latitudes and altitudes, precluding the presence of thermophilous species and permitting true temperate deciduous forests to dominate the vegetated landscape (*Rusco aculeati-Quercetum roboris*); in the same bioclimate, *Calluno vulgaris-Rhododendretum baetici* scrub occurs very sporadically and is present only in sheltered valleys protected by steep slopes. Summer drought increases towards the south and at low altitude, and the Mediterranean climate and plant traits become more evident. In fact, the *Asparago aphylli-Quercetum suberis lauretosum nobilis* forests can be considered true Mediterranean forests, dominated by the sclerophyllous species *Quercus suber*.

Between the coldest forests and the Mediterranean forests we find the *Viburno tini-Quercetum roboris* and the *Arisaro-Quercetum broteroi* formations. The first is considered a true warm-temperate forest occupying thermo-temperate and more humid lower meso-mediterranean areas; we can testify that there is a tendency for *Quercus robur* ssp. *broteroana* to keep a small amount of green foliage during winter (semi-deciduous habit), especially in warmer parts of its range. Probably, however, the winter absolute temperature minima (related to the advent of polar cold fronts) encourage the deciduous habit of the zonal forests and keep the relict laurophyll species restricted to the sheltered valleys as well. The *Arisaro-Quercetum broteroi* formations occupy an intermediate position between the warm-temperate and the Mediterranean forests, being dominated by a particular oak

Table 6 *Myrico fayae-Arbutetum unedonis*

# releve	1	2	3	4	5	6	7
Altitude (m)	50	50	70	60	45	55	
Minimum surface (m^2)	50	50	30	50	50	40	
N° of species/*N° of releves*	20	23	19	27	28	21	*6*
Characteristics							
Myrica faya	4	4	3	2	1	3	V
Arbutus unedo	1	2	3	3	3	3	V
Erica arborea	1	1	2	1	3	3	V
Phillyrea angustifolia	1	2	+	2	2	1	V
Cytisus grandiflorus	2	1	2	1	+	1	V
Hedera maderensis ssp. *iberica*	1	+	2	1	1	+	V
Corema album	2	1	1	1	+	1	V
Daphne gnidium	+	1	1	+	1	1	III
Rubia peregrina	+	+	+	1	1	+	V
Viburnum tinus		2	1	+	2	2	V
Ruscus aculeatus	1	1	+	1	2		V
Smilax aspera		+	1	1	1	+	V
Quercus coccifera	+	1	+		+	1	I
Laurus nobilis		+		1	+	1	III
Pistacia lentiscus		1		1	2	2	II
Rhamnus alaternus			+	+	+	+	V
Asparagus aphyllus	+		+		+	+	
Scilla monophyllus				+	1		
Pulicaria odora		+				+	
Luzula forsteri				+			I
Quercus broteroi							I
Olea sylvestris						+	
Companions							
Pteridium aquilinum	1	1	+	1	1	+	V
Ulex latebracteatus	1	+	2	1	+	1	IV
Pinus pinaster	2	1	2	2	2	1	
Rubus ulmifolius	1	+	+	+	+		II
Halimium halimifolium ssp. *multiflorum*	+		+	1	1	+	
Cistus salviifolius	+	+		+		+	II
Halimium calycinum	+	+		+	+		II
Calluna vulgaris	+		+	+	+		I
Erica scoparia		+	+	+		+	I
Tamus communis	+				+		I
Teucrium scorodonia		+			+		I
Lonicera hispanica				+			I

More: +*Cistus crispus* in 4, +*Rosmarinus officinalis*, +*Iberis welwitschii* in 5

Places: 1Vela Lagoon, Quiaios (Figueira da Foz), 2 Between Quiaios and Murtinheira (Figueira da Foz), 3 Pinhal do Urso (Pombal), 4 Between Ervideira Lagoon and Praia de Pedrogão (Leiria), 5 Between Vieira de Leiria and S. Pedro de Muel (Marinha Grande), 6 Between Vieira de Leiria and Marinha Grande, 7 Capelo and Mesquita (1998)

(*Quercus broteroi*) with very broad, leathery summergreen leaves that wither in winter but fall off only in spring (marcescent habit). This community, even if it is mainly in the meso-mediterranean belt, is mostly related to the limestone-derived substrate. Towards the south and at low elevation, summer drought becomes the limiting factor for the relict laurophyll species that, again, remain restricted to sheltered valleys, occupying azonal (hygrophilous) sites where summer drought is attenuated; this becomes equivalent to a thermo-temperate bioclimate.

The Littoral Beirensean area, where the warm-temperate *Viburno tini-Quercetum roboris* forest is found, was until recently considered part of the Mediterranean region (Costa et al. 1999; Rivas-Martínez 2007). Recent work, however, like the present, suggests that it should rather be included in the Eurosiberian region.

Table 7 *Calluno vulgaris-Rhododendretum baeticae*

# Relevé	1	2	3	4	5	6
Altitude (m)	500	500	500	538	498	517
Characteristics						
Rhododendron ponticum ssp. *baeticum*	5	4	5	4	5	5
Quercus robur	1	1	+	+	1	+
Lonicera periclymenum		+	+		+	+
Rubus ulmifolius	+			1	1	1
Salix atrocinerea	+			2		1
Blechnum spicant			+	+		+
Tamus communis		+	+			
Teucrium scorodonia					+	+
Quercus x *andegavensis*					1	
Osmunda regalis						+
Companions						
Erica arborea	+	1	+	1	+	+
Dactylis lusitanica	+			+	+	+
Agrostis x *fouilladei*	+			+	+	1
Calluna vulgaris		1	+			+
Digitalis purpurea				+		+
Cistus psilosepalus					+	+
Ulex minor					+	+

More: +*Pterospartum tridentatum* ssp. *cantabricum* in 2; 1*Cytisus striatus*, +*Ulex latebracteatus* in 4; +*Carex leporina*, +*Carex pilulifera*, +*Potentilla erecta*, +*Ranunculus repens* in 6

Place: Cambarinho (Vouzela), relevés 2 and 7 from Braun-Blanquet et al. 1956, relevés 1, 4, 5, 6 from Honrado et al. 2007

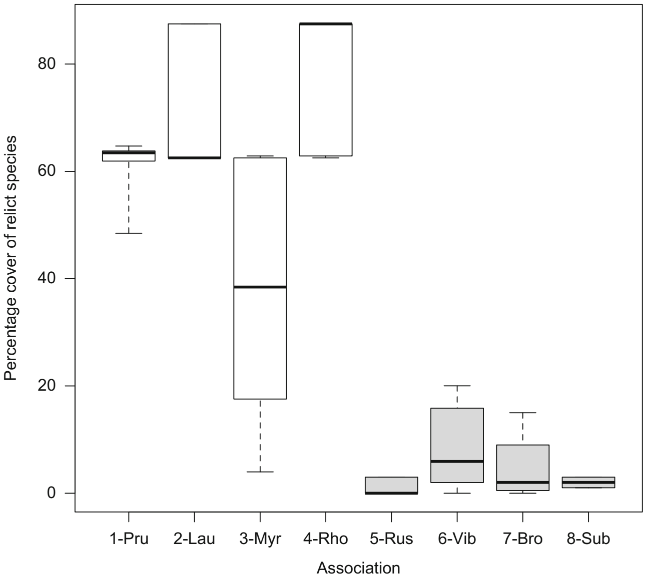


Fig. 6 Total percentage cover of relict species among studied associations (*greyed boxplots* correspond to zonal forests)

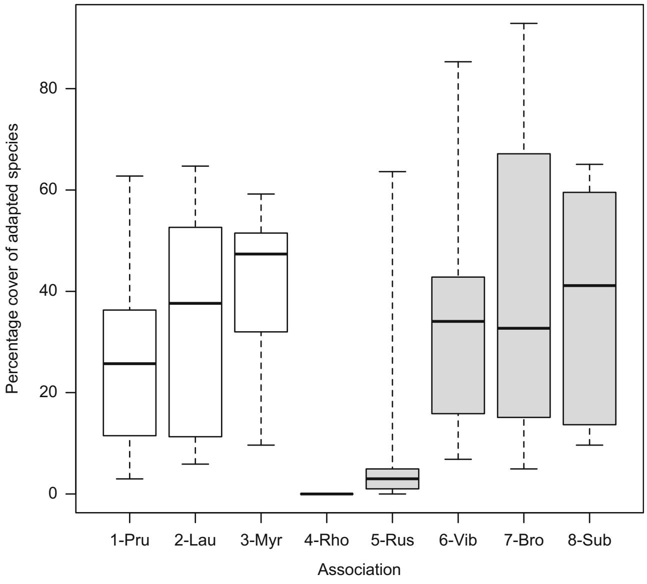


Fig. 7 Total percentage cover of species adapted to present climatic conditions among studied associations (*greyed boxplots* correspond to zonal forests)

Conclusions

The presence of laurophyll relicts in the communities studied is of great value for natural paleohistory. The Portuguese Atlantic archipelagos of Madeira and Azores have maintained some climatic stability since the late Tertiary. As a result, many Miocene and Pliocene laurophyll species have survived there while becoming extinct on the mainland, mostly during the Pleistocene (Capelo et al. 2004, 2005). Some of these species survived on the mainland, but their insular subpopulations went through a process of allopatric speciation, e.g.: *Prunus azorica, Prunus hixa, Ilex azorica, Ilex perado, Laurus azorica* and *Laurus novocanariensis*. The same did not happen, however, to *Myrica faya,* where no evidence of allopatry has yet been found.

In the Azores, *Myrica faya* forms microforests in the thermo-temperate submediterranean humid hyperoceanic bioclimate near the coast (Rivas-Martínez et al. 2002b). In Madeira and the Canarias Islands the optimum for *Myrica faya* is in warmer, edapho-xerophilous situations (Rivas-Martínez et al. 1993; Costa et al. 2004). In mainland Portugal it behaves similarly, occurring on warm sites.

Prunus azorica in the Azores is present in meso-supra-temperate hyperhumid and ultra-hyperhumid hyperoceanic micro-mesoforests (Rivas-Martínez et al. 2002b). Its optimum is on steep slopes, on very moist andosols with gleyic proprieties. This ecology is very similar to that of *Prunus lusitanica*.

Ilex azorica occurs especially at higher elevations of the Azores (Fernández-Prieto et al. 2006), while *Ilex perado* is a characteristic species of Madeiran thermo-meso-temperate submediterranean humid to hyperhumid mesoforests (Costa et al. 2004). The broad temperature range of the *Ilex* genus is evident in *Ilex aquifolium*.

Laurus azorica is very common in meso-supra-temperate hyperhumid microforests growing on andosols (Rivas-Martínez et al. 2002b), and *Laurus novocanariensis* is common in all forest associations of Madeira, from the thermo-mediterranean humid to meso-temperate ultra-hyper-humid belts (Costa et al. 2004). The behaviour of *Laurus nobilis* in mainland Portugal is very similar to that of Madeiran *Laurus novocanariensis*.

Finally, the presence of the relict laurophyll species increases the conservation value of all the communities studied, particularly in the present days as climate change poses new challenges to the conservation of these species (see Calleja et al. 2009).

References

BENNET K.D., TZEDAKIS P.C. & WILLIS K.J. 1991 – Quaternary refugia of north European trees. *J. of Biogeography* **18**: 103–115

BRAUN-BLANQUET J. 1965. – Plant Sociology. The study of plant communities. Hafner, London, 439p.

BRAUN-BLANQUET J., PINTO DA SILVA A.R. & ROZEIRA, A. 1956 – Résultats de deux excursions géobotaniques à travers le Portugal septentrional & moyen II. Chenaies à feuilles caduques (Quercion occidentale) et chenaies à feuilles persistentes (Quercion fagineae) au Portugal. *Agronomia Lusit*. **18** (3): 167–234

CALLEJA J.A., BENITO-GARZÓN M. & SAINZ-OLLERO H. 2009 – Tertiary relict trees in a Mediterranean climate: abiotic constraints on the persistence of Prunus lusitanica at the eroding edge of its range. *J. of Biogeography* **36** (8): 487–498

CAPELO, J. & MESQUITA, S. 1998 – Nota sobre a vegetação natural e potencial das dunas estabilizadas do Superdistrito Costeiro Português. *Silva Lusit*. **6** (2): 257–259

CAPELO J., SEQUEIRA M., JARDIM R. & COSTA J.C**.** 2004 – Guia da Excursão Geobotânica dos V Encontros ALFA 2004 à Ilha da Madeira. In J. Capelo (ed): A paisagem vegetal da Ilha da Madeira. *Quercetea* **6**: 5–45

CAPELO J., SEQUEIRA M., JARDIM R., MESQUITA S. & COSTA J.C. 2005 – The vegetation of Madeira Island (Portugal). A brief overview and excursion guide. *Quercetea* **7**: 105–122

CONSULTATIVE GROUP ON INTERNATIONAL AGRICULTURAL RESEARCH 2008 – CGIAR-Consortium for Spatial Information. SRTM 90m DEM Digital Elevation Database. http://srtm.csi.cgiar.org/(Consulted in: 25 February 2009).

COSTA J.C., AGUIAR C., CAPELO J., LOUSã M. & NETO C. 1999 – Biogeografia de Portugal Continental. *Quercetea* **0**: 5–56

COSTA J.C., LOPES M.C., CAPELO J. & LOUSÃ M. 2000 – Sintaxonomia das comunidades de Prunus lusitanica L. ssp. lusitanica no ocidente da Península Ibérica. *Silva Lusit*. **8** (2): 253–263

COSTA J.C., CAPELO J., HONRADO J., AGUIAR C., & LOUSÃ M. 2002a – Viburno tini-Quercetum roboris (Br.-Bl., P. Silva & Rozeira 1956) ass. nova, stat. nova hoc loco. *In* Rivas-Martínez, S., T.E. Díaz, F. Fernández-González, J. Izco, J. Loidi, M. Lousã & A. Penas ed.- Vascular plant communities of Spain and Portugal. Addenda to syntaxonomical checklist of 2001. *Itinera Geobot*. **15** (1): 225–227

COSTA J.C., CAPELO J., LOUSÃ M. & ESPÍRITO SANTO M.D. 2002b – Os sobreirais do Sector Divisório Português: Asparago aphylli-Quercetum suberis. *Quercetea* **3**: 81–98

COSTA J.C., CAPELO J., JARDIM R. & SEQUEIRA M. 2004 – Catálogo florístico do Arquipélago da Madeira. In J. Capelo (ed): A paisagem vegetal da Ilha da Madeira. *Quercetea* **6**: 187–200

COUDE-GAUSSEN G. 1981 – Les Serras da Peneda et do Gerês: Étude géomorphologique. *Memórias do Centro de Estudos Geográficos*: **5.** I.N.I.C., Lisboa

DUMOLIN-LAPEGUE S., DEMESURE B., FINESCHI S., LE CORRE V. & PETIT R.J. 1997 – Phylogeographic structure of white oaks throughout the European continent. *Genetics* **146**: 1475–1487

FÉRNANDEZ-PRIETO J.A., AGUIAR C. & DIAS E. 2006 – Catálogo Sintaxonómico da vegetação vascular da Ilha Terceira. In Dias, E., J. A. Fernández Prieto & C. Aguiar (eds.) *A Paisagem Vegetal da Ilha Terceira (Açores). Guia da Excursão Geobotânica. VI Encontro ALFA de Fitossociologia. Biodiversidade, Vegetação e Instrumentos de Conservação*: 51–62. Universidade dos Açores. Angra do Heroísmo

FERRIS C., OLIVER R.P., DAVY A.J. & HEWITT G.M. 1993 – Native oak chloroplasts reveal an ancient divide across Europe, *Molecular Ecology*, **2**, 337–344

FERRIS C., OLIVER R.P., DAVY A.J. & HEWITT G.M. 1995 – Using chloroplast DNA to trace postglacial migration routes of oaks into Britain. *Molecular Ecology* **4**: 731–738

FERRIS C., KING R.A., VäINöLÄ R. & HEWITT G.M., 1998 – Chloroplast DNA recognizes three refugial sources of European oaks and suggests independent eastern and western immigrations to Finland. *Heredity* **80**: 584–593

GÉHU J-M. RIVAS-MARTÍNEZ S. 1981 – Notions fondamentales de phytosociologie. In *Syntaxonomie*, ed. Hartmut Dierschke, 5–33. Vaduz: Berichte Internationalen Symposien der Internationalen Vereinigung fur Vegetationskunde. J. Cramer

HONRADO J., AGUIAR C., CALDAS F.B., ALMEIDA DA SILVA R. & CAPELO J.H. 2001 – Palaeoclimatic relicts and climatic disjunctions in the flora of Northern Portugal. *Quaternary Studies* **4**: 49–60

HONRADO J., ALVES P., LOMBA A., TORRES J. & CALDAS F.B. 2007 – Ecology, diversity and conservation of relict laurel-leaved mesophytic scrublands in mainland Portugal. *Acta Bot. Gallica* **154** (1): 63–77

INSTITUTO NACIONAL DE ENGENHARIA, TECNOLOGIA E INOVAÇÃO 2007 – Cartografia e prospecção. http://www.ineti.pt/produtos_e_servicos/prod_e_serv_frameset.aspx (Consulted in: 19 February 2009).

MÉDAIL F. & DIADEMA K. 2009 – Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography* **36** (7): 1333–1345

MONTEIRO-HENRIQUES T. 2010 – Landscape and phytosociology of the Paiva River's hydrographical basin. Tese de doutoramento/Ph.D. thesis, Lisboa: Instituto Superior de Agronomia, Universidade Técnica de Lisboa (TULisbon)

MÜLLER-DOMBOIS D. & ELLENBERG H. 1974 – *Aims and methods of vegetation ecology*. John & Wiley & Sons, New York

MUÑOZ C., RAMIL-REGO P., GÓMEZ-ORELLANA L.& RODRÍGUEZ M. 1996 – Modificaciones del paisaje vegetal durante el Cuaternário en el NW de la Península Ibérica: contextulización con las secuencias del SW de Europa. *Férvedes* **3**: 117–150

OKSANEN, J., R. KINDT, P. LEGENDRE, B. O'HARA, G.L. SIMPSON, P. SOLYMOS, M.H.H. STEVENS & H. WAGNER. 2008 – vegan: Community Ecology Package. R package version 1.15-1. http://cran.r-project.org/, http://vegan.r-forge.r-project.org/.

R DEVELOPMENT CORE TEAM. 2010 – R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org

RAMIL-REGO P., MUÑOZ C., GÓMEZ-ORELLANA L.& RODRÍGUEZ M. 1996 – Cambios globales del clima y de los hábitats terrestres. *Férvedes* **3**: 9–31

RIVAS-MARTÍNEZ S. & SÁENZ LAÍN C. 1991 – Enumeración de los Quercus de la Península Iberica. *Rivasgodaya* **6**: 101–110

RIVAS-MARTÍNEZ S. 2005a – Notions on dynamic-catenal phytosociology as a basis of landscape science. *Plant Biosyst.* **139** (2): 135–144

RIVAS-MARTÍNEZ S. 2005b – Avances en Geobotánica – Discurso de Apertura del Curso Académico de la Real Academia Nacional de Farmacia del año 2005. Madrid: Real Academia Nacional de Farmacia - Instituto de España

RIVAS-MARTÍNEZ S. 2007 – Mapa de series, geoseries y geopermaseries de vegetación de España. *Itinera Geobot.* **17**: 5–436

RIVAS-MARTÍNEZ S., WILDPRET W, DEL ARCO M., RODRÍGUEZ O., PÉREZ DE PAZ P.L., GARCIA-GALLO A., ACEBES J.R., DÍAZ T.E. & FERNÁNDEZ-GONZÁLEZ F. 1993 – Las comunidades vegetales de la Isla de Tenerife (Islas Canarias). *Itinera Geobot.* **7**: 169–374

RIVAS-MARTÍNEZ S., FERNÁNDEZ-GONZÁLEZ F., LOIDI J., LOUSÃ M., PENAS A. 2001 – Syntaxomical checklist of vascular plant communities of Spain and Portugal to association level. *Itinera Geobot.* **14**: 5–341

RIVAS-MARTÍNEZ S., DÍAZ T.E., FERNÁNDEZ-GONZÁLEZ F., IZCO J., LOIDI J., LOUSÃ M., PENAS A. 2002a – Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. *Itinera Geobot.* **15** (1, 2): 5–922

RIVAS-MARTÍNEZ S., LOUSÃ M., FERNÁNDEZ-PRIETO F., COSTA J.C., DIAS E. & AGUIAR C. 2002b – *Lauro azoricae-Juniperetea brevifoliae* classis nova hoc loco. *In* Rivas-Martínez, S., T.E. Díaz, F. Fernández-González, J. Izco, J. Loidi, M. Lousã & A. Penas ed.- Vascular plant communities of Spain and Portugal. Addenda to syntaxonomical checklist of 2001. *Itinera Geobot.* **15** (1):125–132

SAGA USER GROUP ASSOCIATION 2011 – SAGA – System for Automated Geoscientific Analyses. http://www.saga-gis.org/en/index.html (Consulted in: 2 July 2011).

SVENNING J.-C., NORMAND S. & KAGEYAMA M. 2008 – Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *J. of Ecology* **96** (6): 1117–1127

TICHÝ L. & J. HOLT 2006 – JUICE: program for management, analysis and classification of ecological data. Czech Republic: Vegetation Science Group – Masaryk University Brno

WEBER H.F., MORAVEC J. & THEURILLAT J-P. 2000 – International code of phytosociological nomenclature. 3rd edition. *J. Veg. Sci.* **11**(5): 739–768

Marcescent Forests of the Iberian Peninsula: Floristic and Climatic Characterization

Itziar García-Mijangos, Juan Antonio Campos, Idoia Biurrun, Mercedes Herrera, and Javier Loidi

Abstract

Forests dominated by marcescent oak species represent the transition between deciduous forests adapted to rainy summers and cold winters, on the one hand, and evergreen sclerophyllous Mediterranean forests. In the Iberian Peninsula marcescence is shown by some oak species, including *Quercus pubescens, Q. pyrenaica, Q. faginea* and *Q. canariensis*; it suggests an old evergreen habit forced to become deciduous by the cold winters. In this paper we analyse the floristic diversity of marcescent forests in the Iberian Peninsula and their proportion of evergreen broad-leaved and sub-Mediterranean species, and relate them to climatic conditions. This analysis uses 494 phytosociological relevés from the Information System of Iberian and Macaronesian Vegetation (SIVIM) and the BIOVEG data-bases. The data-set was submitted to an agglomerative clustering, which produced four clusters. An NMDS gradient analysis was also applied, in order to assess the relationship between the clusters and bioclimatic variables. The hierarchical and syntaxonomical classifications show a high correspondence, as reflected in the dominance of different *Quercus* species in each cluster. *Quercus broteroi* and *Q. canariensis* forests show a higher proportion of evergreen broad-leaved species, while *Q. pubescens* and *Q. faginea* forests are characterized by sub-Mediterranean species. As for climatic relationships, *Q. broteroi* and *Q. canariensis* forests present the highest values of thermicity (It) and the lowest values of the ombrothermic (Io_2) index. These values indicate their Mediterranean, thermophilous character, which in turn is related to their high proportions of evergreen broad-leaved species. As a conclusion, it can be stated that marcescence is not related to evergreeness, the latter being linked to mediterraneity. Therefore, the idea of considering marcescence as a residual feature of ancient evergreen laurophyll forests is not supported by our results. Those marcescent forests, particularly the basophilous ones, are related to the sub-Mediterranean floristic element.

Keywords

Numerical classification • *Quercus* • Sub-Mediterranean forest • Evergreen broad-leaved • NMDS • Thermicity • Ombrothermic index

1 Introduction

The late Tertiary and Pleistocene were times of dramatic climatic changes, which led to massive extinctions and migrations in the European flora. The changes started with progressive aridification and the emergence of the Mediterranean climate in the late Miocene, with episodes such as the

---

I. García-Mijangos (✉) • J.A. Campos • I. Biurrun • M. Herrera • J. Loidi
Department of Plant Biology and Ecology, University of the Basque Country, UPV/EHU, Ap. 644, 48080 Bilbao, Spain
e-mail: itziar.garcia@ehu.es

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_6, © Springer International Publishing Switzerland 2015

Messinian salinity crisis (Hsu et al. 1977). This resulted in a reversal of the rainfall seasonality from a summer to a winter maximum, with the appearance of summer drought along the southern fringe of the European continent. Subsequently, successive ice ages occurred during the Quaternary. All these events caused deep changes and extinctions in this part of the world. Those episodes, combined with the uplift of several mountain ranges throughout the Cenozoic, fostered the differentiation of mountain floras and set up barriers hampering southward migrations in each of the extension phases of the glacial period. The thermophilous laurophyll flora and vegetation of the mid-Tertiary practically disappeared in Europe, while remaining much better preserved on the Atlantic islands (Macaronesia), i.e., the Azores, Madeira and the Canaries (Rodríguez-Sánchez and Arroyo 2011).

Nevertheless, continental Europe has preserved some remains of the laurophyll vegetation (mesophytic palaeoclimatic relicts, in the sense of Honrado et al. 2001), which is generally recognized based on living populations of *Rhododendron ponticum* ssp. *baeticum* or *Prunus lusitanica* (Calleja et al. 2009). Even the more widespread bay laurel (*Laurus nobilis)* can be related to this group (Rodríguez-Sánchez and Arroyo 2008, 2011; Rodríguez-Sánchez et al. 2010). Some ferns, including *Culcita macrocarpa, Davallia canariensis, Stegnogramma pozoi, Woodwardia radicans, Hymenophyllum tunbrigense* and *Vandenboschia speciosa*, are also related to this relict element from the mid-Tertiary. The three southern European peninsulas, i.e., the Iberian, Italian and Balkan, are known to have been refuges for the thermophilous flora, including *Quercus* species, during the cold periods of the Pleistocene (Dumolin-Lapègue et al. 1997; Brewer et al. 2002; Ferris et al. 1998; Olalde et al. 2002). Nowadays these peninsulas, particularly Iberia, are mainly covered by sclerophyllous, often scrubby vegetation well adapted to the Mediterranean climate. Temperate Europe, on the other hand, is dominated by deciduous summergreen broad-leaved forests that reached their maximum extension by approximately 6,000 BP (Brewer et al. 2002). These forests now extend over most of Europe and are adapted to a seasonal climate with rainy summers and more or less cold winters. The transition between these forests and the evergreen Mediterranean vegetation is formed by forests in which the dominant species are marcescent oaks, whose leaves wither in autumn but remain dry on the branches until spring, when they are shed. This practice is shown by many European oak species: *Quercus pubescens, Q. pyrenaica, Q. faginea, Q. canariensis, Q. cerris, Q. frainetto, Q. ithaburensis, Q. trojana*, etc., and resembles the old evergreen practice, which has been forced into deciduousness by the cold winters. In fact, one of these species, *Q. canariensis*, is even “almost evergreen”: it keeps some of its large leaves functioning during winter until spring, when they are shed immediately before the sprouting of the new leaves.

This woody vegetation dominated by oaks could be interpreted historically as a remnant of the mid-Tertiary vegetation, and these marcescent species as direct descendants of some of the evergreen oaks that covered the mid-latitudes of Europe, as they still do on other continents, particularly in East Asia (Japan, China, and southernmost Korea).

We have carried out a survey of these forests in the Iberian Peninsula, analyzing their flora and the climatic conditions they are linked to. We highlighted the evergreen broad-leaved species living in the canopy or understory of these forests, as they can be used as indicators of evergreens in the communities of Tertiary origin. Many of these species are now considered to be Mediterranean species, as they show a certain sclerophylly (hardness in the leaves); in the context of Mediterranean vegetation, though, they always occur in wet or rainy areas. Another relevant group of plants is the sub-Mediterranean forest species, considered to be the genuine or characteristic species of these forests.

The aims of our study are: (1) to analyse the floristic diversity of the marcescent forests of the Iberian Peninsula; (2) to analyse the proportion of evergreen broad-leaved and sub-Mediterranean species across the different marcescent forest types; and (3) to determine the climatic features linked to different marcescent forests.

We consider the Iberian Peninsula as particularly well suited for performing this survey because of the climatic evolution of the post-glacial Holocene period (Benito Garzón et al. 2007; Rodríguez-Sánchez et al. 2010) and the current climatic variability, from the wettest extreme near the Atlantic to the most extreme Mediterranean climate (summer drought) in some areas of southeastern Spain.

2 Materials and Methods

2.1 Study Area

The study area (Fig. 1) covers the Iberian Peninsula (ca 582,000 km^2), located in the transition zone between the Euro-Siberian and Mediterranean biogeographic regions. The climate changes eastward, from temperate hyperoceanic to semi-continental mediterranean (Rivas-Martínez 2007). In the transition between the mediterranean and temperate climates, we consider the submediterranean variant. This can be defined as the type of climate in which there is only one summer month with $p < 2t$, i.e., only one dry month in the warm season. Formally, Rivas-Martínez (2007) included this variant in the temperate macroclimate, since at least two dry months are needed to be included in the mediterranean macroclimate. This submediterranean variant

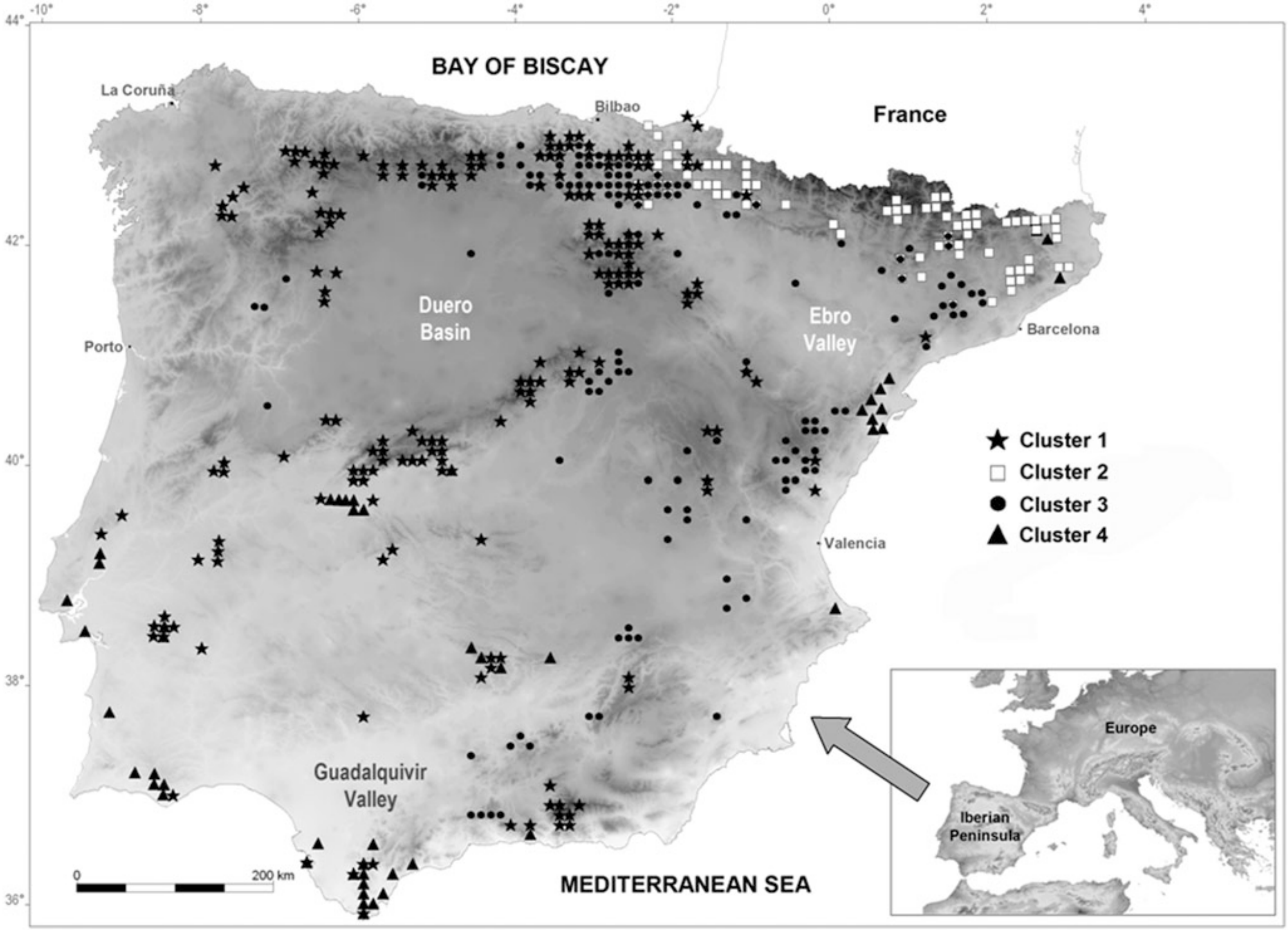


Fig. 1 Location of the study area (*Iberian Peninsula*) in southwestern Europe and distribution of forest cluster types resulting from floristic classification. *Dark areas* correspond to uplands and *light areas* to lowlands

is widespread in the Iberian Peninsula, as well as in other parts of southern Europe, providing a favourable climatic context for this survey. It also seems similar to the concept of warm-temperate deciduous areas in parts of East Asia and southeastern North America.

2.2 Data Collection and Preparation

To construct the primary data-set, phytosociological relevés were obtained from the Information System of the Iberian and Macaronesian Vegetation (SIVIM, Font et al. 2010) and the BIOVEG data-base of the University of the Basque Country. Relevés dominated (tree cover >3) by the marcescent tree species *Quercus pyrenaica, Q. faginea* ssp. *faginea* (from now on *Q. faginea*)*, Q. faginea* ssp. *broteroi* (from now on *Q. broteroi*)*, Q. pubescens* and *Q. canariensis* were selected. All relevés were compiled using the module QUERCUS of the VEGANA Package (De Cáceres et al. 2003). The primary data-set grouped 1,284 relevés representing 39 associations and five communities (see syntaxonomic scheme in Appendix 1). Floristic nomenclature follows *Flora Iberica* (Castroviejo et al. 1986–2011), and *Flora Europaea* (Tutin et al. 1976, 1980) for taxa not included in the former. The references for these sources are listed in Appendix 2.

The effects of possible oversampling of some areas or particular vegetation types were reduced by a stratified re-sampling (Knollová et al. 2005). The data-set was stratified geographically in such a way that only one relevé for each type of dominant tree was selected for each 10 × 10 km UTM grid.

After stratified re-sampling, a floristic homogeneization was performed by removing bryophytes (many relevés have no records of this group) and by assuming that *Hedera helix* s.l. includes *Hedera helix* L., *Hedera maderensis* K. Koch ex A. Rutherf. ssp. *iberica* McAllister and *Hedera hibernica* (G. Kirchn.) Bean; that *Rubus sp*. includes *Rubus* sect. *Corylifolii* Lindl. and *Rubus* sect. *Rubus*; that *Lonicera periclymenum* s.l., *Juniperus oxycedrus* s.l. and *Sanguisorba* *minor* s.l., include all subspecies within each genus in the territory; and that *Viola* gr. *sylvestris* includes *Viola riviniana* Rchb. and *V. reichenbachiana* Jord. ex Boreau. *Quercus faginea* Lam. includes *Q. alpestris* Boiss, and *Q. pubescens* Willd. includes *Q. subpyrenaica* Villar. Finally, all *Quercus* hybrids were included in the parent species dominant in the relevé or in the surroundings. So the dataset was reduced to 494 relevés and 1,003 species.

Climatic variables were calculated from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005), using a grid of 200 m pixel size generated from the existing network of meteorological stations and the official digital elevation model (DEM) of 100 m pixel size. The mean values of annual temperature (°C), annual rainfall (mm) and summer rainfall (sum of rainfall in June, July and August) per 10 × 10 km UTM cell were calculated, as well as five bioclimatic indices proposed by Rivas-Martínez (2007): continentality index (Ic), thermicity index (It) and the ombrothermic index of the warmest 1, 2 and 3-month periods (Ios_1, Ios_2, Ios_3, respectively). In order to reduce colinearity in potential explanatory climatic variables, a Pearson correlation matrix was calculated and variables with pairwise $|r| > 0.75$ were eliminated. In this way, mean annual temperature, summer rainfall, and Ios_1 and Ios_3 were seen as superfluous and excluded.

Ordinal species abundance estimates were replaced by metric average values prior to data analysis (r and +: 0.5%. 1: 5%. 2: 17.5%. 3: 37.5%. 4: 62.5%. 5: 87.5%). Percentages of evergreen broad-leaved species and sub-Mediterranean species were calculated in each relevé and normalized by an arcsine-square-root transformation, as recommended by Sokal and Rohlf (1987) for proportional data. Species present only in three relevés or fewer were deleted (0.6% of the total number). In this way, a definitive matrix with 494 relevés and 521 species was obtained.

2.3 Statistical Analysis

The GINKGO program of the VEGANA package (De Cáceres et al. 2003) was used to perform the floristic-numerical analysis. After transformation of cover values, the relevé data were √-transformed to reduce the impact of large cover values in the subsequent floristic analysis (McCune and Grace 2002). A dissimilarity matrix was constructed using Bray-Curtis distance. The definitive dataset was submitted to agglomerative clustering, according to species composition, using the hierarchical β-flexible cluster algorithm (Lance and Williams 1967; Wesche and von Wehrden 2011), with $\beta = -0.25$.

The Ochiai fidelity index (De Cáceres et al. 2008) of each species, for the four clusters from the numerical classification, was calculated in order to decide which species are the most diagnostic for each cluster.

Gradient analysis by NMDS (Kruskal 1964a, b; Mather 1976) was applied to assess the relationship between clusters and bioclimatic variables. NMDS has the advantage of not relying on a species response-curve model and can be used with various dissimilarity measures (McCune and Grace 2002; Podani 2006). Correlations between ordination axis and variables were evaluated by Pearson's correlation coefficient (r).

Relationships between the clusters and the proportion of both evergreen broad-leaved species (EB) and sub-Mediterranean species (SM) were assessed by the non-parametric Kruskal-Wallis test. The same test was used to evaluate the affinities between clusters and bioclimatic indices. When differences among the clusters were significant ($p < 0.05$), Mann-Whitney's U-test was applied to determine the categories among which those differences were given. All univariate statistical analyses were performed using SPSS 19.0 statistics package.

3 Results

3.1 Forest Classification

Numerical analysis leads to a classification into four main clusters at dissimilarity level 3.3 (Fig. 2), which reflects the syntaxonomical classification. Cluster 1 includes all relevés dominated by *Quercus pyrenaica* belonging to the *Quercion pyrenaicae* alliance (98.5%), except those of the *Arbuto unedonis-Quercetum pyrenaicae* dominated by *Quercus broteroi*. Cluster 2 comprises relevés corresponding to the *Quercion pubescenti-petraeae* (75.6%) and *Quercion roboris* (17.1%) alliances and some relevés of the *Aceri-Quercion fagineae* dominated by *Quercus pubescens*. Relevés of the *Aceri-Quercion fagineae* dominated by *Quercus faginea* are mainly grouped in cluster 3, and those corresponding to the *Quercion broteroi* and *Querco-Oleion sylvestris* alliances inside the *Quercetea ilicis* class are grouped in cluster 4. In this latter the dominant trees are *Quercus broteroi* and *Q. canariensis*, but some relevés from the eastern coastal mountains, dominated by *Quercus faginea* or *Quercus pubescens* and assigned to *Violo willkommii-Quercetum fagineae*, are also included. Table 1 shows the correspondence between clusters, dominant *Quercus* species and alliance.

The geographical distribution of relevés is represented in Fig. 1, with different symbols for each cluster. *Quercus pyrenaica*, *Q. pubescens* and *Q. faginea* forests assigned to the *Querco-Fagetea* class have a sub-Mediterranean distribution, whereas *Q. broteroi* and *Q. canariensis* forests have a Mediterranean distribution and are included in the

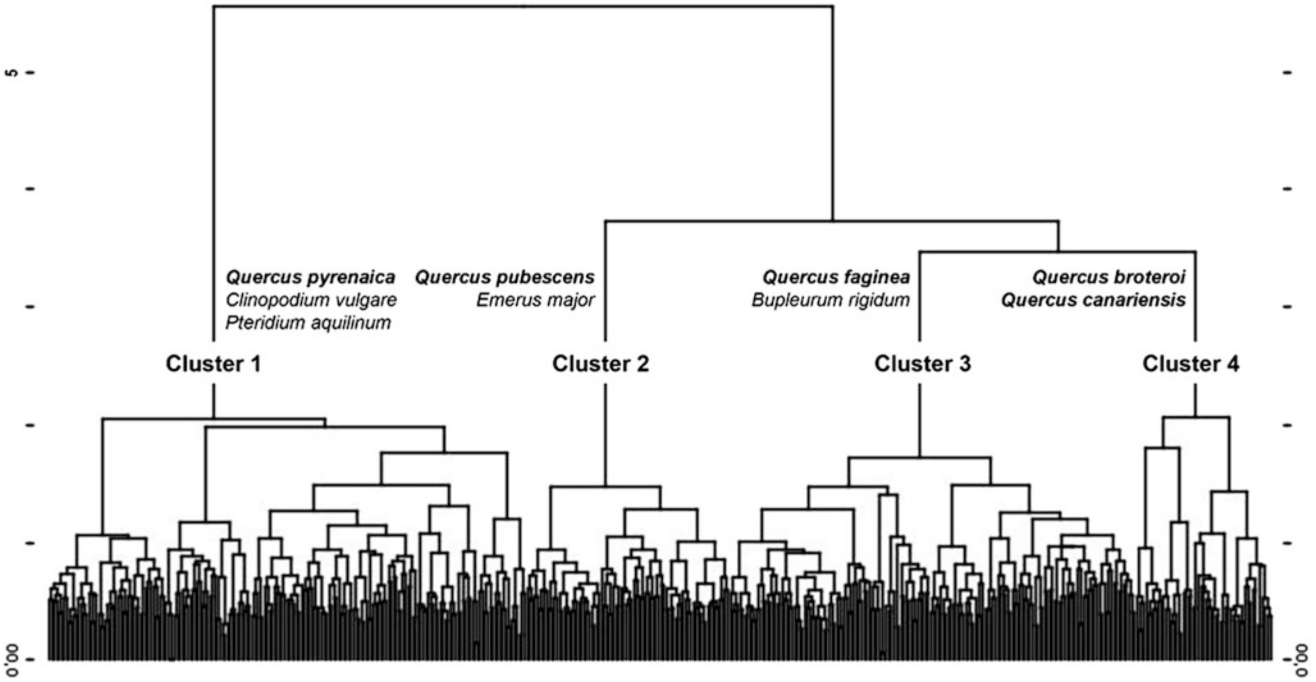


Fig. 2 Dendrogram resulting from the agglomerative clustering analysis explained in the main text. Principal discriminant species, based on their values of the Ochiai fidelity index, are shown. Pearson's *r* cophenetic correlation: 0.758; Spearman's *r* cophenetic correlation: 0.706; Gower Distance (Stress 1): 1472825.37261

Table 1 Correspondence between clusters obtained from hierarchical numerical analysis, tree dominance and alliances for marcescent and related forests in the Iberian Peninsula. The correspondence (%) between clusters, dominant *Quercus* species and alliances is shown in parentheses. N = number of relevés; % EB = percentage of evergreen broad-leaved woody species (median values and interquartile range; $X^2 = 198.89$; df = 3; $p < 0.001$). % SM = percentage of sub-Mediterranean species (median values and interquartile range; $X^2 = 127.1$; df = 3; $p < 0.001$). The values followed by the same letter (a) within a column do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test and a *post hoc* Mann-Whitney U-test

Cluster	N	Tree	Alliance	% EB	% SM
1	193	Q. pyrenaica (98.5%)	*Quercion pyrenaicae* (98.5%)	3 (0–7.1)	7.7 (4.8–10.7)
2	82	Q. pubescens (98.8%)	*Quercion pubescenti-petraeae* (75.6%)	10.4 (4.7–16.2)[a]	12 (7.8–17.6)[a]
			Quercion roboris (17.1%)		
3	164	Q. faginea (98.8%)	*Aceri-Quercion fagineae* (97%)	12.8 (7.1–20)[a]	11 (7.1–15)[a]
4	55	Q. broteroi (47.3%)	*Quercion broteroi* (40%)	40 (27.3–47.4)	2.7 (0–5.3)
		Q. canariensis (21.8%)	*Querco-Oleion sylvestris* (25.5%)		
		Q. faginea (21.8%)[1]	*Aceri-Quercion fagineae* (20%)[2]		

Quercetea ilicis class. *Quercus pyrenaica* forests (Cluster 1) occur mainly throughout the western half of the Iberian Peninsula, associated with acidic soils. Cluster 2 includes *Quercus pubescens* forests from the Pyrenees. Basophilous forests of *Quercus faginea* (Cluster 3) are found in the mountains of the eastern half of the Peninsula. Ecotones are frequent mainly in the north, where the presence and even dominance of hybrids is common.

The classification of the four clusters, with statistically determined diagnostic species for each cluster, is presented in Table 2. Cluster 1 is well defined by *Quercus pyrenaica* (0.97), *Clinopodium vulgare* (0.65), *Pteridium aquilinum* (0.64), *Holcus mollis* (0.63), *Teucrium scorodonia* (0.63), *Arenaria montana* (0.59), *Luzula forsteri* (0.59), *Melampyrum pratense* (0.57), *Lonicera periclymenum s.l.* (0.55), *Physospermum cornubiense* (0.52) and *Poa nemoralis* (0.50). This cluster is characterized by acidophilous species, which supports their inclusion in the *Quercetalia roboris* order.

Clusters 2 and 3 share some diagnostic species with sub-Mediterranean distributions, such as *Viburnum lantana, Primula veris, Acer monspessulanum*, *Buxus sempervirens* (classified as EB)*, Helleborus foetidus* and *Cytisophyllum sessilifolium,* together with other species with a wider distribution, such as *Acer campestre*, *Cornus sanguinea, Juniperus communis, Lonicera xylosteum, Corylus avellana*

Table 2 Floristic interpretation of the clusters obtained (**see main text**). The value of the Ochiai fidelity index is shown for each cluster of the most frequent species

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Diagnostic species of cluster 1					
Quercus pyrenaica	*200*	**0.97**	–	0.03	0.05
Clinopodium vulgare	*145*	**0.65**	0.08	0.14	0.06
Pteridium aquilinum	*154*	**0.64**	0.10	0.11	0.15
Teucrium scorodonia	*113*	**0.63**	0.06	0.01	0.15
Holcus mollis	*81*	**0.63**	0.01	0.01	–
Luzula forsteri	*98*	**0.59**	0.08	0.03	0.08
Arenaria montana	*83*	**0.59**	0.01	0.03	0.04
Melampyrum pratense	*84*	**0.57**	0.02	0.09	–
Lonicera periclymenum s.l.	*134*	**0.55**	0.07	0.18	0.13
Poa nemoralis	*91*	**0.50**	0.17	0.07	0.01
Diagnostic species of cluster 2 and 3					
Juniperus communis	*107*	0.06	**0.40**	**0.46**	0.01
Cornus sanguinea	*85*	0.02	**0.41**	**0.40**	0.01
Acer campestre	*66*	0.04	**0.43**	**0.28**	0.02
Lonicera xylosteum	*65*	0.02	**0.40**	**0.33**	–
Corylus avellana	*70*	0.11	**0.38**	**0.24**	0.03
Amelanchier ovalis	*79*	0.01	**0.34**	**0.45**	–
Diagnostic species of cluster 2					
Quercus pubescens	*97*	–	**0.92**	0.08	0.07
Galium pumilum	*25*	–	**0.38**	0.08	0.08
Campanula trachelium	*19*	–	**0.35**	0.07	0.03
Diagnostic species of cluster 3					
Quercus faginea	*196*	0.06	0.05	**0.91**	0.13
Teucrium chamaedrys	*75*	0.01	0.20	**0.50**	0.03
Genista scorpius	*62*	0.01	0.20	**0.47**	–
Bupleurum rigidum	*60*	0.01	0.11	**0.44**	0.12
Diagnostic species of cluster 4					
Quercus broteroi	*43*	0.11	–	0.01	**0.66**
Quercus canariensis	*16*	–	–	–	**0.54**
Asparagus acutifolius	*32*	0.05	0.04	0.11	**0.43**
Arisarum simorrhinum	*10*	0.02	–	–	**0.38**
Sub-Mediterranean species (SM)					
Physospermum cornubiense	*55*	**0.52**	–	0.01	–
Lathyrus niger	*38*	**0.30**	0.13	0.04	0.04
Genista falcata	*17*	0.24	–	0.06	–
Viburnum lantana	*115*	0.05	**0.34**	**0.55**	–
Primula veris	*78*	0.18	**0.30**	0.28	–
Acer monspessulanum	*74*	0.08	0.28	**0.33**	0.11
Helleborus foetidus	*58*	0.10	0.25	**0.31**	–
Cytisophyllum sessilifolium	*17*	–	0.21	0.17	–
Emerus major	*36*	–	**0.50**	0.10	0.02
Acer opalus	*11*	–	**0.30**	0.05	–
Campanula persicifolia	*11*	–	0.27	0.05	0.04
Hypericum montanum	*13*	0.08	0.21	0.04	–
Saponaria ocymoides	*21*	–	0.07	**0.31**	–
Cephalanthera rubra	*30*	0.07	0.12	0.27	–
Acer granatense	*10*	0.02	–	0.20	0.04
Sorbus aria	*40*	0.17	0.19	0.17	–
Paeonia microcarpa	*14*	0.12	–	0.17	–
Sorbus torminalis	*28*	0.10	0.19	0.16	0.03
Viola hirta	*11*	0.09	0.10	0.09	–

(*continued*)

Table 2 (continued)

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Evergreen broadleaf woody species (EB)					
Rubia peregrina	*220*	0.14	**0.31**	**0.58**	0.36
Hedera helix s.l.	*179*	0.24	**0.35**	**0.43**	0.19
Quercus rotundifolia	*96*	0.06	0.17	**0.51**	0.12
Ligustrum vulgare	*89*	0.05	0.23	**0.51**	–
Buxus sempervirens	*86*	–	**0.57**	**0.32**	–
Ruscus aculeatus	*86*	0.18	0.19	0.13	**0.47**
Daphne gnidium	*66*	0.24	–	0.16	**0.37**
Smilax aspera	*58*	0.09	0.06	0.10	**0.60**
Arbutus unedo	*57*	0.17	0.03	0.06	**0.55**
Rhamnus alaternus	*53*	0.04	0.11	0.28	0.30
Ilex aquifolium	*49*	0.24	0.16	0.15	0.06
Quercus coccifera	*47*	0.03	0.08	0.26	0.31
Viburnum tinus	*45*	0.10	–	0.06	**0.62**
Quercus suber	*39*	0.21	0.04	0.01	**0.39**
Phillyrea latifolia	*36*	–	0.06	0.08	**0.61**
Lonicera implexa	*32*	0.03	0.02	0.11	**0.50**
Pistacia lentiscus	*31*	–	0.02	0.06	**0.63**
Phillyrea angustifolia	*28*	0.05	0.02	0.01	**0.56**
Rosa sempervirens	*25*	–	0.04	0.11	**0.43**
Quercus ilex	*25*	0.04	0.29	0.08	0.11
Daphne laureola	*23*	0.03	0.25	0.13	0.06
Olea europaea	*20*	0.11	–	0.03	**0.33**
Arctostaphylos uva-ursi	*19*	0.05	0.05	0.25	–
Chamaerops humilis	*16*	–	–	–	**0.54**
Cistus populifolius	*15*	0.13	–	–	0.28
Cistus laurifolius	*14*	0.15	–	0.13	–
Myrtus communis	*13*	0.06	–	–	**0.37**
Ruscus hypophyllum	*8*	–	–	–	**0.38**
Vinca difformis	*6*	–	–	0.03	0.28
Rhamnus oleoides	*5*	–	–	–	0.30
Ceratonia siliqua	*4*	–	–	–	0.27
Other species					
Crataegus monogyna	*283*	**0.42**	**0.37**	**0.50**	0.17
Rubus sp.	*191*	0.43	0.27	0.28	0.23
Prunus spinosa	*171*	0.22	**0.34**	**0.53**	0.02
Tamus communis	*140*	0.22	0.26	0.32	0.31
Brachypodium sylvaticum	*134*	0.37	0.30	0.24	0.09
Cruciata glabra	*118*	**0.48**	0.21	0.14	0.05
Stachys officinalis	*108*	0.26	0.27	0.29	0.08
Viola gr. sylvestris	*97*	0.31	0.33	0.19	0.03
Geum sylvaticum	*82*	0.30	0.07	0.28	0.09
Hepatica nobilis	*79*	0.09	0.36	0.33	0.02
Tanacetum corymbosum	*76*	0.21	0.11	0.35	0.05
Carex flacca	*68*	0.03	**0.37**	**0.33**	0.03
Silene nutans	*68*	0.31	0.13	0.21	0.02
Stellaria holostea	*67*	0.37	0.20	0.09	0.02
Lathyrus linifolius	*66*	**0.41**	0.11	0.09	0.05
Viola gr. alba	*65*	0.02	0.36	0.30	0.10
Cytisus scoparius	*64*	**0.43**	0.04	0.04	0.15
Fragaria vesca	*53*	0.19	**0.36**	0.09	0.04
Dactylis glomerata	*53*	0.24	0.26	0.12	0.02
Brachypodium phoenicoides	*52*	0.08	0.17	**0.35**	0.02

(*continued*)

Table 2 (continued)

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Euphorbia amygdaloides	*51*	0.14	0.26	0.20	0.04
Anthoxanthum odoratum	*50*	0.41	0.11	0.02	0.02
Brachypodium retusum	*40*	0.01	0.07	0.32	0.19
Thalictrum tuberosum	*38*	0.01	0.20	0.30	0.04
Juniperus oxycedrus s.l.	*34*	0.02	0.08	**0.35**	0.05
Agrostis capillaris	*29*	0.28	0.08	0.01	0.08
Calluna vulgaris	*29*	0.28	0.08	0.01	0.08
Osyris alba	*28*	0.04	0.04	0.12	**0.38**
Pinus sylvestris	*26*	0.04	**0.37**	0.08	0.03
Pistacia terebinthus	*25*	0.01	0.07	0.17	0.27
Frangula alnus	*25*	0.29	0.02	0.03	0.05
Calamintha nepeta	*22*	0.14	0.05	0.02	0.29
Holcus lanatus	*21*	0.27	0.02	0.02	0.06
Galium maritimum	*19*	0.02	0.28	0.11	0.03
Erica vagans	*92*	0.29	0.21	0.29	–
Brachypodium rupestre	*91*	0.19	0.29	0.34	–
Pulmonaria longifolia	*57*	0.29	0.15	0.18	–
Rosa arvensis	*56*	0.12	0.31	0.24	–
Potentilla montana	*54*	0.27	0.12	0.19	–
Genista occidentalis	*48*	0.07	0.22	0.30	–
Vicia sepium	*48*	0.19	0.37	0.08	–
Festuca rubra	*39*	0.28	0.12	0.10	–
Trifolium ochroleucon	*36*	0.26	0.18	0.05	–
Bromus erectus	*35*	0.02	0.15	0.33	–
Helleborus occidentalis	*31*	0.25	0.04	0.14	–
Hypericum pulchrum	*31*	**0.35**	0.02	0.04	–
Potentilla sterilis	*29*	0.25	0.14	0.04	–
Helictotrichon cantabricum	*27*	0.01	0.19	0.26	–
Daboecia cantabrica	*27*	**0.35**	0.02	0.02	–
Rosa micrantha	*26*	0.07	0.06	0.28	–
Origanum vulgare	*23*	0.05	0.25	0.15	–
Anemone nemorosa	*23*	**0.32**	0.02	0.02	–
Trisetum flavescens	*23*	**0.32**	0.02	0.02	–
Briza media	*22*	0.03	0.09	0.27	–
Ranunculus tuberosus	*21*	0.27	0.05	0.03	–
Coronilla minima	*20*	0.02	0.07	0.28	–
Fraxinus excelsior	*18*	0.03	**0.34**	0.06	–
Trifolium pratense	*17*	0.26	0.03	0.02	–
Helianthemum nummularium	*16*	0.04	0.06	0.23	–
Lonicera etrusca	*59*	–	0.24	0.38	0.09
Carex halleriana	*41*	–	0.07	**0.35**	0.17
Viola willkommii	*37*	–	0.15	**0.36**	0.02
Juniperus phoenicea	*16*	–	0.03	0.25	0.07
Paeonia broteri	*37*	0.25	–	0.05	0.27
Origanum virens	*45*	0.30	–	0.06	0.24
Aristolochia paucinervis	*50*	0.34	–	0.10	0.15
Campanula rapunculus	*49*	0.37	–	0.08	0.12
Sanguisorba minor s.l.	*25*	0.04	–	0.28	0.11
Asphodelus albus	*40*	0.08	–	0.15	0.23
Thapsia villosa	*21*	0.25	–	0.05	0.06
Potentilla erecta	*23*	0.32	–	0.02	0.03
Asphodelus albus	*33*	**0.39**	–	0.01	0.02
Erica arborea	*75*	**0.46**	0.05	–	0.25

(*continued*)

Table 2 (continued)

	Fr	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Festuca heterophylla	*37*	**0.37**	0.07	–	0.04
Knautia nevadensis	*15*	0.09	0.26	–	0.03
Castanea sativa	*18*	0.27	0.03	–	0.03
Hyacinthoides hispanica	*15*	0.11	–	–	0.31
Conopodium marianum	*14*	0.13	–	–	0.25
Cytisus striatus	*20*	0.26	–	–	0.12
Doronicum plantagineum	*24*	0.29	–	–	0.11
Polygonatum odoratum	*23*	0.29	–	0.07	–
Lapsana communis	*20*	0.26	–	0.07	–
Carex lamprocarpa	*18*	0.25	–	0.06	–
Sedum forsterianum	*20*	0.27	–	0.05	–
Genista polygaliphylla	*16*	0.25	–	0.04	–
Avenula sulcata	*24*	**0.32**	–	0.03	–
Rumex acetosa	*23*	**0.33**	–	0.02	–
Ulex gallii	*22*	**0.32**	–	0.02	–
Conopodium pyrenaeum	*20*	**0.31**	–	0.02	–
Erica cinerea	*14*	0.25	–	0.02	–
Quercus robur	*14*	0.25	–	0.02	–
Festuca elegans	*22*	**0.34**	–	–	–
Linaria triornithophora	*21*	**0.33**	–	–	–
Pseudarrhenatherum longifolium	*20*	**0.32**	–	–	–
Crepis lampsanoides	*18*	**0.31**	–	–	–
Vaccinium myrtillus	*17*	0.30	–	–	–
Simethis mattiazzi	*15*	0.28	–	–	–
Hyacinthoides non-scripta	*13*	0.26	–	–	–
Blechnum spicant	*12*	0.25	–	–	–
Deschampsia flexuosa	*35*	0.34	0.13	–	–
Veronica officinalis	*22*	0.29	0.07	–	–
Conopodium majus	*20*	0.27	0.07	–	–
Clematis vitalba	*32*	–	0.31	0.22	–
Aphyllanthes monspeliensis	*30*	–	0.18	0.30	–
Genista hispanica	*26*	–	0.15	0.29	–
Carex humilis	*25*	–	0.20	0.25	–
Pinus salzmannii	*23*	–	0.07	**0.33**	–
Rhamnus saxatilis	*21*	–	0.10	0.29	–
Catananche caerulea	*18*	–	0.05	0.29	–
Spiraea obovata	*16*	–	0.06	0.27	–
Euphorbia nicaeensis	*13*	–	–	0.28	–
Leuzea conifera	*12*	–	–	0.27	–

and *Amelanchier ovalis*. The characteristic species that separate the two groups of relevés are:

- For cluster 2, *Quercus pubescens* (0.92), *Emerus major* (0.50) and *Acer opalus* (0.30) among sub-Mediterranean species and *Galium pumilum* (0.38) and *Campanula trachelium* (0.35) among widespread species; and
- For cluster 3, *Quercus faginea* (0.91), *Teucrium chamaedrys* (0.50), *Genista scorpius* (0.47), *Bupleurum rigidum* (0.44) and the evergreen broad-leaved species *Rubia peregrina* (0.58) and *Quercus rotundifolia* (0.51) (see Table 2).

Finally, cluster 4 is characterized by *Quercus broteroi* (0.66), *Quercus canariensis* (0.54), *Asparagus acutifolius* (0.43), *Arisarum simorrhinum* (0.38) and a large group of evergreen broad-leaved species such as *Pistacia lentiscus* (0.63), *Viburnum tinus* (0.62), *Phillyrea latifolia* (0.61), *Smilax aspera* (0.60), *Phillyrea angustifolia* (0.56), *Arbutus unedo* (0.55), *Chamaerops humilis* (0.54), *Lonicera implexa* (0.50), *Ruscus aculeatus* (0.47), *Rosa sempervirens* (0.43) and *Quercus suber* (0.39). This cluster is quite well defined by thermophilous evergreen broad-leaved species, many of which are sclerophyllous, together with the absence of

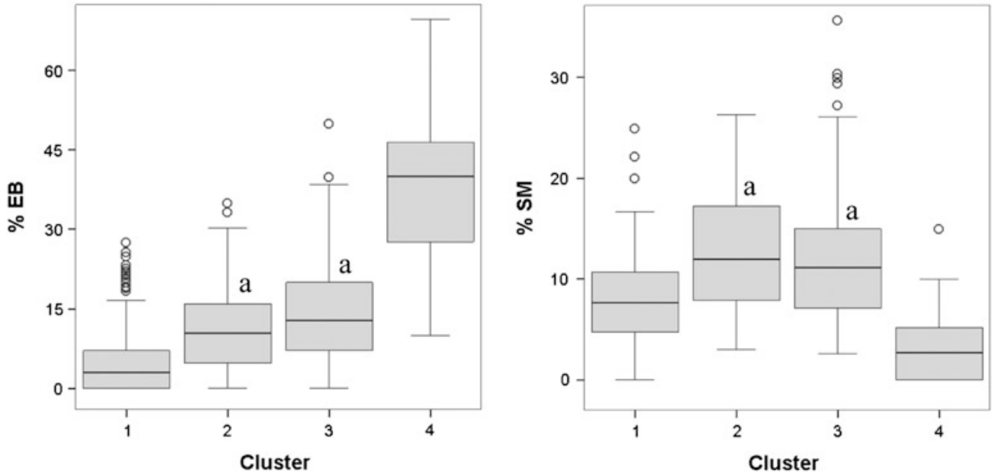


Fig. 3 Comparison of clusters obtained from the clustering analysis (see main text)**,** using the proportions of evergreen broad-leaved species (EB) and sub-Mediterranean species (SM). *Boxes* and *whiskers* include 25–75% and 5–95% of the observed values, respectively, and *lines* inside the *boxes* are medians. Clusters marked with the same letter (a) do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test and a *post hoc* Mann-Whitney U-test

Table 3 Median and interquartile ranges (50% of cases, in parentheses) of climatic parameters for the clusters from hierarchical numerical classification (see main text). Values followed by the same letter (a,b) within a row do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test (X^2) and a *post hoc* Mann-Whitney U-test. N = 494. df = 3. *** = $p < 0.001$. ** = $p < 0.01$

Cluster	1	2	3	4	X^2
P	838 (673–1,141)^{a}	858 (752–1,069)^{a}	652 (567–829)^{b}	699 (626–871)^{b}	80.99***
Ic	16.1 (14.8–18.2)^{ab}	16.7 (15.6–17.9)^{a}	17 (15.3–18.6)^{a}	15.1 (13.7–17.5) ^{b}	16.86**
It	183 (131–247)^{a}	179 (125–207)^{a}	195 (172–216)^{a}	353 (322–382)	123.8***
Io	6.5 (4.9–8.7)^{a}	7.1 (5.5–9.5)^{a}	4.9 (3.8–6.4)	3.6 (3.2–4.4)	122.3***
Ios_2	1.4 (0.7–2.3)^{a}	3 (2.1–4.2)	1.6 (1.1–2.1)^{a}	0.3 (0.2–0.8)	162.3***

nemoral plants of the *Querco-Fagetea* class. In fact, these forests belonging to the *Quercion broteroi* and *Querco-Oleion sylvestris* alliances have traditionally been assigned to the *Quercetea ilicis* class.

3.2 Floristic Analysis

Table 1 summarizes, for each cluster, the proportion of evergreen broad-leaved species (EB) and sub-Mediterranean species (SM) present in the relevés. The highest average percentage of EB species (40%) is in cluster 4, which comprises *Quercetea ilicis* forests (65.5%) and those of the *Aceri-Quercion fagineae* alliance (20%) located in the warmest areas. The average percentages of *Q. pubescens* (cluster 2: 10.4%) and *Q. faginea* (cluster 3: 12.8%) forests are quite similar. Cluster 1 shows the lowest mean value (3%). For SM species, clusters 2 and 3 have the highest values (mean of 12% and 11% respectively), followed by *Q pyrenaica* forests (7.7%), and cluster 4 (2.7%). The Kruskal-Wallis test was significant for the percentage of EB and SM species ($p < 0.001$). Comparison of clusters (Fig. 3) shows that there is no difference between clusters 2 and 3 for both types of species (EB and SM), but clusters 1 and 3 differ significantly from them and also between them for both variables (Table 1).

3.3 Climatic Analysis

Climatic characterization of the four clusters is summarized in Table 3, and clusters for climatic parameters and indices are compared in the box diagram of Fig. 4. The Mediterranean character of a climate is expressed by low values of Ios_2 (the 2-month summer ombrothermic index: Rivas-Martínez 2007). *Quercus pubescens* forests (cluster 2) show the highest median values (3.0), corresponding to a temperate climate, with significant differences ($p < 0.001$) with respect to the other three clusters, which are linked to a more mediterranean climate. Cluster 4 shows the lowest value, which indicates its mediterranean character; clusters 1 and 3 have intermediate values, in agreement with a submediterranean climate. The annual ombrothermic index (Io) also shows significant differences among clusters, but in this case *Quercus*

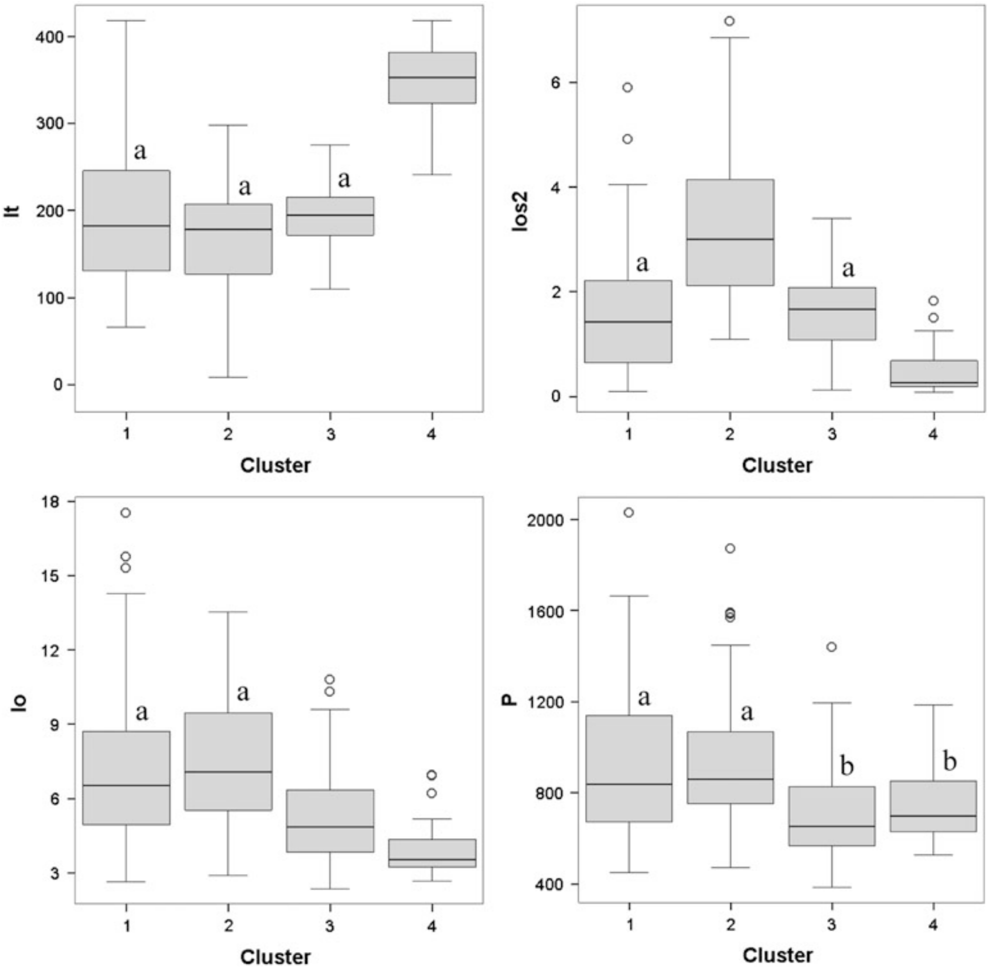


Fig. 4 Comparison of the clusters obtained (see main text) using climatic parameters. *Boxes* and *whiskers* include 25–75% and 5–95% of the observed values, respectively, and *lines* inside the *boxes* are medians. Clusters marked with the same letter (a,b) do not differ at $p < 0.05$, based on a non-parametrical Kruskal-Wallis test and a *post hoc* Mann-Whitney U-test

pyrenaica forests (cluster 1) show values similar to those of *Q*. *pubescens* forests (cluster 2), indicating their affinity for the humid ombrotype; clusters 3 and 4 are related to the subhumid ombrotype (upper and lower, respectively). There is no difference, however, between clusters 3 and 4 in terms of annual precipitation (P), which suggests that temperature controls the dominance by *Q*. *faginea*, *Q*. *broteroi* or *Q*. *canariensis*.

Regarding temperature, cluster 4 bears the highest thermicity index (353) and is significantly different from the other three clusters, which have similar values. This reflects the location of relevés belonging to cluster 4 in the thermo-Mediterranean belt. Continentality does not show any clear differences between clusters ($X^2 = 16.86$).

The diagrams made by NMDS analysis show a clear segregation of the clusters obtained in the hierarchical classification, along axes 1, 2 and 3 (Figs. 5 and 6). These three axes are correlated with climatic indices (Table 4), explaining 33.49% of the accumulated variance. Axis 1 explains the highest accumulated variance (18.25%) and is negatively correlated with annual precipitation (P; $r = -0.319$; $p < 0.001$) and ombrothermic index (Io; $r = -0.313$; $p < 0.001$). Axis 2 shows a large negative correlation with Ios_2 ($r = -0.619$; $p < 0.001$). The diagram representing axes 1 and 2 separates clusters 1, 2 and 3 (Fig. 5). The relevés of cluster 1 (*Q*. *pyrenaica* forests) are grouped in the first quadrant of the diagram, linked to higher precipitation. The position of relevés of cluster 2 (*Q*. *pubescens* forests) indicates their temperate character, due to the positive relation with Ios2. Axis 3, which is negatively correlated with the thermicity index (It; $r = -0.702$; $p < 0.001$), involves relevés of cluster 4 (Fig. 6).

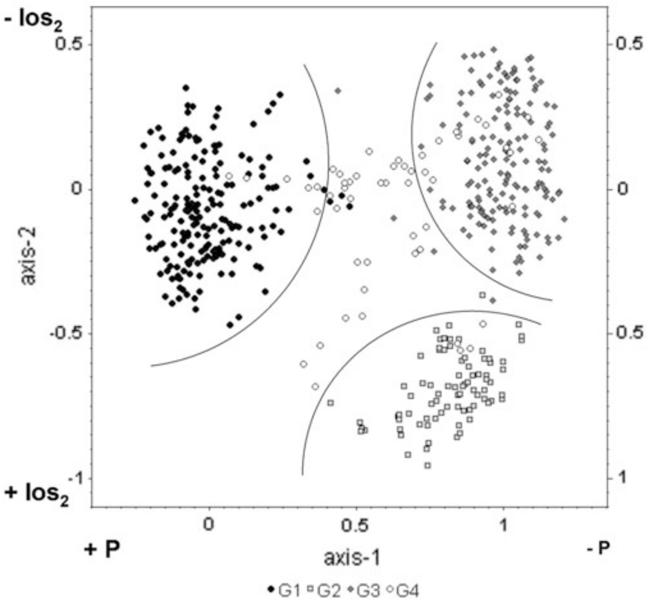


Fig. 5 NMDS ordination of the data-set (see main text), showing axes 1 and 2. G1 – Cluster 1, G2 – Cluster 2, G3 – Cluster 3, G4 – Cluster 4

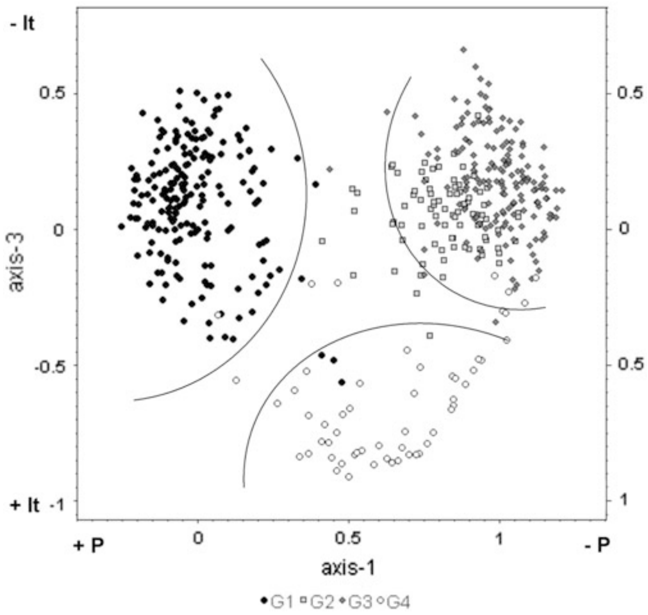


Fig. 6 NMDS ordination of the data-set (see main text), showing axes 1 and 3. G1 – Cluster 1, G2 – Cluster 2, G3 – Cluster 3, G4 – Cluster 4

Table 4 Pearson's correlation coefficients for climatic variables with axes from NMDS ordination analysis (see main text). Accumulated variance explained (Var) by the first three axis = 33.49%. *= $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant

Axe	Var	P	Ic	It	Io	Ios_2
Axis 1	18.25%	−**0.319*****	0.098*	0.078 ns	−0.313***	0.083 ns
Axis 2	8.82%	−0.309***	0.112 ns	0.295***	−0.392***	−**0.619*****
Axis 3	6.42%	0.090*	0.053 ns	−**0.702*****	0.356***	0.419***

4 Discussion

The results of the numerical classification mostly match current syntaxonomy (Rivas-Martínez 2011). Four groups are clearly differentiated, each related to the dominance of one or more *Quercus* species: *Quercus pyrenaica* (cluster 1), *Q. pubescens* (cluster 2), *Q. faginea* (cluster 3) and *Q. broteroi* plus *Q. canariensis* (cluster 4). Nevertheless, some differences can be seen: the associations *Pteridio aquilini-Quercetum pubescentis* and *Carici depauperatae-Q pubescentis*, currently in *Quercion roboris (Quercetalia roboris)*, are included in cluster 2, and we propose to change them from *Quercion roboris* to *Quercion pubescenti-petraeae (Quercetalia pubescenti-petraeae)*.

Relevés of the *Quercion broteroi* and *Querco-Oleion sylvestris* alliances are grouped together into cluster 4, due to the high number of *Quercetea ilicis* species that they share. Thus we accept their current assignment to this class, which groups both sclerophyllous and marcescent forests from Mediterranean Ibero-Atlantic territories with dry to hyperhumid ombrotypes (Rivas-Martínez 2011). Some relevés dominated by *Q. faginea* and *Q. pubescens* from the eastern coast of the Iberian Peninsula are also included in this cluster 4. These relevés belong to the *Fraxino orni-Quercetum fagineae* and *Violo willkommi-Quercetum fagineae* associations in the *Aceri-Quercion fagineae* alliance.

Fraxino orni-Quercetum fagineae was described by Rivas Goday et al. (1960), who included it in the class *Quercetea ilicis* due to the presence of the Mediterranean species *Lonicera etrusca*, *Arbutus unedo*, *Viburnum tinus*, and *Juniperus oxycedrus*. They admitted, however, that it was quite deviant, as shown by the presence of mesophytic species such as *Acer granatense*, *A. monspessulanum, Quercus faginea*, *Rhamnus infectoria*, and *Colutea arborescens*. Later on, Rivas-Martínez (1972) proposed that the new syntaxon *Aceri-Quercion fagineae* within *Quercetalia pubescenti-petraeae* should go together with *Q. faginea* forests and other mixed sub-Mediterranean Iberian forests developed on base-rich soils. This new syntaxon would occupy, according to Rivas-Martínez (1972), the southern and westernmost areas within the range of *Quercetalia pubescentis*. He also proposed the *Fraxino orni-Quercetum fagineae* association as the type of the new syntaxon. On the other hand, the subassociation *Violo willkommii-Quercetum* *fagineae asparagetosum acutifolii* includes marcescent forests from Catalonian coastal ranges (Royo 2006). It is characterized by the presence of many evergreen character species of *Quercetea ilicis (Viburnum tinus, Smilax aspera, Phillyrea angustifolia, Arbutus unedo, Lonicera implexa*, and *Asparagus acutifolius).*

The syntaxonomic location of *Fraxino orni-Quercetum fagineae* and *Violo willkommii-Quercetum fagineae asparagetosum acutifolii* might not be very appropriate, and their future reassignment to the class *Quercetea ilicis* should be considered.

The almost complete correspondence of the numerical classification with dominance by a particular tree species indicates the existence of a companion flora for these forests. This fits with the syntaxonomic classification, in which the alliances are characterized by tree species together with other diagnostic species (Rivas-Martínez et al 2002).

Quercus pubescens and *Q. faginea* forests have many diagnostic species in common, many of them occurring in sub-Mediterranean areas. Most of the diagnostic species common to clusters 2 and 3 are deciduous, whereas the proportion of evergreen broad-leaved species is only 10% and 12% respectively, not enough to support the idea that these forests originated from the evergreen Tertiary forests.

The evergreen broad-leaved species are linked to cluster 4, which includes the most thermophilous, mediterranean forests, mainly *Q. canariensis* and *Q. broteroi* forests belonging to *Quercetea ilicis*, as stated in the syntaxonomic discussion. In fact, these forests hold many of the laurophilous Tertiary species that became adapted to submediterranean conditions (*Viburnum tinus, Arbutus unedo, Myrtus communis* and others) (Costa et al. 2015). *Quercus broteroi* and *Q. canariensis* have been defined as semi-deciduous species with Mediterranean distributions (Sánchez de Dios et al. 2009), in contrast to *Q. faginea* and *Q. pyrenaica,* which are marcescent and have sub-Mediterranean distributions. Abadia et al. (1996) also considered that it is the ability to cope with cold winters that differentiates submediterranean marcescent forests from thermophilous Mediterranean forests. In fact, in thermo-mediterranean areas, *Q. broteroi* and *Q. canariensis* can only live in especially humid places, such as ravines or north-exposed cloud forests (Cantó 2004; Rivas-Martínez et al. 1990; Pinto and Paiva 2005), where they replace evergreen sclerophyllous forests.

The small number of sub-Mediterranean and especially of evergreen broad-leaved species in the *Quercus pyrenaica* forests, grouped in cluster 1, may be caused by the acidic soils combined with cooler conditions and high annual rainfall. The *Q. pyrenaica* forests in the south, where it is warmer, have more evergreen broad-leaved species (Cano and Valle 1990; Pereira 2009). This confirms the relation of such plants with warm climates. A comparative study of these forests together with temperate and true Mediterranean acidophilous forests would be of interest, in order to find out how the submediterranean character is reflected in their floristic composition.

The optimum for marcescent forests seems to be linked to sub-Mediterranean areas characterized by an attenuated summer drought with only one arid month in the warm season (Rivas-Martínez 2007). Studies on forests in Castile and Leon indicated that the ombrothermic indices (Io and Ios) are the best bioclimatic indicators for discriminating between marcescent forests (Del Río and Penas 2006). They concluded that the annual ombrothermic index (Io) discriminates between *Q. pyrenaica* and *Q. faginea* forests, the former requiring more humidity than the latter. This agrees with our results, which show significant differences between these forests and also between *Q. faginea* and *Q. pubescens* forests. On the contrary, regarding Ios_2, there is no difference between *Q. faginea* and *Q. pyrenaica* forests but there are significant differences between these forests and *Q. pubescens* forests, which suffer only one month of summer drought. Values of the continentality and thermicity indices do not show differences among these three forests types. *Q. canariensis* and *Q. broteroi* forests, though, differ clearly from the rest in temperature levels, and this fact could explain the relict character of these latter forests in the Mediterranean area.

Marcescence is thus an adaptation to submediterranean areas with winter frost. Many authors have studied the advantages of marcescent vegetation when competing with deciduous or evergreen forests. Montserrat Martí et al. (2004) attributed it to an early budding in spring and delayed leaf senescence in autumn. Marcescent leaves are capable of some photosynthetic activity in the last 1–2 months of the growing season, unlike senescent ones (Abadía et al. 1996). The companion flora of these marcescent forests is also adapted to a submediterranean and somewhat continental climate, as seen by its distribution; it may have been associated with deciduous forests that could have migrated to the south in the Quaternary, since the Pyrenees may not have formed a strong barrier to colonization after the last ice age (Petit et al. 2003).

Quercus broteroi and *Q. canariensis* forests have high proportions of evergreen species and are related to thermophilous areas with clear summer drought. *Quercus canariensis* is considered to be a semi-deciduous tree (Bingre et al. 2007), as it keeps some of its large leaves functional during winter and then sheds them in spring immediately before the sprouting of the new leaves. This adaptation to mild winters may suggest an evergreen laurophyllous origin partially adapted to summer drought and thus sheltered in especially humid biotopes in thermo-mediterranean territories.

As a conclusion of this survey, it can be stated that the marcescent condition is not related to evergreeness. The abundance of evergreen plants is linked to mediterraneity, and thus the idea of considering marcescence as a residual feature of ancient evergreen laurophyll forests is not supported by our results. Those marcescent forests, particularly basophilous forests, are related to the sub-Mediterranean floristic element.

We propose to move the associations *Pteridio aquilini-Quercetum pubescentis* and *Carici depauperatae-Quercetum pubescentis* into *Quercion pubescenti-petraeae* from the *Quercion roboris* alliance. We also suggest the inclusion of the syntaxa *Fraxino orni-Quercetum fagineae* and *Violo willkommii-Quercetum fagineae asparagetosum acutifolii* in *Quercetea ilicis*. Nevertheless, further studies considering all the associations of *Quercetalia ilicis* and *Quercetalia pubescentis* are necessary.

Acknowledgements Funds from the projects IT299-10 of the Basque Government for research groups and CGL2009-13317-C03-02 of the Spanish Ministry of Science and Innovation (MICINN) have been used for this survey.

Appendix 1. Syntaxonomical Scheme

SALICI PURPUREAE-POPULETEA NIGRAE (Rivas-Martínez & Cantó ex Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González & Loidi 1991) Rivas-Martínez & Cantó 2002

POPULETALIA ALBAE Br.-Bl. ex Tchou 1948

Populion albae Tchou 1948

Fraxino angustifoliae-Ulmenion minoris Rivas-Martínez 1975

1. *Querco pyrenaicae-Fraxinetum angustifoliae* Rivas Goday 1964 corr. Rivas-Martínez, Fernández-González & A- Molina in Fernández-González & A. Molina 1988

QUERCO-FAGETEA SYLVATICAE Br.-Bl. & Vlieger in Vlieger 1937

QUERCETALIA ROBORIS Tüxen 1931

Quercion roboris Malcuit 1929

Quercenion robori-petraeae Rivas-Martínez 1978

2. *Carici depauperatae-Quercetum pubescentis* Zeller 1959 nom. inv. propos.

3. *Carici depressae-Quercetum canariensis* O. Bolòs 1959 nom. inv. propos.

4. *Lathyro linifolii-Quercetum petraeae* (Lapraz 1966) Rivas-Martínez 1983 nom mut. propos.

5. *Pteridio aquilini-Quercetum pubescentis* O. Bolòs 1983

Quercion pyrenaicae Rivas Goday ex Rivas-Martínez 1965

Quercenion pyrenaicae Rivas-Martínez 1975

6. *Adenocarpo decorticantis-Quercetum pyrenaicae* Martínez-Parras & Molero 1983

7. *Arbuto unedonis-Quercetum pyrenaicae* (Rivas Goday in Rivas Goday, Esteve, Galiano, Rigual & Rivas-Martínez 1960) Rivas-Martínez 1987

8. *Arisaro vulgare-Quercetum pyrenaicae* C. Pinto-Gomes, R. Paiva-Ferreira, C. Aguiar, M. Lousã, C. Costa, M. Ladero & S. Rivas-Martínez 2007

9. *Berberido hispanicae-Quercetum pyrenaicae* F. Valle, Gómez-Mercado & Mota 1988 nom. mut. propos.

10. *Cephalanthero rubrae-Quercetum pyrenaicae* O. Bolòs & Vigo in O. Bolòs 1967

11. *Festuco merinoi-Quercetum pyrenaicae* (Rivas-Martínez & Sánchez-Mata in Sánchez-Mata 1989) Sánchez-Mata 1999 corr. Entrocassi, Gavilán & Sánchez-Mata 2004

12. *Genisto falcatae-Quercetum pyrenaicae* Penas & T.E. Díaz ex Rivas-Martínez 2002

13. *Holco mollis-Quercetum pyrenaicae* Br.-Bl., P. Silva & Rozeira 1956

14. *Luzulo baeticae-Quercetum pyrenaicae* Rivas-Martínez 2002

15. *Luzulo forsteri-Quercetum pyrenaicae* Rivas-Martínez 1963

16. *Pulmonario longifoliae-Quercetum pyrenaicae* Oberdorfer & Tüxen in Tüxen & Oberdorfer 1958

17. *Sorbo torminalis-Quercetum pyrenaicae* Rivas Goday ex Rivas-Martínez 1987

Quercenion robori-pyrenaicae (Br.-Bl., P. Silva & Rozeira 1956) Rivas-Martínez 1975

18. *Linario triornithophorae-Quercetum pyrenaicae* Rivas-Martínez, T.E. Díaz, F. Prieto, Loidi & Penas 1984

19. *Lonicero periclymeni-Quercetum pyrenaicae* Rivas-Martínez 2002

20. *Melampyro pratensis-Quercetum pyrenaicae* Rivas-Martínez ex Rivas-Martínez, T.E. Díaz, F. Prieto, Loidi & Penas 1984

21. *Rusco aculeati-Quercetum roboris* Br.-Bl. P. Silva & Rozeira 1956

QUERCETALIA PUBESCENTIS Klika 1933

Quercion pubescenti-petraeae Br.-Bl. 1932 nom. mut. propos.

22. *Buxo sempervirentis-Quercetum pubescentis* Br.-Bl. ex Bannes-Puygiron 1933

23. *Buxo sempervirentis-Quercetum subpyrenaicae* (O. Bolòs & P. Montserrat 1984) Rivas-Martínez in Rivas-Martínez 2011

24. *Roso arvensis-Quercetum pubescentis* Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González & Loidi 1991 nom. mut. propos.

Aceri granatensis-Quercion fagineae (Rivas Goday, Rigual & Rivas-Martínez in Rivas Goday, Borja, Esteve, Galiano, Rigual & Rivas-Martínez 1960) Rivas-Martínez 1987

25. *Berberido hispanicae-Quercetum alpestris* Rivas-Martínez 2011

26. *Cephalanthero rubrae-Quercetum fagineae* Rivas-Martínez in Rivas Goday, Borja, Esteve, Galiano, Rigual & Rivas-Martínez 1960 corr. Rivas-Martínez 1972

27. *Cytiso reverchonii-Quercetum fagineae* Inocencio, Alcaraz & Ríos 1998

28. *Daphno latifoliae-Aceretum granatensis* Rivas-Martínez 1965

29. *Fraxino orni-Quercetum fagineae* Rivas Goday & Rigual in Rivas Goday, Borja, Esteve, Galiano, Rigual & Rivas-Martínez 1960 corr. Rivas-Martínez 1972

30. *Pulmonario longifoliae-Quercetum fagineae* Loidi & Herrera 1990

31. *Sileno melliferae-Quercetum faginae* Rivas Goday & Borja in Rivas Goday, Borja, Esteve, Galiano, Rigual & Rivas-Martínez 1960 corr. Rivas-Martínez, T.E. Díaz, Fernández-González, Izco, Loidi, Lousã & Penas 2002

32. *Spiraeo obovatae-Quercetum fagineae* O. Bolòs & P. Montserrat 1984

33. *Telino patentis-Quercetum fagineae* Rivas Goday & Borja (1960) 1961 corr. Rivas-Martínez 2011

34. *Vinco difformis-Quercetum fagineae* Pérez Latorre & Cabezudo 2009

35. *Violo willkommii-Quercetum fagineae* Br.-Bl. & O. Bolòs 1950 corr. Rivas-Martínez 1972

QUERCETEA ILICIS Br.-Bl. ex A. & O. Bolòs 1950

QUERCETALIA ILICIS Br.-Bl. ex Molinier 1934 em. Rivas-Martínez 1975

Quercion broteroi Br.-Bl., P. Silva & Rozeira 1956 em. Rivas-Martínez 1975 corr. Ladero 1974

Quercenion broteroi Rivas-Martínez, Costa & Izco 1986 corr. Rivas-Martínez 1987

36. *Arisaro-Quercetum broteroi* Br.-B., P. Silva & Rozeira 1956 corr. Rivas-Martínez 1975

37. *Euphorbio monchiquensis-Quercetum canariensis* Malato-Beliz in Rivas-Martínez, Lousã, T.E. Díaz, Fernández-González & J.C. Costa 1990

38. *Pistacio terebinthi-Quercetum broteroi* Rivas Goday in Rivas Goday, Borja, Esteve, Galiano, Rigual & Rivas-Martínez 1960

39. *Quercetum alpestris-broteroi* Carlos J. Pinto & Rodrigo J.P. Paiva 2005

40. *Sanguisorbo hybridae-Quercetum broteroi* M. Pereira 2009

41. *Viburno tini-Quercetum alpestris* Torres & Cano in Cano & al. 2002 corr. Rivas-Martínez 2011

Querco rotundifoliae-Oleion sylvestris Barbéro, Quézel & Rivas-Martínez in Rivas-Martínez, Costa & Izco 1986

42. *Oleo sylvestris-Quercetum alpestris* Galán, A.V. Pérez & Cabezudo in A.V. Pérez, Galán, P. Navas, D. Navas, Y. Gil & Cabezudo 1999 corr. Rivas-Martínez 2011

43. *Rusco hypophylli-Quercetum canariensis* Rivas-Martínez 1975

Appendix 2. Bibliographic Sources of the Relevés

Aguilella, A. (1985). Flora y vegetación de la Sierra del Toro y las Navas de Torrijas; Estribaciones sudorientales del macizo de Javalambre. Tesi doctoral. Universitat de València.

Alonso, R. (2002). Valoración del estado de conservación de la vegetación y propuestas de ordenación y uso del territorio de la margen izquierda de la cuenca alta del río Esla (León). Servicio de publicaciones de la Universidad de León.

Amigo, J. & Romero, M.I. (1994). Vegetación atlántica bajo clima mediterráneo: un caso en el noroeste ibérico. Phytocoenologia, 22(4):583–603.

Amigo, J., Izco, J., Guitián, J. & Romero, M.I. (1998). Reinterpretación del robledal termófilo galaico-portugués: Rusco aculeati-Querc. Lazaroa, 19:85–98.

Amor, A., Ladero, M. & Valle, C.J. (1993). Flora y vegetación vascular de la comarca de La Vera y laderas meridionales de la Sierra de Tormantos (Cáceres, España). Studia Botanica 11: 11–207.

Ascaso Martorell, J. (1990). Estudio fitocenológico y valoración de los recursos pastorales de las zonas forestales y arbustivas del Prepirineo aragonés. Institución Fernando el Católico, 152 pp. Zaragoza.

Asensi, A., Díez-Garretas, B. & Nieto, J. M. (2005). Torcal de Antequera - Desfiladero de los Gaitanes. Guia geobotánica. XX Jornadas internacionales de fitosociología. Academia malagueña de Ciencias. 87 pp. Málaga.

Barrera Martínez, I. (1985). Contribución al estudio de la flora y de la vegetación de la Sierra de Albarracín. Tesis Doctoral. Universidad Complutense de Madrid.

Báscones, J.C. (1978). Relaciones suelo-vegetación en la Navarra húmeda del noroeste. Estudio florístico-ecológico. Tesis Doctoral. Universidad de Navarra

Baudière, A. (1974). Contribution à l'étude structurale des forêts des Pyrénées-Orientales: hêtraies. Coll. Phytosociol. 3:17–44.

Belmonte López, D. (1986). Flora y vegetación del Parque Natural de Monfragüe; Tesis Doctoral. Universidad Complutense de Madrid.

Benito Alonso, J. L. (2006). Vegetación del parque nacional de Ordesa y Monte Perdido (Sobarbe, Pirineo central aragonés). Publicaciones del Consejo de Protección de la Naturaleza de Aragon. Zaragoza.

Bolòs, O. de & Montserrat, P. (1983). Datos sobre algunas comunidades vegetales, principalmente de los pirineos de Aragón y de Navarra. Lazaroa, 5:89–96.

Bolòs, O. de (1954). De Vegetatione Notulae, I. Collect. Bot., 4(2): 253–286.

Bolòs, O. de (1959). El paisatge vegetal de dues comarques naturals: la Selva i la Plana de Vic. Arx. Secc. Ciènc. 26:1–175.

Bolòs, O. de (1967). Comunidades vegetales de las comarca próximas al litoral situadas entre los rios Llobregat y Segura. Mem. R. Acad. Cienc. Art. Barcelona, 38(1):3–281.

Bolòs, O. de (1983). La vegetació del Montseny. Servei de Parcs Naturals. Diputació de Barcelona. Barcelona.

Bolòs, O. de (1988). La roureda acidòfila (Quercion robori-petraeae) a Catalunya. Monogr. Inst. Pir. Ecol. (Hom. a P. Montserrat), 4:447–453.

Bolòs, O. de (1996). Contribució al coneixement de la vegetació del territori Auso-Segàrric. Mem. R. Acad. Cienc. Art. Barcelona, LV 4:147–272.

Braun-Blanquet, J. (1967). Vegetationsskizzen aus dem Baskenland mit Ausblicken auf das weitere Ibero-Atlantikum. II Teil. Vegetatio, 14(1–4):1–126.

Cano, E., Pinto-Gomes, C., Valle, F., Torres, J.A., García Fuentes, A., Melendo, M. & Mendes, S. (2002). Primera aproximación al conocimiento de los quejigares del sur de la Península Ibérica (Portugal y España). Quercetea, 3:175–182

Cano, E. & Valle, F. (1990). Formaciones boscosas en Sierra Morena Oriental (Andalucía, España). Acta Bot. Malacitana, 15:231–237.

Cantó, P. (2004). Estudio fitosociológico y biogeográfico de la sierra de San Vicente y tramo i nferior del valle del Alberche (Toledo, España). Lazaroa, 25:187–249

Carreras, J. Carrillo, E. Ninot, J.M. & Vigo, J. (1997). Contribution to the phytocenological knowledge of Pyrenean forest. Fragm. Flor. Geobot., 42(1):95–129.

Carreras, J., Carrillo, E., Font, X., Ninot, J.M., Soriano, I. & Vigo, J. (1995). La vegetación de las sierras prepirenaicas situadas entre los ríos Segre y Llobregat. 1- Comunidades forestales (bosques, mantos marginales y orlas herbáceas). Ecol. Medit., 21(3/4):21–73.

Carreras, J., Carrillo, E., Masalles, R.M., Ninot, J.M. & Vigo, J. (1993). El poblament vegetal de les valls de Barravés i de Castanesa. I- Flora i Vegetació. Acta Bot. Barcinon., 42:1–392.

Carrillo, E. & Ninot, J. M. (1992). La Flora i la vegetació de les valls d'Espot i de Boí (II). I.E.C. Arx. Secc. Ciènc. 99 (2):1–351.

Casas, I., Díaz, R., Echevarría, J. E. & Gavilán, R. (1989). Datos sobre la vegetación de Morata de Tajuña (Madrid, España). Lazaroa, 11:61–76.

Catalán, P. (1987). Geobotánica de las cuencas Bidasoa-Urumea (NO de Navarra-NE de Guipúzcoa). Estudio ecológico de los suelos y de la vegetación de la cuenca de Artikutza (Navarra). Tesis doctoral. Universidad del País Vasco.

Conesa, J.A. (1991). Flora i vegetació de les Serres Marginals Pre-pirinenques compreses entre els rius Segre i Noguera Ribagorçana. Tesi Doctoral. Universitat de Barcelona.

De la Cruz Rot, M. (1994). El paisaje vegetal de la Cuenca del río Henares (Guadalajara). Tesis Doctoral. Universidad de Alcalá de Henares.

Devis Ortega, J. (2006). Flora i vegetació del territori comprès entre el riu Segre i el Port del Comte (Prepirineus catalans, Lleida). Tesi Doctoral. Universitat de Barcelona.

Díez Garretas, B., Cuenca, J. & Asensi, A. (1986). Datos sobre la vegetación del subsector aljíbico (provincia Gaditano-Onubo-Algarviense). Lazaroa, 9:315–332.

El Aallali, A., López Nieto, J. M., Pérez Raya, F. & Molero Mesa, J. (1998). Estudio de la vegetación forestal en la vertiente sur de Sierra Nevada (Alpujarra Alta granadina). Itinera Geobotanica, 11:387–402.

Fernández González, F. (1991). La vegetación del valle del Paular (Sierra de Guadarrama, Madrid), I. Lazaroa, 12:153–272.

Fernández López, C., Carballo, A. & Guixá, R. (1984). Vegetación natural de Jabalcuz-La Pandera (Jaén). Blancoana, 2:17–38.

Fernández Prieto, J.A. & Vázquez, V. M. (1987). Datos sobre los bosques asturianos orocantábricos occidentales. Lazaroa, 7:363–382.

Ferrer Plou, J. J. (1990). Marojales y quejigales del noroeste de la provincia de Teruel. Teruel, 80–81 (1):181–194.

Ferrer, J. (1993). Flora y vegetación de las Sierras de Herrera, Cucalón y Fonfría. Naturaleza en Aragón nº4. Gobierno de Aragón. 333 pp. Zaragoza.

Fuente, V. de la (1985). Vegetación orófila del occidente de la provincia de Guadalajara (España). Lazaroa, 8:123–219.

Galán de Mera, A. (1993). Flora y Vegetación de los términos municipales de Alcalá de los Gazules y Medina Sidonia (Cádiz, España). Universidad Complutense de Madrid, Facultad de Farmacia, Departamento de Biología Vegetal II. 534 pp.

García González, M.E. (1990). Flora y vegetación de la sierra del Brezo y de la comarca de la Peña (Palencia). Tesis Doctoral. Universidad de León.

García-Abad Alonso, J.J., Gómez Delgado, M. & Rodríguez Espinosa, V.M. (2009). Cartografía detallada de plantas vasculares en un sector de la Alta Alcarria, Guadalajara. Utilidad en la detección de enclaves naturales de interés. Lazaroa, 30:161–175

García-Baquero, Gonzalo (2005). Flora y vegetación del Alto Oja (Sierra de la Demanda, La Rioja, España). Guineana, 11:1–250.

García-Mijangos, I., Biurrun, I., Darquistade, A., Herrera, M. & Loidi, J. (2004). Nueva cartografía de los hábitats en los lugares de interés comunitario (L.I.C.) fluviales de Navarra. Manual de interpretación de los hábitats. Informe para Viveros y Repoblaciones de Navarra

García-Mijangos, I. (1997). Flora y vegetación de los montes Obarenes (Burgos). Guineana 3:1–457.

Gómez Mercado, F. & Valle, F. (1990). Notas fitosociológicas sobre las comunidades arbóreas de las sierras de Cazorla y Segura. Acta Bot. Malacitana, 15:239–246.

Gómez Navarro, J. (2008). Aportaciones al estudio de la flora y vegetación del extremo NE de la provincia de Albacete y zonas adyacentes de la provincia de Valencia (España). Facultad de Ciències Biològiques, Universitat de València, 2:457–926.

Gonçalves Aguiar, C.F. (2000). Flora e vegetação da Serra de Nogueira e do Parque Natural de Montesinho; Universidade Técnica de Lisboa. Inst. Superior de Agronomia. 688 pp. Lisboa

Grüber, M. (1989). Les chenaies acidiphiles à Quercus petraea et Q. pyrenaica de la partie collinéenne des Hautes Pyrénées. Bull. Soc. Hist. Nat. Toulouse, 125:73–78.

Hernández i Cardona, À. M. (1997). Les plantes i el paisatge vegetal d'Olesa de Montserrat. Publicacions de l'Abadia de Montserrat. Col.lecció Vila d'Olesa 6:151–190.

Herrera, M. (1995). Estudio de la vegetación y flora vascular de la cuenca del río Asón (Cantabria). Guineana, 1:1–453.

Herrero Cembranos, L. (1989). Flora y vegetación de la margen izquierda de la cuenca alta del río Pisuerga (Palencia). Tesis Doctoral. Universidad de León

Inocencio Pretel, C., Alcaraz Ariza, F.J. & Ríos Ruiz, S. (1998). El paisaje vegetal de la cuenca albacetense del Guadalmena. Inst. Est. Albacetenses. 327 pp. Albacete.

Ladero Álvarez, M., Luengo Ugidos, M., Santos Bobillo, M.T., González Iglesias, J., Alonso Beato, M.T. & Sánchez Rodríguez, M.E. (2006). Vegetación del entorno del Balneario de Cervantes, Santa Cruz de Mudela (Ciudad Real). An. R. Acad. Nac. Farm., 72:321–368.

Ladero Álvarez, M.T., Luengo Ubigos, M.A., Santos Bobillo, M.T., Alonso Beato, M.T., Sánchez Rodríguez, M. E., González Iglesias, F.J. & Ladero Santos, I. (2008). Vegetación del entorno del Balneario de Valdelateja, Valle de Sedano (Burgos). An. R. Acad. Farm. 74:541–581.

Llamas Garcia, F. (1984). Flora y vegetación de la Maragateria (León). Institución Fray Bernardino de Sahagún, 273 pp. León.

Llansana, R. (1976). Estudio florístico y geobotánico de la zona comprendida entre Balaguer y els Aspres de la Noguera. Tesis de Llicenciatura Universitat de Barcelona.

Loidi Arregui, J., Biurrun Galarraga, I. & Herrera Gallastegui, M. (1997). La vegetación del centro-septentrional de España. Itinera Geobot., 9:161–618.

Loidi, J. & Herrera, M. (1990). The Quercus pubescens and Quercus faginea forests in the Basque Country (Spain): distribution and typology in relation to climatic factors. Vegetatio, 90:81–92

Loidi, J. & Fernández-Prieto, J. A. (1986). Datos sobre la biogeografía y la vegetación del sector Castellano-Cantábrico (España). Doc. Phytosoc. 10:323–362

López Pacheco, M. J. (1988). Flora y vegetación de las cuencas alta y media del río Curueño (León). Institución Fray Bernardino de Sahagun. Diputación provincial de León. 384 pp. León.

López, G. (1976). Contribución al conocimiento fitosociológico de la Serranía de Cuenca I. Comunidades fruticosas: bosques, matorrales, tomillares y tomillar-praderas. Anales Inst. Bot. Cavanilles, 33:5–87.

Martínez Parras, J. M. & Molero Mesa, J. (1982). Ecología y fitosociología de Quercus pyrenaica Willd. en la provincia Bética. Los melojares béticos y sus etapas de sustitución. Lazaroa, 4:91–104.

Medrano, M. (1994). Flora y Vegetación de las Sierras de la Demanda y Cameros (La Rioja). Tesis Doctoral. Universidad de Navarra.

Melendo Luque, M. (1998). Cartografía y ordenación vegetal de Sierra Morena: Parque Natural de las Sierras de Cardeña y Montoro (Córdoba). Tesis Doctoral. Universidad de Jaén.

Mercadé López, A. (2008). Aportació al coneixement dels boscos mesòfils de la Catalunya central, I; Fagedes i Rouredes. Acta Bot. Barcinon., 51:93–125.

Merle Farinós, H., Ferriol Molina, M. (2008). Aportación al conocimiento de los melojares relictos de *Quercus pyrenaica* de la Sierra de Espadán (Castellón, España). Lazaroa, 29:125–128.

Molero, J. & Vigo, J. (1981). Aportació al coneixement florístic i geobotànic de la Serra d'Aubenç. Treb. Inst. Bot. Barcelona, 6:1–82.

Molero, J., Sáez, Ll. & Villar, L. (1998). Interés florístico y geobotánico de la sierra de Alcubierre (Monegros, Aragón). Acta Bot. Barcinon., 45:363–390.

Molina Abril, J. A. & Pertíñez, C. (2005). Adiciones al informe final sobre el estudio integrado de la vegetación de ribera del tramo medio del río Cinca. Centro de Estudios de Monzón y Cinca Medio, 32:51–100.

Molina Cantos, R., Valdés Franzi, A. & Alcaraz Ariza, F. J. (2008). Flora y vegetación del tramo medio del valle del río Júcar (Albacete). Instituto de estudios albacetenses 'Don Juan Manuel' de la excma. Diputación de Albacete. 663 pp.

Navarro Andrés, F. & Valle Gutiérrez, C. J. (1983). Fitocenosis fruticosas de las comarcas zamoranas de Tabara, Alba y Aliste. Studia Botanica, 2:69–121.

Navarro Andres, F. (1974). La vegetación de la Sierra del Aramo y sus estribaciones (Asturias). Rev. Fac. Ci. Oviedo, 15:111–243.

Navarro, G. (1986). Vegetación y flora de las Sierra de Urbión, Neila y Cabrejas. Tesis Doctoral. Universidad Complutense Madrid

Navarro, G. (1989). Contribución al conocimiento de la vegetación del Moncayo. Opusc. Bot. Pharm. Complutensis, 5:5–64.

Nieto, J. M. & Cabezudo, B. (1988). Series de vegetación climatófilas de las sierras Tejeda y Almijara (Málaga-Granada, España). Acta Bot. Malacitana, 13:229–260.

Ninot, J.M. Quadrada, R.V. & Carrillo, E. (2009). Vegetació del Massís de la Fembra Morta (Anoia, Catalunya Central). Miscellanea Aqualatensia, 9:11–136.

Nuet, J. (1983). La vegetació de la muntanya dels Mollons, a la comarca d'Anoia. Miscellanea Aqualatensia, 3:15–52.

Onaindia Olalde, M. (1986). Ecología vegetal de las Encartaciones y Macizo del Gorbea, Vizcaya. Universidad del País Vasco, 271 pp. Bilbao.

Penas, A. & Díaz-González, T.E. (1985). Datos sobre la alianza Corynephoro-Plantaginion radicatae Rivas Goday & Rivas-Martínez 1963 nom. invers. Rivas-Martínez 1975 en el sector Orensano-sanabriense. Acta Bot. Malacitana, 10:155–166.

Penas, A. Rivas-Martínez, S. Díaz González, T.E. (2001). Un itinerario botánico por los alrededores de León. Servicio de Publicaciones de la Universidad de León, pp 47–55.

Peralta, J. Báscones, J.C. & Íñiguez, J. (1990). Bosques de la Sierra de Leyre (Navarra-Zaragoza, NE de España. Botánica pirenaico-cantabrica, 5:559–564.

Pereira, M. (2009). A Flora e Vegetação da Serra de Monfurado (Alto Alentejo-Portugal). Guineana, 15:1–316.

Pérez Badia, M.R. (1997). Flora vascular y vegetación de la comarca de la Marina Alta (Alicante). Colección Técnica 16. Instituto de Cultura Juan Gil Albert. Alicante.

Pérez Latorre, A. V., Caballero, G., Casimiro-Soriguer Solanas, F., Gavira, O. & Cabezudo, B. (2009). Vegetación de la Cordillera Antequerana Oriental (Subsector Torcalense). Málaga-Granada (España). Acta Bot. Malacitana, 34:1–29.

Pérez Latorre, A. V., Galán de Mera, A., Deil, U. & Cabezudo, B. (1996). Fitogeografía y vegetación del sector aljíbico (Cádiz-Málaga, España). Acta Bot. Malacitana, 21:241–267.

Pérez Latorre, A. V., Galán de Mera, A., Navas, P., Gil, Y. & Cabezudo, B. (1999). Datos sobre la flora y vegetación del Parque Natural de los Alcornocales (Cádiz-Málaga, España). Acta Bot. Malacitana, 24:133–184.

Pérez Latorre, A. V., Navas Fernández, D., Gavira, O., Caballero, G. & Cabezudo, B. (2004). Vegetación del Parque Natural de Las Sierras Tejeda, Almijara y Alhama (Málaga-Granada, España). Acta Bot. Malacitana, 29:117–190.

Pérez Morales, C. (1988). Flora y vegetación de la cuenca alta del río Bernesga. Institución Fray Bernardino de Sahagún. Diput. Prov. de León. 437 pp. León.

Pinillos López, J.A. (2000). Estudio de la Vegetación y Flora del Campo de Garcimuñoz: Baja y Media Serranía (Cuenca). Tesis Doctoral. Universidad de Valencia.

Pinto Gomes, C. & Pavia Ferreira, R. (2005). Flora e Vegetação do Barrocal Algarvio (Tavira-Portimão). Comissão de Coordenação e Desenvolvimento Regional do Algarve, pp 9–354.

Pinto-Gomes, Carlos., Paiva-Ferreira, R. & Meireles, C. (2007). New Proposals on Portuguese Vegetation. Lazaroa, 28:67–77.

Pitarch García, R. (2002). Estudio de la flora y vegetación de las sierras orientales del Sistema Ibérico: La Palomita, Las Dehesas, El Rayo y Mayabona (Teruel). Publicaciones del Consejo de Protección de la Naturaleza de Aragón. Serie Investigación. 537 pp. Zaragoza.

Puente García, E. (1988). Flora y vegetación de la cuenca alta del río Sil. Instituación Fray Bernardino de Sahagún. Diput. Prov. de León. 536 pp. León

Ramos Teles, R. J. (2005). Caracterização da flora e vegetação do Vale da Ribeira de Almoster; Universidad de Èvora

Rivas Goday, S. & Borja, J. (1961). Estudio de la vegetación y flórula del macizo de Gúdar y Jabalambre. Anales Inst. Bot. A. J. Cavanilles, 19:1–550.

Rivas Goday, S. (1964). Vegetación y flórula de la cuenca extremeña del Guadiana. Publ. Diput. Prov. Badajoz. 777 pp. Badajoz.

Rivas Goday, S. Borja Carbonell, J. Esteve Chueca, F. Fernández-Galiano, E. Rigual Magallon, A. & Rivas Martínez, S. (1959). Contribución al estudio de la Quercetea ilicis hispánica. Anales Inst. Bot. Cavanilles, 17(2):285–403.

Rivas Goday, S. & Madueño Box, M. (1946). Consideraciones acerca de los grados de vegetación del Moncayo y sobre la habitación de las Digitalis purpurea L. y parviflora Jacq. Farmacognosia, 5(9):97–122.

Rivas Martínez, S. (1962). Contribución al estudio fitosociológico de los hayedos españoles. Anales Inst. Bot. A. J. Cavanilles, 20:97–128.

Rivas Martínez, S. (1975). La vegetación de la clase Quercetea ilicis en España y Portugal. Anales Inst. Bot. Cavanilles, 31(2):205–259.

Rivas-Martínez, S., Báscones, J.C., Díaz, T.E. & Fernández-González, F. (1991). Vegetación del Pirineo-Occidental y Navarra. Itinera Geobot., 5:5–455

Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousa, M. & Penas, A. (2002). Vascular plant communities of Spain and Portugal, addenda to the syntaxonomical checklist of 2001. Itinera Geobot., 15 (1):5–432

Rivas-Martínez, S., Diaz, T.E., Fernández Prieto, J.A., Loidi, J. & Penas, A. (1984). Los Picos de Europa. Ediciones Leonesas.

Rivas-Martínez, Salvador., Lousa, M., Díaz, T. E., Fernández-González, F. & Costa, J. C. (1990). La vegetación del sur de Portugal (Sado, Alentejo y Algarve). Itinera Geobot., 3:5–126

Romero Abello, A. (1991). Contribución al estudio de la flora y vegetación vascular de las cuencas inferiores de los ríos Arlanza, Arlanzón y Carrión (provincias de Palencia y Burgos, España). Tesis Doctoral. Universidad complutense de Madrid

Romo, A.M. (1989). Flora i vegetació del Montsec (Prepirineus catalans). I.E.C. Arx. Secc. Ciènc., 90:1–534.

Roselló, R. (1994). Catálogo florístico y vegetación de la comarca natural del Alto Mijares. Diputació de Castelló. Castelló.

Royo Pla, F. (2006). Flora i vegetació de les planes i serres litorals compreses entre el riu Ebro i la serra d'Irta. Tesi Doctoral. Universitat de Barcelona.

Sánchez Mata, D. (1989). Flora y vegetación del macizo oriental de la Sierra de Gredos (Avila). Institución Gran Duque de Alba. Diputación Provincial de Avila. Avila.

Sardinero, S. (2004). Flora y vegetación del macizo occidental de la Sierra de Gredos (Sistema Central, España). Guineana, 10:1–474.

Sobrino Vesperinas, E. & Sanz Elorza, M. (1998). Datos sobre la flora y vegetación de la Sierra de Alcubierre (Huesca). Lagascalia, 20(2):231–237.

Tüxen, R. & Oberdorfer, E. (1958). Die Pflanzenwelts Spaniens. Teil II. Veröff. Geob. Inst. Rübel Zurich, 32. 328 pp.

Valle, Francisco., Gómez-Mercado, F. & Mota, J. F. (1988). Los robledales de la sierra de Segura y otras comunidades relacionadas con ellos. Anales Jard. Bot. Madrid, 45(1):247–257.

Vicente Orellana, J.A. & Galán De Mera, A. (2008). Nuevas aportaciones al conocimiento de la vegetación Luso-Extremadurense. Estudio de las Sierras de Las Villuercas (Extremadura, España) y San Mamede (Alto Alentejo, Portugal). Acta Bot. Malacitana, 33:1–49.

Vigo, J. (1968). La vegetació del massís de Penyagolosa. I.E.C. Arx. Secc. Ciènc. 37:1–247.

Vigo, J. (1996). El poblament vegetal de la vall de Ribes. Institut Cartogràfic de Catalunya, 468 pp. Barcelona.

Vilar, L. & Viñas, X. (1990). Sobre los robledales del Llano de la Selva. Acta Bot. Malacitana, 15:277–281.

Villaescusa Reig, C. (1998). Flora vascular de la comarca de El Baix Maestrat (Castellón). Tesi Doctoral. Universitat de València.

Villegas i Alba, N. (1993). Flora i vegetació de les muntanyes del Puigsacalm-serra de Milany. Tesi doctoral. Universitat de Barcelona

Viñas, X. & Polo, L. (1992). La vegetació dels enclavaments silicis de l'alta Garrotxa. Actes del Simposi Internacional de Botànica Pius Font i Quer, 2:317–329.

Viñas, X. (1993). Flora i vegetació de l'Alta Garrotxa. Tesi Doctoral. Universitat de Girona.

Vives, J. (1964). Vegetación de la alta cuenca del Cardener. Estudio florístico y fitocenológico comarcal. Acta Geobot. Barcinon., 1:1–218.

Wattez, J.-R. (1979). Affinités phytosociologiques de l'alisier torminal (Sorbus torminalis (L.) Crantz) en Picardie occidentale; Doc. Phytosoc. N.S., 4:951–965

References

Abadía, A., E. Gil, F. Morales, L. Montañés, G. Montserrat, and J. Abadía 1996. Marcescence and senescence in a submediterranean oak (*Quercus subpyrenaica*) E. H. del Villar: photosynthetic characteristics and nutrient composition. *Plant Cell Environ*, 19:685–694

Benito Garzón, M., R. Sánchez de Dios, and H. Sainz Ollero 2007. Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and the Holocene. *Ecography*, 30:120–134

Bingre, P., C. Aguiar, D. Espirito-Santo, P. Arsénio, and T. Monteiro-Henriques (Coord. Cient.) 2007. Guia de campo – as árvores e os arbustos de Portugal continental. 462 pp. In: vol IX dea Sande Silva, J. (Coord. Ed.) Colecção Árvores e Florestas de Portugal. Jornal Público Fundação Luso-Americana par o Desenvolvimento/ / Liga para a Protecção da Natureza. Lisboa

Brewer, S., R. Cheddadi, J. L. de Beaulieu, and M. Reille 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management*, 156:27–48

Calleja, J.A., M. Benito Garzón, and H. Sainz Ollero 2009. A Quaternary perspective on the conservation prospects of the Tertiary relict tree *Prunus lusitanica* L. *J. Biogeography*, 36(8):487–498

Cano, E., and F. Valle 1990. Formaciones boscosas en Sierra Morena oriental (Andalucía, España). *Acta Botánica Malacitana*, 15:231–237

Cantó, P. 2004. Estudio fitosociológico y biogeográfico de la sierra de San Vicente y tramo inferior del valle del Alberche (Toledo, España). *Lazaroa*, 25:187–249

Castroviejo, S., et al. (eds.) 1986–2010. Flora Iberica. Vols. I–VIII, X, XII–XV, XVII, XVIII, XXI. Real Jardín Botánico. C.S.I.C, Madrid.

Costa, J. C., T. Monteiro-Henriques, P. Bingre, and D. Espírito-Santo (2015). Warm-temperate forests of central Portugal: a mosaic of syntaxa. In: Warm-Temperate Deciduous Forests around the Northern Hemisphere (E. O. Box & K. Fujiwara, eds.). Geobotany Studies, Springer-Verlag. DOI 10.1007/978-3-319-01261-2_6.

De Cáceres, M., X. Font, R. García, and F. Oliva 2003. VEGANA, un paquete de programas para la gestión y análisis de datos ecológicos. In: VII Congreso Nacional de la Asociación Española de Ecología Terrestre, July 2003, Barcelona, pp 1484–1497

De Cáceres M., X. Font, and F. Oliva 2008. Assessing diagnostic species value in large data-sets: A comparison between phi-coefficient and Ochiai index. *Journal of Vegetation Science*, 19(6): 779–788

Del Río, S., and A. Penas 2006. Potential distribution of semi-deciduous forests in Castile and Leon (Spain) in relation to climatic variations. *Plant Ecology*, 185:269–282

Dumolin-Lapègue, S., B. Demesure, S. Fineschi, V. Le Come, and R. J. Petit 1997. Phylogeographic structure of white oaks throughout the European continent. *Genetics*, 246:1475–1487

Ferris, C., R. A. King, R. Vaïnölä, and G. M. Hewitt 1998. Chloroplast DNA recognizes three refugial sources of European oaks and suggests independent eastern and western immigrations to Finland. *Heredity*, 80:584–593

Font, X., M. P. Rodríguez-Rojo, C. Acedo, I. Biurrun, F. Fernández-González, C. Lence, J. Loidi, and J. M. Ninot 2010. SIVIM: An on-line data-base of Iberian and Macaronesian vegetation. *Waldökologie, Landschaftsforschung und Naturschutz*, 9:15–22

Honrado, J., C. Aguiar, F. Barreto Caldas, R. Almeida, and J. H. Capelo 2001. Palaeoclimatic relicts and climatic disjunctions in the flora of northern Portugal. *Quaternary Studies*, 4:49–60

Hsu K.-J., L. Montadert, D. Bernoulli, M. B. Cita, A. Erickson, R. E. Garrison, R. B. Kidd, F. Mèliéres, C. Müller, and R. Wright 1977. History of the Mediterranean salinity crisis. *Nature*, 267:399–403

Knollová, I., M. Chytrý, L. Tichý, and O. Hájek 2005. Stratified resampling of phytosociological data-bases: some strategies for obtaining more representative data-sets for classification studies. *J. Vegetation Science*, 16:479–486

Kruskal, J. B. 1964a. Multidimensional scaling by optimizing goodness of fit to a non-metric hypothesis. *Psychometrika*, 29:1–27

Kruskal, J. B. 1964b. Non-metric multidimensional scaling: a numerical method. *Psychometrika*, 29:115–129

Lance, G. N., and W. T. Williams 1967. A general theory of classificatory sorting strategies. 1. Hierarchical systems. *Computational Journal*, 9:373–380

Mather, P. M. 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. J. Wiley & Sons, London

Montserrat Martí, M., S. Palacio, and R. Milla 2004. Fenología y características funcionales de las plantas leñosas mediterráneas. In: *Ecología del bosque mediterráneo en un mundo cambiante* (F. Valladares, ed.), pp 129–162. Ministerio de Medio Ambiente, Madrid

McCune, B., and J. B. Grace 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach (Oregon), USA

Ninyerola, M., X. Pons, and J. M. Roure 2005. Atlas climático digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Editions of Universitat Autònoma de Barcelona, Barcelona.

Olalde, M., A. Herrán, S. Espinel, and P. G. Goicoechea 2002. White-oak phylogeography in the Iberian Peninsula. *Forest Ecology and Management*, 156:89–102

Pereira, M. 2009. A flora e vegetação da Serra de Monfurado (Alto Alentejo-Portugal). *Guineana*, 15:1–316

Petit, R. J., I. Aguinagalde, J.-L. de Beaulieu, C. Bittkau, S. Brewer, R. Cheddadi, R. Ennos, S. Fineschi, D. Grivet, M. Lascoux, A. Mohanty, G. Müller-Starck, B. Demesure-Musch, A. Palmé, J. P. Martín, S. Rendell, and G. G. Vendramin 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. *Science*, 300:1563–1565

Pinto, C. J., and R. J. P. Paiva 2005. *Flora e vegetação do Barrocal Algarvio (Tavira-Portimão)*. Ed. Comissão de Coordenação e Desenvolvimento Regional do Algarve. p 354.

Podani, J. 2006. Braun-Blanquet's legacy and data analysis in vegetation science. *J. Vegetation Science*, 17:113–117

Rivas Goday, S., J. Borja, F. Esteve, E. F. Galiano, A. Rigual, and S. Rivas-Martínez 1960. Contribución al estudio de la Quercetea ilicis hispánica. Conexión de las comunidades hispánicas con *Quercus lusitanica* s.l. y sus correlaciones con las alianzas de Quercetalia ilicis, Quercetalia pubescentis y Quercetalia robori-petraeae. *Anales Inst. Bot. Cavanilles*, 17(2):285–406

Rivas-Martínez, S. 1972. Apuntes sobre la sintaxonomía del orden Quercetalia pubescentis en España. *Anales Inst. Bot. Cavanilles*, 29:123–128

Rivas-Martínez S. 2007. Mapa de series, geoseries y geopermaseries de vegetación de España (Memoria del mapa de vegetación potencial de España). Parte 1. *Itinera Geobotanica*, 17:5–436

Rivas-Martínez, S. 2011. Mapa de series, geoseries y geopermaseries de vegetación de España (Memoria del mapa de vegetación potencial de España). Parte 2. *Itinera Geobotanica*, 18(1):5–424

Rivas-Martínez, S., M. Lousã, T. E. Díaz, F. Fernández-González, and J. C. Costa 1990. La vegetación del sur de Portugal (Sado, Alentejo y Algarve). *Itinera Geobotanica*, 3:5–126

Rivas-Martínez, S., T. E. Díaz, F. Fernández-González, J. Izco, J. Loidi, M. Lousã and A. Penas 2002. Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. Part I. *Itinera Geobotanica*, 15(1):5–432

Rodríguez-Sánchez, F., A. Hampe, P. Jordano, and J. Arroyo 2010. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: A review. *Review of Palaeobotany and Palynology*, 162:507–521

Rodríguez-Sánchez, F., and J. Arroyo 2008. Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. *Global Ecol. Biogeogr.*, 17:685–695

Rodríguez-Sánchez, F., and J. Arroyo 2011. Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past. In: *Climate Change, Ecology and Systematics* (Trevor et al., eds.), pp 280–303. Cambridge University Press

Royo, F. 2006. Flora i vegetació de les planes i serres litorals compreses entre el riu Ebro i la serra d'Irta. PhD. Universitat de Barcelona

Sánchez de Dios, R., M. Benito-Garzón, and H. Sainz-Ollero 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecol.*, 204:189–205

Sokal, R. R., and F. J. Rohlf 1987. *Introduction to Biostatistics*. W. H. Freeman, New York

Tutin, T. G., et al. (eds.) 1976. *Flora Europaea*. Vol. 4. Cambridge University Press, Cambridge. 505 pp.

Tutin, T. G. et al. (eds.) 1980. *Flora Europaea*. Vol. 5. Cambridge University Press, Cambridge. 452 pp.

Wesche, K., and H. von Wehrden 2011. Surveying Southern Mongolia: application of multivariate classification methods in drylands with low diversity and long floristic gradients. *Applied Vegetation Science*, 14(4):561–570

Downy-Oak Woods of Italy: Phytogeographical Remarks on a Controversial Taxonomic and Ecologic Issue

Riccardo Guarino, Giuseppe Bazan, and Bruno Paura

Abstract

The importance of downy oak as an integral component of the "submediterranean" woods has been underscored by many studies. Nevertheless, terms like "submediterranean" and "downy oak" are some of the most poorly understood concepts in European phytogeographic and taxonomic research. Downy oak is well known to be a problematic taxon. The name "*Quercus pubescens*" (= *Q. humilis*) combines populations characterized by increasing phenotypic and genomic polymorphisms along north-south gradients, which is explained as the result of a "founder effect" produced by a relatively fast post-glacial re-colonization of the northern areas through rare long-distance dispersal events.

On the other hand, polymorphisms of downy oak in the south provide evidence for geographic/environmental selection driven by different edaphic conditions along clinal gradients of cold and drought stress, even if the distinction of different species is blurred by systematic hybridization and introgression, which have been enhanced by recent deforestation.

Because downy oak occurs widely throughout the Italian Peninsula, we tried to detect some ecological and geographical borders, which might be useful to identify climate-vegetation feedback mechanisms as well as to sharpen the syntaxonomical and systematic investigation of such a critical species complex. Our work is based on a well-distributed geo-referenced set of vegetation data, combined with layers of environmental variables (elevation, climate, soil chemistry). The statistical significance of the correlation between vegetation and environmental data has been evaluated through the Mantel test.

We assessed that:

- The ecological amplitude of downy oak along the Italian peninsula increases southward;
- The maximum variance in ecological conditions is found in Sicily, where the morphologic variability of downy oak is also maximized and where potential competitors, like *Quercus frainetto*, *Q. trojana*, *Carpinus orientalis*, and others, are missing;
- Discontinuities in the distribution/prevalence of morphologic traits of *Q. pubescens* (regarded here as a species complex) are not determined by sharp ecological or geographical gaps but instead reflect patterns of selection and phenotypic variability in key traits of the geographical range;
- The Ellenberg T and U indicator values for the flora of Italy are correlated well with temperature and precipitation.

R. Guarino (✉) • G. Bazan
Department of Environmental Biology and Biodiversity, University of Palermo, via Archirafi, 38 – 90123 Palermo, Italy
e-mail: riccardo.guarino@unipa.it

B. Paura
Department S.A.V.A., University of Molise, via De Sanctis, 1 – 86100 Campobasso, Italy

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_7, © Springer International Publishing Switzerland 2015

Keywords
Downy oak • Ecological gradients • Syntaxonomy • Phytogeography • Coenologic variability • Distribution patterns • Human impact

1 Introduction

The importance of downy oak as an integral component of the "submediterranean" woods has been underscored by many studies. Nevertheless, terms like "submediterranean" and "downy oak" are some of the most poorly understood concepts in European phytogeographical and taxonomical research. Downy oak is well known to be a problematic taxon. The name "*Quercus pubescens*" (= *Q. humilis*) throws together populations characterized by increasing phenotypic and genomic polymorphisms along north-south gradients, which is commonly explained as the result of a "founder effect" produced by the relatively fast post-glacial re-colonization of the northern areas through rare long-distance dispersal events (Huntley and Birks 1983; Hewitt 1996; Ferris et al. 1998; Brewer et al. 2002).

On the other hand, polymorphisms of downy oak in the south suggest geographic/environmental selection driven by different edaphic conditions along clinal gradients of cold and drought stress, even if the distinction of different species is blurred by systematic hybridization and introgression, which have been enhanced by recent deforestation (Fineschi et al. 2002). Such prominent morphologic variability has been treated in many different ways by taxonomists: from those who lump all the downy-oak populations into a single species, to those who split the variability into countless specific and infra-specific taxa.

Downy oak, in the broad sense, is the single major constituent of the mixed temperate forests of Europe, with the southern European peninsulas acting as refugia during the Quaternary cold phases (Huntley 1990). This isolation, interacting with the ecological diversity of the southern European peninsulas, produced a large array of meta-populations with distinctive characteristics, some broad-ranging and some specialized, that have been investigated in detail genetically (Dumolin-Lapègue et al. 1997; Petit et al. 2002) and morphologically (Rivas-Martínez and Saenz-Lain 1991; Brullo et al. 1998; Schicchi et al. 1998), or both (Bruschi et al. 2000; Fortini et al. 2009; Viscosi et al. 2009). No comparable studies exist to detect latitudinal gradients of floristic variability in the downy-oak meta-populations, even though plenty of data are available in the phytosociological literature, describing forest physiognomy and syntaxonomy.

Because downy oak occurs widely throughout the Italian Peninsula (incl. Sicily and Sardinia), based on phytosociological relevés, ecological indicators and environmental variables, we tried to interpret the floristic diversity as a coenologic response to environmental controls, in order to reveal climate-vegetation feedback mechanisms acting at different latitudes, as well as to support the syntaxonomic and systematic views of such a critical species complex.

2 Methods

2.1 Data Sets

Many phytosociological data on downy-oak woods are available, well distributed throughout the Italian Peninsula, Sicily and Sardinia. Complete bibliographic surveys for the Italian territory have been published by Pignatti (1998), Ubaldi (2003) and, for Sicily, by Brullo et al. (2009, 2012).

In our work, the only criterion used to select the phytosociological associations for data processing was clear dominance by downy oaks. A rough estimate of the surface covered by each association considered was obtained by overlaying the Corine Land Cover map, 4th level (Maricchiolo et al. 2005), over the Map of the Vegetation Series of Italy (Blasi 2010).

Our analyses are based on 290 relevés distributed along the latitudinal gradient 37°–42° N (Fig. 1), mostly taken from literature and involving the 29 phytosociological associations listed in App. 1. All the relevés were normalized to a 100 m^2 standard plot size, by calculating a species-area curve for each association, based on the assumption that species abundance should fit a log-series distribution asymptotic to the mean species number of the relevés sampled in 100 m^2 plots, plus its standard deviation. The species list for the relevés larger than the standard plot size was shortened proportionally by eliminating the most sporadic species; the species list for relevés smaller than the standard plot size was enlarged by adding some sporadic species randomly chosen from the bulk of relevés from the same locality.

For each association, the ten most dissimilar relevés were selected for data processing, in order to portray the maximum floristic variability. The reciprocal dissimilarity of processed relevés was evaluated through the Euclidean distance algorithm. The relevés selected, without explicit indication of their geographical coordinates, were geo-referenced using the Web-GIS of the IGM (Military Geographical Institute), which permits achieving a reasonably good approximation

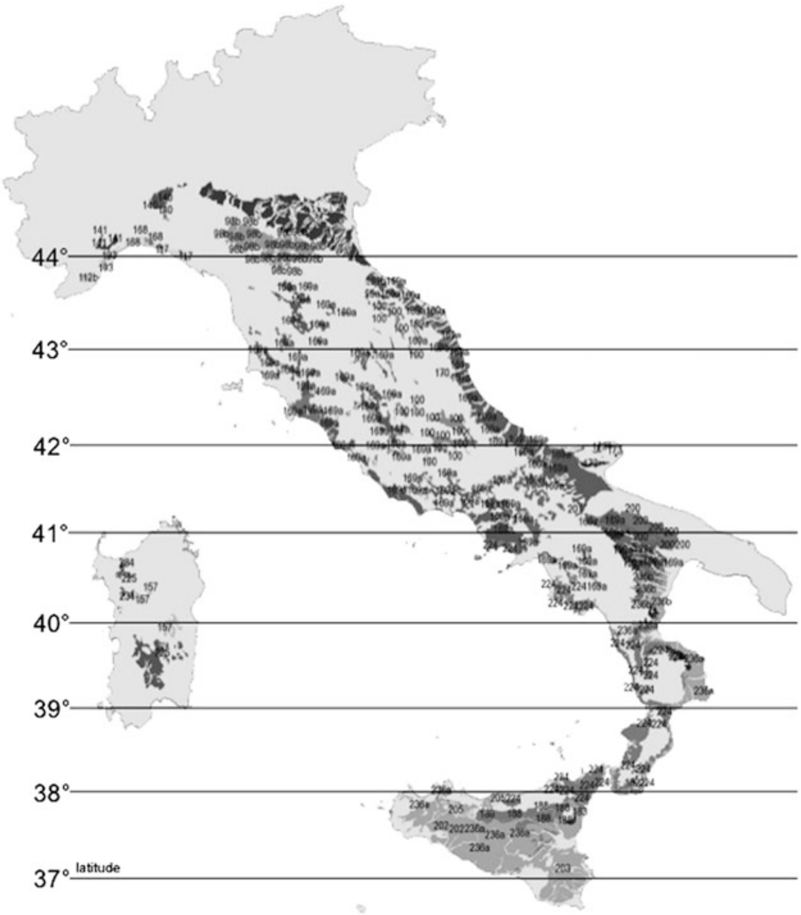


Fig. 1 Distribution map of the phytosociological relevés processed. Numerical codes refer to the associations listed in App. 1. The potential areas of different downy-oak vegetation series (According to Blasi 2010) are depicted in shades of *grey*

through comparison of aerial photographs with the highly detailed IGM data-base of Italian toponyms.

Each site was characterized with respect to the following environmental variables: mean annual temperature, mean annual precipitation (mm), cumulative dry season precipitation (mm/June-September), elevation, and soil reaction (pH).

Climatic variables were interpolated, from meteorological data collected at 85 stations, by means of a multiple-regression model based on geographic coordinates and elevation, incorporated in the global meteorological information system WorldClim (www.worldclim.com). The interpolation procedure was repeated to check the trend of temperatures and the cumulative precipitation during the dry season, in order to express the severity of summer drought at each plot. Graphical plots of monthly rainfall and cumulative rainfall distribution (data not presented) indicated that the maximum difference between station values could be found by integrating data between June and September.

A very rough indication of the soil reaction was obtained from the data-base "Soil Regions of Italy" (www.soilmaps.it), using the following definitions: acidic (pH <5.9); sub-acid ($5.9 \leq$ pH ≤ 6.7); neutral ($6.7 \leq$ pH ≤ 7.3); sub-alkaline ($7.3 \leq$ pH ≤ 8.1); alkaline (pH >8.1). The indications obtained in this way generally agreed quite well with the statements of the authors of the relevés, when available.

In order to get a complementary assessment of the environmental variables, the following Ellenberg indicator values were considered: Temperature (T), Humidity (F), and soil Reaction (R). These values have been described by the author himself as a useful paradigm to summarize interactions between plants and environment, recognising the role of each species as a biological indicator (Ellenberg 1974; Pignatti et al. 2005). Ellenberg's indices have been applied successfully to "fingerprint" the ecological context of plant communities described by floristic composition (Pignatti et al. 1996, 2001a, b; Pignatti 1998, 1999; Guarino and Bernardini 2002; Gristina and Marcenò 2008; Mossa et al. 2008; Brunialti et al. 2010). Latitudinal and altitudinal variations of these indices are therefore expected to correlate quite well with the dimensional measurements of environmental variables (van der Maarel 1993).

Table 1 Percent frequency of the ten most frequently occurring species within phytosociological plots from: (column 1) Sicily, thermo-mediterranean bioclimate, subalkaline soil; (column 2) Sicily, supra-mediterranean bioclimate, acidic soil; (column 3) Piemonte, mesotemperate bioclimate, neutral soil

Oleo-Quercetum virgilianae	%	Agropyro panormitani-Q. congestae	%	Buxo-Quercetum pubescentis	%
Quercus virgiliana	100	Quercus congesta	100	Quercus pubescens	100
Olea europaea var. oleaster	100	Quercus dalechampii	100	Buxus sempervirens	100
Rubia peregrina	100	Agropyron panormitanum	100	Teucrium chamaedrys	100
Rubus ulmifolius	94	Crepis leontodontoides	100	Brachypoium rupestre	97
Carex distachya	94	Brachypodium sylvaticum	100	Corylus avellana	91
Quercus amplifolia	89	Lathyrus pratensis	95	Fraxinus excelsior	86
Osyris alba	89	Silene sicula	95	Cytisus sessilifolius	86
Arisarum vulgare	89	Trifolium semipurpureum	95	Viola hirta	86
Pistacia lentiscus	84	Pteridium aquilinum	95	Sorbus aria	78
Asparagus acutifolius	84	Daphne laureola	95	Hippocrepis emerus subsp. emerus	78
Source: Brullo and Marcenò 1985 tab. 3 (18 rel.)		Source: Brullo et al. 2012, tab. 11 (22 rel.)		Source: Mondino 1992 tab. 5 (38 rel.)	

Botanical nomenclature follows Conti et al. (2005); bioclimatic nomenclature follows Rivas-Martínez (2007).

2.2 Data Processing

Four methods were used to explore the floristic variability of downy-oak forests across the latitudinal gradient considered: (1) percentage of species with restricted distribution; (2) indirect, multivariate ordination, including Non-metric Multidimensional Scaling (NMS); (3) one-way analysis of variance (ANOVA) of the environmental variables along the latitudinal gradient; (4) Mantel test (Mantel 1967).

All analyses were performed by means of the Syntax2000 software package (Podani 2001), the "R" package (Casgrain and Legendre 2000) and the Microsoft® Excel® spreadsheet for Mac® (version 12.2.8). The Euclidean distance algorithm on presence/absence data was adopted for cluster and NMS analysis.

The floristic "spread" along the latitudinal gradient was evaluated on the basis of species groups identified through the cluster analysis and ordination. It must be noted, however, that the restricted distribution observed for many species in the processed relevés is not necessarily indicative of their regional or global distribution range. The multivariate ordination was used, as well, to check the occurrence of a gradient of floristic diversity in the processed phytosociological relevés, in order to support and strengthen the spread and variability of the roughly approximated environmental data available.

The Mantel test was used to measure the pairwise correlation between (1) floristic diversity, (2) environmental variables (temperature, precipitation, soil reaction) and (3) Ellenberg's indicator values. The input included the Euclidean distance of relevés in the first matrix, of environmental variables in the second matrix, of Ellenberg's indicator value in the third matrix.

The Mantel test is a useful tool for checking the independence of the elements of two matrices, or in other words, for testing the significance of the correlation calculated from the initial matrices. Although Mantel tests do not provide graphical outputs, they do have the benefit of providing complementary statistical information about relationships in the data. Overall, the ensemble of data and techniques for data processing was adopted to obtain reliable multiple-entry information for assessing community patterns along the latitudinal gradient considered.

3 Results

3.1 Patterns of Floristic Diversity

Single associations did not show significant differences in floristic richness calculated by multiple measures, including Fisher's and the Shannon diversity index H'; we did, however, find proportionally higher levels of floristic diversity for southern latitudes. This is well reflected by the higher number of phytosociological associations with downy oak described for Sicily and southern Italy (see discussion). Species ranked in Table 1 illustrate the diversity in species composition found within the two most different associations of Sicily.

The southernmost thermo-mediterranean stands (*sensu* Rivas-Martínez) and the sub-montane stands of northern latitudes have contrasting floristic assemblages. Table 1 also illustrates the absence of overlap among the ten most frequent species found in each life zone.

There were no significant differences in the average number of species per relevé. In general, though, shrub density (estimated from the Braun-Blanquet cover values in the relevés) decreased northward and with increasing altitude, with cover decreasing from 60% to 70% in the thermo-mediterranean downy-oak stands of Sicily to 35–45% in the supra-mediterranean stands also on Sicily or 40–45% in the stands in Liguria and the northern Apennines. As a general rule, the thermo-mediterranean stands have greater shrub cover and higher incidence of evergreen species, while evergreens are almost absent in the montane and

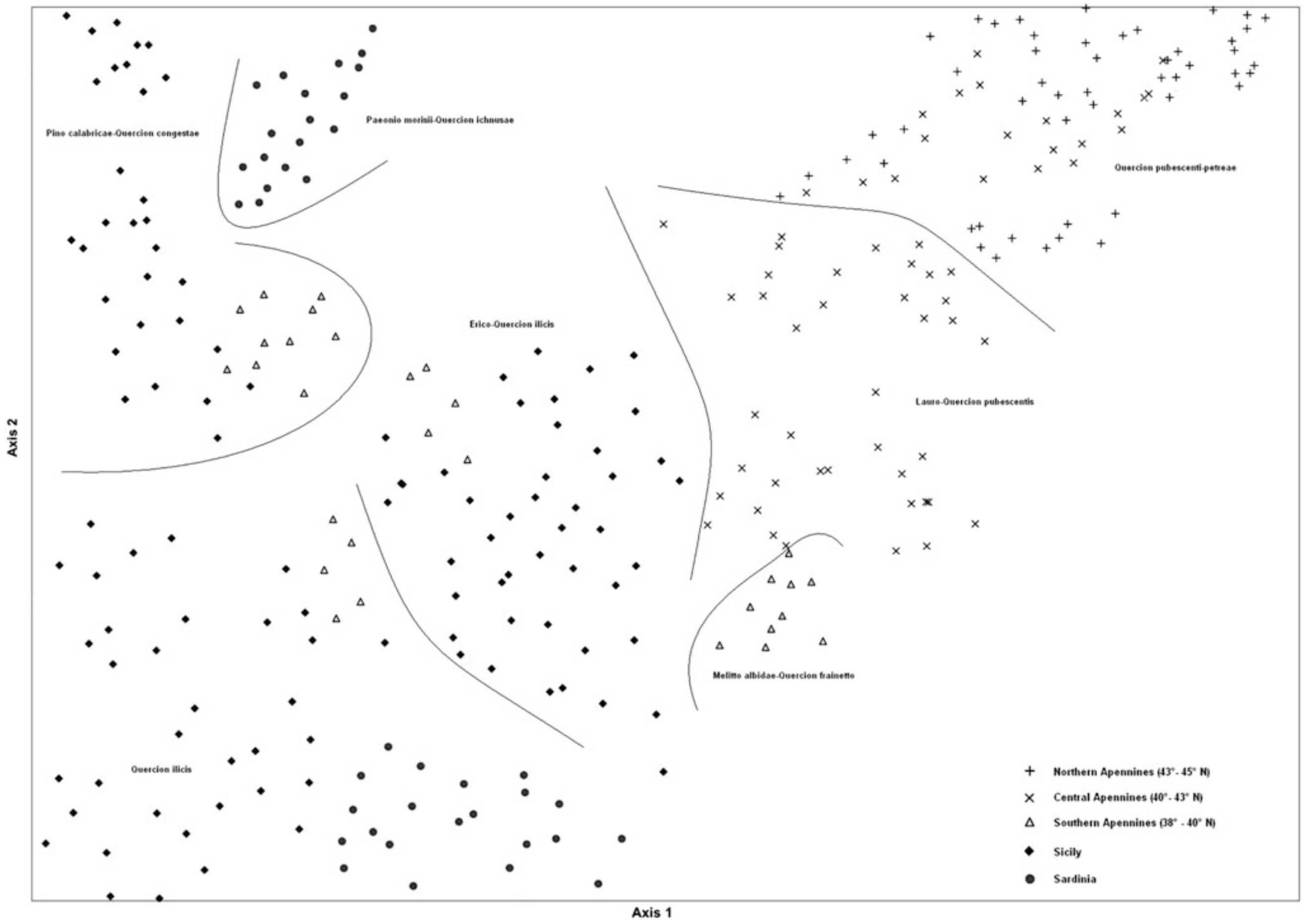


Fig. 2 NMS ordination of the relevés processed. The first axis was fit best by average annual precipitation (p-value < 0.001, $R^2 = 0.58$). The Sicilian, Calabrian and Sardinian plots are stretched along the second axis

northernmost stands. These coenologic differences are certainly due to climatic differences, with which not only different species assemblages but even different life strategies are associated. For instance, the downy oak itself tends to be clearly semi-deciduous when it grows in the thermo-mediterranean climate, with many leaves remaining green in winter; on the other hand, there is a significant shedding of the foliage during the summer drought.

The NMS ordination produced a dense cluster of plots stretching from the warm, dry sites of the thermo-mediterranean region to the colder, moister plots of the northern Apennines (Fig. 2). A more diffuse group is formed by the plots of Sicily and of the isolated Calabrian and Sardinian massifs, stretching along a second axis. These floristic divisions are supported by patterns of species accumulation that occur when crossing ecotones and boundaries between different bioclimatic areas. The restricted distribution observed for many species supports this assumption further (Fig. 3). Many species found in the Sardinian, Sicilian and Calabrian oakwoods are not found in the Apennine plots. This contrasts with the situation along the Apennines, where, despite the scarcity of omnipresent species, many species occur in multiple plots along the latitudinal gradient.

3.2 Patterns of Ecological Gradients

Clear patterns of floristic composition were detected through the indirect gradient analysis. The main gradient appears to run along the Apennine mountain range, paralleling the regional trends in precipitation and dry-season severity inferred from the climate data. If only the 19 pre-Apennine and Apennine phytosociological associations (190 relevés) were included in the analysis, the NMS scores are fit best by average annual precipitation (p-value < 0.001, $R^2 = 0.60$). Mean annual temperature resulted in a slightly worse fit (p-value < 0.001, $R^2 = 0.52$). A randomized Monte Carlo permutation rejected the null hypothesis (no effect by precipitation or temperature) at levels of $\alpha = 0.92$ and 0.85, respectively (precipitation: $r = 0.722$, $p = 0.001$; temperature: $r = 0.382$, $p = 0.001$). Consequently, the test supports a positive association between differences in the main climatic variables and floristic distance as measured by the Euclidean distance. Since climatic conditions and geographic distances are highly correlated along the Apennines, Mantel tests comparing geographic distance and climatic variables indicated a very strong positive association (Standardized Mantel statistic, $r > 0.8$, $p = 0.001$).

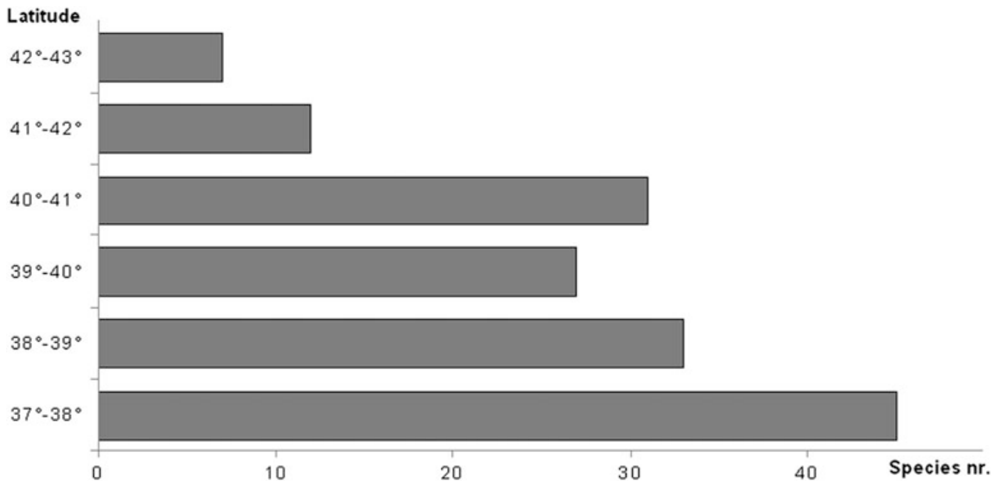


Fig. 3 Percentage of species restricted to one single latitudinal degree within the study area. The restricted distribution of these species is based on their occurrence in the relevés and may not be indicative of their regional or global distribution

The ANOVA of the environmental variables indicated that the ecological amplitude of downy oak increases southward. Altitude and temperature appear to be the two most influential variables on the floristic diversity of the downy-oak stands in Italy, while precipitation appears to be less restrictive (Fig. 4). This general relationship might be blurred partially by the fact that climatic conditions, altitude and geographic distance are highly correlated. This correlation does not apply, however, to the Ellenberg indicator values, which can therefore be used to strengthen the indications provided by the environmental variables. Mantel's asymptotic approximation methods indicated significant correlation, at the alpha = 0.05 level, between the environmental variables and the weighted scores of the Ellenberg indicator values T and F of the relevés processed. This holds true for the comparison between soil reaction and Ellenberg's value R: even if edaphic conditions are not necessarily related to the latitudinal gradient, it is certainly true that soil heterogeneity in the downy-oak stands of Italy is higher between 38° and 40° N latitude. Therefore, geologic and edaphic conditions, superimposed on landscape-scale patterns dominated by climatic and phytogeographic factors, can contribute to local-scale variations in species composition.

4 Discussion

4.1 Regional Classification: North

The phytosociological treatment of the associations considered yielded seven alliances and two different classes (Appendix). The number of syntaxa increases from north to south, reaching its maximum in Calabria and Sicily, where the large number of associations described has been questioned by some authors in the last three decades of the last century (see, for instance, the discussion reported in Brullo and Marcenò 1985), before being accepted as unavoidable, if the principle of floristic homogeneity has to be applied.

In the northern Apennines, downy-oak woods are found mostly between 350 and 750 m above sea level and are all ascribed to the *Quercion pubescenti-petraeae*. This alliance has its barycentre in the continental and pre-Alpine territories of Central Europe, where downy oak behaves like a pioneer tree, colonizing stony slopes and immature soils, particularly on limestone and marl, with dry edaphic conditions. These open xerophilous woods are often rich in grasses and small forbs from the class *Festuco-Brometea* and are characterized by a high frequency of *Trifolio-Geranietea* elements, such as: *Arabis turrita, Campanula persicifolia, Carex montana, Clinopodium vulgare* ssp. *vulgare, Digitalis micrantha, Geranium sanguineum, Hypericum montanum, Inula conyza, Primula veris, Vincetoxicum hirundinaria* ssp. *hirundinaria, Viola hirta, V. scotophylla*, and *V. alba*. The distribution of such woods along the Italian Peninsula reaches Molise, i.e. in the central part of the Apennine range, where they are limited to dry mountain slopes, far from the influence of the sea, in the inner and upper parts of the catchment basins, from 600 to 900 m (Allegrezza et al. 2002; Ubaldi 2003).

4.2 Regional Classification: Centre

Most of the downy-oak woods of the central Apennines are ascribed to the *Lauro-Quercion pubescentis*, the main difference of which (from the previous alliance) is increasing density of the shrub layer; increasing abundance of

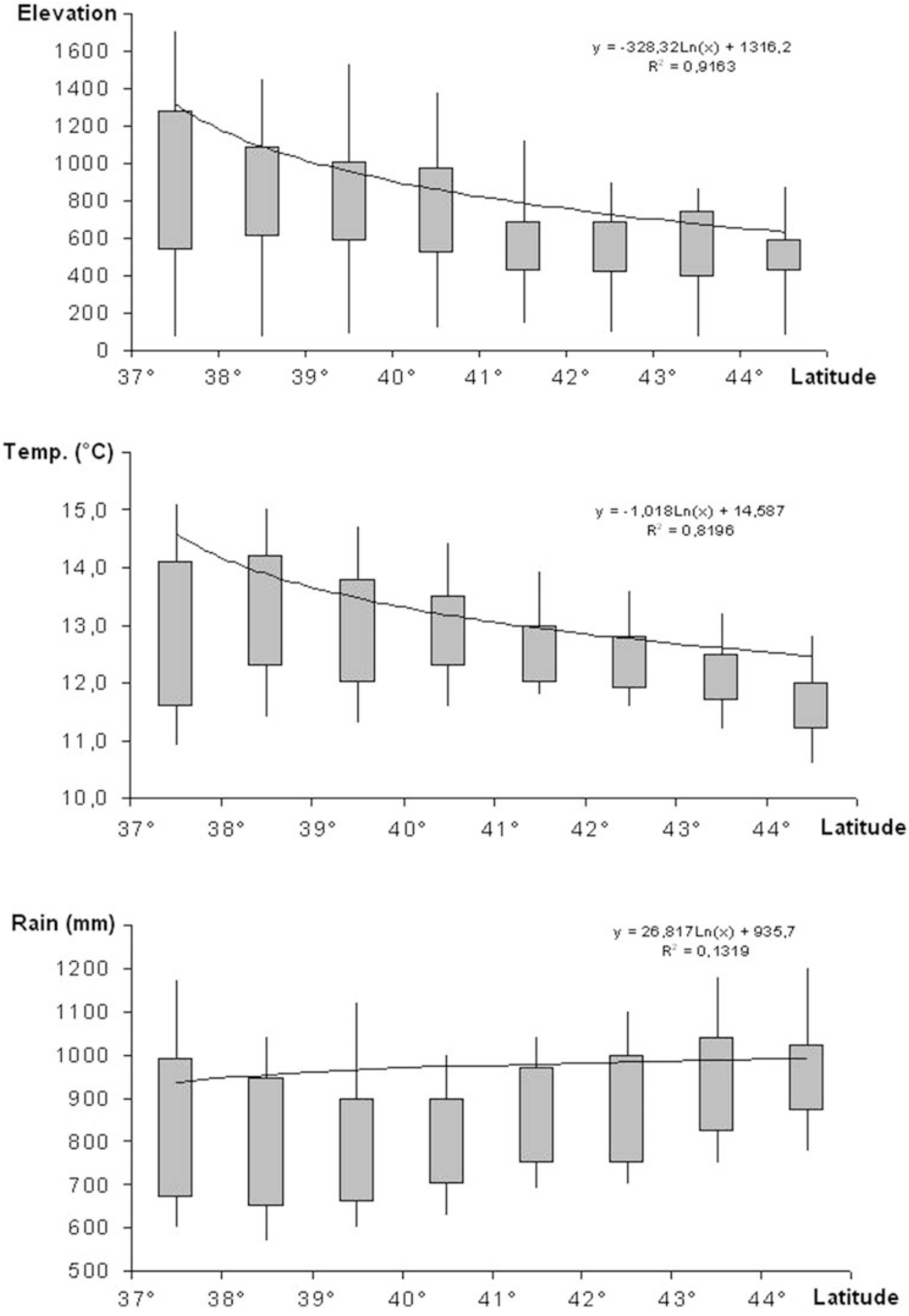


Fig. 4 Histograms showing the decline of environmental variability (altitude, mean annual temperature, average annual rainfall) with latitude

evergreen elements from the class *Quercetea ilicis*, such as *Smilax aspera*, *Laurus nobilis, Asparagus acutifolius*, and *Viburnum tinus*; and occurrence of meso-xerophilous species like *Acer obtusatum, A. neapolitanum, Pyracantha coccinea, Cytisus sessilifolium, Lonicera etrusca, Sorbus torminalis, Cercis siliquastrum, Melittis melissophyllum ssp. albida, Helleborus bocconei*, and *Silene italica*. The alliance *Lauro-Quercion pubescentis* can be considered an Italian vicariant of the *Carpinion orientalis*, a Balkan alliance whose chief species occur widely in central Italy, particularly on the Adriatic side. As a matter of fact, many phytosociologists who studied the northeastern and central sectors of the Italian peninsula prefer to ascribe their relevés to the Balkan alliance, in order to emphasize the remarkable similarity of the woods on both sides of the Adriatic Sea (see, for instance, Allegrezza et al. 2006). These woods are clearly linked to a transitional climate, their optimal stands being on hilly slopes, not too cold in winter and relatively dry in summer, though partially exposed to moisture condensation from the sea. These conditions correspond to the Apennine transitional climate well described by Blasi and Michetti (2005), which blurs the boundary between the Temperate and the Mediterranean ecoregions. The woods ascribed to the *Lauro-Quercion pubescentis* are found at progressively increasing altitudes from Tuscany and the Marche up to the Mt. Pollino massif, on sub-acidic to sub-alkaline soils (Allegrezza et al. 2002; Blasi et al. 2004). In the south-eastern part of the range considered, these woods become progressively enriched in Balkan floristic elements. One of these, described as *Centaureo centauroidis-Quercetum pubescentis*, is included in the alliance *Melitto albidae-Quercion frainetto*, i.e. together with oakwoods dominated by *Quercus trojana* and *Quercus frainetto*, which have the westernmost outposts of their distribution range in central and southern Italy (Biondi et al. 2001, 2004).

4.3 Regional Classification: South and Islands

To the south of Mt. Pollino and in Sicily, the phytosociological treatment of downy-oak woods becomes increasingly complicated: on the one hand it is possible to recognize some orophilous types occurring at 900–1,600 m, typically replacing the beechwoods on xeric edaphic sites; on the other hand, downy-oak woods are also found in the lowlands, under different climatic and edaphic conditions, ranging from thermo- to meso-mediterranean thermotypes, from subhumid to humid ombrotypes, and from alkaline to acidic soils. This justifies the arrangement of the southern downy-oak woods in two different phytosociological classes (*Querco-Fagetea* and *Quercetea Ilicis*), three alliances and several different associations.

The mountain types are ascribed to the *Pino-Quercion congestae*, characterized by a rich pool of southern species with relatively limited distributions, like *Paeonia mascula* ssp. *russii, Thalictrum calabricum, Clinopodium vulgare* ssp. *arundanum, Betula aetnensis, Epipactis meridionalis, Pinus nigra* ssp. *calabrica, Vicia cassubica, Agropyron panormitanum*, and *Symphytum gussonei*. This alliance is replaced on Sardinian mountains by the *Paeonio morisii-Quercion ichnusae*, differentiated by a pool of *Querco-Fagetea* species, like *Sanicula europaea, Taxus baccata, Ilex aquifolium, Viola riviniana*, and *Potentilla micrantha* (which in Sardinia are very localized in this context), plus some Sardinian endemics, such as *Paeonia morisii*, *Glechoma sardoa*, and *Digitalis purpurea* ssp. *gyspergerae* (Bacchetta et al. 2004; Maniscalco and Raimondo 2009; Brullo et al. 2012).

The lowland types are very rich in evergreen shrubs from the Mediterranean maquis, like *Rhamnus alaternus, Pistacia lentiscus, Euphorbia characias, Smilax aspera, Rubia peregrina*, and *Lonicera impexa*. These types are ascribed to the alliances *Quercion ilicis* (neutro-basiphilous) and *Erico-Quercion ilicis* (acidophilous), depending on the edaphic conditions (Brullo et al. 2009).

4.4 Controls on Species Composition

In our results, we have seen that the floristic diversity in downy-oak stands increases progressively toward the south. This fact justifies the wide array of phytosociological units along this gradient. The floristic diversity is explained only partially, however, by the wider ecological amplitude of downy oak in the southern stands. Environmental controls that function as drivers of species assemblages should work in a similar way in both the north and the south of the Italian Peninsula. If the environmental gradients were the only driver of floristic organization at landscape scale, then downy oak should show a similar ecological amplitude all along the Italian Peninsula, up to Sicily, as does the beech (with the exception of Sardinia, where beech forests are missing). So, in our case, the good correlation observed between environmental variables and floristic composition testifies that downy oak has clear patterns of spatial organization, but it does not provide any explanation for its wider ecological amplitude in the south.

The coenologic variability of downy-oak woods is generated by a combination of palaeoclimatic vicissitudes, dispersal limitation and random local processes, interacting across a complex physical landscape. These are, indeed, the same factors accounting for the increasing haplotype diversity and phenotypic polymorphism of downy-oak populations along north-south gradients across Europe (Brewer et al. 2002). Southern Italy was an important refuge area during the Quaternary glaciations, but we did not find proportionally higher species richness (as number of species per relevé) in southern stands. Nor is the observed pattern of species accumulation towards the south produced by proportionally higher percentages of stenochorous species. As we have noticed, the restricted distribution observed for many species in the relevés does not always indicate a restricted regional or global distribution range, although many of the species found in the Sardinian, Sicilian and Calabrian oakwoods are not found in the Apennine relevés. If we exclude Sardinia, where remarkable isolation fostered an abundance of endemic taxa in almost every vegetation type, then it appears that stenochorous species are concentrated in the mountain associations of *Pino-Quercion*

Fig. 5 Agricultural landscape near Muro Lucano (southern Italy) with patches, rows and isolated trees of downy oak (*Quercus virgiliana*)

congestae, and many of them are also found in the beechwoods of southern Italy, well known for having higher species richness and higher percentages of stenochorous species than in the north (Willner et al. 2008; Di Pietro 2009).

So, the Pleistocene glaciations affected downy oaks along the Italian Peninsula in two ways: (I) they enhanced the floristic differentiation in the mountain stands and (II) promoted the migration of Balkan species through the cyclic regressions of the Adriatic Sea. Even so, the greater ecologic amplitude and coenologic differentiation of downy oak in southern Italy can be explained fully only if we admit that what we have intentionally called "downy oak" up to now is in fact a blend of different species, partially blurred by systematic hybridization and introgression.

4.5 The Human Influence

According to the Map of the Vegetation Series of Italy (Blasi 2010), the areas esteemed to be potentially suitable for downy oak account for the 21.8% of the Italian territory. Instead, downy-oak woods are currently covering 0.8 of Italy. The rest has been turned into human settlements, rangelands, vineyards, olive-groves and cereal fields. In many agricultural landscapes of Italy, isolated large individuals of downy oak are the single most frequent landmark (Fig. 5). Many place names, including those of modern commercial infrastructures, recall the pristine vegetation: "Il querceto" (Ital. for "oakwood"). Actually, in Italy, no other autochthonous tree species is so frequently found in close proximity to permanent human settlements.

Centuries of forest management may have altered the structure and composition of the still existing downy-oak woods in many different ways (Chiarucci et al. 2010):

- Downy oaks were commonly used as wooded pastures, particularly for pigs, and are still used in this way in many places of central and southern Italy, including Sicily and Sardinia (Fig. 6). It could be that, in these contexts, oaks have been facilitated in some way, to the detriment of other tree species. Moreover, trampling and herbivory may have enhanced the establishment of non-forest species, which are relatively frequent in the open structure of downy-oak woods (Eriksson 1996);
- Dead wood and litter have been collected for centuries in the downy-oak woods (Fig. 7). This, together with the millennial history of clear-cutting, burning and grazing may have significantly altered the soil formation processes and carbon accumulation (Pignatti & Pignatti, 1968);
- Following the recent land abandonment, many of the current downy-oak woods are developed on soils that had been cultivated for centuries. A significant proportion of the most "untypical" floristic settlements observed in the downy-oak woods may be linked to the past agricultural practices.

The adaptive radiation of the genus *Quercus* in the Mediterranean region dates back to the Tertiary age, and it was influenced little by the glaciations. When human activity began to be significant, all the populations of downy oak

Fig. 6 Open downy-oak wood (*Quercus ichnusae*) in Mandrolisai (Sardinia), used traditionally as rangeland for pigs

Fig. 7 Coppice downy-oak wood (*Quercus congesta*) in the Madonie Mountains (Sicily), with a single, monumental tree left as a landmark. These landscapes were used for charcoal production until recently

along the Italian Peninsula had already been in place for millions of years and had had enough time to specialize, to differentiate, and to become single "species". The massive deforestation started already in pre-historic times, mixing up the genes of formerly distinctive oak populations and causing a chaotic hybridization that blurred the former biogeographic and ecological boundaries (Pignatti 1982; Brullo et al. 1998, 1999); this also influenced the post-glacial routes of recolonization (Dumolin-Lapègue 1997). Nevertheless, it does not seem correct scientifically to throw together, under the name *Quercus pubescens*, all the southern populations of downy oak, unless *Quercus pubescens* is regarded as a species complex whose typical form, described from Central Europe, does not occur in southern Italy and Sicily, where downy oak shows its greatest ecological amplitude.

Conclusions

Coupling climate models with indicator values and phytosociological data across a latitudinal gradient facilitates the exploration of a broad range of issues, including the potential role of downy oak as a major constituent of the Mediterranean and warm-temperate forests, and the impact of climatic and edaphic variations on species assemblages. We assessed that:

- The ecological amplitude of downy oak along the Italian peninsula increases southward;
- The maximum variance in the ecological conditions is found in Sicily, where the morphologic variability of downy oaks is also maximized and where potential competitors, like *Quercus frainetto, Quercus trojana, Carpinus orientalis*, and others, are missing;
- Morphometric analyses (Brullo et al. 1998, 1999) highlighted some discontinuities in the distribution/prevalence of morphologic traits of downy oak in the south; we demonstrated that these boundaries are not determined by any visible ecological or geographical gaps but instead reflect patterns of selection and phenotypic variability in key traits within the geographical range.
- The Ellenberg T and U indicator values for the flora of Italy (Pignatti et al. 2005) show good correlations with temperatures and precipitation.

Our latitudinal approach contributed to the validation of the Italian set of Ellenberg indicator values and provided new arguments for the "splitter's view", i.e. the occurrence of different downy-oak species along the Italian peninsula, blurred by systematic hybridization and introgression and enhanced by the recent deforestation.

Acknowledgments Financial aid from Forum Plinianum is gratefully acknowledged, and Dr. Stefano Perani is thanked for his helpful assistance with the statistical analyses.

Appendix: Syntaxonomical Scheme

QUERCO-FAGETEA Br.-Bl. & Vlieger in Vlieger 1937
QUERCETALIA PUBESCENTI-PETRAEAE Klika 1933
QUERCION PUBESCENTI-PETRAEAE Br.-Bl. 1932
Campanulo medii-Quercetum pubescentis Ubaldi 1995
Clematido flammulae-Quercetum pubescentis Ubaldi et Rondini in Ubaldi et al. 1993
Cytiso sessilifolii-Quercetum pubescentis Blasi 1982
Knautio purpureae-Quercetum pubescentis Ubaldi et al. 1993 ex Ubaldi 1995
Peucedano cervariae-Quercetum pubescentis Ubaldi 1988 ex Ubaldi 1995
LAURO-QUERCION PUBESCENTIS Ubaldi (1980) 1995
Cyclamino hederifolii-Quercetum virgilianae Biondi et al. 2004
Stipo bromoidis-Quercetum dalechampii Biondi et al. 2004
Irido collinae-Quercetum virgilianae Biondi et al. 2004
Roso sempervirentis-Quercetum pubescentis Biondi 1986
MELITTO ALBIDAE-QUERCION FRAINETTO Barbero, Bonin et Quézel in Barbero et Qéezel 1977
Centaureo centauroidis-Quercetum pubescentis Zanotti et al. 1995
PINO CALABRICAE-QUERCION CONGESTAE Brullo, Scelsi, Siracusa et Spampinato 1999
Agropyro panormitani-Quercetum congestae Brullo et al. 1999
Erico arboreae-Quercetum congestae Brullo, Scelsi et Spampinato 1998
Ilici aquifolii-Quercetum leptobalani Maniscalco & Raimondo 2009
Conopodio capillifolii-Quercetum congestae Maniscalco & Raimondo 2009
PAEONIO MORISII-QUERCION ICHNUSAE (Bacchetta et al. 2004) Brullo et al. 2012
Glechomo sardoae-Quercetum congestae Bacchetta et al. 2004
Ornithogalo pyrenaici-Quercetum ichnusae Bacchetta et al. 2004
QUERCETEA ILICIS Br.-Bl. *ex* A. & O. Bolòs 1947
QUERCETALIA ILICIS Br.-Bl. *ex* Molinier 1934 *em.* Rivas-Martínez 1975
QUERCION ILICIS Br.-Bl. *ex* Molinier 1934 *em.* Brullo, Di Martino & Marcenò 1977
Celtido aetnensis-Quercetum virgilianae Brullo & Marcenò 1985
Oleo sylvestris-Quercetum virgilianae Brullo & Marcenò 1985
Sorbo torminalis-Quercetum virgilianae Brullo, Minissale & Spampinato 1995
Lauro-Quercetum virgilianae Brullo, Costanzo e Tomaselli 2001
Lonicero implexae-Quercetum virgilianae Bacchetta et al. 2004
Prasio majoris-Quercetum ilicis quercetosum virgilianae Bacchetta et al. 2004
ERICO-QUERCION ILICIS Brullo, Di Martino & Marcenò 1977
Quercetum leptobalanae Brullo 1984
Mespilo-Quercetum virgilianae Brullo & Marcenò 1985
Erico arboreae-Quercetum virgilianae Brullo & Marcenò 1985

Arabido turritae-Quercetum congestae Brullo & Marcenò 1985

Festuco heterophyllae-Quercetum congestae Brullo & Marcenò 1985

Vicio elegantis-Quercetum congestae Brullo & Marcenò 1985

References

Allegrezza, M., M. Baldoni, E. Biondi, F. Taffetani. & V. Zuccarello 2002. Studio fitosociologico dei boschi a *Quercus pubescens s.l.* delle Marche e delle zone contigue dell'Appennino centro-settentrionale (Italia centrale). *Fitosociologia*, 31(1): 161-171.

Allegrezza, M., E. Biondi, & S. Felici 2006. A phytosociological analysis of the vegetation of the Central Adriatic Sector of the Italian Peninsula. *Achquetia*, 5(2):135-175.

Bacchetta, G., E. Biondi, E. Farris, R. Filigheddu & L. Mossa 2004. A phytosociological study of the deciduous oak woods of Sardinia (Italy). *Fitosociologia*, 41(1):53-65.

Biondi, E., S. Casavecchia, V. Guerra, P. Medagli, L. Beccarisi & V. Zuccarello 2004. A contribution towards the knowledge of semi-deciduous and evergreen woods of Apulia (southeastern Italy). *Fitosociologia*, 41(1):3-28.

Biondi, E., D. Gigante, S. Pignatelli & R. Venanzoni 2001. I boschi a *Quercus frainetto* Ten. presenti nei territori centro-meridionali della Penisola Italiana. *Fitosociologia*, 38(2):97-111.

Blasi, C. (ed.) 2010. La Vegetazione d'Italia con Carta delle Serie di Vegetazione in scala 1: 500000. Palombi Editore, Roma.

Blasi, C., R. Di Pietro & L. Filesi 2004. Syntaxonomical revision of *Quercetalia pubescenti-petraeae* in the Italian Peninsula. *Fitosociologia*, 41(1):87-164.

Blasi, C., & L. Michetti 2005. Biodiversity and climate. In: Biodiversity in Italy – contribution to the National Biodiversity Strategy (C. Blasi et al., eds.), pp 57-66. Palombi Editore, Roma.

Brewer, S., R. Cheddadi, J. L. de Beaulieu & M. Reille 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management*, 156(1-3):27-48.

Brullo S. & Marcenò C., 1985. Contributo alla conoscenza della classe Quercetea ilicis in Sicilia. *Not. Fitosoc*, 19(I):183-229.

Brullo, S., R. Guarino & G. Siracusa 1998. Considerazioni tassonomiche sulle querce caducifoglie della Sicilia. *Monti e Boschi*, 2:33-40.

Brullo, S., R. Guarino & G. Siracusa 1999. Revisione tassonomica delle querce caducifoglie della Sicilia. *Webbia*, 53(2):265-306.

Brullo S., L. Gianguzzi, A. La Mantia & G. Siracusa 2009. La classe *Quercetea ilicis* in Sicilia. *Boll. Acc. Gioenia Sci. Nat*., 41:1-124.

Brullo C., S. Brullo, G. Giusso del Galdo, R. Guarino, G. Siracusa, & S. Sciandrello 2012. The *Querco-Fagetea sylvaticae* class in Sicily: an example of boreal-temperate vegetation in the central Mediterranean Region. Annali di Botanica (IV Serie), in press.

Brunialti, G., L. Frati, M. Aleffi, M. Marignani, L. Rosati, S. Burrascano & S. Ravera 2010. Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. *Plant Biosystematics*, 144(1):221-233.

Bruschi. P., G. G. Vendramin, F. Bussotti, and P. Grossoni 2000. Morphological and molecular differentiation between *Quercus petraea* (Matt.) Liebl. and *Quercus pubescens* Willd. (Fagaceae) in northern and central Italy. *Annals of Botany*, 85:325-333

Casgrain, P., & P. Legendre 2000. The R package for multivariate and spatial analysis. Version 4.0 d3 Available at: http://www.fas.umontreal.ca/BIOL/legendre

Chiarucci, A., M. B. Araùjo, G. Decocq, C. Beierkuhnlein & J. M. Fernández-Palacios 2010. The concept of potential natural vegetation: an epitaph? *J. Veg. Sci*., 21:1172–1178.

Conti, F., G. Abbate, A. Alessandrini & C. Blasi 2005. An annotated checklist of the Italian vascular flora. Palombi Editori, Roma.

Di Pietro, R.. 2009. Observations on the beech woodlands of the Apennines (peninsular Italy): an intricate biogeographical and syntaxonomical issue. *Lazaroa*, 30:89-97.

Dumolin-Lapègue, S., B. Demesure, S. Fineschi, V. Le Corre & R. J. Petit 1997. Phylogeographic structure of white oaks throughout the European continent. *Genetics*, 146:1475-1487.

Ellenberg, H. 1974. Zeigerwerte der Gefässpflanzen Mitteleuropas. *Scripta Geobot*., 9:1-97.

Eriksson, O. 1996. Regional dynamics of plants: A review of evidence for remnant, source–sink and metapopulations. *Oikos*, 77:248–258.

Ferris, C., R. A. King, R. Väinölä & G. M. Hewitt 1998. Chloroplast DNA recognizes three refugial sources of European oaks and suggests independent eastern and western immigrations to Finland. *Heredity*, 80:584-593.

Fineschi, S., D. Taurchini, P. Grossoni, R. J. Petit & G. G. Vendramin 2002. Chloroplast DNA variation of white oaks in Italy. *Forest Ecology & Management*, 156(1-3):103-114.

Fortini, P., V. Viscosi, L. Maiuro, S. Fineschi & G. G. Vendramin 2009. Comparative leaf surface morphology and molecular data of five oaks of subgenus *Quercus* Oerst. (Fagaceae). *Plant Biosystematics*, 143(3):543-554.

Gristina, A. S., & C. Marcenò 2008. Gli indici di bioindicazione di Pignatti-Ellenberg nello studio floristico-vegetazionale del promontorio di Capo Zafferano (Sicilia nord-occidentale). *Naturalista Sicil*., s. 4, 32(1-2):61-96

Guarino, R., & A. Bernardini 2002. Indagine sulla diversità floro-vegetazionale del comprensorio del cuoio (Toscana centro-settentrionale). Tipografia Bongi, S. Miniato.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc*., 58:247-276.

Huntley, B. 1990. European vegetation history: palaeovegetation maps from pollen data - 13000 yr BP to present. *J. Quater. Sci*., 5:103-122.

Huntley, B., & H. J. B. Birks 1983. *An Atlas of Past and Present Pollen Maps for Europe, 0-13,000 Years Ago*. Cambridge University Press, Cambridge, U.K.

Maniscalco, M., and F. M. Raimondo 2009. Phytosociological study of the acidophilous decidous oak woods with *Ilex aquifolium* of Sicily. *Fitosociologia*, 46(2):67-80.

Mantel, N. A. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res*., 27:209–220.

Maricchiolo, C., V. Sambucini, A. Pugliese, M. Munafò, G. Cecchi, E. Rusco, C. Blasi, M. Marchetti, G. Chirici, & P. Corona 2005. La realizzazione in Italia del progetto europeo Corine Land Cover 2000. A.P.A.T. Report, 36:1-86

Mondino, G. P. 1992. La vegetazione forestale del Piemonte, materiali per una tipologia forestale regionale. *Ann. Accad. Ital. Sc. Forest*. 41:85-137.

Mossa, L., A. Aru, M. C. Fogu, R. Guarino & L. Zavattero 2008. Studio geobotanico del Parco Eolico di Ulassai. Edibo, Catania. 193pp.

Petit, R. J., and 28 co-authors 2002. Chloroplast DNA variation in European white oaks: phylogeography and patterns of diversity based on data from over 2600 populations. *Forest Ecology and Management*, 156(1-3):5-26

Pignatti, E., & S. Pignatti 1968. Die Auswirkungen von Kahlschlag und Brand auf das *Quercetum ilicis* von Süd-Toskana, Italien. *Folia Geobot. Phytotax*., 3:17-46.

Pignatti, S. 1982. *Flora d'Italia*, 1: 113-120. Edagricole, Bologna

Pignatti, S. 1998. *I Boschi d'Italia*. UTET, Torino.

Pignatti, S. 1999. La phytosociologie Braun-Blanquetiste et ses perspectives. *Coll. Phytosoc*., 27:1-15.

Pignatti, S., P. M. Bianco, G. Fanelli, R. Guarino, L. Petersen & P. Tescarollo 2001a. Reliability and effectiveness of Ellenberg's indices in checking flora and vegetation changes induced by climatic variations. In: *Fingerprints of Climate Changes: adapted behaviour and shifting species ranges* (J.-R. Walther J.R., et al., eds.), pp 281-304. Kluwer Academic/ Plenum Publishers, New York & London

Pignatti, S., P. M. Bianco, P. Tescarollo & G. T. Scarascia-Mugnozza 2001b. La vegetazione della Tenuta Presidenziale di Castelporziano. In: Il sistema ambientale della Tenuta Presidenziale di Castelporziano. Accademia delle Scienze, Scritti e Documenti, 26(2):441-770.

Pignatti, S., H. Ellenberg & S. Pietrosanti 1996. Ecograms for phytosociological tables based on Ellenberg's Zeigerwerte. *Annali di Botanica*, 54:5-14.

Pignatti, S., P. Menegoni & S. Pietrosanti 2005. Biondicazione attraverso le piante vascolari. Valori di indicazione secondo Ellenberg (Zeigerwerte) per le specie della Flora d'Italia. *Braun-Blanquetia*, 39:1-97

Podani, J. 2001. Syntax 2000 computer program for data analysis in ecology and systematics. Scientia Publishing, Budapest

Rivas-Martínez, S., & C. Saenz-Lain 1991. Enumeración de los *Quercus* de la Peninsula Ibérica. *Rivasgodaya*, 6:101-110.

Rivas-Martínez, S. 2007. Mapa de series, geoseries y geopermaseries de vegetación de España. *Itinera Geobot*., 17:5–436.

Schicchi, R., P. Mazzola & F. M. Raimondo 1998. Eco-morphologic and taxonomic studies on *Quercus* hybrids in Sicily. Proc. IX OPTIMA meeting, Paris, 11-17 May: 50

Ubaldi, D. 2003. La vegetazione boschiva d'Italia (manuale di fitosociologia forestale). Clueb, Bologna.

van der Maarel, E. 1993. Relations between sociological-ecological species groups and Ellenberg indicator values. *Phytocoenologia*, 23:343-362.

Viscosi, V., O. Lepais, S. Gerber & P. Fortini 2009. Leaf morphological analyses in four European oak species (*Quercus*) and their hybrids: a comparison of traditional and geometric morphometric methods. *Plant Biosystematics*, 143(3):564-574.

Willner, W., R. Di Pietro & E. Bergmeier 2008. Phytogeographical evidence for refuge areas and postglacial spread of European beech forests. In: *Frontiers of Vegetation Science — An Evolutionary Angle* (L. Mucina et al., eds), pp 204-205. Keith Phillips Images, Somerset West.

The Status of *Quercus pubescens* Willd. in Europe

Camilla Wellstein and Francesco Spada

A plant's name is the key to its literature – in other words, the key to what we know about it.
(van Steenis 1957)

Abstract

Taxonomic and nomenclatural disagreements are still encountered in the study of *Quercus pubescens* Willd. in Europe and are discussed here. This includes two current antithetical viewpoints on this taxon, i.e. the acceptance of the huge phenotypic variability among and within its populations within a single species vs. the ranking of these phenotypes as distinct species within the subgenus *Quercus* (the European white oaks *sensu* Schwarz).

Up to now many names have been attributed to the European white oaks, especially to the complex included into section Dascia Kotschy *sensu* Schwarz (the "downy oaks"), revealing contrasting opinions among taxonomists since the very first subdivision of the genus. While some schools in southern Europe still emphasize the distinctness and the species status of many taxa described during the earliest botanical surveys, the current trend is toward rejecting many names and considering them as synonyms.

Our review examines the extremely divergent opinions of specialists on these variations and supports the robustness of the current taxonomical status of *Quercus pubescens* Willd. as an inclusive taxon.

Keywords

Functional traits • Infraspecific taxa • Intraspecific variability • Morphology • Oak • Phenotypic plasticity • Phenotypic variability • Phylogeny • Phytogeography • Systematics • Taxonomy

1 Introduction

Quercus pubescens Willd. (see Tutin et al. 1993) is one of the most widespread tree species in Europe south of the Danube, occurring from the Atlantic coast of France to the Black Sea and Crimea, with disjunct outposts in the Caucasus. It is also the dominant tree species in thermophilous and submediterranean forests of southeastern Europe (Horvát et al. 1974). Nevertheless, due to the high degree of phenotypic variability, and possibly also genetic variation, its taxonomic status has been and apparently still is a question of debate, with hardly any analogues in the history of taxonomy and systematics. A veritable confrontation

C. Wellstein (✉)
Facoltà di Scienze e Tecnologie, Libera Università di Bolzano, Piazza Università 5, 39100 Bolzano, Italy

Biogeography, University of Bayreuth, Universitätsstrasse 30, 95447 Bayreuth, Germany
e-mail: camilla.wellstein@unibz.it

F. Spada (✉)
Dipartimento di Biologia Ambientale, Università degli Studi di Roma "La Sapienza", Largo Cristina di Svezia 24, 00165 Rome, Italy
e-mail: francesco.spada@uniroma1.it

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_8, © Springer International Publishing Switzerland 2015

between splitters and lumpers has produced, over the past 200 years, unimaginable consequences for the delimitation and nomenclature of *Q. pubescens* Willd. and its closest relatives among the European white oaks (*Quercus* L. subgenus *Quercus*, see Tutin et al. 1993). This is also having relevant consequences in the geobotanical interpretation of the vegetation patterns and zones in the Mediterranean peninsulas.

Some authors from southern Europe still claim a more restrictive delimitation of *Q. pubescens Willd.*, considering the swarm of closely related taxa (*Q. pubescens* aggregate sensu Ehrendorfer 1973) described by local taxonomists to be truly independent species. Others, though, based on an apparently larger, interdisciplinary consensus (Tutin et al. 1993) consider these names to be mere synonyms.

Here we discuss some aspects of this entangled history, which still divides botanists and has implications for the species concept itself. We evaluate nomenclature, morphology, distribution and hybridization of *Q. pubescens* Willd. in Europe, on the basis of a comprehensive literature review. Distribution data were extracted from Meusel et al. (1978), Tutin et al. (1964; 1968–1980; 1993), Jalas and Suominen (1976), Brullo et al. (1999) and AFE (2010). This treatment of taxonomy and systematics also considers the classic monographs on the genus *Quercus* in Europe by A. Camus (1936–54) and O. Schwarz (1937), as well as the most up-to-date international checklists, indices and concepts (IPNI 2004; Catalogue of Life 2011; Bisby et al. 2012).

The taxonomic background of *Q. pubescens* and phytogeographical consequences of its delimitation have provided intriguing challenges to researchers since the onset of Linnean systematics. We thus also consider some of the most prominent taxa of the *Q. pubescens* aggregate, which reappear in the literature from time to time, in order to provide more clarity for dealing with *Q. pubescens* Willd.

2 Distribution

Quercus pubescens Willd., sensu Tutin et al. (1993), is a medium-sized oak growing in southern Europe, at low and middle altitudes, under (sub-)Mediterranean and temperate climatic conditions (Walter and Straka 1970; Horvát et al. 1974; Meusel et al. 1978; Rivas-Martínez 1994). It ranges (Fig. 1) from the Atlantic coast of France (south of Bretagne and Normandie) to the shores of the Mediterranean Sea, and across peninsular Italy, the Balkan Peninsula and the Aegean regions, to the coasts of the Black Sea and most of Anatolia. Isolated outposts are scattered from the southern Crimea to the Caucasus, and down to the western coast of the Caspian Sea. In the east it reaches the transition between forest biomes and the Eurasian steppe in Dobruja (SE Romania – NE Bulgaria), Bessarabia (Moldova), Anatolia, the Crimea and around the Caucasus, where it often forms (semi-?) natural parklands or isolated groves in the grasslands (forest-steppe: Zohary 1973; Horvát et al. 1974; Walter 1974; Bohn et al. 2003).

The northern limit of *Quercus pubescens* Willd. lies at about 51° N latitude, with the northernmost stand located in Bellinchen (Poland), which Ellenberg (1996) thought might

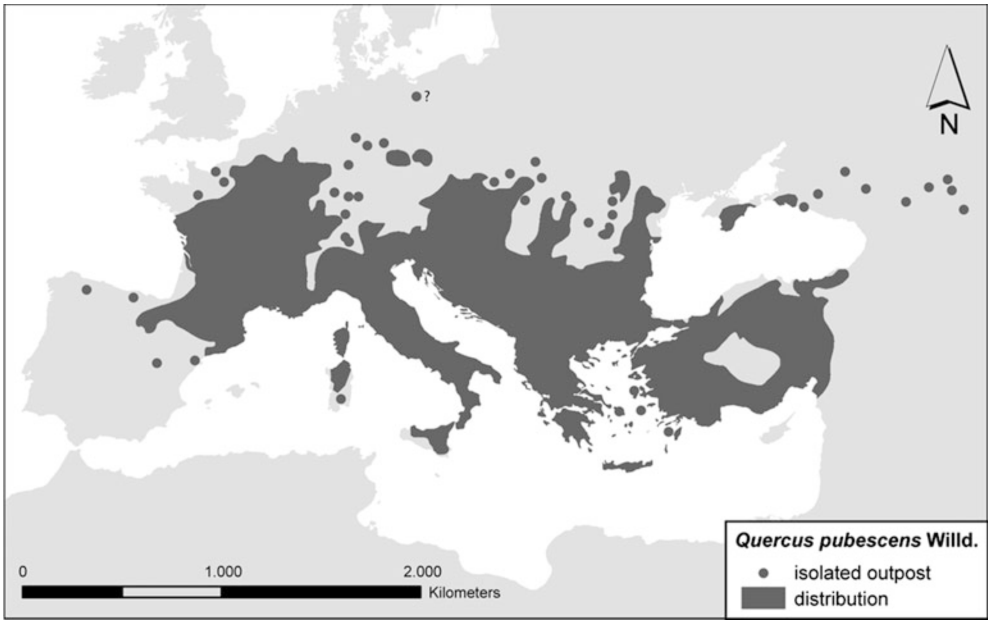


Fig. 1 Distribution of *Quercus pubescens* Willd. in Europe. This map was redrawn from Meusel et al. (1978), adding occurrences according to Tutin et al. (1964; 1968–1980; 1993), Jalas and Suominen (1976), Brullo et al. (1999), and AFE (2010). The northernmost outpost, in the Oder valley (indicated by "?"), might stem from plantation, according to Ellenberg (1996)

have originated from planting. In central Europe the species is widespread south of a line from northern France at the Belgian border, to Thüringen, Bohemia and the Vienna basin (Wagenitz 1981), and on to Odessa. Major gaps occur in the German plains and at the two southern branches of the Carpathian arch. In the Pre-Alps on both sides of the Alpine watershed, and throughout most of southern and central Germany, the species grows only on climatically favorable sites with shallow soils, on limestone, and on rocky outcrops, mainly on south-facing slopes (Sayer 2000). In Mediterranean Europe it is absent from most of the Iberian Peninsula and from the Po plain (northern Italy). Minor gaps are not shown in the distribution map (Fig. 1).

The distribution range is apparently surrounded, except in the south and south–east, where it reaches the Mediterranean shoreline, by a belt of disjunct outposts (Fig. 1), which suggests a widespread process of ongoing range shifts or pulsations. Since a general northward expansion of the white oaks from pleniglacial refugia is to be assumed from the onset of the Holocene, we can infer that the isolated outposts in central Germany, Poland and in the Carpathian regions might be responses to a more recent process of range retreat. However, it is not yet clear whether the species was able to persist during the last pleniglacial in small stands north of the Alps (see Bhagwat and Willis 2008). The possible pleniglacial persistence of white oaks (*Q. pubescens* included) north of the Alps (see Huntley and Birks 1983; Huntley and Webb 1988) and its analogies with the patterns of scattered outposts of *Staphylea pinnata* and *Taxus baccata* in central Europe today (Meusel et al. 1978) suggest that the isolated disjunct populations of *Q. pubescens* may be geographical indicators of former forest refugia rather than stepping-stones of an advancing wave supported by long-distance zoochory.

On the other hand, the complex patterns of introgression and hybridization reported in the Iberian peninsula, with *Q. faginea* (Sánchez de Dios et al. 2006), which is less closely related to the *Q. pubescens* aggregate, suggest that the isolated outposts in Cantabria and Catalonia may be a product of this genetic flow, more than of a late-Holocene or sub-recent range retreat.

This total range of *Quercus pubescens* Willd. involves great diversity in site conditions, encompassing some of the most topographically and climatically heterogeneous landscapes in Europe. The spread of its populations along altitudinal gradients is extremely large, in Italy (see Pignatti 1998) as well as in the Balkans (see Horvát et al. 1974). The coenological fidelity of this species is therefore low (see Zohary 1973; Horvát et al. 1974; Walter 1974; Pignatti 1998).

This eventually leads to the considerable attention always paid by local authors to anomalies, differentiations and changes in morphology exhibited by what we consider here to be a single species, *Q. pubescens* Willd.. This also provides some background for the reiterated splitting into different taxa over the last two centuries. A historical outline of the perception and taxonomy of the downy oak might be useful in order to understand why its controversial status still persists.

3 Taxonomy

3.1 Overview of Historical and Recent Issues

The binomial *Q. pubescens* was first established by Willdenow in 1796 (see Schwarz 1937) to describe a downy white oak growing in southern France. An error in transcription settles the official date later in 1805 (Govaerts 1995, against the opinion of Schwarz), an early harbinger of future nomenclatural misunderstandings. Quotations of apparently similar taxa date back a few decades earlier than 1796, by Miller (1768, see Schwarz 1937) and are mentioned for Spain (*Q. humilis*: see Schwarz 1937). The epithet *lanuginosa*, depicting well the most striking feature of the species, was introduced first by Lamarck in 1783 (*Q robur* δ *lanuginosa* Lam.). This was reinforced soon after (1799) by Thuillier for France (*Q. lanuginosa* Thuill.) but shows up in the nineteenth century only at the level of subspecies or variety (*Q. sessiliflora* ε lanuginosa Lam. et DC. 1806; *Q. robur* ssp. *sessiliflora* ρ *lanuginosa* p.pte DC.1864). It eventually imposes itself over about 50 other, more current binomials of the eighteenth to twentieth centuries, in the interpretation of Gavioli (1935) as variety *lanuginosa* of Q. *robur* ssp. *sessiliflora*.

The other, equally graphic epithet *pubescens*, which appeared first in Willdenow (1796, see Schwarz 1937), was apparently no more successful in attracting taxonomists to the acceptance of downy oak as an independent species or taxon of higher rank, since it is repeatedly downgraded later to an unspecified subtaxon (= variety p.pte) (*Q sessiliflora ε pubescens* Lam. et DC 1806; *Q sessiliflora ζ pubescens* Boiss. 1879; *Q sessiliflora ρ pubescens* DC 1864), or it is doomed to assimilation into taxa considered today (see Schwarz 1937) to be synonyms of *Q. petraea* (Mattuschka) Liebl (*Q. robur* Lam. 1768 p.pte; *Q. sessiliflora* Bert 1854), during the whole nineteenth century.

From the beginning of the nineteenth century (see Schwarz 1937 for a list of synonyms of *Q. pubescens* Willd.), numerous binomials begin to appear, apparently triggered by scanty, unclear diagnoses of downy white oaks. These focused on leaf morphology, acorns or habit and claimed endemic status for each taxon named. Errors in comparing herbarium material or in field surveys, due to obvious communication difficulties between researchers, exacerbated by the use of clearly contrasting traits in different areas (see e.g. the graphically contrasting names *Q. leptobalana* Guss. 1844 in Sicily and *Q. microbalanus* Bor. 1849 in France), reveal overall generally confused perception of downy oaks but also their indubitable polymorphism.

Evident misinterpretations and erroneous reuses of already existing binomials also appear among the names (e.g. *Q. aegylops* Mill. 1768; *Q. cerris* Pall. 1768; *Q. faginea* Rohr et May 1835), in the plausible attempt to stress the existence among white oaks of a third, downy stock, not listed by Linnaeus in 1753, who assigns the trait "foliis [. . .] subtus subtomentosis" only to *Q. cerri*s among all his European species.

This frenetic nomenclatural radiation (or rather, splitting) was mostly based on the degree of pubescence, its persistence on twigs and leaves, and on the form and depth of the leaf lobes. The core area of this excessive pointillism was in the Balkan Peninsula (Vukotinovič: see Schwarz 1937; Pignatti 1982), with the ideological support relying on the work of Ascherson and Graebner (1896–1938).

On the other hand, without reporting his own criteria of choice, Schwarz (1937) lists also the following binomials among the myriad of synonyms of *Q. pubescens* Willd.: *Q. esculus* All. 1785 and *Q. Esculus* Bert. 1854, whose species epithet was used by Linnaeus (1753) as the only clear precursor to the modern *Q. petraea* (Mattuschka) Liebl. This alternative trend of considering downy oak as a mere subtaxon of the modern *Q. petraea* is emphasized, at least in the Italian literature of the nineteenth century, by Cesati et al. (1867), who ranked *Q. pubescens* Willd. as one of the synonyms of a subtaxon called *Q. robur* L. β *sessiliflora* Sm. This status is confirmed as late as the first half of the twentieth century in the interpretation of Gavioli (1935), who ranks the downy oak of Thuillier as variety *lanuginosa* of Q. *robur* ssp. *sessiliflora*, basically following De Candolle's assessment from 1864. The length of the peduncule of the acorn was interpreted consensually as a strong character for the assignment of the subtaxa listed above to the sessile group of the white oaks (*Q. petraea* sensu *latissimo*). This apparently was a reliable attribution in the judgment of most taxonomists of the time, and this view persisted solidly through the nineteenth and the first half of the twentieth century.

The perception of downy oak as independent species, however, rearises with new vigour in southern and southeastern Europe in the early nineteenth century, through the establishment of some new binomials parallel to the taxon of Willdenow. In the judgement of Schwarz, who somewhat daringly treats tens and tens of bi- and trinomials as synonyms of *Q. pubescens* Willd., the most prominent of these are *Q. virgiliana* Ten. (1836), *Q. congesta* Presl. (1822), *and Q. brachyphylla* Ky. (1862). In his monograph, Schwarz (1937) identifies these taxa, along with *Q. pubescens* Willd., as representatives of the series *Lanuginosae* in the section Dascia. He reports them once again in 1964 in the *Flora Europaea* but downgrades them later to synonyms in the 1993 edition. This view is endorsed by Govaerts (1995) and Govaerts and Avishai (2000), confirming them as mere synonyms of *Q. pubescens* Willd. and therefore stating for the first time the 'inclusive' character of this taxon.

Nevertheless, despite this modern consensus shared by Govaerts and Frodin (1998), the IPNI (2004) and the Catalogue of Life (2011), these other taxa are still mentioned persistently in the southern European literature. They appear in surveys (e.g. Trinajstič 1974 for former Yugoslavia: *Q virgiliana*); in keys (Brullo et al. 1999: *Q. virgiliana* and *Q. congesta*; Jahn and Schönfelder 1995: *Q. brachyphylla* Ky); and enter more and more into geobotanical treatises as indicators of distinct vegetation types (e.g. Borhidi 2003; Trinajstič 2007; Rosati et al. 2010: *Q. virgiliana*), of vegetation belts and series (e.g. Blasi 2010: *Q. virgiliana*), vegetation dynamics (e.g. Blasi et al. 2012: *Q. virgiliana*), Natura 2000 Habitats (Biondi et al. 2009: *Q. virgiliana*) and CORINE biotopes (Devillers et al. 1991: *Q. virgiliana*). In this context, the case of *Q. virgiliana* Ten. is really paradigmatic and needs special attention.

3.2 The Case of *Q. virgiliana* Ten.

Throughout the southern and southeastern part of the range of *Q. pubescens* Willd. (see Fig. 1: Corsica-Sardinia, Sicily, peninsular Italy, the Balkan peninsula and the Aegean regions), most local experts claim the occurrence of another taxon, *Q. virgiliana* Ten., suggesting it to be very close phenotypically to, and totally sympatric with, *Q. pubescens* Willd.. *Q. virgiliana* has been described remarkably poorly, by ambiguous, non-discriminatory characteristics, throughout its history. More recent taxonomical revisions consider it to be a synonym of *Q. pubescens* subsp. *pubescens* (Govaerts and Frodin 1998; Conti et al. 2005; Bisby et al. 2012), and include *Q. virgiliana* Ten. within the range of the phenotypic variability of *Q. pubescens* Willd.

Nevertheless, *Q. virgiliana* finds tenacious and persistent support among local researchers and scholars. A recent analytical key to the oak flora of Sicily (Brullo et al. 1999), produces a very detailed description and iconography that apparently states the ultimate, distinct character of *Q. virgiliana* among the Italian oaks. This represented, for Italy, a veritable resurrection of this confused taxon. The same thing happened in recent times in the flora of former Yugoslavia (Trinajstič 1974, 2007). What is so attractive in this controversial oak, so as to split the identity of downy oak and contradict other authoritative sources so openly?

The Work of Tenore

Tenore first establishes *Q. virgiliana* in 1831 as variety B of *Q. robur* Willd., reporting no precise details other than leaf characteristics that have no clear discriminant value in relation to the other poorly described varieties of *Q. robur* Willd. He stresses the semi-deciduousness of *Q. virgiliana* and the edible quality of its acorns, quoting a vernacular name still in use today in C and S Italy ("quercia castagnara").[1] His description refers to anecdotes from classical antiquity and to a *Quercus Aesculus* (the edible oak) named by Pliny and celebrated by Virgil, leaving all possible doubts about its botanical identity, but giving a fascinating patina of a glorious and eminent past for his taxon. Later, (Tenore 1835–1836) Tenore eventually states the distinctness of the taxon, separating his own *Q. virgiliana* from a *Q. robur* Will. (considered by himself a synonym of *Q. sessiliflora* Smith and therefore belonging to the line of the modern binomial *Q. petraea*). The newer description is more comparative and suggests an oak with large, somewhat leathery leaves ("*subsempervirens* [. . .] *laete virens*") and with subpedunculate fruits. No reference to hairiness is reported. In fact, the nature of downy oak is not emerging at all from the description by Tenore, since he explicitly quotes *Q. pubescens* Willd. in 1835–1836 as such. Tenore profusely emphasizes however the dimensions of the tree, the quality of its timber, and once again the edible character of its acorns. It has to be pointed out that populations with edible acorns are to be found in any of the white oaks (B. Schirone, personal communication), which means that this trait is hardly discriminant.

How this vague, scanty information eventually led to later, very detailed descriptions of seemingly distinctive morphological characters versus other white oaks (Schwarz 1937; Brullo et al. 1999), and how it could be sufficient to characterize a taxon still threatening the status of *Q. pubescens* Willd. in most of southern Europe, is a real mystery.

Monographs by A. Camus and O. Schwarz

A. Camus, in her monumental monograph (1936–1954), classifies *Q. virgiliana* Ten. as a variety of *Q. lanuginosa* Lam. (not recognizing *Q. pubescens* Willd.) with larger, edible acorns, relying on no other really distinct characters compared to the other varieties.

The first comprehensive scientific diagnosis therefore was by Schwarz,[2] who first describes the taxon in detail (1937). Apparently, he based his diagnosis on a now vanished (La Valva 1994, pers. comm.) Tenorean *exsiccatum*, formerly preserved in the Herbarium in Naples, and quoted by him as the *holotypus*. Tenore's lectotypes, with original protologues of the author, are preserved today in the Herbarium in Firenze. Each subsequent determination of this species in keys, surveys and recent herbaria should therefore refer to the text of Schwarz. The most important systematic novelty introduced by him is the anchorage of *Q. virgiliana* in Sectio *Dascia* Kotschy (the downy oaks s.l.), Series *Lanuginosae* (the downy oaks s.s.), along with *Q. congesta* C. Presl., *Q. brachyphylla* Ky., and *Q. pubescens* Willd.

Schwarz assigns to *Q. virgiliana* a set of distinctive mesophytic morphological traits within the section *Lanuginosae*. Due to the endless numbers of known synonyms and transitional forms (hybrids) with other closely related species, he highlights the intrinsic difficulty in delimitation of *Q. virgiliana* and recognizes its largely unstable identity. Nevertheless, he stresses explicitly the necessity of keeping *Q. virgiliana* separate from *Q. pubescens* (according to him the most xeromorphic and stunted type within the series *Lanuginosae*), in favor of a geographically and morphologically more consistent interpretation of the variation within the series.

Apparently, though, the clinal and somewhat vague structure of this approach, focused on the dimensions of the trees and on the morphology of their leaves and acorns, did not fully convince him.[3] This can explain his increasing

---

[1] According to our interviews from Umbria to Calabria, peasants in C and S Italy apply the term "quercia castagnara"or "cerqua castagnola" not to a particular sort of downy oak but rather to individuals bearing sweet (and often very small) acorns. These individuals used to be and still are preserved as isolated trees in the rural landscape because of their "once tested" valuable acorns. Due to this, they usually attain old age and large dimensions, and give origin to unlikely legends about intentional plantation, cultivation and even deliberate "selection" by local settlers.

[2] The German of Schwarz (1937) is extremely intricate, wriggling through long, complicated sentences as easy to follow as a Sumerian epigraph. Few people in the new generations of European scientists outside the German-speaking area can read or simply decipher it. His Latin is also a difficult task for all Europeans today. This means that most modern researchers and scholars rely on the quite poor iconography, which on the other hand is extremely useful for understanding the extraordinary message of Schwarz, i.e. the plesiomorphism across lineages. Even so, it is hardly a reliable reference for clear subdivisions based on leaf form. The text has therefore been and still is ignored, except perhaps for the locations mentioned.

[3] The impressive list of synonyms, if critically examined, should also point clearly towards the fuzzy morphological –geographical value of the Schwarz (1937) system. Indeed, a conceptually robust property of his monograph is the natural typological ordination of forms (inherited from Örsted 1866, see Schwarz 1937, p. 10) according to a progression of characters from ancestral to derivative. He considers the "series" as a cline of morphological traits arising from degrees of xeromorphism (leaf outlines, incisions, lobes, hairiness). His classification is functional and considers derivative characters within the series as much as convergence among different series due to environmental constraints. This means that he reviews at the rank of series, all taxa quoted in previous literature in order to emphasize the clinal variation of forms, without any explicit evaluation of "good"or at least not distinct species.

simplification of the systematics and taxonomy of the downy oaks that appeared in *Flora Europaea* (Schwarz 1964, 1993) and the eventual deletion among others, of *Q. virgiliana* Ten. in the last edition, where he considers *Q. pubescens* Willd. the taxon representative of the whole series *Lanuginosae*. His message, so well suited to fruitful revisiting by modern molecular phylogeny, has been completely neglected for decades, in favour of the obstinate persistence of taxa like *Q. virgiliana*, *Q. congesta*, *Q. brachyphylla* in the S European literature up to now.

Examples from the Italian Literature (Floras and Keys, 1923–1999)

In the Italian literature, *Q. virgiliana* is presented by Flora d' Italia (Fiori 1923–1929) as one (κ) out of 18 varieties of *Q. robur*. Eventually it achieves the status of subspecies in Gavioli (1935). In 1976 it is quoted by Zangheri for the first time in modern Italian keys as a distinct species and is eventually upheld in this status by Pignatti (1982) in his *Flora d' Italia*, who points out explicitly its close relation to *Q. pubescens* Willd. After publication of this Flora, *Q. virgiliana* became established as a distinct species, and Italian researchers and scholars began to report it from an increasing number of districts.

The most detailed existing description of *Q.virgiliana* can be found today in the key to the Sicilian oaks by Brullo et al. (1999). These authors present an impressive amount of iconographic and descriptive material about several species, namely *Q. virgiliana*, *Q. congesta*, *Q. leptobalanos*, *Q. amplifolia*, and *Q. humilis* (according to Brullo et al. 1999, = *Q. pubescens* Willd.), reviving older names assigned by earlier scientists to local forms of downy oaks. Their entangled pattern of cross-similarity, which emerges solely from scrutiny of the list of synonyms, mirrors the ambiguous, blurred structure of the alleged distinctive morphological traits (leafe shape, bark morphology and the cupolas scales). It emphasizes the unclear perception of these "species" by those who originally established the binomials.

At best, the scientific community should rather rank these binomials as local "Jordanons" (sensu Davis and Heywood 1963). There is no doubt about the degree of accuracy in the work of Brullo et al. (1999). Their strictly morphological method puts forward undoubtedly existing sets of characters. Less plausible is that these characters might represent geographically distinct phenotypes. The reported populations of these presumptive species are largely coincident in space, suggesting coexistence in the same stands. The clinal character of the traits is evident. The endless number of combinations in nature makes potential recognition, using the keys, anything but easy, at least when outside Sicily. The question is not whether these characters exist but rather where and when they coexist sufficiently often as a set of constant traits in individuals and populations in nature exhibiting a geographical or ecological structure. This is still very far from clear. This work (Brullo et al. 1999) relegitimizes obsolete binomials in an attempt to order into a discrete system what undoubtedly is huge morphological variation among individuals in populations of downy oaks at southern latitudes.

Some characters quoted as discriminates, though used interchangeably in the sources, are illustrated in the following paragraphs.

3.3 Habitus

Tenore (according to the appearance of the *exsiccata* in Florence) probably referred to long-standing, aged, large individuals of downy oak, since his own delimitation of *Q. pubescens* Willd. (1835–1836) is restricted apparently to shrubby individuals. We should remind readers that many oaks in the days of traditional management were seen over large areas as shrubby xeromorphic components of *macchia* (*Q. ilex*, *Q. coccifera*/*calliprinos*) or *šibljak* (downy oaks) and therefore considered as distinc taxa. During the last decades, after this type of disturbance disappeared, many populations turned into different morphological syndromes. Their former shrubby phenotype was revealed to be a growth form due to fire and browsing, a very common pattern in the "disrupted" (sensu Grove and Rackham 2001) Mediterranean and South European landscapes of the nineteenth century. The fact that it has been called *Q. humilis* speaks in favour of this view. This is also the case with *Olea sylvestris* versus *O. europaea*, the persistently juvenile form of the browsed, stunted olive trees outside the cultivated orchards.

Schwarz (1937) speaks about *Q. virgiliana* as a mesic form in the series Lanuginosae of the Section Dascia, and this is what might have attracted Horvát (see references in Horvát et al. 1974) in treating it as a species different from the widespread shrubby form of downy oak (*Q. pubescens*) in the Balkan *šibljak* of his own days. This apparently followed the same logic process which led to the largely ambiguous taxon of Tenore.

It is therefore remarkable that Brullo et al. (1999) consider *Q. virgiliana* the most xero-tolerant and thermophilous among the quoted downy oaks, apparently contradicting the statement of Schwarz. No less confusing is the situation of other morphological characters.

3.4 Cupules

Schwarz (1937) reported humped scales in the cupolas of *Q. virgiliana*, presumably after inspection of herbarium material from Tenore, as opposed to the more flattened scales in *Q. pubescens* Willd. Pignatti (1982) reports flattened scales in the cupolas of both *Q. virgiliana* and *Q. pubescens*, which is in contradiction to Schwarz (1937). Humped scales, first given as characteristic for *Q. dalechampi* Ten. (see Pignatti 1982, among others; Schwarz 1937), were later surprisingly assumed (Brullo et al. 1999) to be a main diagnostic trait for the cupolas of *Q. virgiliana*. This added confusion to the already unclear status of *Q. dalechampi* Ten., itself considered another cryptic downy oak among earlier Italian botanists (see Schwarz 1937), but considered a southern variant of *Q. petraea* by Transalpine taxonomists such as Schwarz (1937, 1964, 1993), and Jalas and Suominen (1976).

These humped scales were clustered more often only at the proximal part of the cupules (Brullo et al. 1999), and were apparently the only ultimately assumed distinctive trait of *Q. virgiliana*. According to our observations, humped scales are found along with flattened scales in individuals in the same stands throughout C. Italy.

3.5 Bark

The same pattern of coexistence of different traits characterizes the bark morphology. Individuals with massively ridged bark, bark fissured into broad ridges, or furrowed and scaly bark are to be seen along topographical discontinuities all together in the same stands, especially in disturbed marginal areas in the rural landscape or in old coppice.

3.6 Leaf Longevity

The (partial) persistence of leaves, as a postulated distinctive character for *Q. virgiliana*, is a universal phenomenon in all submediterranean deciduous oaks (subgenus *Robur*, subgenus *Cerris* sensu Schwarz 1937) in S Europe, where they grow on warmer sites, especially as late-successional species within the broad-leaved evergreen Mediterranean forest belt. In these cases, most tree crowns maintain some green apical leaves during winter, in forest saplings or in young, low, especially shrubby individuals at the forest edge. Also, adults and old trees of all taxa of Sect. Dascia sensu Schwarz (1937) may preserve green or partially green apical leaves during winter on particularly warm sites (e.g. the Colli Albani near Roma: see Montelucci 1978). Leaves may remain green over all their surface or part of it or persist dry on the branches until the new ones sprout, in individuals of the same population on the same site. Kozlowski (1971) reports it as a consequence of individual patterns of different nutrient allocation in lower twigs in comparison to the rest of the crown, due to site, age and health. Most individuals of *Q. robur* as far north as Scandinavia display this ability as well. It can therefore be no specific character for *Q. virgiliana* and especially no morphological discriminant in comparison to *Q. pubescens* Willd.

New Developments

New attempts to delimit *Q. virgiliana* using leaf surface morphology and molecular data are not convincing either. Fortini et al. (2009) are basically tautological, since they use a priori distinct populations in this taxon, which is therefore taken for granted in their study, despite the more cautious position expressed in other recent works, such as Bruschi et al. (2000). When searching for morphological and molecular differentiations across populations, the prerequisite is to take a random sample. Otherwise statistical results are not valid for the treated entities. Non-random sampling does not take into account the natural variation of morphological and molecular characteristics and will therefore lead to artificial separations without meaning.

No convincing comparative or differential trait is reported in the diagnoses of the monographers (Camus 1936–1954; Schwarz 1937), in the later floras (Fiori 1923–1929; Zangheri 1976; Pignatti 1982), or in the modern literature (e.g. Fortini et al. 2009). None of the morphological characters quoted is of any value in discriminating closely related taxa. The vagueness of the descriptions is sometimes buffered by quoting possible hybridisation patterns relying solely on morphology, in order to explain the wide variability of characters. Iconographies portray, for each species, only one of the countless existing leaf shapes as if they were specific, diagnostic elements. The extremely accurate, long list of the Italian *exsiccata* in the national *Herbaria* assigned to this taxon and reported by Brullo et al. (1999) shows that most references appeared soon after the publication of *Flora Italiana* (Zangheri 1976) and *Flora d'Italia* (Pignatti 1982), while older citations of *Q. virgiliana* undoubtedly rely upon the *specimina* and descriptions of Tenore, with all their ambiguities.

Since we are evaluating the internal consistency of a taxonomic identification system, what is relevant is that the morphologically based contraposition between *Q. virgiliana* and *Q. pubescens* seems particularly weak, with apparently no unequivocal set of characters distinguishing these taxa.

It is impressive how much has been erected on this "charismatic" binomial *Q. virgiliana*. We conclude that it attracts at least Italian researchers and scholars emotionally, simply because of its species epithet. Virgil and the appealing references to Pliny, emphasized so brilliantly but somewhat hazardously by Tenore (1831), address educated reminiscences about the Classical world. It seems that authors in S and SE Europe work tirelessly to maintain a taxon at all costs, adding *a posteriori* morphological traits that are not implicit at all in Tenore's description. In this sense, the claimed association between ecology and "the most valid morphological traits assumed distinctive for *Q. virgiliana*" (Frattegiani et al. 2010) and other statements of a unique ecological niche based on syntaxonomy (Rosati et al. 2010) are more the affirmation of a desired outcome of a hazardous taxonomy than the verification of a causal link.

On this basis, the genesis and development of the taxon *Q. virgiliana* Ten. cannot be considered as relying on firm ground at all. We simply see here, in the contraposition between, *Q. pubescens* Willd. and *Q. virgiliana*, the expression of a wide phenotypic variation due first to phenotypic plasticity being visible as intra-individual variability as well as high intra-population variability. The results of Bruschi et al. (2003), for example, on variation in *Q. petraea* suggest the need for biosystematic studies to consider variation also as a quantitative attribute of individual trees. Second, the high genetic variability of *Q. pubescens* Willd. due to a long evolutionary history, as well as gene introgression of the closely related *Q. petraea* and *Q. robur*, contributes to its phenotypic variation (e.g. Petit et al. 2003; Lepais et al. 2009; Lepais and Gerber 2011).

The lack of a convincing geographical or ecological sorting between *Q. pubescens* and *Q. virgiliana* speaks also against ecotypic differentiation. This could be a topic for future investigation. The evidence assumed by the authors supporting distinct morphological species of downy oaks at the local level appears to be, on a broader geographical scale, the manifestation of only a few in a series of morphologically intergrading populations.

To treat the two taxa as separate species does not seem more than the legacy of a prestigious tradition, of the historical accumulation of names and the appealing rehabilitation of older binomials within a general trend of taxonomic splitting.

3.7 The Present Status of *Q. pubescens* Willd.

A general conclusion is that *Q. pubescens* Willd, the first downy oak in the history of oak nomenclature, is an inclusive taxon, characterized by high morphological diversity. So, the many accumulated names is proportional to what seems to be a global misunderstanding, not regardless of patriotic ambitions (see Vuković in Schwarz 1937), of how to interpret classification.

This issue might still re-appear in synonyms and subdivision of *Q. pubescens* in the most updated international sources such as *Flora Europaea* (Tutin et al. 1993) and the annually updated *Catalogue of Life* (2011, now integrated in Bisby et al. 2012). According to *Flora Europaea* there are five synonyms: *Q. infectoria* Olivier, *Q. apennina* auct., *Q. lanuginosa* Thuill., *Q. virgiliana* (Ten.) Ten. and *Q. brachyphylla* Kotschy. There are also three subspecies (*pubescens*, *anatolica* O. Schwarz, *palensis* (Palassou) O. Schwarz) that are included in *Q. pubescens* Willd.

1. *Q. pubescens* Willd. subsp. *pubescens* occurs throughout the range of the species, except Spain and the Pyrenees. There have been listed 273 synonyms for this subspecies in the World Checklist of Selected Plant Families (Catalogue of Life 2011). The new edition of the *Catalogue of Life* (Bisby et al. 2012) confirms *Q. pubescens* subsp. *pubescens* as the accepted name of this infraspecific taxon.
2. *Q. pubescens* Willd. subsp. *anatolica* O. Schwarz ranges between the eastern Balkan peninsula and Crimea (Krym). There have been listed five additional synonyms in the *Catalogue of Life*, edition 2011, namely *Q. anatolica*, *Q. crispata*, *Q. cerris crispata*, *Q. lanuginosa crispata*, *Q. pubescens crispata*. According to the new edition (Bisby et al. 2012) *Q. pubescens* subsp. *crispata* is the accepted name of this infraspecific taxon.
3. *Q. pubescens* Willd. subsp. *palensis* (Palassou) O. Schwarz is restricted to the Pyrenees and northeastern Spain. This taxon is not quoted by the *Catalogue of Life*, edition 2011, and by the new edition (Bisby et al. 2012) as a subspecies of *Q. pubescens* Willd.. These sources report instead *Q. pubescens* subsp. *subpyrenaica* (without reference to an author) as the third subspecies of *Q. pubescens* Willd.. This taxon is erroneously not listed in *Flora Europaea* (neither as subspecies nor as synonym) since the author didn't consider the *Flora Iberica* in which this infraspecific taxon was included (Castroviejo et al. 1990). Eventually, only Govaerts (1995) and *Flora Iberica* (Castroviejo et al. 1990, pp. 27–29) link *Q. subpyrenaica* to *Q. pubescens* subsp. palensis sensu O. Schwarz in Tutin et al. (1993). *Flora Iberica* (Castroviejo et al. 1990) really emphasizes the extraordinary polymorphism of the taxon.

The three subspecies (1–3) of *Q. pubescens* Willd. accepted today (i.e. *pubescens*, *crispata*, and *subpyrenaica*) differ basically in their distribution. Apparently, the westernmost and southeasternmost populations are responsible for this differentiation. Less clear are for taxon (1) and (2) the differences in their morphological characteristics and ecology. The traits quoted in *Flora Europea* (Tutin et al. 1993) are hardly discriminating. They have rather been extracted by the description of some individual herbarium specimens with their own individual manifestations and not by a validation by field surveys. It seems that the need to superimpose an *a posteriori* justification for a broad range with very large phenotypic variation has given rise to this purely self-explaining subdivision according to longitude re-reviving older geographic taxa. In contrast to subspecies (1) and (2), taxon (3) according to Loidi and Herrera (1990), Castroviejo et al. (1990 Fl. Iberica), Govaerts (1995), and Sanchez de Dios (2006) is based on hybridization between *Q. pubescens* Willd. and the Iberian endemic *Q. faginea* Lam.

Hybridization

Interspecific hybridization is common among oaks but usually between species within the same section only and most common in the white oak group (subgenus *Quercus*, section *Quercus*) in Europe. These species are wind pollinated, do not have complete internal barriers against hybridization, and produce fertile hybrid offspring (Arnold 1997). By means of back-crossing, hybrid offspring can subsequently be re-included into the gene pool of one of the parent species, enhancing the level of gene introgression (e.g. Anderson 1949; Petit et al. 2003; Lepais and Gerber 2011). This is an important mechanism that leads to increasing genetic and thus morphologic variation in natural populations. As a consequence, hybridization in *Q. robur*, *Q. petraea* and *Q. pubescens* contributes to increase their adaptation potential without causing a loss of separation among them (Rieseberg 1995; Aas 1998). According to Lepais and Gerber (2011), despite extensive interspecific gene flow, partial species integrity is maintained by genetically controlled pollen discrimination, ensuring preferential matings within purebreds and high parental species fidelity in hybrid reproduction, which impedes complete collapse into a continuous hybrid swarm. From these dynamics it also becomes evident that diverse degrees of introgression have a transitional dynamic character that makes it impossible to give any sound name to the hybrid swarm. It is not yet clear whether the hybrid between *Q. pubescens* and *Q. faginea* in northeastern Spain is stable. However (see Sánchez de Dios et al. 2006), the extent of their hybrid zone and the local environmental gradient suggest possible stabilizing conditions in favour of hybrids.

4 Epilogue

All evidence here points towards the necessity of restarting the analysis of the inclusive taxon *Quercus pubescens* Willd. completely, since there is no ground for accepting any of the phenotypical characteristics named by taxonomists outside the definition of *Q. pubescens* Willd. which could be considered other than parts of the phenome, i.e. the set of phenotypes of an organism, at all organizational levels and at all times through its development (Deans et al. 2012; Parr et al. 2012).

Taxa (ordered entities, from Greek τάξις = arrangement/order) can be characterized as hypotheses about the distribution of variation in nature (see Knapp 2008). In view of the many such hypotheses, recent overviews state that a commitment by scientists is needed to change how we describe biodiversity and to consider critically the relevance of its products (Deans et al. 2012; Parr et al. 2012).

A prerequisite for postulating differentiating, diagnostic morphological species characteristics is knowledge about their variation. The variation has to be taken into account in order to detect discontinuity, which reflects morphological differentiation. Such morphological differences are relatively stable in their differentiation because their characteristic is genetically determined and the environmental impact on it is low. In contrast, unstable or highly variable characteristics are not useful for differentiation.

We recognize the existence of infra-specific variability within *Q. pubescens*. We do not believe, however, that taxa quoted in the historical and recent literature as reviewed describe this variability. This is because their characters are non-discriminate or even contradictory. Since up-to-date methods for morphological, physiological and molecular research are available, sampling that does not consider the intra-individual (i.e. plasticity) and intra-population variation leads to misleading conclusions. Sampled, taxonomically typified morphological variation is often only a part of the phenome (see Deans et al. 2012) and may not provide evidence for any structure according to environmental conditions or geography. Therefore we need to stress the inclusive character of *Q. pubescens* Willdenowii.

While populations may still be defined as belonging to the same species, they might have some functional differences in their gene pools that differentiate them from other populations, not in terms of reproduction but in terms of phenotypic plasticity towards environmental change.

Apart from the focus on the taxonomic definition of a species, the evaluation of its future survival as a species is also crucial. In this context, characteristics that show functional relevance, i.e. *functional traits*, their genetic basis, and their *acclimation and adaptation potential* should be evaluated. Research on ecologically important infra-specific differences, i.e. ecotypic differentiation, is yet to come (see reviews by Jump and Penuelas 2005; Nicotra et al. 2010; Albert et al. 2011; and case studies by Bruschi 2010; Arend et al. 2011 and Wellstein and Cianfaglione in press).

And thus, quo vadis *Quercus pubescens*?

Acknowledgements The authors thank Gregor Aas (Ecological Botanical Garden, University of Bayreuth, Germany) for fruitful discussions, Javier Loidi (University of the Basque Country, Spain) for informations on oaks in the Iberian peninsula, Andreas Gohlke and Reinhold Stahlmann (University of Bayreuth, Germany) for help with producing the distribution map. C. Wellstein was supported by the Bavarian State Ministry of Sciences, Research and the Arts within the FORKAST project.

References

Aas, G. 1998. *Morphologische und ökologische Variation mitteleuropäischer Quercus-Arten: Ein Beitrag zum Verständnis der Biodiversität*. Libri Botanici: Band 19. IHW Verlag, Eching, 221 pp.

AFE 2010. *Atlas Florae Europaeae, Database. Committee for Mapping the Flora of Europe*. Botanical Museum, Finnish Museum of Natural History PO Box 7 (Unioninkatu 44) FI-00014 Helsinki University, Finland.

Albert, C. H., Grassein, F., Schurr, F., Vieilledent, G., & Violle, C. 2011. *When and how should intraspecific variability be considered in trait-based plant ecology?* Perspectives in Plant Ecology, Evolution and Systematics, 13: 217–225.

Anderson, E. 1949. *Introgressive Hybridization*. John Wiley and Sons, New York.

Arend, M., Kuster, T., Günthardt-Goerg, M. S., & Dobbertin, M. 2011. Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiology*, 31:287–297.

Arnold, M. L. 1997. *Natural Hybridization and Evolution*. Oxford University Press, New York.

Ascherson, P., & Graebner, P., 1896–1938. *Synopsis der Mitteleuropaeischen Flora*. 12 vols. Leipzig.

Bhagwat, S. A., & Willis, K. J. 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography*, 35:464–482.

Biondi, E., Blasi, C., Burrascano, S., Casavecchia, S., Copiz, R., Del Vico, E., Galdenzi, D., Gigante, D., Lasen, C., Spampinato, G., Venanzoni, R., & Zivkovic, L. 2009 (E. Biondi & C. Blasi, eds.). *Manuale italiano di interpretazione degli habitat della Direttiva 92/43/CEE*. Ministero dell'ambiente e della tutela del territorio e del mare, società botanica italiana http://vnr.unipg.it:8080/habitat/index.jsp

Bisby, F., Roskov, Y., Culham, A., Orrell, T., Nicolson, D., Paglinawan, L., Bailly, N., Appeltans, W., Kirk, P., Bourgoin, T., Baillargeon, G., & Ouvrard, D. (eds.) 2012. Species 2000 & ITIS Catalogue of Life, 2012 Annual Checklist. Digital resource at www.catalogueoflife.org/col/. Species 2000: Reading, UK.

Blasi, C. (ed.) 2010. *La vegetazione d'Italia*. Palombi, Roma. 539 pp.

Blasi, C., Facioni, L., Burrascano, S., Del Vico, E., Tilia, A. & Rosati, L. 2012. Submediterranean dry grasslands along the Tyrrhenian sector of central Italy: Synecology, syndynamics and syntaxonomy. *Plant Biosystems*. DOI: 10.1080/11263504.2012.656729

Bohn, U., Gollub, G., & Hettwer, C. 2003. *Karte der natürlichen Vegetation Europas; Map of the Natural Vegetation of Europe*. Landwirtschaftsverlag.

Borhidi, A., 2003. *Magyarország nővénytársulásai*. Akad Kiado, Budapest. 610 pp.

Brullo, S., Guarino, R., & Siracusa, G. 1999. Revisione tassonomica delle querce caducifoglie della Sicilia [Taxonomical revision of the deciduous oaks of Sicily]. *Webbia*, 54(1):1–72.

Bruschi, P. 2010. Geographical variation in morphology of *Quercus petraea* (Matt.) Liebl. as related to drought stress. *Plant Biosystems*, 144(2):298–307.

Bruschi, P, Vendramin, G. G., Bussotti, F, & Grossoni, P. 2000. Morphological and Molecular Differentiation between *Quercus petraea* (Matt.) Liebl. and *Quercus pubescens* Willd. (Fagaceae) in Northern and Central Italy. *Annals of Botany*, 85:325–333.

Bruschi, P., Grossoni, P., & Bussotti, F. 2003. Within- and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. *TREES*, 17:164-172.

Camus, A. 1936–1954. *Les Chênes, Monographie du genre Quercus*. 3 vols. Paris.

Castroviejo, S., Lainz, M., Lopez Gonzalez, G., Montserrat, P., Munoz Garmendia, F., Paiva, J., & Villar, L. (eds.) 1990. *Flora Iberica - Plantas vasculares de la Peninsula Iberica e Islas Baleares* Vol. II: Platanaceae-Plumbaginaceae. Real Jardin Botanico (C.S.I.C.), Madrid.

Catalogue of Life, 2011. *Annual Checklist, World Checklist of Selected Plant Families* (accessed through GBIF data portal, http://data.gbif.org/datasets/resource/1566, 2012-02-12)

Cesati, V., Passerini, G., & Gibelli, G. 1867. *Compendio della Flora Italiana*. 2 vols. Milano.

Conti, F., Abbate, G., Alessandrini, A., & Blasi, C., 2005. *An annotated Checklist of the Italian Flora*. Roma, 420 pp.

Davis, P. H., & Heywood, V. H. 1963. *Principles of Angiosperm Taxonomy*. Oliver & Boyd, Edinburgh. xx + 556 pp.

Deans, A. R., Yoder, M. J., & Balhoff, J. P., 2012. Time to change how we describe biodiversity. *Trends in Ecology and Evolution*, 27(2): 78–84.

Devillers, P., Devillers-Terschuren, J., & Ledant, J.-P. 1991. *Habitats of the European Community, CORINE Biotopes manual*. Commission of the European Communities, Luxembourg.

Ehrendorfer, F. 1973. *Liste der Gefäßpflanzen Mitteleuropas*. 2nd ed. Gustav- Fischer-Verlag, Stuttgart.

Ellenberg,H. 1996. *Vegetation Mitteleuropas mit den Alpen*. 5th ed. Verlag Eugen Ulmer, Stuttgart. 1095pp.

Fiori, A. 1923–29. *Nuova Flora analitica d'Italia*. 2 vols. Firenze.

Fortini, P., Viscosi, V., Maiuro, L., Fineschi, S., & Vendramin, G. G., 2009. Comparative leaf surface morphology and molecular data of five oaks of subgenus *Quercus* Oerst. (Fagaceae). *Plant Biosystems*, 143(3):543–554.

Frattegiani, M., Gigante, D., Maneli, F., & Venanzoni, R., 2010. Applicazione del metodo fitosociologico per la definizione dei criteri gestionali di habitat forestali dell'All. I alla direttiva 92/43/CEE. In: Centenaire de la Phytosociologie (Bensettiti, Bioret, Boullet, Pedrotti, eds.), *Braun-Blanquetia*, 46:255–259.

Gavioli, O. 1935. *Archivio Botanico* (Forlì), 1(2):16.

Govaerts, R. 1995. Proposals to conserve or reject three species names in *Quercus* L. (Fagaceae). *Taxon*, 44:1195–1197.

Govaerts, R., & Frodin, D. G., 1998. *World Checklist and Bibliography of Fagales (Betulaceae, Corylaceae, Fagaceae and Ticodendraceae)*, pp 201–394. Royal Botanic Gardens, Kew, Richmond.

Govaerts, R. H. A., & Avishai, M. 2000. The conserved type of the name *Quercus pubescens* Willd. (Fagaceae). *Taxon*, 49:537.

Grove, A. T., & Rackham, O. 2001. *The nature of Mediterranean Europe*. Yale University Press. 524 pp.

Horvát, I., Glavač V. U., & Ellenberg, H., 1974. *Vegetation Südosteuropas*. Stuttgart

Huntley, B., & Birks, H. J. B., 1983. *An atlas of past and present pollen maps for Europe: 0–13 000 years ago*. Cambridge University Press, Cambridge. 667 pp.

Huntley, B, & Webb III, T (eds.), 1988. *Vegetation History*. Handbook of Vegetation Science, vol. 7. Kluwer, Dordrecht. 803pp.

IPNI, 2004. *The International Plant Names Index Published on the Internet* http://www.ipni.org (accessed through GBIF data portal, http://data.gbif.org/datasets/resource/40, 2012-02-12)

Jahn, R., & Schönfelder, P., 1995. *Exkursionsflora für Kreta*. Verlag Eugen Ulmer, Stuttgart.

Jalas, J., & Suominen, J. (eds.) 1976. *Atlas Florae Europaeae. Distribution of Vascular Plants in Europe. 3. Salicaceae to Balanophoraceae*. Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo, Helsinki. 128 pp.

Jump, A. S., & Penuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8:1010–1020.

Knapp, S., 2008. Species concepts and floras: what are species for? *Biological Journal of the Lineean Society*, 95:17–25

Kozlowski, T. T. 1971. *Growth and Development of Trees*. 2 vols. Academic Press, New York.

Lepais, O., Petit, R. J., Guichoux, E., Lavabre, J. E., Alberto, F., Kremer, A., & Gerber, S., 2009. Species relative abundance and direction of introgression in oaks. *Molecular Ecology*, 18: 2228–2242.

Lepais, O., Gerber, S., 2011. Reproductive patterns shape introgression dynamics and species succession within the European white oak species complex. *Evolution*, 65-1:156–170. DOI: 10.1111/j.1558-5646.2010.01101.x

Lineaus, C. 1753. *Species plantarum, exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus,* *synonymis selectis, locis natalibus, secundum systema sexuale digestas*. Lars Salvius, Stockholm.

Loidi, J., & Herrera, M., 1990. The *Quercus pubescens* and *Quercus faginea* forests in the Basque Country (Spain): distribution and typology in relation to climatic factors. *Vegetatio*, 90:81–92.

Meusel, H., Jäger, E. J., Rauschert, S., & Weinert, E., 1978. *Vergleichende Chorologie der zentraleuropäischen Flora*. Vol. 2, Text and.maps. Gustav-Fischer-Verlag, Jena. 171pp.

Montelucci, G., 1978. Lineamenti della vegetazione del Lazio. *Ann. Bot*., 35–36.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15:684–992.

Parr, C. S., Guralnick, R., Cellinese, N., & Roderic, D. M. P., 2012. Evolutionary informatics: unifying knowledge about the diversity of life. *Trends in Ecology and Evolution*, 27(2):94–103.

Petit, R. J., Bodénès, C., Ducousso, A., Roussel, G., & Kremer, A., 2003. Hybridization as a mechanism of invasion in oaks. *New Phytologist*, 161:151–164.

Pignatti, S, 1998. *I boschi d'Italia* [The Forests of Italy]. Unione Tipografico-Editrice Torinese, Torino.

Pignatti, S., 1982. *Flora d'Italia*. 3 vols. Bologna.

Rieseberg, L. H., 1995. The role of hybridization in evolution: Old wine in new skins. *Am. J. Bot*., 82(7):944–953.

Rivas-Martínez, S. 1994. Clasificación bioclimática de la Tierra. *Folia Botan. Matritense*, 13:1–25.

Rosati, L., Filibeck, G., De Lorenzis, A., Lattanzi, E., Surbera, F., Fascetti, S., & Blasi, C., 2010. La vegetazione forestale dei Monti Alburni, nel Parco Nazionale del Cilento e vallo di Diano (Campania): analisi fitosociologica e significato fitogeografico. *Fitosociologia*, 47(2):17–55.

Sánchez de Dios, R., Benito-Garzón, M., & Sainz-Ollero, H., 2006. Hybrid zones between two European oaks: a plant community approach. *Plant Ecology*, 187:109–125.

Sayer, U., 2000. *Die Ökologie der Flaumeiche (Quercus pubescens Willd.) und ihrer Hybriden auf Kalkstandorten an ihrer nördlichen Arealgrenze: Untersuchungen zu Boden, Klima und Vegetation*. J. Cramer, Gebrüder Borntraeger Verlagsbuchhandlung, Berlin.

Schwarz, O., 1937. Monographie der Eichen Europas und des Mittelmeergebiets. *Feddes Repert. Sonderbeih*. D, 1–200.

Schwarz, O. 1964. *Quercus L.* In: *Flora Europaea*, vol. 1: Lycopodiaceae to Platanaceae (T. G. Tutin et al., eds.), pp 61–64. Cambridge University Press, Cambridge.

Schwarz O., 1993 - *Quercus L.* In: Tutin T. G., Heywood V. H., Burges N. A., Valentine D. H. Walters S. M., Webb D. A. (Eds.) Flora Europaea, vol. 1: Lycopodiaceae to Platanaceae. - Cambridge University Press, Cambridge, pp. 72–76.

Tenore, M. 1831. *Sylloge Plantarum Vascolarium Florae Neapolitanae hucusque detectarum*. Napoli

Tenore, M. 1835–1836. *Flora Napolitana*. 5 vols. Napoli.

Thuillier, J. L. 1799. *Flore des Environs de Paris*. 2nd ed. Paris. 502pp.

Trinajstič, I. 1974. *Quercus* L. In: Analitička flora Jugoslavije (I. Trinajstič, ed.), 1(3):460–481. Institut za botaniku Sveučilišta. Zagreb.

Trinajstič, I. 2007. O problemu međusobnog razlikovanja hrastova *Quercus pubescens* Willd. I *Quercus virgiliana* (Ten.) Ten. *Šumarski list*, 131(1–2):57–60.

Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M., & Webb, D. A. (eds.) 1964. *Flora Europaea*. Vol. 1. Cambridge.

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M., & Webb, D. A. (eds.) 1968–1980. Flora Europaea. Vols. 2–5. Cambridge.

Tutin, T. G., Burges, N. A., Chater, A. O., Edmondson, J. R., Heywood, V. H., Moore, D. M., Valentine, D. H., Walters, S. M., & Webb, D. A. (eds.) 1993. Flora Europaea, ed. 2, 1. Cambridge.

Van Steenis, C. G. G. J. 1957. Specific and infraspecific delimitation. *Flora Malesiana*, ser. 1, 5(3):clxvii-cc xxxix. Jakarta.

Wagenitz, G. (ed.) 1981. *Illustrierte Flora von Mitteleuropa*. Vol. III, Part 1. 3rd edition. Parey, Hamburg. 504pp.

Walter, H. 1974. *Die Vegetation Osteuropas, Nord- und Zentralasiens*. Gustav-Fischer-Verlag, Stuttgart. 452 pp.

Walter, H., & Straka, H. 1970. *Arealkunde: Floristisch-Historische Geobotanik*. Verlag Eugen Ulmer, Stuttgart.

Wellstein, C., Chelli, S., Campetella, G., Bartha, S., Galiè, M., Spada, F., Canullo, R. 2013. Intraspecific phenotypic variability of plant functional traits in contrasting mountain grassland habitats. *Biodiversity and Conservation*, 22:2353–2374.

Wellstein, C., & Cianfaglione, K. (in press). Impact of extreme drought and warming on survival and growth characteristics of different provenances of juvenile *Quercus pubescens* Willd. *Folia Geobotanica*.

Zangheri, P. 1976. *Flora Italica*. CEDAM, Padova.

Zohary, M. 1973. *Geobotanical Foundations of the Middle East*. Gustav-Fischer-Verlag, Stuttgart.

On the Potential of *Quercus pubescens* Willd. and Other Species of *Quercus* in the Camerino Syncline (Central Italy)

Kevin Cianfaglione

Keywords
Cental Italy • Camerino Sincline • *Quercus* • Potential • Biological • Geobotanical • Big trees • Development

1 Introduction

In the Umbro-Marchigiano Appenines in central Italy, downy oak (*Quercus pubescens*) does not occur in old-growth forests but only in coppices, the clearly prevalent form of woodland management. Over time, agriculture and livestock grazing have greatly reduced the original forest cover, which today is fragmented into isolated nuclei; in addition, coppicing has modified forest structure and floristic composition and reduced its quality. There has even been the practice, after coppicing, of using the forest topsoil to cultivate cereal species while waiting for coppice regeneration. All this has modified the flora significantly, reduced the quality of the woodland ecosystem, and dried out the soil. In order to understand the potential of *Quercus pubescens* and other *Quercus* species, it is interesting to study the great ancient trees left in the woods, fields, or towns, in order to understand their potential for biological and geobotanical development. In a territory like the Marche, where the woods are very limited and of poor quality, these trees must be viewed not only aesthetically or historically (Ballelli et al. 1981) but also for their potential for woodland improvement and seed collection for elements of genetic biodiversity, in accord with the proposal of Chiarugi (1959). These trees are also important because they promote the process of secondary succession and, consequently, the return of woodlands in areas where this is possible, such as uncultivated or abandoned lands (see also: Cianfaglione 2010, 2011); they are also important for promoting more sustainable silvicultural practices. Today, the oaks that grow in coppices in the study area normally do not exceed 1 m in diameter; more often they are like slender poles, subjected to coppicing that is often done too early. The opposite holds for the ancient oaks in fields, which are often of notable dimensions. When we observe a group of these big oaks, we can imagine how the primordial forests that grew there must have looked, and how they could become some day, were they not dug up or felled (Fig. 1).

2 The Study Area

The study area is the syncline of Camerino, in the Umbro-Marchigiano Apennines between 100 and 1,600 m a.s.l., characterized prevalently by marly-arenaceous hills; this syncline is bordered by two prevalently calcareous mountain chains. The climate is submediterranean, with average annual precipitation between 700 and 900 mm, increasing sometimes to 1,200–1,400 mm above 950 m. In the lowland the mean temperature of the coldest month (January) is 4.9°C and that of the hottest month (July) is 23.6°C; for the higher elevations these values are −2.4°C and 17.4°C, respectively.

K. Cianfaglione (✉)
University of Camerino, School of Environmental Science, Via Pontoni 5, 62032 Camerino, Marche, Italy
e-mail: kevin.cianfaglione@unicam.it

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*,
Geobotany Studies, DOI 10.1007/978-3-319-01261-2_9,

3 Variations in the Vegetation During the Postglacial Period

According to Marchesoni (1957) and Paganelli (1982), the constant presence of *Pinus* and the abundance of *Quercus* in the central levels of deposits in the Fiuminata Plain (5.30–9.40 m) testify the existence of a long anathermic continental period and the transgression of the mediterranean belt during this period. Holm-oak (*Q. ilex*) forests and the "Macchia Mediterranea" thus reached their maximum penetration along the Appenine valleys, and the current stands of holm oak occur on the most sun-exposed, warmest rocky positions, like on the slopes of Monte Primo and Monte Castel Santa Maria. The frequent growths of *Phillirea media*, *Pistacia terebinthus*, *Erica arborea*, and *Osyris alba*, etc., on the driest positions in the deciduous oak wood are in fact relicts of the climactic conditions of that anathermic continental period.

The oldest levels of Colfiorito also have continental characteristics, though the presence of *Pinus mugo*, *Abies* and *Picea* is still an indicator of cold oceanic climatic conditions. The latter two taxa are found occasionally even during the period of maximum continentality, at 4.40 and 3.10 m. The decline of pine marks the limit between the anathermic continental period and the catathermic oceanic period; during this phase there was an expansion of the submontane thermophilous oakwoods. Later, though, more oceanic climatic conditions interrupted the rise of the oakwoods and favored the establishment of beech, to the detriment of *Pinus nigra*. The appearance of *Juglans* and *Castanea* marked the beginning of significant human influence, hastening the disappearance of pine and bringing about a more recent re-expansion of *Quercus*, *Fraxinus ornus* and *Corylus avellana*, the principal components of today's thermophilous bushland (Paganelli 1982).

4 Analysis of the Data

The data in Tables 1 and 2 were extrapolated from the recent regional census by the Corpo Forestale dello Stato [CFS: National Forestry Corps] (see Guidi 2012), indicated by 'a', since the data provided are the most up-to-date, detailed, and precise. In other cases, denoted by 'b', the information was drawn from the "Primo censimento nazionale degli alberi di notevole interesse" [*First national census of trees of notable interest*], by the CFS in 1982. The census by the Provincia di Macerata (2004) is denoted by 'c' and Capodarca (2008) by 'd'. Boldface text is for new reports for the study area (denoted by 'e') published here for the first time. As further information, the last column of the tables provides bibliographic data on the first report, using the same letters.

In trying to compile an accurate database from which to obtain precise data and conclusions on the great old oak trees, the use of bibliographic data is fraught with difficulties because data are often missing, incomplete, incorrect, too generic, or even conflicting. Some discrepancies and errors was found, for example, between the data published in Capodarca (2008). In other hand, some data are according to the last regional census by the National Forestry Corps and with that of Macerata Province. In each case, though, these data as a whole are useful for the study of big oaks, to assure their inclusion in the census of remarkable trees, and to propose measures for their protection.

The data in the lesser literature sometimes indicate trees attributed to erroneous species and genera, or provide other data that do not correspond to reality. In addition, there are discrepancies or errors in toponymy that make it more difficult to identify and to monitor the exemples described. Often the ages of the trees are only estimated, because it is difficult to identify age correctly without precise historic sources or without damaging the tree; at other times, wood damage (knots, scars, and cavities) made it equally difficult to

Fig. 1 In the picture we can observe a remanent fragment of ancient typical rural landscape in *Q. pubescens* belt, with small coppice patches between sowing surfaces, and the last "seminativo arborato" arable land with trees; in similar conditions like in the past, where some big tall oaks remains also if now worked by agricultural machines. Camerino, November 2011 (Photo Karina Piermarteri)

Table 1 List of the biggest *Q. pubescens* trees (veterans or patriarchs) noted in the study area

No.	Municipality	Province	Locality	Place/name	Trunk circumference	h	Canopy circumference	Age	First described by	From
1	Apiro	Macerata	San Leopardo		4.4	22	22	300	c	a
2	Belforte del Chienti	Macerata	Santa Maria	Quercia del Dr. Betti	5.03	20	18	–	d	a
3	Caldarola	Macerata	Bozzolone		4.5	25	26	200	d	a
4	Caldarola	Macerata	Vestignano	San Pietro	5.2	19	16	300	d	a
5	**Camerino**	**Macerata**	**Canepina**	**Incrocio**	**4.1**	**20**	**16**	–	**e**	a
6	Camerino	Macerata	Torrone	Case Micozzi	4.3	18	19.65	300	a	a
7	Camerino	Macerata	Villa San Vito	Villa Battibocca 1	5.62	18	21.5	350	b	a
8	Camerino	Macerata	Villa San Vito	Villa Battibocca 2	4.82	21	16	300	c	a
9	Camerino	Macerata	Colle Altino		4.3	20	20	20	a	a
10	Camerino	Macerata	Le Scalette		4.45	19	24.5	300	a	a
11	**Camerino**	**Macerata**	**Via per Rocca d'Aiello**	**1**	**4**	**17**	**12**	–	**e**	–
12	**Camerino**	**Macerata**	**Via per Rocca d'Aiello**	**2**	**4.1**	**16**	**14**	–	**e**	–
13	**Camerino**	**Macerata**	**Via per Rocca d'Aiello**	**3**	**4**	**18**	**16**	–	**e**	–
15	Cascia	Perugia	Avendita		4.4	15	–	–	b	b
16	Cascia	Perugia	Capanne di Collegiacone		4.1	15	–	–	b	b
17	Cascia	Perugia	Roccaporena		4.15	16	–	–	b	b
18	**Castelraimondo**	**Macerata**	**Castello di Lanciano**	**1**	**4.8**	**18**	**21**	–	**e**	–
19	**Castelraimondo**	**Macerata**	**Castello di Lanciano**	**2**	**4.06**	**20**	**21.3**	–	**e**	–
20	Castelraimondo	Macerata	Villa De Luca	1	4.4	24	27.9	300	a	a
21	Castelraimondo	Macerata	Villa De Luca	2	4.18	23	21.05	250	a	a
24	Cerreto d'Esi	Ancona	Fontanelle		4.66	20	28	≈300	d	d
25	Cerreto d'Esi	Ancona	Centro abitato		4.7	16	–	–	d	d
26	Cerreto d'Esi	Ancona	Casale Piergiò		4.4	15	–	–	d	d
27	Cingoli	Macerata	Santa Maria del Rango	Case Foltrani	4.8	23	35	≈300	c	a
28	Cingoli	Macerata	Mummuiola	Fonte del piano	4.41	26	26	250	c	a
29	Cingoli	Macerata	S. Maria del Rango	Case Foltrani	4.9	23	32.5	300	c	a
30	Cingoli	Macerata	Botontano	Villa Castiglioni	5.3	23	22.2	300	c	a
31	Cingoli	Macerata	Colcerasa		4.15	24	22.4	250	a	a
32	Cingoli	Macerata	Lioni		4.13	21	23.25	250	a	a
33	Colmurano	Macerata	Contrada Fiastra		4.1	18	28.35	250	a	a
34	Corridonia	Macerata	Sarrocciano		4.95	20	27	≈350	d	a
35	Fabriano	Ancona	Putido	Casa dei Piani	4.5	21	26	100	b	a
36	Fabriano	Ancona	Fraz. Nebbiano		4.8	20	27.65	110	b	a
37	Fabriano	Ancona	Monte civita	Villa Rotondo	4.4	11	20	–	b	a
38	Fabriano	Ancona	Località Grotte	Fonte comunale	4.5	24	21.5	–	a	a

(*continued*)

Table 1 (continued)

No.	Municipality	Province	Locality	Place/name	Trunk circumference	h	Canopy circumference	Age	First described by	From
39	Fiastra	Macerata	Colle		4.5	18	15	250	c	a
40	Gualdo Tadino	Perugia	Loc. Tomaiolo st. ferroviaria		4	18	–	–	b	b
41	Macerata	Macerata	Villa Potenza	Via dei Velini/ Casa Bianchini	5.35	22	28	350	b	a
42	Macerata	Macerata	Sforzacosta	Fosso Narducci	5.44	22.8	27	350	b	a
43	**Macerata**	**Macerata**	**Sforzacosta**	**1**	**5.3**	**17**	**20**	–	**e**	–
44	**Macerata**	**Macerata**	**Sforzacosta**	**2**	**4.4**	**15**	**18**	–	**e**	–
45	**Macerata**	**Macerata**	**Sforzacosta**	**3**	**4.1**	**13**	**16.5**	–	**e**	–
46	Matelica	Macerata	Casafoscola	C.Foscoli Bassa	4.33	22.2	21.8	300	b	a
47	Norcia	Perugia	Valcaldara loc. Badia		4.05	20	–	–	b	b
49	Norcia	Perugia	San Pellegrino loc. Caricaia		4.1	20	–	–	b	b
50	Norcia	Perugia	San Pellegrino periferia Sud		4.3	16	–	–	b	b
51	Norcia	Perugia	Parrocchia di Nottoria		5.1	22	–	–	b	b
52	Pievebovigliana	Macerata	Rocca Maia		4.3	16.35	20	250	b	a
53	Pievetorina	Macerata	Villarella	Pian di Salto	4.6	22.5	22.5	300	a	a
54	Pievetorina	Macerata	Acqua Morta		4.6	16	19.6	300	d	a
55	Pollenza	Macerata	C.da Morico		4.6	23.8	22	300	c	a
56	Sassoferrato	Ancona	Serrasanta	Aspro	4.4	20	30	300	b	a
57	S. Severino Marche	Macerata	Berta		4.65	23.2	27.2	300	d	a
58	Serrapetrona	Macerata	Ventigliano, C.da Colli	Quercia dei Frati	4.55	9.7	13.7	300	c	a
59	Tolentino	Macerata	Mulino Bandini		4.6	22	27	300	a	a
60	Tolentino	Macerata	Cisterna n. 60		4.25	20.4	24	250	a	a
61	Tolentino	Macerata	Regnano		4.45	20.8	26.5	300	a	a
62	Tolentino	Macerata	Contrada divina pastora		5	24	27	≈300	d	a
63	Tolentino	Macerata	Piane del Chienti		4.82	21	16	260	d	a
64	Tolentino	Macerata	Vicino superstrada 1		4.6	–	27	–	d	d
65	Tolentino	Macerata	Vicino superstrada 2		4.32	–	–	–	d	d
66	Tolentino	Macerata	Vicino superstrada 3		4.4	–	–	–	d	d
67	Treia	Macerata	Passo di Treia	San Marco vecchio	6.46	29.7	35	450	c	a
68	Urbisaglia	Macerata	C.da Fiastra, 30		4.38	21.1	26.05	250	a	a
69	Urbisaglia	Macerata	Contrada Fiastra		4.1	24.2	30	250	a	a
70	Urbisaglia	Macerata	Zona industriale		4.3	15.7	22.1	200	a	a
71	Urbisaglia	Macerata	Area archeologica	Tempio dea Salus	5.35	18	20	350	d	d
72	Urbisaglia	Macerata	Selva		4.1	16.5	20.8	250	a	a
73	Ussita	Macerata	Palazzo		4.1	12	8	200	c	a
74	Visso	Macerata	Fematre		4.25	14	16.5	400	c	a

Table 2 List of the more notable big trees of *Quercus cerris* in the study area, all these oaks are in Macerata Province; boldface type indicates examples identified and reported for the first time

No.	Municipality	Locality	Trunk circumference	h	Canopy circumference	Age	First described by	From
1	Castelsantangelo sul Nera	Valle di Vallinfante	3.1 (2.5 at the base)	15	11	150	c	**a**
2	**Castelsantagelo sul Nera**	**Frazione di Macchie**	**2.7**	**9**	**8**	–	**e**	–
3	**Sefro**	**Alta piana di Montelago**	**2.6**	**15**	**8**	–	**e**	–
4	**Sefro**	**Alta piana di Montelago**	**3.76**	**20**	**15**	–	**e**	–
5	Serravalle del Chienti	Fonte delle Mattinate	3.37	16.1	19.7	120	(d) a	**a**

estimate age scientifically. In addition, the oaks examined almost always bear signs of pruning, other removal of limbs, or pollarding, which can nullify the current development of dimensions. An extreme case is that of the Serrapetrona downy oak, the large trunk of which was sawn 6 m above ground about 20–50 years ago, so that today its height and crown are distinctly different from those of other nearby oaks of the same species.

To evaluate the potential vegetation, the flora and characteristic plant associations were evaluated. For dendrological potential, the great trees in the study area were analyzed species by species, and a dendrochronological study was done at the University of Tuscia (Viterbo). The diameters and circumferences, when not otherwise specified, were all measured at the standard height of 1.30 (chest-high circumference) from the closest soil line.

5 *Quercus* Species Present in the Study Area

The following oak (*Quercus*) species were examined in the study area: *Q. pubescens* s.l., *Q. ilex*, *Q. cerris*, *Q. robur*, *Q. suber*, *Q. crenata*, *Q. petraea* and *Q. frainetto*.

Quercus pubescens s.l. [downy oak, pubescent oak, or Mediterranean white oak; *roverella* in Italian]. This is the most common in the study area and forms zonal forests. Numerous examples with a circumference over 3 m are present, for the most part in fields and rarely in woods, which are normally managed by coppicing. The biggest examples reach circumferences of as much as 6 m. Because of alterations by man, downy oak can be found even at high altitudes, even above 1,500 m. In this regard Prof. Vittorio Marchesoni reported *Q. pubescens* in Forca Canapine above Norcia (Perugia) in arid areas between 1,300 and 1,500 m, substituting for pre-existing beech woods (*Fagus sylvatica*) (Ballelli et al. 2005). It is well known that *Q. pubescens* is very variable, partly because of hybridization with other species in the study area, especially with *Q. petraea* and *Q. frainetto*. Saplings from acorns collected on the hills to the orographic right of Polverina Lake (Cianfaglione 2012) were compared with saplings from other European sites and were found to develop earlier in the spring than the others (see also: Wallstein e Cianfaglione, in preparation). In addition, there are sporadic and widespread phenotypes with acorns marked by a lower tannin content, known as *querce castagnole* (Sweet-acorn oak or Chestnut oak, sometimes controversially attributed to *Q. picena* Spad. and *Q. virgiliana* Ten.), which were once eaten by people and used for forage. There is little probability that *Q. dalechampi* is present in the study area. *Quercus pubescens*, on marly-arenaceous substrates, forms the two associations *Peucedano cervariae-Quercetum pubescentis* and *Erico arboreae – Quercetum pubescentis*. The latter is also found on calcareous substrates in a shrubby oak wood, in a precocious stage of secondary succession, near the Gole di Pioraco, toward Località Costa, a report worthy of further attention. Instead, the *Cytiso sessilifolii-Quercetum pubescentis* association forms on calcareous substrates and is also present in the *Orno-ostryetum* (*Fraxinus ornus – Ostrya carpinifolia* woods) along with the *Scutellario columnae-Ostryetum carpinifoliae* association. In terms of phytosociological potential, it should be noted that the current plant associations of downy oak present and described are all in more or less degraded stages. A different floristic composition is possible for the understorey of mature woods, that have examples over 5 m average in circumference, except for *Peucedano cervariae-Quercetum pubescentis*, which has a floristic composition fairly close to the potential vegetation. All these associations have been described in coppices and thus have many mantle species, with significant numbers of edge and herbaceous-fringe presences and even archeophytes/neophytes. Thus, if they become mature forests, it is not necessarily the case that they will maintain a similar floristic composition. The *Peucedano cervariae-Quercetum pubescentis* prevail on hills where the most large specimens of *Q. pubescens* are found today. Also, the *Erico arboreae – Quercetum pubescentis* would be much richer in *Q. cerris* (ecologically more suitable and similar heather *E. arborea*), until, in case, to become *Erico arboreae-Quercetum cerridis*. In a more natural situation of potential vegetation, the *Q. pubescens* forest would certainly be more extensive than today. On the other hand, in some cases it would also be absent from some locations where it occurs today, in substitution of many other kinds of woodland, including *Q. petraea*, *Q. robur*, *Q. frainnetto*, *Q. cerris* and *Fagus sylvatica*.

Normally, oaks in this area are spread throughout the coppices and never exceed a meter in diameter; in fact, more often than not they are like slender poles. In most cases the great oaks are located in rural settings, where they are often of notable dimensions, even though their limbs may have been cut off (pollarding) and they may have many knots and cavities. In these cases, the longevity of the oaks is undermined not only by the danger of cutting but also by planting and digging activity, by destruction of the roots, and by excessive pruning. For example, in Table 1, the oak no. 63 died recently because of such strong pruning; the same happened to the Sarrocciano, Corridionia downy oak, killed because of plowing; oak no. 2 is suffering and wilting because of plowing around its base. On the other hand, oak trees also die or are removed because they are considered mistakenly to be dangerous or because they were inconvenient for roadwork. In some cases, bad management and lack of respect cause trees to suffer and become vulnerable to attack by pathogens like *Cerambix cerdo*, other insects and some *fungi*.

The cross-section was analyzed at chest height (circumference: 4.43 m).

In the oak analyzed, average annual diameter growth was 3.71 mm, and the total growth 1.76 m. The basal trunk circumference without bark was 5.52 m, the width of the bark being 2.3 cm, and the total basal trunk circumference was 5.98 m. The trunk sample was analyzed a year after felling and was still of good quality: the wood had only slight scattered traces of fungal attack, with a small cavity (2 cm^2) between the alburnum and the duramen. In Fig. 2 we can note the classical growth trend, maximum in the first years and decreasing with the passage of centuries. Maximum growth was interrupted in 1910, when the tree was about 45 years old, and then growth remained fairly constant until 2010. There were four periods of limited growth, perhaps caused by xerothermic conditions or road work near the tree base, in 1783–1793, 1808–1817, 1833–1837, and 1872–1884. The oak was well developed and vital when cut, its cause of death being just the cutting. After the cut, no polloniferous root activity or basal resprouting was observed. Some sections of the longitudinal section show evident trauma from an impact 22 years before felling, on the side facing away from the road, probably due to impact by a tractor maneuvering close to the tree. The wound had completely healed without weakening the woody tissue.

Given the good distribution of big trees of *Q. pubescens* in the study area, this survey considered trees with circumference no less than 4 m. Trunk circumference, when not otherwise specified, was measured at the standard height of 1.30 m from the closest soil line.

Coordinates of new findings: (5) 43° 9′ 42.48″ N, 13° 3′ 35.23″ E at 357 m elevation; (11) 43° 10′ 27.80″ N, 13° 3′ 31.02″ E at 351 m; (12) 43° 10′ 48.48″ N, 13° 3′ 43.00″ E at 395 m; (13) 43° 10′ 44.58″ N, 13° 3′ 54.89″ E at 458 m; (18) 43° 11′ 20.82″ N, 13° 2′ 21.77″ E at 316 m; and (19) 43° 11′ 21.34″ N, 13° 2′ 22.62″ E at 315 m; (43–44–45) are without coordinates because they are all on a single piece of private property, the owners of which accompanied me out of kindness and respect for science but did not want to be make public the locations of these oaks.

The average circumference of this class of big trees is 4.53 m, and the average height is 19.5 m. The average diameter of the crown is 23.41 m; the average ratio of height to trunk circumference is 4.4, and the average age is 278 years. The oaks examined are often isolated, in loose groups or in rows. These oaks are notably in the Marche Region, but except for the great oak on the Count Battibocca property and the one in Treia, they are not particularly noteworthy, as compared to the largest downy oaks in Italy and in the world; this is due to human intervention, which did not allow greater development.

6 Brief Observations on Others Oak Species Present in the Study Area

Q. petraea (Mattuschka) Liebl. [sessile oak, cornish oak or durmast oak] is *rovere* in Italian. This species, often hybridized with *Q. pubescens*, is very rare today and thus does not form its own associations. Prof. Vittorio Marchesoni reported this species in Amandola, in the province of Ascoli Piceno, at 400–500 m, specifying it as "*quercie gigantesche*" [gigantic oaks], and in Pievetorina (Macerata), at 600 m, indicating it as "*albero grande*" [big tree] (Ballelli et al. 2005). None of these trees are found today. Other reports concern sporadic examples in the *Q. cerris* woods of Madonna del Piano (Colfiorito, Perugia, Umbria) and between Sellano and Casenove, also in Umbria (Pedrotti 1969; Pedrotti and Sanesi 1969). The Pioraco gorge is another site (Pedrotti, personal communication 2011), where it grows in the *Scutellario columnae-Ostryetum carpinofoliae*.

The closest example of notable dimensions is in Osimo (Ancona), with a circumference of 4.3 m and a height of 20 m. Another, in Guardea (Terni), Località Ontorello, has a circumference of 4.5 m and a height of 20 m.

Because of variability of form, over time various hybrids or intermediate forms have been reported that are currently considered synonymous; in any case, in the study area the examples generally do not exceed a meter in circumference because they are subjected to cutting.

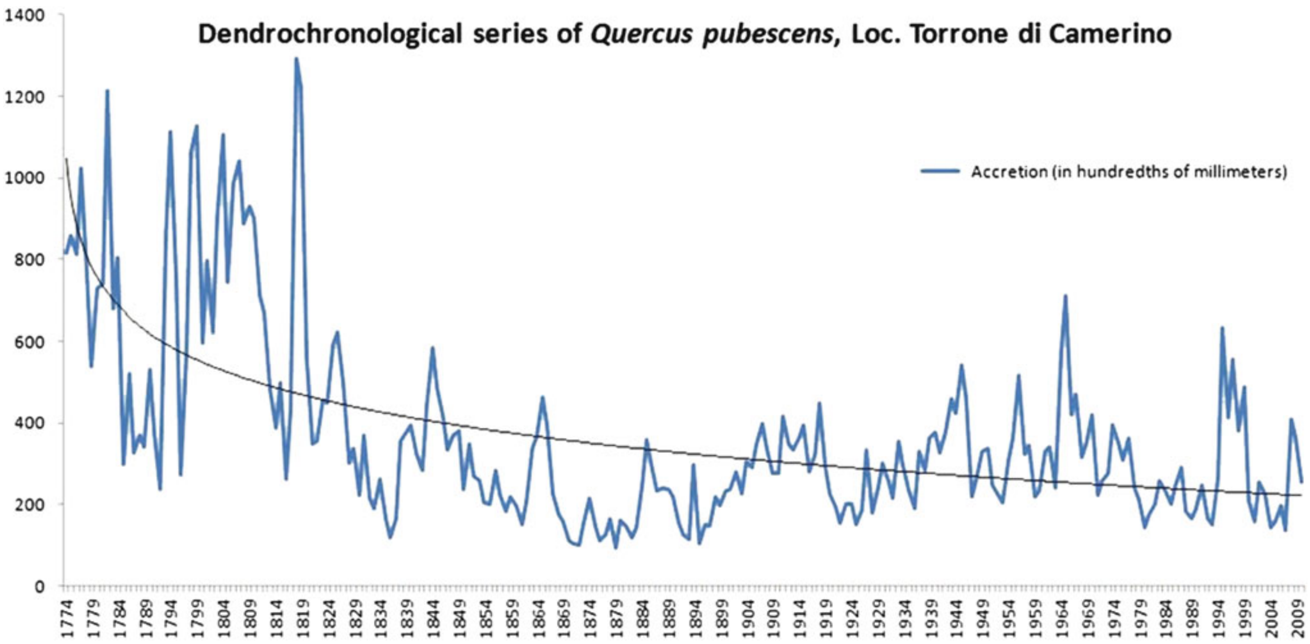


Fig. 2 In the figure above, *blue* indicates the annual growth rate, in hundredths of millimeters, while *black* indicates the annual growth curve (Log.)

Q. cerris L. [Turkey Oak] is *cerro* in Italian. This species forms intrazonal woods and prefers soils with lower pH levels that are rich, more clayey, mesophilous and without waterlogging. These woods of 'turkey oak' (not to be confused with *Q. laevis* in North America, also called 'turkey oak') grow between the deciduous submediterranean oak woods and beech groves; although this turkey oak is widespread in the Marche Region, we cannot say that it forms a true altitudinal belt (Pedrotti 1969). According to Marchesoni (1958, 1959) the climax of the turkey oak occurred much more widely than at present, because some species such as *Taxus baccata*, *Ilex aquifolium*, *Tilia* spp. *Acer obtusatum*, *Prunus avium*, *Euonymus latifolius*, *Crataegus oxyacantha* and *Staphylea pinnata* can also be identified within the so-called climax belt of *Q. cerris*. In addition, much of the *Q. cerris* woods in the study area has been substituted by chestnut stands (*Castanea sativa*), in particular on the subacidic soils over sandstone. These *Q. cerris* woodlands can be divided into two main categories: a "xeric" one with *Q. pubescens*, *Fraxinus ornus* and more rarely *Q. petraea*, developed on rocky terrain; and a "cooler" one with *Fagus sylvatica*, *Carpinus betulus* and *Acer obtusatum* (Pedrotti 1969). Spadoni (1826–1828) distinguished between *Q. cerris* and *Q. haliphlaeos*, now synonyms. Agreeing with Spadoni, Reali (1871–1876) says that this species was common in other woodlands in Sammaroto (San Maroto), but today, in the same area, it is not so common. In San Maroto only a few trees (some suffering) still remain between the *Q. pubescens* (lower) and *Q. ilex* (upper) woodlands.

The closest example of notable dimensions is in Pennabilli (Pesaro), Località Poggio Bianco, with 4.3 m circumference and 17 m height. Another, in Sant'Angelo di Amatrice (Rieti), has a trunk circumference of 6.97 m, height of 22 m, and crown circumference of 25 m.

In the study area it is possible to find a few examples with circumference around 2 m, but only those that exceed 2.50 should be considered interesting for their age. Because of coppicing at brief intervals, this species usually does not grow more than a meter in circumference in the study area.

The *Q. cerris* trees of more noteworthy dimensions in the study area are shown in Table 2.

Coord.: (2) 42° 53′ 59.54″ N, 13° 10′ 26.13″ E, at 1,290 m elevation; (3) 43° 6′ 9.63″ N, 12° 58′ 32.86″ E at 953 m; (4) 43° 6′ 9.89″ N, 12° 57′ 59.73″ E at 953 m.

The most notable individual of *Q. cerris* found in the study area is on the high plain of Montelago. It has a trunk circumference of about 3.76 m, measured at 1.30 m above the closest soil line, and a height of about 20 m.

Quercus robur [English oak, Pedunculate oak or French oak] is *farnia* in Italian. This species has behaves azonally in the study area, preferring valley bottoms. It was more common in the past but today is very rare because of land reclamation in past centuries; it is very rare in the study area because of the concentration of human activity there. Around Camerino there are only four examples of *Q. robur*, along a ditch near S. Luca in the Sfercia Valley; one of these is of greater interest because it has a circumference over 3 m. The presence of this species was already reported by Pedrotti and Gafta (1996), but the dendrometric measurements are reported here for the first time. This residual example grows on a cultivated, mowed terrace close to fragments of a *Salicetum albae* along the ditch. This species was previously more common in the study area, grew mainly beyond the valley bottom and probably occurred at one time along ditches and brooks, extending out onto cooler clayey and arenaceous soils slopes, with shallow groundwater. This situation is also seen with taxa such as *Ulmus*, *Carpinus betulus*, *Prunus avium*, *Tilia* and *Fraxinus excelsior*, which are still present in sporadic populations now mixed with the *Quercus pubescens* that has remained as substitute vegetation. On the other hand, this oak could be mixed with *Salix alba* on rivers terraces, now attributable to the *Salicetum albae*.

The largest individual tree in the S. Luca group measures 3.54 m in circumference, 16 m in height and has a crown diameter of 12 m (coordinates: 43° 7′ 7.60″ N, 13° 4′ 57.54″ E, at 417 m). Spadoni (1826–1828) cites two large specimens under the name *Q. racemosa* Willd., which can no longer be found: one was in the mountains of Vestignano in Camerino and the other was in those of Chiggiano, Villetta San Severino. He measured the trunk circumferences himself between 1813 and 1815 and recorded the values as 26 and 27 palms (i.e. both between about 7 and 8 m). In addition, he also indicated the presence of this species within the woods of San Maroto (see also Reali 1871–1876) and most others near Fabriano, including Isola, Cantìa and Torre di Cecchino (most no longer able to be confirmed; only a few, extremely rare, scattered specimens still exist in the Fabrianese, along the waterways). One tree with trunk circumference of 2 m, height of 17 m and crown diameter of 11.5 m, grows near the Abbadia di Fiastra, Urbisaglia. The big English oak closest but outside the study area is in Filottrano (Ancona), with a circumference of 4.4 m and a height of 23 m. Two other noteworthy examples are in Foligno (Perugia), Località Belfiore, via Innamorato, with a circumference of 3.77 m and height of 20 m; the other is in Gubbio (Perugia), Località Piaggiola, Via Frate Lupo, with a circumference of 4.5 m and height of 20 m. For the English oak, various hybrids or intermediate forms have been reported over time because of the variability of the forms. These include *Q.* x *thellungii* A. Camus 1939, which should be a multi-species hybrid of *Q. pubescens* x *Q. robur* x *Q. petraea* that can be used as a general name for the intermediaries of *Q. robur*. The phenotype found in the study area is non-pubescent or has very little pubescence on the underside of leaves and thus is more similar to forms occurring outside Italy, such as in France, Poland and Romania (personal observations) but not at other Mediterranean sites. This has often led to the hypothesis of hybrid forms with *Q. pubescens*, but they should all be considered variants of the same species, in view of the ongoing debate about possible hybridization between the two species (see also Dupouey and Badeau 1993) and the impossibility of crossing with the two other species.

Quercus ilex [Holm Oak or Holly Oak] is *leccio* or *elce* in Italian. In the study area this species occurs in populations on calcareous cliffs and gorges, under extrazonal conditions, and always as coppice. Since these oaks often grow in xeric situations on rocky, nutrient-poor substrates and are subjected to coppicing, they are usually short and shrubby. According to Marchesoni (1958), these relict strips of vegetation also grow in the montane belt, in special rocky areas in the cold *lauretum* in which some accompanying species, such as *Arbutus unedo* and *Pistacia lentiscus*, are always missing. Some nuclei of holm oak reach the altitude of the beech, up to 1,500 m a.s.l., and in some cases are mixed in the *Fagus sylvatica* woods. There are no large examples of *Q. ilex* in the study area, but in the Rocca dei Borgia city park in Camerino there is an allée of large holm-oak trees, two of which have a circumference of 4.05 and 4.10 m, height of 12 m and crowns of about 8 m (repeatedly pruned and pollarded over the years). These were measured and are reported here for the first time (coordinates: 43° 7′ 51.97″ N, 13° 3′ 49.64″ E, at 641 m; and 43° 7′ 51.47″ N, 13° 3′ 50.15″ E, at 638 m). These trees are all about the same age, but the growth of trunk circumference varies greatly. The garden was designed by Luigi Napoleone (Bittarelli 1978), then head gardener of the University of Camerino Botanical Garden. The trees were probably planted between 1924 and 1927, when the monument to soldiers killed in World War I was installed and the public garden was created (see also: Pedrotti 2009; Remiddi 1989), in an area that until then had been a cattle market *Foro boario*. According to testimonies of some elderly local people, these oaks were transplanted by a local worker, Agostino Impecora, when they were about 10 years old, from the nearby holm-oak wood of Roccamattea, where today, however, there are no holm oaks of similar dimensions. Another noteworthy holm-oak wood in the study area is in the park of the Abbadia di Fiastra estate, in the municipality of Urbisaglia (Macerata); an example there has a trunk circumference of 4.4 m. Another large holm oak is also present there, with a trunk circumference of 3.5 m, height of 26 m and average crown diameter of 21 m; the last big one is in the courtyard of the monks. With a trunk circumference of 4.2 m. All of these are cultivated trees in gardens.

Q. suber [cork oak] is *sughera* in Italian. It is another sclerophyllous oak, described by Spadoni (1826–1828) with two examples in Urbisaglia (Macerata), in the Abbadia di Fiastra, and another one in Roti (Macerata), on Monte San Vicino; there were also others in the area of Urbino and four examples near Ascoli Piceno. Today there is only one large example near the Abbadia di Fiastra, Urbisaglia, with a circumference of 4.1 m, height of 22.5 m, and crown circumference of 18.85 m. The tree is still standing in the park of the abbey villa and in the past sometimes was confused as *Q. x crenata*. In any case, it should be considered an extrazonal example, probably planted there in 1780; 8 years ago Bongarzoni estimated its age as 210 years, by the resitographic method. Another specimen, cited by Reali (1871–1876), was cultivated in a cold-winter climate, in the Botanical Garden of the University of Camerino. Brilli Cattarini and Gubellini (1985) noted that *Q. suber* never grows spontaneously in the Marche but is present only as cultivated examples. This enigmatic presence, in each case, and the current climatic conditions and degree of human impact in the favorable area make it improbable that this species could form its own woods here.

Quercus crenata [Spanish oak, Lucombe oak, Crenate oak] is *cerrosughera* or *pseudosughera* in Italian. This species is cited by Spadoni (1826–1828), with its synonym *Q. pseudo-suber* Willd., in the territory of Fabriano (Ancona) near Località Macchia del Bango, above Cupo. Spadoni (1826–1828) and Reali (1871–1876) both reported some other examples of Spanish oak scattered throughout the mountains of San Maroto, in the area of Camerino, which can no longer be found. This species, often confused in the past because of its hybrid form, is present today in Fiastra (Macerata), at Località Podalla, Monte Frascare (1,020 m), as an tree with a trunk circumference of 1.30 m, a height of 7.65 m and a presumed age of 100 years. Another notable example in the study area is in Serravalle del Chienti (Macerata), at Località Civitella (918 m), with a trunk circumference of 1.7 m, 18 m of height and 9.45 m of crown circumference (presumed age of about 80 years). Other specimens have been found (Ballelli, personal communication 2011) around Camerino, near Sabbieta (about 600 m), including Gualdo and Forca di Castelsantangelo sul Nera, along the road on the edge of the forest (about 1,100 m) and in the forest of Fabriano, above the village Campodonico (about 1,100 m). This species is found sporadically in the woods but does not seem to have the potential to form its own woods.

Quercus frainetto [Hungarian Oak or Italian Oak], is *farnetto* in Italian. Spadoni (1826–1828) reported this species as *Q. apennina* near Fabriano, at Macchia Castiglioni, Montemaggio, near Cacciano and in some woods from Pioraco. Recently this species has not been reported for the Marche and is reported here for the first time, near Camerino. The relevés are mostly characterized by *Q.* x *szechenyana* Borbas 1886, which is an intermediate form between *Q. frainetto* and *Q. pubescens*. The trees occur as: (1) forest trees, near Pontelatrave, on the right bank of the Chienti River (43° 4′ 44.0″ N, 13° 5′ 4.78″E, at 408 m); (2) trees subjected to coppicing in the *macchia*, between Casale and state road "S.S. 250" (43° 6′ 19.39″ N, 13° 2′ 25.33″ E, at 568 m); and (3) forest trees growing in fields near Canepina (43° 9′ 41.32″ N, 13° 3′ 38.79″ E, 359 m), a sample of which is preserved in the herbarium of the University of Camerino (CAME 26335, Unresolved), dated November 2009. In just one case (3), an oak growing in a field seems closer to the species per se, perhaps because of the variability of the species. It would be interesting to study this further through morpho-genetic analyses. Because of variability of forms, various hybrid or intermediate forms with *Q. pubescens* have been reported over time, more or less considered in synonyms. Among these are *Q.* x *szechenyana* Borbas 1886 (= *Q.* x *braunii* Borbas 1887; *Q.* x *topaliae* A. Camus 1939) reported for Hungary, Turkey and SE Europe; and *Q.* x *vulcanica* Borzi, reported for Bosnia, Serbia, Greece, Italy, and Turkey. The example closest to the Hungarian oak, and of large dimensions, is in Canepina, outside Camerino, beside the crossing for Montagnano (site number 3), with a circumference of 3.27 m, height of 13 m and crown diameter of 6 m. Puletti (2010) reports another individual of Italian oak, presumably hybrid with *Q. Cerris*, in Borgo village near Fabriano, on the crossing of the railway line Fabriano-Pergola. In each case these data are useful to indicate a certain past and probably still actual presence of this species in the Region Marche.

7 Final Considerations

The most common oak species found with large dimensions in the study area is *Quercus pubescens*, because the study area falls well within the vegetation range of this species. It is best adapted to the conditions here, both on marly-arenaceous and on calcareous slopes. The potential of this species involves two aspects: the potential of individuals (height, diameter, age) and the potential distribution.

The largest oak is the Downy Oak of Treia (No. 62 in Table 1), which has a trunk circumference of 6.46 m, height of 29.7 m, and estimated age of 450 years. It should be remembered that measurements given in this work normally refer to oaks found in agricultural areas, which in each case may be subject to significant anthropogenic influences.

In terms of potential vegetation, the associations described and known in the study area are related to: *Peucedano cervariae-Quercetum pubescentis*, *Erico arboreae – Quercetum pubescentis* and *Cytiso-Quercetum pubescentis*. The *Peucedano cervariae-Quercetum pubescentis* has the larger range, occurring on marly-arenaceous substrates. Currently such areas are almost entirely under cultivation, with some nuclei of downy oak remaining. In each case, the agricultural and forestry practices have modified the potential development of the trees and other vegetation in this area. The oaks in the study area are much smaller than the largest oaks of Italy or of the world. Their vegetation potential has been undermined as well, and thus the associations described and noted today are for the most part in a degraded state. Past environmental governance had simplified and impoverished the vegetated landscape, including the woodlands. In this regard, it would be absolutely necessary to define some oakwoods as protected areas, in order to restore habitats, stop biodiversity loss, promote diversification of forest production, and analyze better the potentials and stages of evolution up to the maximum natural condition of these formations.

Acknowledgments I would like to thank Professors Bartolomeo Schirone and Gianluca Piovesan (University of Tuscia, Viterbo) for their courtesy and helpfulness in using their equipment; and the collaboration of the personnel of the laboratory of dendrology, Department of Sciences and Technology for Agriculture, Forests, Nature and Energy, where it was possible to conduct the dendrological analyses of *Quercus pubescens*.

References

Ballelli S., Biondi E., Cortini Pedrotti C., Francalancia C., Orsomando E., Pedrotti F., 1981. Il patrimonio vegetale delle Marche. Ancona, Servizio ambiente e urbanistica della Regione Marche.

Ballelli S., Lucarini D., Pedrotti F. 2005. *Catalogo dell'erbario dei Monti Sibillini, di Vittorio Marchesoni*. Braun Blanquetia, 38:1–259.

Bittarelli, A.A., 1978. Camerino, viaggio dentro la Città. Litotip. S. Giuseppe

Brilli Cattarini, A.J.B., Gubellini L., 1985 – *Note di floristica marchigiana: sul supposto indigenato di Quercus suber L. nelle Marche*. Informatore Botanico Italiano 17(1-2-3): 87–89

Capodarca V., 2008. *Alberi monumentali delle Marche*. Macerata, Roberto Scocco Ed.

Guidi G., 2012. *Le formazioni vegetali monumentali delle Marche*. C.F. S.-Corpo Forestale dello Stato e Regione Marche. Urbania, Arti grafiche Stibu

Chiarugi A., 1959. *La selezione genetica degli alberi nel quadro della protezione della natura*. Suppl. Ricerca Scientifica, 29: 103–106.

Cianfaglione K., 2010. *Chi può contribuire a salvare il bosco?*. In: Andrei E. (coord.), Pădurea Plămânul Planetei - Lucrările simpozionului. Craiova (Romania), Info Ed.: 5–7

Cianfaglione K., 2011. *Il bosco e i paesaggi culturali*. In: Pignatti S., Aree protette e ricerca scientifica - Atti del Convegno dell'Accademia dei Lincei (Roma, 16 Ottobre 2009): 127–134. Pisa, ETS Ed

Cianfaglione K., 2012. Impact of extreme weather events on functional traits in young specimens of Quercus pubescens of different geographical origin. Università di Camerino, Tesi di laurea sperimentale in Ecologia.

Marchesoni V., 1957. *Storia climatico-forestale dell'Appennino umbro-marchigiano*. Ann. Bot., 25(3):1–39.

Marchesoni V., 1958. *Importanza del Pino nero, dell'Abete, del Tasso e dell'Agrifoglio nella storia climatico forestale dell'Appennino Umbro-marchigiano*. Monti e Boschi IX: 535–541

Marchesoni V., 1959. *Importanza del fattore storico-climatico e dell'azione antropica nell'evoluzione della vegetazione forestale dell'Appennino Umbro marchigiano*. Firenze, Annali Acc. It. Sc. For., VIII: 326–343

Dupouey J. L., Badeau V., 1993. *Morphological variability of oaks (Quercus robur L, Quercus petraea (Matt) Liebl, Quercus pubescens Willd) in northeastern France: preliminary results*. Ann. For. Sci. 50: 35–40.

Paganelli A., 1982. Histoire paleobotanique. In: Guide itineraire excursion internat. Phytosociologie Italie centrale (2-11 julliet 1982). Camerino: 39–74

Pedrotti F., 1969. *Introduzione alla vegetazione dell'Appennino centrale*. Mitteil ostalp.-din. pflanzensoz. Arbeitsgem., 9:21–57

Pedrotti F., 2009. *I prefetti dell'Orto Botanico*. In: Pedrotti et al.; L'Orto botanico "Carmela Cortini" dell'Università di Camerino. Trento, Temi Ed.: 269–309

Pedrotti F., Gafta D., 1996. *Ecologia delle foreste ripariali e paludose dell'Italia*. L'Uomo e l'Ambiente, Camerino, 23:1–163.

Pedrotti F., Sanesi G., 1969. *Resoconto delle escursioni sull'Appennino Umbro-Marchigiano (25-27 giugno 1968)*. Mitt. ostalp. - din. pflanzensoz. Arbeitsgem., 9: 365–388.

Provincia di Macerata, 2004. *Alberi custodi del tempo*. Piediripa di Macerata, litografia Biemmegraf

Puletti E., 2010. *Bisogna salvare quella quercia. Si trova al Borgo ed è un ibrido naturale particolarmente interessante*. L'Azione (Fabriano-Matelica), 6 novembre, 42 (XCIX): 7

Reali A., 1871-76. Gli alberi e gli arbusti del circondario e dell'Appennino camerte. Borgarelli, Camerino

Remiddi G., 1989. *Il parco sulla Rocca Borgesca di Camerino*. In: Atti dell'incontro "L'Orto botanico e il verde di Camerino", (Camerino, 7 maggio 1988). L'Uomo e l'Ambiente, 11:71–80

Spadoni P., 1826-28. Xilologia picena applicata alle arti. Tomo II, Macerata, presso Antonio Cortesi.

Wellstein C., Cianfaglione K., (in press). Impact of extreme drought and warming on survival and growth characteristics of different provenances of juvenile Quercus pubescens Willd. Folia Geobotanica.

Chorology and Phytosociology of Sessile Oak [*Quercus petraea* (Mattuschka) Liebl.] in Trentino-Alto Adige (East-Central Alps) of Northern Italy

Franco Pedrotti

Abstract

Sessile oak (*Quercus petraea*) in Trentino-Alto Adige (east-central Alps, northern Italy) forms the *Luzulo niveae-Quercetum petraeae* association, which develops between 200 and 1,300 m above sea level on siliceous substrates (granites, porphyries, and gneiss). This association occurs in three sectors: pre-Alpine (hygric-pluvial continentality below 45°), Alpine (index between 40° and 66°) and endo-Alpine (index above 52°). The *Quercus petraea* series [*Luzulo niveae-Querceto petraeae* sigmetum] is composed of forests (*Luzulo niveae-Quercetum petraeae*), xeric meadows (*Stipo-Seselietum variae*, *Festuco-Caricetum supinae* and *Tunico-Koelerietum gracilis*), heaths (*Chamaecytiso hirsuti-Callunetum*) and mantles (*Pteridio-Sarothamnetum* and *Corylo-Populetum avellanae*).

Keywords

Central Alps • *Luzulo niveae-Quercetum petraeae* • *Quercus petraea* • *Series of Quercus petraea* • Sessile oak • Trentino-Alto Adige

1 Introduction

Sessile oak [*Quercus petraea* (Mattuschka) Liebl.] occurs throughout the east-central Alps (northern Italy), in the regions Lombardy, Trentino-Alto Adige, Veneto and Friuli-Venezia Giulia (Pignatti 1982). In these areas it contributes to forming the following associations: *Phyteumato betonicifolii-Quercetum petraeae* and *Cytiso nigricantis-Quercetum petraeae* in Lombardy; *Luzulo niveae-Quercetum petraeae* in Trentino-Alto Adige; and *Melampyro vulgati-Quercetum petraeae*, *Carici umbrosae-Quercetum petraeae* and *Seslerio autumnalis-Quercetum petraeae* in Veneto and Friuli-Venezia Giulia (Verde et al. 2010; Pedrotti 2010; Buffa et al. 2010; Poldini and Vidali 2010). The purpose of this contribution is to examine the chorology and phytosociology of *Quercus petraea* (Mattuschka) Liebl. in Trentino-Alto Adige.

2 Study Area

The *Regione* Trentino-Alto Adige is located between 45° 40′ and 47° 6′ N latitude and between 10° 23′ and 12° 28′ E longitude, in the east-central Alps. It includes the hydrographic basins of the Chiese, Sarca, Adige and Brenta Rivers. The lowest altitude is at Riva del Garda (67 m) and the highest is the Ortles peak (3,905 m).

This territory can be divided into three sectors based on pluvial and hydric continentality indices: pre-Alpine (index below 45°), Alpine (index between 40° and 66°) and endo-Alpine (index above 52°). The bioclimatic belts are the following: lower and upper meso-temperate, lower and upper supra-temperate, oro-temperate, cryo-orotemperate and nival (Gafta and Pedrotti 1998).

3 Chorology

In Trentino-Alto Adige, *Quercus petraea* is widespread in the Val Venosta, Valle dell'Adige and its lateral valleys (Passiria, Sarentina, Isarco, Pusteria, Tures, Cembra,

---

F. Pedrotti (✉)
University of Camerino, Via Pontoni 5, 62032 Camerino, Marche, Italy
e-mail: franco.pedrotti@unicam.it

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*,
Geobotany Studies, DOI 10.1007/978-3-319-01261-2_10,

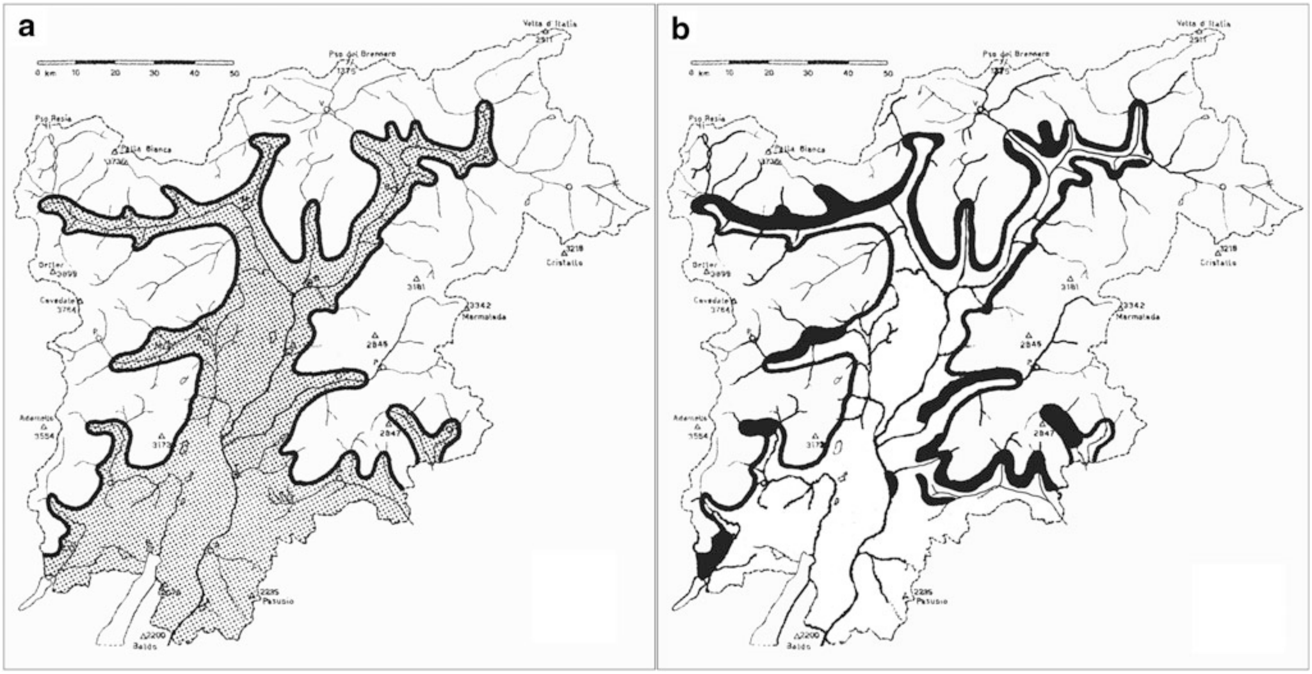


Fig. 1 (**a**) Northern distribution limit of *Quercus petraea* in Trentino-Alto Adige; (**b**) woods of *Luzulo niveae – Quercetum petraeae* in Trentino-Alto Adige

Fersina, Non, Sole), in Valsugana, the Valle di Canal S. Bovo, the Val di Genova and the Valle del Chiese (Fig. 1). The species prevails on sites with siliceous substrates but is also common on carbonate substrates (Marchesoni, in Pedrotti 1995). The altitudinal limits of distribution are between 200 m at Gocciadoro (near Trento, Val d'Adige) and 1,300 m at Monte Celentino (Val di Sole).

The bioclimatic thresholds that restrict the natural spreading of *Quercus petraea* are the sum of positive average monthly temperatures ≥855°C and the average minimum temperature of the coldest month ≥−9°C. In comparison, these values are respectively ≥1,000°C and ≥−8°C for downy oak (*Quercus pubescens*), and ≥1,450°C and ≥−2.5°C for Holm oak (*Quercus ilex*) (Gafta and Pedrotti 1998).

The area of *Quercus petraea* in Trentino-Alto Adige extends into all three phytoclimatic sectors, the pre-Alpine, Alpine and endo-Alpine.

4 Phytosociology

Oakwoods of *Quercus petraea* in Trentino-Alto Adige belong, phytosociologically, to the association *Luzulo niveae-Quercetum petraeae* Gafta et Pedrotti 1999, the alliance *Quercion petraeae* Zolyomi et Jakucs ex Jakucs 1960, the order *Quercetalia pubescenti-sessiliflorae* Klika 1933, and the class *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959.

In these oakwoods, *Quercus petraea* is almost always dominant, while *Fraxinus ornus*, *Tilia cordata*, *Prunus avium* and sometimes *Fagus sylvatica* (Table 1) appear with lower frequency. The herb layer is characterized by the abundance of graminoid species (*Luzula nivea*, *Poa nemoralis*, *Festuca heterophylla*) and species of *Hieracium* (*H. sabaudum*, *H. sylvaticum*, *H. racemosum*, *H. laevigatum*). Other contributors are transgressive species of the *Fagetalia* and *Quercetalia roboris* orders. Species of the *Fagetalia* reflect the intermediate altitudinal position of the *Luzulo niveae-Quercetum petraeae* between the hornbeam (*Carpinus*) woods below and the beech (*Fagus*) woods above; the presence of *Quercetalia* species is conditioned by the acidic substrate, which also favors some species of the *Vaccinio-Piceetalia* order.

Two surveys conducted in the Valle del Chiese (Table 1) revealed *Teucrium scorodonia*, which is absent in all the other surveys. For this reason, these two surveys show a certain affinity with the *Phyteumato betonicifolii-Quercetum petraeae* of Lombardy, where *Teucrium scorodonia* is very frequent. It should be remembered that *Teucrium scorodonia* is a west-European species (subatlantic), reported by Marchesoni (1947) for six locations of Trentino, including one in the Valle del Chiese and two in Valsugana, in the zone with presence of *Quercus petraea*.

Table 1 Classes of presence in *Luzulo-Quercetum petraeae* (seven records)

Sp. of all. (Quercion petraeae), ord. (Quercetalia pubescenti-sessiliflorae) and cl. (Quercetea pubescentis)	
Quercus petraea (three)	V
Quercus petraea (shrub)	V
Fraxinus ornus (three)	III
Lathyrus niger	III
Hypericum montanum	I
Sorbus torminalis (three)	I
Melittis melissophyllum	I
Tanacetum corymbosum	I
Ostrya carpinifolia (shrub)	I
Coronilla emerus	I
Quercus cerris (three)	I
Quercus cerris (shrub)	I
Cornus mas	I
Potentilla micrantha	I
Quercus pubescens (shrub)	I
Arabis turrita	I
Sp. transgr. of order Quercetalia roboris	
Hieracium sabaudum	IV
Melampyrum pratense ssp. vulgatum	IV
Castanea sativa (three)	II
Hieracium laevigatum	II
Lathyrus montanus	II
Pulmonaria australis	II
Teucrium scorodonia	I
Sp. transgr. of order Fagetalia sylvaticae	
Prunus avium (three)	III
Tilia cordata (three and shrub)	III
Campanula trachelium	II
Fagus sylvatica (three)	II
Fagus sylvatica (shrub)	II
Dryopteris filix-mas	II
Fraxinus excelsior (three and shrub)	II
Salvia glutinosa	II
Laburnum alpinum	II
Vinca minor	II
Neottia nidus-avis	II
Epilobium montanum	II
Veronica urticifolia	II
Acer pesudoplatantus (three)	I
Primula vulgaris	I
Galium laevigatum	I
Prenathes purpurea	I
Polygonatum multiflorum	I
Ribes alpinum	I
Scrophularia nodosa	I
Euphorbia dulcis	I
Daphne mezereum	I
Acer platanoides (three)	I
	I
Sp. transgr. of cl. (Querco-Fagetea)	
Poa nemoralis	
Festuca heterophylla	V
Luzula nivea	V
Viola reichenbachiana	IV
Carex digitata	III
Hedera helix	III
Lonicera xylosteum	II
Melica nutans	II
Acer campestre (three)	II
Malus sylvestris (three)	I
Luzula albida	I
Convallaria majalis	I
Cephalanthera longifolia	I
Melampyrum italicum	I
Ulmus minor (three)	I
Brachypodium sylvaticum	I
Pirus pyraster	I
Aquilegia vulgaris	I
	I
Sp. transgr. of cl. (Rhamno-Prunetea)	
Corylus avellana	
Crataegus monogyna	IV
Ligustrum vulgare	II
Rhamnus catharticus	II
Populus tremula (shrub)	II
Rubus sp.	I
Prunus mahaleb (shrub)	I
Clematis vitalba	I
Berberis vulgaris	I
Tamus communis	I
Euonymus europaeus	I
Viburnum lantana	I
Cornus sanguinea	I
Prunus spinosa	I
	I
Other sp.	
Solidago virgaurea	
Hieracium sylvatium	V
Hieracium racemosum	V
Polypodium vulgre	V
Vincetoxicum hirundinaria	V
Juniperus communis	IV
Sedum maximum	IV
Lembotropis nigricans	IV
Fragaria vesca	IV
Polygonatum odoratum	IV
Silenr nutans	IV
Cruiata glbra	IV
Vaccinium myrtillus	III
Phyteuma betonicifolium	III
Genista tinctoria	III
Carex humilis	III
Sorbus aucuparia	III
Mycelis muralis	III
Genista germanica	III
Platanthera sp.	III
Veronica officinalis	III

(*continued*)

Table 1 (continued)

Calamagrostis arundinacea	III
Chamaecytisus hirsutus	II
Pteridium aquilinum	II
Clinopodium vulgare	II
Teucrium chamaedrys	II
Dianthus seguieri	II
Asplenium adiantum-nigrum	II
Vaccinium vitis-idaea	II
Vicia cassubica	II
Potentilla alba	II
Stachys officinalis	II
Primula veris	II
Digitalis lutea	II
Trifolium medium	II
Maianthemum bifolium	II
Avenella flexuosa	II
Frangula alnus	I
Geranium robertianum	I
Geum urbanum	I
Serratula ticnctoria	I
Moehringia muscosa	I
Astragalus glyciphyllos	I
Peucedanum oreoselinum	I
Hieracium umbellatum	I
Lilium bulbiferum ssp. crocetum	I
Viola hirta	I
Campanula perisicifolia	I
Orthilia secunda	I
Calluna vulgaris	I
Carex montana	I
Athyrium filix-femina	I
Cytisus scoparius	I
Sedum cepaea	I
Cyclamen purpurascens	I
Molinia arundinacea	I
Sorbus aria	I
Juniperus sabina	I
Erica arborea	I
Polygala chamaebuxus	I
Potentilla erecta	I
Orchis maculata	I
Pyrola rotundifolia	I
Lychnis flos-cuculi	I
Lathyrus sylvestris	I
Monotropa hypopytis	I
Peucedanum latifolium	I
Chamaecytisus purpureus	I
Peucedanum cervaria	I
Anthericum ramosum	I
Saxifraga cuneifolia	I
Ribes uva-crispa	I
Carex contigua	I
Oxalis acetosella	I
Brachypodium pinnatum	I
	I

Still in the Valle del Chiese, which is on the border with Lombardy, the oakwoods have mantles formed by the *Pteridio-Sarothamnetum* association, which is common in Lombardy (Verde et al. 2010) but has been reported in Trentino-Alto Adige so far only in the Valle del Chiese.

In Trentino-Alto Adige *Quercus petraea* was also found in other associations, namely: *Fraxino orni-Ostryetum carpinifoliae* (shrub layer) in two surveys done on the Doss Trento and in Ponte Gardena (Braun-Blanquet 1961) and in a survey conducted in the Marocche di Dro (Pedrotti and Minghetti 1994); also in *Salvio glutinosae-Fraxinetum excelsioris* (tree layer) in a survey conducted in the Val di Cembra (Pedrotti and Gafta 1999); and in *Vaccinio vitis-idaeae – Pinetum sylvestris* (shrub layer) in 17 surveys conducted in various locations of Trentino-Alto Adige and in one survey from the high plain of Piné above Trento (Minghetti 2003; Pedrotti 2004).

Quercus petraea (*Luzulo niveae-Quercetum petraeae*) oakwoods are not present everywhere in the distribution area of this species, but only in valleys with the particular geomorphology and lithologic substrate identified above (Fig. 1, part A).

5 Distribution of the Oakwoods (*Luzulo niveae-Quercetum petraeae*)

In the past, *Quercus petraea* formed very extensive oakwoods. Over time they have been reduced progressively for various human purposes, including agriculture, logging, and reforestation with conifers (Scots pine, Norway spruce, European larch). Today these oakwoods are found almost exclusively on very steep, rocky sites, where the geomorphology has limited man's intervention. These are almost always residual coppice forests, very fragmented and of limited extension but of great phytogeographic interest.

The distribution of *Quercus petraea* forests in Trentino-Alto Adige is conditioned by the lithology and the orientation of the valleys. These forests are present above all on siliceous substrates (granites, porphyries, and gneiss) and not on carbonate substrates, where Sessile oak can grow only very subordinately in other associations. Valleys can be oriented north-south, east-west, or obliquely. In north-south valleys the oakwoods grow on both slopes, but only on south-facing slopes in east-west valleys, because of the strong ecological asymmetry. The east-west valleys are the Venosta, Pusteria, Sole, Genova, and Valsugana (in part); east-west valleys are the Isarco (in part), Adige, Chiese, and Canal San Bovo. The following are oriented more obliquely and show intermediate, more complex conditions: Isarco (in part), Cembra, Fiemme, and Valsugana (in part).

In Trentino-Alto Adige, the *Quercus petraea* series corresponds to the *Luzulo niveae-Querceto petraeae* sigmetum, which includes xeric meadows (*Stipo-Seselietum variae*, *Festuco-Caricetum supinae* and *Tunico-Koelerietum gracilis*), heathlands (*Chamaecytiso hirsuti-Callunetum*) and mantles (*Pteridio-Sarothamnetum* and *Corylo-Populetum avellanae*).

In particular, oakwoods are present in the following locations (see also Fig. 1, part B):

- Val Venosta: southern slope from 500 to 950 m; at higher altitudes it follows the belt of xeric pinewoods (*Astragalo-Pinetum sylvestris*). The series is composed of meadows (*Stipo-Seselietum variae* and *Festuco-Caricetum supinae*) and of mantles (*Berberido-Rosetum* and *Corylo-Populetum tremulae*).
- Alta Val Passiria: both slopes up to altitudes of 900–950 m; this is followed by the belt of montane spruce forests (*Luzulo-Piceetum*).
- Bassa Val Passiria: both slopes, at altitudes above the belt of the *Fraxino orni-Ostryetum* variant with *Quercus pubescens*. (A *Fraxino orni-Ostryetum carpinifoliae* variant with *Quercus pubescens* was reported for the Adige Valley by Braun-Blanquet 1961).
- Val d'Adige between Merano and Bolzano: only on the south slope, 800–1,000 m; above this there are acidophilous pinewoods of *Vaccinio vitis-idaeae-Pinetum sylvestris*.
- Val d'Adige south of Trento: there is only one nucleus of oakwoods, today very degraded, on the porphyries of Gocciadoro, at 200–310 m; it is in contact with the *Galio laevigati-Carpinetum betuli*. The series is composed of xeric meadows (*Tunico-Koelerietum gracilis*).
- Val Pusteria: while the potential area for oakwoods is very vast, today only a few residual nuclei remain. The oakwoods reach to the bottom of the Val di Tures (where they are present on both slopes of the north-south valley); at higher altitudes one can find pinewoods (*Antherico liliaginis-Pinetum sylvestris* and *Vaccinio vitis-idaeae-Pinetum sylvestris*) and montane spruce forests (*Luzulo-Piceetum*).
- The high Val d'Isarco: a zone between Bressanone and Fortezza, where, however, the oakwoods develop on lower slopes and do not have Manna Ash (*Fraxinus ornus*) or Hop hornbeam (*Ostrya carpinifolia*). The oakwoods rise to just beyond Fortezza, at 500–550 m; the series is composed of xeric meadows (*Tunico-Koelerietum gracilis*).
- Low Val d'Isarco: between Bolzano and just before Ponte Gardena, on medium slopes, bordered at lower slope positions by the *Fraxino orni-Ostryetum carpinifoliae* and *Quercus pubescens*, and above by acidophilous pinewoods (*Vaccinio vitis-idaeae-Pinetum sylvestris*); the series is composed of xeric meadows (*Tunico-Koelerietum gracilis*).
- The Cembra and Fiemme valleys: the oakwoods occupy the south slope, with southwest exposure, in an intermediate band between the *Fraxino orni-Ostryetum carpinifoliae* variant with *Quercus pubescens* and the pinewoods and sometimes the montane sprucewoods (*Vaccinio vitis-idaeae-Pinetum sylvestris*, *Antherico liliaginis-Pinetum sylvestris* and *Luzulo-Piceetum*); the series is composed of heathlands of *Chamaecytiso hirsuti-Callunetum*.
- Valle del Fersina: high plains of S. Colomba (850–990 m) and Piné (800–1,000 m) and on the slopes below; at the base of the slopes it is in contact with *Galio laevigati-Carpinetum betuli*. The series is composed of heathlands of *Chamaecytiso hirsuti-Callunetum*.
- Valsugana: very widespread on south-facing slopes, where it forms a belt between the *Galio laevigati-Carpinetum betuli* (below) and montane spruce forests (*Luzulo-Piceetum*) above; the series is composed of heathlands of *Chamaecytiso hirsuti-Callunetum*.
- Valle di Canal S. Bovo: on both slopes in an irregular band up to 900–950 m; the upper limit is established by the appearence of montane spruce forests (*Luzulo-Piceetum*).
- Alta Val di Sole (from Mezzana to Ossana), up to m 1,300; above are montane spruce forests (*Luzulo-Piceetum*) and perhaps in some cases also subalpine (*Homogyno-Piceetum*). The series is composed of xeric meadows (*Tunico-Koelerietum gracilis*) and of mantles (*Corylo avellanae-Populetum tremulae*).
- Bassa Val di Sole (from Caldes to Mezzana, including the lower part of the Val di Rabbi): only on south-facing slopes, up to 1,300 m, above which are montane spruce forests (*Luzulo-Piceetum*). The series is composed of xeric meadows (*Tunico-Koelerietum gracilis*) and mantles (*Corylo avellanae-Populetum tremulae*).
- Val di Genova: an irregular band only on south-facing slopes at 850–1,200 m; above this are beech forests and acidophilous pinewoods (*Calamagrostio villosae-Fagetum*, *Calamagrostio villosae-Abietetum albae*).
- Valle del Chiese (between Condino and the Lago d'Idro): only on south-facing slopes, at 500–700 m, on siliceous substrates; oakwoods are absent on north-facing slopes, formed of carbonate substrates. Below the band of oakwoods are hornbeam woods of *Galio laevigati-Carpinetum betuli*; above are beech forests and acidophilous pinewoods (*Luzulo niveae-Fagetum sylvaticae*, *Luzulo niveae-Abietetum albae*). The series is composed of heathlands of *Chamaecytiso hirsuti-Callunetum* and mantles of *Pteridio-Sarothamnetum*.

Based on the data listed, one can observe that the oakwoods (*Luzulo niveae-Quercetum petraeae*) in Trentino-Alto Adige occur normally on slopes between 500 and 1,300 m, except for the nucleus south of Trento (200 m), thus in the colline and montane belts.

The band of *Luzulo niveae-Quercetum petraeae* at lower altitudes, where the substrate permits, is in contact with the *Fraxino orni-Ostryetum carpinifoliae*, with *Quercus pubescens* (on porphyries) and with *Galio laevigati-Carpinetum betuli* (on quartziferous phyllites). The chain-like relationship at higher altitudes can involve four groups of forest associations: pinewoods, beech forests, silver-fir forests and montane spruce forests.

Scots-pine woods can belong to three associations, according to bioclimatic sector: *Astragalo-Pinetum sylvestris* in the endo-Alpine sector (Val Venosta), and *Antherico liliaginis-Pinetum sylvestris* and *Vaccinio vitis-idaeae-Pinetum sylvestris* in the Alpine (Val d'Adige and Valle dell'Isarco) and pre-Alpine sectors (Val di Cembra and Valle del Fersina).

Beech forests and silver-fir forests, which occur only in the Alpine and pre-Alpine sectors, correspond to the *Luzulo niveae-Fagetum sylvaticae*, *Calamagrostio villosae-Fagetum*, *Luzulo niveae-Abietetum albae*, *Calamagrostio villosae-Abietetum albae* associations.

The montane spruce forests, which occur only in the Alpine and endo-Alpine sectors, correspond to *Luzulo-Piceetum.*

References

BRAUN-BLANQUET, J. 1961. *Die inneralpine Trockenvegetation*. Gustav-Fischer-Verlag, Stuttgart.

BUFFA, G.,U. GAMPER, L. GHIRELLI, C. LASEN, D. MION, & G. SBURLINO 2010. Le serie di vegetazione della Regione Veneto. In: *La vegetazione d'Italia*.(C. Blasi, ed.), pp 111–137. Palombi, Roma.

GAFTA, D., & F. PEDROTTI 1998. Fitoclima del Trentino-Alto Adige. *St. Trent. Sc. Nat*., 73:55–111

MARCHESONI, V. 1947. Analisi fitogeografica degli elementi floristici del bacino atesino. III e IV. Elemento subatlantico ed elememto orientale. *Mem. Museo St. Nat. Venezia Tridentina*, VIII(III):1–40.

MINGHETTI, P. 2003. Le pinete a Pinus sylvestris del Trentino-Alto Adige (Alpi Italiane). Tipologia, ecologia e corologia. *Braun-Blanquetia*, 33:1–95.

PEDROTTI, F. 1995. Le osservazioni del Prof. Vittorio Marchesoni sulla corologia di specie arbustive e arboree nella Regione Trentino-Alto Adige. *St. Trent. Sc. Nat*., 70:107–137.

PEDROTTI, F. 2004. Ricerche geobotaniche al Laghestel di Piné (1967–2001). *Braun-Blanquetia*, 35:1–55.

PEDROTTI, F. 2010. Le serie di vegetazione della Regione Trentino-Alto Adige. In: *La vegetazione d'Italia* (C. Blasi, ed.), pp 83–109. Palombi, Roma.

PEDROTTI, F., & D. GAFTA 1999. Sintassonomia e distribuzione di alcuni boschi di caducifoglie nel Trentino-Alto Adige. *Doc. Phytosoc*., XIX:495–508.

PEDROTTI, F., & P. MINGHETTI 1994. Le Marocche di Dro. In: Guida all'escursione della Società Italiana di Fitosociologia in Trentino (1–5 luglio 1994) (F. Pedrotti), pp 29–65. Camerino, Dipartimento Botanica Ecologia.

PIGNATTI, S. 1982. *Flora d'Italia*. Bologna, Edagricole.

POLDINI, L., & M. VIDALI 2010. Le serie di vegetazione della Regione Friuli-Venezia Giulia. In: *La vegetazione d'Italia* (C. Blasi, ed.), pp 139–163. Palombi, Roma.

VERDE, S., S. ASSINI, & C. ANDREIS 2010. Le serie di vegetazione della Regione Lombardia. In: *La vegetazione d'Italia* (C. Blasi, ed.), pp 53–81. Palombi, Roma.

Quercus suber Distribution Revisited

Bartolomeo Schirone, Francesco Spada, Marco Cosimo Simeone, and Federico Vessella

Abstract

The complex evolutionary history of *Quercus suber* is still under debate. Also, data and evidence at the eastern end of the species range are largely incomplete. In this study, historic floras, fossil data, and local toponyms were surveyed and genetic analyses and linguistic research used in order to point towards a previously neglected occurrence of *Q. suber* east of Italy. Such a multidisciplinary approach depicts a scenario in which cork oak survived in the Balkan Peninsula until recently and suggests how *Q. suber* might have been evicted and relegated westward, due to climate changes, ecologic competition and human impact. Our findings also suggest that the differentiation core of *Q. suber* was in a yet unidentified area corresponding to present-day central Europe to southwestern Asia. Radiation occurred during the Middle Miocene, with a later extension into southern Europe, Iberia and North Africa, as documented by samples collected from the late Miocene-early Pliocene. The causes of extinction in the east, however, should be investigated further and may lead to investigations about other species that might have experienced range shifts similar to that of cork oak.

Keywords

Quercus suber • Distribution • East Mediterranean • Etymology • Evolution

1 Introduction

Along with disturbance, habitat loss and fragmentation, climate change is one of the main drivers of terrestrial biotic change. Climate change affects all levels of life, from the individual, population, species, community and ecosystem to the eco-region level (Lepetz et al. 2009). Understanding possible reactions and adaptations of the forest tree species in the future scenarios is a fundamental issue for landscape and biodiversity conservation.

It is generally hard to predict long-term biological responses, as we have little knowledge concerning timeframes between climatic effects and related responses. In fact, to show and understand impact of climate changes on forest biodiversity, it would be essential to monitor individuals/populations/species over a long period, usually spanning several decades, since effects are detectable only after many years (e.g. Yoccoz et al. 2001; Walther et al. 2002). Therefore, it is necessary to approach alternative multispecific, multiscale and multidisciplinary investigations to improve our current knowledge.

Among the most important challenges for forest ecologists and evolutionary biologists, quantifying and monitoring the trends of genetic diversity, interpreting the geographic patterns of population migration have a key role in understanding climate change biome modifications. Genetic

B. Schirone (✉) • M.C. Simeone • F. Vessella
Dipartimento di Scienze e Tecnologie per l'Agricoltura, le Foreste, la Natura e l'Energia (DAFNE), Università degli Studi della Tuscia, Via S. Camillo de Lellis, snc, I-01100 Viterbo, Italy
e-mail: schirone@unitus.it

F. Spada
Dipartimento di Biologia Vegetale, Università degli Studi di Roma "La Sapienza", Piazzale Aldo Moro 5, 00185 Rome, Italy

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_11,

backgrounds may account for species adaptation, and species can react by expanding their distribution or, rather the ultimate threat, getting extinct (Thomas et al. 2004). Therefore, estimating the past and present changes in genetic variation and the accurate definition of a species range through space and time are imperative to predict the trends of biodiversity and to make adjustments to population management and conservation (Parmesan 2006, 2007).

In this view, conservation and characterization of populations in marginal areas of the species distribution should also be considered of high importance (Channel and Lomolino 2000; Petit et al. 2005). Marginal populations might be genetically depauperated as a result of genetic drift or, in contrast, might harbour a significant share of the intra-specific diversity; for instance they could show particular genetic combinations due to adaptation to extreme environmental conditions (Hunter and Hutchinson 1994; Lesica and Allendorf 1995). In addition, marginal stands may reveal interesting signs of distant migration routes and even help identifying large scale shift of a species range in geological times (Lorenzo et al. 2009).

The cork oak (*Quercus suber* L., Fagaceae) is an emblematic sclerophyllous tree, which may represent an ideal model for investigating the effect of historical processes based on its biology and distribution (Hampe and Petit 2007). The species is semi-domesticated, distributed rather continuously along the coasts of the west-central Mediterranean Basin, and the easternmost stands of the species are considered some small enclaves scattered along the Apulian coast (southeastern Italy); its occurrence in the Balkans is historically contradictory and generally not considered (De Philippis 1935 and reference therein).

By combining molecular and palaeoecological data, recent studies indicate that: (1) the present cork oak distribution range was already established during the pre-glacial period; (2) cork-oak genetic diversity is strongly structured across its range and geographical patterns of chloroplast DNA (cpDNA) may date back to the Tertiary (Lumaret et al. 2005; Lopez de Heredia et al. 2007; Magri et al. 2007); (3) cork oak populations share inter-specific genetic components with *Q. ilex* L. and *Q. coccifera* L. (in the west) and with *Q. cerris* L., *Q. trojana* Webb and *Q. ithaburensis* Decne. (in the east) (Jimenez et al. 2004; Simeone et al. 2009).

However, the issue of the *Q. suber* differentiation core has not been assessed fully. A late Oligocene-early Miocene origin in the Iberian peninsula was suggested as the most appropriate explanation, based on the genetic results obtained by Magri et al. (2007), but cork-oak fossil records available to support this hypothesis are scarce and later (late Miocene-Pliocene, see Quézel 1995). On the other hand, almost all other fossil evidence currently reported (cf. Palamarev 1989) would agree with the plausible occurrence of supposed cork-oak precursor(s) in east-central Europe and Asia Minor all through the Oligocene and Miocene. Noteworthy is that this wide region is also where all sister species of the modern cork oak still occur.

Beyond the absence of exhaustive phylogenetic investigations, and the difficulty of conducting palynological studies (the pollen of *Q. suber* is hard to differentiate from that of *Q. cerris*, cf. Mariani Colombo et al. 1983), the weak point in the latter hypothesis is the absence of the cork oak forests in the Eastern Mediterranean.

An East Mediterranean past occurrence of cork oak, with a gradual erosion and survival only in the western regions, would be of great importance for the future management of the species, as it would help clarify the strategies adopted to overcome the climate crisis since the Tertiary, motivating species relationships and identifying past extinction events and migration routes. Furthermore, new insights into the species' centre of origin might be acquired.

The aim of this research is to investigate all available evidence about the occurrence of *Q. suber* in the Eastern Mediterranean Basin, giving new information to enrich the study. Our study focused on the yet neglected distribution of cork oak east of Italy and searched eventual historical occurrence as far east as possible, theoretically assuming a distribution range similar to other sclerophyll oaks, such as *Q. ilex* and *Q. coccifera*, and sister species such as *Q. cerris*, *Q. trojana* and *Q. ithaburensis*. In this context, historic floras, fossil data, linguistic research and local toponyms were surveyed and discussed.

2 Exploring the Value of Words: The Etymology

Linguistic study is essential in the search for possible ancient locations of cork oak outside its present territory, along with examination of historical sources of its range (Schirone et al. 2006). In the Mediterranean region, the basic names traditionally used for cork oak are the Latin *suber* and the Greek φελλόςτΘ (see Appendix 1), even though the original meaning of these terms is not necessarily clear and unequivocal.

The etymology of the name *suber* has been carefully investigated by Schulten (1930), Bertoldi (1947, 1951) and Alessio (1961).[1] This last author highlights the relation between the Latin *suber* and a Greek term σῦφαρ, stressing that the latter cannot be the source of the former, as claimed by many linguists (cf. Vaniček 1877; Walde 1910; Meyer-Lübke 1911; Boisacq 1916; Hofmann 1950; Ernout and Meillet 1951), except Bertoldi (1947). Both terms suggest

---

[1] Very few Authors dealt with this topic. After Alessio (1961) no relevant contribution is known.

their origin from a common source, evolved in the central Mediterranean area, probably Sicily, where indigenous populations used to come in contact with visitors from the East, and later with Greek colonists (Alessio 1961). According to Alessio, this source can be traced back to a basis **sūφar* belonging to a Tyrrhenian linguistic substrate (apparently pre-Indo-European).

Of course the Tyrrhenian linguistic substrate, according to some scholars, might have originated in the East as well, in Anatolia (Heubeck 1961), and only later expanded to westward around the middle of the second millennium BC, if the hypothesis of a linguistic connection between Etruscan, Lemnian (Anatolian) and Caucasian languages is accepted (De Palma 2003; Robertson 2006). This makes the geographical origin of the term σῦφαρ in the West particularly intriguing, since the "Tyrrhenian" languages, represent either widespread persistence of an older, autochthonous Mediterranean substrate or their later westward radiation from an Aegean-Anatolian core area.

From a more remote linguistic antiquity, or from the west, the main range of *Q. suber*, the term σῦφαρ might have spread eastwards, where it melted into the concept "wrinkled" (which was never used for cork but rather used to describe snake skin, the peel of dried figs, and the film that forms on milk before boiling). It apparently did not spread from east to west. The statement of Alessio (1961) seems persuasive and should not require the further insights that the author strives to produce, searching for a trans-Hellenic link to names in use for holm oak (*Q. ilex*) or kermes oak (*Q. coccifera*), through the unrealistic reference to ὕφεαρ, meaning mistletoe (*Viscum album* L.), which grows on πρίνοςτΘ (*Q. coccifera*) but also on other oaks. This etymological construction reveals the remarkable propensity shared by many, often prominent glottologists to misunderstand the principles of assigning names to plants used among the ancients (and therefore missing the real semantic roots of names), based clearly on the type of product or practical use of plants. Any other assessments of different nature, particularly "educated" references or references relying on Linnean taxonomy or on modern analogues, are to be rejected vigorously. So we can assume that the two terms *suber*/σῦφαρ might have designated the material itself, the cork (and subsequently cork oak), essential for the production of floats for fishing nets, and nothing else.

In the Aegean area, the concept of "cork" is expressed by the Greek word φελλόςτΘ, a term of putative Indo-European origin. It is a widespread opinion that this term, possibly related to φλοιόςτΘ (> φελ-jόςτΘ) for bark, might derive from the Indo-European root **bhl-* (**bhel-*), "to inflate", "to blow", shifting to **bhlo-* and **bhle-* and from here to the Greek φλέω, "to swell", "to overflow" (cf Latin *flare*, "to blow") (Alessio 1961; Devoto 1968; Calonghi 1969; Rocci 1974; Pontillo 1993; Κουλάκη 1993).

The study of toponymy related to cork oak needs, therefore, the use of both terms *suber* and φελλόςτΘ.

Some inevitable questions arise. First, following the opinions of some authors that cork oak never grew in Greece, it is puzzling that the inhabitants, who consequently should have known cork only through trade with western Mediterranean countries (where *Q. suber* grows), did not use the imported name σῦφαρ but rather the autochthonous name φελλόςτΘ.

As mentioned above, some scholars (cf. Bertoldi 1947; Alessio 1961) suggest φελλόςτΘ to be simply a synonym of bark, but this is not supported by Pausanias, who writes in 320 BC:

> Τοῦ τάφου δὲ τοῦ Ἐπαμινώνδα μάλιστά που σταδίου μῆκοςτΘ Διὸσἀφέστηκεν ἱερὸν ἐπίκλησιν ΧάρμωνοςτΘ. Ἀρκάδων δὲ ἐν τοῖςτΘ δρυμοῖςτΘ εἰ̓σιν αἱδρῦςτΘ διάφοροι, καὶ τὰςτΘ μὲν πλατυφύλλουςτΘ αὐτῶν,τὰςτΘ δὲ φηγοὺςτΘκαλοῦσιν: αἱ τρίται δὲ ἀραιὸν τὸν φλοιὸν καὶ οὕτω δή τι παρέχονταικοῦφον, στε ἀπ᾽ αὐτοῦ καὶ ἐν θαλάσση ποιοῦνται σημεῖα ἀγκύραιςτΘ καὶδικτύοιςτΘ: ταύτηςτΘ τῆςτΘ δρυὸςτΘ τὸν φλοιὸν ἄλλοι τε Ἰώνων καὶ ρμησιάναξ ὁτὰ ἐλεγεῖα ποιήσαςτΘ φελλὸν νομάζουσιν.
>
> [Just about a stade from the grave of Epaminondas there is a sanctuary of Zeus named Charmon. The oaks in the woods of the Arcadians are of different sorts; some of them are called "broad-leaved" and others "edible oaks." A third kind has a porous bark, which is so light that they actually make from it floats for anchors and nets. The bark of this oak is called "cork" by the Ionians, for example by Hermesianax, the elegiac poet].

It is clear that the two terms φλοιόν (bark) and φελλόν (cork), underlined in the Greek text, are very different in meaning and have been used as such by the author, although they can be traced back to the same root. Over time they could have been used in a semantic path with a result similar to that of the Latin word *cortex* (see ags. cork, kork; sp. corcho; fr. liège from (*cortex-*) *levius*, lighter) (cf. Calonghi 1969; Scardigli and Gervasi 1978).

Pausanias refers to the Ionians. Among the three basic Hellenic nations (Ionians, Eolians, Dorians), the Ionians were the earliest invaders in Pelasgian (pre-Hellenic) Greece, so their idiom was crucial, along with Attic, for the later development of classical Greek.

Now, if we list in chronological order all authors who ever reported the word φελλόςτΘ (Theophrastus, Hesiodus, Licofronide, Pindarus, Aeschylus, and Plato), we date the first quotations of the term back to VIII-VII BC, in the early days of writing in the Greek world, i.e. the time of the more or less legendary Homer, who, on the other hand, apparently never reports the word. Conversely, the word σῦφαρ is first reported much later, by Sophronides of Syracuse (around 430 BC). It was taken up in the following centuries by Callymachus and Lucianus, but not applied to cork.

The Latin word *suber* appears first in Virgilius (70–19 BC) and later in Livius, Plinius, Traianus, Columella, Isidorus, Sidonius, Vitruvius, Horatius, and Servius

Honoratus. The oldest reports are probably to be found in Lucilius (180–102 BC), who uses the word *suberies*, apparently for a type of product (see analogy with *materies*/*materia*), and in Livius himself, who in his *Historiae* refers to the year 211 BC, a *Forum Subertanum*, probably named after the Subertani, a people settled in southern Etruria, close to Viterbo of the day. According to Alessio (1961) and Bertoldi (1947), the word is an ethnic word related to *suber*.

We can therefore infer that, in classical Greek, a completely independent word was in use to describe a light type of bark, as opposed to common bark. We can also infer that both σῦφαρ and *suber*, words presumably "from the West", i.e. from the core area of cork oak, might be words that appeared later than φελλόςτΘ, the word from the east, at least in the literary tradition.

This supports the opinion that Greeks used their own word, apparently independent of any alloctonous influence, only because they had first-hand knowledge of cork and of the cork oak itself; or alternatively, they came in contact with it already during their earlier migrations east of the easternmost range limit of *Q. suber* (20°E, at present).

For these reasons, toponyms related to φελλόςτΘ might be particularly valuable, for example φελλὶνη. Place names which would seem connected to this term occur in Greece and Apulia (SE Italy), where a form of ancient Greek (locally "Griko") has been in use up to our times, spoken by a large and culturally very active linguistic minority. They call the cork *feddò* or *fiddò* locally (cf. Rohlfs 2007).[2] Moreover, north of the river Megerda, in Tunisia, where *Q. suber* grows naturally, there formerly was a location that the Greeks called Φελλίνη. In fact, at present, cork is called *fellîn*(*e*) in Arabic. This assonance might suggest that the Arabs imported the Greek word into North Africa. If not mere assonance, then this is further evidence for the independent status of the word φελλόςτΘ and for a historical link to *Q. suber* in Greek. Meanwhile, we should also search for a reliable North African root for "cork" among the native Berber languages. Local Berber words for cork oak are *ifernan* and *nelfernan*, probably derived from an ancient root **fern* comparable to the Greek πρὶνοςτΘ (cf. *Quercus ilex*) (Alessio 1961).

We might argue that the link between a Hamitic and an Indo-European language is quite hazardous. There is consensus that Berber might be one aspect of the old Mediterranean, non-Indo-European substrate, so the relationship between **fern* and πρὶνοςτΘ is dubious. Nevertheless, the assonance is intriguing. In fact, πρὶνοςτΘ, a word of presumable Indo-European origin, might refer to the concept "to be pointed" or"acorn" or "nut" (Friedrich 1970) and may originally be a morphonym.

Since Berbers relied on an agro-pastoral economy focused mainly on acorns for feeding their cattle, it is likely that, from their point of view, there was no reason to distinguish between *Q. ilex* and *Q. suber*, something which might support the idea of an obscure ancient link between the two words through the acorns or resulting from a common ancestor to be found in the Mediterranean substrate (consider also *sindiane felline*, in note 3).

The first Greek colonies in North Africa and Andalusia, however, were founded by the Ionians long before the Arab invasion and colonization. Thus we can not conclude that Arabic in the early Middle Age might simply have reinforced a local, already existing word. This is especially true since today, in the Maghreb, cork oak is called *ballout* and *kerrouche*, words etymologically much closer to oaks (and acorns) than to cork itself and surprisingly close to the many Indo-European roots for acorns, if we want to ignore the suggestions implicit in the root of the word *kerrouche*[3] (Friedrich 1970).

Still unresolved remains the etymology of *suber*. According to Bertoldi (1947) and Alessio (1961), the root of the word might be sought within a western wing of the Mediterranean linguistic substrate, roughly coincident with the main range of *Q. suber*. Nevertheless, none of these ideas addresses the question of its underlying semantic connections. In the framework of the present study, detection of the etymology of *suber* and φελλόςτΘ might be of minor relevance but can be useful in the solution of toponymical questions.

One initial hypothesis, based on indirect references by Alessio (1961), suggests a link between the basic meaning of a word reported in Etruscan sources, namely *sūpl-*/*sūϕl-* (meaning flute or whistle) and a Latin base **sūfilare*/**sūbilare* (Latin *sibilare* to blow, Italian *zufolare* to play a flute).

If this were confirmed by new evidence, then the semantic link with "to blow" would lead directly to the meaning of the word φλέω. Considering the roots *phl*. . ., *s*..*b*..*l*, *sp*..*r* as

---

[2] Rohlfs (2007) demonstrated at phonetic, structural and grammatical levels, that the griko spoken in Southern Apulia (Salento) is the direct descendant of the ancient Greek, also stating a pronounce more similar to the modern Greek, i.e. Reuchlian, than Erasmian. In conclusion, the griko would be the same of the Hellenic settlers in Salento, thus the hypotheses about a byzantine origin of this dialect has to be rejected. As consequence, toponyms like *Felline* (*Fiddine* in salentine dialect) would derive from Greek (cf. Alessio 1961) instead of the pre-byzantine Latin stratum, for instance *fig*(*u*)*lina*, clay pit.

[3] In North Africa, cork oak and cork are also indicated with other terms. Arab: *sindiane fellini* (Morocco, from sindiyānah = holm oak); *felline*, *fernan*, *fernoun*, *fernana* (Algeria); *fernan fernoun*, *fernana*, *kerrouch* (Tunisia). Berber: *ballaut*, *ferchi*, *fersi*, *iggui* (Anti-Atlas); *fernane*, *dlem*, *chuber* (Rif).

onomatopoeic morphemes (cf. Devoto 1968), whatever their origin is, what is cork if not “swollen” bark? (Fig. 1).

This etymology might be supported by another path of semantic, linguistic and toponymical connections. According to an alternative hypothesis (cf. Alessio 1961), *suber* could be linked to such hydronyms as *Subi* (a river in Iberia), *Subur* (Σούβουρ) a river and settlement in Mauritania, or ΣύβαριςτΘ (a place name in Achaia, at Parnassus, in Greece, and in Magna Graecia). In this case, the shifting of a hydronymic base **sub*- (meaning “river” or “stream”) to a geonymic base like “furrow”, “gorge” or eventually “valley”, could be taken into account (Alessio 1961). The shift of hydronyms into geonyms and vice-versa is claimed by some scholars as a universal semantic link in toponymy and can be applied usefully to this case (see the paradigmatic examples Aventinus, Velinus), as is also suggested in parallel, linguistically related or not related, very ancient families of roots (Spada and Passigli 2006).

Based on these assumptions, the reported place names assumed to be based on water might rather have originated in the geomorphology of the riverbed, and may have been applied to gorges, slopes and, at the end of the semantic path, to ridges and mountains, endorsing an origin of the name *suber*/σῦφαρ in what gives the idea of “protruding” or “swollen”.

Quite misleading is the postulated ecological relation between stony sites and cork oak claimed by Alessio (1961), who surprisingly does not see the connection between swollen bark and protruding (geo-) morphology. This is implicit in the pair of names φελλόςτΘ (cork) and φελλεύςτΘ (“stony ground” or “rocky outcrop”)[4] (Call. Fr. 49, in Rocci 1974). These terms lead us inevitably to address the issue of Mediterranean toponymy, its etymology and its overlapping, entangled patterns of Mediterranean, (pre?-), proto-, and Indo-European substrates, with their highly uncertain phyletic and historical relationships.

After this complicated proposition of circumstantial evidence, it is appropriate to approach again the subject of toponymy related to *Q. suber* and to test whether or not it provides, realistically, at least linguistic evidence for a former occurrence of cork-oak stands further east than its modern eastern range boundary, as speculated earlier.

Most of the Indo-European tree names refer either to the pointed shape of the leaves or to the spherical form of the fruits, including nuts, acorns and drupes. Moreover, the linguistic roots of both organs are very often the same or overlap (Friedrich 1970). These roots are in turn related to forms and show up in the aboriginal description of the landscape as well. We could summarize this, quoting the semantic path from Kern to Kirsch to the root **ker*-, **kar* for mould, mountain, region and earth, indicating, in Indo-European language families, a fruit, its tree and a geonym. The pattern of this semantic sequence, which appears in a wide range of ancient roots, stresses the importance of detecting possible geonyms, that radiated into coronyms and morphonyms or vice-versa, in the assessment of Mediterranean (and non) toponymy.

Fig. 1 The common bark of an adult tree of *Quercus suber* L. still unstripped

Many settlements and geomorphological outcroppings can be traced back to a root *PL- and a huge series of derivatives *Pal-, *Pyl-, *Pel-, *Per-, *Kar-, *Gor-, *Fal-, *Fel-, *Vel, *Vul-, which apparently are geonyms. A quite reasonable origin of this semantic equivalence of human settlement – place (earth), or topographic top to which most of the names of ridges, cliffs, hills in Mediterranean countries can be related, finds a simple paradigm in the German pair Berg/Burg and the Slavonic equivalent Gora/Grad, connecting artificial and natural outcroppings. This root belongs to the ancient Mediterranean substrate, already a form of Pre-Indo-European idiom since the many legacies left in the Indo-European languages. In this light, the link between Berber **fern* and Greek πρὶνοςτΘ also becomes less unrealistic.

---

[4] The difference of semantic value is determined, at the toponomastic level, by the word morphology (Alessio 1961; Pieraccioni 1990; Sivieri and Vivian 2006).

As shown above, the words φλοιόςτΘ (bark), φελλόςτΘ (cork), φελλεύςτΘ (stony ground, rocky outcrop), φλέω (to blow), *suber*/σῦφαρ (swollen?), and the morphemes *phl*, *s..b..l*, *sp..r*, can all be traced back to the root of a morphogeonym describing surface. It is significant to notice that these words with the root *PL- may be related, not only by assonance but also on the basis of the relationship of these words to an inflated, swollen, outcropping morphology. Moving along this logical sequence, we might even venture to say that the term σῦφαρ itself sounds very close to (oro-)coronyms like Iberia (the present-day Iberian peninsula, and formerly also in the Caucasus, cf. Semitic Sephardic); but this may be too speculative.

In synthesis, there is some kind of circumstantial evidence for the recognition of reliable semantic and linguistic links between the outstanding, inflated, wrinkled, furrowed bark of "virgin" cork and ancient morphemes converging into families of prehistorical geonyms indicating corrugated (geo-) morphology, supporting the hypothesis of a more eastern limit of the range of *Q. suber* in prehistoric/protohistoric times.

3 Collecting All Data and Evidence

Data and evidence for the occurrence of *Q. suber* in the eastern Mediterranean region are reported and discussed here.

3.1 Adriatic and Ionian Italy

3.1.1 Abruzzi

No natural occurrence of *Quercus suber* in Abruzzi is recorded at present, but clues to a past presence are given by a description of natural vegetation in the Middle Ages, collected at the Museo Archeologico dell'Abruzzo Bizantino ed Alto Medievale [Museum of the Byzantine and High Middle Ages] in Crecchio, in Chieti Province. Such testimony accounts for the occurrence of cork oak, Aleppo pine, and Carob tree (now absent) in neighbouring valleys. This report is not actually supported by reliable evidence, but two toponyms in Torino di Sangro (Chieti) and close to Crecchio are unambiguous: *Sughero* (GPS X: 959124; Y: 4687729) and *Sùvaro* (X: 955179; Y: 4688363) (Giammarco 1990). These toponyms are in the vicinity of a holm-oak stand where *Quercus crenata* Lam. (*Q. suber x Q. cerris*) also occurs. This last species, even if rare, is reported in several localities of Abruzzi: Pratelle di Fagnano (L'Aquila), San Nicolao (Caramanico, L'Aquila) at 950 m, and Lecceta di Casoli (Chieti) (Pirone 1995).

3.1.2 Molise

The occurrence of cork oak in Molise is restricted to a single individual recorded in Jelsi (Fascia), in cadastral unit no. 324, sheet 6 (GPS X: 487777; Y: 4590265). It is a tree of 250 cm of circumference and an estimated age of 200 years, growing within a private field and protected by the Regional Authority. The naturalness of this tree is not certain, but other young plants and seedlings have been reported in the nearby town of Venafro (Isernia) (see: www.provincia.campobasso.it/ambiente/banca_dati/alberi.htm#ielsi). On the other hand, neither attestations of past cork-oak occurrence nor toponyms can be found in Molise.

3.1.3 Apulia

Cork oak occurs in southern Apulia, in the provinces of Brindisi and Lecce, and covers about 120 ha. Around Brindisi, scattered populations and isolated trees are present in the municipalities of Ostuni, Brindisi, Fasano, San Vito dei Normanni, and San Pancrazio Salentino. These stands are the remnants of wider cork-oak forests, currently fragmented due to agricultural activity. In particular, Fascist land reclamations (1927–1935) and land reforms in the 1950s affected the natural vegetation strongly, including cork-oak forests. At the beginning of the 1930s, wide oak stands were still reported around Brindisi (cf. Musci 1932).

Nowadays small populations and isolated cork-oak trees are also recorded in Lecce, at Torre Rinalda (at the boundary with Brindisi privince), at Masseria Gagliardi (Lecce), Palmariggi, Masseria Pacciana (Gallipoli), and between Uggiano la Chiesa and Otranto. Stands that have disappeared since 1979 were the Bosco Brancasi and Bosco di Casignano, in Brindisi (Beccarisi et al. 2010).

The occurrence of cork oak in Apulia is known since the nineteenth century (cf. Tenore 1831; Marinosci 1870; De Giorgi 1884; Carano 1934; Crivellari 1950; Novembre 1964; Monaci 1994), but the most interesting evidence is given by Adamović (1906), who showed a distribution map of *Q. suber* and *Q. trojana* Webb. (Fig. 2). Here it is possible to assess a significant presence of cork oak in the past, also in the part of Apulia north of Bari. In this way, it is feasible to explain the existence of several toponyms of otherwise ambiguous origin: *Sovereto* (*Suberitum*), *Santa Maria de Suberito*, *. . . in loco Sober*, *grotticella del Sovero*, all of which are close to Terlizzi (north of Bari) (Colella 1941); *Lamie del Sughero* between Ostuni and Locorotondo, *Felluzza* (Oria), and *Masseria Sovereto* (Fasano) in Brindisi province (Alessio 1942; Portale Cartografico Nazionale, PCN, available at http://www.pcn.minambiente.it); and *Felline* (Alliste), *Felloniche* (Castrignano del Capo), and *Surano* in Lecce province (Alessio 1942; Rohlfs 2007).

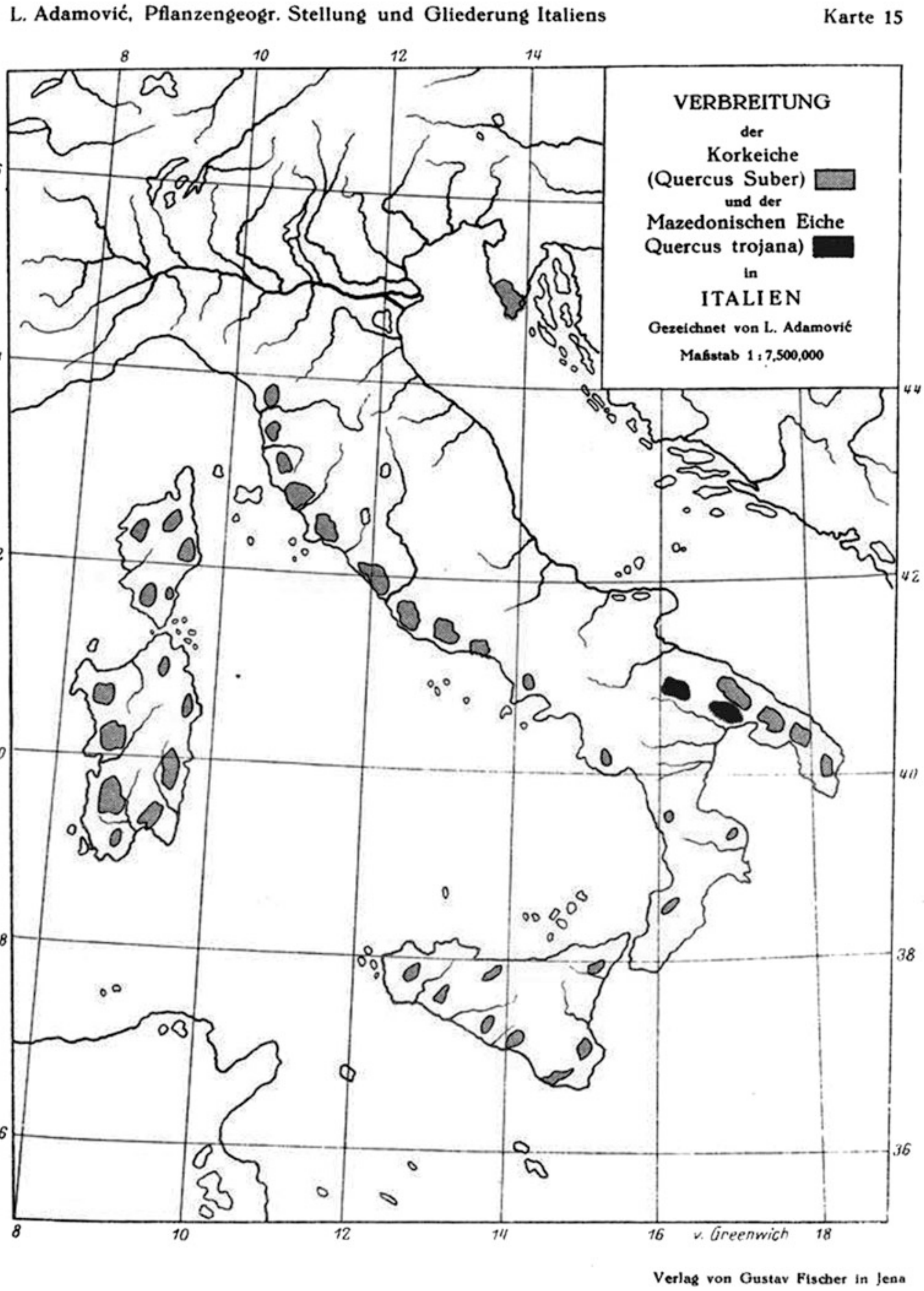


Fig. 2 Distribution map of *Q. suber* and *Q. trojana* Webb in the Italian peninsula, retrieved from Adamović (1906)

Furthermore, the assessment of *Q. suber* occurrence in Apulia since prehistoric time is evidenced by palynological surveys (Di Rita and Magri 2009). These authors found traces of cork-oak pollen sediments of the Alimini Lakes (Lecce) that dated back to 5000 BP, in a period when the main part of Salento was covered by a vegetation dominated by *Quercus* spp. Concerning this ancient presence of cork oak, it is interesting to note that there was apparently a drought crisis between 4350 and 3900 BP, with a resulting regression of the arboreal vegetation for about 300 years, also involving the evergreen oaks (Di Rita and Magri 2009). Other palynological studies concerned Lago Battaglia (Gargano peninsula, Foggia), with stratigraphic sections similar to those of the Alimini Lakes, where pollen samples of *Q. suber*/*Q. cerris* group were found dating from 5950 to 290 BP (Caroli and Caldara 2007).

Finally, it is necessary to mention the cork-oak hybrids *Q. crenata* Lam., which is not present in Apulia except as a single tree near Cassano delle Murge, in inland southern Bari province (Carella 2006); and *Q. morisii* Borzì (*Q. suber x Q. ilex*), whose numerous individuals occur in small, mixed cork oak-holm oak stands in Brindisi province (Scarascia Mugnozza and Schirone 1983).

3.1.4 Basilicata

Cork oak is present in Basilicata currently with only five individuals, in Grottole (Chiaromonte, Potenza province; GPS X: 1112079; Y: 4460097). This reference is particularly interesting because of the nearby occurrence of a small population of *Q. coccifera* ssp. *calliprinos* (Webb) Holmboe (Bianco et al. 1981-82) and some individuals of *Q. trojana* (Spicciarelli 1996), in Senise near Chiaromonte. For these last two species, such populations are the westernmost in peninsular Italy, so, it might be possible to hypothesize that the area surrounding Senise-Chiaromonte was a *refugium* for these *Quercus* species, including cork oak.

Information on the past occurrence of *Q. suber* in this region is available in Rikli (1943), who included Basilicata in the species' eastern distribution but without indicating detailed stand locations. A wider earlier occurrence might be presumed also based on some toponyms, such as *Sùvero* (Carbone, of Potenza; GPS X: 1101666; Y: 4465284) and *Suggarrone* (Matera; X: 1142725; Y: 4528119), although this second might also indicate a sort of "crag" in a local dialect.

3.2 Slovenia, Croatia and Montenegro

3.2.1 Slovenian Kras (Carso) and Istria[5]

The present-day occurrence of *Q. suber* in the Istrian peninsula is recorded at Šijana Forest (Pula), with several individuals of large dimensions (Trinajstić 2005; Simeone et al. 2009) (Fig. 3). Although the natural origin of this Imperial Wood (Kaiserwald) is under debate, this site is the only one mentioned for Istria since the Middle Ages. Biasoletto (1841) and Fiori (1923-29) reported an isolated population of *Q. coccifera* in the Istrian area, and Marchesetti (1930) cited *Q. calliprinos* on Cres Island. It can be hypothesized that the southern Istrian region could have been a *refugium* for cork oak as well, under unfavourable climatic periods (Medail and Diadema 2009).

Fig. 3 Picture from the Šijana Forest (*Pula*) with cork oak trees (property of Marco Cosimo Simeone, 2008)

In the second half of the nineteenth and beginning of the twentieth century, many authors included Istria in the natural distribution range of cork oak, for instance: Kotschy (1862), De Candolle (1864), Parlatore (1867), Borzì (1880), Piccioli (1890), Müller (1900), Schneider (1906), Rikli (1912), Chancerel (1920), Klauber (1920), Pavari (1934), and De Philippis (1935). Other botanists mentioned a corky oak but adopted different scientific names. This is the case of De Visiani (1842), who cited a *Q. ilex* var. *suberosa* sine auct. syn. *Q. suber* L. Also, De Candolle (1864) reported a single tree of *Q. pseudosuber* Santi; Strobl (1872) mentioned it at Šijana Forest, Freyn (1877) at Lusinamore, Munisca, Magran and Veruda forests (Pula: 44° 49′ 56″ N, 13° 51′ 45″ E) and between Stignano and Gallesano (44° 55′ 57″ N, 13° 51′ 49″ E); Grisebach (1875) named some individuals of *Q. pseudosuber* Desf. at Volosko; Richter (1897) cited *Q. pseudosuber* Santi again, in addition to *Q. pseudosuber* var. *aegylopifolia* (Lam.) DC, without site details; and Ascherson and Graebner (1908-13) listed *Q. pseudosúber* sine auct. at Dragonja (Pula: 44° 52′ 20″ N, 13° 51′ 33″ E), Tinjan (45° 12′ 49″ N, 13° 50′ 20″ E), Pazin (45° 14′ 32″ N, 13° 56′ 5″ E), the Mirna river (45° 14′ 49″ N, 13° 37′ 12″ E), Wege (45° 24′ 9″ N, 13° 39′ 33″ E), Lovran (45° 16′ 57″ N, 14° 12′ 12″ E) and Volosko (45° 20′ 54″ N, 14° 18′ 13″ E). Also, Hayek (1927) mentioned *Q. pseudosuber* Santi in Istria and Schneider (1906) more precisely in Pula and Volosko.

---

[5] After the Balkan war in 1992, Yugoslavia was dismembered and the present country boundaries not always match with the previous federal regions. Also for this reason, in this work we will refer to the historic names of the study areas, as usually in biogeography.

Conversely, cork oak is never described for the Kras region, although De Visiani (1842) reported *Q. ilex* var. *suberosa* without indicating a specific site, while Ascherson and Graebner (1908-13) talked about *Q. pseudosùber* sine auct. as occurring at Vremšćica (45° 41′ 6″ N, 14° 3′ 36″ E) and to the west in Italy (Gorizia, Süd-Tirol, Monte Baldo, Garda Lake and Verona province).

Some individuals of *Q. crenata* Lam. (= *Q. pseudosuber* Santi) with regeneration have been observed in Kras, as the last remnants of a wider past presence of this hybrid, along the Reva river (Brkini hilly area: 45° 34′ 26″ N, 13° 57′ 45″ E) (Brus 1996; Brus and Žitnik 2003), in Zagrajec (two individuals at 45° 48′ 41″ N, 13° 41′ 54″ E), Sežana (a single tree at 45° 43′ 6″ N, 13° 52′ 56″E) and Makole (south of Maribor, at 46° 18′ 12″ N, 15° 40′ 31″ E) in eastern Slovenia (Brus, personal observation).

3.2.2 Dalmatia

The Dalmatian islands are interesting because of some cork-oak populations cited by Trinajstić (2005), at Rab (Dundo Forest: 44° 46′ 31″ N, 14° 41′ 23″ E), Korčula (Blato: 42° 55′ 58″ N, 16° 46′ 14″ E) and on the Mljet Islands (42° 44′ 40″ N, 17° 32′ 31″ E).

As with Istria, Dalmatia is often included by past authors in their descriptions of the range of cork oak (cf. De Philippis 1935 and reference therein). Again, different names were used and the exact species observed is often hard to discern. De Visiani (1842) indicated *Q. ilex* var. *suberosa* at Česmina (43° 31′ 23″ N, 16° 28′ 39″ E) and Pelješac (42° 58′ 51″ N, 17° 10′ 4″ E) on the Dalmatian coast. Parlatore (1867) mentioned *Q. suber* in Dalmatia, giving a detailed species description and matching it with the De Visiani's *Q. ilex* var. *suberosa*. Grisebach (1875) considered cork oak as native in Istria and Dalmatia. Poscharsky (1896) distinguished *Q. suber* from *Q. pseudosuber* Desf., the first as occurring in northern Dalmatia, as a shrub, but more common in southern Dalmatia (e.g. at Lesina, Hvar Island: 43° 10′ 24″N, 16° 26′ 22″E) as a tree also in open lands; he considered the second as present with some individuals at Volosko. Hirc (1903-12) identified *Q. suber* (*plutnjak* in Croatian) at Rječina (45° 22′ 46″ N, 14° 26′ 25″ E) and Rab, thus in line with the observations of Trinajstić (2005).

Richter (1897) and Hayek (1927) cited *Q. pseudosuber* Santi, and Ascherson and Graebner (1908-13) referred to *Q. pseudosùber* sine auct. at Dragutina Tomića (45° 20′ 13″ N, 14° 27′ 56″ E). Adamovic (1911) is the most prolific author in terms of site references for Dalmatia, reporting *Q. pseudosuber* (but using together the terms *Korkeiche* and *Črna Česvina*, black holm oak) on the same islands as Trinajstić, in addition to Brac Island (43° 18′ 12″ N, 16° 36′ 3″ E), Pelješac, Zaton (42° 41′ 25″ N, 18° 2′ 5″ E), Konavle (42° 34′ 29″ N, 18° 14′ 7″ E), and Hercegnovli (42° 27′ 49″ N, 18° 31′ 4″ E).

A tree of a presumed cork-oak hybrid, *Q. crenata* or *Q. x viridis* Trin., is reported north of Zadar, at the village Islam Latinski (Jedlowski 1955; Trinajstić 1974; Borzan and Stabentheiner 2002), while a reliable *Q. crenata* has been observed in Rijeka by Martina Temunović (University of Zagreb, personal observation).

3.2.3 Montenegro

Specific detailed references to cork oak in Montenegro are missing, both now and in the past. In 2005 several adult individuals of *Q. crenata* Lam. were identified in the Tara Valley within the Durmitor National Park in a mixed stand on a south exposure at an elevation of 600 m, growing with *Acer campestre* L., *Acer monspessulanum* L., *Carpinus betulus* L., and *Ostrya carpinifolia* Scop. (Daniele Buzi, personal observation). Past testimonies of presumed hybrids of cork oak are available: Nyman (1878-82), Richter (1897), Schneider (1906), Ascherson and Graebner (1908-13), and Hayek (1927) reported the occurrence of *Q. pseudosuber* Santi or simply *Q. pseudosuber* (with no patronymic) in Montenegro, without indicating specific sites. Further information about cork oak occurrence in these regions could be retrieved from toponomastic study, taking into account that cork oak is known as *surva* in the Dalmatian dialect and *šiuri* in Istria.

3.3 Albania

There is no current evidence for the presence of *Q. suber* in Albania (cf. Demiri 1983; Paparisto 1988; Paparisto et al. 1992), but several testimonies were noted in the past. The first references comes from Grisebach (1843), who cited *Q. ilex* var. *suberosa* syn. *Q. suber* L. north of Dukagjin (41°47′15″N, 19°39′14″E), about 25 km in the direction of Rruga Lek Dukagjini (northern Albania) on the western side of the Candavia mountains. Tchihatcheff (1860) referred to *Q. suber* in the country with no site details. Parlatore (1867) described and distinguished accurately both *Q. suber*, associated to *Q. ilex* var. *suberosa* of De Visiani, and *Q. pseudosuber* sine auct. Ørsted (1871) mentioned *Q. suber* in north Albania, in mixed stands with *Q. pubescens*; Grisebach (1875) did too but called it *Q. pseudosuber*. Finally, Hayek (1927) and Horvát (1951) referred generally to *Q. pseudosuber* and *Q. suber* in Albania, with no further details. On the other hand, Von Mannagetta (1901) and Markgraf (1949), two of the most important students of the Albanian flora, never stated the occurrence of cork oak there. Only Richter (1897) and Schneider (1906) referred to *Q. pseudosuber* Santi in Albania, distinguished from *Q. suber*, which was considered absent.

Nowadays, we are only able to confirm a herbarium sample collected in Albania in 1909 by E. Koelher (Fig. 4)

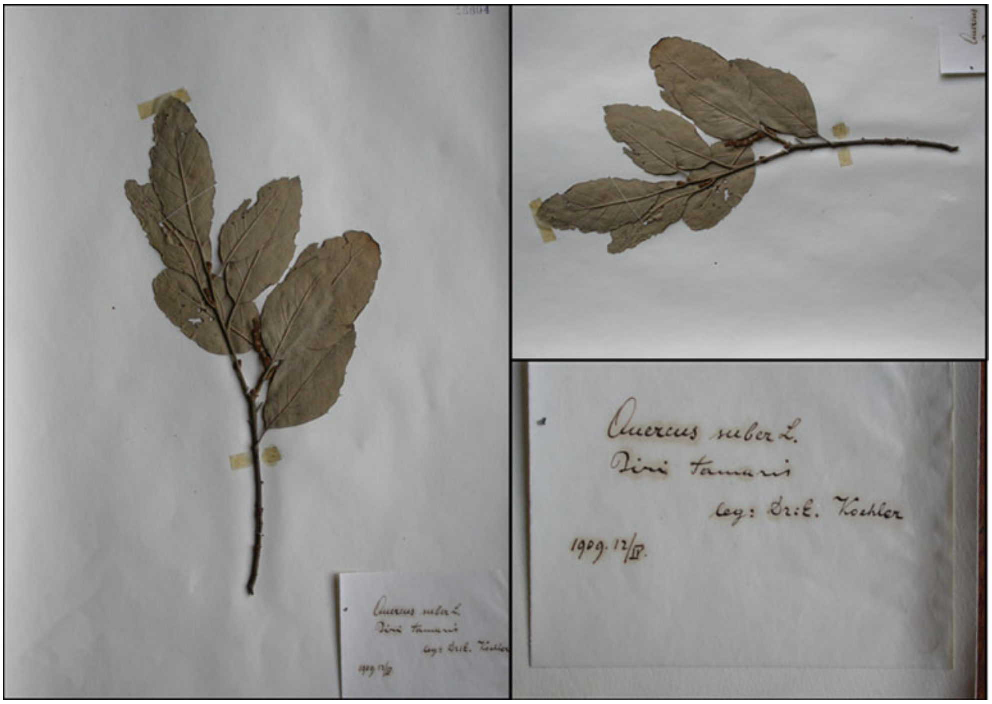


Fig. 4 Herbarium specimen sampled in Albania by E. Koelher and stored at the Botanic Institute of the Bulgarian Academy of Sciences in Sofia (voucher no. SOM16804)

and stored at the Herbarium of the Botanic Institute of the Bulgarian Academy of Sciences Sofia (voucher no. SOM16804). This sample has been examined by Uzunova et al. (1997) for a comparative study on foliar epidermis of extant and fossil Euro-Mediterranean oaks. The label reports the location as Biri Tamaris, not currently identified in Albania; on modern Albanian maps there is a village named Tamarë, near Montenegro, but the geographic position and the surrounding environmental characteristics seem not to allow the occurrence of cork oak. In the same study, Uzunova et al. (1997) compared the Albanian cork-oak sample with those of *Q. crenata* Lam. (*Q. pseudosuber* Santi) from Italy, Istria and Spain, stating that the Albanian sample is different and more similar to some Italian cork-oak provenances. Such results might speak in favour of the past occurrence of *Q. suber* also in Albania.

3.4 Greece

Nowadays only three individuals occur in Greece. One of them is on Ikaria Island (Aegean Sea), planted about 1920 and growing near the village of Monokampi in inland Aghios Kyrikos district (www.nikaria.gr). The other two trees, also planted in the early 1900s, are on Zakynthos and Kerkyra Islands (www.naturazante.com/2011/01/querqus-suber.html). No evidence of natural cork-oak stands has been stated up to now, but many clues to a possible occurrence in the past are evident from fossils, citations and toponyms.

The clearest testimony of an ancient presence of cork oak is from a fossil record found during the archaeological mission in 1968–1978, coordinated by Nicole Lambert, at the Kitsos Cave (2 km north of St. Constantine of Kamariza, Cape Sounion, Attiki), populated by humans in several periods since the Pleistocene. The fossil is a carbonized piece of wood from the Neolithic (ca. 6,900 years BP), which was found together with fossils of *Pinus pinaster* Aiton. (Mavrommatis 1981). This pine has a western Mediterranean distribution now that overlaps partially with that of cork oak, forming also wide mixed forests with it in France and the Iberian Peninsula; it also has a quite similar geographical distribution of the DNA variation patterns (Magri et al. 2007). Since it is hard to imagine such material being imported from Iberia or France during that period, we might hypothesize that both species occurred also in the Eastern Mediterranean Basin in a sub-recent period. For this, it is important to look at the investigation of past climatic and other environmental conditions for pollen and the fossil analyses by Lambert's team, who stated a humid climate with temperate winter in the stratum where the cork-oak fossil was found. Radiocarbon dating places this phase at 4,900 (± 150)–4,200 (±200) years BC, matching the warmest, wettest period of the last postglacial (Atlantic). This scenario is consistent with the environmental requirements of cork oak and of *P. pinaster*, suggesting favourable climatic conditions for these species in the area at least as late as in the fifth millennium BC, a time when local agriculturalists were already affecting the assessment of the natural plant cover. We might therefore infer subrecent anthropogenic destruction of this last refugial outpost of mesophytic trees of the Western Mediterranean geoelement in the Aegean region and pre/proto-historic occurrence of cork oak in Greece.

A detailed investigation of cork-oak references in the Classic Greek literature has been performed by Amigues (1988, 1991), who also translated Theophrastus into French. In the *Historia Plantarum* (c. 320-300 BC), the oldest known Botanic Essay, Theophrastus gave an accurate but ambiguous indication of cork oak in Greece. In fact, the author himself reveals that he wrote about cork oak based only on descriptions by local woodmen.

The first brief mention of cork oak is made in Book I (9, 3), within the list of evergreen and deciduous plants: "Τῶν μὲν ἡμέρων ἀείφυλλα ἐλαία φοῖςτΘιξ . . . τῶν δέ ἀγρίων ἐλάτη πεύκη . . . καὶ ἣν ἈρκάδεςτΘ καλοῦσι φελλόδρυν" ["The domestic species with persistent leaves are the olive, the palm tree. . .; the wild species, the fir, the pine. . . and the one called φελλόδρυςτΘ (cork oak) by the Arcadians."]

In Book III (16, 1) Theophrastus' exact words are: " δὲ καλοσιν οἱ ἈρκάδεςτΘ φελλόδρυν τοιάνδε ἔχει τὴν φύσιν · ςτΘ μὲν ἁπλωςτΘ εἰπεῖ, ἀνὰ μέσον πρίνου καὶ δρυόςτΘ ἐστι, καί ἔνιοί γε ὑπολαμβάνουσιν εἶναι θῆλυν πρινον · διὸ καὶ ὅπου μὴ φύεται πρινοςτΘ τούτῳ χρῶνται πρὸςτΘ τὰςτΘ ἁμάξαςτΘ καὶ τὰ ποιαῦτα, καθάπερ οἱ περὶ Λακεδαίμονα καὶ λείαν. Καλοῦσι δὲ οἵ γε ΔωριεῖςτΘ καὶ ἀρίαν τὸ δένδρον. Ἔστι δὲ μαλακώτερον μὲν καὶ μανότερον τοῦ πρίνου, σκληρότερον δὲ καὶ πυκνότερον τῆςτΘ δρυόςτΘ · καὶ τὸ χρῶμα φλοισθέντοςτΘ τοῦ ξύλου λευκότερον μὲν τοῦ πρίνου, οἰνωπότερον δὲ τῆςτΘ δρυόςτΘ. Τὰ δὲ φύλλα προσέοικε μὲν ἀμφοῖν, ἔχει δὲ μείζω μὲν ςτΘ πρῖνοςτΘ, ἐλάττω δὲ ςτΘ δρῦςτΘ. Καὶ τὸν καρπὸν τοῦ μὲν πρίνου κατὰ μέγεθοςτΘ ἐλάττω, ταῖςτΘ ἐλαχίσταιςτΘ δὲ βαλάνοιςτΘ ἴσον, καὶ γλυκύτερον μὲν τοῦ πρίνου, πικρότερον δὲ τῆςτΘ δρυόςτΘ. Καλοῦσι δέ τινεςτΘ τὸν μέν τοῦ πρίνου καὶ τὸν ταύτηςτΘ καρπὸν ἄκυλον, τὸν δὲ τῆςτΘ δρυὸςτΘ βάλανον. Μήτραν δὲ ἔχει φανερωτέραν ὁ πρῖνοςτΘ. Καὶ ἡ μέν φελλόδρυςτΘ τοιαύτην τινὰ ἔχει φύσιν."

["(The tree) called φελλόδρυςτΘ (cork oak) by the Arcadians has this feature: it is, in brief, something in between πρίνοςτΘ (*Q. coccifera* according to Amigues; collective name for *Q. coccifera* and *Q. ilex* according to Di Bérenger) and δρῦςτΘ (deciduous oak), and somebody considered it a female πρίνοςτΘ; so, where the πρίνοςτΘ does not grow, its wood (of the φελλόδρυςτΘ) is used for making baggage wagons and other similar products, as people do in Laconia and Elide. The Dorians named this tree αρία (*Q. ilex* according to Amigues, and hypothesized with reservations also by Di Bérenger). It is softer and less stiff than πρίνοςτΘ, harder and thicker than δρῦςτΘ; also the color of its wood, after removing the bark, is whiter than πρίνοςτΘ, more purplish than δρῦςτΘ. The leaves are similar to both oaks, but the φελλόδρυςτΘ leaves are larger than πρίνοςτΘ and smaller than δρυςτΘ. The fruit is smaller than πρίνοςτΘ, even though equal to its smallest acorns, sweeter than πρίνοςτΘ, and more bitter than δρῦςτΘ. Somebody used the name άκυλοςτΘ (acorn) for the fruits of πρίνοςτΘ and the species under discussion (φελλόδρυςτΘ), and βαλάνοςτΘ (acorn) for those of δρῦςτΘ (nowadays this distinction is not made). (The φελλόδρυςτΘ) has a more rendered pith than does πρίνοςτΘ. These are more or less the distinctive characters of the φελλόδρυςτΘ."]

Again in Book III (17, 1), Theophrastus mentioned φελλόςτΘ: ""Ἔνια δ' ἰδιώτερα, καθάπερ καὶ ὁ φελλόςτΘ · γίνεται μὲν ἐν Τυρρηνίᾳ, τὸ δὲ δένδρον ἐστὶ στελεχῶδεςτΘ μὲν καὶ λιγόκλαδον, εμηκεςτΘ δ' ἐπιεικῶςτΘ καὶ εὐαυξέςτΘ. Ξύλον ἰσχυρόν, τὸν δὲ φλοιὸν παχὺν σφόδρα καὶ καταρρηγνύμενον σπερ ὁ τῆςτΘ πίτυοςτΘ, πλὴν κατὰ μείζω, τὸ δὲ φύλλον ὅμοιον ταῖςτΘ μελίαιςτΘ παχὺ προμηκέστερον. Οὐκ ἀείφυλλον ἀλλὰ φυλλοβολοῦν. Καρπὸν δὲ αἰεὶ φέρει βαλανηρὸν ὅμοιον τῇ ἀρίᾳ. Περιαιροῦσι δὲ τὸν φλοιὸν καὶ φασι δεῖν πάντα διαιρεῖν, εἰ δὲ μὴ χεῖρον γίνεται τὸ δένδρον. Ἐξαναπληροῦται δὲ πάλιν σχεδὸν ἐν τρισὶν ἔτεσιν."

["Some species are typical, such as φελλόςτΘ; it is original from Tyrrhenia, is monocormic, has few branches, but it is quite big and hairy-chested. It has hard wood, very thick bark that cracks as does that of Aleppo pine, but in larger plates, and the leaves (are) like the ash, thick and quite elongated. (The species has) non-persistent leaves but is deciduous.[6] It produces a fruit similar to the acorn of the αρία. The bark is removed all around (the trunk), and it is said that it needs to be removed lest the tree become worse. It grows (the bark) again in about 3 years."].

Amigues (1988, 1993), after a deep analysis of the Theophrastus essay, in which he focused on the confusion between *Q. suber* and *Q. crenata*, spoke in favour of the presence of cork oak in Greece, in particular in the Peloponnesus, at least by the second century BC, even if cork extraction and utilization were never organized

---

[6] The description of a deciduous cork oak is not to be acritically refuse. Indeed, Camus (1938–1954) mentioned a *Q. suber* var. *caduca* Batt. et Trab., in Algeria near Taourirt-Ighil (Tawrirt Iyil), Kabylie, with "Feuilles se renouvelant complètement au primtemps" (Battendier et Trabut 1888-1890, 1902). On the other side, it has to remark as *Q. afares*, widespread in that area, sometimes could have a corky bark, so the hybrid *Q. suber x Q. afares* is not to be excluded. Worthy of note, is also *Q. ilex* subvar. *caduca* Camus, identified near Saint-Tropez: «Feuilles se renouvelant entièrment au primptemps, à bord dentés, rappellant un peu celles du *Q. x hispanica*» (Camus 1936-1954). Also Daubeny (1865) focused on the evergreen crown of cork oak, affirming that «Commentators have tried to get over this difficulty, by pointing out that there is actually a variety of Cork-tree, which sheds its leaves in April, and which has been observed near Bayonne».

activities. To support her thesis, Amigues (1988) referred other testimonies, such as by Eratosthenes and Pausanias, since the ambivalent use of the terms φελλόςτΘ and φελλόδρυςτΘ by Theophrastus does not allow one to make definitive distinctions between *Q. suber* and *Q. pseudosuber* (*Q. crenata*) and their geographic distribution.[7]

Nevertheless, φελλόδρυςτΘ, identified as *Q. pseudosuber* by several authors (cf. Kavvadas 1956-64), is described by Theophrastus in two paragraphs (I, 9, 3 and III, 16, 1) as evergreen, while φελλόςτΘ (considered the real cork oak by the same authors) is defined as deciduous (III, 17, 1). The Dorian description, though, must also be pointed out, in which φελλόδρυςτΘ was called αρία. To support the conclusion of Amigues about the past occurrence of cork oak in Greece there are also some toponyms in the Peloponnesus cited and located by the same authors: Φελλία (Laconia) and Φελλόη (Achaia) mentioned by Pausanias (*Description of Greece*, III, 20, 3 and VII, 26, 10); and Φελλών reported by Strabo (*Geographica*, VIII, 3, 14). Finally, Amigues considered the ecological and vegetation characteristics of the study areas to be suitable for cork oak, also at present, to back up her hypothesis (Barbero and Quezel 1976).

Di Bérenger (1859-1863)[8] proposed an interpretation of φελλόςτΘ and φελλόδρυςτΘ in Theophrastus' text based on the species' morphology: φελλόςτΘ would be *Q. pseudosuber* and φελλόδρυςτΘ the real *Q. suber*,[9] also considering that cork oak was called φελλόδρυςτΘ by Pliny the Elder (*Naturalis Historia* XVI, 8, 13) and believed to be an *ilex feminea*.[10] This hypothesis contrasts with that suggested by Amigues. Anyway, Di Bérenger accepted the occurrence of cork oak in Greece but suspected that Theophrastus confused *Q. suber*, *Q. pseudosuber* and one of the several varieties of *Q. ilex*, which "not rarely have a corky bark".

Also interesting is the interpretation of Theophrastus' text proposed by Daubeny (1865), where he affirmed that φελλόςτΘ is surely *Q. suber* and *Q. pseudosuber* should be identified with ΑντίφελλοςτΘ (Book III, 8, 4), i.e. the *Haliphloeos* of Pliny the Elder, considered as *Q. cerris* by all other authors with the exception of Di Bérenger (1859-1863), who ascribed it to *Q. infectoria* Oliv. Saint-Lager (1880) following the same conclusion in his botanic nomenclature. Hort (1916), in the English translation of Theophrastus, used φελλόςτΘ for *Q. suber*, while φελλόδρυςτΘ is intended to be *Q. ilex* var. *agrifolia* DC., i.e. *Q. ilex x Q. coccifera* according to Camus (1936-54).

Finally, Thanos (2005) argued that φελλόδρυςτΘ can be recognized as *Q. pseudosuber*, thus supporting Kavvadas (1956-1964) and Amigues, after a misinterpretation of her studies.

Other botanists cited the occurrence of *Q. suber* in Greece in the past two centuries. Fraas (1845), who admitted to not having seen the species directly, considered cork oak as still occurring rarely in Greece, as reported also by Tchihatcheff (1860). Baldacci (1893), based on personal observations, cited *Q. suber* along streets in the valleys around Louros (Pindus mountainside), where it grows under good conditions.

Other references to species that could be cork oak include: De Halácsy (1904) about a *Q. hispanica* Lam. (= *Q. pseudosuber* Santi) "Inter Tschungeri et Malakasi in Pindo tymphaeo, ubi silvas latas aliis speciebus intermixtas consituit" (Haussknecht 1899) and in Arcadia "si *Q. suber* Fraas huc pertineat"; Richter (1897) about *Q. pseudosuber* var. *aegylopifolia* (Lam.) DC in Rhodes; Scnheider (1906) about *Q. pseudosuber* Santi; and Rikli (1943), cited also by Horvát (1951), about the same species in the Pindus region.

At the toponomastic level, we can add other phytonyms to the ones cited by Amigues: Φελλούσα (Tozer 1882), and Φολόη, a name still persisting today for a village and an oak-pine-forested mountain north of Olympia that may well be a linguistic relict of the ancient presence of false cork oak in the Peloponnesus (Thanos 2005). Also, on Andros Island (Cyclades), there is a village called ΦελλόςτΘ (from Ιστορικό Λεξικό τηςτΘ ΑκαδημίαςτΘ Αθηνών).

Finally, a present-day occurrence of *Q. pseudosuber* in western Greece is cited in a paper published in *Amphibion*, a journal edited by the Greek Center for Biotopes (ΝταφηςτΘ 2000).

A full list of the references mentioned in these paragraphs is given in Table 1, while Fig. 5 and the sub-frames 1, 2, 3 show a summary of past and presence testimonies of *Q. suber* and its hybrids on the Adriatic coast, Kras, and in Montenegro, Albania, Greece and Turkey.

3.5 Turkey

Evidence of present-day occurrence of cork oak in Turkey is absent, and scarce or vague in the past. Fraas (1845) did mention cork oak as common in Asia Minor and very rare in

---

[7] It has to be pointed out that in the first translation of Theophrastus from Greek to Latin, Theodorus Gaza (1483) translated φελλόςτΘ with *Q. suber*, while φελλόδρυςτΘ was left in its original form. Daléchamps and Des Moulins (1615) followed a similar criteria, but accurately describing both cork oak (of which he indicated two forms) and φελλόδρυςτΘ (of which he stated five entities).

[8] The essay of Adolfo Di Bérenger (1815–1895) is worthy of particular consideration because the author, Franco-German and acknowledged as founder of the Scuola Forestale Italiana, got a Ph.D. in Philosophy in Wien before engage in forest sciences. For this reasons, he knew Italian, French, German, ancient Greek and Latin, then he interpreted the original texts basing on his knowledge both of languages and forestry.

[9] Di Bérenger followed the same translation proposed by Sprengel (1822), the German translator of Theophrastus.

[10] Despite the dioecism of many plant species, both the ancients and the present rural cultures consider as female the tree that provides a product like fruits, but also bark and cork as well.

Table 1 Summary of past and present evidence of *Q. suber* and its hybrids in the study area

Region	Species	Locality/Area	Reference	Type of evidence[a]
Abruzzi	*Q. suber*	Crecchio (CH)	Museum of the Byzantine and High Middle Age Abruzzi	Informative panel
	””””	Torino di Sangro (CH)	Giammarco 1990	*Sughero*
	””””	Torino di Sangro (CH)	Giammarco 1990	*Sùvaro*
	Q. crenata	Pratelle di Fagnano (AQ)	Pirone 1995	Present occurrence
	””””	Caramanico (AQ)	Pirone 1995	Present occurrence
	””””	Lecceta di Casoli (CH)	Pirone 1995	Present occurrence
Molise	*Q. suber*	Jelsi (CB)	This work	Present occurrence
	””””	Venafro (IS)	Database Isernia Province	Present occurrence
Apulia	*Q. suber*	Ostuni (BR)	Monaci 1994	Present occurrence
	””””	Brindisi (BR)	Monaci 1994	Present occurrence
	””””	Fasano (BR)	Monaci 1994	Present occurrence
	””””	San Vito dei Normanni (BR)	Monaci 1994	Present occurrence
	””””	San Pancrazio Salentino (BR)	Monaci 1994	Present occurrence
	””””	Torre Rinalda (LE)	This work	Present occurrence
	””””	Masseria Gagliardi (LE)	This work	Present occurrence
	””””	Palamriggi (LE)	This work	Present occurrence
	””””	Masseria Pacciana (LE)	This work	Present occurrence
	””””	Uggiano la Chiesa – Otranto (LE)	This work	Present occurrence
	””””	Bosco Brancasi (BR)	Beccarisi et al. 2010	Past occurrence
	””””	Bosco Casignano (BR)	Beccarisi et al. 2010	Past occurrence
	””””	Bari, Brindisi and Lecce Provinces	Tenore 1831; Marinosci 1870 De Giorgi 1884; Adamovic 1906; Carano 1934; Crivellari 1950; Novembre 1964; Monaci 1994	Past occurrence
	””””	Terlizzi (BA)	Colella 1941	*Sovereto*
	””””	Terlizzi (BA)	Colella 1941	*Santa Maria de Suberito*
	””””	Terlizzi (BA)	Colella 1941	*...in loco Sober, grotticella del Sovero*
	””””	Ostuni-Locorotondo (BR)	Alessio 1961	*Lamie del Sughero*
	””””	Oria (BR)	PCN	*Felluzza*
	””””	Fasano (BR)	PCN	*Masseria Sovereto*
	””””	Alliste (LE)	Alessio 1942	*Felline*
	””””	Castrignano del Capo (LE)	Rohlfs 2007	*Felloniche*
	””””	Surano (LE)	PCN	*Surano*
	””””	Alimini Lakes (LE)	Di Rita and Magri 2009	Pollen records
	””””	Battaglia Lake (FG)	Caroli and Caldara 2007	Pollen records
	Q. crenata	Cassano delle Murge (BA)	Carella 2006	Present occurrence
	Q. morisii	Province of Brindisi	Scarascia Mugnozza and Schirone 1983	Present occurrence
Basilicata	*Q. suber*	Chiaromonte (PZ)	This work	Present occurrence
	””””	Lucania	Rikli 1943	Past occurrence
	””””	Carbone (PZ)	PCN	*Sùvero*
	””””	Matera (MT)	PCN	*Suggarrone*
Kras	*Q. ilex* var. *suberosa*	Çarnika	De Visiani 1842	Past occurrence
	Q. pseudosúber	Vremšcića	Ascherson and Graebner 1908–13	Past occurrence
	Q. crenata	Brkini	Brus 1996; Brus and Žitnik 2003	Present occurrence
	””””	Zagrajec	Brus, pers. obs.	Present occurrence
	””””	Sežana	Brus, pers. obs.	Present occurrence
	””””	Makole	Brus, pers. obs.	Present occurrence

(*continued*)

Table 1 (continued)

Region	Species	Locality/Area	Reference	Type of evidence[a]
Istria	*Q. suber*	Šijana Forest (Pula)	Trinajstić 2005	Present occurrence
			Simeone et al 2009	
	’’’’	Istrian peninsula	Kotschy 1862	Past occurrence
			De Candolle 1864	
			Parlatore 1867	
			Grisebach 1875	
			Borzì 1880	
			Piccioli 1890	
			Müller 1900	
			Schneider 1906	
			Rikli 1912	
			Chancerel 1920	
			Klauber 1920	
			Pavari 1934	
			De Philippis 1935	
	Q. ilex var. *suberosa*	Istrian peninsula	De Visiani 1842	Past occurrence
	’’’’	Svida	De Visiani 1842	Past occurrence
	Q. pseudosuber	Istrian peninsula	De Candolle 1864	Past occurrence
			Richter 1897	
			Hayek 1927	
	’’’’	Šijana Forest (Pula)	Strobl 1872	Past occurrence
	’’’’	Lusinamore	Freyn 1877	Past occurrence
	’’’’	Munisca	Freyn 1877	Past occurrence
	’’’’	Magran	Freyn 1877	Past occurrence
	’’’’	Veruda Forest	Freyn 1877	Past occurrence
	’’’’	Stignano-Gallesano	Freyn 1877	Past occurrence
	’’’’	Pula	Schneider 1906	Past occurrence
	’’’’	Volosko	Schneider 1906	Past occurrence
	Q. pseudosúber	Dragonja	Ascherson and Graebner 1908–13	Past occurrence
	’’’’	Tinjan	Ascherson and Graebner 1908–13	Past occurrence
	’’’’	Pazin	Ascherson and Graebner 1908–13	Past occurrence
	’’’’	Mirna River	Ascherson and Graebner 1908–13	Past occurrence
	’’’’	Wege	Ascherson and Graebner 1908–13	Past occurrence
	’’’’	Lovran	Ascherson and Graebner 1908–13	Past occurrence
	’’’’	Volosko	Ascherson and Graebner 1908–13	Past occurrence
	Q. pseudosuber Desf.	Volosko	Grisebach 1875	Past occurrence
	Q. pseudosuber var. *aegylopifolia*	Istrian peninsula	Grisebach 1875	Past occurrence
Dalmatia	*Q. suber*	Dundo Forest (Rab Isl.)	Trinajstić 2005	Present occurrence
	’’’’	Blato (Korčula Isl.)	Trinajstić 2005	Present occurrence
	’’’’	Mljet Island	Trinajstić 2005	Present occurrence
	’’’’	Dalmatia	Kotschy 1862	Past occurrence
			Parlatore 1867	
			Grisebach 1875	
			Borzì 1880	

(*continued*)

Table 1 (continued)

Region	Species	Locality/Area	Reference	Type of evidence[a]
			Piccioli 1890	
			Poscharsky 1896	
			Müller 1900	
			Schneider 1906	
			Rikli 1912	
			Chancerel 1920	
			Klauber 1920	
			Hayek 1927	
			Pavari 1934	
			De Philippis 1935	
	””	Lesina (Hvar Island)	Poscharsky 1896	Past occurrence
	””	Rječina and Rab Island	Hirc 1903–12	Past occurrence
	Q. ilex var. *suberosa*	Česmina	De Visiani 1842	Past occurrence
	””	Pelješac	De Visiani 1842	Past occurrence
	””	Dalmatian Islands	De Visiani 1842	Past occurrence
	Q. pseudosuber	Dalmatia	Richter 1897	Past occurrence
			Hayek 1927	
	””	Rab	Adamovic 1911	Past occurrence
	””	Korčula	Adamovic 1911	Past occurrence
	””	Mljet	Adamovic 1911	Past occurrence
	””	Brac Island	Adamovic 1911	Past occurrence
	””	Pelješac	Adamovic 1911	Past occurrence
	””	Zaton	Adamovic 1911	Past occurrence
	””	Konavle	Adamovic 1911	Past occurrence
	””	Hercegnovli	Adamovic 1911	Past occurrence
	Q. pseudosúber	Dragutina Tomića	Ascherson and Graebner 1908–13	Past occurrence
	Q. crenata,	Islam Latinski (Zadar)	Jedlowski 1955	Present occurrence
	Q. x viridis ?		Trinajstić 1974	
			Borzan and Stabentheiner 2002	
	Q. crenata	Rijeka	Temunović, pers. obs.	Present occurrence
Montenegro	*Q. crenata*	Tara Valley	Buzi, pers. obs.	Present occurrence
	Q. pseudosuber	Montenegro	Nyman 1878–82	Past occurrence
			Richter 1897	
			Schneider 1906	
			Hayek 1927	
	Q. pseudosúber	Montenegro	Ascherson and Graebner 1908–13	Past occurrence
Albania	*Q. suber*	Albania	Tchihatcheff 1860	Past occurrence
			Parlatore 1867	
			Horvat 1951	
	””	North Albania	Ørsted 1871	Past occurrence
	””	Biri Tamaris (?)	collected by Khoeller in 1906	Herbarium Sample
	Q. ilex β Q. suber	Dukagjin	Grisebach 1843	Past occurrence
	Q. pseudosuber	Albania	Grisebach 1843	Past occurrence
			Richter 1897	
			Schneider 1906	
			Hayek 1927	
Greece	*Q. suber*	Ikaria Island	Web Source	Living but planted
	””	Zakynthos Island	Web Source	Living but planted
	””	Kerkyra Island	Web Source	Living but planted
	””	Kitsos Cave (Attiki)	Mavrommatis 1981	Fossil wood
	””	Greece	Tchihatcheff 1860	Past occurrence

(*continued*)

Table 1 (continued)

Region	Species	Locality/Area	Reference	Type of evidence[a]
	’’’’	Arcadia	Fraas 1845	Past occurrence
	’’’’	Louros (Pindus)	Baldacci 1893	Past occurrence
	’’’’	Laconia	Pausanias III BC	*Φελλία*
	’’’’	Achaia	Pausanias III BC	*Φελλόη*
	’’’’	Elis	Strabo, I BC	*Φελλών*
	’’’’	Greece	Tozer 1882	*Φελλούσα*
	’’’’	North of Olimpia	Thanos 2005	*Φολόη*
	’’’’	Andros Island	Historic Dictionary of the Accademy of Athens	*Φελλό*ςτΘ
	Q. pseudosuber	Western Greece	ΝταφήςτΘ 2000	Present occurrence
		Rhodes Island	Schneider 1906	Past occurrence
	’’’’	Pindus	Rikli 1943	Past occurrence
			Horvat 1951	
	’’’’	Thessaly	Hayek 1927	Past occurrence
	’’’’	Greece	Hayek 1927	Past occurrence
	Q. hispanica Lam.	Tschungeri-Malakasi (Pindus)	Haussknecht 1899	Past occurrence
			De Halácsy 1904	
	Q. pseudosuber var. *aegylopifolia*	Rhodes Island	Richter 1897	Past occurrence
	*Φελλόδρυ*ςτΘ – *Φελλό*ςτΘ – *Αλιφλοίο*ςτΘ [b]	Arcadia (Peloponnesus)	Theophrastus, Erathostenes, Pausanias, Pliny the Elder	Past occurrence
Turkey	*Q. suber*	North of Asia Minor (District of Istanbul)	Fraas 1845	Past occurrence
	’’’’	Lycia	Tchihatcheff 1860	
			Elian II BC	*Φελλό*ςτΘ
			Plutarch I BC	
			Strabo I BC	
	’’’’	Lycia	Elian II BC	*Αντίφελλο*ςτΘ
			Plutarch I BC	
			Strabo I BC	
	’’’’	near Lesbo Island	Pliny the Elder I BC	*Phellusa*
	Q. cerris var. *pseudocerris*	Kahramanmaraş Province	Mιhçιoğlu 1942	Present occurrence
			Kayacik 1959	
			Yaltirik 1984	
			Mayer and Aksoy 1986	
	’’’’	Hatay Province	Mιhçιoğlu 1942	Present occurrence
			Kayacik 1959	
			Yaltirik 1984	
			Mayer and Aksoy 1986	

[a] Toponyms are in *italics*;

[b] We preferred to report in this context the original words used by the authors; see the “Data and Evidence” section (Sect. 3) in the main text for detailed argumentation of their meanings

Greece, while Tchihatcheff (1860) considered it rare in Greece and very rare on the northern coasts of Asia Minor (reading his essay, we suppose that he referred to the north-eastern Aegean coast, in the district of Istanbul). The oldest interesting testimonies that might suggest something referable to cork oak are the toponyms of ΦελλόςτΘ and ΑντίφελλοςτΘ in Lycia, cited by Plutarch (*Moralia* 976), Elian (*De natura animalium* 8.5) and Strabo (*Geographica*, 14.3.7). Nowadays, ΑντίφελλοςτΘ is known as Kaş, while ΦελλόςτΘ (Felen in Turkish) is a historic site 12 km far away in inland Kaş. At the same time, the Island of *Phellusa*, near Lesbo according to Pliny the Elder (*Naturalis Historia*, V, 31), was mentioned (Bischoff and Moeller 1829).

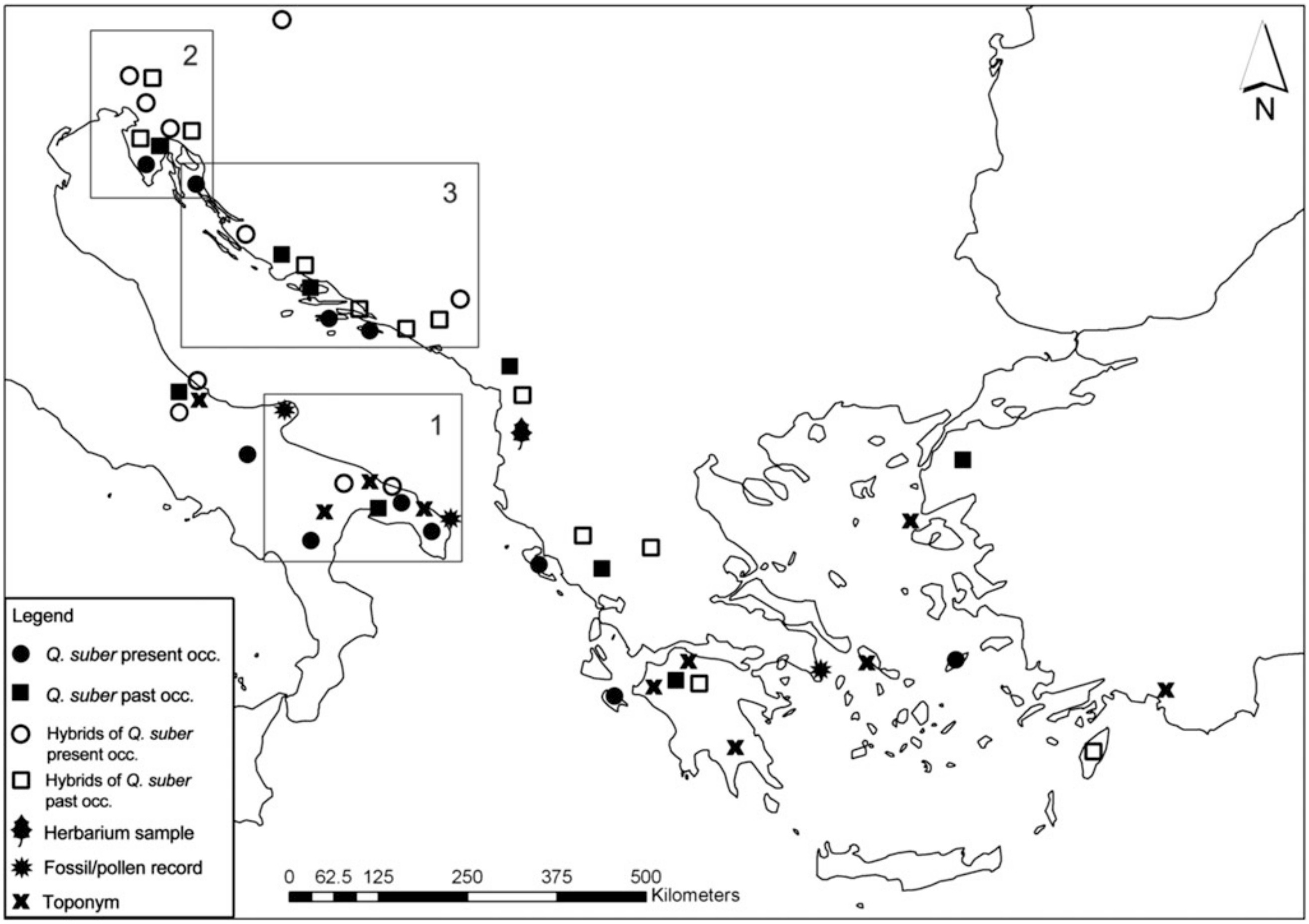


Fig. 5 (continued)

There is, however, also another species in Turkey that should be mentioned in this study, namely *Hatay meşesi*, i.e. *Q. cerris* var. *pseudocerris* Boiss. (now *Q. cerris* var. *cerris*) (Fig. 6). This variety, distinguished by Yaltirik (1984) from *Q. cerris* var. *austriaca*, has deeply lobed leaves; it is widespread throughout the country except in the east and northeast (Yaltirik 1984; Mayer and Aksoy 1986). In Kahramanmaraş and Hatay provinces of southeastern Turkey, *Q. cerris* var. *pseudocerris* has a conspicuous corky bark that is generally thicker than that of other *Quercus* species.[11] Because of this character, and due to scarcity of imported material during World War II, *Q. cerris* var. *pseudocerris* bark was used in Turkey as an alternative to cork from *Q. suber* in order to produce agglomerates for insulation and later for bottle stoppers for the alcoholic drink *raki* (Mıhçıoğlu 1942). Kayacik (1959) mentioned 5,915 trunks stripped in 1942 to obtain 66 t of bark. This was possible because the species had a wide range, with ca. 235,000 ha in the Andirin district, in Kahramanmaraş Province (Mıhçıoğlu 1942). Furthermore, Kayacik also mentioned two small factory farms in Osmaniye, still working in the 1950s. Nowadays there is a new economic interest in the Turkish "pseudo-cork" (Şen et al. 2011a, b).

Although *Q. cerris* var. *pseudocerris* has corky bark, it is easily distinguishable from cork oak by its deciduous *habitus*, its leaves and the cupule shape. We can not exclude a priori that the authors who studied the Turkish flora, except from Tchihatcheff, would have reported the occurrence of this species, based on woodmen testimony or on personal observations of corky pieces of trunks. In any case, the occurrence in Turkey of a variety of *Q. cerris* with a corky bark seems to be of great interest to evolutionary understanding.

---

[11] *Q. cerris* var. *pseudocerris* differs from *Q. cerris* var. *cerris* and var. *austriaca* because of its corky bark and its restricted distribution in Kahramanmaraş and Hatay Provinces, so that it is called Hatay meşesi (oak of Hatay). For these reasons, the deletion of *pseudocerris* category might have been inappropriate, also because the var. *cerris* is still unapproved at international level.

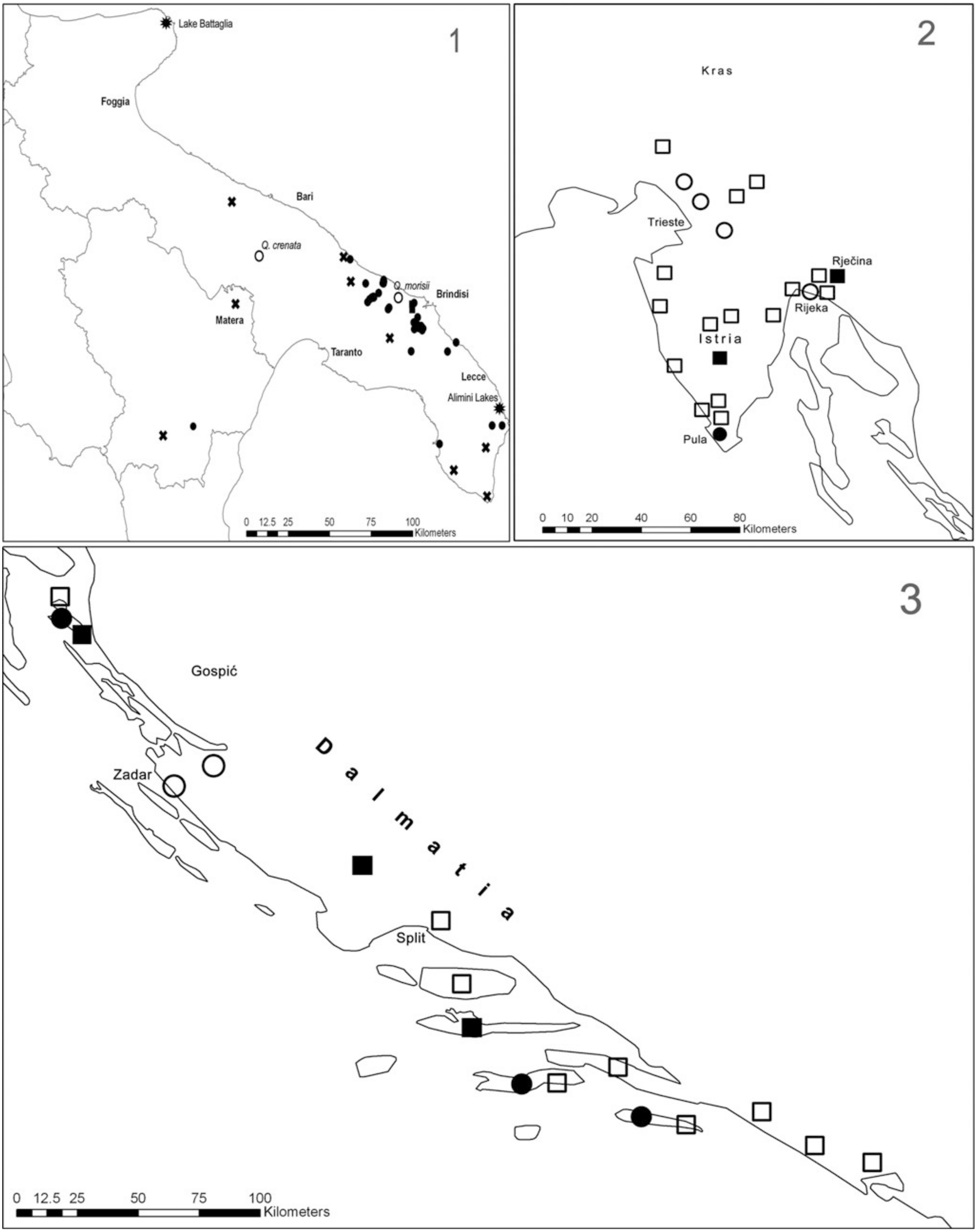


Fig. 5 Summary map of past and present evidence of *Q. suber* and its hybrids in the Eastern Mediterranean Basin, with insets for southeastern Italy (*1*), Istria and Kras (*2*), and Dalmatia (*3*). *Symbol* meanings are the same in all views

Resim. 3. Hatay mesesine ait muhtelif boyuttaki yapraklar
Abb. 3. Die Blätter von Q. pseudo-cerris in verschiedenen Grössen.

Fig. 6 Leaf morphology of several *Q. cerris* var. *pseudocerris* Boiss. samples, retrieved from Kayacik (1959) and optimized digitally

4 Searching for Ancient Proofs: Relationships Between *Q. suber* and Other Species of Subgenus *Cerris*

In order to understand the epiontology of *Q. suber*, it is useful to compare its present distribution with those of other oaks of subgenus *Cerris* (sensu Schwarz 1964). Only a few species belong to this group (13 of 531 actually accepted; Govaerts and Frodin 1998), mainly occurring in the Old World and particularly in Europe. These are: *Q. acutissima* Carruth. (E Asia, deciduous, semi-corky); *Q. afares* Pomel (E Algeria – W Tunisia, deciduous/semi-evergreen, semi-corky); *Q. brantii* Lindl. (E Mediterranean – Asia Minor, deciduous/semi-evergreen); *Q. castaneifolia* Mey. (E Caucasus – N Iran, deciduous); *Q. cerris* L. (SE Europe – Asia Minor, deciduous); *Q. chenii* Nakai (E Asia, deciduous, semi-corky); *Q. crenata* Lam. (Italy – SW France – NE Slovenia – Croatia, semi-evergreen, semi-corky); *Q. ithaburensis* Decne. (E Mediterranean – Asia Minor, semi-evergreen); *Q. libani* Olivier (Asia Minor, deciduous); *Q. look* Kotschy (Israel, deciduous); *Q. trojana* Webb. (E Mediterranean – Asia Minor, deciduous); and *Q. variabilis* Blume (E Asia, deciduous, corky). Some of them have a deciduous/semi-evergreen habit, with a range of variability linked with the local habitat. The present distribution of these species, except those from East Asia, seems to follow an east-west gradient with the number of taxa decreasing westward (Fig. 7). Only *Q. suber* and *Q. afares* occur in the Western Mediterranean Basin. However, investigations of fossil records of Tertiary *Quercus* species performed by Palamarev (1989) and Kovar-Eder et al. (2006) showed a wide presence of the *Q. sosnowskyi* group (e.g. the suggested ancestor of present-day *Q. suber*, including *Q. sosnowskyi* Kolak., *Q. suber-pliocenica* N. Boul., *Q. pseudosuber* Santi foss. and *Q. cerriscarpa* Kolak.) in eastern Europe. This distribution is similar to that of the ancestors of other species of subgenus *Cerris* (cf. Palamarev 1989), as well as to that of *Q. mediterranea* Ung. (probable ancestor of *Q. coccifera* s.l.) (Fig. 8) and *Q. praeilex* Sap. (= *Q. paecursor* Sap., *Q. ilex* L. foss., ancestor of *Q. ilex*), the other two typical evergreen oaks of the Mediterranean forests. *Q. mediterranea* and *Q. praeilex* were also found in Spain and dated back to the Oligocene, while the first evidence of *Q. sosnowskyi* is from the Miocene, all through Europe except the Iberian peninsula.

Such paleobotanical records, together with the distribution of the whole *Cerris* group, make questionable the hypothesis of the differentiation of *Q. suber* in Iberia.

A further interesting evolutionary item of the subgenus *Cerris*, linked to the species distribution, is the habit of the tree crown: eight of 13 species are deciduous, four species show an intermediate deciduous/semi-evergreen habit, and only cork oak is evergreen, although leaf persistence is only about 1 year.

Species distributions do not case these seasonality habits. A progressive westward segregation of species evergreeness in the Mediterranean region can be seen in Fig. 7: the highest concentration of semi-evergreen species is in the central Mediterranean. Two species are of particular interest. *Q. ithaburensis* has its westernmost limit in Apulia and seems to exhibit stable species features; *Q. crenata* is often mentioned along the Adriatic coasts and for Greece, and it involves a highly variable taxon group that does not allow well defined characterization.

Q. crenata certainly deserves a closer look. As reviewed by Cipollini (2008), the first mention of a taxonomic entity afterwards called *Q. crenata* is ascribed to Jean-Baptiste

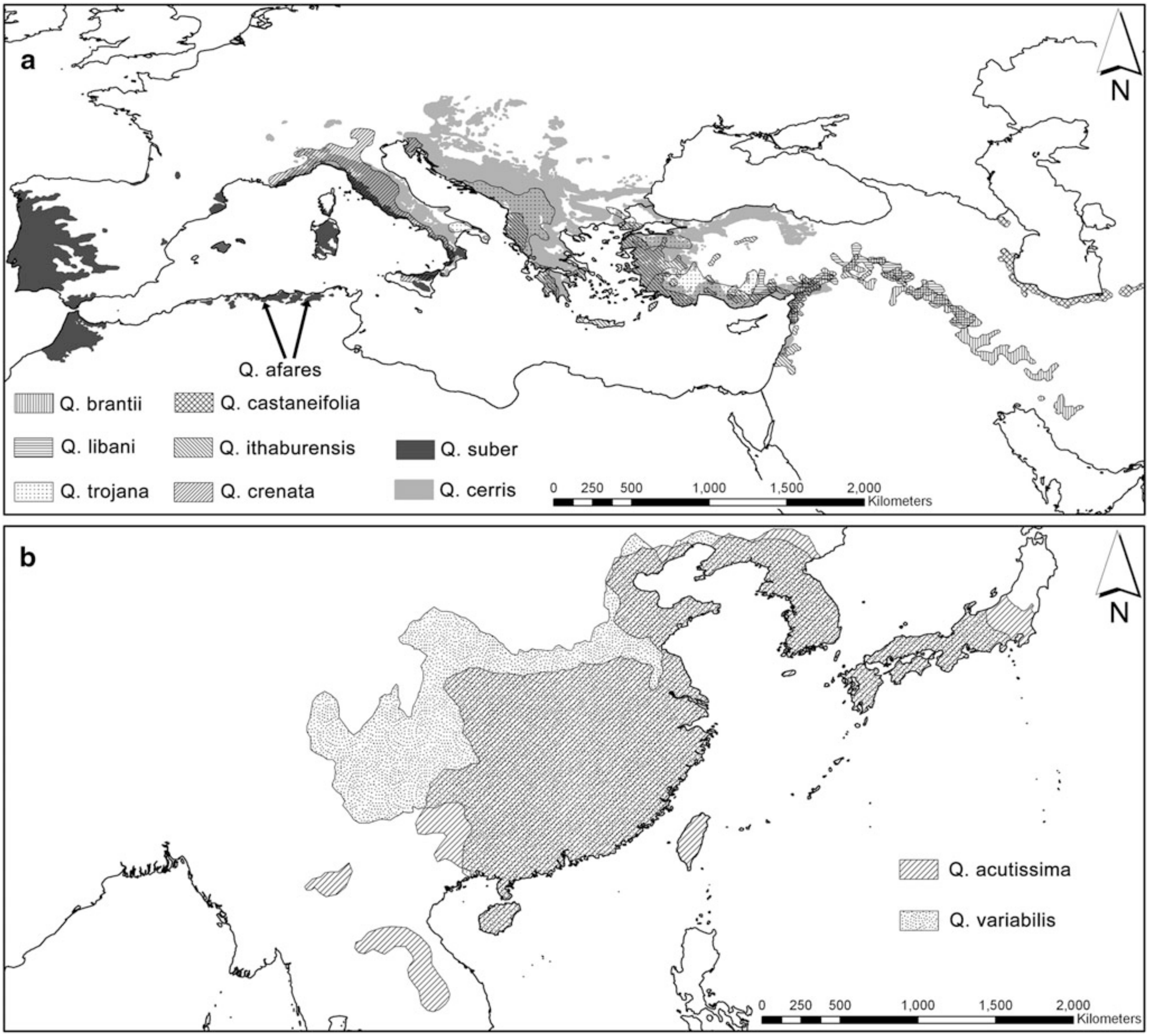


Fig. 7 Distribution maps of species belonging to subgenus *Cerris*: Mediterranean – Mid-East (**a**) and East Asia (**b**)

Lamarck in the "Encyclopédie Méthodique Botanique" (1783) (Fig. 9). The author describes this plant as: "a well-distinguished species, with respect to *Q. ilex* varieties and *Q. suber*. It seems to reach the maximum dimension of a small tree: the bark is slightly corky. The smallest twigs are tomentose, hosting alternate leaves with very short stems, oblong-elliptic, saw-toothed, green on both sides, [with] evident nervature on the lower side, and slightly coarse. The nervatures are a little pubescent, forming a small mucrone at the tip of each saw-tooth. The leaves are two inches in length and one inch or a bit more in width. This oak is found in southern Europe. The black *Phellodris* (*Phellodres* in the edition of 1785) of Dalechamp, with medium size and large leaves, seems to belong to this species; these grow on the Rhône riversides. I named this tree *Chêne le combe*, and I believe it is the *Quercus exoniensis* of the English. Its leaves are sometime pale coloured, and whitish on the lower-side."

Such a species classification was done from a single young individual observed in the Royal Garden of Versailles (Jardin du Roi, Trianon), and Lamarck gave to it his patronymic, thus assigning the rank of species. This tree is supposed to have been planted, since Lamarck did not mention any other occurrence in France and the species distribution is currently limited by the Alps.

After Lamarck, Giorgio Santi (Professor in the University of Pisa) wrote a detailed report in 1795 about his expeditions at Monte Amiata (Tuscany). He focused on a tree called "cerrosughera" locally. The morphological description by Santi matches that of Lamarck. Santi stated also that the

Fig. 8 Reconstruction of Europe during the Miocene (13 Ma), with fossil records of *Q. sosnowskyi* (*white solid circles*) and of *Q. mediterranea* (*black solid circles*). For details see Palamarev (1989), Knobloch and Kvacek (2003), Kovar-Eder et al. (2006), and references therein

leaves of this entity were more leathery and less saw-toothed than those of *Q. cerris*, and that the rhytidome was a half-ounce thin and unworkable with respect to *Q. suber*. Although this "cerrosughera" showed intermediate characters between the two species above, Santi defined it as a species with the name *Quercus pseudosuber* Santi.

The hybrid origin of *Q. crenata*, from *Q. cerris* and *Q. suber*, was proposed only at the beginning of the twentieth century. The first authors supporting this hypothesis, also based on morphology, were Locajono Pojero (1904) and Borzì (1911). The latter author tried to clear up the nomenclatural confusion about *Q. crenata* by considering *Q. pseudosuber* Santi (also identifying a *Q. pseudosuber* var. *castanophylla*), *Q. hispanica* Lam., and *Q. fontanesii* Guss. all as synonyms.

There are, however, many historical descriptions of taxa that could refer at least to *Q. crenata* (*Q. pseudosuber* Santi and *Q. fontanesii* Guss. among them), reviving a more difficult systematic frame for the species. Lamarck (1783) described an "Oak of Spain", *Q. hispanica* Lam., that was comparable morphologically to cork oak, with three varieties: (α) "Oak of Gibraltar", (β) "Oak with the leaves of gilops", and (γ) "Oak *turnere*". All of these occurred in the western Mediterranean, even if variety γ were cultivated in Great Britain. Gussone (1843) referred to *Q. fontanesii* Guss. as a kind of deciduous "sugherella", found in Calabria in 1825 (at Bocca di Falco). Tenore (1831) considered *Q. pseudosuber* Santi as a species and described it in detail as different from *Q. fontanesii*. Bertoloni (1854) depicted both *Q. pseudosuber* Santi and *Q. fontanesii* Guss., supposing the

724 CHE

lancéolées, groſſiérement dentées en leurs bords, liſſes, luiſantes & d'un verd foncé en deſſus, cotonneuſes & blanchâtres en deſſous. Ces feuilles ont deux pouces & demi à trois pouces de longueur. Les glands viennent communément deux ou trois enſemble ſur de très-petites grappes; leur cupule eſt hériſſée de pointes molles ou d'écailles étroites, lâches & pubeſcentes. Ce beau *Chêne* croît, à ce qu'on prétend, aux environs de Gibraltar. ♄. (*v. v.*)

La variété β, que nous appelons *Chêne à feuilles d'Ægylops*, a ſes feuilles oblongues, bordées de dents plus groſſières & plus profondes, preſqu'inciſées, liſſes & vertes en deſſus, imperceptiblement cotonneuſes en deſſous, & d'une couleur pâle. ♄. (*v. v.*)

Le *Chêne turnère*, qui fait la troiſième variété de notre *Chêne d'Eſpagne*, & qu'on prétend avoir été trouvé dans des ſemis faits en Angleterre, & depuis multiplié par la greffe, eſt ſinguliérement remarquable par la forme & la conſiſtance de ſes feuilles. Ses rameaux, qui ſont glabres, portent des feuilles ovales, très-planes, groſſiérement dentées, un peu coriaces, liſſes & d'un verd foncé en deſſus, d'un verd plus clair, & preſqu'entiérement glabres en deſſous, n'ayant dans leur jeuneſſe que des poils rares ſur leur côte poſtérieure. Ces feuilles ſont plus larges que celles des deux *Chênes* précédens, ſans les ſurpaſſer en longueur; & dans leur développement parfait, elles ſont entiérement glâbres de deux côtés; ces différences n'empêchent point que les autres caractères de cet arbre n'indiquent clairement qu'il n'eſt qu'une variété des deux *Chênes* ci-deſſus. ♄. (*v. v.*)

18. CHÊNE à Cochenille, *Quercus coccifera.* Lin. *Quercus foliis ovatis indiviſis ſpinoſo-dentatis utrinque glabris.* Lin. Mill. Dict. n°. 15. *Ilex aculeata cocciglandifera.* Bauh. Pin. 425. Tournef. 583. Duham. Arb. 1. p. 314. t. 125. Garid. Aix. t. 53. *Coccus infectoria.* Lob. Ic. 2. p. 153. Vulg. *le Kermès.*

CHE

d'écarlate, qui n'eſt autre choſe qu'un inſecte du genre des Cochenilles (*Coccus ilicis.* Lin. Syſt. Nat. 2. p. 740.), qui s'attache ſur ſes branches & ſur ſes feuilles pour y prendre ſa nourriture. Le Kermès ſert pour la teinture & pour l'uſage de la Médecine.

19. CHÊNE crênelé, *Quercus crenata. Quercus foliis oblongo-ellipticis crenatis utrinque viridibus, crenis mucrone ſpinuloſo terminatis.* N. *An phellodris nigricans anguſtifolia.* Bauh. Pin. 424. & *phellodris nigra, mediocribus foliis Dalechampii.*

Nous ne connoiſſons de ce *Chêne* qu'un individu encore fort jeune, qui eſt cultivé au Jardin du Roi; néanmoins nous le regardons comme une eſpèce très-diſtincte, qu'on ne peut confondre avec les *Chênes verds*, ni avec le liége. Il nous paroît ne devoir former qu'un petit arbre: l'écorce de ſon tronc eſt un peu ſubéreuſe. Ses plus petits rameaux ſont velus, & chargés de feuilles alternes, à pétioles très-courts, oblongues-elliptiques, crênelées, vertes des deux côtés, très-nerveuſes en deſſous, & un peu rudes au toucher. Leurs nervures ſont légérement velues, & forment au ſommet de chaque crênelure une petite ſaillie ſpinuliforme. Ces feuilles ſont longues d'environ deux pouces, & larges d'un pouce ou quelquefois un peu plus. On trouve ce *Chêne* dans l'Europe auſtrale. Les *Phellodris* noirs à feuilles moyennes & à feuilles larges de Dalechamp, nous paroiſſent appartenir à cette eſpèce; ils croiſſent ſur les coteaux qui ſont près du Rhône. ♄. (*v. v.*) Nous avons entendu nommer cet arbre *Chêne le combe*, & nous croyons que c'eſt le *Quercus oxonienſis* des Anglois. Quelquefois ſes feuilles ſont d'une couleur pâle & légérement blanchâtre en deſſous.

20. CHÊNE hétérophylle, *Quercus heterophylla. Quercus foliis oblongo-ellipticis, coriaceis; aliis integerrimis aliiſque ſubangulato-dentatis.* N. *Ilex folio non ſerrato in ſummitate quaſi triangulo.* Duham. Arb. 1. p. 314. *Non verò ſynonymon Cateſbii. An ilex major.* Cluſ. Hiſt. p. 23. & *ilex*

Fig. 9 Excerpt from the Encyclopédie Méthodique Botanique (1783) by Jean-Baptiste Lamarck showing paragraphs about *Q. crenata*, extracted from a digital copy retrieved from http://www.archive.org/details/texts

latter to be a synonym; this hypothesis was confirmed later by Parlatore (1867), who described *Q. pseudosuber* Santi precisely. This entity is considered similar to *Q. afares* Pom., with corky bark, and was ranked as a species by Locajono, with the name *Q. pseudo-austriaca* Lojac. Rouy (1910), supported the hybrid origin of *Q. pseudosuber* Santi but justified its occurrence in areas without cork oak by assuming crossbreeding between *Q. cerris* and *Q. ilex*, thus suggesting a new denomination: *Q. pseudocerris* Rouy. Camus (1936–1954) agreed with Fiori (1923–1929) about the hybrid origin of *Q. crenata*, confirmed that this tree occurred also in areas without cork oak, and described two forms based on the morphological similarity of the parentals. Vicioso Martinez (1950) supported the hybrid origin but disagreed with Schwarz (1936) about the first description of the species being assigned to Lamarck. In fact, Vicioso Martinez assessed that *Q. crenata* Lam. is different from *Q. pseudosuber* Santi (corresponding to the hybrid) and defined this latter as another entity, with respect to *Q. hispanica* Lam., based on fruit maturation (biannual), anther features (with thricomes and mucronate), and styles (lower position). Hegi (1957) defined *Q. crenata* Lam. as a species, introducing the new synonym *Q. aegylopifolia* Pers. Barbero et al. (1972), and supported the rank of species for *Q. crenata*; *Q. pseudosube*i would include several hybrids between *Q. suber* and other species. Finally, Pignatti (1982) considers *Q. crenata* Lam. as the probable hybrid *Q. cerris x Q. suber*, normally *inter parentes*, although it occurs sometimes in areas with the parental missing (e.g. *Q. suber* in Piemonte).

According to Govaerts and Frodin (1998), the several forms of *Q. hispanica* Lam. are coincident with *Q. morisii* Borzì (*Q. ilex x Q. suber*) and *Q. x turneri* A.DC (*Q. ilex x Q. robur*, a natural hybrid used for ornamental purposes since the eighteenth century).

Another hybrid between *Q. cerris* and *Q. suber* is cultivated in many parks and gardens in central-western Europe. The individuals belonging to this entity are divided into varieties *lucombeana*, *ambrozyana* and *fulhamensis*, all derived from a vegetative tree multiplication performed by William Lucombe in 1765.

Beyond *Q. crenata* Lam., other hybrids of cork oak are also acknowledged. *Q. hispanica* Lam. is an epithet previously adopted as a synonym of *Q. crenata* but is used now to indicate presumed *Q. suber x Q. faginea* hybrids in the Iberian peninsula (Vicioso Martinez 1950; Oliveira et al. 2003). *Q. afares* Pomel, considered in the past a species able to hybridize frequently with *Q. suber*, was suggested to be an introgressive form between *Q. suber* and *Q. canariensis*, based on nuclear and plastid DNA markers (Mir et al. 2006); it occurs in Algeria and Tunisia, where the parentals still coexist. *Q. x kabylica* Trab. (*Q. suber x Q. afares*), probably a synonym of *Q. pseudosuber* var. *castaneifolia* Wenz. and *Q. numidica* Trab., could be an intermediate introgression form of *Q. afares*, endemic in Algeria. *Q. fontanesii* Guss., an ascertained Sicilian endemic, was considered a synonym of *Q. pseudosuber* Santi by many authors despite its deciduous habit. Pignatti (1982) recently supposed *Q. fontanesii* to be a variety of *Q. cerris* restricted to the Salerno area (Campania) and to Sicily; it was described as a natural hybrid between *Q. suber* and *Q. gussonei* Borzì by Brullo and Marcenò (1985). This latter is related morphologically to *Q. crenata* Lam., which grows in the Nebrodi Mountains and at Bosco della Ficuzza (Schicchi et al. 2000).

In our opinion, a cluster of entities hard to place taxonomically, encompassing hybrids of the first generation, introgressive forms, hybrispecies and micro-species, has been collected under the name *Q. crenata*. Such material might never be distinguished into homogeneous groups without extreme nomenclaturism, beyond the morphological variability of a single species.

For instance, in agreement with Barbero et al. (1972), the samples of *Q. crenata* (now *Q. pseudosuber*) collected in Andalusia (Camus 1936-1954) could be hybrids between *Q. suber* and other species (*Q. faginea*?), since *Q. cerris* does not occur in the Iberian peninsula. On the other hand, we can not exclude that other plants of *Q. crenata* found between Italy and the Balkans were hybrids between cork oak and other taxa not corresponding to *Q. cerris*. In this sense, the value assigned to *Q. ilex* var. *suberosa* cited by De Visiani (1842) should be reconsidered. This name surely evokes the θηλή πρίνοςτΘ of Theophrastus, and the *ilex feminea* of Pliny the Elder as well. Parlatore (1867) recovered it, but we lose all traces of this name after him: Camus (1936-1954), Schwarz (1936) and others did not mention it any more. May we suppose this name really refers to *Q. crenata*, or that it includes different entities, such as *Q. x morisii* Borzì?

All the comments above might be useful to understand better the meaning of the evergreen habit of cork oak, as compared with other species of the *Cerris* group, especially if we consider that cork oak is the only representative of the subgenus in the west. The hypothesis of evergreen habits in the evolutionary history of the perennial plants, prior to deciduousness, is deeply shared. This would support the theory of a western differentiation of cork oak, unless we take into account some ideas proposed for instance by Ne'Eman (1993), who considered the semi-evergreen habit of *Q. ithaburensis* as an ongoing transition from deciduous to evergreen. Such an alternative explanation could be useful to explain the evolution of cork oak in a wider evolutionary model within subgenus *Cerris*. In fact, according to Ne'Eman (1993), leaf longevity (or persistence) is an adaptive plant character that might be more advantageous than deciduousness under mediterranean climatic conditions and on poor soils (Moore 1980; Goldberg 1982). Based on this, we could speculate that *Q. suber* originated in the speciation core of the (evergreen/semievergreen) *Cerris* group, placed in the east, and then developed its current habit during a westward migration in times characterized by adverse climatic and edaphic conditions, such as the Messinian, which favoured evergreeness (or longer leaf persistence) as an advantageous feature. Such a migration probably left a swarm of semi-evergreen taxa, including *Q. crenata*, still occurring along the migration routes (the Adriatic coasts and the Balkans). More adverse climatic conditions there, and the historical human impact, almost extinguished the cork oak, which survived only in a few isolated shelters.

5 Inferences from Genetics

Investigation of genetic features of different *Q. suber* populations may aid understanding of the easternmost occurrence of the species, giving more insight into its pattern of

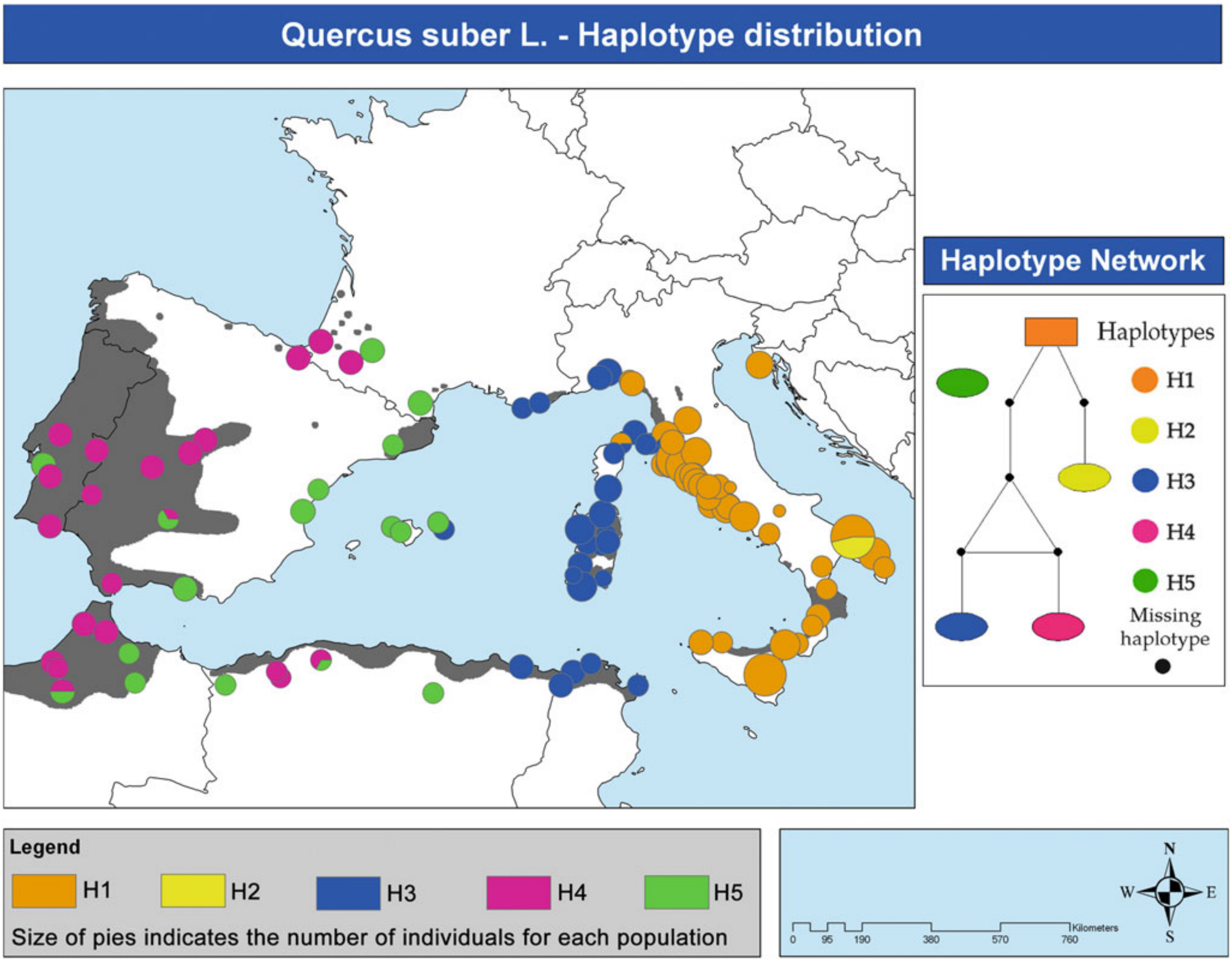


Fig. 10 Distribution of cpDNA haplotypes within *Q. suber* populations throughout its range: total genetic diversity (hT), the average of total gene natural range, and phylogenetic reconstruction of the relationships among haplotypes using statistical parsimony. Size of the *circles* indicates the number of individuals for each population (1-13)

evolution. For this purpose, several molecular analyses were performed on the most significant cork oak stands.

The cork oak population from Pula (Croatia) was sampled and analysed, by means of PCR-RFLP (Appendix 2), at five chloroplast DNA loci (Simeone et al. 2009). Data were included in a broader framework, up to a total of 95 cork-oak stands from the entire species range.

A geographical organization of the plastid genetic variation is evident from the haplotype frequency map (Fig. 10). Among the five total haplotypes detected in the entire cork-oak distribution range, three (H3, H4 and H5) occur in the western part of the range (Iberia, France, and the Mediterranean coast of North Africa); the remaining lineages (H1, H2) appeared exclusive to the Italian peninsula and, coherently, the Croatian stand exhibited the most common of the Italian haplotypes. Consistent with previous studies, the following lineage-area relationships can be outlined for cork oak, based on cpDNA variation: the Atlantic coasts (France, Portugal, Spain, Morocco), the Western Mediterranean (southwestern France, eastern Spain, east-central, west-central Algeria), the central Mediterranean (northeastern France, northwestern Italy, Corsica, Sardinia, Tunisia, eastern Algeria), and the Eastern Mediterranean (Italian Peninsula, Sicily, Croatia).

After comparing *Q. suber* with sympatric oak species, the following reports could be documented: *Q. suber*-*Q. ilex* in the west and *Q. suber*-*Q. crenata*-*Q. cerris*, and *Q. suber*-*Q. trojana*-*Q. ithaburensis* in the east; the latter two relations include all the central Mediterranean species of the *Cerris* group. The eastern lineages are separated by at least four mutations from the western haplotype groups. No haplotype colonisation of the Mediterranean seems to have occurred from west to east, at least in recent times. This finding might be interpreted in the light of an early separation of two

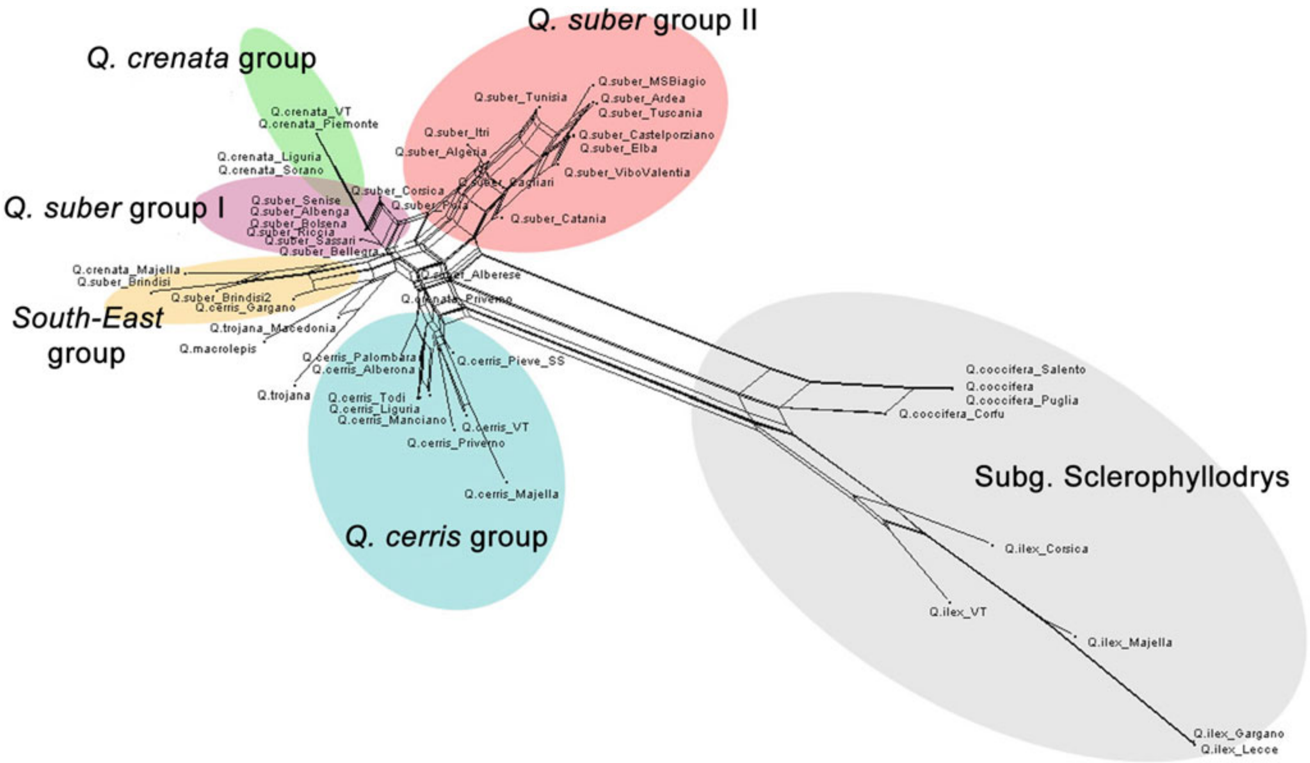


Fig. 11 Phylogenetic Network of 50 ITS sequences belonging to subgenus *Cerris* and *Sclerophyllodrys* from Italy and bordering areas, using Neighbor-Net method with K2P distance

ancient lineages favoured by a strong geographical disjunction, unless broad-scale hybridization and introgression processes are taken into account.

Sequence variation of the nuclear ribosomal ITS spacer was also investigated (Simeone et al. 2009). Even though most of the ribotypes were largely unresolved, due to the known limitations of this marker to provide adequate phylogenetic information in oaks (Denk and Grimm 2010), two major findings did result: the ITS sequences of the Croatian stand (Pula) clustered in a clade with provenances located rather uniformly in the western (Morocco, Portugal, central Spain, western France), central (Mallorca, northern Sardinia, Corsica), and eastern districts (Italian Peninsula) of the species range; a basal group of sequences collected provenances of cork oak located both in the east and west of the present range.

Closer inspection within the eastern *Q. suber* provenances was performed by use of SplitsTree and the NeighborNet methods (Bryant and Moulton 2004; Huson and Bryant 2006), allowing improved intraspecific genetic analyses with a more accurate representation of the evolutionary relationships given by sets of parallel branches; this supports the hypothesis of a closer connection between the southeastern cork oak and the Middle Eastern members of the same taxonomic group. A set of 50 ITS sequences was collected from the Italian peninsula and bordering areas, including five members of subgenus *Cerris*; an additional eight from subgenus *Sclerophyllodrys* (*Q. ilex* and *Q. coccifera*) were used as outgroups. As shown in Fig. 11, a monophyletic clade for subgenus *Cerris* was produced. Five main groups (A to E) were recognized within the clade: A refers to *Q. cerris*; B collects *Q. suber* and *Q. crenata* from the Adriatic coast, strongly connected with *Q. cerris* (from Apulia) and, secondarily to *Q. ithaburensis* and *Q. trojana* (i.e., three species with Eastern Mediterranean ranges). The remaining groups collected *Q. crenata* of the Tyrrhenian coast (included as a subset of group D, dominated by *Q. suber* populations from Tyrrhenian coast, north Sardinia and Corsica) and further *Q. suber* provenances ranging from isolated, disjunct regions: Croatia, Algeria, Tunisia, Sicily and south Sardinia. Similarly, Fig. 12 represents the relative position of *Q. suber* and *Q. crenata* in a wider frame of oaks (109 records) belonging to the three main groups, i.e. *Cerris*, *Quercus* and *Sclerophyllodrys*. This network, derived from the combination of ITS and cpDNA sequences, shows clearly that cork oak and its hybrid belong to a rather homogeneous phylogenetic group (subgenus *Cerris*), in which only a sub-clade with the Asian species of subgenus *Cerris* is distinguishable.

Allele sharing between two (or more) species resulting from shared ancestral variation has been documented extensively for closely related and for recently diverging species, and it could be emphasized by stochastic processes of

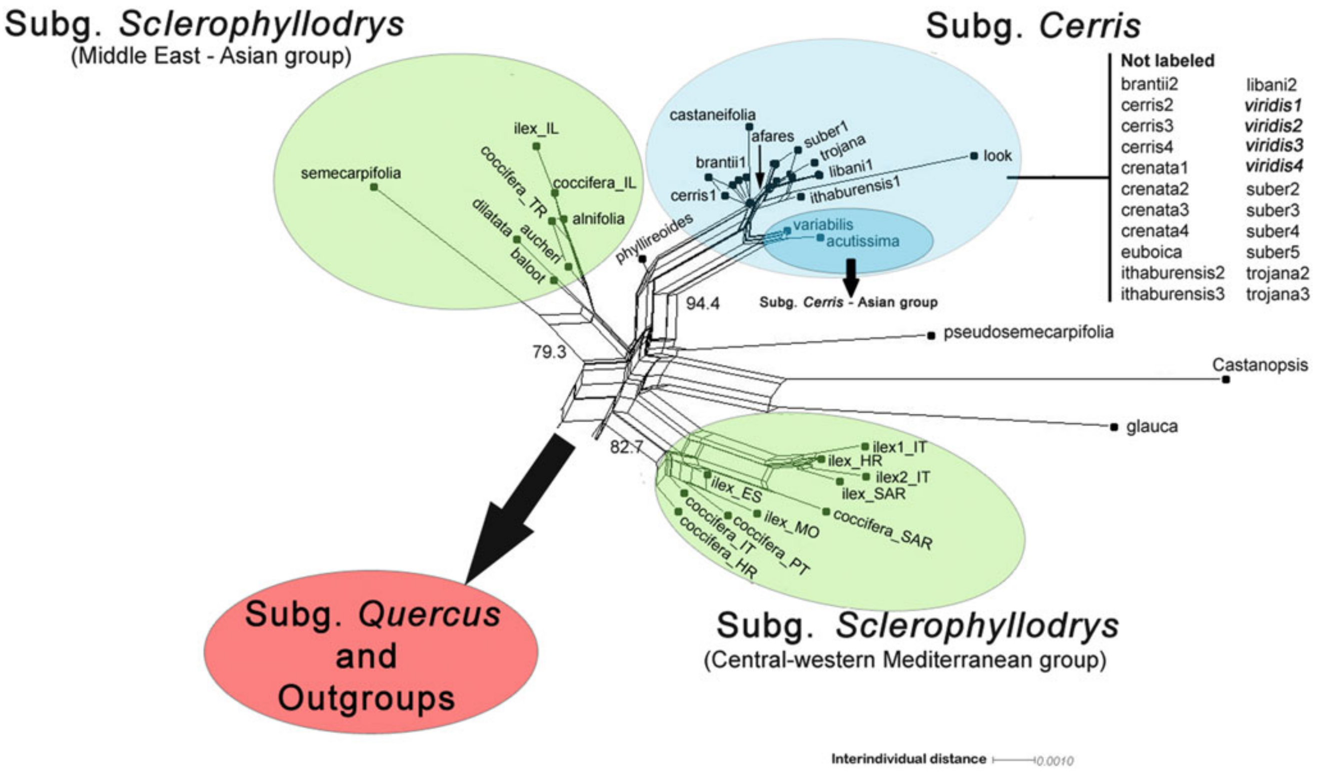


Fig. 12 Phylogenetic network (Neighbor-Net splits graph) of 109 oaks and related taxa based on ITS + cpDNA data set, drawn using the Equal Angle method. Bootstrap percentages (non-parametric bootstrapping) based on 1,000 replicates are indicated on the main edges, corresponding to phylogenetic splits observed under maximum likelihood. Fit index = 96.5

lineage sorting which followed genetic drift after strong climatic oscillations (Muir and Schlotterer 2005; Ran et al. 2006). Besides extensive hybridization and introgression events among closely related taxa, sharing of cpDNA polymorphisms between divergent taxa (in phenology, ecology, range, etc.) may account for reticulation during recent species radiation, as well as in the early diversification of taxonomic groups (Soltis and Kuzoff 1995; Cronn and Wendel 2004; Guo et al. 2004). In this case, divergence of the plastid lineages would suggest hybridization with different groups of species at the two ends of the Mediterranean or, alternatively, vicariance between western and eastern haplotypes, and fixation of the ancestral cytotype(s).

Indeed, both hypotheses are valid and can be used to interpret the available data; nevertheless, one should not necessarily exclude the other. For instance, we might reconcile them both by assuming persistence of the oldest plastid lineages in those areas closer to the differentiation center of the *Cerris* group (e.g., the eastern areas of the *Q. suber* range) and reiterated hybridizations with *Q. ilex* in the west. This hybridization apparently never happened (or it was very rare) in the eastern cork-oak range, despite the broad co-occurrence of the two species. On the other hand, the conclusion that every single cork-oak lineage (with no exceptions) currently present in peninsular Italy is derived from introgression with three species of the *Cerris* group seems unrealistic.

Besides cpDNA sharing, the ITS region can provide evidence of inter-specific geneflow when the hybrids retain the repeat types that each parental species contributed (Hershkowitz et al. 2006). In diploid hybrids, however, one of the parental ribosomal DNA loci may be lost quickly through recombination and segregation. At the same time, concerted evolution can act to homogenize variation between repeat types. The roles played by timing of the hybridization events and long generation periods are still unclear, as they may both be correlated with one fate or another: some woody groups have shown partial to little homogenization (Sang et al. 1995; Campbell et al. 1997), whereas in other cases inter-locus homogenization may be complete (Aguilar et al. 1999) or absent (Ritz et al. 2005). If hybrids are very recent, both parental types are almost always present (Bellarosa et al. 2005), and direct sequencing can quickly reveal hybridization through an additive pattern of sequence variation. When direct sequencing fails to find a second parental repeat in a suspected hybrid, cloning and search for the second repeat is the next step. If the missing repeat is relatively rare, however, it may be necessary to screen a large number of clones, costing much labour and time.

Genetic analyses of the combined ITS and plastid DNA datasets showed that two Italian *Q. suber* haplotypes are highly shared within subgenus *Cerris* and that the ITS sequence of *Q. crenata*, a species of presumed hybrid origin (*Q. cerris x Q. suber*), clusters within the *Q. suber* clades. These results might indicate, respectively, an extensive introgression of *Q. suber* in sympatric oak species in the Italian territories and ITS repeat homogenization following hybridization between disjoint *Q. suber* populations and sympatric oaks; in *Q. crenata*, the ITS loci of *Q. suber* would thus have replaced those of *Q. cerris*.

Along with these assumptions, *Q. crenata* could be interpreted as an intermediate step, originating from still ongoing introgression phenomena and capable of reverting to either parent, except where one or both are missing; or it may be evidence of more distant reticulation events between *Q. suber* and *Q. cerris*, with early formation of a hybrispecies that experienced evolutionary success thanks to acquisition and maintenance of its own species identity across space and time.[12] Obviously, contemporary interplay of these phenomena cannot be excluded, but establishing the likeliness of these hypotheses would require larger samplings and the use of more powerful molecular tools. Cristofolini and Crema (2005), based on morphometric analyses of the *Q. crenata* species complex, showed that populations in southern Italy retain greater morphological heterogeneity than northern populations, suggesting the southern to be offspring of ongoing introgression processes, while the northern, far away from the range limits of one of the putative parental species (*Q. suber*), may be the legacy of more ancient hybridization events.

6 Closing

All data gathered seem to point toward a previously neglected occurrence of *Q. suber* east of Italy. The species apparently was eroded and pushed westward in recent times, because many clues of its occurrence were retrieved in the Balkans up to the early twentieth century.

The causes of this extinction should be investigated, as we may learn much from what the species experienced during the hard times it passed through. The Messinian crisis, the glacial-interglacial cycles (from Riss/Wurm to Eemian), and the post-glacial climatic fluctuations might have caused the species to withdraw westward, except for short periods of range expansion, such as during the Atlantic. The steadily increasing rareness of cork oak might be due to its poor competition on carbonate and alkaline soils, more common in the eastern Mediterranean, during climatic deterioration (marked by progressive aridity) and aggravated by increasing human impact (Böhner et al. 2008). In addition, the pioneer/intermediate position of *Q. suber* in vegetation succession, due to its marked lack of shade tolerance, would reduce its competitiveness further.

Variations in the range limits of central-eastern oaks are known for a long time (Francini Corti 1966, 1967; Schirone and Spada 1995), but they have not yet been studied adequately, because of limited data. In many cases, students and botanists observed a few scattered, rare individuals and probably overlooked the species or considered it not native. Trinajstić (2005), for instance, argued that cork oak is not recognized in Croatia or is simply mistaken for *Q. crenata*, since the individuals found were never stripped, thus conflicting with the common picture of cork oak as having a red trunk without bark. Such a priori exclusion of the parental species lead to missing some possible cork-oak hybrids in the trans-Adriatic and trans-Ionic areas, such as *Q. morisii*.

Relict, isolated stands, single individuals and even genetic imprints of *Q. suber* can still be found east of Italy and call for further studies and protection, which might be accomplished with a well-aimed in-situ and ex-situ conservation strategy.

Finally, even if larger samplings and the use of more powerful molecular tools are required to assess the center of origin of cork oak, our findings do suggest that *Q. suber* might have differentiated during the Middle Miocene in a yet unidentified area somewhere from present-day central Europe to southwestern Asia (Palamarev 1989; Kvaček et al. 2002; Khondkarian et al. 2004; Kovar-Eder et al. 2006) and then spread into southern Europe, Iberia and North Africa, where evidence of a late Miocene-early Pliocene presence of the species has been collected (Depape 1932; Carvalho 1957; Quézel 1995). Identifying when these events occurred is still under debate, but many timeframes, such as the Messinian (7.2–5.3 Ma), should probably be reconsidered and not discarded summarily.

The next question arising from the present study is: "how many other species are there like *Q. suber*"? The answer of course is particularly complex and would certainly require a multidisciplinary approach such as the one we applied in this work. Searching for historical data, however, we found several pieces of evidence that range shifting and extinction in the Eastern Mediterranean may not be as rare as one would expect. For instance, the same destiny as that of *Q. suber* could have been shared by *P. pinaster* Ait., an ecologically similar Western Mediterranean pine.

---

[12] The hybrid nature of *Q. crenata* in populations from central Italy was supported by means of morphometric and molecular analysis (seed storage proteins resolving, restriction fragment length polymorphism -RFLP- of nuclear ribosomal genes and nuclear internal transcribed spacers -ITS- sequencing) (Schirone et al. 1990, 1995; Bellarosa et al. 1996, 2005). However, the results could not be generalized because of the restricted sampling in Tuscany and Latium.

Acknowledgements We are deeply in debt with Prof. Maura Fracassini for the revision and support of our Ancient Greek translation of Theophrastus. Thanks to Tamara Kirin, Ph.D. student of our working group, for helping translate Croatian into Italian. Most of the ancient books we consulted were retrieved freely form Google Books, the Biodiversity Heritage Library (http://www.biodiversitylibrary.org), the Internet Archive Digital Library (http://archive.org), the Gallica Digital Library (http://gallica.bnf.fr), the Digital Library of the Real Jardín Botánico de (Royal Botanical Garden of) Madrid (http://bibdigital.rjb.csic.es/spa/index.php), the Digital Library of the Hrvatska Akademija znanosti i umjetnosti (http://dizbi.hazu.hr/index.php), or Austrian Literature Online (http://www.literature.at/default.alo). We would like to express our gratitude to the efforts of all such institutions, which allow easy access to a great amount of information and rare texts.

Appendix 1

Transliteration from Greek to Latin

Greek	Latin	Meaning
άκυλοςτΘ	akylos	acorn
αλιφλοίοςτΘ	aliphloios	*Q. cerris*
ΑντίφελλοςτΘ	Antiphellos	The name of an ancient town
αρία	aria	*Q. ilex*
βαλάνοςτΘ	balanos	Acorn
δρῦςτΘ	drys	Oak
φελλεύςτΘ	phelleus	Rocky
Φελλία	Phellia	The name of an ancient settlement
Φελλίνη	Pheline	The name of an ancient settlement
φελλόδρυςτΘ	phellodrys	*Q. suber* (or *Q. pseudosuber*)
Φελλόη	Phelloe	The name of an ancient settlement
φελλόςτΘ	phellos	Cork (cork oak)
Φελλούσα	Phellousa	The name of an ancient Island
Φελλών	Phellon	The name of an ancient settlement
Φλέω	phleo	To overflow
ΦλοιόςτΘ	phloios	Bark
Φολόη	Pholoe	The name of an ancient settlement
ΠρίνοςτΘ	prinos	*Q. coccifera* (*Q. ilex*)
Σούβουρ	Soubour	The name of an ancient settlement
ΣύβαριςτΘ	Sybaris	The name of an ancient settlement
σῦφαρ	syphar	Wrinkled skin
ῦφεαρ	yphear	*Viscum album*

Appendix 2: Materials and Methods for the Genetic Investigations

Plant material – Plants were all sampled in the wild. Leaves were dried in silica gel, preserved as herbarium specimens and liophilised. Vouchers with institutional accession numbers were prepared for each sample and are stored at the Forest DNAbank of the University of Tuscia (Italy). DNA extractions were performed with the Dneasy Plant Minikit (QIAGEN), following the maufacturer's instructions.

Chloroplast DNA PCR-RFLP – Chloroplast DNA was amplified with universal primers (fragments TF, CD, DT, AS, SR; Taberlet et al. 1991; Demesure et al. 1995). Amplification, digestion, and electrophoretic procedures followed Jimenez et al. (2004). Statistical parsimony was used to reconstruct phylogenetic relationships between haplotypes (TCS, version 1.21; Clement et al. 2000).

Nuclear and Chloroplast DNA sequencing – Plastid primers for matK and trnH-psbA fragments, and PCR conditions were the same as in Piredda et al. (2011); oligos for the nuclear ribosomal ITS were designed as follows: 5′-ACGACTCTCGGCAACGGATA-3′ (5,8S_Fw), 5′-CAGCGGGTAGTCCCGCCTGA-3′ (25S_Rev); thermocycling conditions were 98°C for 3 min, followed by 35 cycles of 98°C for 30 s (s), 60°C for 30 s and 72°C for 30 s, with a final extension step of 5 min at 72°C. DNAs (ca. 40 ng) were amplified with RTG PCR beads (GE Healthcare). PCR products were cleaned with the Illustra DNA Purification Kit (GE Healthcare), and standardized aliquots were then submitted to Eurofins MWG Operon (http://www.eurofinsdna.com) for sequencing. Electropherograms were edited with CHROMAS 2.3 (http://www.technelysium.com.au) and checked visually. Potential ITS pseudo-genes were filtered according to Denk and Grimm (2010). ITS boundaries were determined by comparison with Bellarosa et al. (2005). Optimal multiple alignments were obtained with CLUSTALW 1.81 (Thompson et al. 1994) and checked visually. The phylogenetic investigation was performed on both the cpDNA (joined matK + trnH-psbA sequences) and cpDNA + ITS datasets. Split networks for the ITS, CpDNA, and ITS + CpDNA data sets were generated with the Neighbor-Net method implemented in SplitsTree4 (Bryant and Moulton 2004).

References for Appendix 2

Bellarosa R, Simeone MC, Papini A, Schirone B (2005) Utility of ITS sequence data for phylogenetic reconstruction of Italian *Quercus* spp. Mol Phylogenet Evol 34:355–370

Bryant D, Moulton V (2004) Neighbor-Net: An Agglomerative Method for the Construction of Phylogenetic Networks. Mol Biol Evol 21:255–265

Clement MD, Posada MD, Crandall KA (2000) TCS: a computer program to estimate gene genealogies, Mol Ecol 9:1657–1660

Demesure B, Sodzi N, Petit RJ (1995) A set of universal primers for amplification of polymorphic non-coding regions of mitochondrial and chloroplast DNA in plants. Mol Ecol 4:129–131

Denk T, Grimm GW (2010) The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers. Taxon 59:351–366

Jimenez P, Lopez-de-Heredia U, Collada C, Lorenzo Z, Gil L (2004) High variability of chloroplast DNA in three Mediterranean evergreen oaks indicates complex evolutionary history. Hered 93:510–515

Piredda R, Simeone MC, Attimonelli M, Bellarosa R, Schirone B (2011) Prospects of barcoding the Italian wild dendroflora: oaks reveal severe limitations to tracking species identity. Mol Ecol Resour 11:72–83

Taberlet P, Gielly L, Patou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA, Plant Mol Biol 17:1105–1109

Thompson JD, Higgins DG, Gibson TJ (1994) ClustalW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. Nucl Acids Res 22:4673–4680

References

Adamović L (1906) Die Pflanzengeographische stellung und gliederung der Balkanhalbinsel. Vienna-Kais, Akad. d. Wissensch, pp 405–495

Adamović L (1911) Die Pflanzenwelt Dalmatiens. Verlag von Dr. Werner Klinkhardt, Leipzig

Aguilar JF, Rossello JA, Feliner JN (1999) Nuclear ribosomal DNA (nrDNA) concerted evolution in natural and artificial hybrids of Armeria (*Plumbaginaceae*). Mol Ecol 8:1341–1346

Alessio G (1942) Appunti sulla toponomastica pugliese. Iapigia, n.s., n. 13, fasc. III, pp 166–189

Alessio G (1961) I *Subertani* dell'Etruria e il problema dell'origine del lat. *suber*. Atti dell'Accademia Pontaniana 9: 293–321

Amigues S (1988, 1989, 1993, 2003) Théophraste. Recherche sur les Plantes (in ancient Greek, translator and commentator S. Amigues). Les Belles Lettres, Paris

Amigues S (1991) Le témoignage de l'antiquité classique sur des espèces en régression. Rev For Fr 43:47–58

Ascherson P, Graebner P (1908-13) Synopsis der Mitteleuropäischen Flora. Verlag Wilhelm Engelmann, Leipzig, pp 463–465

Baldacci A (1893) Ricordi di un viaggio botanico fra Prevesa e Janina. N Giorn Bot It XXV:84–88

Barbero M, Loisel R, Ozenda P (1972) Répartition et écologie de *Quercus cerris* et *Quercus crenata* dans les Alpes maritimes et ligures. Bull Soc Bot Fr 119:121–125

Barbero M, Quezel P (1976) Les groupements forestiers de Grèce centroméridionale. Ecol Medit 2:3–86

Battandier JA, Trabut LC (1888-1890) Flore de l'Algérie. Dicotylédones. Argel, París, 4 fasc. et 2 appendices

Battandier JA, Trabut LC (1902) Flore Analytique et Synoptique de l'Algérie et de la Tunisie. Giralt, Alger

Beccarisi L, Biondi E, Casavecchia S, Ernandes P, Medagli P, Zuccarello V (2010) La quercia da sughero (*Quercus suber* L.) nel Salento: analisi diacronica e sinfitosociologica (Adriatico meridionale, Italia). Fitosociologia 47(2):3–16

Bellarosa R, Schirone B, Maggini F, Fineschi S (1996) Inter- and Intraspecific variation in three mediterranean oaks. Proceedings workshop "Inter- and intraspecific variation in European oaks: Evolutionary implications and practical consequences". Eur Comm Sc Res Develop, 15-16 June 1994, Bruxelles. Off. Publ. of European Community, Luxembourg, pp 239-276

Bellarosa R, Simeone MC, Papini A, Schirone B (2005) Utility of ITS sequence data for phylogenetic reconstruction of Italian *Quercus* spp. Mol Phyl Evol 34:355–370

Bertoldi V (1947) La Iberia en el sustrato étnico-linguistico del Mediterraneo occidental. Nueva Revista de Filologia Hispanica 1:128–147

Bertoldi V (1951) Tradizione mediterranea di lingua e cultura. In: Les belles Lettres (ed) Essai de Philologie Moderne, Paris, pp 133–154

Bertoloni A (1854) Flora italica, sistens plantas in Italia et in insulis circumstantibus sponte nascentes. 10 Vols, R. Masi, Bologna

Bianco P, Castellano MA, Piro G, Schirone B (1981-82) Sulla distribuzione della quercia spinosa in Puglia. Annali della Facoltà di Agraria, Università di Bari, 32:255–291

Biasoletto B (1841) Relazione del viaggio fatto nella primavera dell'anno 1838 dalla Maestà de Re Federico Augusto di Sassonia nell'Istria, Dalmazia e Montenegro. H.F. Favager, Trieste

Bischoff FHT, Moeller JH (1829) Vergleichendes Wörterbuch der alten, mittleren und neuen Geographie. 8 Vols. Gotha, Becker

Böhner J, Blaschke T, Montanarella L (2008) SAGA – Seconds Out. Hamburger Beiträge zur Physischen Geographie und Landschaftsökologie, vol 19

Boisacq E (1916) Dictionnaire etymologique de la langue grecque. Carl Winter/Klincksieck, Amsterdam

Borzan Ž, Stabentheiner E (2002) Biological and taxonomical investigations of some oak species. Acta Bot Croat 61(2):135–144

Borzì A (1880) Flora forestale italiana. Fasc. II, Firenze

Borzì A (1911) Le Querce della Flora italiana. Boll R Orto Bot Palermo 10:41–66

Brullo S, Marcenò C (1985) Contributo alla conoscenza della classe Quercetea ilicis in Sicilia. Not Fitosoc 19(1):183–229

Brus R (1996) Hrast oplutnik (*Quercus crenata* Lam.) tudi na Krasu. Gozdarski vestnik 54:511–515

Brus R, Žitnik S (2003) Slovenia (Country Report). In: Bozzano M, Turok J (compilers) Mediterranean Oak Network, Report of 2nd meeting, 2–4 May 2002, Gozo, Malta. International Plant Genetic Resources Institute, Rome, Italy, pp. 44–47

Bryant D, Moulton V (2004) NeighborNet: an agglomerative algorithm for the construction of planar phylogenetic networks. Mol Biol Evol 21:255–265

Calonghi F (1969) Dizionario Latino-Italiano. Rosenberg e Sellier, Torino

Campbell CS, Wojciechowsky MF, Baldwin BG, Alice LA, Donoghue MJ (1997) Persistent nuclear ribosomal DNA sequence polymorphism in the Amelanchier agamic complex (*Rosaceae*). Mol Biol Evol 14:81–90

Camus A (1936-1954) Les chênes, Monographie du genre Quercus et Monographie du genre Lithocarpus. Encyclopédie Economique de Sylviculture. Vol. VI, VII, VIII. Lechevalier (ed), Paris

Carano E (1934) Il suolo e la flora delle Puglie. Atti della Soc. Ital. per il progresso delle Scienze, XXII riunione. Bari, 12-18 ottobre 1933, Roma

Carella R (2006) Management of pastures of Alta Murgia National Park (Puglia, Italy). Conference proceedings "Management of forest ecosystems in national parks and other protected areas". Zbornik radova, Jahorina - NP. Sutjeska, 5-8 Jul 2006, pp 223–230

Caroli I, Caldara M (2007) Vegetation history of Lago Battaglia (Eastern Gargano coast, Apulia, Italy) during the middle-late Holocene. Veget Hist Archaeobot 16:317–327

Carvalho A (1957) Identificaçao de um possivel fossil de sobreiro (*Quercus suber* L.) proveniente de solos do mioceno lacustre do Alentejo. Bol Soc Broter 32:75–81

Chancerel L (1920) Flore forestière du Globe. Gauthier-Villars et C., Paris

Channell R, Lomolino MV (2000) Dynamic biogeography and conservation of endangered species. Nature 403:84–86

Cipollini C (2008) Distribuzione e caratterizzazione di *Quercus crenata* Lam. nella provincia di Viterbo. Graduated Thesis. Tutor Prof. M.C. Simeone. Faculty of Agronomy, University of Tuscia, Viterbo, Italy

Colella G (1941) Toponomastica pugliese dalle origini alla fine del Medio Evo. Vecchi e C., Trani

Cristofolini G, Crema S (2005) A morphometric study of the *Quercus crenata* species complex (Fagaceae). Bot Helv 115:155–167

Crivellari D (1950) Inchiesta sulla distribuzione del genere *Quercus* in Puglia. N Giorn Bot Ital n.s. 57:335–350

Cronn RH, Wendel JF (2004) Cryptic trysts, genomic mergers, and plant speciation. New Phytol 161:133–142

Daubeny C (1865) Essay on the trees and shrubs of the Ancients. Henry & Parker, Oxford & London

Daléchamps J, Des Moulins J (1615) Histoire générale des Plantes. Vol. 1, Guillaume Rouille, Lyon

De Candolle A (1864) Prodromus systematis naturalis regni vegetabilis, XVI. Paris, pp 1–160

De Giorgi C (1884) Cenni di geografia fisica della provincia di Lecce. Edizioni Salentina, Lecce

De Halácsy E (1904) Conspectus Florae Graecae, Vol. III. G. Englemann, Lipsia

De Palma C (2003) Il paese dei Tirreni, Studi dell'Accademia Toscana di Scienze e Lettere "La Colombaria", Olschki (ed), Firenze

De Philippis A (1935) La sughera (*Q. suber*) e il leccio (*Q. ilex*) nella vegetazione mediterranea. Saggio di fitogeografia ed ecologia comparate. Bull Silva Medit, X:1–109

De Visiani R (1842) Flora Dalmatica, Vol. I. F. Hofmeiter, Lipsia, pp 208–209

Demiri M (1983) Flora ekskursioniste e Shqiperise. Shtepia Botuese e Librit Shkollor, Tirana

Denk T, Grimm GW (2010) The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers. Taxon 59:351–366

Depape G (1932) Recherches sur la flore Pliocène de la vallée du Rhone. Ann Sc Nat IV (10e sér.): 73–265

Devoto G (1968) Dizionario etimologico. Avviamento alla etimologia italiana. Le Monnier, Firenze

Di Bérenger A (1859-1863) Dell'antica storia e giurisprudenza forestale in Italia. Stabilimenti Tipo-litografici G. Longo, Treviso e Venezia

Di Rita F, Magri D (2009) Holocene drought, deforestation and evergreen vegetation development in the central Mediterranean: a 5500-year record from Lago Alimini Piccolo, Apulia, southeast Italy. The Holocene 19(2):295–306

Ernout A, Meillet A (1951) Dictionaire etymologique de la langue latine. Libraire C. Klincksieck, Paris

Fiori A (1923-1929) Nuova Flora Analitica d'Italia. Edagricole, Bologna

Fraas C (1845) Synopsis plantarum florae classicae. Verlag von E. A. Fleischmann, München, p 254

Francini Corti E (1966) Aspetti della vegetazione pugliese e contingente paleoegeico meridionale nella Puglia. Ann Acc Sc For 15:137–193

Francini Corti E (1967) Problemi di Fitogeografia della Puglia. Arch Bot Biogeogr Ital 43:195–226

Freyn J (1877) Ueber einige Pflanzen, insbesondere der österr.-ungar. Flora. Österreichische Botanische Zeitschrift 27(1):26–28

Friedrich P (1970) Proto-Indo-European Trees: The Arboreal System of a Prehistoric People. University of Chicago Press, Chicago and London

Gaza T (1483) (trad.) Theophrastus: Historia Plantarum. V. Vechel, Paris (Edition 1529)

Giammarco E (1990) TAM Toponomastica abruzzese e molisana, vol. VI del DAM Dizionario Abruzzese e Molisano, Edizioni dell'Ateneo, Roma

Goldberg DE (1982) The distribution of evergreen and deciduous trees relative to soil type: an example from the Sierra Madre, Mexico and a general model. Ecology 63:942–951

Govaerts R, Frodin DG (1998) World checklist and bibliography of Fagales (Betulaceae, Corylaceae, Fagaceae and Ticodedraceae). Kew (UK): Royal Botanical Garden

Grisebach A (1843) Spicilegium Florae rumelicae et bithynicae, Vol. IF Vieweg & Sons, Brunsvig

Grisebach A (1875) La Flore du Globe, Vol. I. Guérin et C., Paris

Guo YP, Ehrendorfer F, Samuel R (2004) Phylogeny and systematics of *Achillea* (*Asteraceae-Anthemideae*) inferred from nrITS and plastid trnL-F DNA sequences. Taxon 53:657–672

Gussone G (1843) Florae Siculae synopsis. Vol 2 (pars I), ex Typis Tramater, Napoli

Hampe A, Petit RJ (2007) Ever deeper phylogeographies: trees retain the genetic imprint of Tertiary plate tectonics. Mol Ecol 16:5113–5114

Haussknecht C (1899) Symbolae ad floram graecam. Aufzählung der im Sommer 1885 in Griechenland gesammelten Pflanzen. Mittheilungen des Thüringischen Botanischen Vereins, XIII-XIV:18–77

Hayek A (1927) Prodromus Florae peninsulae Balcanicae, Vol. I. Dalhem, Berlin, p 72

Hegi G (1957) Illustrierte Flora von Mittel-Europa, Vol. III. Lehman's Verlag, Munchen

Hershkowitz MA, Hernandez-Pellicer CC, Arroyo MTK (2006) Ribosomal DNA evidence or the diversification of *Tropaeolum* sect. *Chilensia* (*Tropaeolaceae*). Pl Syst Evol 260:1–24

Heubeck A (1961) Myk. *ra-o λᾶαςτΘ "Stein" und Verwandtes. IF 66:29–34

Hirc D (1903-12) Revizija hrvatske flore (Revisio florae croaticae). Izrađena u botaničko-fiziologijskom zavodu kr. sveučilišta Franje Josipa I. u Zagrebu, p 153

Hofmann JB (1950) Etymologisches Wörtebuch des Griechischen. Verlag von R. Oldenbourg, München

Hort A (1916) (trad.) Theophrastus: historia plantarum, 2 vols. Heinemann W & Putnam's GP Sons, London & New York

Horvát A (1951) Prilog poznavanju uzgoja plutnjaka (*Q. suber* L.). Šumarski List 78:1–11

Hunter ML, Hutchinson A (1994) The virtues and shortcomings of parochialism: conserving species that are locally rare, but globally common. Conserv Biol 8:1163–1165

Huson DH, Bryant D (2006) Applications of Phylogenetic Networks in Evolutionary studies. Mol Biol Evol 23(2):254–267

Jedlowski D (1955) Zeleni hrast. Anali Instituta za eksperimentalno šumarstvo JAZU:487–489

Jimenez P, Lopez-de-Heredia U, Collada C, Lorenzo Z, Gil L (2004) High variability of chloroplast DNA in three Mediterranean evergreen oaks indicates complex evolutionary history. Hered 93:510–515

Kavvadas DS (1956-1964) Illustrated botanical-plant dictionary, 3. Athens (in Greek)

Kayacik H (1959) Hatay Meşesi (*Quercus pseudo-cerris* Boiss.) ve kabuklarindan faydalanma imkânlari. İstanbul Üniversitesi Orman Fakültesi Dergisi A, 9(1):11–21

Khondkarian IG, Shcherba IG, Popov SV (2004) Latest Miocene. Lithological-Palaeogeographic maps of Paratethys. Ten maps Late Eocene to Pliocene. In: Popov SV et al. (eds) Cour Forsch.Inst Senckenberg, Frankfurt

Klauber A (1920) Die Monographie des Korkes. A. Weber, Berlin

Knobloch E, Kvaček Z (2003) Miocene macroflora of the opencast mine Oder (Germany). doi:10.1594/PANGAEA.125553

Kotschy T (1862) Die Eichen Europas und des Orients. Hölzel, Wien

Κουλακη Γ (1993) Το μεγάλο ετυμολογικό λέξικό τηςτΘ νεσελληνικήςτΘ γλόσσαςτΘ. ΜαλλιάρηςτΘ-Παιδεία, Αθήνα

Kovar-Eder J, Kvaček Z, Martinetto E, Roiron P (2006) Late Miocene to Early Pliocene vegetation of southern Europe (7-4 Ma) as reflected in the megafossil plant record. Palaeogeogr Palaeclim Palaeoecol 238:321–338

Kvaček Z, Velitzelos D, Velitzelos E (2002) Late Miocene Flora of Vegora, Macedonia, N Greece. University of Athens, Athens

Lamarck J-B (1783) Encyclopédie Méthodique, ou par Ordre de Matieres. Vol 1. Panchkoucke, Paris

Lepetz V, Massot M, Schmeller DS, Clobert J (2009) Biodiversity monitoring: some proposals to adequately study species' responses to climate change. Biodiv Conserv 18:3185–3203

Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? Conserv Biol 9:753–760

Lojacono Pojero M (1904) Flora sicula: descrizione delle piante vascolari spontanee o indigenate in Sicilia. Vol. 2(2), Edizione 8 di Bibliotheca Botanica, PalermoZ

Lopez de Heredia U, Jimenez P, Collada C, Simeone MC, Bellarosa R, Schirone B, Cervera M, Gil L (2007) Multi-marker phylogeny of three evergreen oaks reveals vicariant patterns in the Western Mediterranean. Taxon 56: 1209–1220

Lorenzo Z, Burgarella C, Lopez de Heredia U, Lumaret R, Petit RJ, Soto A, Gil L (2009) Relevance of genetics for conservation policies: the case of Minorcan cork oaks. Ann Bot-London 104:1069–1076

Lumaret R, Tryphon-Dionnet M, Michaud H, Sanuy A, Ipotesi E, Born C, Mir C (2005) Phylogeographical variation of chloroplast DNA in cork oak (*Quercus suber*). Ann Bot-London 96:853–861

Magri D, Fineschi S, Bellarosa R, Buonamici A, Sebastiani F, Schirone B, Simeone MC and Vendramin GG (2007) The distribution of *Quercus suber* choloroplast haplotypes matches the palaeogeographic history of the western Mediterranean. Mol Ecol 16:5259–5266

Marchesetti C (1930) Flora dell'isola di Cherso. Archivio botanico VI (1-2):16–59,113–157

Mariani Colombo P, Chiesura Lorenzoni F, Grigoletto F (1983) Pollen grain morphology supports the taxonomical discrimination of Mediterranean Oaks (*Quercus, Fagaceae*). Pl Syst Evol 141:273–284

Marinosci M (1870) Flora salentina. Edizioni Tip. Salentina, Lecce

Markgraf F (1949) Eine neue Höhenstuffenkarte der Vegetation in Albanie. Bericht über das Geobotanische Forschunsinstitut Rübel in Zürich, Zürich, pp 109–118

Mavrommatis G (1981) Évolution de la Flore et de la Végétation à Kitsos. In: Lambert N (ed) La Grotte Préhistorique de Kitsos (Attique). Missions 1968–1978. L'occupation néolithique. Les vestiges des temps paléolithiques, de l'antiquité et de l'histoire récente. 2 Tomes. A.D.P.F., Paris, pp 667–677

Mayer H, Aksoy H (1986) Wälder der Türkei. Gustav Fischer Verlag, Stuttgart, New York

Medail F, Diadema K, 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J Biogeogr 36:1333–1345

Meyer-Lübke W (1911) Romanisches Etymologisches Wörterbuch. C. Winter's Universitätsbuhhandlung, Heidelberg

Mıhçıoğlu K (1942) Türkiye'de Saçlı Meşeden Mantar İstihsaline Dair Bir Araştırma. Orman ve Av 1:151–166

Mir C, Toumi L, Jarne P, Sarda V, Di Giusto F, Lumaret R (2006) Endemic North African *Quercus afares* Pomel originates from hybridisation between two genetically very distant oak species (*Q. suber* L. and *Q. canariensis* Willd.): evidence from nuclear and cytoplasmic markers. Heredity 96:175–184

Monaci L (1994) Al limite estremo dell'areale della sughera: i popolamenti relitti della Puglia meridionale. Dissertation in Botanica Forestale (under Prof. B. Schirone), Facoltà di Agraria, Università degli Studi della Tuscia, Viterbo

Moore PD (1980) The advantages of being evergreen. Nature 285:535

Muir G, Schlotterer C (2005) Evidence for shared ancestral polymorphism rather than recurrent gene flow at microsatellite loci differentiating two hybridizing oaks (*Quercus* spp.). Mol Ecol 14:549–561

Müller R (1900) Ueber die Korkeiche (*Q. suber* L. und *Q. occidentalis* Gay). Abhandl, der K.K. Geograph, Gesell, Wien

Musci G (1932) La bonifica integrale in Puglia nel primo decennio della rivoluzione fascista. Iapigia (ed), fasc. IV, pp 494–510

Ne'Eman G (1993) Variation in leaf phenology and habit of *Quercus ithaburensis,* a Mediterranean deciduous tree. J Ecol 81(4):627–634

Novembre D (1964) Aree antiche e recenti della macchia del Salento. Atti del XIX Congresso Geografico Italiano, Como (Villa Olmo), 18–23 maggio 1964, pp 179–193

ΝτάφηςτΘ Σ (2000) ΦελλοφόροςτΘ ΔρῦςτΘ, Ένα χρυσοφόρο δένδρο. ΑΜΦΙΒΙΟΝ 34:8–11

Nyman CF (1878-1882) Conspectus Florae Europaeae. Typis Officinæ Bohlinianæ, Örebro, Sweden, p 662

Oliveira P, Custódio AC, Branco C, Reforço I, Rodrigues F, Varela MC, Meierrose C (2003) Hybrids between Cork Oak and Holm Oak: Isoenzyme analysis. For Gen 10(4):283–297

Ørsted AS (1871) Bidrag til Kundskab om Egefamilien i Nutid og Fortid. Bianco Lunos Bogtrykkeri ved F. S. Muhle, Copenhagen, pp 67–76

Palamarev E (1989) Palaeobotanical evidence of the Tertiary history and origin of the Mediterranean schlerophyll dendroflora. Plant Syst Evol 162:93–107

Paparisto K (1988) Flore de l'Albanie, Vol. I. Acad Sci RPS Albanie, Tirana

Paparisto K, Demiri M, Mitrushi I, Qosja Xh, Vangjeli J (1992) Flora e Shqiperise. Vol. II, Tirane, pp 446

Parlatore F (1867) Flora Italiana Vol. IV. Tipografia dei successori Le Monnier, Firenze

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Ann Rev Ecol Evol Syst 37:637–669

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob Chang Biol 13:1860–1872

Pavari A (1934) Sulle condizioni di vegetazione della sughera. Memoria presentata al I Convegno Nazionale del Sughero, Sassari, maggio 1934

Petit RJ, Hampe A, Cheddadi R (2005) Climate changes and tree phylogeography in the Mediterranean. Taxon 54:877–885

Piccioli L (1890) Le piante legnose italiane. Salvadore Landi, Firenze

Pieraccioni D (1990) Grammatica greca. Sansoni, Firenze

Pignatti S (1982) Flora d'Italia. Edagricole, Bologna

Piredda R, Simeone MC, Attimonelli M, Bellarosa R, Schirone B (2011) 1146 Prospects of barcoding the Italian wild dendroflora: oaks reveal severe limitations to tracking species identity. Mol Ecol Resour 11:72–83.

Pirone G (1995) Alberi, arbusti e liane d'Abruzzo. Cogecstre Edizioni, Penne

Pontillo T (1993) Dizionario sanscrito. Vallardi, Milano

Poscharsky GA (1896) Beiträge zur Flora von Croatien und Dalmatien. Buchdruckerei von Arthur Schönfeld, Dresden

Quézel P (1995) La flore du bassin méditerranéen: origine, mise en place, endémisme. Ecol Medit 21:19–39

Ran JH, Wei XX, Wang XQ (2006) Molecular phylogeny and biogeography of *Picea* (*Pinaceae*): implications for phylogeographical studies using cytoplasmic haplotypes. Mol Phyl Evol 41:405–419

Richter K (1897) Plantae Europaeae, Vol. II, Fasc. I. Verlag von Wilhelm Engelmann, Leipzig

Rikli M (1912) Lebensbedingungen und Vegetationsverhältnisse der Mittelmeerländer und der atlantischen Inseln. G. Fischer, Jena

Rikli M (1943) Das Pflanzenkleid der Mittelmeerländer. H. Huber, Bern, Vol. 1, pp 171–173

Ritz CM, Schmuths H, Wissemann V (2005) Evolution by reticulation: European dog roses originated by multiple hybridization across the genus Rosa. J Hered 96:4–14

Robertson E (2006) Etruscan's genealogical linguistic relationship with Nakh-Daghestanian: a preliminary evaluation. Retrieved from http://www.nostratic.ru/books/(329)EGRWND.pdf. 2009-07-13

Rocci L (1974) Vocabolario Greco Italiano. Società editrice Dante Alighieri, Milano

Rohlfs G (2007) Vocabolario dei dialetti salentini (Terra d'Otranto). Congedo Editore, Galatina

Rouy G (1910) Flore de France: ou, Description des plantes qui croissant spontanément en France, en Corse et en Alsace-Lorraine. Asnière(Seine), France

Saint-Lager JB (1880) Reforme de la nomenclature botanique. Ann Soc Bot Lyon 7:1–154

Sang T, Crawford DJ, Stuessy TF (1995) Documentation of reticolate evolution in peonies (*Paeonia*) using internal trascriber spacer sequenze of nuclear ribosomal DNA: implication for biogeography and concerted evolution. Proc Natl Acad Sci USA 92:6813–6817

Santi G (1795) Viaggio al Monte Amiata. Pisa, 1795-1806

Scarascia Mugnozza G, Schirone B (1983) Un bosco di sughera presso Brindisi. Monti e Boschi 6:47–52

Scardigli P, Gervasi T (1978) Avviamento all'etimologia inglese e tedesca. Le Monnier, Firenze

Schicchi R, Mazzola P, Raimondo FM (2000) Eco-morphologic and taxonomic studies of *Quercus* hybrids (Fagaceae) in Sicily. Bocconea 13:485–490

Schirone B, Schirone A, Romagnoli M, Angelaccio C, Bellarosa R (1990) Considerazioni preliminari sulla tassonomia di *Quercus crenata* Lam. In Orantes (ed) Approcci metodologici per la definizione dell'ambiente fisico e biologico mediterraneo, Gruppo di Lavoro Bioritmi vegetali e Fenologia della S.B.I., Congreas, pp 423–452

Schirone B, Pelosi C, Piovesan G, Schirone A, Bellarosa R, La Fiandra D (1995) Utility of seed proteins to assess different levels of genetic variability in forest trees. In: Baradat P, Adams WT, Muller-Stark G (eds) Population genetics and genetic conservation of forest trees. SPB Academic Publishing, Amsterdam, pp 55–70

Schirone B, Spada F (1995) Anomalies in reproductive phenology and vegetation history: the case of SE Italy. Colloq Phytosociol XXIV:847–857

Schirone B, Spada F, Passigli S, Agrillo E, Casella L (2006) Toponimi e distribuzione di *Quercus suber* L. in Italia. In: IUFRO (ed.) Cultural heritage and sustainable forest management: The role of traditional knowledge. Proceedings of the Conference, 8-10 June 2006, Warszawa, Vol. 2, pp 524–530

Schneider CK (1906) Illustriertes Handbuch der Laubholzkunde, Vol. I. Verlag von Gustav Fischer, Jena

Schulten A (1930) Die Etrusken in Spanien. Klio 23:365–432

Schwarz O (1936) Entwurf zu einen natürlichen System der Cupuliferen und der Gattung *Quercus* L. Notizbl Bot Gart Berlin-Dahlem 8:1–22

Schwarz O (1964) Quercus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (eds) Flora Europaea, vol. 1: Lycopodiaceae to Platanaceae. Cambridge University Press, Cambridge, pp 61–64

Şen A, Quilhó T, Pereira H (2011a) Bark anatomy of *Quercus cerris* L. var. *cerris* from Turkey. Turk J Bot 35:45–55

Şen A, Quilhó T, Pereira H (2011b) The cellular structure of cork from *Quercus cerris* var. *cerris* bark in a materials' perspective. Ind Crops Prod 34:929–936

Simeone MC, Papini A, Vessella F, Bellarosa R, Spada F, Schirone B (2009) Multiple genome relationships and a complex biogeographic history in the eastern range of *Quercus suber* L. (*Fagaceae*) implied by nuclear and chloroplast DNA variation. Caryologia 62:236–252

Sivieri A, Vivian P (2006) Grammatica greca. D'Anna, Firenze

Soltis DE, Kuzoff RK (1995) Discordance between nuclear and chloroplast phylogenies in the *Heuchera* group (*Saxifragaceae*). Evolution 49:727–742

Spada F, Passigli S (2006) Variazioni della copertura vegetale, documentazione storica e toponomastica nel Lazio appenninico. In: IUFRO (ed.) Cultural heritage and sustainable forest management: The role of traditional knowledge. Proceedings of the Conference, 8-10 June 2006, Warszawa, Vol. 2, pp 333–342

Spicciarelli R (1996) Alberi Padri. Quaderni di Basilicata Regione

Sprengel K (1822) (trad.) Theophrastus: Historia Plantarum. 2 Vols. Hammerick JF, Altona

Strobl PG (1872) Aus der Frühlings-Flora und Fauna Illyriens. Verh zool.-bot Ges XXII:577–616

Tchihatcheff de P (1860) Asie Mineure. Description physique, statistique et archéologique de cette contrée. III Botanique. Gide, Paris, p 477

Tenore M (1831) Sylloge Plantarum Vascularium Florae Neapolitanae. Ex Typographia Fibreni, Neapoli

Thanos CA (2005) Theophrastus on Oaks. Bot Chron 18(1):29–36

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend Peterson A, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

Tozer HF (1882) Lectures on the geography of Greece. J Murray, London

Trinajstić I (1974) Taxa nova et combinationes novae in flora Jugoslavie II. *Fagaceae*, *Q. x viridis* Trinajstić, hybr. nov. =? *Q. cerris* f. *austriaca* x *Q. ilex*. Suppl Fl Anal Jugosl 2:1–17

Trinajstić I (2005) Hrast plutnjak (*Quercus suber* L.) u dendroflori Hrvatske. Rad Šumar Inst. 40:199–206

Uzunova K, Palamarev E, Ehrendorfer F (1997) Anatomical changes and evolutionary trends in the foliar epidermis of extant and fossil Euro-Mediterranean oaks (*Fagaceae*). Pl Syst Evol 204:141–159

Vaniček A (1877) Griechisch-Lateinisches Etymologisches Wörterbuch. B. G. Teubner, Leipzig

Vicioso Martinez C (1950) Revisión del Género Quercus en España. Bol Inst Forest Invent Exp 51:1–194

Von Mannagetta BGR (1901) Die vegetationsverhältnisse der illyrischen Länder. Verlag von Wilhelm Engelmann, Leipzig

Walde A (1910) Lateinisches Etymologisches Wörterbuch. C. Winter's Universitätsbuchhandlung, Heidelberg

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Yaltırık F (1984) Türkiye Meşeleri Teşhis Kılavuzu. İstanbul Yenilik Basımevi

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. Trends Ecol Evol 16:446–453

Phenorhythms and Forest Refugia

Bartolomeo Schirone, Francesco Spada, Gianluca Piovesan, and
Marco Cosimo Simeone

Abstract

Anomalous phenoryhthms such as reiterated anthesis and annual, biennial and intermediate fruiting are recorded for evergreen oaks (*Quercus* sect. *Sclerophyllodrys*: *Q*. *ilex*, *Q*. *coccifera* s.l. and *Quercus* sect. *Cerris*: *Q*. *suber*) in southern peninsular Italy. The same patterns are known from populations of evergreen oaks of the same sections in the western Himalaya, in areas where climatic conditions are intermediate between mediterranean and monsoons regimes, thus resembling border-line mediterranean climates. This suggests persistence of atavistic adaptations in areas with similar, "relaxed" climatic conditions. In the Italian peninsula, such areas would have acted as small isolates where a less intense climatic deterioration during the Late Quaternary affected the forest stands that survived across pleni-glacial events, preserving the main features of evergreenness with anomalous phenorhythms. These areas are today particularly dense in Arctotertiary taxa of Caucasian affinity, which coexist where oak populations with anomalous phenorhythms have been recorded. This suggests that present-day anomalies in reproductive cycles, along with a rich woody flora and local altitudinal zonations with mixed forest stands of Caucasian affinity, might represent the legacy of cryptic forest refugia during the last pleni-glacial.

Keywords

Anomalous phenorhythms • Forest refugia • Reproductive cycles • *Quercus sclerophyllodrys*

1 Introduction

Sites that acted as shelters for whole ecosystems during glaciations or other unfavourable climatic periods are the focus of a vast body of research for a long time (Battandier 1894; Haffer 1982; Bennett 1997; Taberlet et al. 1998; Hampe and Petit 2005). In recent years, search and description of such refugia have been urged greatly by growing awareness of the dramatically increasing biodiversity loss in ecosystems and by unforeseeable effects of the ongoing climate change (Walther et al. 2002; Thomas et al. 2004; Petit et al. 2005; Lepetz et al. 2009). In this context, the Mediterranean region represents a symbolic, crucial area as one of the world ecoregions where high levels of biodiversity occur together with long-standing, exceptionally strong human pressure (cf. Bailey 1998; Quézel and Médail 2003).

A detailed inventory of Mediterranean plant refugia has been compiled recently by Médail and Diadema (2009), who reviewed many studies based mostly on paleo- and phylogeography, and correlated them with all currently acknowledged biodiversity hotspots in the Mediterranean basin. Nevertheless, additional bio-ecological evidence may play an important role in implementing the excellent

B. Schirone (✉) • G. Piovesan • M.C. Simeone
Dipartimento DAFNE, Università della Tuscia, Via S.C. De Lellis, 01100 Viterbo, Italy
e-mail: schirone@unitus.it

F. Spada
Dipartimento di Biologia Vegetale – Orto Botanico, Università "La Sapienza", Largo Cristina di Svezia, 24. 00165 Roma, Italy

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_12,

work by these two authors and help to discover refugial areas that have been overlooked up to now.

Populations of trees exhibiting anomalous phenophases have been recorded on sites scattered at low altitude in subcoastal districts throughout peninsular Italy (Schirone and Spada 1995). In these areas, woody Rosaceae (*Prunus*, *Amygdalus*, *Crataegus*: nomenclature according to Pignatti 1982) may exhibit autumnal anthesis as soon as climatic conditions in autumn become persistently mild. Individuals of *Cercis* from many sites in central and southern Italy and in Greece are known to perform in the same way. In mid-Tyrrhenian Italy and Apulia, however, populations of evergreen oaks (*Q. ilex*, *Q. coccifera s.l.* and *Q. suber*) exhibit such phenological anomalies as reiterated anthesis, or annual, biennial and intermediate fruiting (Bianco and Schirone 1982; Schirone and Codipietro 1992), which are apparently not dependent on local meteorological circumstances.

Significant differences can be detected in the behaviour of these taxa. While autumnal antithesis in woody Rosaceae and Fabaceae does not lead to any reproductive output, autumnal flowers in *Quercus* do lead to the production of fruits. The maturation processes in oaks are simply suspended during the harsh season and restart as soon as climatic conditions turn favourable. Both phenotypic plasticity and genetic polymorphism seem therefore to be involved. In *Quercus* the anomalous reproductive mechanisms suggest the nature of genetically inherited adaptive traits. In some populations these anomalies are rather the rule than the exception. The geographical distribution of the anomalies shows spatial coincidence with outstanding patterns of phytogeographical affinities in the plant cover of central-southern Italy, which might be crucial in understanding events of the local vegetation history. These affinities point out the importance of areas where the forest cover was able to persist across the reiterated climatic deteriorations of the late Quaternary, i.e. the forest refugia. The nature of these coincidences is discussed here in the form of a hypothetical historical mechanism which might account for the patterns.

2 Reproductive Cycles and Phenological Anomalies in Quercus

Among the Italian oaks, anomalies are unusual in the subgenus *Quercus* (sensu Schwarz 1936-39) but are common in the subgenus *Sclerophyllodrys* (*Q. ilex*, *Q. coccifera s.l.*) (Corti 1959; Bianco and Schirone 1982; Schirone and Codipietro 1992). Such anomalies are very rare as well among the deciduous representatives of subgenus *Cerris*; cases are recorded otherwise also in semi-evergreen species (*Q. macrolepis*: Scaramuzzi 1960) of this subgenus, but anomalies are more common among its evergreen representatives (*Q. suber*: Corti 1954, 1955; Scarascia Mugnozza and Schirone 1983). In these species the divergence from the normal phenoryhthm is displayed by reiterated male and female flowerings in autumn, in winter and exceptionally in summer (in August by *Q. coccifera* on Corfù, Greece: Bianco and Schirone 1984). These flowerings initiate annual-abbreviated (*Q. ilex*, *Q. coccifera*), annual, biennial and sub-biennial reproductive cycles (*Q. coccifera*, *Q. suber*). Mixed cycles are also recorded, i.e. anthesis starting in autumn and ending in autumn of the next year, often on different branches of the same tree. In Apulia (southeasternmost Italy), *Q. coccifera* may flower extra-periodally in mid-winter as well.

Complex reproductive cycles seem to be processes that affected significantly the evolutionary history of oaks of both the subgenera *Sclerophyllodrys* and *Cerris*.

Q. ilex flowers annually and *Q. suber* as well, but some populations (cf. Barros Gomes 1876; Pereira Coutinho 1888; Corti 1954, 1955) or a whole geographical sub-taxon, *Q. occidentalis* Gay, may flower biennially (cf. Fiori and Paoletti 1933). In the *Q. coccifera*-*Q. calliprinos* complex, the cycle is predominantly biennial, but populations displaying annual, sub-continuous flowering and “reduced” biennial cycles are known (flowering and fecundity in autumn, alternatively fecundity during the subsequent spring with fruit maturation in autumn of the second year (cf. Bianco and Schirone 1985).

Such manifestations were ignored initially by most researchers. They gained more attention since 1950, thanks mainly to the scientific activity of the Italian “Scuola di Embriologia Vegetale di Firenze-Bari”, through which a general model to explain the phenomenon at a ecophysiological level was developed (cf. Corti 1954, 1955; Francini Corti 1960; Scaramuzzi 1960; Bianco 1961; Bianco and Schirone 1982, 1984, 1985; Ciampi 1987). Unfortunately, their studies have remained largely unknown to most of the international scientific community, as they were all written in Italian. They were also unknown to the French author Lavarenne-Allary (1963, 1964), who subsequently developed analogous models for the vegetative growth cycles of oaks and suggested the same evolutionary patterns. Even more surprisingly, no recent phenological investigations (cf. Milla et al. 2010) recognize the former or the latter.

The Italian scientists interpreted the origin of the anomalies as the “re-emergence” and activation of atavistic characters, never erased from these species during their evolutionary history but “silenced” in order to survive during unfavourable climatic periods with high water or thermal stress during reproductive phases (cf. Scharfetter 1953). Since anomalous autumnal flowering leads to fecundity in autumn or the following spring, the interruption of reproductive processes during winter only provides a delayed but successful maturation. Oaks exhibiting this reproductive cycle seem therefore to cope with the effects of an unfavourable season by a phenorhythm pre-adapted to (sub)continuous flowering. They are apparently not in harmony with local seasonality and could be defined as "out of phase" (cf. Francini Corti 1960; Axelrod 1973; Mitrakos 1980). This suggests that biennial cycles in evergreen oaks (and in *Q. macrolepis*, a quasi-evergreen species sensu Ne'Eman 1993) might represent an attempt to withstand the constraints of a local climate which no longer matches their environmental demands but which is not harsh enough to damage any phase of the reproductive process. Consequently, cycles based on (sub)continuous flowering seem to represent a basic primary structure in these oaks, on which the modern climate superimposes new secondary constraints (Francini Corti 1960). In fact, red oaks in the tropical montane climate of Central America lack strong seasonality in flowering and fruiting (Nixon 2006; see Fig. 2.3 in Deacon 2010), due to the absence of freezing stress (Koehler et al. 2012).

Recurrent, "out of time" anthesis and anomalous fruiting can be set within the complex phenomenon of recurrent flushing, which is recorded at different degrees of intensity in several woody species. In particular, this phenomenon has been deeply investigated by Lavarenne-Allary (1964) and co-workers (Alatou et al. 1989; Barnola et al. 1986, 1990; Alaoui-Sossé et al. 1996), who analyzed the vegetative growth patterns of *Quercus robur*. They stressed that the English oak can display both winter and summer dormancy, and that the two phenophases are of a different nature. Winter dormancy is a cold-induced steady state that can be removed easily by physical and chemical treatments. In contrast, summer dormancy can be reduced strongly by favourable climatic conditions, although it cannot be removed totally. In fact, plants growing under constant favourable environmental conditions (e.g., in growth chambers) maintained an active growth cycle consisting of alternating periods of 25 days, of which 14 are of active flushing and 11 are of growth interruption. Such a rhythmic growth would be a fixed behaviour, very probably under genetic, developmental control, and no chemical or hormonal treatments could remove or even alter this attitude. Furthermore, the alternating, summer growth cycle is more evident in young individuals and in sprouts (cf. Lavarenne-Allary 1964; Schirone et al. 1988), due probably to the higher availability of soil nutrition and stump storage (Willaume and Pagès 2011). Congruently, sucrose synthase is involved in the active growth phases, by determining the mobilization of the stored energies that are required to sustain the growth flux (Le Hir et al. 2005).

These growth patterns were given different names (St. John twigs, lamma shoots, etc.) by the authors who first described them (cf. Kramer and Kozlowski 1979). They can be traced back to the general rhythm of sub-continuous growth, distinctive for species living under tropical climatic conditions (Greathouse et al. 1971; Borchert 1973). These manifestations are explained more consistently as the remains of an aboriginal rhythm, at present obscured by periods of dormancy mostly due to summer drought or winter cold, rather than by exceptional events that break dormancy (Fig. 1). According to this, favourable climatic conditions might trigger the restart, at least partly, of an ancestral vegetative cycle that was never completely deleted by a true adaptive dormancy (Scharfetter 1953; Borchert 1975; Bianco and Schirone 1982).

The phenology of woody plants has been widely investigated in mediterranean climates (e.g. Mooney and Kummerow 1981; Kummerow 1983; Montenegro 1987; Correia et al. 1992; De Lillis and Fontanella 1992; Perez-Latorre et al.1996; Castro-Díez et al. 2005; Milla et al. 2010), and several patterns have arisen from this research. There are two main, generally acknowledged clues: (1) Vegetative growth should occur in the optimal period of the year, while reproductive phenophases could spread more over the year. This implies that vegetative growth should show higher phenological flexibility, for development under optimal conditions each year, since Mediterranean areas show very high inter-annual variation in climate (Di Castri and Mooney 1973). (2) Flower development does not require environmental conditions as favourable as for vegetative growth (Mooney and Kummerow 1981; Kummerow 1983). Flowering, however, occurs predominantly in spring in Mediterranean areas (cf. Orshan 1989), although some species like *Arbutus unedo* wait until autumn to perform this phenophase (Guitian and Guitian 1990; Aronne and Wilcock 1997). Other phenophases, such as fruiting, display a more variable chronology (Orshan 1989).

No particular attention has ever been paid to the phytogeographical significance of the sites studied, nor to the evergreen or deciduous habits of the species investigated. For this reason, the models proposed still show some gaps. For instance, during the summer, vegetative growth tends to be continuous in Australian and South African mediterranean sites (Specht et al. 1981), whereas in the Mediterranean basin, summer growth is allowed only after rooting has penetrated deeply enough (Hoffmann and Kummerow 1978; Castro-Díez et al. 2005). In other words, a clear phenological model based on rhythmic growth has never been proposed for the evergreen species in the Mediterranean basin, since the phenomenon involves the whole plant and can be observed also in cambial activity. In fact, in the Mediterranean region, spring, summer and autumn flushings can be recorded at the level of cambial activity in different species, such as *Olea europaea*, *Pistacia lentiscus*, *Rhamnus alaternus*, and *Ceratonia siliqua*, along with many species of oak (de Paolis 1949; Maugini 1949; Fahn 1953; Arbel 1969; Ephrat 1971; Scaramuzzi et al. 1971; Arzee

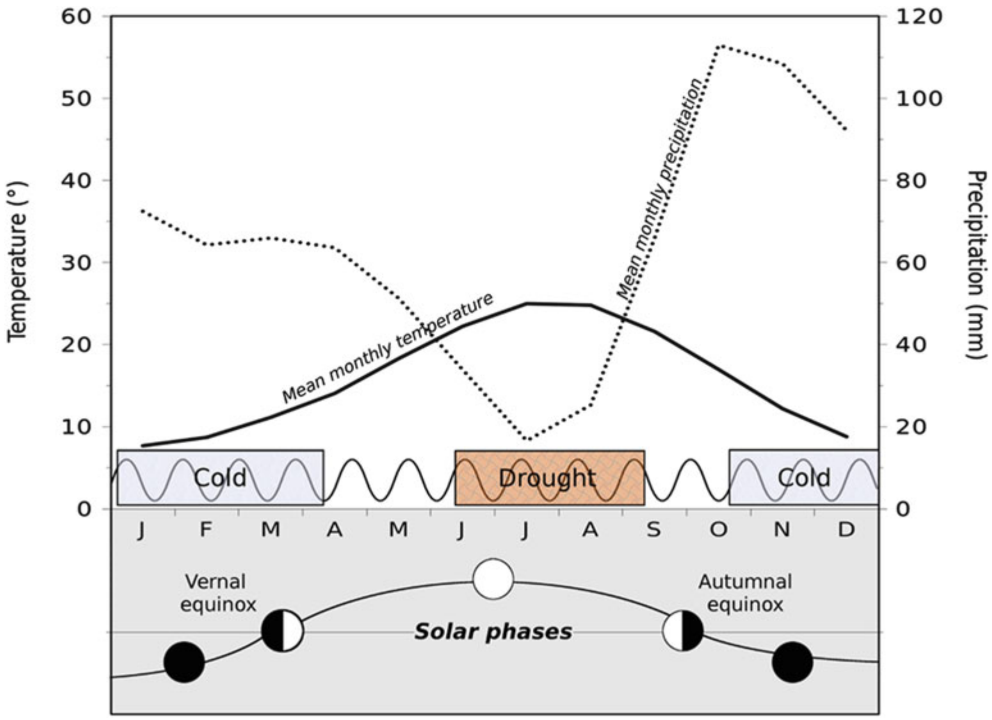


Fig. 1 Growth of Oaks in the Mediterranean Environment. The model shows the periods of vegetative growth in coastal Latium (province Viterbo, Italy). The *curves* of rainfall and temperature correspond to the average climatic conditions of the station. The *sinusoidal curve* indicates the original growth rhythm based on constantly favourable thermal and water conditions (the period of about 25 days is probably connected to the lunar cycle). The *shaded areas* indicate the periods of dormancy (suspension of the vegetative activity imposed by cold or drought). The *bottom curve* shows the solar cycle. Dormancy is broken near the time of the vernal equinox, with buds opening 3 weeks later (cf. Schirone et al. 1996)

et al. 1977; Liphschitz et al. 1985). If environmental conditions are particularly favourable, like mild temperatures in winter or water availability in the dry summer, cambial activity can persist all year long (Liphschitz and Lev-Yadun 1986).

Flowering follows a similar model in many instances. According to Francini Corti (1960), some oaks preserved, during their evolutionary history, adaptive traits typical of a tropical climate, constantly warm and wet. In those climates, endogenous rhythms prevail over external factors, so we can frequently observe vegetatively growing plants together with flowering and fruiting individuals of the same species, or even different phenological phases displayed by different branches of the same plant. The genus *Quercus* started its differentiation under similar environmental conditions, developing sub-continuous anthesis, i.e. a type of anthesis not linked to changing climatic parameters but only endogenously controlled. This attitude is actually displayed by the ability to interrupt the reproductive cycle when external conditions are unfavourable (summer drought or winter cold) and to restart as soon as they turn favourable.

This simple model still needs deeper insight. Indeed, some biological patterns are not yet investigated; it is not clear why and where phen-atavistic rhythms appeared, or why only some species were affected by these phenomena.

3 At the Origin of the Anomalies

Outside the Italian peninsula, these phenomena have been recorded as well in coastal districts in Spain (Elena-Rosselló et al. 1993; Diaz-Fernandez et al. 2004; Pons and Pausas 2012), Greece and Turkey (Bianco and Schirone 1982, 1984, 1985), and as far as the piedmont regions of W Himalaya, in north-central Pakistan (i.e. Murraee Hills, Kagan Valley, Nanga Prabat: cf. Schirone and Spada 1995, 2001). In these areas, a border-line mediterranean climate (sensu Daget 1977), with features intermediate between mediterranean and monsoon regimes (sensu Walter 1968), provides permanently “relaxed” climatic conditions. Here the local vegetation has not been so severely affected by pleni-glacial events, since this mild climate preserved a pre-glacial character. According to this model, species like *Q. suber* or *Q. coccifera*, traditionally considered to exhibit anomalous reproductive cycles, show “complete” cycles.

Direct field observations, analyses of herbarium samples (e.g. Pakistan Museum of Natural History, Islamabad) and information from classic monographs on Fagaceae (cf. Camus 1936-54), show that multiple reproductive cycles are recorded in many species of *Quercus* (i.e. *Q. baloot* Griff., *Q. leucotrichophora* A. Camus, *Q. semecarpefolia*

Smith) and in some species of the closely related genus *Lithocarpus* (Camus 1936-54). All these species share the evergreen habit, which belongs to taxa that differentiated earlier in the evolutionary history of their genera, under tropical climatic conditions. They apparently were not forced to adapt to harsher climates but in some cases to some degree of sclerophylly (cf. De Lillis 1991). Therefore, in the evergreen species, reiterated anthesis and fruiting can be sustained by uninterrupted photosynthetic activity.

On the other hand, deciduous species evolved later, in order to match the climatic deterioration of more recent epochs. The deciduous oaks share the same florogenetic origin of their evergreen ancestors, but they are likely to have adapted to seasonality much earlier and under different evolutionary constraints. In deciduous oaks the necessity to reconstitute foliage in spring requires a large amount of energy. This exhausts metabolic reserves, preventing any additional energy flow into reiterated reproductive processes and inhibiting continuous flowering. The St. John's long shoots (sensu Kramer and Kozlowski 1979) are the only "constant" manifestation left of their subtropical montane atavistic traits dating back to the early Neogene (Schwarz 1936-39). On the other hand, evergreen species have energy left for flowering, thus keeping many more atavistic traits still alive (non-seasonal flowering).

Since phenorhythms in plants are considered to be manifestations of equilibrium between adaptations, competitive demands and local climatic conditions, and since the reproductive organs are very sensitive to environmental changes, anomalies in anthesis or foliation suggest either ongoing changes in the environmental scenario or persistence of previously achieved adaptations.

Sub-continuous anthesis is a primary reproductive strategy in non-seasonal, florogenetically tropical-subtropical humid ecosystems, due to absence of limiting climatic constraints. (Interruptions in this case are due solely to the endogenous control of an intrinsic physiological rhythm). Seasonality induces cyclical patterns in this process. In temperate ecosystems, this pattern is induced by the climatic deterioration of the cold season and, to the south (on continental west sides), by the increasing summer drought, which produce long seasonal gaps in reproductive activity. But in mediterranean climates, on sites where latitude or aspect mitigate winter cold and soil or topography mitigate summer drought, the environmental conditions may become very close to mesic subtropical.

In the central Mediterranean Basin, such habitats are concentrated along the Italian coasts, in areas where topography provides suitable conditions for sufficient increase in local precipitation. Coastal ridges and inselbergs of the Tyrrhenian and southernmost Adriatic districts induce orographic precipitation, dew and mist in many areas with steep coastal slopes or cliffs. These climatic enclaves are indeed the areas where the populations of oaks exhibiting the described anomalies have been recorded: Ausoni-Aurunci Mountains, Mt. Circeo, Mt. Argentario, Mt. Gargano, and southern Apulia, especially along the coast of Salento.

This suggests that the "relaxed" climatic characteristics of these areas do provide conditions favourable to the manifestation of atavistic traits in *Quercus*, which account for adaptations achieved earlier in their evolutionary history under subtropical climatic conditions. Moreover, there is sufficient circumstantial evidence to support the statement that the anomalies in reproductive cycles of locally important oak taxa are frequent enough in these areas to represent the rule (cf. Fig. 2 in Schirone and Spada 1995).

Anomalous phenorhythms, in the form of complex reproductive mechanisms, might thus reveal local persistence of genetically inherited adaptive traits not yet deleted by the climatic conditions of the present-day oak species ranges. We therefore consider the geographical concentration of the anomalous reproductive cycles as the legacy of ancient, relic genomes adapted to climatic conditions which might have been occurring in parts of a previous ancient range of the species, prior to the establishment in those areas of a Mediterranean–type climate. This relict nature seems to be consistent with a not yet completely achieved (or necessary) harmony with the mediterranean seasonality.

If this line of evidence is accepted, many patterns in the biographies of these species might be clarified.

4 Evolution During Environmental Change

The oaks were involved more than other taxa in the environmental changes that eventually shaped the Mediterranean climate in Paleo-Europe since the onset of mid-Neogene. Among them, the evergreen species are likely to have been less affected by the Messinian and Pliocene climatic deteriorations, which are likely to have triggered the development of deciduousness in many sections of the genus *Quercus* (Schwarz 1936-39).

The reiterated establishment of arid conditions in the western Mediterranean after the dramatic Messinian events favoured, during the Pliocene, in situ evolution of scleromorphic evergreens from subtropical ancestors, which had survived up to 3.2 Myr BP (Estabrook 2001), at least in areas corresponding to present-day southeastern France (Suc 1984) and northwestern Italy (Principi 1942).

Quercus subg. *Sclerophyllodrys* (e.g. *Q. ilex s.l.*) is therefore likely to have developed sclerophylly during this long time span and part of the Pleistocene from an originally laurophyllous stock of subtropical, eastern origin (Zohary 1973). The process is apparently not yet fully developed (De Lillis 1991), as suggested by comparison of real drought-adapted sclerophylls (e.g. *Ceratonia*, *Pistacia*, cf. Mai 1989). This process is probably even more incomplete in *Q. suber*, which is likely to have originated from a more continental stock of oaks. This suggests that different types of climatic constraints related to the increasing seasonality of the late Neogene and the Quaternary interfered eventually with a pre-existing attitude toward continuous flowering exhibited by these lineages.

Other characteristics in oaks stress their non-complete release from the subtropically adapted syndrome. Genera of tropical florogenetic origin still have representatives in the Mediterranean regions today (*Ficus*, *Olea*, *Pistacia*, *Rhamnus*, *Ceratonia*) that show sub-continuous cambial activity, apparently as adaptation (sensu Begon et al. 1996) to the low degree of seasonality in the original ecosystems. The Mediterranean evergreen oaks *Q. ilex*, *Q. coccifera* and *Q. suber* also show sub-continuous cambial activity, in addition to anomalous phenotypic reproductive cycles, suggesting parallel evolutionary histories.

The processes determining adaptation (i.e. sclerophylly) to the modern Mediterranean climate and seasonality would seem more likely to have operated on subtropical ancestors in areas where ubiquity of scleromorphic, drought-tolerant evergreens is recorded earlier and persisted for a longer time. In southern France and the western Mediterranean, extremely dry conditions are documented many times from 3.2 up to 1.2 Myr BP. This is likely to have induced, along with in situ evolution of subtropical species into lineages adapted to seasonality and drought, also the local extinction of most of the subtropical flora (cf. Suc 1984) in the north-westernmost outposts of the Mediterranean domain.

On the other hand, a long period of cooler climate is documented during part of that time span (3.4 to 2.4 Myr BP), in parts of emerging southern Italy (Bertoldi et al. 1989). This area hosted a mesic, temperate arboreal flora up to the onset of Northern Hemisphere glaciation around 2.4 Myr BP, when species adapted to seasonal drought recolonized the area. This is likely to have provided, in south-Tyrrhenian areas of the late Pliocene, at least in maritime districts, the environmental diversity and gradients needed to preserve ancestral (subtropical) traits in part of the arboreal flora up to more recent times.

This "Italian delay" might suggest a less intense extinction process in the subtropical mesic flora of the Tertiary and a lower degree of in situ evolution to seasonality in more eastern areas in the Mediterranean. This means the establishment of a NW-SE gradient in the mesic subtropical legacy in the area already in the late Tertiary. The gradient tracks, in the opposite direction, the more remote westward spread of laurophyllous stocks of Indo-Malesian origin (*Q. ilex*-*Laurus*: cf. Zohary 1973) during the early Neogene (including ancestors of *Quercus* subg. *Sclerophyllodrys*: cf. Palamarev 1989; Mai 1989). This suggests increase toward the east of the taxonomic and adaptive legacy of the subtropical laurophyllous florogenesis.

5 Modern Phytogeographical Affinities

With the onset of the glacial cycles of the Quaternary, major range pulsations and a gradual decimation of the arboreal flora in the Mediterranean regions occurred (Walter and Straka 1970), leading to the final taxonomic turnover of the Mediterranean vegetation into the modern assessment, around 1.6 Myr BP (Estabrook 2001). The climate achieved a high degree of seasonality, with winter cold stress (temperate continental climate) or summer drought stress (mediterranean climate, sensu stricto), according to latitude and elevation. Apparently, enclaves of subtropical climate dwindled gradually throughout the Mediterranean during this time (Thunell et al. 1985; Rio et al. 1990), with partial recovery during the earlier interglacials.

Nevertheless, evidence for the persistence of the pre-Quaternary legacy can still be found in the present-day phytogeography of the Italian peninsula. Here, the areas where a particularly high concentration of evergreen oaks with anomalous reproductive cycles has been recorded coincide with the present-day westernmost isolated outposts on the European continent of two prominent temperate deciduous taxa with Caucasian-Himalayan affinity: *Acer lobelii* (see *A. cappadocicum*) and *Alnus cordata* (see *A. cordifolia*). These species are locally frequent in stands of mesic deciduous forests from S Latium to Calabria (Schirone and Spada 1995). This outstanding spatial coincidence has major implications for the understanding of the pattern. Both species are widespread in the mesic, species-rich, broad-leaved forests of the Colchis, in the western Caucasus (Euxinian floristic domain), where abundant orographic precipitation in summer meets the basically mediterranean regime that rules along the coasts of northern Anatolia, producing very humid, warm-temperate, climatic conditions (Walter 1968). These occur as well along the steep slopes south of the Caspian sea (Hyrcanian domain), where similar conditions with low seasonality favour luxuriant, species-rich broad-leaved forests dominated by a Euro-Siberian flora (e.g. *Carpinus betulus*, *Taxus*) in a fully subtropical climatic enclave (Walter 1968; Browicz 1982). *A. cappadocicum* occurs as well in the western Himalaya, where anomalous phenorhythms of oaks have been recorded (Schirone and Spada 1995, 2001) and where this species reaches its easternmost range limit in Eurasia (Zohary 1973; Browicz 1982). The rich floristic structure of these Euxino-Hyrcanian and W Himalayan forests is considered to be the result of a particularly low impact by the climatic disturbance during the last pleni-glacial (Zohary 1973). In this sense, the combined concentration of the Caucasian-Himalayan *Acer* *lobelii* and *Alnus cordata* in mesic deciduous forests in central and southern Italy might suggest that the Italian areas have also been scarcely affected by the late-Quaternary climatic deterioration. These areas might therefore be interpreted as the legacy of a lower degree of local forest disturbance during last pleni-glacials (Schirone and Spada 1995).

It has to be stressed that these stands are spatially contiguous or even in catenal contact with the stands of evergreen oaks that display the anomalous phenorhythms and continuous flowering described herein. Since these areas escaped major forest disturbance during the last pleni-glacial, the outlines of the pattern become clear. If the spatial occurrence of phenological anomalies in evergreen oaks is superimposed on the pattern of these phytogeographical affinities, a satisfactory delimitation can be drawn of presumptive areas where forest refugia survived during the last pleni-glacial. In these isolates, the low constraints of environmental selection due to the lesser climatic changes in the late Quaternary enhanced the accumulation of genetic variation and the conservation of atavistic traits in local evergreen oaks.

6 Additional Evidence

Some significant spatial coincidences stress the refugial status of these areas. Site coexistence of *Fagus* and *Laurus* in forest communities is recorded in Tyrrhenian Italy at 42° N latitude (the coastal inselberg Tolfa). This suggests similarities with Plio-Pleistocene fossil aggregations, which persisted in the region as late as the middle Holocene (climatic optimum) on sites with nearly subtropical conditions.

In other parts of Tyrrhenian Italy where the anomalies occur, some of the highest densities of arboreal species are to be recorded today. In Campania (Mts. Picentini), where all the Italian trees but *Picea excelsa* coexist along with many taxa of Caucasian, Euxinic and Himalayan affinity (e.g. *Alnus*, *Acer*, *Staphylea*, *Hypericum*), the low degree of altitudinal differentiation reminds one of the pattern of floristic accumulation characteristic for the eastern coast of the Black Sea (Colchis), where relic laurophyllous taxa (e.g. *Laurus*, *Rhododendron*, *Prunus laurocerasus*) suggest the area to be one of the largest late-Quaternary forest refugia in western Eurasia.

Similar patterns can be observed in many forest areas in Latium (the chains of Mts. Lucretili, Sabini, Aurunci). There is a high degree of polymorphism south of 42° N latitude in oaks of Sect. *Robur*. This, the outstanding occurrence of *Styrax officinalis* in the Roman area, and the development of an altitudinal *Genisteae* belt on the Roman volcanoes (Colli Albani: *Citysus scoparius*, *Spartium junceum*, *Adenocarpus complicatus*) (Montelucci 1976-1977) and on Mt. Vesuvio (*Spartium junceum*) all stress a complex pattern of phytogeographical nestedness along the NW-SE gradient of the Italian peninsula, along which species with relic (Tertiary) status are scattered: Liguria (Cinque Terre), Tuscany (Etruscan coast), southern Abruzzi (Mts. Frentani), Calabria, Sicily, Sardinia, and Corsica. This parallels the NW-SE extinction gradient of pre-Quaternary woody species (Schirone and Spada 1995).

In many areas of Apulia and some of Basilicata (Senise), the phenomenon is even more impressive. Here, along with the absence of *Fagus* and its common associates, at low altitude, there is a significant concentration of almost all the Italian oak species, both mesophytic and xerophytic (cf. Fig. 1 in Schirone and Spada 1995). Moreover, in these areas, the atavistic phenorhythms in oaks nearly displace the common modern ones. Here, the species that Francini Corti (1966, 1967) recognized as "southern paleo-Aegeic stock" (i.e. *Q. trojana*, *Q. macrolepis*, *Periploca graeca*, *Salvia triloba*, *Phlomis fruticosa*, *Asyneuma limonifolium*, and *Campanula versicolor*), which belong to modern east-Mediterranean vegetation types, are probably the last remnants of a global southeastward retreat of the flora of the late Tertiary (cf. Schirone and Spada 1995).

Several genetic studies on Italian evergreen oaks (Bellarosa et al. 2005; Simeone et al. 2009) support this evidence. A geographical organization of the *Quercus suber* plastid genetic variation was evident from the PCR-RFLP haplotype frequency map reported in Simeone et al. (2009). Among the total of five haplotypes detected in the entire cork-oak distribution range, three occur in the western part of the species range (Iberian Peninsula, France, North African Mediterranean coast); the remaining lineages only appeared outside the Italian peninsula, separated by at least four mutations from the western haplotype groups. A closer haplotype relationship with eastern members of the *Cerris* group (*Q. trojana*-*Q. macrolepis*) could be documented in the Salento region. Another exclusive cork-oak haplotype was detected by Magri et al. (2007), based on microsatellite markers, located in north-central Italy and with its southernmost occurrence in central Latium. On the other hand, *Q. ilex* and *Q. coccifera* shared haplotypes with *Q. suber*, especially in the western part of the cork-oak range, whereas the Italian samples were unique or identical to the Greek and Balkan samples. Congruently, the high variation and eastern-Mediterranean affinities of nuclear ribosomal ITS spacer variants of Italian oaks were discussed in Bellarosa et al. (2005), and the occurrence of suggested ancestral *Q. suber* ITS sequences was detected in Salento (Simeone et al. 2009).

Additional evidence supporting the refugial status of these areas might be found in the unexpectedly large individuals of *Quercus*, *Taxus*, *Fagus*, *Carpinus betulus* and *Pinus halepensis* recorded in many stands in Apulia and in one of the last old-growth forests in Abruzzi

("Abetina di Rosello"). These trees of uncommon heights and diameters are by no means the result of particularly favourable edaphic conditions, which do not occur at least at the Apulian sites. Since no direct correlation between height, diameter and age of trees has been found (cf. Piovesan et al. 2005; Schirone et al. 2005), the large, local populations of huge trees are rather likely to be the legacy of relic genotypes preserved in these areas, which acted as refugia for "nemoral" genotypes with large leaves, high levels of evapotranspiration and increased sensitivity to frost during the harsh pleni-glacials.

Conclusions

Refugial areas are crucial in the history of a local vegetation. Here, forest stands, arboreal species and genomes of interglacial and late-Tertiary affinities were preserved from local extinction in restricted enclaves, thanks to the persistence of favourable meso- or micro-climatic conditions during periods when widespread climatogenic steppes and semi-deserts dominated most of southern Europe. The post-glacial recolonization processes started from here and developed according to the relic biotypes that differentiated there during long periods of glacial isolation, often giving origin to lineages of neo-endemisms. These areas are of major importance for nature conservation. According to the most recent simulation-based predictions, in the changing environmental scenario of the near future, the refugial areas of the past are likely to become the locations where species and plant communities will be able to withstand the most severe climatic deterioration. Identification of such areas in the present-day landscape is therefore a major issue in conservation policies and resource management.

Traditionally, identification of refugial areas was based on macrofossils and on palynological data (cf. Huntley and Birks 1983) that pointed out sites with highest concentrations of arboreal species during pleni-glacials. More recently, phylogeographical data, which relate genetic components and allele frequencies to species ranges (Avise 2000), improved the delimitation of potential refugial areas for forest stands. These methods supported the established opinion that the Mediterranean peninsulas and the Caucasian districts facing the Black Sea (Colchis: cf. Brewer et al. 2002) were the main refugial macro-districts in Europe, where the oldest genotypes of arboreal species have been preserved. But these districts are not necessarily characterised by high intra-specific genetic diversity. As shown by Petit et al. (2002), the greatest genetic diversity in woody species is found in populations scattered through central Europe. This is a consequence of the post-glacial recolonization processes, which started from refugia in southern Europe, where only few genotypes survived, and converged eventually further north.

Indeed, reconstructed geographical patterns of genetic diversity produced valuable results to characterize numerous forest refugia across the Mediterranean and Europe. These regions, however, are among the most complex and heterogeneous areas of the world from environmental and biogeographical points of view. A merely optimistic application of the phylogeographic approach here is likely to produce ambiguous or incomplete information. Researchers should be aware of the multiple caveats concerning phylogeographic data analysis and inference, recognizing that the stochastic variance of the coalescent process, the influence of broad (geographic) and fine scale (landscape) environmental variables, and the exceptional complexity of tree evolutionary pathways could only be avoided by an open-minded, pluralistic approach (Weiss and Ferrand 2007). For instance, in an explicit phylogeographic context, artefacts may result from questionable reliability on single-site data sets, non-application of the most appropriate statistical tools for making inferences, and lack of consistent sampling across a whole biogeographical region, often combined with an oversampling of some putative key populations within a pre-defined area.

Several areas still remain poorly explored (e.g. North Africa, the Middle East), and future attention should focus on integration of a vast array of data and on improved sampling of these regions. According to the data presented here, (at least) two Italian regions described in this work belong to the group of yet overlooked areas (Fig. 2). In fact, all phenological observations, phytogeographical studies and historical recordings agree with previous genetic work based on well-aimed, dense samplings and multi-gene approaches to indicate the central Thyrrenian coast of peninsular Italy and the Salento region in southeastern Italy to have acted as glacial refugia (Bellarosa et al. 2005; Magri et al. 2007; Simeone et al. 2009). Moreover, these regions could constitute a model to select conservation areas according to the principles of conservation biogeography (cf. the case of red oaks in Mexico and Central America: Torres-Miranda et al. 2011)

The possibility to identify areas of forest refugia during the last pleni-glacial through combined investigations of species biorhythms and distribution ranges has been tested successfully in this work. A method based on study of spatial coincidence between anomalous phenorhythms, relaxed climatic conditions and local concentration of phytogeographically significant taxa seems therefore to be a highly reliable approach to involve genetics, demographic dynamics, species biology, evolutionary legacy

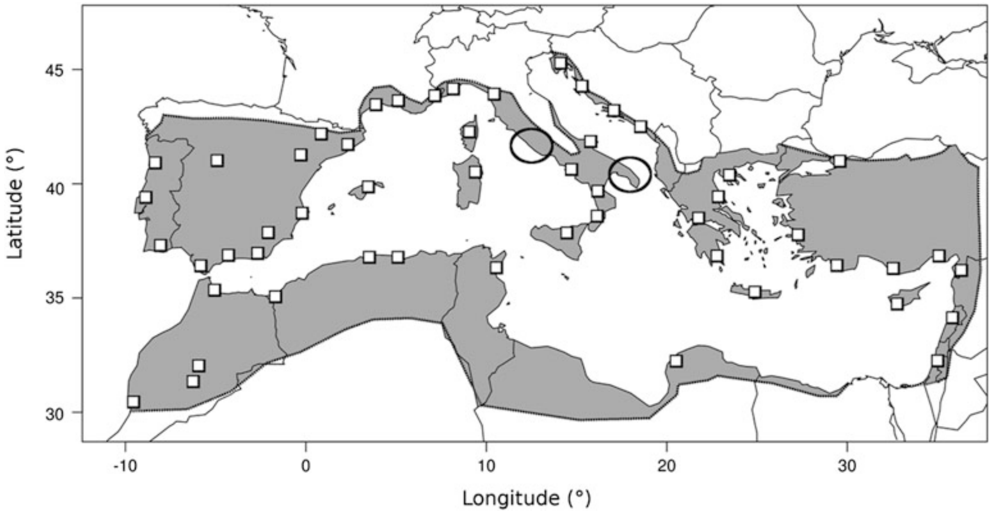


Fig. 2 Geographical Distribution of Plant Refugia within the Mediterranean Region (*grey area*). *Squares* indicate the hotspots identified by Médail and Diadema (2009), *circles* the refugial areas proposed in this work

and habitat requirements at the organismic level to understand the true nature of the genetic structure of species and the importance of still existing segments of forest refugia from the last full-glacial period.

Acknowledgements We thank Emanuele Ziaco for drawing the figures.

References

Alaoui-Sossé B., Ricaud S., Barnola P., Dizengremel P., 1996. Rhythmic growth and carbon allocation in *Quercus robur*. Sucrose metabolizing enzymes in leaves. Physiol. Plant., 96: 667–673.

Alatou D., Barnola P., Lavarenne S., Gendraud M., 1989. Caractérisation de la croissance rythmique du chêne pédonculé. Plant Physiol. Biochem., 27: 275–280.

Arbel E., 1969. The development of cork in *Ceratonia siliqua* L. (Carob tree). M. Sc. Thesis, Tel-Aviv Univ. (in: Liphschitz and Lev-Yadun, 1986).

Aronne G., Wilcock C.C., 1997. Reproductive phenology in Mediterranean macchia vegetation. Lagascalia 19: 445–454.

Arzee T., Arbel E., Cohen L., 1977. Ontogeny of periderm and phellogen activity in *Ceratonia siliqua* L. Bot. Gaz., 138: 329–333.

Avise J.C., 2000. Phylogeography: the history and formation of the species. Harvard University Press. Cambridge, Ma, London, UK.

Axelrod, D.I., 1973. History of the Mediterranean Ecosystem in California. In Mediterranean Type Ecosystems: Origin and Structure, eds. F. di Castri and H. A. Mooney, pp. 225–277. Berlin, Springer-Verlag

Bailey R.G., 1998. Ecoregions: The ecosystem geography of oceans and continents. Springer-Verlag. New York.

Barnola P., Alatou D., Lecointe A., Lavarenne S., 1990. Étude biologique et biochimique du déterminisme de la croissance rythmique du chêne pédonculé (*Quercus robur*). Effets de l'ablation des feuilles. Ann. Sci. For., 21: 619–631.

Barnola P., Crochet A., Payan E., Gendraud M., Lavarenne S., 1986. Modifications du métabolisme énergétique et de la perméabilité dans le bourgeon apical et l'axe sous-jacent au cours de l'arrêt de croissance momentané de jeunes plants de chênes. Physiol. Veg., 24 : 307–314.

Barros Gomes B., 1876. Etude sur les éspèces de chênes forestiers du Portugal. J. Sci. Mat., Phys., Nat., 5: 235–241.

Battandier M., 1894. Considarations sur les plantes refugiees rares ou en voie d'extinction de la flore algerienne. Association Francaise pour l'Avancement des Sciences, Congres de Caen, Paris

Begon M., Harper J.L., Townsend C.R., 1996. Ecology individuals populations and communities. Blackwell, Oxford.

Bellarosa R., Simeone M.C., Papini A., Schirone B., 2005. Utility of ITS sequence data for phylogenetic reconstruction of Italian *Quercus* spp.. Molecular Phylogenetics and Evolution, 34: 355–370.

Bennett K.D., 1997. Evolution and ecology. Cambridge University Press, Cambridge

Bertoldi R., Rio D., Thunell R., 1989. Pliocene-Pleistocene vegetational and climatic evolution of the South-Central Mediterranean. Palaeo, Palaeo, Palaeo, 72: 263–275.

Bianco P., 1961. Ricerche sul ciclo riproduttivo di specie del genere *Quercus* della Flora italiana. VI. Contributo alla biologia di *Q. trojana* Webb. in Puglia. Annali Accademia Italiana di Scienze Forestali, 10: 59–96.

Bianco P., Schirone B., 1982. Nuove osservazioni sul ciclo riproduttivo della quercia spinosa in Puglia. Annali Accademia Italiana di Scienze Forestali, 31: 3–52.

Bianco P., Schirone B., 1984. Osservazioni sui cicli riproduttivi della quercia spinosa in Grecia. Atti e Relazioni dell'Accademia Pugliese delle Scienze. Nuova serie. Vol. 42 (2): 3–37.

Bianco P., Schirone B., 1985. On *Quercus coccifera* L. s.l.: variation in reproductive phenology. Taxon, 34(3): 436–439.

Borchert R., 1973. Simulation of Rhythmic Tree Growth under Constant Conditions. Physiologia Plantarum, 29: 173–180.

Borchert R., 1975. Endogenous Shoot Growth Rhythms and Indeterminate Shoot Growth in Oak. Physiologia Plantarum, 35: 152–157.

Brewer S., Cheddadi R., de Beaulieu J.L., Reille M., 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. Forest Ecology and Management, 156: 27–48.

Browicz K., 1982. Chorology of trees and shrubs in South-West Asia and adjacent regions. Polish Scientific Publishers, Warszawa, Poznan.

Camus A., 1936-54. Les Chênes. Monographie du genre *Quercus* and monographie du genre *Lithocarpus*. Encycl. Econ. de Sylvic., Vol. VI, VII, VIII. Lechevalier, Paris.

Castro-Díez P., Milla R., Sanz V., 2005. Phenological comparison between two cooccurring Mediterranean woody species differing in growth form. Flora, 200: 88–95.

Correia O.A., Martins A.C., Catarino F.M., 1992. Comparative phenology and seasonal foliar nitrogen variations in mediterranean species in Portugal. Ecol. Mediterr., 18: 7–18.

Ciampi C., 1987. Reproductive cycles and ecological considerations in woody plants. Atti Soc. Tosc. Sci. Nat., Mem., Serie B, 94: 25–42.

Corti R., 1954. Ricerche sul ciclo riproduttivo di specie del genere *Quercus* della Flora italiana. I. Osservazioni sul ciclo riproduttivo in *Quercus coccifera* L. Annali Accademia Italiana di Scienze Forestali, 2: 234–264.

Corti R., 1955. Ricerche sul ciclo riproduttivo di specie del genere *Quercus* della Flora italiana. II. Contributo alla biologia e alla sistematica di *Q. suber* L. e in particolare della forma a sviluppo biennale della ghianda. Annali Accademia Italiana di Scienze Forestali, 4: 55–133.

Corti R., 1959. Ricerche sul ciclo riproduttivo di specie del genere *Quercus* della Flora italiana. IV. Osservazioni sulla embriologia e sul ciclo riproduttivo di *Q. ilex* L. Annali Accademia Italiana di Scienze Forestali, 8: 19–42.

Daget P., 1977. Le bioclimat Mediterraneen: caractères généraux, modes de caractérisation. Vegetatio, 34: 1–20.

Deacon N 2010. Population genetic structure, pollen dispersal, and local adaptation in *Quercus oleoides* forests of Costa Rica. PhD Thesis, University of Minnesota

De Lillis M., 1991. An ecomorphological study of the evergreen leaf. Braun-Blanquetia, vol. 7.

De Lillis M., Fontanella A., 1992. Comparative phenology and growth in different species of the Mediterranean maquis of central Italy. Vegetatio, 99/100: 83–96.

de Paolis D., 1949. Ciclo di accrescimento e differenziazione delle gemme in piante perenni nel territorio di Bari. V. L'evoluzione della cerchia legnosa in *Rhamnus alaternus* L. dal dicembre 1946 al marzo 1949. Nuovo Gior. Bot. Ital., n.s., 56: 328–338.

Diaz-Fernandez P.M., Climent J., Gil L., 2004. Biennial acorn maturation and its relationship with flowering phenology in Iberian populations of *Quercus suber*. Trees, 18: 615–621.

Di Castri F., Mooney H.A. (Eds.), 1973. Mediterranean Type Ecosystems. Origin and Structure. Ecological Studies, 7. Springer-Verlag, Berlin, 405 pp.

Elena-Rosello R., de Rio J.M., Garcia Valdecantos J.L., Santamaría I. G., 1993. Ecological aspects of the floral phenology of the cork-oak (*Q. suber* L.): why do annual and biennial biotypes appear? Ann. Sci. For., 50: 114–121.

Ephrat Y., 1971. Periderm development and the annual rhythm of phellogen and cambial activity in *Quercus suber* and *Quercus calliprinos*. M. Sc. Thesis, Tel-Aviv Univ. (in: Liphschitz and Lev-Yadun, 1986).

Estabrook G.F., 2001. Vicariance or dispersal: the use of natural historical data to test competing hypotheses of disjunction on the Tyrrhenian coast. J. Biogeogr., 28: 95–103.

Fahn A., 1953. Annual wood ring development in maquis trees of Israel. Palest. J. Bot. Jerusalem series, 6: 1–26.

Fiori A., Paoletti G., 1933. Flora italiana illustrata. Firenze

Francini Corti E., 1960. Aspetti evolutivi desunti dal ciclo ontogenetico nella sistematica dei generi *Pinus* e *Quercus*. Quaderni Accademia Nazionale dei Lincei, 47: 71–103.

Francini Corti E., 1966. Aspetti della vegetazione pugliese e contingente paleoegeico meridionale della Puglia. Annali Accademia Italiana di Scienze Forestali, 15: 137–194.

Francini Corti E., 1967. Problemi di fitogeografia della Puglia. Archivio Botanico e Biogeografico Italiano, 12: 195–226.

Greathouse D.C., Laetsch W.M., Phinney B.O., 1971. The shoot-growth rythm of a tropical tree, *Theobroma cacao*. American Journal of Botany, 58: 281–286.

Guitian J., Guitian P., 1990. Fenología de la floracíon y fructificacíon en plantas de espinal del Bierzo (León, Noroeste de España). An. Jard. Bot. Madrid, 48: 53–61.

Haffer J., 1982. General aspects of the refuge theory. Biological diversification in the tropics (G. Prance Ed.), pp. 6–24. Columbia University Press, New York

Hampe A., Petit R.J., 2005. Conserving biodiversity under climate change: the rear edge matter. Ecology Letters, 8, 461–467.

Hoffmann A., Kummerow J., 1978. Root studies in the Chilean matorral. Oecologia, 32: 57–69.

Huntley B., Birks H.J.B., 1983. An atlas of past and present pollen maps of Europe: 0–13,000 years ago. Cambridge University Press, Cambridge (UK).

Koehler K., Center A., Cavender-Bares J., 2012. Evidence for a freezing tolerance-growth rate trade-off in the live oaks (*Quercus* series *Virentes*) across the tropical-temperate divide. New Phytologist, 193 (3): 730–744.

Kramer P.J., Kozlowski T.T., 1979. Physiology of Woody Plants. Academic Press, New York, San Francisco, London.

Kummerow J., 1983. Comparative phenology of Mediterranean-type plant communities. In: Kruger F.J., Mitchell D.T., Jarvis J.U.M. (Eds.). Mediterranean-Type Ecosystems. The Role of Nutrients. Springer, Berlin, pp. 300–317.

Lavarenne-Allary S., 1963. Les caractères et la nature de la dormance des bourgeons chez le chêne. C.R. Acad. Sci. Fr., 256: 2217–2219

Lavarenne-Allary S., 1964. Recherche sur la croissance des bourgeons du chêne et de quelques autres espèces ligneuses, Ann. Sci. For., 22: 1–203.

Le Hir R., Pelleschi-Travier S., J.-D. Viémont, Leduc N., 2005. Sucrose synthase expression pattern in the rhythmically growing shoot of common oak (*Quercus robur* L.). Ann. For. Sci., 62: 585–591

Lepetz V., Massot M., Schmeller D.S., Clobert J., 2009. Biodiversity monitoring: some proposals to adequately study species' responses to climate change. Biodiv. Conserv., 18: 3185–3203.

Liphschitz N., Lev-Yadun S., Waisel Y., 1985. The annual rhythm of activity of the lateral meristems (cambium and phellogen) in *Pistacia lentiscus* L., IAWA Bullettin n.s., 6: 239–244

Liphschitz N., Lev-Yadun S., 1986. Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. IAWA Bulletin, 7 (2): 145–153.

Magri D., Fineschi S., Bellarosa R., Buonamici A., Sebastiani F., Schirone B., Simeone M.C., Vendramin G.G., 2007. The distribution of *Quercus suber* choloroplast haplotypes matches the palaeogeographic history of the western Mediterranean. Mol. Ecol., 16: 5259–5266.

Mai D.H., 1989. Development and regional differentiation of the European vegetation during the Tertiary. Pl. Syst. Evol., 162: 79–91.

Maugini E., 1949. L'evoluzione della cerchia legnosa in *Quercus pubescens* L. e in *Quercus ilex* L. nel clima di Firenze. Nuovo Gior. Bot. Ital., n.s., 56: 593–611

Medail F., Diadema K., 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J. Biogeogr., 36: 1333–1345.

Milla R., Castro-Díez P., Montserrat-Martí G., 2010. Phenology of Mediterranean woody plants from NE Spain: Synchrony, seasonality, and relationships among phenophases. Flora, 205: 190–199.

Mitrakos K.A., 1980. A theory for Mediterranean plant life. Acta Oecologica, 1: 245–252.

Montelucci G., 1976-1977. Lineamenti della vegetazione del Lazio. Ann. Bot (Roma), 35–36: 1–107

Montenegro G., 1987. Quantification of Mediterranean plant phenology and growth. In: Tenhunen J.D., Catarino F.M., Lange O.L., Oechel W.C. (Eds.). Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems. Springer, Berlin, pp. 469–488.

Mooney H.A., Kummerow J., 1981. Phenological development of plants in Mediterranean-climate regions. In: Di Castri F., Goodall

D.W., Specht R.L. (Eds.). Mediterranean-Type Shrublands. Elsevier, Amsterdam, pp. 303–307.

Ne'Eman G., 1993. Variation in leaf phenology and habit of *Quercus ithaburensis,* a Mediterranean deciduous tree. J. Ecol., 81(4): 627–634.

Nixon K.C., 2006. Global and Neotropical Distribution and Diversity of Oak (genus *Quercus*) and Oak Forests. In: M. Kappelle (Ed.), Ecology and Conservation of Neotropical Montane Oak Forests. Ecological Studies, Vol. 185. Springer-Verlag, Berlin, Heidelberg

Orshan G., 1989. Plant pheno-morphological studies in Mediterranean type ecosystems. Dordrecht: Kluwer.

Palamarev E., 1989. Palaeobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora. Pl. Syst. Evol., 162: 93–107.

Pereira Coutinho A.X., 1888. Os *Quercus* de Portugal. Boletim de Sociedade Broteriana, 6: 47–116.

Perez-Latorre A.V., Cabezudo B., Nieto Caldera J.M., Navarro T., 1996. Caracterizacíon fenológica y ecomorfológica de alcornocales andaluces (Malaga, España). An. Jard. Bot. Madrid, 54: 554–560.

Petit R.J., Brewer S., Bordács S., Burg K., Cheddadi R., Coart E., Cottrell J., Csaikl U.M., van Dam B.C., Deans J.D., Fineschi S., Finkeldey R., Glaz I., Goicoechea P.G., Jensen J.S., König A.O., Lowe A.J., Madsen S.F., Mátiás G., Munro, R.C., Popescu F., Slade D., Tabbener H., de Vries S.M.G., Ziegenhagen B., de Beaulieu J.-L., Kremer A., 2002. Identification of refugia and post-glacial colonization routes of European white oaks based on chloroplast DNA and fossil pollen evidence. Forest Ecology and Management, 156: 49–74.

Petit R.J., Hampe A., Cheddadi R., 2005. Climate changes and tree phylogeography in the Mediterranean. Taxon, 54: 877–885.

Pignatti S., 1982. Flora d'Italia. Edagricole, Bologna

Piovesan G., Biondi F., Bernabei M., Di Filippo A., Schirone B., 2005. Spatial and altitudinal vegetation zones of the Italian peninsula identified from a beech (*Fagus sylvatica* L.) tree-ring network. Acta Oecologica, 27 (3): 197–210.

Pons J., Pausas J.G., 2012. The coexistence of acorns with different maturation patterns explains acorn production variability in cork oak. Oecologia, on line. doi 10.1007/s00442-011-2244-1

Principi P., 1942. La geologia e la pedologia della provincia di Firenze. L'Universo, n. 7–9, 153 p.

Quézel P., Médail, F., 2003. Ecologie et biogéographie des forêts du bassin méditerranéen. Elsevier (Collection Environnement), Paris

Rio D., Sprovieri R., Thunell R., Vergnaud Grazzini C., Glacon G., 1990: Pliocene-Pleistocene paleoenvironmental history of the western Mediterranean: a synthesis of ODP Site 653 results. Proceedings of the Ocean Drilling Program, Scientific Results, 107: 695–704. Washington

Scaramuzzi F., 1960. Ricerche sul ciclo riproduttivo di specie del genere *Quercus* della Flora italiana. V. Osservazioni sul ciclo riproduttivo e sull'embriologia di *Quercus aegilops* L. Annali Accademia Italiana di Scienze Forestali, 9: 289–322.

Scaramuzzi F., Porcelli Armenise V., de Gaetano A., 1971. Recherches sur le comportment et le rhytme de la callogenèse de fragments de tiges de certains arbres. C.R. Acad. Sci. Paris, 272: 2544–2547

Scarascia Mugnozza G., Schirone B., 1983. Un bosco di sughera presso Brindisi. Monti e Boschi, 6: 47–52.

Scharfetter R., 1953. Biographien von Pflanzensippen. Springer. Wien.

Schirone B., Codipietro G., 1992. Periodicity and aperiodicity in flowering rhythm of trees. Atti del V Congresso Nazionale "Habitat e Salute" dell'Associazione Italiana di Aerobiologia. Montecatini Terme, 14–17 ottobre. pp. 211–216.

Schirone B., Parlante A., Sandoletti L., Tamantini M., 1988. Prime osservazioni sui ritmi fenologici di una cerreta. Informatore Botanico Italiano, 20 (2–3): 704–711.

Schirone B., Spada F., 1995. Anomalies in reproductive phenology and vegetation history: the case of SE Italy. Colloques Phytosociologiques, 24: 847–857.

Schirone B., Codipietro G., Bellarosa R., Schirone A., 1996. Phenological rhythms and heat sums for rest breaking in *Quercus cerris* L. Proceeding workshop in "Inter- and intraspecific variation in European oaks: Evolutionary implications and practical consequences". Eur. Comm. Sc. Res. Develop, 15–16 June 1994, Bruxelles. Off. Publ. of the European Communities, Luxembourg, pp 337–353

Schirone B., Spada F., 2001. Some remarks on the conservation of genetic resources of Mediterranean oaks. Mediterranean Oaks Network, Report of the first meeting, 12–14 October 2000, Antalya, Turkey, pp. 21–26. International Plant Genetic Resources Institute, Rome, Italy

Schirone B., Pedrotti F., Spada F., Bernabei M., Di Filippo A., Piovesan G., 2005. La hêtraie pluri-séculaire de la Vallée Cervara (Parc National des Abruzzes, Italie). Acta Botanica Gallica, 152(4): 519–528.

Schwarz O., 1936-39. Monographie der Eichen Europas, besonders des Mittelmeergebietes. Feddes Rep., Sonderbeih. D. 1–5. Berlin.

Simeone M.C., Papini A., Vessella F., Bellarosa R., Spada F., Schirone B., 2009. Multiple genome relationships and a complex biogeographic history in the eastern range of *Quercus suber* L. (*Fagaceae*) implied by nuclear and chloroplast DNA variation. Caryologia, 62:236–252

Specht R.L., Rogers R.W., Hopkins A.J.M., 1981. Seasonal growth and flowering rhythms: Australian heathlands. In: Specht, R.L. (Ed.). Heathlands and Related Shrublands of the World. B, Analytical Studies. Elsevier Scientific, Amsterdam. pp. 5–13

Suc J.-P., 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. Nature, 307: 429–432.

Taberlet P., Fumagalli L., Wust-Saucy A.G., Cosson J.-F., 1998. Comparative phylogeography and postglacial colonization routes in Europe. Molecular Ecology, 7, 453–464.

Thomas C.D., Cameron A., Green R.E., Bakkenes M., Beaumont L.J., Collingham Y.C., Erasmus B. F. N., Ferreira de Siqueira M., Grainger A., Hannah L., Hughes L., Huntley B., van Jaarsveld A. S., Midgley G.F., Miles L., Ortega-Huerta M.A., Townsend Peterson A., Phillips O.L., Williams S.E., 2004. Extinction risk from climate change. Nature, 427:145–148.

Thunell R.C., Williams D.F., Rio D., Raffi I., Sprovieri R., 1985. Pliocene-Pleistocene history of the Mediterranean: results from deep sea and land-based marine records. Terra Cognita, 5: 89.

Torres-Miranda A., Luna-Vega I., Oyama K., 2011. Conservation biogeography of red oaks (*Quercus*, section *Lobatae*) in Mexico and Central America. Am. J. Bot., 98: 290–305.

Walter H., 1968. Vegetation der Erde in oeko-physiologischer Betrachtung. Stuttgart, 3 Voll.

Walter H., Straka H., 1970. Arealkunde Floristich-historische Geobotanik. Ulmer Verlag, Stuttgart.

Walther G.-R., Post E., Convey P., Menzel A., Parmesan C., Beebee T. J., Fromentin J.M., Hoegh-Guldberg O., Bairlein F., 2002. Ecological responses to recent climate change. Nature, 416: 389–395.

Weiss S., Ferrand N., 2007. Current perspectives in phylogeography and the significance of South European refugia in the creation and maintenance of European biodiversity. In: S. Weiss and N. Ferrand (Eds.), Phylogeography of Southern European Refugia. Springer, Dordrecht, Netherlands.

Willaume M., Pagès L., 2011. Correlated responses of root growth and sugar concentrations to various defoliation treatments and rhythmic shoot growth in oak tree seedlings (*Quercus pubescens*). Annals of Botany, 107: 653–662.

Zohary M., 1973. Geobotanical Foundations of the Middle East. Gustav Fischer, Stuttgart. Swets & Zeitlinger, Amsterdam.

Warm-Temperate Deciduous Forests of Eastern North America

Elgene O. Box

Abstract

Eastern North America has a large region of humid temperate climate, extending from southeastern Canada to south-central Florida and west to Missouri, eastern Oklahoma and eastern Texas. Within this area is a large region of temperate deciduous forest, perhaps the world's largest, with a large area of "southern" forests that may correspond to Kira's concept of warm-temperate deciduous forest. These forests are dominated mainly by *Quercus* species, but *Fagus*, *Liquidambar*, *Nyssa*, and other deciduous trees can also dominate or co-dominate, depending largely on topography. Some important tree species span the full north-south range of the deciduous forests, but some genera have clear "northern" and "southern" species. Oak-hickory forests cover the largest parts of this southern region, but other types include beech and other mesophytic forests, so-called "southern mixed hardwoods", and rich bottomland forests. Some of these southern deciduous forests occur on the coastal plain, which has climates clearly warm enough for broad-leaved evergreen trees. The coastal plain, however, is geologically young and has complex vegetation mosaics determined more by topography and substrate than by climate. As a result, some coastal-plain deciduous forests are permanent and probably not successional to zonal warm-temperate evergreen broad-leaved forests.

Keywords

Absolute minimum temperature • Bottomland forests • Evergreenness • Oak forests • Southeastern US coastal plain • Southern mixed hardwoods • Warm-temperate climate • Zonal vegetation

1 Introduction

Eastern North America has a large region of humid temperate climate that extends from southeastern Canada to south-central Florida and west to Missouri, eastern Oklahoma and eastern Texas. This includes a large area of typical four-season temperate climate, a strip of warm-temperate climate along the outer southeastern coastal plain, and a rather large region of transition from cold to mild winters across the inner coastal plain and piedmont. Most of this region is covered by temperate deciduous forests (e.g. Küchler 1964, Eyre 1980, Vankat 1990, Delcourt and Delcourt 2000, Dyer 2006), although the climate in the south is clearly warm enough for broad-leaved evergreen trees (e.g., Greller 1989).

Warm-temperate climates are well recognized as having warm summers, mild winters, and no consistent dry season. In a global sense (cf Rübel 1930, Schmithüsen 1968; Walter 1970, 1985; Kira 1977, 1991; Greller 1989, Box 1995, Box and Fujiwara 2012), the warm-temperate climate is normally understood as a mostly humid temperate climate with:

– warmer summers and longer growing seasons than in other parts of the temperate zone, and

---

E.O. Box (✉)
Geography Department, University of Georgia, Athens, Georgia 30602, USA
e-mail: boxeo@uga.edu

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*,
Geobotany Studies, DOI 10.1007/978-3-319-01261-2_13, © Springer International Publishing Switzerland 2015

- milder winters, with mostly light frost and no lasting snow cover.

Winter mean temperatures are generally above 0°C and can be above 10°C. Absolute minima are generally not below about –15°C. As a result, the zonal vegetation is normally evergreen broad-leaved forest (cf Woodward 1987), such as the laurel forests of East Asia, southern Brazil, northern New Zealand, and even some montane belts in the tropics. Thermally, some mediterranean and submediterranean climates are also warm-temperate, as in southern Europe. Some drier, more continental climates can also be seen as warm-temperate, including those of the live-oak woodlands of central Texas and the open sclerophyll woodlands of interior Australia.

The concept of warm-temperate deciduous forest was introduced by Kira (1949) for deciduous forests that occur in climates that are warm enough during the growing season for broad-leaved evergreen trees but too cold for them in winter. This suggests climates that are more continental or at least subcontinental, as occur especially on continental east sides in the mid-latitudes. Such forests would be composed of more southern deciduous tree taxa, especially species of *Quercus*.

Some initial goals of the IAVS special session on warm-temperate deciduous forests were to:

- Document the composition and structure of these forests, as well as their landscape dynamics;
- Examine their environmental situations, especially climatic similarities and differences; and
- Understand why these deciduous forests are not replaced by evergreen broad-leaved forests.

The purpose of this chapter is to look at these questions in eastern North America by describing the forest types involved, their composition and dynamic structure, and their environmental constraints.

2 Physiographic Regions of Eastern North America

Eastern North America is a relatively low-lying region, except for the Appalachians, an old mountain chain that reaches only slightly over 2,000 m at its highest points. Most of the remainder of the region can be divided into the following physiographic provinces:

- a piedmont, which extends from Maryland to Georgia and then westward toward the Mississippi river valley;
- an interior lowland (west of the Appalachians) that merges with the piedmont in the south and extends well beyond the Mississippi river to eastern Oklahoma and Texas; and
- an eastern-southeastern coastal plain, that extends from southern New England to Florida and westward along the Gulf of Mexico to Texas and northeastern Mexico.

All three of these physiographic provinces lie entirely within the temperate climatic zone, except for the southernmost parts of the coastal plain.

The climate of eastern North America is generally subcontinental, with large differences between summer and winter temperatures right up to the Atlantic coast and southward to the Gulf coast. Diurnal temperature ranges are also relatively large, as compared for example, with much of Europe and East Asia (cf Box 1995). Some climatic data for eastern North America are given in the Appendix and in the “Overview” chapter (Box and Fujiwara, herein: Tables 8). In eastern North America, mean summer temperatures are generally near or above 25°C (as in East Asia) and mean winter temperatures range from below 0°C in the north to above 10°C in the south. Thus, snow may remain and the soil may be frozen or nearly so for long periods in the north but not in the south.

Winter mean temperatures in eastern North America are generally higher than at the same latitude and corresponding geographic position in East Asia, but extreme minima are lower (Box 1995). As a result, forests in the southeastern USA are deciduous, at positions that would already be (broad-leaved) evergreen in East Asia. The differences in winter temperatures are decisive, both winter means and absolute minima. Winter means in the southeastern USA are always above freezing, but evergreen (broad-leaved) forests only occur where the absolute minima do not go below about −15°C or do so only very infrequently, perhaps only once in a century.

All around the Northern temperate zone, one can usually recognize more northern areas with cooler summers and more southern areas with milder winters. In eastern North America, though, this leaves a large gap in the subcontinental middle, roughly from New York to Tennessee to Missouri (see data in the Appendix). This pattern argues strongly for a division into three parts (cf Box and Fujiwara, herein):

- A cool-temperate zone mainly in New England, with cooler summers (due to higher latitude) and mixed broadleaf-conifer forests involving both non-boreal and boreal conifers;
- A main, generally subcontinental ‘typical temperate’ zone, with four seasons of roughly equal expression and more completely deciduous forests (without conifers at maturity); and
- A warm-temperate zone with milder winters, quite warm-sultry summers, and the potential for evergreen broad-leaved forests, unless winters are too cold or other factors intervene.

While deciduous forest is the zonal vegetation type of the piedmont and interior lowlands, evergreen broad-leaved forest would be the zonal vegetation type on at least the outer portion of the southern coastal plain. In fact, however, both cold temperatures and other factors, namely substrate and topography, do intervene to preclude evergreen broad-leaved forests from most of the southern coastal plain. Deciduous forests occur across much of this warm-temperate region, not only as successional stages but also as permanent vegetation even where winters are "mild" enough for evergreens.

In many ways the coastal plain is the most interesting region because it constitutes one of the world's largest regions in which the substrate does not match the current climate. The substrate is mostly recently deposited sand, ranging from fine-humic sands to coarse, sterile sandhills. These sand substrates are quite different from the zonal clay soils of warm-temperate climates, from the "fossil" red-clay soil of the piedmont, from the brown forest soils further north and northwest, and from the loess deposits in the wide lower-Mississippi floodplain. On the generally flat, low-lying topography, small differences in relief have large consequences for drainage, soil aeration, availability of soil water, soil type (mineral vs histosol), and vegetation type. As a result, there is actually relatively little zonal vegetation on the coastal plain and no extensive expanse of zonal evergreen broad-leaved forest. Instead, most of the region was covered originally by a matrix of fire-maintained pine savannas plus mosaics of topogenic wetlands and dry scrub on upland and other dry sand (cf Wells 1942, Christensen 1988). Closed forest is confined largely to lowlands and other areas of better, wetter but aerated soils.

Such lowlands include in particular the floodplains of major rivers, which overflow occasionally beyond their channels, resulting in erosion-deposition cycles and the building of natural levees and backwater areas. Floodplains are especially wide on the flat coastal plain but also extend sometimes well up into the piedmont. On the coastal plain the floodplains take the form of broad alluvial valleys called 'bottoms' or 'bottomland', which include not only the streamside inundation terraces but also the backwater areas behind the levees (called first bottoms); deep-water areas in depressions, sloughs and old river channels; and the transition to the adjacent uplands. On these very gradual slopes one can recognize zones that are semi-permanently flooded, seasonally flooded (usually in winter and early springtime), temporarily flooded (not every year), and eventually only occasionally flooded (i.e., the final transition to the uplands). These bottomlands support, in particular, characteristic bottomland hardwood forests and deep-water alluvial swamps. Especially good descriptions of bottomland zonation and forest types are given by Sharitz et al. (1993) and by Wharton (1978).

The boundary between the coastal plain and piedmont, especially through the Carolinas and Georgia, runs along old shorelines and their old dune systems, now recognizable as "sandhills" along the "fall line" (the innermost reaches of navigable rivers). The sand can be fairly deep, slightly mobile, and very sterile. This boundary is also the boundary between coastal-plain sand substrates and the quite different red clay of the piedmont, left from an earlier, warmer climate. Interestingly, this topographic/substrate boundary also coincides largely with the $-15°C$ isotherm for absolute minimum temperature, often considered the lower temperature limit for evergreen broad-leaved trees (cf Woodward 1987).

3 Forest Regions of Eastern North America

At a time when men could be shot for entering private rural land, E. Lucy Braun (cf Stuckey 1973) was able to gain the trust of landowners and survey much of the deciduous forest area of the eastern United States. Her results were presented as a classification of main forest types, a map of their extent, and detailed descriptions of the composition and structure of these forest types (Braun 1950). The resulting regionalization, with subsequent modification by Greller (1988, see below) is shown in Fig. 1.

Sugar maple (*Acer saccharum*), the leaf on the Canadian flag, is the main dominant across the mixed-forest zone in the north, which extends from the western Great Lakes area to Atlantic Canada. Sugar maple is joined in the most continental area, the Maple-Basswood region (southern Wisconsin and Minnesota) mainly by *Tilia americana* (basswood) and across much of Ohio, Indiana and southern Michigan, in a Beech-Maple region, by *Fagus grandifolia* (American beech).

The richest forests, in terms of species, are the Mixed Mesophytic Forests, which occur on the wetter (windward) western side of the Appalachians, mainly on the Allegheny Plateau and Cumberland Plateau from southwestern Pennsylvania to northeasternmost Alabama (see also Hinkle et al. 1993, and their extensive bibliography). The canopy in these forests can reach 40 m in height and may contain about ten co-dominant species (but potentially more than 20), especially *Liriodendron tulipifera* and species of *Fraxinus*, as well as character species *Tilia heterophylla* and *Aesculus octandra*. Further west, and extending from the lower Ohio Valley to northernmost Mississippi, is the Western Mesophytic Forest, in which *Quercus* is becoming more important westward but many other canopy trees still remain, including *Liriodendron*, *Nyssa*, *Tilia*, *Carya* and *Liquidambar* (cf Greenberg et al. 1997). Unlike the mixed mesophytic forests, this western mesophytic region "is not characterized by a single climax type" (Braun 1950) but is rather a

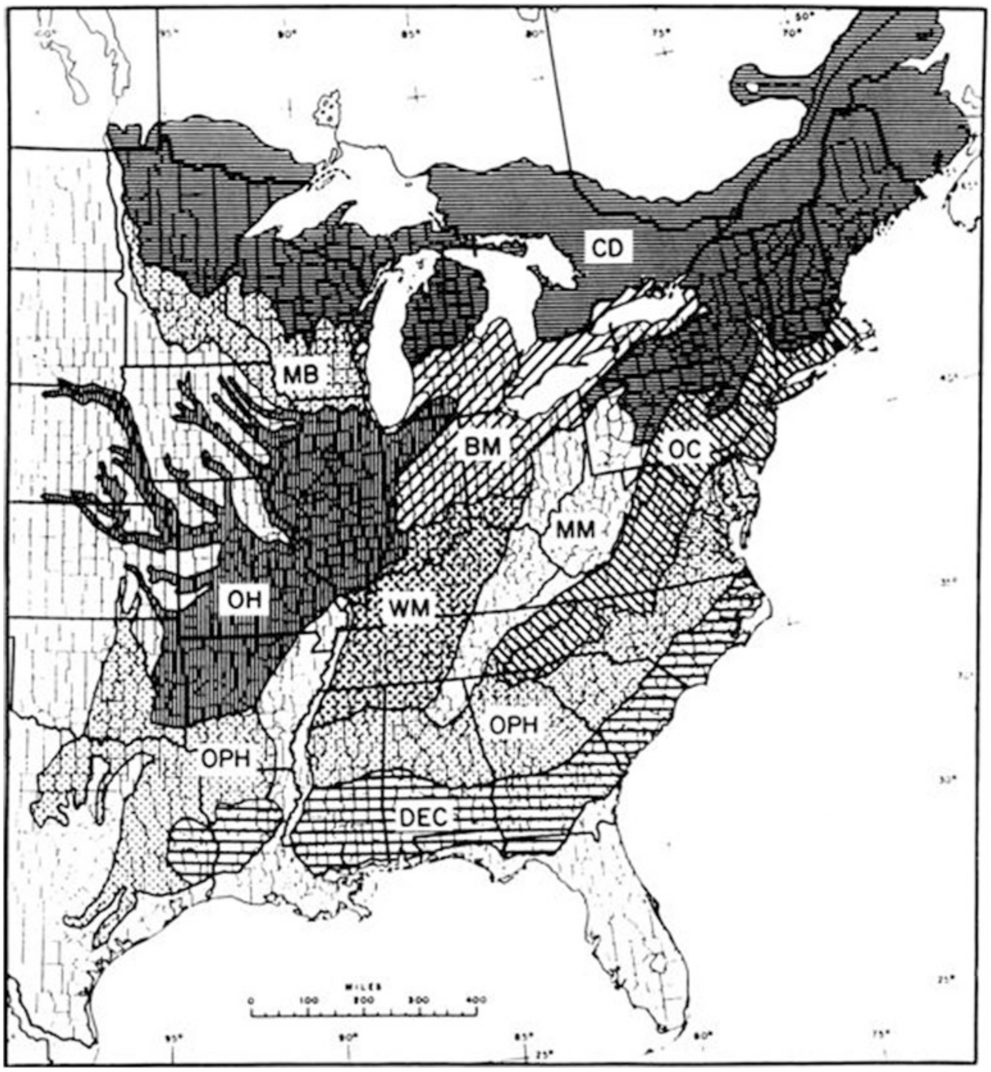


Fig. 1 Forest types of Eastern North America (from Lucy Braun 1950, modified by Greller 1988). All types represent deciduous forests except the mixed conifer-deciduous forests (CD) in the north and the semi-evergreen forests with conifers (DEC) in the south. Types in boldface are mainly southern forest types; these are potentially warm-temperate deciduous forests except for the Appalachian oak-chestnut (OC) forests, which occur at higher elevation and lower summer and winter temperatures. Southern mixed hardwoods (under DEC) are largely deciduous and also represent warm-temperate deciduous types. *CD* Conifer-Deciduous Mixed Forest, *MM* Mixed Mesophytic Forest (many species, no dominant), *WM* Western Mesophytic Forest (Quercus + co-dominants), *OC* Appalachian Oak Chestnut Forest (Quercus-Castanea, *BM* Beech-Maple Forest (Fagus grandifolia-Acer saccharum), *MB* Maple-Basswood Forest (Acer saccharum-Tilia, *OH* Oak-Hickory Forest (Quercus-Carya), *OPH* Oak-Pine-Hickory Forest (pine successional), *DEC* Deciduous-Evergreen-Conifer Forest ("Southern Mixed Hardwoods")

complex mosaic resulting from substrate and other heterogeneity. Braun and subsequent authors have recognized various subregions, including an *Acer-Quercus-Carya-Fraxinus* association in Tennessee; *Fagus-Quercus* forests especially in uplands of Kentucky and Tennessee; more oak-dominated forests toward the southwest; and the "big meadow" of *Fraxinus-Quercus-Carya* savanna-woodlands in the Kentucky Bluegrass region (cf Bryant et al. 1993).

The remaining three forest types are all dominated by oaks and are far enough south to be candidates for warm-temperate deciduous status. From the southern and central Appalachians to the mid-Atlantic coast (e.g., New Jersey) and into southernmost New England is an Oak-Chestnut region (cf Stephenson et al. 1993). The once dominant *Castanea dentata* was eliminated by chestnut blight in the early 1900s, and its place in these forests has subsequently been filled largely by its canopy companions, especially *Quercus prinus* (chestnut oak). Across the extensive southern piedmont is the Oak-Pine-Hickory region that reaches westward as far as eastern Texas and Oklahoma, with a gap in the wide Mississippi River floodplain (cf Skeen et al. 1993). The name of this main region of southern oak forests is a slight misnomer, however, since the pines are mostly heliophilic successional species that would disappear in

Table 1 Traditional forest types of Eastern North America (Based on Lucy Braun 1950, modified by Greller 1980; 1988)

Sub-boreal mixed forest	Northern broad-leaved deciduous trees (*Acer*, *Betula*, etc.) + boreal conifers (*Picea* + *Abies*) + temperate conifers (*Pinus strobus*, *P. resinosa*)
Deciduous forests	Northern Hardwood [Mixed] Forest (*Acer saccharum*, *Betula* spp., *Fagus*, etc. + *Pinus strobus*)
	Beech-Maple Forest (*Fagus grandifolia* + *Acer saccharum*)
	Maple-Basswood Forest (*Acer saccharum* + *Tilia americana* spp.)
	Mixed Mesophytic Forest (*Fraxinus*, *Tilia*, *Liriodendron*, etc. (no clear dominant, ***Quercus*** less importamt)
	Western Mesophytic Forest (***Quercus*** + other dominants) (*Fraxinus*, *Tilia*, *Liriodendron*, *Acer* etc.)
	Appalachian **Oak-Chestnut** Forest (***Quercus*** + *Castanea*) (eliminated by chestnut blight: → mixed *Quercus* forest)
	Piedmont **Oak-Hickory** Forest (***Quercus*** + *Carya*) (with *Pinus* important in successional stages)
	Western **Oak-Hickory** Forest (***Quercus*** + *Carya*) (S: mainly *Q. stellata* + *Q. marilanidca*, N: *Q. macrocarpa*)
Southern mixed forest	"Southern Mixed Hardwoods" Forest (southern deciduous + few evergreen broad-leaved trees)
Warm-temperate region	Potentially Evergreen Broad-Leaved Forest (*Q. virginiana* forest on uplands/coastal strand, laurophyll "bay forest" in moist depressions)

The locations of these forest types are shown in Fig. 1. The concept of "southern mixed hardwoods" (mainly deciduous but with some broad-leaved evergreens), as the potential "climax" vegetation of the southeastern coastal plain, was proposed by Quarterman and Keever (1962). A warm-temperate evergreen *Quercus virginiana-Magnolia grandiflora* region, mainly in northern and peninsular Florida, was recognized and separated by Daubenmire (1978, 1990).

closed mature forests, and the hickories (*Carya* spp.) are not always important (cf Ware 1992) and do not always quite reach the canopy in large numbers. Finally, covering most of (drier) Illinois, Missouri and Arkansas is an Oak-Hickory region that differs by not having the southern pines and by being shorter (12–15 m near their western limit) and simpler, co-dominated eventually by only two oak species.

The map and forest types of Braun quickly became the paradigm for understanding the deciduous forest area of eastern North America. On the southern coastal plain, though, the actual vegetation was not Oak-Pine-Hickory so much as vast areas of fire-maintained pine savanna, dominated by *Pinus palustris*, the only pine with seedlings adapted to survive frequent fire (cf Bartram 1791; Sargent 1884; Harper 1913, 1928; Frost et al. 1986; Christensen 1988; see map in Ware et al. 1993: Figure 4). What would be the potential vegetation if fire were eliminated? This question was answered by Quarterman and Keever (1962), who proposed "southern mixed hardwoods" as the "climax" vegetation of the coastal plain, i.e. a forest composed of mostly deciduous southern tree species plus a smaller number of evergreen canopy and understorey companions. The deciduous trees named were *Fagus grandifolia*, *Quercus alba*, *Liquidambar styraciflua*, *Q. nigra*, *Carya tomentosa*, *C. glabra*, *Q. falcata*, and *Nyssa sylvatica* (in that order). The evergreens included *Quercus laurifolia* and successional *Q. hemisphaerica*; *Magnolia grandiflora* and *M. virginiana*; *Ilex opaca* (which can reach > 25 m with enough time); *Persea borbonia*; and *Prunus caroliniana*. Southern mixed hardwoods (SMH) were included by Küchler (1964) as "southern mixed forest" in his map and booklet on the vegetation of the entire United States. SMH also became the paradigm for understanding the forests of the problematic southern coastal plain and is generally represented (cf Ware et al. 1993) as the successor of the former "longleaf pine forest". Lieth (1973) used the term "warm-temperate mixed forest", which is still widely used, especially in East Asia.

Some evergreen species do not extend to the northern limit of SMH but do become more important to the south. In northern Florida, for example, evergreen *Quercus virginiana*, with its spreading crown and long lifespan, becomes the potential dominant, and Daubenmire (1978, 1990) recognized a mainly evergreen *Magnolia grandiflora-Quercus virginiana* association, separate from the region of [more deciduous] southern mixed hardwoods. A related distinction was made by Greller (1980), who redefined SMH to require that evergreen broad-leaved species appear in the canopy and recognized a "temperate broad-leaved evergreen forest" region mainly in northern and peninsular Florida. The zonation of Braun was modified by Greller (1988, 1989) to show a "deciduous-evergreen-conifer" region corresponding largely to southern mixed hardwoods (see Fig. 1). These main forest types, including the modifications, are listed in Table 1, along with dominant tree taxa.

The single most complete description of southeastern forest types is probably the two-volume *Biodiversity of the Southeastern United States* (Martin et al. 1993). Other comprehensive descriptions have been presented, *inter alia*, by Christensen (1988) for the southeastern coastal plain and by Greller (1988) and Delcourt and Delcourt (2000) for the eastern deciduous forest region in general. More phytosociological treatments were presented by chapters in Lieth and Landolt (1979) and by Miyawaki et al. (1994). More details on composition and dynamics of the "southern mixed hardwoods" forests are given, among others, by Pessin (1933), Oosting (1956), Monk (1965, 1968), Mills and Jones (1969), Ware (1970, 1978), Harcombe and Marks (1977),

Table 2 Main trees of temperate deciduous forests in the Southeastern USA

Appalachian forests (including foothills)	
Oak-chestnut forests:	*Quercus prinus*, *Q. alba*, *Q. rubra*, *Q. velutina*; formerly with *Castanea*
Tall, mesophytic cove forests, especially with *Tilia*, *Liriodendron*, *Fraxinus*, etc. (no oaks)	
Upland forests (piedmont, overwhelmingly deciduous)	
(a) Typical oak-hickory forests:	*Quercus alba*, *Q. rubra*, *Q. coccinea*, *Q. velutina*, plus *Carya* spp.
(b) Upland mixed hardwoods:	*Fagus*, *Quercus*, *Carya*, *Liriodendron*, *Liquidambar*, *Nyssa*, etc.
(c) Drier upland oak woods:	Upland *Quercus prinus*, *Q. alba*, *Q. velutina*
	Western *Quercus stellata*-*Q. marilandica*
	Sandhill oakwoods (*Q. laevis*, also with ***Pinus***)
Southern mixed hardwoods (coastal plain; with evergreens)	
Classically:	*Fagus*, *Q. alba*, *Liquidambar*, ***Q. laurifolia/hemisphaerica***, ***Magnolia grandiflora***, *Q. nigra*, *Carya* spp, *Q. falcata*, *Nyssa sylvatica* [var. *dilatata*] (Quarterman and Keever 1962)
Oak-hardwoods without beech:	*Quercus falcata*, *Q. nigra*, *Q. alba*, ***Magnolia grandiflora***, *Nyssa*, *Liriodendron*, *Liquidambar*; successionally, with ***Q. hemisphaerica***, ***Q. virginiana***
Bottomland mixed hardwoods:	***Magnolia* spp.**, *Liriodendron*, *Quercus nigra*, *Q. lyrata*, ***Q. laurifolia***, *Q. michauxii*, *Nyssa* spp, *Fraxinus*, *Liquidambar*
Beech-magnolia forests:	*Fagus grandifolia*-***Magnolia grandiflora***
Floodplain forests:	***Quercus laurifolia***, *Q. nigra*, *Q. michauxii*, plus *Nyssa*, ***Magnolia* spp.**, *Liriodendron*, *Liquidambar*

Forests in the southern Appalachians and piedmont are overwhelmingly deciduous (except for successional pines). Admixtures of broad-leaved evergreen trees (indicated by boldface type) appear in the coastal plain, in forests described by Quarterman and Keever (1962) as "southern mixed hardwoods". Beech-magnolia has been considered the potential climatic-climax forest type on the coastal plain but is rare due to fire, other disturbances, and substrate and topographic limitations. More or less equally mixed semi-evergreen broad-leaved forests, as have been described for central China, do not occur – except perhaps the beech-magnolia forests.

DeWitt and Ware (1979), Quarterman (1981), Gibson (1992), and Ware et al. (1993). An ordination of the original "southern mixed hardwoods" forest was done by Ware (1988), and succession over more than 50 years was described by Hartnett and Krofta (1989). A classification of deciduous forests of eastern North America was given by Monk et al. (1989) and of oak forests by Monk et al. (1990). This long history of forest interpretation in the southeastern coastal plain is summarized well by Ware et al. (1993).

4 Methodology and Data

The following description of warm-temperate deciduous forests in the southeastern USA is based primarily on analysis of the climatic relationships of the various main tree taxa and forest types. Climatic data are from the world climatic data-base compiled by the author, from many sources, over the past 40 years. These data include long-term mean monthly temperatures, average precipitation amounts, and extreme temperature minima at several thousand sites worldwide. Except for the absolute minima, measurement periods generally stop in the 1980s, in order to avoid effects of recent global warming, to which trees and vegetation types have not yet had time to adapt.

Vegetation data involve species range maps and Braun-Blanquet relevés of forest types. The main sources of range maps were Little (1971-78) and Brockman (1986), plus Iverson et al. (1999), who studied potential range shifts with global warming. Relevés were collected mostly during the Eastern North American Vegetation Survey (1988–90), from eastern Canada to south Florida and west to southern Louisiana (see Miyawaki et al. 1994). About 1,400 relevés were available (plus a few collected later), all made following the field methodology of Fujiwara (1987). Most forest relevés were about 25 × 25 m in area. Species names follow the main floristic manuals available at the time of the fieldwork, including in particular Radford et al. (1968), Kurz and Godfrey (1982), Duncan and Duncan (1988), and Godfrey (1989).

The climatic analysis relies also on the interpretation of climatic "breaks" and vegetation boundaries suggested in the "Overview" chapter (Box and Fujiwara, herein: see Table 8). Descriptions of forest types are presented through summary tables of up to four relevés from different locations. These tables were constructed by RELTABLR and other routines written by the author in the 1990s (before it became unthinkable not to use commercial software). The climatic and relevé data-bases, and the processing routines, were all described briefly by Box and Fujiwara (2010).

5 Warm-Temperate Deciduous Taxa

As elsewhere around the Northern Hemisphere, the deciduous forests of warmer parts of eastern North America are mainly oak forests – but with many other trees too. The main tree taxa of deciduous forests in the southeastern USA are shown in Table 2.

The main oak species include *Quercus alba* (white oak) and *Q. velutina* (black oak), which have wide north–south ranges, as well as *Q. rubra* (northern red oak), which gives way gradually (southward) to *Q. falcata* (southern red oak) and *Q. coccinea* (scarlet oak). All of these except *Q. alba* are red oaks (section *Erythrobalanus*), which are endemic to the Western Hemisphere but are at least as important throughout North America as are the white oaks (section *Quercus*, synonym *Leucobalanus*). *Q. prinus* (chestnut oak) appears in drier uplands and in the oak-chestnut forests found especially on the leeward eastern side of the southern and middle Appalachians. To the west, the main oaks in the shorter oak-hickory forests are *Q. stellata* (post oak) and *Q. marilandica* (blackjack oak), which occur in the east but have more xeromorphic leaves and become more important in the drier west. Deciduous oaks also occur, though, in wetter situations, especially *Q. lyrata*, *Q. michauxii* (swamp chestnut oak), and tardily deciduous *Q. phellos* and *Q. nigra* (water oak). Semi-evergreen to evergreen *Q. laurifolia* often dominates in floodplains. Especially good descriptions of the leaf and other morphology of the different oak species have been given by Kurz and Godfrey (1982) and by Hunt (1994).

Hickory (*Carya*, which occurs in China but not Europe) is the prototypical canopy companion in most oak forests. The main species are *C. tomentosa*, *C. glabra*, *C. ovata*, *C. ovalis* and *C.cordiformis* (plus *C. aquatica* in wet bottoms, mainly in Florida). Non-native pecan (*C. illinoiensis*) has become naturalized and appears sporadically, especially in bottomlands. Other common overstorey companions in oak forests include *Nyssa sylvatica* (uplands to bottomlands), *N. biflora* (mainly in bottomlands), and *N. aquatica* (in swamps), as well as evergreen *Magnolia grandiflora* (uplands to bottomlands).

Liriodendron tulipifera and *Liquidambar styraciflua* play particular roles in forests from uplands to floodplains. These species often appear in early succession, but both grow relatively straight and tall, and thus are not shaded out in late succession. *Liriodendron* (Magnoliaceae) is a monotypic genus; *Liquidambar* (Hamamelidaceae) also has only one species in eastern North America but does occur in China, with one species (*L. formosana*). Evergreen *Magnolia virginiana* occurs commonly in bottomlands and floodplains but also sometimes on uplands.

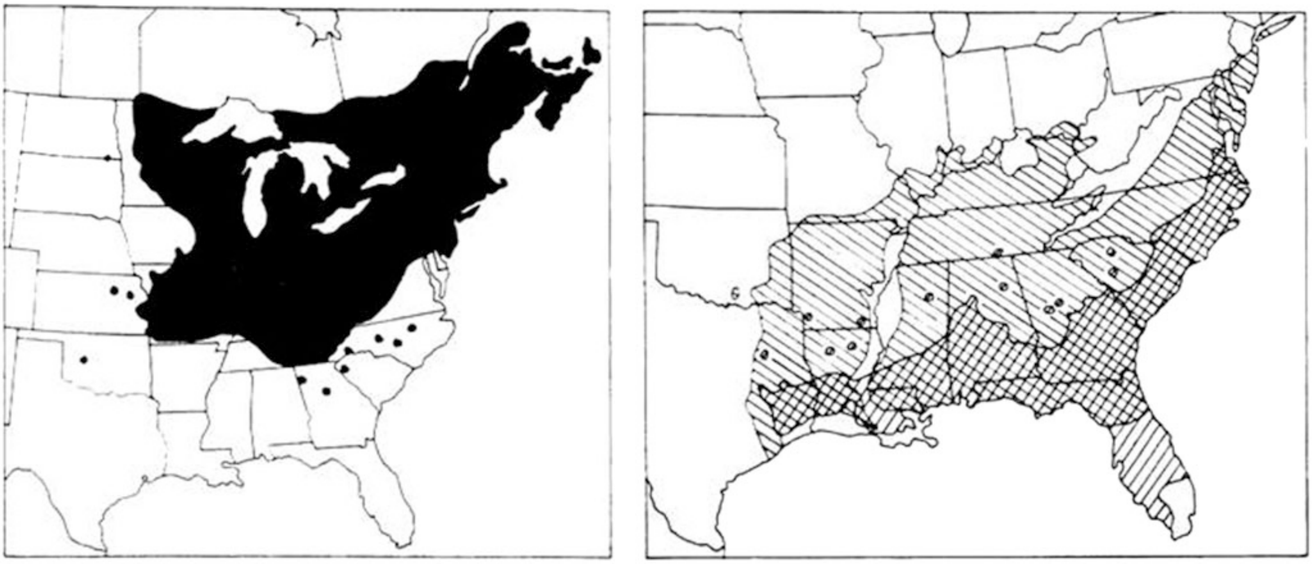
Other canopy tree species are important in more mesic situations and occur as canopy co-dominants in forests that sometimes have no oaks at all. The only beech species, *Fagus grandifolia*, occurs in upland and more mesic forests but is usually not mono-dominant in forest canopies, unlike the situation of *F. sylvatica* in Europe and of other *Fagus* species in Japan and China. *Tilia* and *Fraxinus* species occur in most mesic forests and co-dominate the canopies of mesic Appalachian and some mesic, north-slope piedmont forests. Floodplain forests in the piedmont generally involve *Platanus occidentalis*, *Celtis* spp., *Ulmus* spp., and *Betula nigra*, in characteristic zonations that also include the floodplain oaks.

Although some tree species span most or all of the north–south range of the deciduous forest, some genera have clear "northern" and "southern" species, as seen in Fig. 2 (from Daubenmire 1978, pp. 121 and 132). *Acer saccharum* has outliers in the south, but it and also-northern *A. nigrum* are largely replaced in southern forests by smaller-leaved *A. barbatum*, *A. leucoderme*, and *A. floridanum*. Among oaks, the "southern" status of some deciduous species, such as *Q. stellata*, was corroborated by projecting their climatic envelopes to Europe, where these fell in the submediterranean area (Box and Manthey 2006; see also Box and Fujiwara, herein); other deciduous species with "southern" distributions include upland species like *Q. shumardii*, *Q. laevis* and *Q. incana*. Perhaps more important, though, are several bottomland oaks, especially *Q. lyrata*, *Q. michauxii*, *Q. nigra* and *Q. phellos*. *Quercus laurifolia* (see Fig. 2) is evergreen further south but only semi-evergreen in the northern part of its range. Other important tree genera with northern and southern species include *Celtis* and *Tilia*. *Liquidambar* and *Nyssa sylvatica*, on the other hand, are somewhat more southern, extending northward only into southernmost New England, and the former not far upward in the Appalachians.

On the other hand, *Acer rubrum* occurs from the Gaspé Peninsula to subtropical south Florida and westward to central Texas; relevé data from the Eastern North American Vegetation Survey suggested that it is perhaps the most abundant tree in the forests of eastern North America. *Fagus grandifolia* also occurs from Nova Scotia southward to near the Gulf of Mexico and westward slightly into eastern Texas. Other important canopy or understorey trees with wide north–south ranges, generally from southern New England southward, include *Liriodendron tulipifera*; the main *Carya* species; *Fraxinus americana* and *F. pennsylvanica*; *Ulmus americana* and *U. rubra* (but not southern *U. alata*); and floodplain species *Platanus occidentalis*. Most of the important understorey trees also have wide north–south ranges, including *Carpinus caroliniana* and *Ostrya viriginiana* (Betulaceae, though all true birches are clearly "northern" except *B. nigra*); *Prunus serotina*, *P. americana* and *Amelanchier arborea* (unlike most other Rosaceae trees); and *Cornus florida*, *Cercis canadensis* and *Morus rubra*.

Dynamics in the piedmont forests, excluding floodplains, generally follows a classic successional pattern that begins with pine colonization. The first broad-leaved, potentially tall trees to invade the growing pinewoods are usually sweet gum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*). These are

Northern and Southern Range Types



Range of *Acer saccharum*

Ranges of *Quercus falcata* (north) and *Q. laurifolia* (semi-evergreen)

Fig. 2 Northern versus Southern species ranges in eastern North America. Several tree genera in eastern North America have distinctly "northern" and "southern" species. The range of *Acer saccharum* (left), the maple on the Canadian national flag, is typical for northern tree species. The range of *Quercus falcata* (right, extending further north), is typical for many southern tree species, including other oaks, *Nyssa*, *Liquidambar*, *Liriodendron*, and some hickories (*Carya*). The other range at right is that of *Q. laurifolia*, a semi-evergreen southern species that is restricted to the coastal plain but occurs frequently with warm-temperate deciduous species in bottomlands. The maps are from Daubenmire (1978)

followed, on the more xeric uplands, by the oaks and hickories, plus tupelo (*Nyssa sylvatica*) and perhaps beech (*Fagus*). An oak-hickory forest, sometimes with considerable beech, is established after 50–100 years.

On the coastal plain, the main early invaders include evergreen *Quercus hemisphaerica*, followed especially by *Q. nigra*, *Q. falcata*, and sometimes evergreen *Magnolia virginiana* if it is not too dry. Even so, such forests remain mainly deciduous unless conditions and seed sources permit the eventual establishment of evergreen *Q. virginiana*, the potential canopy dominant of southern warm-temperate forests. This succession is similar to that in East Asia, except that the geologically young, sandy substrate of the southeastern US coastal plain does not permit widespread occurrence of the laurophyllous evergreens that dominate in East Asia. Laurophyll trees (called "bay" species, i.e., *Magnolia virginiana*, *Persea borbonia*, and *Gordinia lasianthus*) do occur on the southeastern US coastal plain but mostly only in shallow, moist depressions, typically over thin peat accumulations that insure water availability even in dry summers (see graphics in Wharton 1978).

Winter tempertures seem to delimit the ranges of evergreen tree species in the southern US. Evergreen broad-leaved trees usually do not tolerate even short-term exposure to temperatures below about −15°C (cf Woodward 1987), although some harder-leaved trees such as *Q. virginiana* tolerate infrequent minima to perhaps −18°C. Some temperature differences between interior and coastal locations in the southeastern US are shown in Table 3, which juxtaposes inland and coastal sites at the same latitudes. Evergreen *Ilex opaca*, on the other hand, occurs in deciduous-forest understoreys as far north at least as Pennsylvania.

Some of the advantages of deciduous and evergreen habits in humid warm-temperate climates have been considered in other chapters in this book; other useful insights are given, *inter alia*, by Monk (1966), Van Auken et al. (1981), and Givnish (2002). Adaptations to the transitional nature of warm-temperate climates include marcescence (see García-Mijangos, herein; Sánchez de Dios et al. 2009) and semi-evergreenness. A third adaptation appears in the southeastern US in the form of the "tardy deciduousness" (e.g., Kurz and Godfrey 1982) shown by *Quercus nigra* and *Q. phellos*, which do not lose their leaves until December, well after all other trees, and which may remain partly marcescent, depending on winter severity. Both species have relatively entire leaves without deeply indented lobes, more like evergreen oak species. *Q. nigra* is in fact evergreen in the southern part of its range (central to south-central Florida).

Table 3 Temperatures at inland-deciduous and coastal or near-coastal sites in the Southeastern USA

Inland deciduous							Coastal / near coastal					
Lat	Location	Tmax	Tmin	Tabmin	BT	Lwarm	Location	Tmax	Tmin	Tabmin	BT	Lwarm
39.3	Baltimore Md	25.7	1.5	−21.7	13.5	7						
38.0	Charlottesville	24.7	2.0	−23.3	13.6	7						
37.5	Richmond Va	25.6	3.3	−24.4	14.5	7						
36.9	Chatham Va	23.6	1.0	−22.8	12.6	7	Norfolk Va	25.7	4.9	−19.4	15.2	8
35.9	Raleigh-Durham	25.6	4.7	−22.8	15.3	9	Manteo NC	26.2	6.1	−18.9	16.6	9
35.4	New Holland NC	26.1	6.4	−24.4	16.6	9	Cape Hatteras NC	25.6	7.7	−14.4	16.7	9
35.1	Fayetteville	26.3	6.2	−20.6	16.3	9						
34.7	Lumberton NC	26.4	6.4	−18.9	16.9	9	Morehead City NC	26.4	7.7	−17.2	17.0	9
34.3	Darlington SC	26.6	7.1	−20.0	16.9	9	Wilmington NC	26.5	8.4	−17.8	17.4	9
33.9	Columbia SC	27.1	7.9	−18.9	17.7	9	Conway SC	26.9	8.5	−15.6	17.9	9
33.4	Augusta Ga	27.4	7.4	−18.3	17.5	9	Georgetown SC	26.9	8.6	−15.6	17.9	9
32.8	Macon Ga	27.7	8.8	−21.1	18.4	9	Charleston SC	27.7	10.1	−12.2	19.0	12
31.8	Cordele Ga	27.6	8.7	−19.4	18.9	11	Savannah Ga	27.6	10.5	−16.1	19.3	12
31.2	Moultrie Ga	27.2	9.7	−17.8	19.1	11	Brunswick Ga	27.8	11.5	−15.0	20.0	12
30.4	Tallahassee Fla	27.3	11.5	−18.9	19.8	12	Jacksonville	27.9	12.8	−13.9	20.6	12
							Pensacola Fla	27.5	11.4	−15.0	19.9	12
29.6	Gainesville Fla	27.3	12.7	−14.4	20.6	12	Palatka Fla	28.1	14.2	−11.7	21.6	12
29.2	Ocala Fla	27.5	14.4	−15.0	21.3	12	Daytona Beach	27.4	14.5	−9.4	21.3	12
28.6	Brooksville Fla	27.3	15.1	−17.8	21.8	12	Titusville Fla	27.6	15.8	−7.8	22.1	12
28.0	Plant City Fla	27.7	15.8	−9.4	22.3	12	Tampa Fla	27.9	15.9	−7.8	22.2	12

Sites are arranged in pairs, one inland and one coastal or near-coastal, from north to south. The latitude (lat) given is the average for the juxtaposed sites, which deviate by no more than about 0.1° from the average.

Tmax = mean temperature of the warmest month (°C, as are all temperatures)

Tmin = mean temperature of the coldest month

Tabmin = absolute minimum temperature (lowest ever measured, over a minimum of about 50 years)

BT = Holdridge's biotemperature, which is actually the mean annual temperature since no month is $< 0°\mathrm{C}$

Lwarm = number of consecutive months with mean monthly temperature $\geq 10°\mathrm{C}$

All sites in the left-hand column, north of Florida, have deciduous or mostly deciduous forest as the natural vegetation. Deciduous trees are still important even in northern Florida, where Tabmin is still around the critical minimum of −15°C (except Plant City, inland from juxtaposed Tampa).

All sites in the right-hand column have at least some evergreen broad-leaved trees surviving, even in coastal Virginia and North Carolina, since the absolute minima come very infrequently and there are sheltered micro-sites. From Georgetown (South Carolina) southward, the natural forest is overwhelmingly broad-leaved evergreen, generally dominated by *Quercus virginiana*.

Note that Wilmington and Savannah (right column) are a bit inland from the coast and show lower absolute minima, as does Pensacola on the Gulf of Mexico coast. There is even some inland effect on minimum temperatures in central Florida.

On the other hand, some 'evergreen' species in the southeastern US are only semi-evergreen in the northern parts of their ranges, including *Q. laurifolia* and *Cyrilla racemiflora* (cf Godfrey 1989).

Finally, successful reproduction is also a major determinant of the natural range of a species. *Magnolia grandiflora*, for example, despite its evergreen broad leaves, grows well as a planted ornamental tree at least as far north as Washington, where infrequent nighttime temperatures below −20°C have been recorded. *M. grandiflora* does not reproduce well, however, north or inland from the southern coastal plain, which is its natural range.

Reproduction potential of the main trees in the region of potential evergreen broad-leaved forests, mainly northern and central Florida, was summarized by Ware et al. (1993). Among oaks, invasive successional *Quercus hemisphaerica* (evergreen) was considered to reproduce well everywhere, while potential dominant *Q. virginiana* (also evergreen) was seen to reproduce poorly and perhaps to be maintaining its dominance mainly through its longevity. Bottomland deciduous *Q. nigra* reproduces best in mesic to moist situations, although it does also occur in uplands. *Liquidambar styraciflua*, a pioneer that tends to remain in mature forests, reproduces well everywhere but better on moister substrates, including bottomlands. Slow-growing *Magnolia grandiflora* (evergreen) also reproduces best on moist sites but was seen as more important in forest canopies on dry-mesic sites, perhaps because these have less competition from other trees. Evergreen *Ilex opaca* is also more abundant on drier sites. *Carya* species and understorey *Cornus florida* and *Ostrya virginiana* reproduce best or only on mesic to dry sites, while *Carpinus caroliniana* reproduces only on wetter sites. This may explain why *Carpinus* and *Ostrya* were almost never found in the same ENAVS relevé samples.

6 Warm-Temperate Deciduous Forests

The ranges of important "southern" species, such as *Quercus falcata* (see Fig. 2), *Q. stellata* (cf Box and Fujiwara, herein: Fig. 2), and others (see Little 1971-78; Brockman 1986), all suggest that forests that could be called warm-temperate deciduous occur across the southern piedmont and coastal plain, but not further north. This means from New Jersey to eastern Texas and south of the Ohio River, including piedmont Virginia, essentially all of lowland Kentucky and Arkansas, but not Missouri. Warm-temperate deciduous forests with significant admixtures of evergreen broad-leaved trees, such as *Q. laurifolia* (cf Fig. 2), should be restricted mainly to the coastal plain.

The climatic analysis in the "Overview" chapter (Box and Fujiwara, herein: Table 8) suggested that regions with warm-month mean temperature approaching or exceeding 25°C are distinct from more northern forests. This means the region southward from Maryland and the Ohio River, coinciding generally with the pattern suggested by species ranges. New York city and Indianapolis are suggested as borderline locations.

In terms of Braun-Greller forest regions (see Fig. 1), the potential region of warm-temperate deciduous forests would thus include the DEC (deciduous-evergreen-conifer) region on the coastal plain, most of the OPH (oak-pine-hickory) region on the piedmont, and most of the WM (western mesophytic) region of western Kentucky-Tennessee and northern Mississippi. The Appalachian MM (mixed mesophytic) and OC (oak-chestnut) regions have cooler summers and would mostly be excluded; similarly most of the continental OH region (oak-hickory, without pines), in Illinois, Missouri and northwestern Arkansas (Ozark Plateau), would be too far north to be included.

If we recognize three general topographic provinces, namely the lower mountains and foothills, the piedmont, and the coastal plain, then a general scheme for the occurrence of the various forest types may be as appears in Table 4. The main division of deciduous forest types in the southeastern US is between oak-dominated forests and what are often called 'mesophytic' forests, meaning those that occur in more mesic situations and are not dominated by oaks. The following sections describe what appear to be the main types of warm-temperate deciduous forest in the southeastern USA.

6.1 Oak and Related Forests

The most widespread and typical oak forests in the southeast are the upland oak-hickory (*Quercus-Carya*) forests of the piedmont (see, for example, Greller 1988, Monk et al. 1990, Skeen et al. 1993, Delcourt and Delcourt 2000; cf Box and Manthey 2005; see also Photo 1). The compositions of three typical stands, from piedmont Virginina, North Carolina and Georgia, are shown in Table 5. The Virginia stand was on a 13° north-facing slope, but the more typical other two stands were on very slight slopes, as are representative of the usually gently rolling piedmont terrain.

The most consistent canopy species was *Quercus alba*, which is consistently present if not at least co-dominant throughout the oak-hickory forests of the piedmont and westward at least to the Mississippi River. *Quercus rubra* is the main canopy species at the more northern site (Virginia) but is often replaced southward by *Q. coccinea*, as here in north Georgia. The hickories (*Carya*) are not always in the canopy (cf Ware 1992) but are usually present, especially *C. tomentosa* in the piedmont, with *C. glabra* more on the coastal plain. *Liriodendron tulipifera* also occurs reliably in piedmont oak-hickory forests, usually

Table 4 Warm-temperate deciduous forests of Southeastern North America, by composition and topographic situation

	Oak forests	Mesophytic forests
Mountains and foothills	**Appalachian Oak-Chestnut forests** (*Q. prinus*, *Q. alba*, *Q. rubra*, *Q. velutina*; formerly *Castanea*)	**Appalachian Cove forests** (tall *Tilia*, *Liriodendron*, *Fraxinus*, etc.; little oak)
Uplands (piedmont)	**Southern Oak-Hickory forests** (*Q. alba*, *Q. rubra*, *Q. coccinea*, *Q. velutina*, plus *Carya* spp.)	Upland Mixed Hardwoods (*Fagus*, *Quercus*, *Carya*, *Nyssa*, *Liriodendron*, *Liquidambar*, etc.)
	Western: *Q. stellata*-*Q. marilandica*	
Coastal-plain uplands	Southern Oak Hardwoods (no beech) (*Q. falcata*, *Q. nigra*, *Q. alba*, *Magnolia grandiflora*, *Nyssa*, *Liriodendron*, *Liquidambar*)	
	Successional: *Q. hemisphaerica*, *Magnolia*, deciduous hardwoods (eventually: *Q. virginiana*)	
	Sandhills (*Q. laevis*, also with *Pinus*)	
(uplands/bottomlands:)		**Southern mixed hardwoods** (*Fagus*, *Q. alba*, *Liquidambar*, *Q. laurifolia/hemisphaerica*, *Magnolia grandiflora*, *Q. nigra*, *Carya*, *Q. falcata*, *Nyssa sylvatica*)
Bottomlands/floodplains (coastal plain)	*Quercus laurifolia*, *Q. nigra*, *Q. michauxii*, plus *Nyssa*, *Magnolia*, *Liriodendron*, *Liquidambar*, etc.	Bottomland Mixed Hardwoods (*Magnolia*, *Liriodendron*, *Q. nigra*, *Q. lyrata*, *Q. laurifolia*, *Q. michauxii*, *Nyssa* spp, *Fraxinus*, *Liquidambar*)
		Beech-Magnolia forests (*Fagus-Magnolia grandiflora*)

Oak-dominated forests occur especially in more xeric situations (but also some floodplains); forests in more mesic situations often have more and perhaps many canopy species, are called mesophytic forests, usually include beech, and may or may not contain oaks at all. Boldface indicates well recognized Southern forest types, including especially the types of Braun (1950) and the "southern mixed hardwoods" of Quarterman and Keever (1962), which may occur both in bottomlands and in more mesic upland situations.

entering in early to mid-succession and remaining in the canopy (due to its height and straight growth form). Other fairly consistent companion trees include *Oxydendrum arboreum* (Ericaceae), common on drier sites, and *Nyssa sylvatica*. As understorey trees, *Acer rubrum* occurs everywhere and *Cornus florida* is especially common in these drier piedmont forests.

Liquidambar styraciflua and *Fagus grandifolia* did not appear in these stands but often do occur. Other characteristic understorey trees include *Ostrya virginiana*, *Prunus serotina*, and *Disopyros virginiana*. There is usually no *Carpinus* in these drier forests, and the characteristic understorey trees do not occur everywhere. The two more typical stands (Duke and Oconee) have moderately diverse herb layers, but the Virginia stand has mostly seedlings in its understorey. The warm-temperate nature of these forests is suggested by the various evergreen understorey vines and forbs, especially at the two more southern sites. Like most forests over the region, these stands are secondary, having developed after land abandonment and a subsequent "pine stage" involving colonization especially by *Pinus taeda*.

Further west, from Missouri and southern Illinois to eastern Oklahoma and Texas, the oak-hickory forest becomes shorter and simpler, with dominance shared mainly by only two main species, *Quercus stellata* and *Q. marilandica*. Both of these species occur in the east, but they become more important toward the drier western limit of the deciduous forest, where canopy height is typically only 10–15 m (cf Rice and Penfound 1959). In eastern and central Texas these species are joined by *Q. texana* (red group), which can be mono-dominant.

The presence of beech (*Fagus grandifolia*) has been considered a major characteristic distinguishing coastal-plain mixed hardwood forests from piedmont oak-hickory forests (Ware et al. 1993, p 470). As shown by the relevés in Table 6, however, beech occurs also in piedmont oak-hickory forests and can be fairly prominent, especially on lower, north-facing slopes and in ravines. The examples shown,

Table 5 Representative oak-hickory forest stands in the Southeastern US Piedmont

	Twin Lakes Va				Duke Forest NC				Oconee Forest			
	(US-176, 1989)				(AM-160, 1988)				(KF-2, 1999)			
	N slope				Upland kaolinite				Slight slope			
	30m	16m	6m	.3m	30m	15m	6m	.5m	27m	15m	6m	.4m
	80%	30%	40%	20%	70%	30%	20%	35%	75%	30%	35%	25%
Canopy Trees												
Quercus prinus	1.1	1.1	+	+.2								
Quercus rubra	3.3			+.2	1.2		+.2					
Quercus velutina	1.1						+	+.2	+			+
Quercus alba	2.2		+		4.3				3.3	2.2	2.2	+
Quercus coccinea					1.1				3.3		+	2.3
Quercus falcata									1.1			
Quercus nigra									+			1.1
Carya tomentosa		2.2	2.2		2.2		+.2	+.2			2.2	+.2
Carya ovata			+.3				1.2					
Carya glabra			+				+.2	+.2		1.1	2.2	
Liriodendron tulipifera	2.2	1.1	1.1	+	1.1		+		1.1	1.1	+	
Oxydendrum arboreum	1.1	1.1	+			3.3				2.2	1.1	
Nyssa sylvatica	1.1	1.1		1.1			1.2				2.2	+
Fagus grandifolia								+		1.1	1.2	+
Liquidambar styraciflua											1.1	
Understorey Trees												
Acer rubrum		2.3	2.2	+.2		2.2	2.3			1.1	1.1	
Cornus florida		+	2.3	1.2		1.2	1.2				1.2	
Castanea dentata			+	+								
Ilex opaca			2.2									
Juniperus virginiana			2.2	+		1.1						
Magnolia grandiflora											1.1	1.1
Diospyros virginiana							+				+	
Prunus serotina							+	+.2		+	1.2	+
Ostrya virginiana								+			1.1	+
Amelanchier arborea										+	+	
Crataegus flava											+	+
Morus rubra											+	+
Shrub Layer												
Chionanthus virginicus			1.1				+					
Sassafras albidum			+				+.2					
Viburnum prunifolium			+				+					
Viburnum acerifolium							2.3	2.3				
Viburnum rafinesquianum							2.2					
Vaccinium vacillans				+.2				+.2				
Vaccinium stamineum				+				1.2			1.1	1.1
Dioscorea quaternata				+							+	
Asimina triloba											1.1	
Euonymus americanus							+	1.2			+.2	1.1
Diervilla lonicera											+.2	+
Lianas and other Vines												
Vitis rotundifolia							+	1.2		+		2.3
Parthenocissus quinquefolia								+.2				+
Lonicera sempervirens							+	+.2				
Smilax glauca			+	+				+				1.1
Smilax hispida											1.1	+.2
Smilax bona-nox											+.2	+.2
Herb Layer												
Chimaphila maculata				+				1.2				+.2
Tipularia discolor				+				+				
Hexastylis arifolia												1.1
Uvularia perfoliata				+.2				+				
Polygonatum biflorum								+.2				+.2
Danthonia spicata												1.1
Scleria triglomerata												1.1
Panicum dichotomum												1.2

Species shown in boldface type (above only) are evergreen. Additional species occurring only as "+" and only in one relevé:

a) Twin Lakes: S-layer Rhododendron sp.; and H-layer Vitis aestivalis, Vaccinium angustifolium, Galium latifolium, Smilacina racemosa, Goodyera pubescens, Desmodium sp., Galium sp., Carex sp.

b) Duke Forest: T2-layer Fraxinus sp.; S-layer Ilex montana; and H-layer Carya ovalis, Quercus phellos, Viburnum rufidulum, Aureolaria virginica, Desmodium nudiflorum, Euphorbia corollata, Potentilla simplex, Hieracium sp., Carex 2 spp.

Photo 1 Oak-hickory forest in the Piedmont of central North Carolina. Oak-hickory forests are dominated by deciduous oaks (*Quercus*), with hickories (*Carya*) mainly in the subcanopy. The most common oaks are *Q. alba* (white oak: see two trees with scaly bark in the center and left of the photo), *Q. rubra* (northern red oak), *Q. coccinea* (scarlet oak) and *Q. velutina* (black oak). All of these species have wide north–south ranges (from New England southward), though scarlet oak is more common in the southern piedmont. The most common hickories are *Carya tomentosa*, *C. ovata*, *C. ovalis*, and *C. glabra*, the last also common in otherwise mainly evergreen oak forests of the coastal plain. Although somewhat “xeric”, these forests can have leaf area indices near 5–6 and can be quite shady in summer. Canopy height is typically 20–25 m. Oak-hickory forests extend throughout the southeastern piedmont, from Maryland to central Georgia, then westward (not along the coast) into eastern Texas, where *Q. texana* becomes prominent (see OHP in Fig. 1). Shorter, more xeromorphic counterparts, dominated by two canopy trees, *Q. stellata* (post oak) and *Q. marilandica* (blackjack oak), cover large parts of Missouri, Arkansas, and eastern Oklahoma (see OH in Fig. 1)

though, are all from rather slight (5°–10°) north-facing slopes, from the piedmont in North Carolina and Georgia, and from the coastal plain in southern Mississippi. *Quercus alba* is again the most consistent oak, and *Carya* is less common. *Liriodendron* is still a canopy component, with *Acer* and *Cornus florida* still occurring in the tree understoreys. The occurrence of *A. negundo* at Indian Springs, as well as *Quercus michauxii*, a bottomland oak, suggests that this is a moister site (cf Howel 1991). It also has fairly dense *Styrax americana*, more vines and forbs, and no *Ostrya*, which is usually found on drier sites. Unusually, though, both *Ostrya* and *Carpinus* were found at the Mississippi site, the secondary nature of which is suggested by the remaining large pines.

The forests of Braun’s Western Mesophytic region (mainly Kentucky and western Tennessee) are also dominated by *Quercus* species, moreso westward (cf Bryant et al. 1993). Much of this deciduous forest area also appears to be warm-temperate.

c) Oconee Forest: S-layer Vaccinium arboreum, Vaccinium elliottii, Elaeagnus pungens, Smilax smallii; and H-layer Celtis occidentalis, Lonicera japonica, Rhus radicans, Baptisia leucophaea, Clitoria mariana, Desmodium dillenii, Solidago arguta v. caroliniana, Corallorhiza maculata, Galium circaezans, Galium obtusum v. filifolium, Panicum boscii, Aristolochia sp., Croton “pubescent”.

The first stand, with a total of 34 species on 25 × 30 m, was on a 13° north-facing slope at Twin Lakes State Park, about halfway between Richmond and Lynchburg in the piedmont of south-central Virginia. The second stand, with 45 species on 30 × 40 m, was on relatively level, kaolinite-rich clay near the Wooden Bridge Road in the Korstian Division of the Duke Forest, west of Durham, in the piedmont of central North Carolina. Robert K. Peet and Dawson Sather were the accompanying local botanical authorities. The last stand, with 55 species on 25 × 30 m, was on a slight NW slope in the Oconee Forest Park near the University of Georgia campus in Athens, in the upper piedmont of northeast Georgia. This was one of two relevés done after the ENAVS inventory and was done by Kazue Fujiwara and the author

Table 6 Representative samples of beech-oak forest in the Southeastern USA

	Duke Forest				Indian Springs				P Quin St Pk			
	(AM-156, 1988)				(AM-102, 1988)				(US-289, 1989)			
	Mild NW slope				Lower N slope				Dry low NW slope			
	30m	17m	6m	.5m	38m	22m	6m	.8m	31m	15m	6m	.5m
	80%	20%	20%	20%	90%	20%	40%	20%	80%	40%	30%	30%
Canopy Trees												
Fagus grandifolia	3.4		1.2	1.2	4.3		2.3		2.2	2.2	2.2	
Quercus rubra	2.1		+									
Quercus alba	1.1			+.2	1.1		+		3.3	1.1		1.2
Quercus falcata	1.1								1.1	+		
Quercus coccinea	1.1											
Quercus michauxii					1.1		+					
Quercus nigra								+				+
Carya glabra	2.2	2.2	+.2				+					
Carya ovalis			+.2	+.2								
Carya ovata					1.1							
Carya tomentosa			+			2.3					+	
Liriodendron tulipifera	1.1	1.1			2.1				2.2			
Liquidambar styraciflua									1.2			
Oxydendrum arboreum		1.2	2.3								+	
Nyssa sylvatica			1.2						1.1		1.1	
Pinus taeda	2.2								2.2			
Pinus echinata	+											
Understorey Trees												
Acer rubrum		2.2	2.3								+	+.2
Acer negundo							1.2	+.2				
Cornus florida		+.2	+.2			2.2	2.3					+
Ostrya virginiana										2.3	2.2	
Carpinus caroliniana							1.2			1.1	1.2	
Magnolia grandiflora										1.1		
Morus rubra							+.2				+	
Prunus serotina			+				+.2				+	
Shrub Layer												
Styrax americana							3.3					
Viburnum acerifolium			2.3					+				
Rhododendron nudiflorum			+.2	+							+	
Vaccinium vacillans				2.2								
Vaccinium stamineum				1.2								
Asimina parviflora							+				+	
Hamamelis virginiana											+	+
Sassafras albidum				+.2			+					
Ilex opaca							+				+	
Ilex vomitoria											+.2	+
Lianas and other Vines												
Vitis rotundifolia				+.2				+	+.2	+		
Rhus radicans							+	1.2	+	+		+.2
Lonicera japonica							+	3.3				+.2
Parthenocissus quinquefolia								2.3				
Herb Layer												
Chimaphila maculata				1.2								
Hexastylis arifolia				+				1.1				2.2
Euonymus americanus				+								1.2
Mitchella repens												1.2
Goodyera pubescens				+				+				
Desmodium nudiflorum								3.3				
Epifagus virginiana				1.2								
Galium circaezans								1.2				
Podophyllum peltatum								1.2				
Prenanthes sp.								1.2				
Carex "himekuwazu"								2.2				
Carex sp.												1.2
Panicum "big"								1.2				

Species shown in boldface type (above) are evergreen. Some taxa not identified completely carry descriptive epithets in quotation marks, sometimes Japanese names of similar species. Additional species occurring only as "+" and only in the understorey of one relevé:

(a) Duke Forest: S-layer Juniperus virginiana, Viburnum rafinesquianum; and H-layer Quercus velutina, Amelanchier sp., Ilex decidua, Vaccinium tenellum, Polygonatum biflorum, Smilacina racemosa, Luzula sp., Carex "fine"

6.2 Appalachian Forests

On drier uplands and especially on the drier leeward side of the Appalachians, *Quercus prinus* (chestnut oak) becomes more important and often dominant; *Q. velutina* may also become more important. The compositions of three typical stands of such upland oak forest are shown in Table 7, all on significant slopes (in different directions). The first two stands were along the Blue Ridge Parkway, a scenic road that runs from northern Virginia to the Smoky Mountains of North Carolina. The third stand is from Johns Mountain in the Appalachian foothills of northwestern Georgia.

All three stands involve *Q. prinus*, but *Q. alba* was strongly dominant in the higher-elevation North Carolina stand (1240 m). *Q. rubra* is also consistently important in the mountains, but *Q. velutina* and *Q. falcata* become more important in the north-Georgia foothills. Forbs are more prominent than seedlings in the herb layers, none of which, however, has more than 20% cover. The higher-elevation North Carolina site, probably less xeric, has the characteristic southern Appalachian “wild azalea” understorey of deciduous *Rhododendron calendulaceum* plus lower-growing, evergreen *Kalmia latifolia* (both Ericaceae). All three stands represent examples of Braun’s Oak-Chestnut Forest, and chestnut (*Castanea dentata*) can still be found, albeit growing to only a few meters in height before being found and killed by the chestnut blight that eliminated the once-dominant trees during the first half of the twentieth century. Mean summer temperatures at the higher-elevation sites are below 22°C and January means are below freezing, so these forests should not be considered warm-temperate, even though they are similar to the piedmont oak-hickory forests, with many of the same species. One difference in these cooler forests is the prominence of *Quercus rubra* (northern red oak).

The degree of local variation on different slope positions and orientations is illustrated by the stands shown in Table 8, from the “The Pocket” of Crockford-Pigeon Mountain in the Appalachian foothills of northwestern Georgia. The Pocket is a concavity with steep slopes and a “gorge” with a small stream. Elevations range between about 240 m and 320 m, with (nearby) mean July temperatures around 24–25°C and January means above freezing at 2–3°C. The first stand was on a 28° northeast-facing slope, the second in the narrow floodplain, and the third on an adjacent, more exposed, more xeric south slope (15°).

The first stand, with 51 species, was a true “cove forest” growing in a humid concavity of the steep slope; it is also an example of Braun’s Mixed Mesophytic forest (cf Hinkle et al. 1993). The canopy reached 40 m in height and was composed of typical cove-forest species, including *Liriodendron*, *Tilia heterophylla*, *Liquidambar*, *Fraxinus americana*, and *Magnolia acuminata* (deciduous), all of which usually grow relatively straight and tall. *Acer saccharum*, *Juglans nigra*, some *Carya* were also in the canopy, but no *Quercus*. The floodplain forest, near the stream mouth, was also tall (35 m) and had 46 species, dominated by *Liriodendron* with other mesophytic species and *Platanus*. It may be seral. The forest on the adjacent south slope was of more normal height (26 m) and was a typical upland oak forest, dominated by *Quercus alba*, with *Liquidambar*, other oaks, and *Carya*. It also had a quite different understorey and a total of 66 species.

6.3 Upland Mixed Hardwoods of the Coastal Plain

Upland forests on the coastal plain may also be mainly deciduous, both indefinitely and as secondary forests successional to zonal evergreen broad-leaved forests dominated mainly by live oak (*Q. virginiana*) (cf Monk 1965, Wharton 1978, Christensen 1988, Hartnett and Krofta 1989, Platt and Schwartz 1990). These upland forests are also mainly oak forests, but with admixtures of more evergreen taxa. Three examples are shown in Table 9, all on humic sand and very slight if any slope.

The first stand was on a mesic sand flat in Reed Bingham State Park in inland southern Georgia. It had only 30 species, was dominated by *Q. alba*, and is a typical coastal-plain

(b) Indian Springs: S-layer Tilia americana, Cercis canadensis, Halesia carolina, Decumaria barbara, Hydrangea arborescens; and H-layer Smilax hispida, Sanicula marilandica, Thalictrum thalictroides, Fraxinus sp., Galium “medium”, Sanicula sp., Viola sp., Carex “medium”

(c) Percy Quin: T2-layer Prunus caroliniana; S-layer Magnolia virginiana, Symplocos tinctoria, Castanea floridana, Rhamnus caroliniana, Ulmus alata, Viburnum dentatum, Halesia sp., Berchemia scandens, Dioscorea quaternata; and H-layer Callicarpa americana, Smilax rotundifolia, Smilax pumila, Anisostichus capreolata, Brintonia dicoidea, Collinsonia anisata, Elephantopus carolinianus, Lilium philadelphicum, Lygodium japonicum, Polystichum acrostichoides, Sanicula canadensis, Spigelia marilandica, Uvularia perfoliata, Uniola laxa, Lactuca sp., Carex “narrow”, Acanthaceae sp.

The first stand, with a total of 37 species on 30 × 30 m (previous an old pasture), was on a 5° NW-facing slope in the Korstian Division of the Duke Forest, near Durham, in the piedmont of central North Carolina. Robert K. Peet and Dawson Sather were accompanying local botanical authorities. The second stand, with 43 species on 30 × 30 m, was on a 10° north-facing slope in Indian Springs State Park, near Monticello in the lower piedmont of north-central Georgia. The vegetation of this park is described in more detail by Carol Howel (1991), who was our local botanical authority. The last stand, with 56 species on 30 × 30 m, was on a 7° NW-facing lower slope, on dry loam, in the Percy Quin State Park south of McComb in southwestern Mississippi, neat the Louisiana boundary. Much of forest vegetation in this area was clearly secondary and still in mid-succession, with numerous stately, large pines (mainly *Pinus taeda*)

Table 7 Appalachian and other upland oak-chestnut forests

	Va BR Pkwy (US-165, 1989) Mid NW slope				NC BR Pkwy (AM-133, 1988) SE slope				Johns Mtn (US-237, 1989) Ridge slope			
	22m	14m	3m	.5m	25m	15m	6m	.8m	22m	14m	5m	.9m
	80%	40%	20%	8%	80%	30%	40%	20%	85%	30%	25%	20%
Canopy Trees												
Quercus prinus	3.3			1.2	1.1	2.2	1.2		3.3	2.2	2.2	1.1
Quercus rubra	3.3	2.2			3.2		1.2	1.2				
Quercus alba					4.3	2.2				+		
Quercus velutina		+							2.2	1.1	1.2	1.1
Quercus falcata									1.1			
Carya ovalis	2.3	2.2				1.1	+					
Carya glabra									2.2	1.1	1.1	
Carya tomentosa		+							1.1	1.1		
Carya ovata	+	1.1										
Oxydendrum arboreum						2.3	1.2			2.2	1.1	
Acer rubrum		2.2		+			+	+.2		1.2	1.2	+.2
Betula lenta	+	+					+					
Fraxinus americana		+	+.2	+						+		
Prunus serotina							+			+	+	
Pinus echinata									1.2			
Pinus virginiana									1.1			+
Understorey Trees												
Cornus florida		1.2	2.3	1.1							2.2	+.2
Hamamelis virginiana		+		+								
Amelanchier arborea							1.2					
Shrubs												
Rhododendron calendulaceum							3.3	1.1				
Kalmia latifolia							2.3					
Lindera benzoin			1.2									
Viburnum acerifolium			1.2	1.1							+.2	+.2
Hydrangea arborescens				1.2								
Sassafras albidum				1.1			1.2	+			+	+.2
Acer pensylvanicum							1.2					
Castanea dentata			+				+				+	
Lianas and Vines												
Vitis rotundifolia									2.2		+	+.3
Parthenocissus quinquefolia			+	+								+.2
Smilax glauca								+.2			+	1.2
Herb Layer (incl. seedlings)												
Dryopteris marginalis				1.2								
Galium latifolium				1.2								
Polystichum acrostichoides				1.2								
Viola stoneana				1.2								
Conopholis americana								2.3				
Vaccinium vacillans								1.2				
Robinia pseudoacacia				+				+				
Carex pensylvanica												1.2
Chimaphila maculata				+								1.2
Desmodium nudiflorum												1.1
Panicum commutatum												1.2
Gramineae "narrow"												1.2
Gramineae "hairy"												1.1
Amphicarpa bracteata				+								+
Coreopsis major								+				+

Species shown in boldface type (above) are evergreen. Some taxa not identified completely carry descriptive epithets in quotation marks. Additional species occurring only as "+" and only in an understorey of one relevé:

(a) Va Pkwy: S-layer Betula lutea, Rosa multiflora; and H-layer Dioscorea quaternata, Desmodium sp., Aster divaricatus, Stellaria media, Monotropa uniflora, Tiarella cordifolia, Galium aparine, Eupatorium sp., Smilax sp., Viola sp., Vitis sp., Polygala sp., Galium "small", and Carex "1 cm wide"

(b) NC Pkwy: S-layer Cornus alternifolia, Vaccinium stamineum, Viburnum cassinoides; and H-layer Heuchera americana, Smilacina racemosa, Solidago "virgaurea", Gillenia trifoliata, Dioscorea villosa, Houstonia purpurea, Arabis laevigata, Eupatorium rugosum, Cypripedium acaule, Pedicularis canadensis, Zizia trifoliata, Dryopteris sp., Polygonatum pubescens, Polygonatum sp., Carex "wide"

(c) Johns Mtn: S-layer Quercus stellata, Carya pallida, Cercis canadensis, Diospyros virginiana, Juniperus virginiana, Ulmus alata, Vaccinium corymbosum, Viburnum rufidulum; and H-layer Gaylussacia frondosa, Anisostichus capreolata, Smilax rotundifolia, Aster shortii, Cacalia atriplicifolia, Desmodium paniculatum, Eupatorium aromaticum, Helianthus microcephalus, Hystrix patula, Lespedeza hirta, Silene stellata, counterpart to the piedmont oak-hickory forests. On the coastal plain, however, such forests can also have *Magnolia grandiflora* and *Quercus nigra*, the latter suggesting (as does the presence of *Carpinus*) that the water table may be within reliable reach. The second stand, also from inland southern Georgia, was on a gentle 5° SE-facing slope in the Grassy Pond military reservation near the Florida border. It had 34 species and represents a classic *Quercus hemisphaerica* secondary forest that, despite the current lack of *Q. virginiana*, will probably succeed eventually to live-oak dominance, in the absence of disturbance. The third stand was on dark humic sand on a slight knoll in the Paul Johnson State Park on the Mississippi coastal plain just south of Hattiesburg. The original forests of this area were eliminated completely in the 1800s (for cotton plantations), and the area was reforested with pines during the 1900s. This stand, with 41 species, is still only mid-successional, with *Q. falcata* and other oaks in the canopy but also many large pines, including the native longleaf pine (*Pinus palustris*) of the fire-maintained pine savannas; slash pine (*P. elliottii*), also native on fairly sterile sand but especially in flatwoods with high groundwater; and loblolly pine (*P. taeda*), the successional pine more important on the piedmont but which may have been the main pine used in reforestation efforts.

Mean January temperature is around 10°C at all three sites, and much of the shrub layer in these forests is evergreen. Many deciduous or only somewhat evergreen forests of the coastal plain are in fact on trajectories that would lead, in the absence of fire, to dominance by live oak (evergreen *Q. virginiana*). Many of these forests are dominated now by *Q. hemisphaerica*, a secondary species with quite small acorns that colonizes disturbed and abandoned areas rapidly. The best places to see such forests are in many of the state parks in Florida, which were established typically in the 1930–1940s after land abandonment. These areas had grown up (at the time of our sampling, in the 1980–1990s) into stands like the one at Grassy Pond (middle column) in Table 9. Although *Q. hemisphaerica* is evergreen, everything else in that stand is deciduous except for *Magnolia grandiflora* and a few saplings of *Q. virginiana*. Such forests are warm-temperate deciduous now but may not be so permanently, as in the piedmont and Appalachian foothills.

There was no common oak or other canopy tree species in these three stands, only understorey *Ilex opaca* and *Vitis rotundifolia*. At the south Georgia sites, the dominance by *Q. alba* at one site and varying amounts of *Q. hemisphaerica* and *Q. virginiana* suggest mainly a difference in history and seed availability. Both sites are potentially *Q. virginiana* forest, though the deciduous secondary stage may be long. The presence of *Carpinus* at Reed Bingham suggests a lower, more mesic situation, and the site was indeed a low-lying sand flat. This site also has a diverse evergreen understorey that is lacking on the slightly sloping site at Grassy Pond.

Upland deciduous woodlands on the coastal plain also include open woodlands of *Q. laevis* (turkey oak) on deeper sand, usually in association with *Pinus palustris* (longleaf pine). These “longleaf pine-turkey oak sandhills” (Wells and Shunk 1931, Laessle 1942; cf Christensen 1988) occur especially along the fall-line sandhills through the Carolinas and Georgia but also in much of southern Mississippi, in the Piney Woods of western Louisiana-eastern Texas, and scattered throughout northern Florida (see map in Stout et al. 1993). Some stands may also have *P. taeda* or *P. elliottii*, or evergreen oaks, especially *Q. geminata* but also shorter individuals of *Q. virginiana* (plus shrubby *Q. chapmanii* and *Q. inopina* if conditions are not too sterile). The dependence of stand composition on fire and substrate is explained and illustrated by Wharton (1978, pp 180), who called these stands “dwark oak forest”. An unusually dense stand with both *Q. laevis* and pines is shown in Photo 2, but most stands are more open and too short to be forest (and too densely wooded to be savanna).

6.4 Piedmont Floodplain Forests

Southern floodplain forests, at least on the piedmont, are not unlike floodplain forests further north, which often involve *Salix* on the mostly frequently disturbed shoreline areas and taxa such as *Platanus*, *Ulmus* and *Fraxinus* on the adjacent

Solidago odora, Solidago sphacelata, Vernonia noveboracensis, Asplenium platyneuron, Polypodium polypodioides, Galium tinctorium, Viola palmata, Rubus “dewberry”, Euphorbia “hairy”, Ruellia “inubiwa”, Viola sp., Carex “big”, Compositae “hairy”.

The first stand, with a total of 41 species on 30 × 25 m, was on an 18° NW-facing mid-slope at 700 m elevation, below a tourist overlook, along the Blue Ridge Parkway in Virginia, near Waynesboro (west of Charlottesville). The second stand, with 37 species on 30 × 20 m, was on a 15° SE-facing slope along the Blue Ridge Parkway in western North Carolina, at an elevation of 1,240 m near mile marker #371. Michael Baranski was our local botanical authority. The last stand, with 59 species on 25 × 30 m, was on the “dry” soil of a 17° east-facing ridge slope on Johns Mountain (about 350 m), in the Chattahoochee National Forest near Floyd Springs in the Ridge and Valley Province of northwestern Georgia.

Mean summer temperatures at the first two sites (higher elevations) are below 22°C and January means are below freezing (Johns Mountain is much warmer). These higher-elevation deciduous forests thus should not be considered warm-temperate, even though they are similar to the piedmont oak-hickory forests, with many of the same species. One difference in these cooler forests is the prominence of *Quercus rubra* (northern red oak).

Table 8 Appalachian foothill forests at "The Pocket" of pigeon mountain (NW Georgia)

	NE-facing slope (US-246)				Floodplain (US-242)				S-facing slope (US-238)			
	T1	T2	S	H	T1	T2	S	H	T1	T2	S	H
	40m	18m	6m	.8m	35m	20m	6m	.5m	26m	18m	6m	.5m
	85%	20%	30%	30%	80%	20%	40%	30%	75%	20%	30%	50%
Canopy Trees												
Tilia heterophylla	3.3	1.1					1.2	+			+	
Liriodendron tulipifera	3.3				3.3							
Liquidambar styraciflua	2.2				2.2	1.2			2.2	2.2	2.2	+.2
Magnolia acuminata	2.2				1.1							
Fraxinus americana	2.2		+		1.2		+				+	
Acer saccharum	2.2	2.3	2.2	+.2		2.3	3.3			1.1	+	
Carya glabra	2.2				+						+	
Carya ovata	1.1								1.1	1.1		
Juglans nigra	2.2	1.1										
Carya cordiformis			+	1.1	2.2			+				
Platanus occidentalis					1.2							
Ulmus rubra		1.1	+			1.2		+				
Ulmus americana		+					+					
Fagus grandifolia				+						+		+
Quercus alba									3.3			+.2
Quercus rubra									1.1			
Quercus velutina									1.1		1.1	
Quercus prinus										+	+.2	
Acer rubrum											1.2	
Pinus virginiana											+	+
Understorey Trees/Arborescents												
Aesculus octandra			2.2				1.2					
Carpinus caroliniana		+	+				1.2					
Cornus florida			1.2			1.2	1.2				1.1	
Cercis canadensis			+								+	+
Ostrya virginiana							+					+
Ulmus alata										+	1.2	
Juniperus virginiana										+		+
Morus rubra							+				+	
Prunus serotina											1.2	+
Shrub Layer												
Lindera benzoin			2.2				2.2					
Asimina triloba							2.3					
Euonymus americanus				+.2								+.2
Callicarpa americana											+	+
Sambucus canadensis				1.2								+
Rhamnus carolinianum											+	+
Viburnum rufidulum											+	+
Lianas and other Vines												
Vitis rotundifolia	1.2	+.2			1.2	1.2				+		
Anisostichus capreolata		+		+.2								+
Parthenocissus quinquefolia		+		+								
Rhus radicans					+	+						+
Smilax bona-nox											+	+.2
Herb Layer												
Hydrophyllum canadensis				3.3				2.2				
Polystichum acrostichoides				2.3				2.3				
Dryopteris celsa								2.2				
Athyrium pycnocarpum				1.2				+.2				
Cystopteris protrusa				1.1				+				
Osmorhiza claytonii				1.2								
Carex platyphylla				1.2				+				
Stellaria pubera				1.1				+				
Viola rostrata				1.2								
Uniola laxa								1.2				
Panicum commutatum												2.2
Aster shortii				+								2.2
Aster patens												1.2
Cacalia atriplicifolia												1.2
Chimaphila maculata												1.2
Lobelia puberula												1.1
Rhus aromatica												1.2
Polygonum virginianum				+				+				
Actaea pachypoda				+				+				
Botrichyum virginianum				+								+
Eupatorium rugosum				+								+
Laportea canadensis				+				+				
Polymnia uvedalia				+								+
Sanicula canadensis								+				+
Sanicula gregaria				+				+				
Solidago sp.												1.1
Agrimonia sp.												1.2
Desmodium sp.												1.1

Species shown in boldface (above) are evergreen. Additional species occurring only as "+" and only in one relevé:

terraces. On the southern piedmont, floodplain forests are still overwhelmingly deciduous but can be quite different, depending on floodplain topography. The structures of four rather different stands are shown in Table 10.

The first stand was along an alluvial flat in the Twin Lakes State Park in the upper piedmont of south-central Virginia. It was 35 m tall, had 75 species, and was dominated strongly by *Liriodendron*, with some *Liquidambar* also in the canopy. Although some other bottomland taxa were present (e.g. *Acer rubrum*, *Ulmus americana*, *Celtis laevigata*), typical dominants of southern floodplains were not. One of these typical dominants, *Platanus occidentalis*, was dominant in the second stand, from behind a riverine levee in the Duke Forest in central North Carolina. This classic *Platanus* floodplain-forest stand had 62 species, including typical southern floodplain species *Betula nigra* and *Acer negundo*, along with *Liriodendron*, *Acer rubrum*, some *Juglans* and *Fraxinus*, a viny understorey, and fairly dense herb-layer coverage by *Glechoma hederacea*. The third, quite different stand, with 44 species, was from a low flat at the UNC botanical garden (also in central North Carolina) and was dominated by *Quercus phellos*. This oak is one of the two "tardily deciduous" species and occurs also, in almost pure stands, around the "sag ponds" on the limestone substrate of northwestern Georgia. *Q. phellos* is widely planted as a street tree but is not otherwise abundant in most natural forests. Somewhat surprisingly, the other "tardily deciduous" oak, *Q. nigra* (also widely planted), did not appear in any of the floodplain stands in Table 10. The last stand, with only 29 species, was on a levee in the Coosa River floodplain near Rome, in northwestern Georgia. The stand shown was part of a typical floodplain zonation and represents the zone (behind *Platanus*) that is usually dominated by *Betula nigra* and *Celtis occidentalis*, with significant *Juglans nigra*, *Fraxinus pennsylvanica* and even *Tilia americana*. Unfortunately, like most Southern floodplains now, this one was infested with evergreen *Ligustrum sinense* (Chinese privet).

The four stands shown have no common species except *Ulmus alata* and the ubiquitous vines *Rhus radicans*, *Smilax rotundifolia*, and *Lonicera japonica*. Each stand represents a characteristic type of floodplain forest in a particular situation of topography and inundation regime (see, for example, Wharton 1978, Sharitz et al. 1993). Cover in the herb layer is at least 20%, at least 40% for three of the four, indicating that the inundation regime is not long. This is normal on the more sloping piedmont topography. Even so, the canopies of all four are completely deciduous, as are the tree understoreys except for *Juniperus virginiana* at one site. The only woody broad-leaved evergreen species is the invasive *Ligustrum sinense* (plus the vines, which did not climb higher here than the shrub layer).

6.5 Bottomland Mixed Hardwoods

The concept of "southern mixed hardwoods" (Quarterman and Keever 1962) finds its fullest expression in the bottomland forests of the southeastern coastal plain, which extends from Delaware and southeastern Maryland to southeastern Texas (cf Nixon et al. 1990). As on the piedmont, these forests can be quite different in different places, with different topographies and inundation regimes. Even so, the following bottomland forest zones can be identified: river swamps with almost continuous flooding; lower hardwood swamp forests flooded most years during part of the growing season; the forests of backwaters and flats flooded especially in early spring; and transitional areas flooded only briefly and not every year. The species occurring in these forests are determined by the different hydroperiods. A detailed description of this floodplain forest zonation and the hydroperiods and tree species involved is given by Sharitz et al. (1993).

a) NE slope: S-layer Hydrangea arborescens; vines Clematis virginiana and Smilax hispida; and H-layer Collinsonia canadensis, Dentaria diphylla x laciniata, Disporum maculata, Pelea sp., Phacelia bipinnitrifida, Solidago flexicaulon, Tiarella colorilifolia var. collina

b) floodplain: S-layer Acer negundo, Staphylea trifoliate; and H-layer Adianthum pedatum, Allium lineale, Campsis radicans, Cystopteris bulbifera, Disporum lanuginosum, Hepatica sp., Osmorhiza longistylis, Viola sp.

c) S slope: understorey trees/shrubs Aesculus glabra, Diospyros virginiana, Robinia pseudoacacia, and Vaccinium arboreum; Amphicarpa bracteata, Coreposis major, Desmodium rotundifolia, Elephantopus tomentosus, Galium tinctorium, Goodyera pubescens, Hypericum stragalum, Lespedeza sp., Panicum dichotomum, Pycnanthemum incanum, P. sp., Salvia lyrata, Smilax rotundifolia, Solanum americanum, Symphoricarpos sp., Vernonia noveboracensis, three Carex spp. and Gramineae sp.

Crockford-Pigeon Mountain is in northwestern Georgia, near Lafayette; "The Pocket" is a concavity with steep slopes and a "gorge" with a small stream. Elevations range between about 240 m and 320 m, with mean July temperatures around 24–25°C and January means above freezing at 2–3°C. The first stand, with 51 species on 40 × 30 m, was a true "cove forest", on a steep 28° NE–facing lower. The main canopy species include *Liriodendron*, *Tilia heterophylla*, *Liquidambar*, *Fraxinus americana*, and *Magnolia acuminata* (deciduous), all of which grow relatively straight and tall, here to 40 m. The second stand, with 46 species on 20 × 40 m, was part of the *Liriodendron*-dominated floodplain forest in the "gorge", i.e., on the floor of the "Pocket". The slope was slight, only 3° to the northeast, near the mouth (delta) of this stream. This stand can be considered seral. The last stand, with 66 species on 25 × 30 m, was just outside the "Pocket", on a 15° south-facing slope. This is a typical upland oak forest, quite different from the other two stands, and is dominated in this case by *Q. alba*. Steve Bowling and Jim Renner were local botanical authorities for these relevés

Table 9 Upland mixed hardwood forests on the Southeastern US coastal plain

	Reed Bingham Ga				Grassy Pond Ga				P Johnson St Pk			
	(US-1190, 1990)				(US-1188, 1990)				(US-284, 1989)			
	Humic sand flat				Upslope humic sand				Humic-sand knoll			
	22m	14m	3m	.5m	29m	15m	7m	.5m	20m	10m	4m	.4m
	80%	30%	30%	15%	75%	20%	50%	40%	80%	30%	30%	15%
Canopy Trees												
Quercus virginiana		1.1	+				+.2					
Quercus hemisphaerica		1.1		+	4.4	2.3		3.3				
Magnolia grandiflora	1.1	2.2				1.1	3.2	1.3				
Quercus nigra	1.1	1.1							2.2	1.2		1.1
Quercus alba	4.4			+.2						+		
Quercus falcata					2.2		+	1.1	3.3			
Quercus stellata									2.2			
Quercus arkansana									1.1		1.2	1.2
Carya glabra					2.1		+					
Carya tomentosa							1.1	+.2				
Carya ovalis							1.1					
Nyssa sylvatica									1.2			+.2
Liquidambar styraciflua						+				1.2	+	+
Pinus palustris									3.3	1.1		
Pinus elliottii									2.2			
Pinus taeda									2.2			
Understorey Trees												
Carpinus caroliniana		2.3										
Cornus florida										2.3	2.2	+.2
Cercis canadensis						1.1	+.2					
Prunus serotina						+	1.1					
Amelanchier arborea		+.2										+
Ilex opaca			+				+	+.2		+	1.1	+
Prunus caroliniana							+	+				
Symplocos tinctoria		+	+.2									
Shrub Layer												
Callicarpa americana							3.3					
Aralia spinosa							1.2					
Lyonia lucida			2.3	1.2								
Lyonia ferruginea			1.2									
Serenoa repens			1.2									
Vaccinium elliottii			1.2								+	
Vaccinium arboreum											2.2	
Ilex vomitoria											2.2	+
Ilex coriacea											1.2	+
Osmanthus americanus			+.2								+	
Asimina triloba			1.2									
Myrica inodora											1.2	
Vaccinium stamineum			+									+
Lianas, Vines and Epiphytes												
Vitis rotundifolia				1.2		1.1		1.2			+.2	2.3
Rhus radicans				+						+	+	+.2
Anisostichus capreolata			+	+.2		+	+	1.2				
Smilax bona-nox			+				2.3	2.2				
Smilax glauca							2.2					+.2
Lonicera japonica											+	+.2
Tillandsia usneoides					+.2	2.2	1.2					
Herb Layer (incl. seedlings)												
Galium "4 lvs"								1.1				
Panicum "big"								1.2				

Species shown in boldface type (above) are evergreen and include the native longleaf pine (*Pinus palustris*) of the fire-maintained pine savannas; slash pine (*P. elliottii*), which is also native on fairly sterile sand but especially in flatwoods with high groundwater; and loblolly pine (*P. taeda*), the successional pine more important on the piedmont. Much of the shrub layer in these forests is evergreen

Additional species occurring only as "+" and only in one relevé:

(a) Reed Bingham: canopy and T2-layer Pinus sp.; S-layer Persea borbonia, Chionanthus virginicus, Smilax laurifolia; and H-layer Mitchella repens, Tipularia discolor, Campsis radicans, Uniola laxa, Carex "narrow", Panicum "small"

(b) Grassy Pond: S-layer Viburnum nudum, Ilex ambigua, Diospyros virginiana, Morus rubra, Erythrina herbacea, Crataegus sp., "bumelioid shrub"; and H-layer Celtis laevigata, Rhus copallina, Desmodium paniculatum, Oplismenus setarius, Rubus sp., "jacquemontioid"

(c) P Johnson St Pk: S-layer Magnolia virginiana, Acer rubrum, Sassafras albidum, Juniperus virginiana, Vaccinium corymbosum, Crataegus sp.; and H-layer Vaccinium vacillans, Gaylussacia dumosa, Gelsemium sempervirens, Smilax pumila, Rubus flagellaris, Hypericum hypericoides, Pteridium aquilinum, Eupatorium rotundifolium, Pinus seedling, Malvaceae sp., "euphorbiaceous vine"

Only the less inundated (non-swamp) forests of the backwater flats and upland transition can be considered potential warm-temperate deciduous forests. A diverse selection of such forests is shown in Table 11.

The first stand represents the very unusual occurrence of a beech-dominated floodplain forest on the coastal plain of North Carolina (Croatan National Forest), first recognized and described by Nesom and Treiber (1977). This *Fagus* forest, with 55 species, was on a flat upper terrace above what was then a cut bank on both sides of a slow-moving stream. *Fagus* is strongly dominant but is joined by trees with relatively wide ecological amplitudes, including *Nyssa sylvatica*, *Liriodendron* and *Acer rubrum*. This, plus the dominance by *Fagus* and the understorey of *Cornus florida* (with *Ostrya virginiana*, *Stewartia malacodendron*, and *Mitchella repens*), all suggest that the soil is not waterlogged and that conditions are generally not hydric.

The second stand, with 52 species, was on a riverside terrace in a floodplain (noted as a "seasonal swamp") in Blue Springs State Park in southeastern Alabama. This stand is more typical of southern floodplains, being dominated by *Quercus nigra* (water oak). Other tree species common in lowlands were also present significantly, namely *Nyssa biflora*, *Acer rubrum*, and *Carpinus caroliniana*; also present were other bottomland oaks (*Q. laurifolia* and *Q. lyrata*), *Liquidambar*, *Fraxinus*, *Platanus*, and *Magnolia virginiana*.

The third stand, with 51 species, was on a moist flat above a depression in the Honey Island Swamp along the Pearl River in southeastern Louisiana. It had a canopy dominated by *Liquidambar* but also containing the various bottomland oaks, *Q. nigra*, *Q. michauxii*, *Q. lyrata* and *Q. phellos*, plus *Nyssa sylvatica* and evergreen *Ilex opaca* and *Magnolia virginiana*. The fairly dense herb layer (60% cover) included *Oplismenus setarius* and *Carex louisianica* but also *Lygodium japonicum* and other graminoids. Bottomland and floodplain forests and swamps are especially well developed in southern Louisiana and have been described, among others, by White (1983) and Tanner (1986).

The last stand was on a mesic-moist flat above a main stream channel at the Edisto Nature Trail, a protected area in the bottomlands along the Edisto River on the low-lying coastal plain west of Charleston (South Carolina). This stand, with 74 species, is a typical *Quercus laurifolia* floodplain forest on an elevated flat, but similar stands can also occur on gentle streambanks and in shallow depressions if not inundated too long. Although *Q. laurifolia* is dominant and evergreen, this stand could still perhaps be considered a warm-temperate deciduous forest since the other canopy trees are all deciduous (except for some pines), including the swamp species *Carya aquatica*, and *Carya glabra*. The understorey was viny, with some lianas reaching the canopy, and the herb layer (60% cover) was diverse, largely with graminoids but also with much *Tovara virginiana* and vines.

These stands show a more consistent canopy and understorey composition, except for the unusual *Fagus* stand. All the others have (semi-evergreen) *Quercus laurifolia* plus either *Q. nigra* or *Q. lyrata* and *Q. michauxii*. All also have *Liquidambar*, *Acer rubrum* (s.l.), and *Carpinus* (the *Fagus* stand has both *Carpinus* and *Ostrya*). All are viny, but only *Rhus radicans* and *Anisostichus* (*Bignonia*) *capreolata* occur in all four, and canopy lianas are significant only at Edisto, which also has the richest herb layer. The shrub and herb layers are all different. The herb layer is least, only 10%, at Blue Springs, suggesting that it has the longest inundation period, as does its designation as a "seasonal swamp" and the presence of *Nyssa biflora* and *Q. lyrata*. Even so, the most typical "southern mixed hardwoods" stands may be Blue Springs and Honey Island, with their components of evergreen *Magnolia* species and *Ilex opaca*.

Species composition can be very patchy on the mosaics of flats, sloughs, channels, depressions and other features in floodplains and their adjacent backwater areas. Nevertheless, Sharitz et al. (1993) made the following generalizations, which seem to fit our relevé data also:

- *Liquidambar* is a common dominant or co-dominant on riverside flats;
- *Quercus nigra* (and *Q. phellos*) are most common on relatively poorly drained flats;
- *Quercus laurifolia* is mainly topogenic and remains if sites are stable; and
- *Acer rubrum* can occur almost everywhere, often also *A. negundo*.

Even so, we found *Q. laurifolia* to be especially abundant and often apparently permanent. A bottomland forest dominated by *Liquidambar*, from northern Florida, is shown in Photo 3.

The first stand, with only 30 species on 30 × 20 m of humic sand, was on a mesic flat (120 m elevation) in Reed Bingham State Park east of Moultrie in southern Georgia. The second stand, with 34 species on 15 × 25 m of humic sand (denoted as "mesic"), was on a gentle 5° SE-facing slope in the Grassy Pond military reservation near Valdosta, near the Florida border a bit further south. This is a classic *Quercus hemisphaerica* secondary forest that, despite the current lack of *Q. virginiana*, probably would succeed to live-oak dominance in the absence of disturbance. The last stand, with 41 species on 30 × 30 m of dark humic sand, was on a slight knoll in the Paul Johnson State Park near McLaurin, on the Mississippi coastal plain just south of Hattiesburg. This area was stripped completely of its original forests in the 1800s (for cotton plantations) and was reforested with pines during the 1900s, many of which remain. Mean January temperature is around 10°C at all three sites, and July means are around 27°C

Photo 2 Unusually dense sandhill oak-pine scrub, in South Carolina. The main tree on this 'longleaf pine-turkey oak sandhill' (Wells and Shunk 1931; cf Christensen 1988) is *Quercus laevis* (turkey oak), a short, deciduous oak that occurs almost exclusively on sand, especially deeper sandhills. The pine overstorey is mainly *Pinus palustris*, although *P. taeda* and *P. elliottii* also occur. Spanish moss (*Tillandsia usneoides*, Bromeliaceae) is hanging from many trees. Both fire and the sterile white sand normally preclude dense vegetation, but this stand had been protected from fire for some time and was near a wetland, suggesting groundwater and perhaps more humic sand not far below the surface. More xeric sites often have pines only. Relationships of stand composition, i.e. pines with or without oaks, to topography, sand depth, and fire are described well by Wharton (1978), who shows a similar photo and calls this vegetation 'dwarf oak forest'. This photo was taken in the Biedler Forest, near the Four Holes Swamp, on the coastal plain of South Carolina southeast from Columbia

6.6 Beech-Magnolia Forests

The potential climax on the sandy Southern coastal plain, in the absence of fire and other disturbance and on sites with at least somewhat humic soil, has been considered by some to be a forest dominated by *Fagus grandifolia* and *Magnolia grandiflora* (cf Delcourt and Delcourt 1974, 1977; Harcombe and Marks 1983). This Southern magnolia is a lauro-sclerophyll, which means that it is shade tolerant but grows slowly. So a beech-magnolia climax would take many years to develop. Such forests are rare but do occur in several locations, three of which are represented in Table 12. All three stands are on flat or only slightly sloping terrain, but the flat stands are at least elevated above adjacent floodplains.

The first stand is at the Zemurray Estate in Louisiana, which protects one of the very best areas of beech-magnolia forest, surviving in the loop of a river where it was thus protected from fire (see White 1987). The forest here is overwhelmingly beech-magnolia, with only small canopy admixtures of *Liquidambar* and a few oaks. Over much of the area there was a fairly dense shrub layer of evergreen, aromatic *Illicium floridanum*, which is usually confined to bottomlands. The stand shown here, with only 35 species, was on a slightly elevated loess flat. The total number of species in a (typically) 25 × 25 m relevé was usually not large and was sometimes below 30. Even so, being in this forest was like being in a cathedral, with the canopy formed by large, straight-growing trees reaching 40 m in height and an understorey tree layer reaching 20 m (see Photo 4).

The other two stands are from western Florida, one at Wakulla Springs south of Tallahassee and the other at Apalachicola Bluff preserve, along the Apalachicola (=Chattahoochee) River south of the Georgia-Alabama border (cf Delcourt and Delcourt 1977). Both of these stands are more diverse, with *Fagus* and *Magnolia* joined in the canopy by *Liquidambar*, 2–3 *Quercus* species (deciduous), and *Carya glabra* (the most common of the coastal-plain hickories). The stand at Wakulla Springs, with 63 species, was on mesic humic sand along a nature trail above a floodplain. This forest is an especially rich example of the beech-magnolia type of southern mixed hardwoods; the understorey was mainly evergreen, with *Ilex opaca* and *Persea borbonia* joining *M. grandiflora*. The stand at

Table 10 Several types of upland floodplain forest on the Southeastern Piedmont of the USA

	Twin Lakes Va				Duke Forest NC				UNC Bot Garden				Marshall Forest			
	(US-178, 1989)				(AM-162, 1988)				(AM-164, 1988)				(US-227, 1989)			
	Alluvial				Behind levee				Low flat				Levee			
	35m	20m	6m	.6m	38m	20m	6m	1.0m	32m	16m	5m	.8m	30m	14m	4m	.3m
	70%	30%	30%	40%	80%	30%	40%	60%	70%	10%	20%	40%	80%	20%	70%	20%
Canopy Trees																
Platanus occidentalis	+				5.4	1.2										
Liriodendron tulipifera	4.4	1.1	+.2		3.2											
Liquidambar styraciflua	2.2	1.2	+		1.1											
Betula nigra					2.1								3.4			
Juglans nigra					1.1		+.2						2.3			
Fraxinus pennsylvanica					1.1						1.1		2.1			
Fraxinus americana			+				+									
Ulmus americana	1.1		+			1.2	1.2				+			2.1		
Celtis laevigata		1.2													+	
Celtis tenuifolia							1.1									
Celtis occidentalis													3.3	2.2	1.2	
Tilia americana													2.1			
Acer rubrum	1.2		2.2	+		2.2					2.3	+.2				
Nyssa sylvatica			1.1						1.1		1.2					
Quercus phellos									4.3		+	+				
Quercus pagodaefolia									2.2					+		
Quercus lyrata									1.1							
Quercus michauxii										1.1		+				
Quercus falcata													1.1			
Carya cordiformis							1.2								1.2	
Carya glabra	1.1										+.2					
Carya ovata											1.2					
Understorey Trees																
Carpinus caroliniana		1.1	+											+		
Cornus florida		1.2	2.3													
Juniperus virginiana		1.1		+							+					
Prunus serotina		1.1										+.2				
Acer negundo						3.3	+.2								1.1	
Acer saccharum							1.2									
Morus rubra						+.2								1.1	+	
Shrub Layer																
Asimina triloba			2.3				1.2									
Lindera benzoin			+.2				2.2									
Aesculus sylvatica							1.1									
Rubus argutus							+				+.2					
Ilex decidua											2.2					
Ligustrum sinense							1.2								4.4	
Arundinaria gigantea															2.2	
Rosa multiflora			+												1.3	
Sambucus canadensis				+			+.2								+	
Lianas and Vines																
Rhus radicans			+	+.2				3.3		1.2				1.2		+
Smilax glauca			1.2	+.2												
Smilax rotundifolia				+				+.2			1.2				+	+
Lonicera japonica				2.2			2.2	1.2				1.2			2.2	2.2
Parthenocissus quinquefolia				+			+	+.2			1.2	1.2				
Campsis radicans				1.2				+								
Vitis rotundifolia				+								+.2				
Anisostichus capreolata												+.2			+	1.2
Herb Layer (incl. seedlings)																
Polystichum acrostichoides				2.3												
Carex big hairy"				2.2												
Viola rotundifolia				1.2												
Elephantopus carolinianus				1.2												
Glechoma hederacea								3.4								
Boehmeria cylindrica				+				1.2								
Festuca obtusa								1.2								
Laportea canadensis								1.2								
Viola papilionacea								1.2								
Carex "kawazusuge"												3.3				
Carex stipata												1.2				
Microstegium vimineum								+.2								2.2
Dioscorea sp.																1.1
Rudbeckia sp.				1.1												
Solidago sp.				1.2												
Carex "shirasuge"				1.2												
Carex "itosuge"								1.2								
Luzula sp.												1.2				
Panicum "small"												1.2				
Asarum canadense				+.2				+								
Euonymus americanus				+.2				+				+.2				
Amphicarpa bracteata				+				+								
Botrychium virginianum				+				+								
Menispermum canadense				+												+
Tovara virginiana								+								+

Species shown in boldface (above) are evergreen and occurred only in understoreys. Some taxa not identified completely carry descriptive epithets in quotation marks, sometimes Japanese names of similar species. Additional species occurring only as " + " and only in one relevé:

(a) Twin Lakes: S-layer Fagus grandifolia, Carya tomentosa, Alnus serrulata, Cercis canadensis, Corylus americana, Sassafras albidum; and H-layer Botrychium dissectum, Onoclea sensibilis, Smilax laurifolia, Actaea rubra, Fragaria virginiana, Galium aparine, Lycopus uniflorus, Pilea pumila, Smilacina racemosa, Tiarella cordifolia, Tipularia discolor, Uvularia perfoliata, Agrimonia sp., Rubus sp., Clematis sp., Aster sp., Eupatorium 2 spp., Agrostis sp., Desmodium sp., Desmodium "big", Sanicula sp., Allium sp., Galium "small", Geum sp., Spiranthes sp., Viola 2 spp., Carex "small", Carex "aobasuge", Panicum "big", Acanthaceae sp.

Apalachicola Bluff, also rich (62 species), was on fine humic sand at a "steephead" (upper stream course), on a gentle 5° west-facing slope. The understorey here, on the other hand, was largely *Ostrya virginiana*, with *Carpinus*, *Cornus florida*, and some *Ilex opaca*.

In these stands, *Fagus* is always more abundant in the canopy than *Magnolia*, though both are always significant and slower-growing *Magnolia* is generally more abundant in the understorey, where it survives the shade better than does beech. Even though beech and magnolia are the co-dominants, the canopy of all three stands also included generalists *Liquidambar* and *Quercus alba*, and bottomland species *Q. michauxii*. *Fagus* usually requires continuously moist conditions but also well drained soil (though apparently exceptional "wet beech" flatwoods were reported by Braun). Soil aeration appears to be provided here by the loess or humic-sand substrate, even if flat and only slightly elevated. All the other common trees are known to be tolerant of moist conditions. *Carpinus* occurs on the flats and gentle slope, but *Ostrya* only on the slope (last stand). Woody broad-leaved evergreens are significant in all stands, including *Magnolia virginiana*, *Ilex opaca*, *I. vomitoria*, *Persea*, *Prunus caroliniana*, and *Symplocos tinctoria*, plus a dense *Illicium* shrub layer at Zemurray and dense herb-layer *Smilax* at Wakulla.

7 Mexican Temperate Deciduous Forests

Many deciduous tree genera and even species from eastern North America reappear in some montane forests of the Sierra Madre Oriental in eastern Mexico, especially on slopes facing the Gulf of Mexico (see Miranda and Sharp 1950, Rzedowski 1978, Velázquez et al. 2000). Major taxa include *Fagus mexicana* (Martínez 1940, Little 1965), deciduous *Quercus* (with many Mexican species), *Liquidambar macrophylla* (Velázquez et al. 2000), *Carpinus caroliniana* and *Cornus florida*, plus *Nyssa sylvatica*, *Ostrya virginiana*, *Prunus serotina*, *Tilia floridana*, *T. mexicana*, and the evergreen understorey shrub *Illicium floridanum*. These forests are scattered from Tamaulipas to Chiapas (see map in Miranda and Sharp 1950) and are especially common in Veracruz state (cf Gomez-Pompa 1977). These Mexican mountain locations have shorter, milder winters than in the eastern USA, and some deciduous taxa, including *Fagus*, have been reported as "almost evergreen" (e.g. Peters 1995). It is not possible here to assess the warm-temperate status of these forests definitively, but Greller (1990) did ascribe them to the transitional VI-Ve (not Ve-VI) zone. These Mexican deciduous forests certainly invite further study and may well represent counterparts to warm-temperate deciduous forests in other mountainous areas, such as China and the Hyrcanian region.

Conclusions

The shape of eastern North America, with its large land area to the north and winter-warm Gulf of Mexico to the south, results in a southern region, roughly south of Chesapeake Bay and the Ohio River valley, that has the mild winters characteristic of a warm-temperate climate – except when interrupted (often almost weekly) by sudden, forceful cyclonic intrusions of cold, dry northern air. This southern climate, with its sudden changes and up-and-down winter temperatures, is subcontinental right up to the Atlantic and Gulf coasts. Almost the entire region, except the southern Appalachian Mountains, has long, warm summers with mean temperatures generally well above 24°C. January mean temperatures are generally near or above 10°C along the Gulf coast, above 5°C across the interior South and not below 0°C over most of the rest of the region. The unusual, infrequent low-temperature extremes, however, reach well below −20°C

(b) Duke Forest: S-layer Staphylea trifolia, Smilax sp.; and H-layer Lonicera sempervirens, Dioscorea batatas, Dioscorea villosa, Arisaema triphyllum, Cimicifuga racemosa, Clematis virginiana, Cryptotaenia canadensis, Geum canadense, Hystrix patula, Impatiens pallida, Oxalis florida, Pilea fontana, Polygonatum biflorum, Ranunculus abortivus, Rudbeckia sp., Saururus cernuus, Sedum ternatum, Allium sp., Eupatorium "4 lvs", Solidago sp., Carex sp., Carex "big", Labiatae sp.

(c) UNC Botanical Garden: T2-layer Ilex opaca; S-layer Ulmus alata, Ulmus rubra, Ilex verticillata, Leucothoë racemosa, Viburnum rafinesquianum, Viburnum prunifolium, Gelsemium sempervirens; H-layer Rhododendron nudiflorum, Dicliptera brachiata, Goodyera pubescens, Lycopus virginicus, Athyrium sp., Galium "very narrow", Scutellaria sp., Carex "toboshigara-suge", Carex "yariho"; and moss-layer Polytrichum sp. and Sphagnum sp.

(d) Marshall Forest: S-layer Cocculus carolinus, Ipomoea hederacea; and H-layer Verbesina virginica, Carex sp.

The first stand, with a total of 75 species on 10 × 40 m, was along an alluvial flat at Twin Lakes State Park in the piedmont of south-central Virginia. The second stand, with 62 species on 30 × 50 m, was behind a levee along a stream off the Old Chapel Hill Road in the Korstian Division of the Duke Forest, in the piedmont of central North Carolina (near Durham). This is a classic *Platanus* floodplain forest, with *Liriodendron* and *Betula nigra*. Robert K. Peet and Dawson Sather were local botanical authorities in the Duke Forest. The third stand, with 44 species on an area recorded as 40 × 50 m, was on a low flat in the Big Oak Woods at Mason Farm (UNC Botanical Garden) in central North Carolina (near Chapel Hill). Local authorities here were Dawson Sather, Peter S. White and Kathleen Kron. The last stand, with only 29 species on 15 × 30 m, was on a levee in the Coosa River floodplain, in the Marshall Forest near Rome (northwestern Georgia). Philip Greear was the local botanical authority here.

Table 11 Representative, mainly deciduous bottomland forest stands on the Southeastern US coastal plain

	Croatan Nat Forest (AM-220, 1988) Terrace > cut bank				Blue Springs St Pk (US-254, 1989) (seasonal swamp)				Honey Island (US-307, 1989) > depression				Edisto Nature Trail (US-1150, 1990) Mesic-moist flat			
	30m	15m	6m	.7m	20m	12m	6m	.8m	25m	14m	6m	.3m	30m	20m	6m	.8m
	80%	30%	40%	30%	70%	40%	30%	10%	85%	30%	20%	60%	80%	20%	30%	60%
Canopy Trees																
Quercus laurifolia					1.1				2.2	+.2	+.2	+.2	4.4	2.2		
Quercus nigra					3.3	1.1	+		1.2		+.2	+.2				
Quercus lyrata					1.1	1.2								1.1	1.2	
Quercus michauxii				+	+				2.2							
Quercus phellos										+.2	+		1.1		+	1.1
Quercus alba			+													
Liquidambar styraciflua			+		1.1				3.3				1.1		1.2	
Nyssa biflora					2.2		+									
Nyssa sylvatica	1.1		+						1.2	2.2	1.1					
Fagus grandifolia	4.4	2.3		2.3												
Liriodendron tulipifera	1.1															
Acer rubrum	1.2				2.2		+							1.2	+.2	+.2
Acer rubrum v. drummondii										1.1	+	+				
Fraxinus pennsylvanica					1.1	2.2	+	+								1.1
Carya aquatica													3.3	1.1		
Carya glabra												+	2.3			
Celtis laevigata													1.1	2.2		1.1
Platanus occidentalis					1.1											
Ulmus americana														1.1	+	
Magnolia virginiana					1.1	2.2		+	1.2	+						
Magnolia grandiflora						+	+									
Ilex opaca		1.1	+				1.2	+	1.1	2.2	1.1	+.2			+	
Pinus glabra											+			1.1		
Pinus taeda													1.2		+	+
Understorey Trees																
Carpinus caroliniana			1.2		2.2	2.3	1.2			2.2	2.2			1.1		
Cornus florida		2.3	1.2													
Ostrya virginiana		1.2	2.3													
Acer saccharum		1.2		+.2												
Crataegus marshallii							+				1.1					
Ilex decidua						+.2					+.2	+				
Morus rubra			+				+									
Persea borbonia			+													+
Persea palustris											+					
Shrub Layer																
Stewartia malacodendron			2.2	+.2												
Viburnum dentatum							2.2									
Sebastiana fruticosa							1.2	1.2								
Itea virginica							1.2	1.2								
Viburnum ashei											2.2	+				
Lygodium japonicum											+	2.3				
Rubus argutus												1.2				
Sabal minor								+.2							2.3	+.2
Myrica cerifera															1.2	
Rhamnus caroliniana															1.2	
Callicarpa americana				+							+					
Ulmus alata							+									+.2
Euonymus americanus				+							+	+				
Symplocos tinctoria											+	+				
Lianas, Vines and Epiphytes																
Vitis rotundifolia				+	+.2	+.2		+					1.2	1.2		
Vitis aestivalis													1.1	1.2		
Anisostichus capreolata		+		+				+.2		+	+.2	+.2				1.2
Berchemia scandens								1.2		1.2	+		1.2	2.3		+
Rhus radicans				+		+		+.2		+.2		+.2		1.2	1.1	2.2
Campsis radicans							+	+				+		1.2		
Lonicera japonica				+											1.2	2.2
Ampelopsis arborea												+.2				1.1
Mikania scandens												+			+	1.3
Decumaria barbara							1.2									
Smilax bona-nox				+				+								1.2
Smilax glauca				+												+.2
Smilax hispida								+				+.2				
Smilax rotundifolia								+				+				
Gelsemium sempervirens							+									+
Tillandsia usneoides						2.2	+									
Herb Layer (and seedlings)																
Mitchella repens				2.3								+.2				+.2
Polystichum acrostichoides				1.2												
Podophyllum peltatum				1.2												
Hexastylis arifolia				1.2												
Galium circaezans				1.2												
Commelina virginica								1.2								
Pontederia cordata								1.2								
Carex sp.								1.2								
Carex "cyperoid"																3.3
Tovara virginiana												+				3.2
Oplismenus setarius												2.3				2.3
Carex louisianica												2.3				
Carex abscondita												1.2				
Botrychium biternatum								+				1.1				+.2
Chasmanthium sessiliflorum												1.2				
Leersia lenticularis																2.3
Uniola laxa																2.3
Carex debilis																2.2
Carex intumescens																2.3
Carex "narrow"				1.2												2.3
Carex (sketch)																2.2
Carex sp.																2.2
Aster linariifolius																1.1
Aster dumosus																1.2
Boehmeria cylindrica												+				1.1
Lycopus rubellus												+				+
Onoclea sensibilis								+								+.3
Panicum "long"																1.2
Panicum "wide"																1.2

Species shown in boldface type (above only) are evergreen. Some taxa not identified completely carry descriptive epithets in quotation marks, sometimes Japanese names of similar species. Additional species occurring only as "+" and in only one relevé:

(a) Croatan: Oxydendrum arboreum in canopy; S-layer Magnolia tripetala, Carya cordiformis, and Hamamelis virginiana (all also H layer), plus Vaccinium arboreum, Juniperus virginiana, Lindera benzoin, Juglans sp.; H-layer Thelypteris hexagonoptera, Th. phegopteris, Chimaphila throughout the interior and below −15°C even near the Gulf and southern Atlantic coasts.

The result, except along the coasts, is a region of warm-temperate deciduous forests, perhaps the world's largest, dominated largely by oaks. In fact, during the Eastern North American Vegetation Survey, Prof. Miyawaki and his Japanese colleagues were so impressed by the oak dominance throughout eastern North America that they referred to the region as one of "oak-forest culture", as a counterpart to the "laurel-forest culture" of East Asia (e.g. Ueyama 1969) and what they perceived as the "beech-forest culture" of central Europe. Oak-hickory forests cover much of the interior South and extend onto the coastal plain. There are, however, also more mesophytic upland forests (e.g., with *Fagus*), "southern mixed hardwoods" across the coastal plain, and various bottomland forest types, these last two with admixtures of broad-leaved evergreen trees (see relevé summaries in Tables 5 to 12). The greatest species richness and diversity of forest types (except where hydroperiods are long) are generally found in the bottomlands, including floodplain terraces with various inundation regimes. Some oak forests of the southern Appalachians are similar to piedmont forests, but these foothill and lower-montane areas are cooler and their forests are not included as warm-temperate deciduous.

In terms of existing zonations, the warm-temperate deciduous forests of eastern North America would include Braun's largely piedmont and interior-lowland regions of oak-hickory and western mesopnhytic forests, plus the region of "southern mixed hardwoods", including the 'deciduous-evergreen-conifer' region of Greller. This southern mixed-hardwood region includes interior areas without *Magnolia grandifolia* (further north) and coastal-plain areas with *Quercus alba* and *Fagus* (plus *Magnolia*), which disappear further south. The region of the 'live oak-magnolia association' association of Daubenmire, mainly in northern Florida and which Greller called the 'temperate broadleaf evergreen forest' region, is not deciduous and is not included. In his later zonations, Greller (1989, 1990) appeared to place the northern/interior boundary for Walter's Ve climate near the −15°C isotherm for absolute minimum temperature, the lower limit for broad-leaved evergreen trees (cf Woodward 1987; Box 1995). If one accepts this delimitation of a warm-temperate climate proper, then the warm-temperate deciduous forests occupy the transitional climate zones Ve-VI and VI-Ve, some southern portions of zone VI, but do not extend far into zone Ve except in floodplains, on particular substrates, or as successional secondary forests.

Two features of the region of "southern" deciduous forests are relatively unique. One is the coupling of relatively high mean winter temperatures and much lower extremes, which favors deciduous trees and forests even in areas where broad-leaved evergreen trees can grow well until the next unusual cold event (which may be 50 years away). The other feature is the sandy substrates and low-lying topography of the coastal plain, which may also favor deciduous forests or woods in some places, such as where groundwater can be reached reliably or soil nutrient levels are higher, as in the deeper soils of

maculata, Desmodium nudiflorum, Goodyera pubescens, Luzula echinata, Melica nutans, Phryma leptostachya, Polygonatum biflorum, Sanguinaria canadensis, Athyrium sp., Botrychium sp., Sanicula sp., Galium "narrow", Carex "juzu-suge", C. "yachikawazu", Panicum "big", Poa sp.

(b) Blue Springs: S-layer Vaccinium elliottii, Rhododendron canescens, Bumelia reclinata, Clematis viorna (also H layer), Cornus stricta, Ligustrum sinense, Leucothoe racemosa, Rubus sp.; epiphytic Polypodium polypodioides; and H-layer Arundinaria gigantea, Lobelia cardinalis, Eupatorium rugosum, Hydrocotyle verticillata, Solidago sp., Gramineae sp.

(c) Honey Island: S-layer Sambucus canadensis, Halesia diptera (also H layer); H-layer Aristolochia serpentaria, Clematis crispa, Clematis virginiana, Hypericum galioides, Aster lateriflorus, Elephantopus carolinianus, Polygonum punctatum, Brunnichia cirrhosa, Panicum commutatum, Carex tribuloides.

(d) Edisto Nature Trail: S-layer Diospyros virginiana, Ilex myrtifolia, Sabal palmetto, Parthenocissus quinquefolia, Wisteria sp., plus Hypericum hypericoides and Crataegus sp. (both also H layer); and H-layer Vaccinium corymbosum, Ligustrum obtusifolium, Rubus trivialis, Asplenium platyneuron, Commelina communis, Elephantopus tomentosus. Lobelia elongata. Matelea carolinensis, Cirsium sp., Desmodium "narrow", D. "round", Juncus sp., Poa "big", Polygonum "white", Ranunculus sp., Labiatae sp.

The first stand, with 55 species on perhaps 30 × 30 m, was on a relatively flat upper terrace above the cut bank of slowly moving Island Creek, in the Croatan National Forest of southeastern North Carolina between New Bern and Morehead City. This forest is described further by Nesom and Treiber (1977). The second stand, with 52 species on 20 × 30 m, was in the floodplain of the Choctawhatchee River, in Blue Springs State Park in southeastern Alabama. Though not inundated when sampled, this is in fact a seasonal swamp. The third stand, with 51 species on 25 × 25 m, was on a moist flat above a depression in the Honey Island Swamp along the Pearl River in southeastern Louisiana. Local botanical authorities were Sidney McDaniel, C. Patrick O'Neil, and David A. White (see also White 1983). The last stand, with 74 species on 15 × 25 m, was on a mesic-moist section of creek floodplain along the Edisto Nature Trail, a protected area of diverse bottomland communities near Jacksonboro, on the low coastal plain of South Carolina west of Charleston. This site was sampled in 1990 and revisited for confirmation in 1996. Temperatures at all sites are quite high enough to be considered warm-temperate.

Photo 3 Bottomland hardwood forest in northern Florida, on a floodplain terrace dominated here by *Liquidambar styraciflua*. This secondary forest developed on former pastureland, next to Paynes Prairie, a former lake (now dry lake bottom) in northern Florida just south of Gainesville. The former lake, over limestone, once held enough water for commercial riverboat service – until it drained suddenly and almost completely in one night. Although dominated strongly here by *Liquidambar*, the photo is nevertheless very representative of the appearance of Southern bottomland forests in general, most of which are included in the concept of "southern mixed hardwoods". Since the climate of northern Florida is clearly warm-temperate, such forests are also a type of warm-temperate deciduous forest, although the bottomland topography may play a large role in favoring deciduous trees over evergreens. Most Southern bottomland forests also include some broad-leaved evergreen species, such as *Magnolia virginiana*, *M. grandiflora*, and *Quercus laurifolia*. For other main species in Southern bottomland forests, see the main text

bottomlands. Land-use history and other kinds of disturbance also favor deciduous trees, since disturbance breaks up forest canopies and raises light levels, which may be exploited more by the faster-growing malacophyllous deciduous tree species. Even in the region of potential dominance by the live oak-magnolia (*Quercus virginiana-Magnolia grandiflora*) association, mainly northern Florida, low nutrient levels and frequent drought on the sandy substrates make replacement of deciduous trees by broad-leaved evergreens a slow process. Zonal broad-leaved evergreen forests would be dominated by semi-sclerophyllous *Quercus virginiana*, which does not reproduce reliably, grows slowly, and usually becomes established following colonzation by *Q. hemisphaerica*, another semi-sclerophyllous evergreen, which does however grow much faster.

As in East Asia, the warm-temperate deciduous forests of the warmest areas (outer coastal plain) are composed mainly of tree species from the secondary forests that could be replaced by more shade-tolerant zonal evergreen broad-leaved forests. The difference, in North America, is that there are only two native broad-leaved evergreens, *Quercus virginiana* and *Magnolia grandiflora*, which are capable of reaching a deciduous forest canopy on the uplands. Both are rather sclerophyllous and grow slowly, as does *Ilex opaca*. Tall, true laurophylls (shade tolerant but not sclerophyllous), such as *Magnolia virginiana*, *Persea borbonia* and *Gordonia lasianthus*, are confined to moister bottomland, as are also shorter laurophylls such as *Cyrilla racemiflora*, *Symplocos tinctoria*, *Osmanthus americanus*, *Ilex vomitoria* and *I. cassine*. Of the other evergreen oaks, *Quercus laurifolia* is confined largely to floodplains, *Q. geminata* is shorter and quite sclerophyllous, and *Q. hemisphaerica* is a short-lived colonizer. The role of *Fagus* is interesting in that it occurs in the warm-temperate South as well as the typical-temperate and cool-temperate zones further north. This may also happen, marginally, in Japan but does not happen in China because northern China is too dry.

With global warming, deciduous forests with "southern" species would be expected to expand or at least shift northward, where some of their key species already occur

Table 12 Beech-Magnolia forests in the Southeastern coastal plain of North America

	Zemurray				Wakulla Springs				Apalachicola Blf			
	(US-292, 1989)				(US-1245, 1990)				(DFL-1,1991)			
	Loess				Mesic humic sand				Fine humic sand			
	40m	20m	5m	.2m	32m	13m	6m	.8m	40m	20m	3m	.6m
	80%	20%	60%	10%	80%	20%	30%	35%	80%	20%	15%	20%
Canopy Trees												
Fagus grandifolia	4.4		1.1		3.3		+	+	3.3			
Magnolia grandiflora	2.2	1.1	1.2		2.2	2.2	+	+	2.3	1.2	+.2	
Liquidambar styraciflua	2.2				2.2		+	+	2.2		+	
Quercus alba	2.1				2.2				1.1			
Quercus michauxii	1.1	1.1			2.2		+.2	+.2	1.1		+	+
Quercus shumardii					2.2	1.1	+					
Quercus nigra	+					1.1	+.2				+	
Quercus hemisphaerica							2.3				1.1	+
Carya cordiformis					2.2		+					
Carya glabra					1.1	1.1	1.2		2.2		+	
Tilia americana					2.2		1.1					
Fraxinus americana					1.1		+.2					
Liriodendron tulipifera									1.1			
Nyssa sylvatica		+								+	+	
Magnolia virginiana			+									
Pinus glabra	+			+								
Understorey Trees												
Ostrya virginiana										2.2	2.2	
Carpinus caroliniana		1.2	1.2	+			+			1.2		+.2
Symplocos tinctoria		1.2	2.2	+.2								
Halesia diptera		1.2	1.2									
Cornus florida							1.1			1.1	1.2	+
Cercis canadensis							1.1				+	+
Quercus austrina											+.2	+
Ilex opaca						2.2	3.3	1.2		1.1	+	+
Ilex vomitoria			+.2				1.2					
Persea borbonia						1.1	1.1				+.2	
Prunus caroliniana			1.1			1.2					+.2	+.2
Juniperus virginiana											+	+
Shrub Layer												
Illicium floridanum			3.4	2.2							+.3	
Asimina parviflora							2.2					
Osmanthus americanus							1.2					
Callicarpa americana							1.1				+	+
Hamamelis virginiana			+				+.2	+.2			+	
Cornus foemina							+.2				+	
Dioscorea quaternata							+					+
Lianas, Vines and Epiphytes												
Smilax laurifolia							1.1					
Smilax bona-nox								3.4				
Smilax pumila								2.2				
Smilax smallii			+	+								
Rhus radicans				+		+.2		1.1				+
Anisostichus capreolata				+.2				+				+
Vitis cinerea					+							
Tillandsia usneoides										+	+	
Polypodium polypodioides										+	+	
Herb Layer (incl. seedlings)												
Carex sp.				2.2								
Carex "narrow"												2.2
Euonymus americanus								2.2				
Hexastylis arifolia				1.2								+.2
Chasmanthium sessiliflorum				1.2								
Mitchella repens				+				1.2				+
Oplismenus setarius								1.2				+.2
Asplenium platyneuron								1.2				
Viola walteri								1.2				
Arisaema dracontium								+				+
Polystichum acrostichoides												1.2
Thelypteris kunthii												1.3
Tradescantia subaspera												1.1
Carex baltzellii												1.2
Panicum sp.								1.2				

Species shown in boldface type (above) are evergreen. Some additional species, occurring only as "+" in the understorey of only one relevé were: (a) Zemurray Estate: epiphytic Trichomanes petersii; and H-layer Erythrina herbacea, Epifagus virginiana, Vaccinium tenellum, Ligustrum sinense, Elephantopus tomentosus, Smilax rotundifolia, Smilax glauca, Smilax sp., Vitis sp., Panicum sp., Liliaceae sp.

(e.g. *Quercus alba*, *Q. prinus*, *Fagus grandifolia*, *Liriodendron tulipifera*). Evergreen broad-leaved forests (especially those dominated by *Quercus virginiana*) could move northward too, but only if they can grow successfully on the piedmont red clay and its lower water table, which are so different from the humic sand of the coastal plain.

Photo 4 Beech-magnolia forest in Louisiana. Forests dominated at maturity by beech (*Fagus grandifolia*) and Southern magnolia (*Magnolia grandiflora*, evergreen) have been considered the potential climatic climax forest type on the interior southeastern coastal plain (e.g. Delcourt and Delcourt 1974, 1977). Such forests are rare, however, because of recurring fire, which made fire-climax pine savanna the dominant landscape over much of the coastal plain. This beech-magnolia forest is at the Zemurray Estate in southeastern Louisiana, growing in a river loop where it has been protected from fire. The canopy reached about 40 m and was dominated by the two species only. Beech-magnolia also represents one type of "southern mixed hardwoods" forest, considered the general potential climax forest type on the coastal plain (Quarterman and Keever 1962). This forest has been described by David A. White (1987), who is shown standing against the largest tree, along with members of the ENAVS team (in 1989)

Acknowledgments The author is indebted to Akira Miyawaki and his team for the ENAVS inventory and resulting data-base of about 1400 relevés. This team included Kazue Fujiwara, who assisted the author with many other relevés in eastern North America, outside the ENAVS framework, and who provided many insights into vegetation structure and environmental relationships. All of us are indebted moreover to the various local botanical experts who helped us at one time or another in the southeastern coastal plain and piedmont, including especially Robert K. Peet, David A. White, Daniel Ward, Michael Baranski, and Wilbur Duncan.

References

Bartram, W. 1791 [1973]. *Travels through North and South Carolina, Georgia, East and West Florida*. Beehive Press, Savannah. 142 pp (see also 1955 reprint by Dover).

Box, E. O. 1995. Climatic relationships of the forests of East and South-East Asia. In: *Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and southeast Asia* (E. O. Box et al., eds.), pp. 23–55. Kluwer Academic Publishers, Dordrecht.

Box, E. O., and K. Fujiwara 2010. What else can one do with relevé data: Eastern North America? *Braun-Blanquetia*, 46:139–142.

Box, E. O., and K. Fujiwara 2012. A comparative look at bioclimatic zonation, vegetation types, tree taxa and species richness in Northeast Asia. *Botanica Pacifica* (Vladivostok), 1:5–12.

Box, E. O., and K. Fujiwara (herein). Warm-temperate deciduous forests: concept and global overview. In: *Warm-Temperate Deciduous Forests* (E. O. Box and K. Fujiwara eds.), Geobotanical studies.

Box, E. O., and M. Manthey 2005. Oak and other deciduous forest types of eastern North America and Europe. *Botanika Chronika* (Greece), 18(1):51–62.

Box, E. O., and M. Manthey 2006. Conservation of deciduous tree species in Europe: Projecting potential ranges and changes. In: *Nature Conservation: Concepts and Practice* (D. Gafta and J. Akeroyd, eds.), pp. 241–253. Springer-Verlag, Berlin.

(b) Wakulla Springs: T2-layer Vitis rotundifolia; S-layer Aralia spinosa, Bumelia lanuginosa, Chionanthus virginicus, Crataegus marshallii, Crataegus viridis, Ilex ambigua, Morus rubra, Prunus serotina, Sabal palmetto, Ulmus alata, Vaccinium stamineum, Viburnum nudum, Menispermum canadense; and H-layer Botrychium dissectum, Desmodium galactia, Rubus flagellaris, Ruellia caroliniensis, Sabal minor, Solanum americanum, Uniola laxa, Desmodium "big", Sanicula sp., Carex "short", Carex "big"

(c) Apalachicola Bluff: T2-layer Halesia caroliniana, Prunus "deciduous"; S-layer Aesculus pavia, Hydrangea quercifolia, Pinus taeda, Smilax auriculata, Vaccinium arboreum; and H-layer Agrimonia microcarpa, Ampelopsis arborea, Chasmanthium latifolium, Cnidoscolus stimulosus. Croomia pauciflora, Parthenocissus quinquefolia, Passiflora lutea, Sabal etonia, Asplenium sp., Aster sp., Elephantopus sp., Senecio sp., Viola sp., Panicum "narrow", Panicum "wide". Found nearby: canopy Quercus muhlenbergii and Platanus occidentalis, T2-layer Planera aquatica

The first stand, with only 35 species on 30 × 30 m, was on a loess flat behind the "tallest magnolia" in the protected area at the Zemurray Estate in Louisiana, near Hammond (northwest of Lake Pontchartrain). The canopy reaches 40 m and the understorey tree layer reaches 20 m. The accompanying local authority was David A. White, who has described this forest in detail (White 1987; cf Delcourt and Delcourt 1974). The second stand, with 63 species on 30 × 30 m, was on mesic humic sand above the floodplain, along the nature trail, in Wakulla Springs State Park in western Florida south of Tallahassee. This forest was an especially rich example of the beech-magnolia type of "southern mixed hardwoods". The last stand, with 62 species on 30 × 30 m, was on the fine humic sand of a "steephead", on a gentle 5° west-facing slope above the Apalachicola River in western Florida, in the Apalachicola Bluff preserve owned at that time by The Nature Conservancy. This relevé was made in May 1991, after the ENAVS inventory, with E. Dennis Hardin as local botanical authority. This was also an impressive forest (cf Delcourt and Delcourt 1977)

Braun, E. L. 1950. *Deciduous Forests of Eastern North America*. Philadelphia: Blakiston Co. 596 pp.

Brockman, C. F. 1986. *Trees of North America*. Revised edition. New York: Golden Press. 280 pp.

Bryant, W. S., W. C. McComb, and J. S. Fralish 1993. Oak-Hickory Forests (Western Mesophytic/Oak-Hickory Forests). In: *Biodiversity of the Southeastern United States: Upland Terrestrial Communities* (W. H. Martin et al., eds.), pp 143–201. Wiley, New York.

Christensen, N. L. 1988. Vegetation of the Southeastern Coastal Plain. In: *North American Terrestrial Vegetation* (M. G. Barbour and W. D. Billings, eds.), pp. 317–363. Cambridge University Press.

Daubenmire, R. F. 1978. *Plant Geography with special reference to North America*. Academic Press, New York. 338 pp.

Daubenmire, R. 1990. The *Magnolia grandiflora-Quercus virginiana* forest in Florida. *Amer. Midland Naturalist*, 123:331–347.

Delcourt, H. R., and P. A. Delcourt 1974. Primeval magnolia-holly-beech climax in Louisiana. *Ecology*, 55:638–644.

Delcourt, H. R., and P. A. Delcourt 1977. Presettlement magnolia-beech climax of the Gulf Coastal Plain: quantitative evidence from the Apalachicola River Bluffs, north-central Florida. *Ecology*, 58:1085–1093.

Delcourt, H. R., and P. A. Delcourt 2000. Eastern Deciduous Forests. In: *North American Terrestrial Vegetation* (M. G. Barbour and W. D. Billings, eds.), 2nd ed., pp. 357–395. Cambridge University Press.

DeWitt, R., and S. Ware 1979. Upland hardwood forests of the central coastal plain of Virginia. *Castanea*, 44:163–174.

Duncan, W. H., and M. B. Duncan 1988. *Trees of the Southeastern United States*. University of Georgia Press, Athens. 322 pp.

Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. *BioScience*, 56(4):341–352.

Eyre, F. H. (ed.) 1980. *Forest Cover Types of the United States and Canada*. Soc. Amer. Foresters, Washington. 148 pp.

Frost, C. C., J. Walker, and R. K. Peet 1986. Fire-Dependent Savannas and Prairies of the Southeast: Original Extent, Preservation Status and Management Problems. In: *Wilderness and Natural Areas in the Eastern United States* (D. L. Kulhavy and R. N. Conner, eds.). S. F. Austin University, Nacogdoches.

Fujiwara, K. 1987. Aims and methods of phytosociology or "vegetation science." In: *Papers on Plant Ecology and Taxonomy to the Memory of Dr. Satoshi Nakanishi* (Y. Takeda, ed.), pp. 607-628. Kōbe Geobotanical Society.

García-Mijanos, I., J. A. Campos, I. Biurrun, M. Herrera, and J. Loidi (herein). Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: *Warm-Temperate Deciduous Forests* (E. O. Box and K. Fujiwara eds.), Geobotanical Studies.

Gibson, D. J. 1992. Vegetation-environment relationships in a Southern Mixed Hardwood forest. *Castanea*, 57:174–189.

Givnish, T. J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica*, 36:703–743.

Godfrey, R. K. 1989. *Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia and Alabama*. University of Georgia Press, Athens.

Gomez-Pompa, A. 1977. *Ecología de la Vegetación del Estado de Veracruz*. Cia. Editorial Continental, S. A. de C. V., México. 91 pp.

Greenberg, C. H., D. E. McLeod, and D. L. Loftis 1997. An Old-Growth Definition for Western and Mixed Mesophytic Forests. Report SRS-16, Southern Research Station, US Forest Service, Asheville.

Greller, A. M. 1980. Correlation of some climatic statistics with distribution of broadleaved forest zones in Florida, USA. *Bull. Torrey Botan. Club*, 107:189–219.

Greller, A. M. 1988. Deciduous Forest. In: *North American Terrestrial Vegetation* (M. G. Barbour and W. D. Billings, eds.), pp. 287–316. Cambridge University Press.

Greller, A. M. 1989. Correlation of warmth and temperateness with the distributional limits of zonal forests in eastern North America. *Bull. Torrey Botan. Club*, 116:145–163.

Greller, A. M. 1990. Comparison of humid forest zones in eastern Mexico and southeastern United States. *Bull. Torrey Botan. Club*, 117(4):382–396.

Harcombe, P. A., and P. L. Marks 1977. Understory structure of a mesic forest in southeast Texas.*Ecology*, 58:1144–1151.

Harcombe, P. A., and P. L. Marks 1983. Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). *Oecologia*, 57:49–54.

Harper, R. M. (1913) (1928). Economic botany of Alabama. 2 parts, monographs 8 and 9. Geological Survey of Alabama, University (Alabama).

Hartnett, D. C., and D. M. Krofta 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. *Bull. Torrey Bot. Club*, 116:107–113.

Hinkle, C. R., W. C. McComb, J. M. Safley jr., and P. A. Schmalzer 1993. Mixed Mesophytic Forests. In: *Biodiversity of the Southeastern United States: Upland Terrestrial Communities* (W. H. Martin et al., eds.), pp 203–253. Wiley, New York.

Howel, C. L. 1991. Floristics of two state parks in the piedmont of Georgia: Indian Springs and High Falls. *Castanea*, 56:38–50.

Hunt, D. M. 1994. Morphology and Ecology of *Quercus* Series *Laurifoliae*, *Marilandicae* and *Nigrae*. In: *Vegetation in Eastern North America* (A. Miyawaki et al., eds.), pp. 99–120. Tokyo University Press.

Iverson, L., A. M. Prasad, B. J. Hale, and E. K. Sutherland 1999. Atlas of current and potential future distributions of common trees of the Eastern United States. US forest service, general technical report NE-265. US Dept. of Agriculture, Washington. 245 pp.

Kira, T. 1949. Nippon-no shinrin-tai [Forest zones in Japan]. *Ringyō Kaisetsu*, 17:105-141. Nippon Ringyō Gijutsu Kyōkai, Tokyo; reprinted in Kira 1971, pp 105-141 (in Japanese).

Kira, T. 1977. A Climatological Interpretation of Japanese Vegetation Zones. In: *Vegetation Science and Environmental Protection* (A. Miyawaki, ed.), pp. 21–30. Maruzen, Tokyo.

Kira, T. 1991. Forest ecosystems of East and Southeast Asia in a global perspective. *Ecol. Research* (Japan), 6:185-200. Reprinted: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 1-21. Kluwer, Dordrecht.

Küchler, A. W. 1964. *Potential Natural Vegetation of the Conterminous United States*. Amer. Geogr. Soc., Special Publ. 36, New York.

Kurz, H., and R. K. Godfrey 1982. *Trees of Northern Florida*. University Presses of Florida, Gainesville. 4th printing (original 1962), 311 pp.

Laessle, A. M. 1942. The plant communities of the Welaka Area. *Biol. Sci. Series* (UFla Press), 4(1):5–141.

Lieth, H. 1973. Primary production: terrestrial ecosystems. *Human Ecology*, 1(4):303–332.

Lieth, H., and E. Landolt (eds.) 1979. *Contributions to Knowledge of Flora and Vegetation in the Carolinas*. 3 vols. Zürich: Veröff. Geobotan. Inst. Rübel.

Little, E. L. 1965. Mexican beech, a variety of *Fagus grandifolia*. *Castanea*, 30(3):167–170.

Little, E. L. 1971–1978. *Atlas of United States Trees*. Misc. Publs. US Forest Service. US Govt. Printing Office, Washington. 5 vols.

Martin, W. H., S. G. Boyce, and A. C. Echternacht (eds.) 1993. *Biodiversity of the Southeastern United States*. 2 vols. New York: Wiley. 502 + 373 pp.

Martínez, M. 1940. Una nueva especie forestal (*Fagus mexicana* Sp. nova). *Anales del Instituto de Biología, Universidad de México*, 11:85–89.

Mills, R. H., and S. B. Jones 1969. The composition of a mesic Southern Mixed Hardwood Forest in south Mississippi. *Castanea*, 34:62–66.

Miranda, F., and A. J. Sharp 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology*, 31 (3):313–333.

Miyawaki, A., K. Iwatsuki, and M. M. Grandtner (eds.) 1994. *Vegetation in Eastern North America*. Tokyo: Univ. of Tokyo Press. 515pp.

Monk, C. D. 1965. Southern mixed hardwood forest of north-central Florida. *Ecol. Monogr*., 35:335–354.

Monk, C. D. 1966. An ecological significance of evergreenness. *Ecology*, 47:504–505.

Monk, C. D. 1968. Successional and environmental relationships of the forest vegetation of north-central Florida. *Amer. Midl. Nat*., 79:441–457.

Monk, C. D., D. W. Imm, R. L. Potter, and G. G. Parker 1989. A classification of the deciduous forest of eastern North America. *Vegetatio*, 80:167–181.

Monk, C. D., D. W. Imm, and R. L. Potter 1990. Oak forests of eastern North America. *Castanea*, 55:77–96.

Nesom, G. L., and M. Treiber 1977. Beech-mixed hardwoods communities: a topo-edaphic climax on the North Carolina coastal plain. *Castanea*, 42:119–140.

Nixon, E. S., G. A. Sullivan, S. D. Jones, G. D. Jones and J. K. Sullivan 1990. Species diversity of woody vegetation in the Trinity River Basin, Texas. *Castanea*, 55:97–105.

Oosting, H. J. 1956. *The Study of Plant Communities*. 2nd ed. W. H. Freeman, San Francisco.

Pessin, L. J. 1933. Forest associations in the uplands of the lower Gulf Coastal Plain (longleaf pine belt). *Ecology*, 14:1–14.

Peters, R. 1995. Architecture and Development of Mexican Beech Forest. In: *Vegetation Science in Forestry* (E. O. Box et al., eds.), Handbk. Veg. Sci., vol. 12a, pp. 325–343. Dordrecht: Kluwer.

Platt, W. J., and M. W. Schwartz 1990. Temperate Hardwood Forests. In: *Ecosystems of Florida* (R. L. Myers and J. J. Ewel, eds.), pp. 194–229. Orlando: Univ. Central Florida Press.

Quarterman, E. 1981. A fresh look at climax forests of the coastal plain. *ASB Bulletin*, 28:143–148.

Quarterman, E., and Ch. Keever 1962. Southern mixed hardwood forest: climax in the southeastern coastal plain, USA. *Ecol. Monogr*., 32:167–185.

Radford, A. E., H. E. Ahles, and C. R. Bell 1968. *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, Chapell Hill. 1184 pp.

Rice, E. L., and W. T. Penfound 1959. The upland forests of Oklahoma. *Ecology*, 40:593–608.

Rübel, E. F. 1930. *Pflanzengesellschaften der Erde*. Verlag Hans Huber. 464 pp.

Rzedowski, J. 1978. *Vegetación de México*. Limusa, Mexico (city). 432pp.

Sánchez de Dios, R., M. Benito-Garzón, and H. Sainz-Ollero 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology*, 204:189–205.

Sargent, C. S. 1884. *Report on the Forests of North America*. US Dept. Interior, Census Office, Washington.

Schmithüsen, J. 1968. *Allgemeine Vegetationsgeographie*. 3rd edition. Walter de Gruyter, Berlin. 463pp.

Sharitz, R. R., and W. J. Mitsch 1993. Southern Floodplain Forests. In: *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities* (W. H. Martin et al., eds.), pp 311–372. Wiley, New York.

Skeen, J. N., Ph. D. Doerr, and D. H. Van Lear 1993. Oak-Hickory-Pine Forests. In: *Biodiversity of the Southeastern United States: Upland Terrestrial Communities* (W. H. Martin et al., eds.), pp 1–33. Wiley, New York.

Stephenson, S. L., A. N. Ash, and D. F. Stauffer 1993. Appalachian Oak Forests. In: *Biodiversity of the Southeastern United States: Upland Terrestrial Communities* (W. H. Martin et al., eds.), pp 255–303. Wiley, New York.

Stout, I. J., and W. R. Marion 1993. Pine Flatwoods and Xeric Pine Forests of the Southern (Lower) Coastal Plain. In: *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities* (W. H. Martin et al., eds.), pp 373–446. Wiley, New York.

Stuckey, R. L. 1973. E. Lucy Braun (1889-1971), outstanding botanist and conservationist: A biographical sketch with bibliography. *Michigan Botanist*, 12:83–106.

Tanner, J. T. 1986. Distribution of tree species in Louisiana bottomland forests. *Castanea*, 51:168–174.

Ueyama, S. (ed.) 1969. [Culture in the Laurel Forest Zone]. Chūō-Kōron-sha, Tokyo. (In Japanese)

Van Auken, O. W., A. L. Ford, and J. L. Allen 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. *Amer. J. Bot*., 68(9):1249–1256.

Vankat, J. L. 1990. A classification of forest types of North America. *Vegetatio*, 88:53–66.

Velázquez, A., V. M. Toledo, and I. Luna 2000. Mexican Temperate Vegetation. In: *North American Terrestrial Vegetation*, 2nd edition (M. G. Barbour and W. D. Billings, eds.), pp 573–592. Cambridge University Press.

Walter, H. 1970. *Vegetationszonen und Klima*. Verlag Eugen Ulmer, Stuttgart. 382 pp. (3rd ed. 1977, 309pp).

Walter, H. 1985. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*. 3rd edition. Springer-Verlag, New York. 318 pp (1st edition 1970).

Ware, S. 1970. Southern mixed hardwood forest in the Virginia Coastal Plain. *Ecology*, 51:921–924.

Ware, S. 1978. Vegetation role of beech in the southern mixed hardwood forest in the Virginia Coastal Plain. *Virginia J. Science*, 29:231–235.

Ware, S. 1988. Ordination of Quarterman and Keever's original Southern Mixed Hardwoods forest. *Castanea*, 53:197–206.

Ware, S. 1992. Where are all the hickories in the piedmont oak-hickory forest? *Castanea*, 57:4–12.

Ware, S., C. C. Frost, and Ph. D. Doerr 1993. Southern Mixed Hardwood Forest: the Former Longleaf Pine Forest. In: *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities* (W. H. Martin et al., eds.), pp 447–493. Wiley, New York.

Wells, B. W. 1942. Ecological problems of the southeastern United States coastal plain. *Botan. Review*, 8:533–561.

Wells, B. W., and I.V. Shunk 1931. The vegetation and habitat factors of coarser sands of the North Carolina coastal plain: an ecological study. *Ecolog. Monographs*, 1:465–520.

Wharton, C. H. 1978. *The Natural Environments of Georgia*. Georgia Dept. Natural Resources, Atlanta. 228 pp.

White, D. A. 1983. Plant communities of the lower Pearl River basin, Louisiana. *Amer. Midland Naturalist*, 110:381–396.

White, D. A. 1987. An American beech-dominated original growth forest in southeast Louisiana. *Bull. Torrey Botan. Club*, 114:127–133.

Woodward, I. 1987. *Climate and Plant Distribution*. Cambridge University Press. 174 pp.

Deciduous Woodlands in Mediterranean California

Mark A. Blumler

Oak woodlands scattered over grass-covered hills represent the characteristic landscape of California.
– Mensing (2005, p. 1)

Abstract

Despite the widespread perception of dominance of evergreen sclerophylls, some Mediterranean climate regions have significant representation of winter-deciduous species. In California, deciduous oaks dominate extensive regions. In central California, the blue oak, *Quercus douglasii*, dominates interior foothills that have wet winters and long dry summers; valley oak, *Q. lobata*, and garry oak, *Q. garryana* also are found in interior, hot summer locations. In southern California, the Englemann oak, *Q. englemannii* is found in interior, hot summer regions while the evergreen *Q. agrifolia* dominates nearer the coast where summers are less severe. Deciduous species can occur alone, or mixed with broadleaved evergreen trees or shrubs, and/or conifers. As severity of summer drought increases, whether due to climate or soil conditions, deciduousness becomes increasingly favored.

Keywords

California vegetation • Subtropical dry ecosystems • Deciduousness as Mediterranean adaptation

1 Introduction

Longtime California residents would tend to agree with Mensing's statement (above), and the oaks referred to are much more often winter-deciduous than evergreen (Fig. 1). Barbour and Major (1977) calculated the areas occupied by different vegetation types California, based on Küchler's (1964) map of potential natural vegetation (see Table 1). Creosote bush is desert vegetation, and mixed conifer forest is montane. Thus, the most widespread types within the mediterranean parts of California are "steppe" (really grassland, as there is very little admixture of bushes) and oak woodland, primarily deciduous. Within the mediterranean vegetation, chaparral (sclerophyllous evergreen scrub, involving both shrubs and arborescents) comes in third place and is generally associated with coarse-textured soils (Hanes 1977). Küchler (1977) also produced a more detailed map, for the Barbour and Major volume, but the areas of the major vegetation types were not significantly different.

Even so, evergreen sclerophyllous shrubland characteristic of the Mediterranean-type climate has long been considered the classic example of ecological convergence at the biome scale (Schimper 1898; di Castri and Mooney 1973; Cody and Mooney 1978). The widespread dominance of winter-deciduous species in California (and elsewhere – see the companion paper), especially oaks, raises questions regarding the supposed correlation between evergreen sclerophylls and the mediterranean climate. I am by no means the first to point out that the correspondence of the

---

M.A. Blumler (✉)
SUNY-Binghamton, Binghamton, NY, USA
e-mail: mablum@binghamton.edu

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_14, © Springer International Publishing Switzerland 2015

Fig. 1 Characteristic deciduous oak woodland in California (Photo by S. Mensing)

Table 1 The most widespread California vegetation types and their areas, calculated from Küchler's (1964) map of potential natural vegetation (Barbour and Major 1977)

Vegetation type	Area (hectares)
Creosote bush	6,542,395
Mixed conifer forest	5,522,676
California steppe	5,288,897
California oakwoods	3,821,807
Chaparral	3,400,234

two may be more apparent than real (cf Freitag 1971, 1982; Minnich 1985; Barbour and Minnich 1990; Valiente-Banuet et al. 1998).

Describing and explaining vegetation-environment patterns is a classic task of biogeography, dating back to Alexander von Humboldt (Blumler et al. 2011). After Clement's (1916) climatic climax swept the field, the subject became less interesting to American biogeographers, as everything already seemed well worked out. Meanwhile, detailed classification, vegetation mapping, and associated explanations continued to flourish in Germany and on the Continent. Box's (1981) pioneering global model was an exception within the Anglo-American tradition, subsequently picked up and utilized when concerns about climatic warming and its impacts caused a rebirth of the study of vegetation-environment relations (Woodward 1987). Biome modeling has tended to focus on climate, which is entirely appropriate: climate is the primary determinant of plant distribution at broad scales, and climatic data are much more readily available than soil characteristics or other salient factors, such as herbivory. In any case, it made sense to use only the most important factor, climate, in the first modeling attempts, in order to keep the models as simple as possible. Two implications of the subsequent discussion in this paper and the companion piece on the Middle East are that climate is not the sole determinant of vegetation type and that evolutionary history is important too.

Dominance of winter-deciduous species in a summer-dry climate is surprising, and it has thus taken a long time for this fact to become widely known. Scientists in mediterranean regions have noted this fact for single regions, but that the pattern is widespread has remained essentially unrecognized.

2 Definitions

In subhumid and semi-arid regions, such as much of California, woody vegetation often appears as savanna, park-forest (parkland), steppe-forest (forest-steppe), or woodland, rather than true forest. That is, the vegetation tends to be open, though dense forest can be found here and there. Also, in addition to deciduous and evergreen species, a few species are sometimes classified as "semi-evergreen". Depending on who is using the term, semi-evergreen can refer to trees that are briefly deciduous (losing their leaves for only a very short time) or semi-deciduous (losing many but not all of their leaves during the cool season). The former is regarded here as deciduous, but the latter is at least quasi-evergreen. Reports about the phenologies of these species conflict frequently, and it is not always clear whether this is weather-related or due to only casual observation. Leaves may be slower to drop during a mild winter than in a subsequent winter that happens to be considerably colder. An additional complication is that many oaks and a few related species, even if entirely seasonal in a photosynthetic sense, often fail to drop many of their dead leaves (cf marcescence, see García-Mijangos et al., herein). I would define such species as deciduous, but not everyone does, and clearly there is some legitimate room for alternative classifications.

3 Climate

Coastal California has mild summer temperatures, while hot summers are characteristic of the interior; the rainy season is longer to the north, and the annual total precipitation is greater (Fig. 2). In addition, of course, the high mountains produce pronounced altitudinal temperature and precipitation gradients. In comparison to other regions of "Mediterranean" climate, the California rainfall and temperature patterns are most similar to those of Morocco (with a northward extension into Portugal, corresponding reasonably well to the southern portion of the redwood zone in central California).

Winter cold is also a limiting factor for broad-leaved evergreens (Larcher 1981; Woodward 1987). There has been considerable discussion in the literature as to the cutoff point below which they are likely to be eliminated, with a January mean of 0ºC perhaps the most widely accepted rule-of-thumb (Blumler 2005b). Of course, the validity of this or any value would depend on wind velocity, temperature variability (frequency of extremes), and so on. Scientists frequently explain the presence of winter-deciduous vegetation in mediterranean regions, and near absence of evergreens, as being due to winter cold, but without actually examining the temperature data. As will be discussed below, the Central Valley of California is surrounded by a chaparral belt located at higher elevation than most deciduous oak woodlands, i.e., the chaparral belt experiences colder winter temperatures than do the deciduous woodlands (see temperature data in Blumler 2005b).

4 Climate and Vegetation History

Given that recent glacial periods were about ten times as long as interglacials, and given also the dramatic and abrupt climate swings that are known to have occurred, it is unlikely that ecosystems today can be considered to be at equilibrium (Davis 1981). General climatic trends over the course of the Tertiary and Quaternary included cooling, drying, and increasing seasonality of both temperature and precipitation (Cox and Moore 2005). Mensing (2005) reviewed the fossil evidence for California oaks and concluded that: (a) the mediterranean climate is recent in California; and (b) oaks evolved before the appearance of the mediterranean climate. A possible exception is the blue oak, *Quercus douglasii*, which has not been found outside California and does not show up in the fossil record until late (Mensing 2005, p. 5). Axelrod (1973, 1983) argued that many California oaks were Madro-Tertiary in origin, but Mensing's review shows that the early fossils tend to come from the north, from Washington, Oregon and Idaho. This should not be surprising, given the Tertiary cooling trend: an equatorward retreat would be a more likely plant response than the reverse. Mensing (2005) also found that oaks mostly disappeared during glacial periods, only to rebound during interglacials such as the present interval (see also Byrne et al. 1991; Davis 1999). So, although all three subgenera of oaks are represented in California, including both evergreen and deciduous species in the two major lineages (Nixon 2002), Holocene communities were built out of whatever remained after surviving through the far longer Wisconsin glacial period.

5 California Vegetation at European Contact

Early descriptions of California vegetation are sufficient to reconstruct the general distributions of the major communities, and even today, despite massive conversion to agriculture and housing developments, most are still present in a zonation (see Table 2) that reflects tolerance of summer drought and to some extent winter cold, as one goes up in elevation.

The Central Valley is mostly agricultural today, but it is well established that it was originally a grassland, with some (deciduous) valley oak, *Quercus lobata*, though much of that almost certainly was phreatophytic. Then, as one leaves the valley and climbs the foothills on both the east and west sides, one encounters *Quercus douglasii* (blue oak, deciduous), with admixtures of *Pinus sabiniana* (digger pine), *Quercus lobata*, interior live oak (evergreen *Q. wislezenii*), and chaparral shrubs. At the lowest (driest and hottest) elevations, though, and on the more fertile, heavier-textured soils, there is pure blue oak (cf. Gartner et al. 1957; Baker et al. 1981). As Griffin (1977, p. 400) put it: "On uplands around the Central Valley, the lowest savanna fringe usually has *Quercus douglasii* as the only tree." Higher up, one encounters the chaparral zone, then deciduous black oak (*Q. kelloggii*) still higher, and then conifers and winter snow cover.

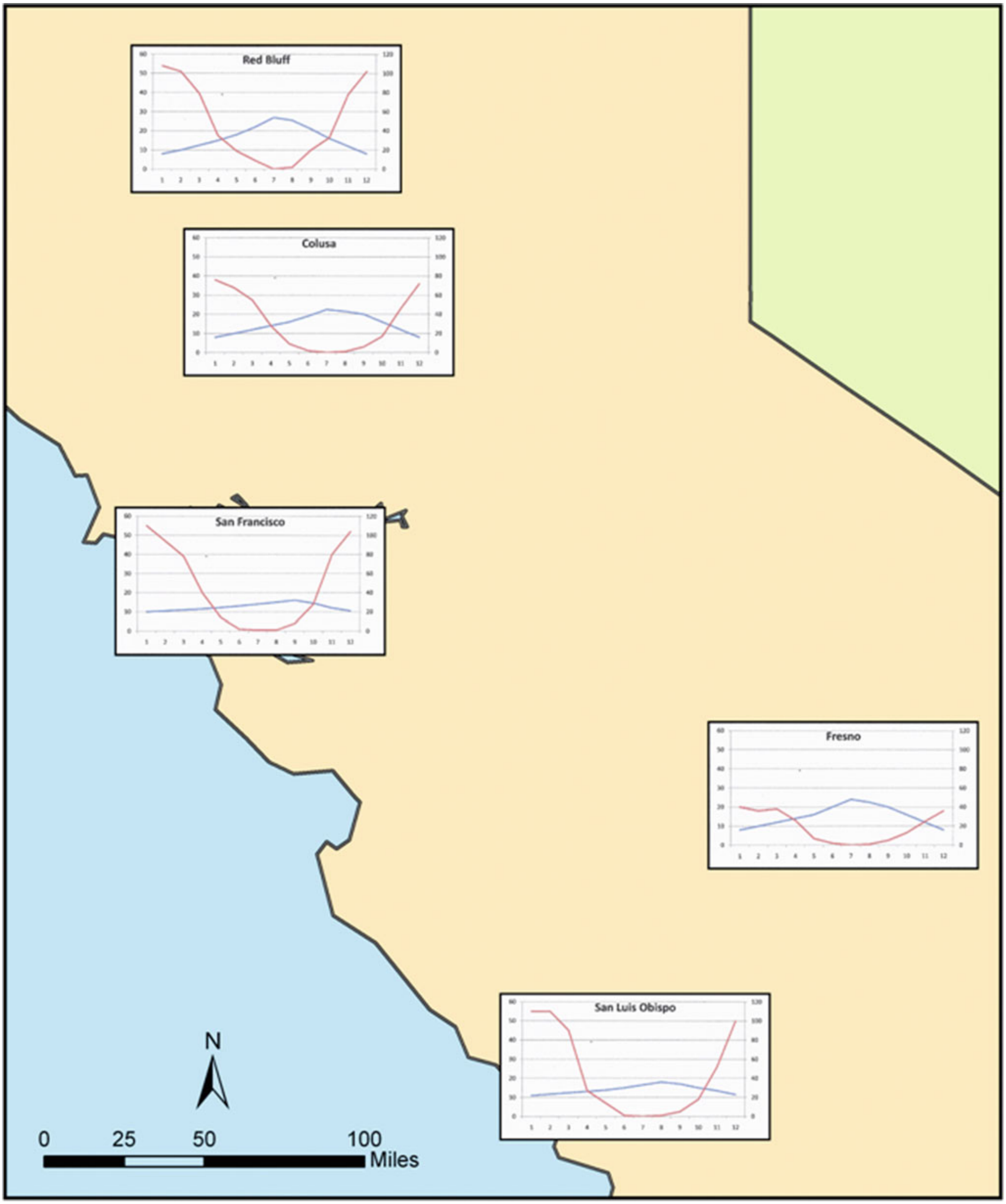


Fig. 2 Representative climate diagrams in California (Based on Walter and Lieth 1967; Walter et al. 1975)

Table 2 The elevational gradient of plant communities in central California

Central Valley:	Grassland, some valley oak (*Quercus lobata*)
Lower foothills:	Blue oak alone or with digger pine (*Pinus sabiniana*)
Upper foothills:	Chaparral
Montane (winter snow cover):	Black oak (*Q. kelloggii*) and conifers

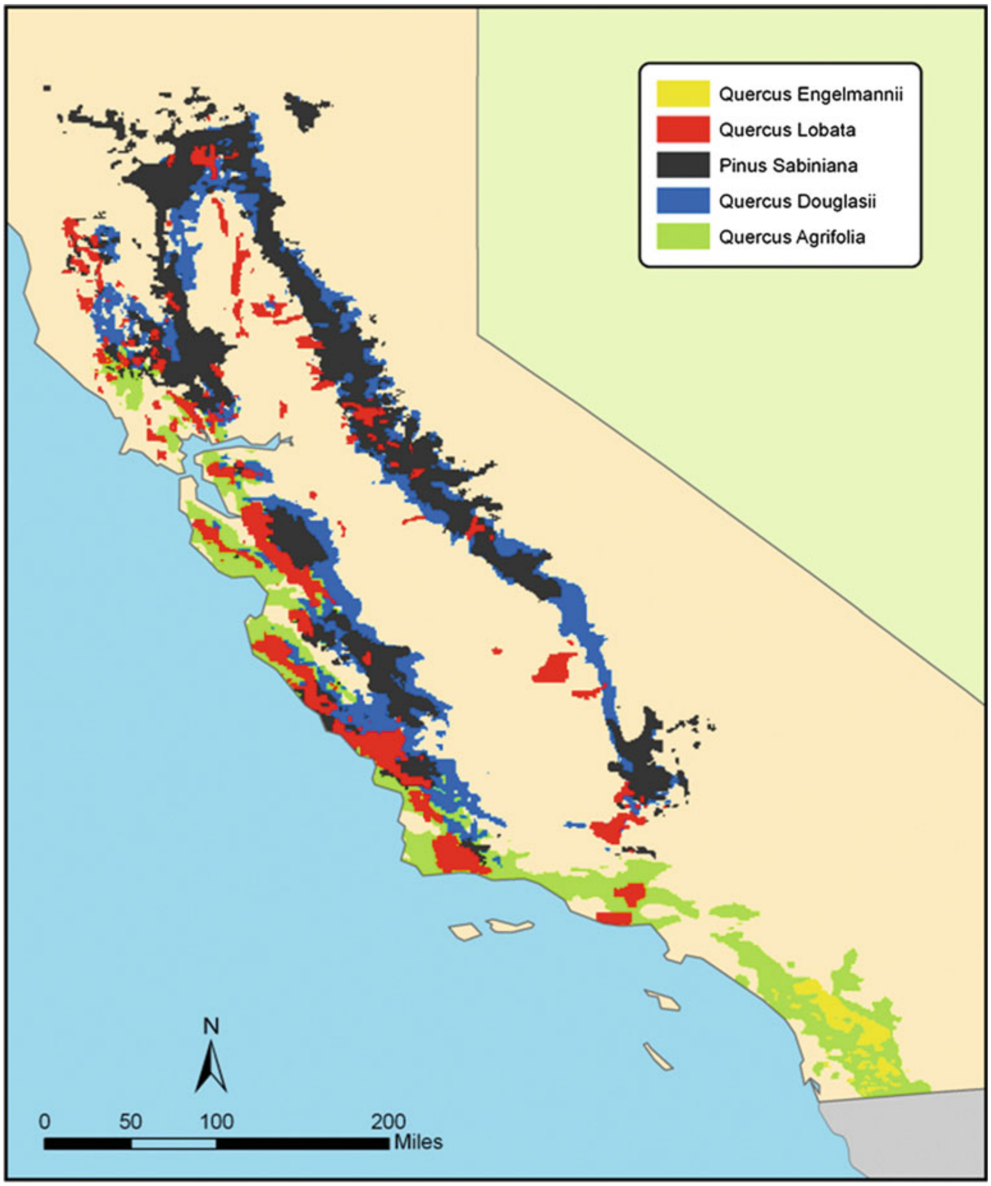


Fig. 3 Distribution of Oaks and Digger Pine in California (Redrawn from Griffin and Critchfield 1972). Not included is garry oak, which is found primarily in the northwest part of California, and black oak, which occurs mostly above the Mediterranean zone

Before GIS made such projects more routine, Griffin and Critchfield (1972) carefully mapped the distribution of California tree species; these maps illustrate how evergreen and deciduous species compare in terms of their adaptation to California's mediterranean climate (Fig. 3). Because of the extreme topographic gradients in California, the maps are difficult to interpret visually. Note, however, that blue oak generally extends down lower around the Central Valley than does digger pine (where it appears not to, the black of digger pine is masking the blue of blue oak); note also that extensive areas in the driest foothills (southeastern Sierra Nevada and the southern interior Coast Ranges) lack the pine altogether but that blue oak is present.

Blue oak, valley oak, and (also deciduous) Oregon oak (*Q. garryana*) are all characteristic at or below the chaparral belt, although Oregon oak is more northern in its distribution and typically appears to be replaced by conifers in the absence of disturbance. Even black oak (*Q. kelloggii*), which usually is montane, occasionally forms stands at low elevation, in true mediterranean climatic conditions (Griffin 1977).

Coast live oak (*Q. agrifolia*), as its name suggests, is evergreen and more coastal, i.e. it grows where summers are relatively mild on the whole. It extends farther south than do the other oaks, into Baja California, but according to Minnich and Franco-Vizcaino (1998), it becomes restricted to riparian environments there. In contrast, semi-evergreen Engelmann oak (*Q. engelmannii*) occurs in interior southern California. It typically co-occurs with coast live oak, but then it is on the "droughtier" (heavier, more rock-free) soils (Snow 1972; Scott 1991).

This may sound counter-intuitive, but as Noy-Meir (1973) pointed out, in dry regions one encounters an "inverse texture effect": taller woody vegetation is found more commonly on sand than on clay, because the latter dries out more during long drought periods. In contrast, during the rainy season, coarse-textured soils are drier than heavy soils. Rock outcrops are similar to coarse-textured soils in this respect, and infertile soils are as well. The latter hold moisture well through drought periods because the vegetation cannot grow fast enough to utilize the available water. Noy-Meir wrote about deserts, but the pattern is also characteristic, and in some ways more salient, in semi-arid regions featuring a long dry season (Blumler 1991).

The California buckeye, *Aesculus californica*, often co-occurs with oaks on slopes (Fig. 4). It might be called "long-deciduous" in that it loses its leaves early in summer and does not grow them again until spring. Black walnut (*Juglans californica*), also deciduous, forms small areas of park forest in southern California; it is not known if it is phreatophytic.

Griffin (1971, 1973, 1976, 1977) investigated the physiological ecology and regeneration of oaks at Hastings Reservation, in the Carmel Valley of central California, demonstrating that blue oak does not need to tap the water table in summer. Snow (1972) showed that Englemann oak is probably similar in southern California. In contrast, Griffin (1973) found that coast live oak and valley oak are phreatophytic at Hastings. In very dry years, blue oaks drop "much of their foliage" in late August-September (Griffin 1977:406). That is, blue oak is facultatively drought-deciduous.

6 Classification

Classification in the US has traditionally and generally been in terms of "associations' named for dominant species. Such classification and vegetation mapping generally lacked in detail until recently. With increasing concern for conservation, due to the spectacular number of species now becoming endangered, this has changed. Led by Michael Barbour and the California Native Plant Society, an ongoing effort was organized to classify and map vegetation in much more detail, including the use of relevés and related phytosociological terminology (Sawyer and Keeler-Wolf 1995; Sawyer et al. 2009). Hierarchical classification is being attempted. The number of associations is great; listed below are those for blue oak, with evergreen or deciduous species noted (Table 3).

7 Human Impacts

Mensing (2006) suggested that California Indians maintained and even expanded the area of oak woodlands through the use of fire. Since the adoption of a fire suppression policy, conifers have replaced many oak woodlands at higher altitudes and in wetter areas. Some low-elevation blue-oak savannas have also become more dense since fires were stopped, though remaining oak-dominated (Mensing 1998). It is undeniable that the Indians burned frequently, and that this sometimes would have favored oaks (Reynolds 1959; Lewis 1973). On the other hand, it is notable that blue oak shares dominance with digger pine and chaparral shrubs on coarser substrates but tends to be alone on heavier soil. It is difficult to explain this pattern as being due to fire. The same is true of Engelmann oak: its best stands are on basalt, which typically produces heavy-textured soils. Basalt plateaux all over the world tend to be vegetated with grassland or open woodland, at least under semi-arid to subhumid conditions.

8 The Savanna Problem

In the Old World, temperate savanna or "park forest" is generally, though not always, regarded as seral (Walter 1973). In contrast, in the US, savannas are sometimes considered to be ecotonal, for example the Midwestern "oak openings" at the ecotone between the eastern deciduous forest and the tall-grass prairie. In California, oak savannas

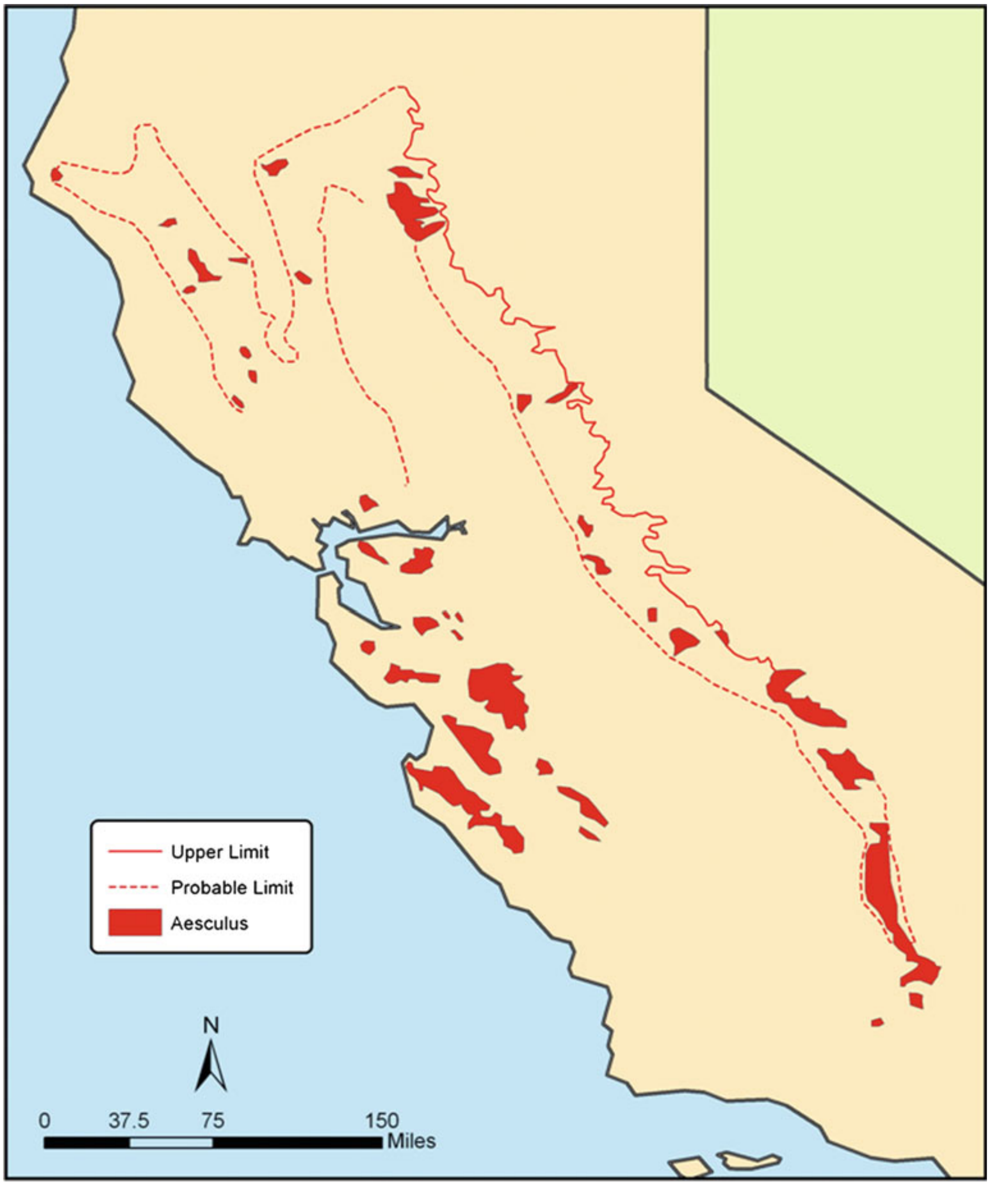


Fig. 4 Approximate distribution of California Buckeye (*Aesculus californica*) in California (Redrawn from Griffin and Critchfield 1972)

grade into forests on their wet side and into grassland (without trees) on their dry side. The first may well be seral, as shown by recent vegetation change (Mensing 2006), but this is less likely on the dry side. Mensing (1992, 2006) noted that pulses of oak regeneration occurred during periods when fire and/or grazing were suppressed. While he opted for a conventional explanation, it is quite possible that the oaks, and many other species, establish in pulses during changes in conditions, rather than being adapted to particular conditions such as lack of disturbance. Many oaks (in the Old World as well as California, see Grove and Rackham 2001) can persist almost as a ground cover for many decades and then spring up when fire and grazing cease for a short period (J. W. Bartolome, personal communication). Their establishment in the first place, though, may require fire or grazing to eliminate competitors (for a similar example in California bunchgrass, see Bartolome and Gemmill 1981).

9 California Summary

Several deciduous or semi-evergreen oaks flourish where summer drought is most severe, to the exclusion of evergreens. In California, at least blue oak and Engelmann oak do so apparently without need to tap the water table. Drought-deciduousness may confer an advantage where summer drought is long and hot. Also, acorns from deciduous oaks typically germinate in fall and grow through the

Table 3 List of associations in the blue oak Alliance of California's state vegetation classification. **Boldface** type indicates whether the associated woody species are **deciduous** or **evergreen**. No boldface is shown for herbaceous species

Quercus douglasii – Aesculus californica/ Asclepias fascicularis (**deciduous**)
Quercus douglasii – Aesculus californicus/ grass (**deciduous**)
Quercus douglasii – Pinus sabiniana (**evergreen**)
Digger Pine Oak Woodland
Quercus douglasii – Pinus sabiniana/ Arctostaphylos viscida (**evergreen**)
Quercus douglasii – Pinus sabiniana/ Ceanothus cuneatus – Cercocapus montanus (**evergreen**)
Quercus douglasii – Pinus sabiniana/ Cercocarpus montanus (**evergreen**)
Quercus douglasii – Quercus agrifolia (**evergreen**)
Quercus douglasii – Quercus lobata (**deciduous**)
Quercus douglasii – Quercus wislizeni (**evergreen**)
Quercus douglasii – Quercus wislizeni – Pinus sabiniana (**evergreen**)
Quercus douglasii – Quercus wislizeni (**evergreen**)*/Bromus spp. – Daucus pusillus*
Quercus douglasii – Quercus wislizeni/ Ceanothus cuneatus (**evergreen**)
Quercus douglasii – Quercus wislizeni/ Lithophragma cymbalaria
Quercus douglasii/ Juniperus californica – Cercocarpus montanus (**evergreen**)
Quercus douglasii/ Achnatherum lemmonii
Quercus douglasii/ Amsinckia intermedia – Plagiobothrys nothofulvus
Quercus douglasii/ Arctostaphylos Manzanita (**evergreen**)*/ herbaceous*
Quercus douglasii/ Brachypodium distachyon
Quercus douglasii/ Bromus hordeaceus – Lolium multiflorum
Quercus douglasii/ Bromus hordeaceus – Madia gracilis
Quercus douglasii/ Bromus hordeaceus – Triteleia laxa
Quercus douglasii/ Bromus spp. – Daucus pusillus
Quercus douglasii/ Ceanothus cuneatus (**evergreen**)
Quercus douglasii/ Cercocarpus montanus (**evergreen**)*/ Bowlesia incana – Lithophragma affine*
Quercus douglasii/ Collinsia sparsiflora – Rigiopappus leptocladus
Quercus douglasii/ Delphinium parryi – Phacelia imbricata
Quercus douglasii/ Ericameria linearifolia
Quercus douglasii/ Ericameria linearifolia – Juniperus californica (**evergreen**)
Quercus douglasii/ Eriogonum elongatum/ Lotus subpinnatus – Plantago erecta
Quercus douglasii/ Eriogonum fasciculatum/ herbaceous
Quercus douglasii/ Erodium moschatum – Hordeum leporinum
Quercus douglasii/ Euphorbia spathulata – Pentagramma triangularis
Quercus douglasii/ Galium andrewsii – Lupinus concinnus
Quercus douglasii/ grass
Quercus douglasii/ Hordeum leporinum – Viola pedunculata
Quercus douglasii/ Juniperus californica (**evergreen**)
Juniper Oak Cismontane Woodland
Quercus douglasii/ Juniperus californica – Ceanothus cuneatus (**evergreen**)
Quercus douglasii/ Juniperus californica – Quercus john-tuckeri (**evergreen**)
Quercus douglasii/ Lotus subpinnatus – Nassella pulchra
Quercus douglasii/ Lupinus concinnus – Trifolium ciliolatum
Quercus douglasii/ Ribes californica (**deciduous**)*/ Bromus diandrus*
Quercus douglasii/ Selaginella hansenii – Navarretia pubescens
Quercus douglasii/ Toxicodendron diversilobum (**deciduous**)*/ grass*
Quercus douglasii/ understory oak

Source: www.cnps.org/cnps/vegetation/manual.php (last accessed 31 May 2012)

first rainy season, emphasizing root growth, since they can subsist on their seed reserves until the leaves unfold in the spring (Matsuda and McBride 1986; Matsuda et al. 1989; Griffin and Muick 1990). In contrast, some evergreen sclerophylls do not germinate until spring (Blumler 1991). Griffin (1976) found that valley-oak seedlings were killed primarily by browsing but were unaffected by competition from grasses; coast live oak, in contrast, was unaffected by browsing but established only in shade. This latter result suggests that coast live oak cannot compete with the herbaceous vegetation that flourishes in the open. In short, deciduousness does not inhibit seedling establishment, and may even give the plant an advantage in competition with fast-growing herbs, compared to the slower-growing evergreen oaks. This and other aspects of comparative evergreen/ deciduous advantages are discussed more fully in the companion paper, on the Middle East (herein).

Acknowledgements I wish to express my heartfelt thanks to Elgene Box, for inviting me to a most stimulating set of sessions on Warm Temperate Deciduous Forests, and also for not having allowed fashion to dictate what he has studied, but instead for having continued to pursue vegetation-environment research and modeling. I also thank my dissertation advisor, Roger Byrne, who has always understood what biogeography is all about, and who ran a pollen lab in which the topics of discussion ranged far beyond palynology. Kevin Heard, of Binghamton University's GIS Core facility, drew the distribution maps.

References

Axelrod, D. I. 1973. History of the Mediterranean ecosystem in California. In di Castri, F., and H. A. Mooney (eds.), *Mediterranean Type Ecosystems: Origin and Structure*, pp. 225–277. Springer Verlag, New York.

Axelrod, D. I. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden* 63:24–41.

Baker, G. A., P. W. Rundel, and D. J. Parsons 1981. Ecological relationships of *Quercus douglasii* (Fagaceae) in the foothill zone of Sequoia National Park, California. *Madrono* 28:1–12.

Barbour, M. G., and J. Major 1977. Introduction. In: *Terrestrial Vegetation of California* (M. G. Barbour and J. Major, eds.), pp. 1–10. John Wiley and Sons, New York

Barbour, M. G., and R. A. Minnich 1990. The myth of chaparral convergence. *Israel J. Botany* 39:453–463.

Bartolome, J. W., and B. Gemmill 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madrono* 28:172–184.

Blumler MA (1991) Winter-deciduous versus evergreen habit in mediterranean regions: a model. In: Davis (R. B. Standiford, tech. coord.) (ed) Proceedings of the symposium on Oak Woodlands and Hardwood Rangeland management, October 31-November 2, 1990, USDA, Forest Service, Gen. Tech. Rep. PSW-126, Berkeley, pp 194–197

Blumler, M. A. 2005a. History of the biome concept, with implications for practical application to global change prediction and management. *Research in Contemporary and Applied Geography: A Discussion Series* 29(3):1–43.

Blumler, M. A. 2005b. Three conflated definitions of mediterranean climates. *Middle States Geographer 38*:52–60.

Blumler, M. A., A. Cole, J. Flenley, and U. Schickoff 2011. History of biogeographical thought. In Millington, A. C., M. A. Blumler, and U. Schickoff (eds.) *Handbook of Biogeography*, pp. 23–42. Sage Publications, London.

Box, E. O. 1981. *Macroclimate and Plant Forms: an Introduction to Predictive Modeling in Phytogeography*. Dr W. Junk, The Hague.

Byrne R, Edlund E, Mensing S (1991) Holocene changes in the distribution and abundance of oaks in California. In Standiford RB, tech. coord (ed) Proceedings of the symposium on Oak Woodlands and Hardwood Rangeland management, October 31-November 2, 1990, Davis, CA. USDA, Forest Service, Gen. Tech. Rep. PSW-126, Berkeley, pp 182–188

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. *Carnegie Institute of Washington Publications* 242:1–512.

Cody, M. L., and H. A. Mooney 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* 9:265–321.

Cox, C. B., and P. D. Moore 2005. *Biogeography: an ecological and evolutionary approach*. 7th ed. Blackwell, Malden (Massachusetts).

Davis, M. B. 1981. Quaternary history and the stability of forest communities. In West, D. C., H. H. Shugart, and D. B. Botkin (eds.), *Forest Succession*, pp. 132–153. Springer Verlag, New York.

Davis, O. K. 1999. Pollen analysis of Tulare Lake, California: Great Basin-like vegetation in central California during the full-glacial and early Holocene. *Review of Palaeobotany and Palynology* 107:249–257.

Di Castri, F., and H. A. Mooney (eds.) 1973. *Mediterranean Type Ecosystems: Origin and Structure*. Springer Verlag, New York.

Freitag, H. 1971. Studies in the natural vegetation of Afghanistan. In Davis, P. H., P. C. Harper, and I. C. Hedge(eds.), *Plant Life of South West Asia*, pp. 89–106. Royal Botanic Garden, Edinburgh

Freitag, H. 1982. Mediterranean characters of the vegetation in the Hindu Kush Mts., and the relationship between sclerophyllous and laurophyllous forests. *Ecologia Mediterranea* 8: 381–388.

García-Mijanos I, Campos JA, Biurrun I, Herrera M, Loidi J (herein) Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: Box EO, Fujiwara K (eds) Warm-temperate deciduous forests. Geobotanical Studies.

Gartner, F. R., A. M. Schultz, and H. H. Biswell 1957. Ryegrass and brush seedling competition for nitrogen on two soil types. *Journal of Range Management* 10:213–220.

Griffin, J. R. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* 52:862–868.

Griffin, J. R. 1973. Xylem sap tension in three woodland oaks of central California. *Ecology* 54: 152–159.

Griffin, J. R. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. *American Midland Naturalist* 95:422–435.

Griffin, J.R. 1977. Oak woodland. In Barbour, M. G., and J. Major (eds.), *Terrestrial Vegetation of California*, pp. 383–415. John Wiley and Sons, New York.

Griffin JR, Critchfield WB (1972) The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82

Griffin, J. R., and P. C. Muick 1990. California native oaks: past and present. *Fremontia* 18(3): 4–10.

Hanes, T. L. 1977. Chaparral. In: Barbour, M. G., and J. Major (eds.), *Terrestrial Vegetation of California*, pp. 417–469. John Wiley and Sons, New York.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. *American Geographical Society Special Publication* 36:1–116 + map

Kuchler, A. W. 1977. Appendix: The map of the natural vegetation of California. In Barbour, M. G., and J. Major (eds.), *Terrestrial Vegetation of California*, pp. 909–938. John Wiley and Sons, New York.

Larcher, W. 1981. Low temperature effects on Mediterranean sclerophylls: an unconventional viewpoint. In Margaris, N. S., and H. A. Mooney (eds.), *Components of productivity of Mediterranean-climate ecosystems: basic and applied aspects*, pp. 259–266. Dr W. Junk, The Hague.

Lewis, H. T. 1973. *Patterns of Indian Burning in California: Ecology and Ethnohistory*. Ballena Press, Ramona (California).

Matsuda, K., and J. R. McBride 1986. Difference in seedling growth morphology as a factor in the distribution of three oaks in central California. *Madrono* 33:207–216.

Matsuda, K., J. R. McBride, and M. Kimura 1989. Seedling growth form of oaks. *Annals of Botany* 64:439–446.

Mensing, S. A. 1992. The impact of European settlement on blue oak (*Quercus douglasii)* regeneration and recruitment in the Tehachapi Mountains, California. *Madrono* 19:36–46.

Mensing, S. A. 1998. 560 years of vegetation change in coastal central California. *Madrono* 45: 1–11.

Mensing, S. A. 2005. The history of oak woodlands in California, Part I: The paleoecologic record. *The California Geographer* 45:1–38.

Mensing, S. A. 2006. The history of oak woodlands in California, Part II: The Native American and historic period. *The California Geographer* 46:1–31.

Minnich, R. A. 1985. Evolutionary convergence or phenotypic plasticity? Responses to summer rain by California chaparral. *Physical Geography* 6:272–287.

Minnich, R. A., and E. Franco–Vizcaino 1998. Land of chamise and pines: historical descriptions of vegetation in northern Baja California. *University of California Publications in Botany* 80: 1–166

Nixon KC (2002) The oak (*Quercus*) biodiversity in California and adjacent regions. In Oaks in California's changing landscape. USDA Forest Service General Technical Report PSW-GTR-184, pp 3–20

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25–52.

Pavlik, B. M., P. C. Muick, S. G. Johnson, and M. Popper 1991. *Oaks of California*. Cachuma Press, Los Olivos, CA.

Reynolds RD (1959) Effect of natural fires and aboriginal burning upon the forests of the central Sierra Nevada. M. A. thesis, Geography, University of California, Berkeley, p 262

Sawyer, J. O. and T. Keeler-Wolf 1995. A Manual of California vegetation. California Native Plant Society Press, Sacramento CA.

Sawyer, J. O., T. Keeler-Wolf, and J. Evens 2009. A Manual of California Vegetation. 2nd ed. California Native Plant Society Press, Sacramento CA.

Schimper, A. F. W. 1898. *Pflanzengeographie auf Physiologischen Grundlage*. Gustav Fischer, Jena.

Scott TA (1991) The distribution of Engelmann Oak (*Quercus engelmannii*) in California. In RB Standiford, tech. coord (ed) Proceedings of the symposium on Oak Woodlands and Hardwood Rangeland management, October 31-November 2, 1990, Davis, CA. USDA, Forest Service, Gen. Tech. Rep. PSW-126, Berkeley, pp 351–359

Snow GE (1972) Some factors controlling the establishment and distribution of *Quercus agrifolia* Nee and *Quercus engelmannii* Greene in certain southern California woodlands. Ph. D. dissertation, Oregon State University

Valiente-Banuet, A., N. Flores-Hernandez, M. Verdu, and P. Davila 1998. The chaparral vegetation in Mexico under non-Mediterranean climate: the convergence and Madrean-Tethyan hypotheses reconsidered. *American Journal of Botany* 85:1398–1408.

Walter, H. 1973. *Vegetation of the Earth*. Springer-Verlag, New York.

Walter, H., E. Harnickell, and G. Mueller-Dombois 1975. *Climate-Diagram Maps of the Individual Continents and the Ecological Climatic Regions of the Earth*. Springer Verlag, Berlin.

Walter, H., and H. Lieth 1967. *Klimadagramm-Weltatlas*. Gustav Fischer, Jena.

Woodward, F. I. 1987. *Climate and Plant Distribution*. Cambridge University Press, Cambridge.

Deciduous Woodlands in the Near Eastern Fertile Crescent, and a Comparison with California

Mark A. Blumler and Joel C. Plummer

Abstract

In the Near East, Mediterranean climate extends eastward from the northern Levant and southeast along the Zagros foothills. Evergreen sclerophylls are almost completely absent from the Zagros; instead, several deciduous tree species dominate, from genera such as *Pistacia* and *Zizyphus*, as well as oaks. In the Levant, deciduous and evergreen species co-occur, with the deciduous species predominating noticeably on the soils that are most fertile and drier in summer. Distribution patterns suggest that evergreen sclerophylls are not strictly Mediterranean but rather subtropical semi-arid in their adaptation, while deciduous species outcompete them under the most purely Mediterranean conditions. Comparison with California shows that the regions display similar patterns, probably for similar reasons.

Keywords

Keywords • Mediterranean ecosystems • Fertile Crescent climate • Evergreen sclerophylls • Subtropical dry ecosystems • Deciduousness as Mediterranean adaptation

1 Introduction

The Fertile Crescent is variously defined. Historically, it included the Mesopotamian lowlands which, much like the southern San Joaquin Valley of California, are too arid to support woodlands except along rivers. More recently, some authorities have come to give the Fertile Crescent a more ecological definition, as comprising the semi-arid "hilly flanks" (Braidwood and Howe 1960) that stretch from Israel, Palestine and Jordan northward along the Mediterranean coast to southeastern Turkey and then east and southeast along the Zagros Mountains to Shiraz or thereabouts. This region is wet enough to support dry farming and is the region covered in this review. Other parts of the Mediterranean region and of the Near East also support Warm-Temperate Deciduous Woodlands, but I will mention only a few such areas, and only tangentially.

The hilly flanks of the Fertile Crescent have a California analogy in the blue oak (*Quercus douglasii*) woodlands of the foothills surrounding the Central Valley (Blumler, herein). As is true of California, the Fertile Crescent of the Near East has a mediterranean climate, with mild wet winters and extreme summer drought and heat. In both cases, winter-deciduous species, especially oaks, dominate the vegetation over extensive areas, which raises questions regarding the supposed correlation of evergreen sclerophylls and mediterranean climate. As in California, evergreen sclerophylls cover only a small percentage of the total area. They are more characteristic of the western part of the Fertile Crescent, also known as the Levant (Israel, Palestine, western Jordan, Lebanon, coastal Syria, and the region of the Amanus Mountains in Turkey). Even in the Levant, though, sclerophylls are probably not more common than deciduous vegetation. Also as in California, woody vegetation appears typically as savanna, park-forest (parkland), steppe-forest, or

M.A. Blumler (✉)
SUNY-Binghamton, Binghamton, NY, USA
e-mail: mablum@binghamton.edu

J.C. Plummer
NASA Goddard Space Flight Center, Greenbelt, MD, USA
e-mail: diekarte@juno.com

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_15, © Springer International Publishing Switzerland 2015

woodland, rather than true forest, though the latter is not entirely absent. "Semi-evergreen" species (see Blumler, herein) are sometimes present.

2 Climate

> California doesn't have a real Mediterranean climate. It doesn't have summer thunderstorms. (R. Degouvenain, personal communication, 1980)

Blumler (2005) pointed out that scholars have conflated three different definitions of Mediterranean climate:

1. Climates around the Mediterranean Sea;
2. Climates that favor evergreen sclerophylls; and
3. Winter-wet, summer-dry climates.

Climates around the Mediterranean are diverse, and not all feature summer dryness. The quote above from a native of Montpellier who immigrated to California reflects the fact that, in southern France, 25% of the precipitation falls in summer. In general, summer dryness and winter rain increase as one transects the Mediterranean region from north to south and especially from west to east – toward the Fertile Crescent (Fig. 1). As Trewartha (1961, p. 11) put it:

> Although the Mediterranean Basin has given its name to one of the earth's most distinctive climate types, the region as a whole is not a good model of subtropical summer-dry climate (Cs) in its simple or pure form. Only the southern and eastern parts can so qualify.

In contrast, evergreen sclerophyll (*maquis*) vegetation occurs in some parts that receive 25% of precipitation in summer, such as southern France, while some of the most summer-dry areas feature winter-deciduous species rather than evergreens. If winter rain and summer dryness are taken together as the defining feature of the Mediterranean-type climate, then the Fertile Crescent is the purest mediterranean region on Earth: it is hotter and drier in summer than any other winter-rain region. Blumler (1992) ranked mediterranean and submediterranean regions according to seasonality of precipitation, i.e., degree to which they correspond to definition 3, above, and found the following:

$$\begin{aligned}\text{Fertile Crescent} &\geq \text{Eastern Mediterranean} > \text{California}\\ &= \text{Morocco} > \text{N. Afghanistan}\\ &> \text{Central Chile} = \text{Western Australia, etc.}\end{aligned}$$

It is noteworthy that the three most mediterranean regions, in this sense, also are the regions that show the least dominance of evergreen sclerophylls. It seems likely that, as summer drought increases, the quantity of winter precipitation required to support trees would also increase. So if 350 mm of annual precipitation are sufficient to support tree vegetation in southern France, the same sort of vegetation might need 400 mm to survive the much longer drought of the Fertile Crescent. Finally, Blumler's classification ignores winter cold, which is generally felt to be a significant limiting factor for evergreen sclerophylls (Larcher 1981). Those areas with significant winter cold, however, might also fail to qualify as "warm temperate" regions.

There is considerable confusion concerning the extent of mediterranean-type climate in the Near East, in part because weather stations are scattered and not always operational, but primarily because of the conflation of sclerophylls with summer drought discussed above and in Blumler (2005b). Browicz (1978, 1982-1988) had mapped the distribution of arboreal Near Eastern species. Plummer (2004) entered these into a GIS and overlaid climate data, after co-kriging, to produce continuous surfaces. Although evergreen sclerophylls are rare in the Near East, a few species are present, such as oleander (*Nerium* spp.) and myrtle (*Myrtus communis*) (Fig. 2). Plummer's careful review demonstrated that oleander and myrtle are more susceptible to cold than most Mediterranean sclerophylls. Thus, where they are present, winter cold is not the factor that excludes the other taxa. Oleander is phreatophytic, growing typically in gravelly or rocky wadis. By comparing myrtle distribution to the climate overlays, though, Plummer (2004, p. 111) was able to conclude that the mediterranean climate zone should conform to areas with January mean temperature of 0°C or greater and total annual precipitation of 350 mm or more. This result is in excellent agreement with consensus thinking about Mediterranean climates. Plummer's (2004) map of Mediterranean climate within the Near East is reproduced as Fig. 3.

3 Climate History

The Mediterranean climate is recent in Europe, as in California and elsewhere (Raven 1973; Suc 1984). The Near East fossil record is poor, but presumably the same story applies there as in the Mediterranean region proper. As in California, evergreen sclerophylls and deciduous oaks were much more restricted during the last glacial period, especially in the northern Mediterranean and Near East (Bottema 1982 (1985); van Zeist and Bottema 1982; Huntley and Birks 1983; Roberts 1998; Blumler 2007).

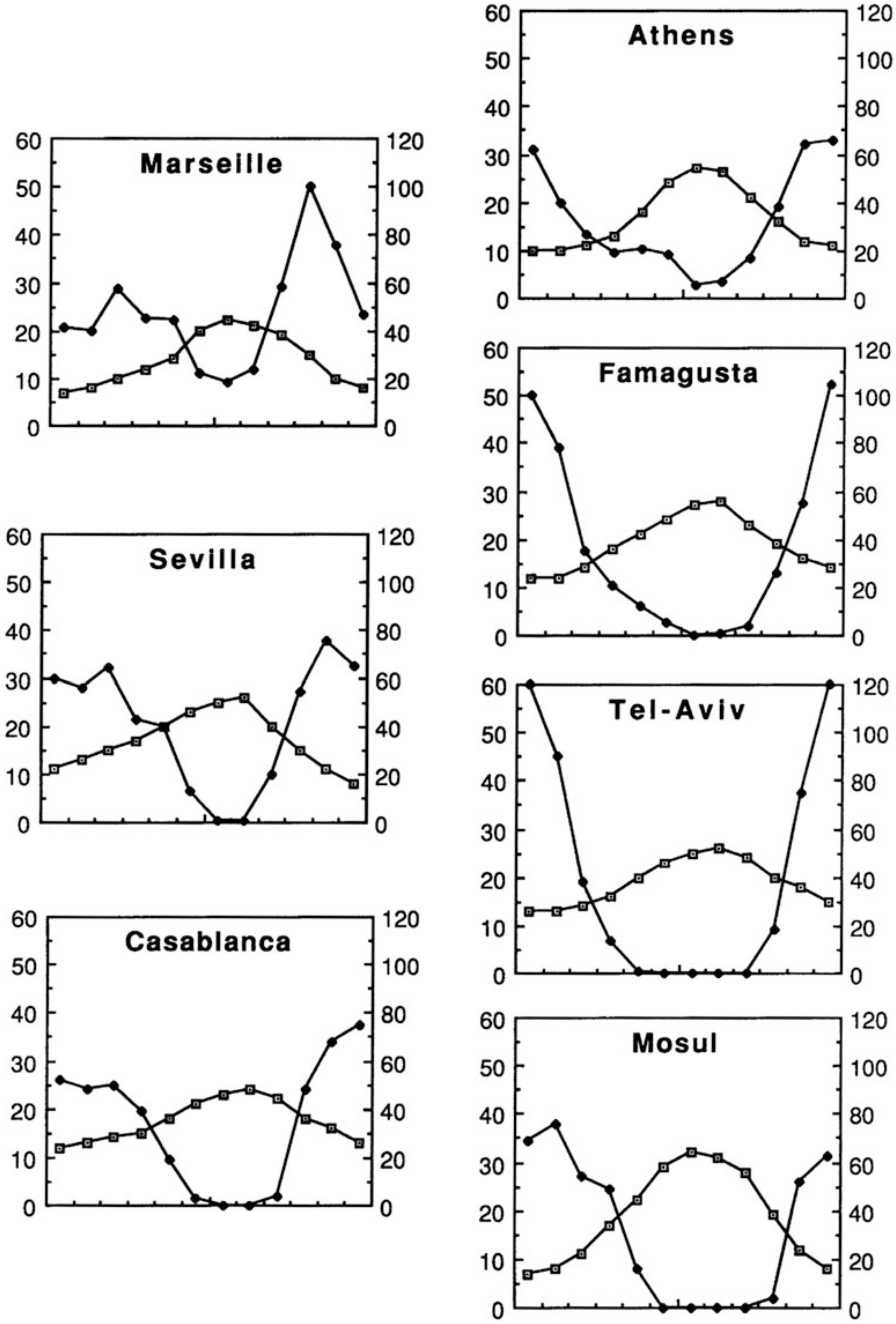


Fig. 1 Climate diagrams (without shading) for selected Mediterranean/Near Eastern Cities. These show how seasonality increases from north to south and especially from west to east (Blumler 1993, after Walter and Lieth 1967; Walter et al. 1975)

4 The Zagros Gap

Blumler (2005b) described one of the more striking aspects of Near Eastern plant distribution, namely the “Zagros Gap” in which sclerophylls are missing. Several broad-leaved evergreen species, as well as conifers (which are also evergreen sclerophylls, though needle-leaved), are present in the eastern Mediterranean region but disappear shortly to the east. They, or their vicariant sibling species, re-appear in Pakistan and neighboring Afghanistan. Although no two taxa have identical distributions, olive is characteristic (see

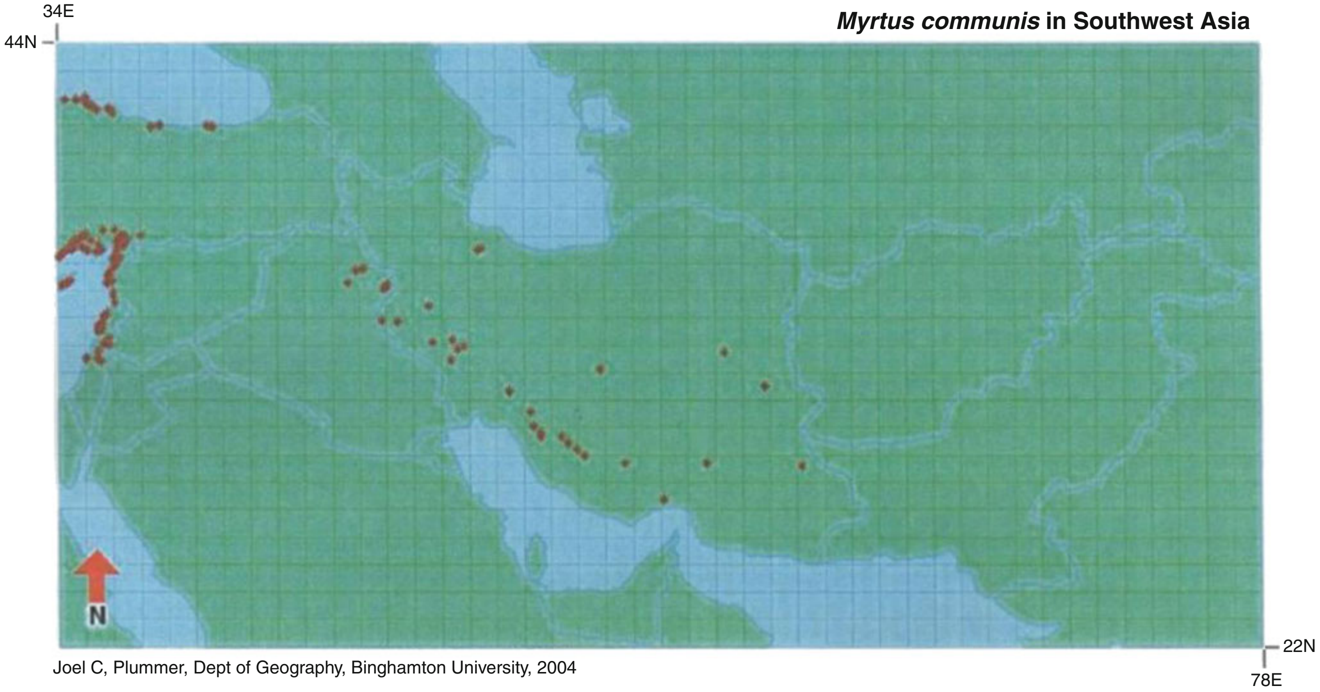


Fig. 2 Distribution of *Myrtus communis* in the Near East (Plummer 2004, from Browicz 1982-1988)

Fig. 3). *O. europaea* occurs in the eastern Mediterranean, in northeast Turkey where summer precipitation is plentiful, and in southern Iran and Oman (Ghazanfar 1991), which is very dry (only slightly more than 100 mm annually) but can have rain in winter or summer, located as it is between the Mediterranean and the tropics. The sibling species *O. ferruginea* (only doubtfully distinct) occurs mainly in Pakistan, where there is both winter and summer rain, though at most stations there is a summer maximum, due to the monsoon (Trewartha 1961; Walter et al. 1975; Blumler 2005b). *O. europaea* has a huge gap in its distribution, corresponding to the region Plummer outlined as Mediterranean in Fig. 3.

This gap is reflected in the cuisine of the region. Wherever the olive grows, it is the preferred cooking oil. In eastern Turkey, Iraq, and areas to the east and south, though, the fat from the tail of the fat-tailed sheep has been the traditional mainstay. Examination of olive agricultural statistics illustrates this point clearly (Held 2006): small amounts of olive are cultivated in Iraq, but given its high value today, it would undoubtedly be grown much more extensively if it were possible to do so without summer irrigation, as in the Mediterranean Basin. Yet the olive is more tolerant of cold than myrtle, which is widespread in Iraq and Iran (see Fig. 2), though never a dominant (Plummer 2004).

Table 1 lists species pairs that occur on opposite sides of the Zagros Gap. A slightly different example is the cypress, *Cupressus sempervirens*, which ranges east to the Levant and then is absent until the shores of the Caspian Sea or southern Iran and Pakistan (Browicz 1978). Almost all other Mediterranean sclerophylls do not range east of the Levant. Freitag (1971, 1982) pointed out that the vicariant evergreen taxa drop out on the Afghanistan side of the high mountains, where there is winter precipitation but no monsoon rain. Although much of Afghanistan may be too cold for evergreen broad-sclerophylls, it is difficult to see how cold could exclude conifers. As Sakai and Larcher (1987) and Woodward (1987) have discussed, many conifers have super-cooled water in their tissues, enabling them to tolerate temperatures down to around – 40°C or lower.

Myrtus communis (Fig. 2) and *Juniperus excelsa* are exceptions, in that they are not excluded from the Zagros Gap. Another exception, one that “proves the rule” is oleander (*Nerium oleander*/*N. indicum*) (Fig. 4). Oleander is phreatophytic and grows in gravelly wadis; consequently, it is essentially unaffected by summer drought. Since it grows right through the region, and is one of the most cold-sensitive sclerophylls, it is clear once again that winter cold is not what is excluding most evergreen species. There is one small gap in oleander’s distribution, where the two species separate, but this is in the rugged, little explored Bakhtiari country. It would not be surprising if oleander grows there too but has been overlooked.

In contrast, many deciduous species grow in the Zagros Gap, and at least some occur within the area that Plummer determined to be mediterranean in climate. *Quercus brantii* is the dominant tree species in the Zagros (Guest 1966; Zohary 1963, 1973), and its distribution at least overlaps

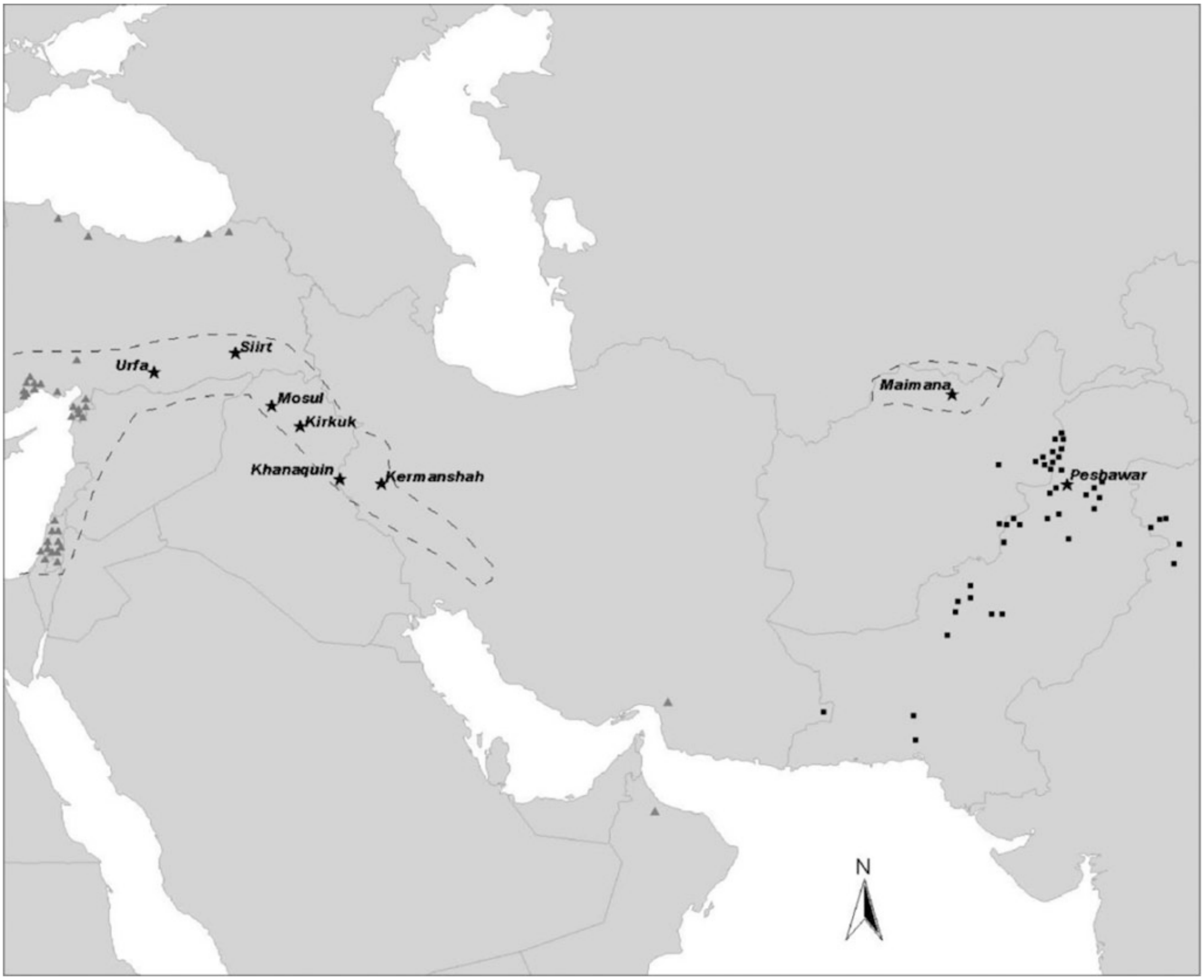


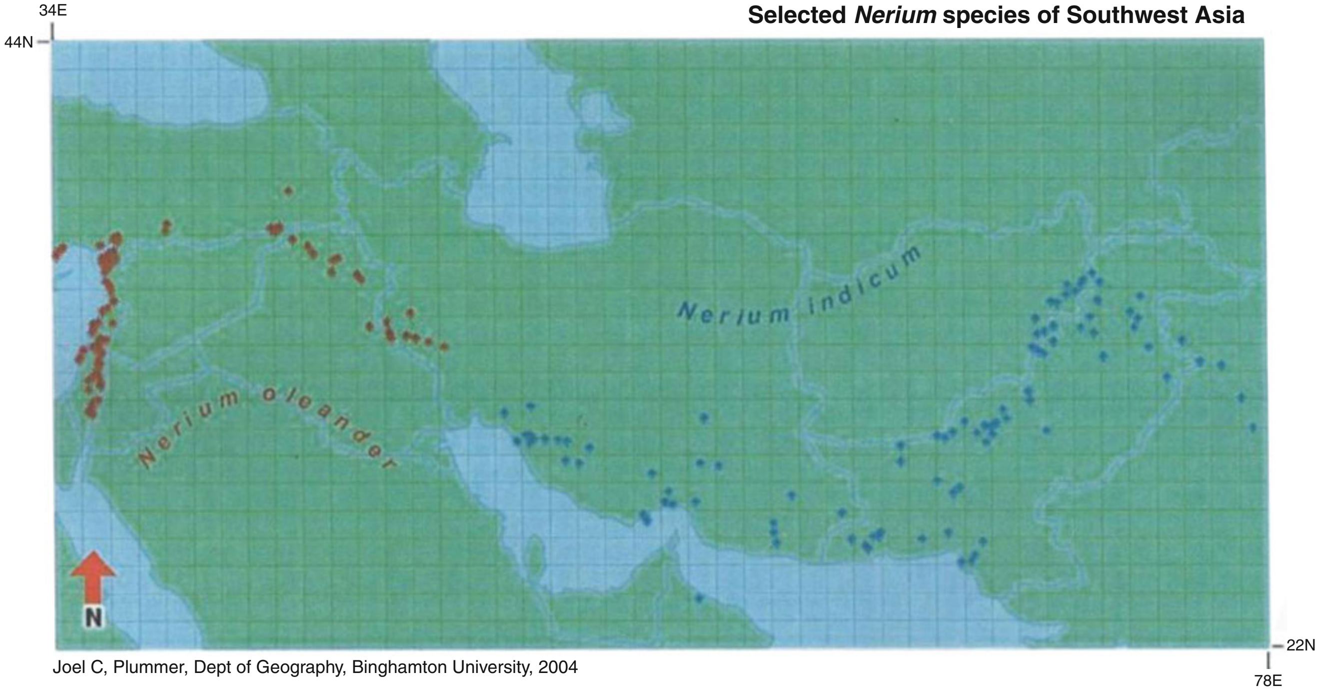
Fig. 3 Regions of Mediterranean climate (*dashes*) within the Near East, with the distribution of wild olive (*Olea europaea* = *triangles*; *O. ferruginea* = *squares*) (From Plummer 2004, modified to include information from Ghazanfar 1991)

Table 1 Middle Eastern evergreen vicariants. These are pairs of sibling species (in some cases only doubtfully distinct) that occur in the eastern Mediterranean or in monsoon Pakistan and neighboring regions, but which are absent from the intervening summer-dry region (Sources: Browicz 1978, 1982-1988; Freitag 1971, 1982)

Eastern Mediterranean	Monsoon Afghanistan/Pakistan
Olea europaea	*O. ferruginea*
Quercus ilex	*Q. baloot*
Cedrus libani	*C. deodara*
Juniperus communis	*J. communis*
Pinus brutia (to northern Iraq)	*P. roxburghii*
Abies cillicica	*A. spectabilis*

with oleander and myrtle, though it also ranges to higher elevations. Table 2 lists some of the many other deciduous species that, at least in some cases, overlap the Mediterranean climate zone.

In the Zagros Mountains, *Pistacia atlantica* and *Zizyphus spina-christi* are the most common trees at lower elevations, below the *Q. brantii* belt, where winters are milder and summers hotter. Zohary (1963, 1973) asserted that they constitute natural steppe-forest vegetation, though today the trees are very widely scattered – sometimes kilometers apart! *P. atlantica* is deciduous, and *Z. spina-christi*, although sometimes classified as evergreen, is in my experience semi-evergreen. The descriptions of Zohary (1963, 1973) and others (e.g. Guest 1966) do not clarify entirely how many other deciduous Zagros species are found only at higher elevations, where winters are cold, and how many extend down to elevations with mild winters, as *Q. brantii* does. There is a need for more detailed mapping and correlation with climate data for this region. It is clear, however, that the old argument that evergreens would dominate, were it not for human disturbance, cannot apply to the Zagros,



Joel C, Plummer, Dept of Geography, Binghamton University, 2004

Fig. 4 Distribution of Oleander in the Middle East (Plummer 2004; from Browicz 1982-1988)

Table 2 Deciduous or semi-evergreen species that grow within the Zagros Gap (Sources: Browicz 1978, 1982-1988; Zohary 1973 (taxonomy may be dated))

Acer monspessulanum	*Cerasus mahaleb*
Quercus brantii	*Crataegus aronia*
Q. infectoria	*Pyrus syriaca*
Q. libani	*Celtis caucasica*
Q. macrolepis	*Pistacia atlantica*
Amygdalus spp.	*P. khinjuk*
Zizyphus spina-christi	

because the most tree-like evergreen, *Juniperus excelsa*, is a poor candidate to replace oaks in a successional sequence.

Plummer (2004) also identified a small area within northern Afghanistan, around Maimana, as having a mediterranean climate (Fig. 3). Freitag (1971, 1982) described this area as a steppe involving *Pistacia vera* (true wild pistachio, deciduous), frequently with an understory of wild barley (*Hordeum spontaneum*).

A striking contrast with California is that, while oaks predominate in both regions, there exists a much greater diversity of accompanying deciduous species in the Fertile Crescent/Near East. Mensing (2005) pointed out that, during the Tertiary and Quaternary, the western US progressively lost deciduous species that today are characteristic of the eastern US, until the oaks were almost all that remained. Although arboreal cover is low in the Middle East, it does not seem to have suffered the same degree of loss. In contrast, conifers are much better represented in California, including types such as pinyon pines that have no Old World equivalent.

5 The Levant

Phytogeographers, especially Israeli, have described Levantine vegetation patterns in more detail than the rather cursory reports on the Zagros. This is convenient, since both evergreen and deciduous species can dominate in the Levant. Close attention to soils, in particular, is necessary to understand the conditions that favor one habit over the other. A problem with the Israeli literature, which will be the focus here, is that wide-ranging taxa are frequently split, and a species epithet is given to the doubtfully distinct form that grows within Israel. So for instance, the evergreen kermes oak *Q. calliprinos* is closely related to, and doubtfully distinct from, the widespread *Q. coccifera*; deciduous *Pistacia palestina* is doubtfully distinct from *P. terebintha*; and the semi-evergreen tabor oak, *Q. ithaburensis*, is doubtfully distinct from *Q. macrolepis*.

Tabor oak (see Fig. 5) is the closest equivalent to California's blue oak (see Blumler, herein). It grows at low altitudes (the kermes oak ranging to higher elevations), on fertile, often clayey soils that dry out severely during summer. It mixes sometimes with kermes oak and other *maquis* species on Cenomanian hard limestone, where water relations are somewhat more favorable, but it is more likely

Fig. 5 Tabor oak woodland on nari in Lower Galilee, Israel

to occur alone or with other deciduous trees and shrubs such as *P. atlantica*, *Zizyphus lotus*, and *Rhamnus palaestina* (Zohary 1962; Naveh and Whittaker 1979; Rabinovitch-Vin 1983; Blumler 1992).

One well-studied formation is the tabor-oak community on dark rendzina, which is an unusual, fertile, clay-rich soil that forms over a calcrete, locally called "nari", that itself has formed over chalk (Dan et al. 1972). (Although derived from chalk, dark rendzina is unlike other rendzinas in that it is largely decalcified). The nari serves as a barrier to root penetration, and so the vegetation must deal with extreme moisture depletion late in the dry season. It is generally accepted that tabor oak is not seral to some other woody vegetation on the nari (Eig 1933; Oppenheimer 1950; Zohary 1962; Blumler 1992). Blumler (1993) pointed out that one can observe evergreen sclerophylls arising from the underlying chalk where it is exposed on slopes, but not on the nari. Just as Griffin (1973) pointed out for blue oak in California, Oppenheimer (1950) suggested that summer drought in Israel tends to produce open woodland stands due to competition for limited water.

Blumler (1992, 1993) studied succession in an exclosure on nari and found that no new woody plants were able to become established during the study period. Apparently, competition from tall wild-cereal grasses was so severe that seedling establishment of perennials was completely halted, except on rock outcrops. Tabor oak seedlings appeared occasionally but did not survive, for reasons that were unclear. It may be that they were taken by rodents, or alternatively that they could not withstand the drying of the soil by the fast-growing annual grasses. Regardless, the nari environment is clearly hostile to the establishment of woody plants. Woody plants were more frequent where there was moderate grazing, though even then the species were deciduous.

Zohary (1962) emphasized that fully half the species in the Mediterranean maquis of Israel are deciduous. Moreover, the deciduous species are frequently co-dominant with evergreens. *Quercus calliprinos-Pistacia palestina* maquis occurs at 150–800 m+, especially on terra rossa, which is neither as fertile nor as clayey as most soils that support dominance by tabor oak. Also, in low-elevation Israel one encounters savanna forests of *Z. spina-christi*, and there are also several deciduous rosaceous trees, such as almond (*Amygdalus communis*) and hawthorn (*Crataegus azarolus*), that occasionally form steppe-forest remnants, according to Zohary.

6 Classification

Zohary (1962) presented this classification of the arboreal vegetation of Palestine:
Quercetea calliprini Class
Quercetalia calliprini Order
Pinion Halepensis Alliance

- *Pinus halepensis* – *Hypericum serpyllifolium* Association
- *Pinus halepensis* – *Juniperus oxycedrus* Association
- *Pinus halepensis* – *Cupressus sempervirens* Association

Quercion ithaburensis Alliance

- Quercetum ithaburensis arenarium Association
- *Quercus ithaburensis* – *Styrax officinalis* Association
- *Quercus ithaburensis* – *Pistacia atlantica* Association

Quercion calliprini Alliance
  Quercus calliprinos – Pistacia palaestina Association
  Quercus calliprinos – Juniperus phoenicea Association
Ceratonia-Pistacion Alliance
  Ceratonieto-Pistacietum lentisci typicum Association
  Ceratonieto-Pistacietum lentisci arenarium Association
  Ceratonieto-Pistacietum lentisci orientale Association

Artemisetea herbae-albae Class
Zizypho – Pistacietalia Order
Pistacion Atlanticae Alliance
  Pistacietum atlanticae

Zizyphion Loti Alliance
  Zizyphetum Loti
  Zizyphus lotus – Retama raetam Association
  Zizyphus lotus – Zizyphus spina-christi Association

The associations featuring Aleppo pine (*P. halepensis*) are found on light rendzina, a highly calcareous substrate that is less fertile but has better water retention than the heavier-textured soils alluded to above. The first of the three tabor forest associations occurs on sandy clay loam of the coastal plain; the second is found on nari; and the last is on basalt and Eocene hard limestone, both heavy clay types that dry out in summer. Within the Quercion calliprini Alliance, the first association is the typical maquis alluded to above, with about 50% of species deciduous. The other association covers only a small area and is found in Jordan. Although the two named species are evergreen, the association also includes several deciduous species, such as *Crataegus azarolus*, *Pistacia palaestina*, *P. atlantica*, and *Rhamnus palaestina*. Carob (*Ceratonia siliqua*) and mastic (*Pistacia lentiscus*) are evergreen species that dominate low-elevation communities, especially on consolidated sand dunes, rendzina, and terra rossa, i.e. soils that are probably water-retentive on the whole.

Zohary regards other wooded associations as Irano-Turanian and, consequently, places them in the Class Artemisetea herbae-albae. These include scattered stands dominated by *Pistacia atlantica* and *Zizyphus* spp., which may be analogous to the vegetation of the lower foothills of the Zagros.

7 Discussion: Patterns and Explanations

Mensing (2006) suggested that oak parks in California were favored by the Indians' practice of burning. Vegetation patterns in the Fertile Crescent are highly analogous, yet fire does not seem to be such a significant player. Certainly pastoralists do set fires, but they do not do so on the scale or with the frequency that is claimed for Native Americans prior to the coming of Europeans.

The Mediterranean is beyond the purview of this paper, but it is perhaps germane to mention briefly that similar patterns appear to present themselves in its more summer-dry portions. See, for instance, Rackham (1982, 1990; Grove and Rackham 2001) for Crete and Greece.

Deciduous species are capable of higher rates of photosynthesis under optimum conditions (e.g., Ne'eman 1993) but are not "present" year-round. Evergreen species are capable of some photosynthetic production even under poor conditions, and thus are better adapted to environments fostering slow steady growth. These differences lead to some predictions. Where soils are fertile and summer drought is severe, advantage should go to fast-growing but drought-deciduous species; where soils are infertile or where drought is shorter (for instance, in Pakistan there is a short drought in spring and another in fall), the advantage should go to evergreens that do not drop their leaves and then need to re-grow them again. Because light availability is low under the canopy, growth rates there are less than optimum, shifting the advantage to evergreens (Blumler 1991). Thus, where woods can become denser, evergreens may be able to replace the deciduous trees. In a mediterranean climate, though, as Griffin (1973) showed and Oppenheimer (1950) also suggested, drought stress increases as tree density increases. This tends to limit the ability of trees to develop dense forests, except where the water table is freely accessible. On fertile soils, open vegetation would probably mean competition from fast-growing herbs, which would favor the fast-growing deciduous species over evergreens. Winter cold can be a problem for evergreen sclerophylls, and it seems likely, though not yet investigated, that they would revive from cold damage better where there is some summer precipitation. If so, the threshold minimum temperature would in effect be higher where there is extreme summer drought, such as in the Fertile Crescent.

Long ago, geographer Preston James (1959) suggested that evergreen sclerophylls were limited not only by winter cold but also by summer drought. Although this was ignored completely at the time and for long after, it may be that he was correct.

8 Implications Regarding Biome Modeling

Evergreen sclerophylls are characteristic of subtropical semi-arid regions, regardless of seasonal rainfall pattern, but drop out in favor of deciduous woodland where seasonal drought is severe. This somewhat counter-intuitive conclusion illustrates some of the problems encountered in applying climatic biome modeling to semi-arid regions such as those that feature a mediterranean climate. The biome concept works best where it is wet (forest), cold (tundra), or dry (desert), though "desert" subsumes considerable diversity (Blumler 2005a). The biome concept becomes highly problematic in semi-arid regions because many different growth forms, and thus several different types of vegetation, can compete on close-to-equal terms. Under these circumstances, edaphics and types of disturbance play more prominent roles in determining the type of vegetation that will prevail.

Acknowledgements We thank Florence Margai for assisting the junior author in learning the strengths and weakness of interpolation techniques such as co-kriging; and Kevin Heard for providing cartographic assistance to the senior author. We also acknowledge the late, great Heinrich Walter, who kept the study of vegetation-environment relationships flourishing during those decades of American neglect of the subject.

References

Blumler, M. A. 1991. Winter-deciduous versus evergreen habit in mediterranean regions: a model. In Standiford, R. B., tech. coord., *Proceedings of the Symposium on Oak Woodlands and Hardwood Rangeland Management*, October 31-November 2, 1990, Davis, CA, pp. 194–197. USDA, Forest Service, Gen. Tech. Rep. PSW-126, Berkeley.

Blumler, M. A. 1992. Seed weight and environment in mediterranean-type grasslands in California and Israel. Ph. D. dissertation, Geography, University of California, Berkeley.

Blumler, M. A. 1993. Successional pattern and landscape sensitivity in the Mediterranean and Near East. *In* Thomas, D. S. G., and R. J. Allison, eds., *Landscape Sensitivity*, pp. 287–305. John Wiley & Sons, Chichester.

Blumler, M. A. 2005a. History of the biome concept, with implications for practical application to global change prediction and management. *Research in Contemporary and Applied Geography: A Discussion Series* 29(3):1–43.

Blumler, M. A. 2005b. Three conflated definitions of mediterranean climates. *Middle States Geographer 38*:52–60.

Blumler, M. A. 2007. Near Eastern pollen diagrams and "deforestation." *Middle States Geographer* 40:150–157.

Blumler, M. A. (herein). Deciduous woodlands in mediterranean California. In: Warm-Temperate Deciduous Forests: Not so Unusual around the Northern Hemisphere (E. O. Box & K. Fujiwara, eds.).

Bottema, S. 1982 (1985). Palynological investigations in Greece with special reference to pollen as an indicator of human activity. *Paleohistoria* 24:257–289

Box, E. O. 1981. *Macroclimate and Plant Forms: an Introduction to Predictive Modeling in Phytogeography*. Dr W. Junk, The Hague, 258pp.

Braidwood, R. J., and B. Howe 1960. *Prehistoric Investigations in Iraqi Kurdistan*. University of Chicago Press, Chicago.

Browicz, K. 1978. *Chorology of Trees and Shrubs in South-West Asia*. Vol. 1. Polish Academy of Sciences, Institute of Dendrology, Kornik.

Browicz, K. 1982-1988. *Chorology of Trees and Shrubs in South-West Asia and Adjacent Regions*. Vols. 2-5. Polish Academy of Sciences, Institute of Dendrology, Warsaw

Dan, J., D. H. Yaalon, and H. Koyumdjisky 1972. Catenary soil relationships in Israel 2. The Bet Guvrin catena on chalk and nari limestone crust in the Shefela. *Israel Journal of Earth Sciences* 21:99–114.

Di Castri, F., and H. A. Mooney (eds.) 1973. *Mediterranean Type Ecosystems: Origin and Structure*. Springer Verlag, New York.

Eig, A. 1933. A historical-phytosociological essay on Palestinian forests of *Quercus aegilops* L. ssp. *ithaburensis* (Desc.) in past and present. *Beihefte zum Botanischen Zentralblatt* 51B:225–272

Freitag, H. 1971. Studies in the natural vegetation of Afghanistan. In Davis, P. H., P. C. Harper, and I. C. Hedge (eds.), *Plant Life of South West Asia*, pp. 89–106. Royal Botanic Garden, Edinburgh.

Freitag, H. 1982. Mediterranean characters of the vegetation in the Hindu Kush Mts., and the relationship between sclerophyllous and laurophyllous forests. *Ecologia Mediterranea* 8:381–388.

Ghazanfar, S. A. 1991. Vegetation structure and phytogeography of Jabal Shams, an arid mountain in Oman. *Journal of Biogeography* 18:299–309.

Griffin, J. R. 1973. Xylem sap tension in three woodland oaks of central California. *Ecology* 54: 152–159.

Grove, A. T. and O. Rackham 2001. *The Nature of Mediterranean Europe: An Ecological History*. Yale University Press, New Haven CT.

Guest, E. 1966. *Flora of Iraq*.Vol 1. Introduction. Minister of Agriculture, Baghdad

Held, C. C. 2006. *Middle East Patterns: Places, People, and Politics*. 4th ed. Westview Press, Boulder, CO.

Huntley, B., and H. J. B. Birks 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0-13 000 Years Ago*. Cambridge University Press, Cambridge.

James, P. E. 1959. *The Geography of Man*. Ginn & Co., New York

Larcher, W. 1981. Low temperature effects on Mediterranean sclerophylls: an unconventional viewpoint. In: *Components of productivity of Mediterranean-climate ecosystems: basic and applied aspects* (N. S. Margaris & H. A. Mooney, eds.), pp. 259–266. Dr W. Junk, The Hague.

Naveh, Z., and R. H. Whittaker 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other mediterranean countries. *Vegetatio* 41:171–190.

Mensing, S. A. 2005. The history of oak woodlands in California, Part I: The paleoecologic record. *The California Geographer* 45:1–38.

Mensing, S. A. 2006. The history of oak woodlands in California, Part II: The Native American and historic period. *The California Geographer* 46:1–31.

Ne'man, G. 1993. Variation in leaf phenology and habit in *Quercus ithaburensis*, a Mediterranean deciduous tree. *Journal of Ecology* 81:627–634.

Oppenheimer, H. R. 1950.The water turn-over of the Valonea oak. *Palestine Journal of Botany* (Rehovot) 7:177–179.

Plummer, J. C. 2004. A bio-climatic approach to determining the extent of a Mediterranean climate in southwest Asia. M. A. thesis, SUNY-Binghamton

Rabinovitch-Vin, A. 1983. Influence of nutrients on the composition and distribution of plant communities in mediterranean-type ecosystems of Israel. In: *Mediterranean-type Ecosystems: The Role of Nutrients* (F. J. Kruger et al., eds.), pp. 74–85. Springer-Verlag, Berlin.

Rackham, O. 1982. Land use and the native vegetation of Greece. In: *Archaeological aspects of Woodland Ecology* (M. Bell & S. Limbrey, eds.), pp. 177–198. BAR, Oxford.

Rackham, O. 1990. The greening of Myrtos. In: *Man's Role in the Shaping of the Eastern Mediterranean Landscape* (S. Bottema et al., eds.), pp. 341–348. Balkema, Rotterdam.

Raven, P. H. 1973. The evolution of Mediterranean floras. In:.*Mediterranean Type Ecosystems: Origin and Structure* (F. di Castri & H. A. Mooney, eds.), pp. 213–224. Springer-Verlag, New York

Roberts, N. 1998.*The Holocene*. 2nd ed. Blackwell, Oxford.

Sakai, A., and W. Larcher. 1987. *Frost Survival of Plants: Responses and Adaptations to Freezing Stress*. Springer Verlag, New York.

Suc, J.-P. 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* 307:429–432.

Trewartha, G. 1961. *The Earth's Problem Climates*. University of Wisconsin, Madison.

Van Zeist, W., and S. Bottema. 1982. Vegetational history of the eastern Mediterranean and the Near East during the last 20 000 years. In: *Palaeoclimates, Palaeoenvironments and Human Communities in the Eastern Mediterranean Region during later Prehistory* (J. L. Bintliff & W. van Zeist, eds.), pp. 277–321. BAR, Oxford.

Walter, H., E. Harnickell, and G. Mueller-Dombois. 1975. *Climate-Diagram Maps of the Individual Continents and the Ecological Climatic Regions of the Earth*. Springer Verlag, Berlin.

Walter, H., and H. Lieth. 1967. *Klimadagramm-Weltatlas*. Gustav Fischer, Jena.

Woodward, F. I. 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge.

Zohary, M. 1962. *Plant Life of Palestine*. Ronald Press, New York

Zohary, M. 1963. On the geobotanical structure of Iran. *Bulletin of the Research Council of Israel* 11D(suppl.):1–113.

Zohary, M. 1973. *Geobotanical Foundations of the Middle East*. 2 Vols. Gustav Fischer, Stuttgart

Zohary, M. 1982.*Vegetation of Israel and Adjacent Areas*. Ludwig-Reichert-Verlag, Wiesbaden.

Quantitative Delimitation of Warm-Temperate Deciduous Forest Areas

Elgene O. Box

Abstract

The zonal vegetation of [humid] warm-temperate regions is normally considered to be evergreen broad-leaved forest, as in East Asia, southern Brazil, and much of New Zealand. Kira, however, proposed the term ‘warm-temperate deciduous’ for forests composed of deciduous trees that do not occur in the adjacent cool–temperate or subtropical zones in Japan but do occur in parts of the otherwise warm-temperate zone that have colder winters. This concept also fits some deciduous forests on other continents, and some such forests are described in other chapters of this book. In addition, in the Overview chapter of this book, an attempt was made to delimit such forest areas quantitatively, using climatic data. In this chapter an attempt is made to identify these and other potential temperate forest areas geographically, based on their climatic envelopes, and to map them worldwide. Limiting values for the envelopes are based on the “breaks” in climatic response identified in the Overview chapter, but with a compromise threshold for summer temperatures, in order to show European areas that occur at lower summer temperatures than on continental east sides. The resulting map shows the expected three main regions, plus some additional smaller areas, thus suggesting that warm-temperate deciduous does represent a consistent sub-zonal climatic and potential forest type. The regions shown, though, are too large in eastern North America and East Asia, in order to show some areas in Europe.

Keywords

Absolute minimum temperature • Cool-temperate climate • Kira index • Summer warmth threshold • Submediterranean climate • Thermophilous deciduous forest • Typical temperate climate • Warm-temperate climate

1 Introduction

The zonal vegetation of [humid] warm-temperate regions is normally considered to be evergreen broad-leaved forest, such as the “laurel forests” in East Asia, southern Brazil, and much of New Zealand. Observing the vegetation of Japan and other parts of East Asia, however, Kira (1949) suggested that some deciduous *Quercus* species do not occur in either the cool-temperate (deciduous) or the subtropical (evergreen) zone and eventually proposed the concept of warm-temperate deciduous forests, composed especially of *Quercus* species. These species occur in the drier climates of interior Honshū, especially around Nagano, where summers are warm enough but winters are too cold for evergreen broad-leaved forest. This concept also fits parts of middle-eastern China and lowland Korea, where most of the same *Quercus* species also occur. Analogous warm-temperate deciduous forests beyond Asia appear to include, *inter alia*, the *Quercus-Carya* forests of interior southeastern North America and the *Quercus pubescens* forests of southern Europe. In East Asia, some main deciduous species are

---

E.O. Box (✉)
Geography Department, University of Georgia, Athens, Georgia 30602, USA
e-mail: boxeo@uga.edu

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2_16, © Springer International Publishing Switzerland 2015

Quercus variabilis, *Q. serrata*, *Q. aliena* and *Q. dentata*, all occurring on relatively dry sites. These species also form the canopy of secondary deciduous forests that are eventually replaced by the zonal warm-temperate evergreen broad-leaved (laurel) forests.

In the foregoing chapters of this book a strong case has been made for recognition of warm-temperate deciduous forest as a consistently occurring forest type in (otherwise) warm-temperate climatic areas that may (or may not) be a bit too cold in winter for zonal evergreen broad-leaved forests. Warm-temperate deciduous forests should thus also be seen as a zonal forest type, occupying especially the transition between the typical temperate (deciduous) and warm-temperate (evergreen) zones, i.e. between climates Ve and VI in the (expanded) global climatic zonation system of Walter (1968, 1970, 1985; cf Box 1995b, 2002; Box and Fujiwara 2004). Warm-temperate deciduous forests also occur, as permanent vegetation types (albeit perhaps less zonally), in some parts of the warm-temperate zone proper, due perhaps to topographic or substrate factors as well as climatic aberrations.

If warm-temperate deciduous forests occur consistently in particular climatic situations, it should be possible to define these situations, to delimit them quantitatively, and to map them globally. In order to confirm the concept of warm-temperate deciduous forest as a consistent type, though, it is also necessary to quantify and map the other humid temperate climates, and in turn the adjacent boreal, humid subtropical and dry temperate climates. The purpose of this chapter is to do this mapping, in order to identify areas of possible warm-temperate deciduous forest and to demonstrate that these and other zonal forest types represent consistent responses to particular climatic situations.

2 Data

The factors involved in the response and delimitation of warm-temperate deciduous forests, as well as their adjacent forest types (and corresponding climatic zones), are mainly aspects of temperature, since all such areas must be humid enough to support forest. Experience modeling climatic limitation of plant and vegetation types as well as particular taxa (e.g. Box 1981, 1994, 1995a; Box et al. 1993) has suggested that some expression of the following factors will probably be required to delimit the climate types:

- Mean temperatures of the warmest and coldest months (Tmax, Tmin)
- Temperature extremes, especially minima (e.g. absolute minimum temperature)
- Some expression of the “magnitude” of growing-season warmth (not just a threshold temperature)
- Some measure of overall climatic moisture balance
- Some measure of precipitation during the driest period of the year (Pmin).

Total growing-season warmth may be expressed by a temperature sum, such as Kira’s Warmth Index, or by the length of the warm period, e.g. the number of consecutive months above some temperature threshold.

Data are required in two forms, namely measurements at sites (meteorological stations) for developing the model and interpolated values in pixel rasters for the mapping. The main sources of these data are:

- The world data-base of site values for long-term mean monthly temperature and precipitation, plus absolute minimum temperatures, compiled by the author over the past 40 years (see partial description in Box and Fujiwara 2010); and
- The 0.5 × 0.5-degree pixel fields for mean monthly temperature and average monthly precipitation, interpolated from meteorological station data, provided by Leemans and Cramer (1990, improved version).

All variables must be derived from these primary data.

Tmax, Tmin and Pmin are included as such in the site data-base. The moisture index normally used is the ratio of annual precipitation (in the data-base) to potential evapotranspiration, which is estimated from monthly temperatures (cf Box 1986; Box and Meentemeyer 1991). Length of the warm period (as a measure of overall growing-season warmth) requires only a specified threshold and monthly temperatures. Absolute minimum temperature (Tabmin), i.e. the lowest ever measured, is available for some sites but not all, and sometimes only for short observation periods. As a result, Tabmin is always estimated, as an offset from Tmin, based on the Tmin-Tabmin difference at nearby sites that have Tabmin from sufficiently long observation. Lower estimates for Tabmin replace measured values if the measurement period was short. This methodology, embodied in program TXTRAP, was suggested by the characteristic regional offset patterns shown in Box (1995b) and has been used in various other modeling and other studies (e.g. Box 1994; Box and Choi 2003). Some site data and derived values are shown in the book Appendix.

Pixel rasters for the necessary variables were made in the essentially same way, except that Tmax, Tmin and Pmin also had to be made. Rasters for Tmax, Tmin and Pmin were made by TPSUBS, which identifies the mean value of a running “month” (30-day period) centered on the time of the extreme, rather than simply using the value for the calendar month. Rasters for the derived variables were made by applying the same operations to pixel values as for sites, by means of programs PIXVARS and PIXTRAP. All programs were written by the author and are unpublished (but available by request).

3 Methodology

The modeling and mapping herein involve the various humid temperate climates plus the adjacent boreal and humid subtropical zones and one category for drier temperate regions. The humid temperate climate types are cool-temperate, typical temperate, warm-temperate deciduous and warm-temperate evergreen. The first step in the modeling requires definition of each climate type in terms of biologically relevant distinguishing features. This is done in the next section.

The second step is construction and calibration of the envelope model, which involves, *inter alia*, determination of climate variables needed to express the distinguishing features of the climates; calculation of values for derived variables, from the primary data; construction of a climatic envelope for each type by estimating upper and lower limiting values; and iterative envelope calibration by evaluating predictions and refining limiting values accordingly. Calculation of derived variables was explained briefly in the previous section, including the construction of the pixel field for each variable. The normal steps in envelope modeling, as relevant here, are treated mainly in the next section.

Since this project involves mapping, the third step is to apply the calibrated envelope model to the pixel values to generate geographic results. This requires creating a global pixel raster for each envelope variable, based on the Leemans-Cramer fields (see Sect. 2, above). The climatic regions are then identified and mapped in one step, by program ENVMAP (Box, unpublished), which does the envelope screening at each pixel and provides a single result.

Finally, the resulting map is colored by PIXPAINT (Box, unpublished), by converting the integer code for predicted climate type, at each pixel, into an integer representing position in the RGB palette of Adobe Photoshop ("indexed color" mode).

Since local climatic conditions cannot always be represented well by interpolations to large pixels, the envelope model was run also on a global selection of site data. These sites include those in the Appendix to this book, which also shows the envelope-model result for each site.

4 Defining the Climates

Seven climatic regions are delimited and mapped. The defining features of the five main zones are as follow:

Boreal: pleasantly warm but short summers, with long, severely cold winters except in maritime areas. Mean and absolute winter temperatures are well below freezing, which insures that the warm period is short, usually less than the time needed by most temperate-zone trees to produce viable fruit. This delimitation holds both for the large, distinctly continental expanses of boreal climate with severely cold winters and for maritime areas in the boreal latitudes, like Iceland, which have much milder winters, longer periods above a mean temperature of 0°C, but still do not have longer summers. At least 30 days of mean temperature above about 10°C are normally required for the tree growth that separates boreal from polar landscapes (e.g. Walter 1968).

Cool-Temperate: cool summers, as found in maritime areas and at higher latitudes, especially on continental west sides. The warm season (generally above about 10°C) should be at least 4 months, as for all temperate climates (cf Walter 1968, 1970, 1985). Warm-season mean temperatures are not high, however, generally below about 22°C, which is not reached in Europe, for example, until one approaches the Mediterranean region. Winters may be mild to quite cold, as it is the summer temperature that is distinguishing.

Typical Temperate: most typical of temperate four-season climates, which are found on continental east sides and are rather subcontinental in their temperature regimes. At least five consecutive warm months are required, since summers should be warmer than in cool-temperate climates of higher-latitude and maritime areas. Winters should be fairly cold (continental), but no binding limit is set.

Warm-Temperate: warmer summers and mild winters. This means at least six consecutive warm months, lowest monthly mean temperature above 0°C, and absolute minima not below about −15°C (cf Woodward 1987), in keeping with the idea that the zonal vegetation is normally evergreen. Such conditions may also be met in highly oceanic areas, as in the Southern Hemisphere, where the warm period is long but summer mean temperatures are much lower than in the more continental Northern Hemisphere (cf Troll 1961).

Subtropical: almost tropical, which means mild winters with almost complete absence of frost, usually also with generally warm conditions throughout the year (cf Crumpacker et al. 2001). Light frost has been recorded infrequently in most subtropical areas, such as Guangzhou (−2°C), Simao (−2.5°C), Miami (−2.8°C), and Yakushima (−0.2°C), as well as some Mediterranean locations sometimes considered to be subtropical, such as Lisboa (−1.7°C) and Cairo (−1°C) (see Appendix). The warm period approaches 12 months, the mean temperature of the warmest month is usually well above 15°C and that of the coldest month well above 0°C.

Within this framework we can thus also define the climate of potential warm-temperate deciduous forests. This climate differs from the general warm-temperate (evergreen) climate by having winter mean temperatures that can go significantly below freezing and absolute minima that can go well below −15°C. Also, Kira's original concept was for inland areas of Japan, meaning that warm-temperate deciduous climates are at least subcontinental, with summers warmer than in the cool-evergreen forest areas of the Southern Hemisphere.

Finally, a less well defined dry temperate climate is included in order to suggest gradations of warmer temperate forest regions into adjacent drier areas, which largely have evergreen woodlands and scrub (e.g. Mediterranean, Texas, Australia). All other climates are humid, potentially forest climates. Typical temperate represents the middle of the temperate range and is large only in North America.

5 Building the Model

Six variables were chosen to express the main features of each climate type, especially summer and winter temperatures:

- Mean temperature of the warmest month (Tmax)
- Mean temperature of the coldest month (Tmin)
- Absolute minimum temperature (Tabmin)
- Length of the warm period (Lwarm: consecutive months with mean temperature at least 10°C)
- Annual moisture index (MIy: precipitation divided by potential evapotranspiration)
- Average precipitation of the driest month (Pmin).

Summer warmth is thus expressed by warm-month mean temperature (Tmax) and number of consecutive warm months. The threshold 10°C is commonly used for the beginning of growth in temperate areas and as the warmth threshold that separates boreal from polar climates (e.g. Walter 1968, p. 522; cf Walter 1970, 1985; Box and Fujiwara 2012). Winter cold is represented by cold-month mean temperature (Tmin) and the absolute minimum (Tabmin), i.e. the lowest temperature ever measured; in cases with short measurement records, Tabmin is estimated from its offset from Tmin at nearby stations, as discussed in the Sect. 2 above. The delimitations are only for forest and woodland climates, as represented in the model by threshold values for the annual moisture index (MIy; cf Box 1995a). Since the emphasis in this study is on temperature limits, these climates are permitted to extend significantly into adjacent, drier areas of mainly open woodland. All potential forest climates except the boreal are truncated, though, at a minimum MIy value of 0.6. Limitation by a value of MIy is more artificial in boreal climates, where slowly melting permafrost can compensate for scant precipitation during summer.

Limiting values for the particular variables and climate types are based partly on fairly well recognized physiological limits and partly on geographic observations of forest limits. The main physiological limits seem to be:

- the short-term occurrence of temperatures below about −15°C that preclude temperate-zone evergreen broad-leaved trees (cf Woodward 1987) and below about −3°C that preclude subtropical (and tropical) trees (see Sect. 4, above); and
- the need by most temperate-zone broad-leaved trees of 4 months or more of temperatures above about 10°C in order to produce viable seeds.

In addition, for broad-laurophyll (evergreen) trees, Tmin must be above about 0.5°C for temperate taxa (e.g. *Castanopsis*, not *Persea*; Fujiwara 1982) and generally much higher for subtropical taxa. This and the Tabmin limit of about −15°C (Woodward 1987; Box 1995a, b; cf Sakai 1971) generally define the warm-temperate evergreen climate. Short exposures to a bit lower absolute minima may be tolerated by sclerophyllous or lauro-sclerophyllous trees, such as *Quercus virginiana* or *Magnolia grandiflora*.

The final values for limiting temperatures used in the envelope model are shown in Table 1. The moisture-balance threshold for all types is 0.6 (except for boreal), and Pmin limits are set such that they never come into play. Apparent temperature thresholds for the three main deciduous forest regions of the Northern Hemisphere were identified in the Overview chapter (Box and Fujiwara, herein), and those for typical temperate and warm-temperate deciduous regions are summarized in Table 2, as a basis for valuation of some envelope limits.

The climate types (except dry temperate) are processed, at each pixel, in order from north to south. This means that, if there is envelope overlap and multiple types are predicted, taking the latter type in the list will correspond to the typical pattern of more southern forest types replacing more northern types as conditions become warmer and growing seasons become longer.

For the boreal and cool-temperate zones, limiting values are fairly straightforward, based on insight from a recent zonation for Northeast Asia (Box and Fujiwara 2012). Boreal climates require Tmax of at least 10°C for at least 1 month (but generally not as many as four, cf Walter 1968). Winter mean temperature (Tmin), though, is <0°C (if not <<0°C) and absolute minimum usually far below 0°C.

For the temperate deciduous forest climates, temperature patterns are somewhat consistent among the three main regions. Cool-temperate climates may have cool or quite cold winters, but summers must be relatively cool, as at higher latitudes and in maritime areas. The upper limit for Tmax is set at 22°C, based on the 21–22°C threshold for typical temperate (see Table 2). This limit depicts almost all of temperate Europe as cool-temperate (Tmax typically 17–20°C), except for quite southern areas. The boreal climate is replaced by cool-temperate when there are at least four consecutive warm months.

Typical temperate climates represent the mid-range and are generally subcontinental, with warmer summers and significantly cold winters. As suggested in Table 2, Tmax should be at least 21°C and at least 5 months should be warm (means above 10°C). If overlap occurs, typical-temperate replaces cool-temperate where these two criteria are met.

Table 1 Quantitative delimitation of temperate and adjacent climates

	Warm Months	Tmax	Tmin		Tabmin
Boreal	<4	>10°C	<0°C		<<0°C
Temperate	≥4				
Cool-temperate		<22°C			
Typical temperate	≥5	>21°C			
Dry temperate (P/PET<0.70)					
Warm-temperate deciduous	≥6	>23°C	<0°C	or	<−15°C
Warm-temperate (evergreen)	≥6	>19°C	>0°C	and	>−15°C
Subtropical (evergreen)	→12	>>15°C	>>0°C	and	>−3°C

These climatic limits define the envelopes used for mapping the various temperate and adjacent climate types shown on the map in Fig. 1. Warm months are defined as consecutive months with mean temperature 10°C or above; temperate-zone trees generally require four consecutive warm months in order to produce viable seeds. Tmax is the mean temperature of the warmest month, and Tmin is the mean temperature of the coldest month. Tabmin is absolute minimum temperature, i.e. the lowest ever measured (or which could reasonably be estimated, in the absence of sufficiently long data records)

The warm-temperate evergreen climate herein is actually a humid temperate warm/cool evergreen type, with a lower Tmax threshold in order to include oceanic climates of the Southern Hemisphere. The delimitation is for forests and woodlands only, with annual moisture balance (precipitation/potential evapotranspiration) of at least 0.6, except for boreal climates (where slowly melting permafrost can compensate scant precipitation during summer). Dry temperate climates include areas of short or open woodland, scrub, grassland and steppe, both continental and mediterranean

The summer warmth threshold for warm-temperate deciduous (23°C) is a compromise between the warmer summers of East Asia and eastern North America, on the one hand, and cooler summers in Europe. This threshold predicts warm-temperate deciduous areas in eastern North America that extend significantly further north than the ranges of most "southern" tree species. On the other hand, this threshold excludes some deciduous forest areas of southern Europe usually denoted as "thermophilous" or "submediterranean". It may be that there can be no strictly climatic definition that will work for all areas of the Northern Hemisphere

Table 2 Apparent temperature thresholds in temperate deciduous forest regions of the Northern hemisphere

	East Asia	Eastern N America	Europe
Typical temperate (deciduous)			
Tmax	21°	21°	21–22°
Warmth index	60	60+	80
Warm months	5	5–6	6
Tmin	–	−10°	−6°
Warm-temperate deciduous			
Tmax	25°	25°	23°
Warmth index	90	90	90
Warm months	6	6–7	7
Tmin	−5°	−4°	−1°

Values are for typical-temperate and warm-temperate deciduous forest regions, as discussed in the main text. The values were estimated from patterns of change in forest type (i.e. occurrence of boundaries) along north–south temperature gradients, as explained in Tables 7–9 in the "Overview" chapter (Box and Fujiwara, herein)

Variables and abbreviations:

Tmax = mean temperature of warmest month; Tmin = mean temperature of coldest month

Warm months = number of consecutive months with mean temperature at least 10°C

Warmth Index is from Kira (1977, 1991), defined as the sum of monthly mean temperatures ≧5°C

All temperatures are in °C. No consistent Tmin threshold was suggested for typical temperate climates in East Asia

Warm-temperate climates, including deciduous, have at least six warm months, as suggested in Table 2. Summer mean temperatures (Tmax) generally reach 25°C in East Asia and eastern North America. As the data in Table 2 show, though, the 'thermophilous' and 'submediterranean' deciduous forests of southern Europe occur at lower summer temperatures of only about 22–23°C. This presents a problem for delimitation and mapping. Use of a Tmax threshold of 25°C, as in East Asia and eastern North America, would eliminate the deciduous forests of southern Europe from consideration as warm-temperate deciduous. The European threshold of 22–23°C, on the other hand, pushes the warm-temperate region much too far north in North America and includes most of lowland Hokkaidō and lowland Chinese Manchuria. Given their low winter mean and minimum temperatures (see Appendix), these areas in East Asia could never be considered warm-temperate. In the end, a compromise threshold of 23°C was chosen for warm-temperate deciduous forests, since this value will show the magnitude of the regional disagreement on the map.

The normal warm-temperate climate, with zonal evergreen broad-leaved forests, is distinguished from warm-temperate deciduous by having mean monthly temperature always >0°C, albeit sometimes barely, and absolute minima not below about −15°C, as discussed above. Summer means generally reach about 25°C or higher, except in some parts of southern Europe (where the climate may, however, already be mediterranean, with drier summers). Even so, the warm-temperate evergreen climate depicted here, for global mapping, is actually a "warm/cool" evergreen climate, with a lower Tmax threshold in order to include oceanic areas in the Southern Hemisphere. The Tmax threshold is set at 19°C (which does not, however, let in

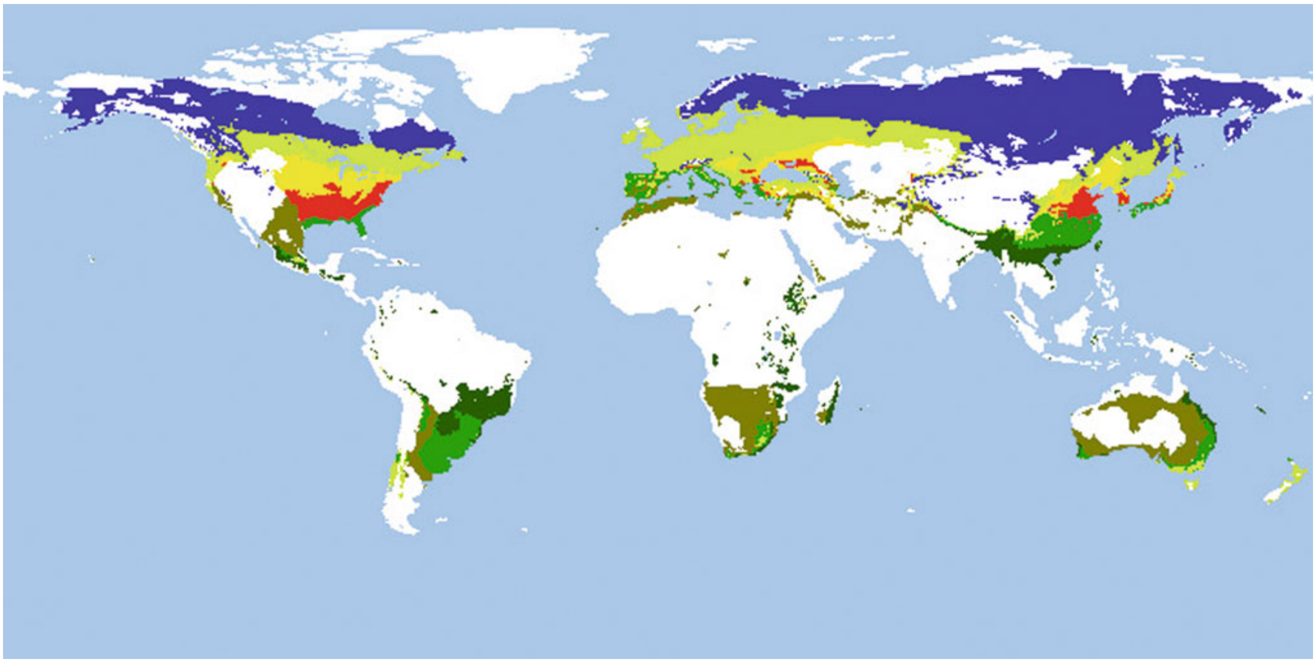


Fig. 1 World temperate and adjacent climatic regions, including potential areas of warm-temperate deciduous forest, as identified from constant-valued limits for selected climatic variables (see main text). All climates are humid, potentially forest climates except the last. Typical temperate represents the middle of the temperate range and is large only in North America. The summer warmth threshold used for warm-temperate deciduous was a compromise, which permits Europe to appear but makes the regions too large in eastern North America and in East Asia. Evergreen broad-leaved (BL) forests are composed mainly of temperate taxa in the warm-temperate zone and of subtropical or tropical taxa in the subtropical zone. Dry warm-temperate is less well defined but is included here to show extensions of warm-temperate forest regions into adjacent drier areas of largely evergreen woodlands and scrub (e.g. Mediterranean, Texas, Australia). Note that no red, blue or yellow is predicted to occur in the Southern Hemisphere. The regions were identified and mapped by ENVMAP (Box, unpublished), based on climatic envelopes described in the main text (Table 1). Mapping resolution is 0.5 × 0.5°, based on the global pixel fields for mean monthly temperature and average monthly precipitation provided by Leemans and Cramer (1990, improved version)

Northern Hemisphere areas too cool for warm-temperate evergreen because winters in those areas are too cold for broad-leaved evergreens).

Finally, the humid subtropical bioclimate replaces warm-temperate types where Tabmin is no longer below about −3°C, assuming that there are six warm months at the very least and that Tmin is well above freezing. Tmax is normally well above 15°C in lowlands, but this threshold is used here in order to accommodate tropical mountain areas that meet the other criteria for subtropical.

The climate type predicted by this envelope model is shown, with the climatic data for the selected sites, in the Appendix (as well as on the map in Fig. 1). Note that, for a given site, the model-generated climate type in the Appendix is not always the same as the interpreted climate type shown in Tables 7–9 of the “Overview” chapter (Box and Fujiwara, herein).

6 Results

The resulting map of projected climatic regions, based on the envelope model, is shown as Fig. 1. Shown are regions of the following climate types, with the expected zonal vegetation type:

Boreal (blue)	Coniferous forests, including larch
Cool-temperate (light green)	Deciduous and mixed forests
Typical temperate (yellow)	Deciduous forests
Dry warm-temperate (olive brown)	Short/open non-forest, mainly evergreen
Warm-temperate deciduous (red)	Warm-temperate deciduous forests
Warm-temperate (rich green)	Evergreen forests, temperate taxa
Subtropical (dark green)	Evergreen forests, [sub]tropical taxa

All forest types are broad-leaved forests except where stated (boreal and cool-temperate mixed).

In general, the pattern shown is as one would expect. Boreal forests appear across the northern higher latitudes, various temperate forests appear over much of the mid-latitudes, and evergreen forests appear to the south, with subtropical (evergreen) forests when frost disappears completely or almost completely, as in southern China, other parts of south Asia, and in south Florida and the Caribbean area. Dry (but not necessarily mediterranean) warm-temperate climates appear adjacent to the warm-temperate evergreen climates but further inland, as in Texas. Note that no red, blue or yellow is predicted to occur in the Southern Hemisphere.

Kira's original concept of warm-temperate deciduous was for somewhat more continental regions with growing seasons warm enough for evergreen broad-leaved forest but with winters too cold for evergreens. Areas of potential warm-temperate deciduous forest (in red) appear especially in the three main regions expected: the interior southeastern USA, parts of mainly mainland East Asia, and parts of southern Europe. In East Asia, the areas include much of northeastern China (i.e. between Beijing and Shanghai, not Manchuria), the southern part of the Korean peninsula, and small parts of Japan. In Japan the red areas appear on the map only along the coasts of Honshū, not in the interior, as was Kira's concept. This is frustrating but is an artifact of the spatial interpolation that produced the spatially averaged 0.5 × 0.5-degree pixel rasters, as was seen by examining the actual pixel values and values at corresponding data sites. At actual meteorological stations, such as Nagano, warm-temperate deciduous forest is predicted as expected (see site results in the book Appendix).

In southern Europe, the main areas of red appear in parts of the central and southern Balkans (especially Bulgaria, not Greece) and in Insubria (south of the Alps). There are also small areas in the western Mediterranean, in interior Iberia (two separated pixels) and along the interior Moroccan-Algerian border in North Africa (two nearby pixels). Expected larger areas of warm-temperate deciduous forest in northern Iberia (cf Garcia-Mijanos et al., herein) were precluded, in the envelope model, by low values of the climatic moisture index, i.e. the region was seen as "too dry". Small areas in Portugal, as described by Costa et al. (herein), were seen by the model as not warm enough in summer (Tmax only 22°C vs threshold of 23°C). Finally, expected areas over large parts of interior peninsular Italy, where *Quercus pubescens* is prominent (cf. Guarino et al., herein, and Cianfaglione, herein), were seen as mild enough for evergreen woods, or too dry in summer, or not warm enough.

Further east, there are also areas of warm-temperate deciduous forest projected in southernmost Russia, just north of the Black Sea and the Greater Caucasus, and in western Turkey, where deciduous oak forests have been described (e.g. Ugurlu and Gökhan Senol 2005). Smaller areas appear across central and southern Turkey and in the inter-Caucasian region (Georgia, Armenia, Azerbaijan). An especially rich deciduous forest on the lower southern flank of the Caucasus in northeastern Georgia was described by Box et al. (2000), but climatic data were not available near the site.

Finally, small areas of possible warm-temperate deciduous forest are also projected in some drier regions. In the northwestern USA, small areas appear in interior northern California and in the Palouse region (mainly grassland), probably representing uplands, as in eastern Washington and Idaho. Unlike the extensive deciduous forests of the west side of Eurasia, these are the only areas shown for the mountainous west side of North America. Small areas also appear in the western Himalaya (and sporadically into the Hindu Kush to the southwest) and in the Tian-Shan divide between Middle Asia and Central Asia (two areas).

The summer warmth threshold for warm-temperate deciduous forests (23°C) was a compromise between the warmer summers of East Asia and eastern North America, on the one hand, and cooler summers in Europe. This compromise permits southern European forests to appear in the warm-temperate deciduous category but makes the regions too large in eastern North America and in East Asia. In particular, the areas of warm-temperate deciduous forest go too far north in Manchuria and eastern North America. On the other hand, this compromise also excludes some deciduous forest areas of southern Europe usually denoted as "thermophilous" or "submediterranean". It may be that there can be no strictly climatic definition that will work for all areas of the Northern Hemisphere.

Conclusions

The mapped results show warm-temperate deciduous regions where expected and where described in some of the other chapters in this book. This suggests fairly strongly that warm-temperate deciduous forest is a consistent response to a particular climatic situation and deserves to be seen as an alternative zonal forest type in some parts of the warm-temperate zones, especially in the transition to typical temperate climates with colder winters.

In order to show possible warm-temperate deciduous forest areas in southern Europe, a compromise threshold value for summer warmth had to be used, which projects warm-temperate deciduous forests too far north in East Asia and especially in eastern North America. This suggests that it may not be possible to quantify warm-temperate deciduous forest areas rigorously but rather that warm-temperate deciduous potentials should be seen as relative to the particular geographic position, i.e. continental east sides versus west sides. In the two east-side regions, the summer warmth threshold (and other apparent limits) do seem to be quite consistent (cf Table 1).

Some other regions of possible warm-temperate deciduous forest are also suggested by the mapping, including small areas in interior Asia, in Turkey, in southernmost Russia and the Caucasus region, in North African mountains, and in the interior northwestern USA. An area is also suggested at the node of the great Asian mountain systems, especially the western Himalaya and the Hindu Kush, but Zobel (personal communication) seemed doubtful that this region (or the Himalaya in general) would have deciduous forests in our warm-temperate sense (cf Zobel and Singh 1997). At any rate, these areas should be studied in more detail. In order to understand the zonal status of such regions, however, especially in mountainous terrain, true local climatic data (i.e. from sites, not pixels) are badly needed.

References

Box, E. O. 1981. *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Tasks for Vegetation Science, vol. 1. The Hague: Dr. W. Junk BV. 258 pp.

Box, E. O. 1986. Some climatic relations of the vegetation of Argentina, in global perspective. Special issue on "Contributions to the Knowledge of the Flora and Vegetation of Northern Argentina". *Veröff. Geobot. Inst. ETH, Stiftung Rübel* (Zürich), pp. 181-216.

Box, E. O. 1994. Global Potential Natural Vegetation: Dynamic Benchmark in the Era of Disruption. In: *Toward Global Planning of Sustainable Use of the Earth – Development of Global Eco-engineering* (Sh. Murai, ed.), pp.77-95. Proceedings of 8th Toyota Conference, November 1994, Mikkabi (Japan). Elsevier, Amsterdam.

Box, E. O. 1995a. Factors determining distributions of tree species and plant functional types. *Vegetatio*, 121:101-116.

Box, E. O. 1995b. Climatic relationships of the forests of East and South-East Asia. In: *Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and Southeast Asia* (E. O. Box et al., eds.), pp. 23-55. Handbook Vegetation Sci., vol. 12/1. Kluwer, Dordrecht.

Box, E. O. 2002. Vegetation analogs and differences in the Northern and Southern Hemispheres: a global comparison. *Plant Ecology*, 163:139-154 (appendix missing! – request from author).

Box, E. O. (herein). Appendix: Climatic Data for Representative Humid-Temperate Sites around the Northern Hemisphere. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O., and J. N. Choi 2003. Climate of Northeast Asia. In: *Forest Vegetation of Northeast Asia* (J. Kolbek et al., eds.), pp. 5-31. Kluwer, Dordrecht.

Box, E. O., D. W. Crumpacker, and E. D. Hardin 1993. A climatic model for plant species locations in Florida. *J. Biogeography*, 20:629-644.

Box, E. O., K. Fujiwara, G. Nakhutsrishvili, N. Zazanashvili, R. J. Liebermann, and A. Miyawaki 2000. Vegetation and landscapes of Georgia (Caucasus), as a basis for landscape restoration. *Bull. Inst. Environm. Sci. Technol., Yokohama National University*, 26:69-102.

Box, E. O., and K. Fujiwara 2004 (2nd ed. 2013). Vegetation Types and their Broad-Scale Distribution. In: *Vegetation Ecology* (E. van der Maarel, ed.), pp. 106-128. Blackwell, Oxford.

Box, E. O., and K. Fujiwara 2010. What else can one do with relevé data: Eastern North America? *Braun-Blanquetia*, 46:139-142.

Box, E. O., and K. Fujiwara 2012. A comparative look at bioclimatic zonation, vegetation types, tree taxa and species richness in Northeast Asia. *Botanica Pacifica* (Vladivostok), 1:5-12.

Box, E. O., and K. Fujiwara (herein). Warm-Temperate Deciduous Forests: Concept and Global Overview. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Box, E. O., and V. Meentemeyer 1991. Geographic Modeling and Modern Ecology. In: *Modern Ecology: Basic and Applied Aspects* (G. Esser and D. Overdieck, eds.), pp. 773-804. Amsterdam: Elsevier.

Cianfaglione, K. (herein). On the potential of *Quercus pubescens* and other *Quercus* species in Camerino. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Costa, J. C., T. Monteiro-Henriques, P. Bingre, and D. Espírito-Santo (herein). Warm-temperate deciduous forests of central Portugal: a mosaic of syntaxa. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Crumpacker, D. W., E. O. Box, and E. D. Hardin 2001. Temperate-subtropical transition areas for native trees and shrubs in Florida: Present locations, predicted changes under climatic warming, and implications for conservation. *Natural Areas Journal*, 21(2):136-148.

Fujiwara, K. 1982. [Phytosociological investigations of evergreen broad-leaved forests of Japan: II. Regional distribution of the evergreen broad-leaved forest]. *Bull. Inst. Environm. Sci. Techn., Yokohama National University*, 8:121-150 (in Japanese).

García-Mijanos, I., J. A. Campos, I. Biurrun, M. Herrera, and J. Loidi (herein). Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Guarino, R., G. Bazan, and B. Paura (herein). Downy-oak woods of Italy: Phytogeographical remarks on a controversial taxonomic and ecologic issue. In: *Warm-Temperate Deciduous Forests around the Northern Hemisphere* (E. O. Box and K. Fujiwara, eds.). Geobotanical Studies.

Kira, T. 1949. Nippon-no shinrin-tai [Forest zones in Japan]. *Ringyō Kaisetsu*, 17:105-141. Nippon Ringyō Gijutsu Kyōkai, Tokyo; reprinted in Kira 1971, pp 105-141 (in Japanese).

Kira, T. 1977. A Climatological Interpretation of Japanese Vegetation Zones. In: *Vegetation Science and Environmental Protection* (A. Miyawaki, ed.), pp. 21-30. Maruzen, Tokyo.

Kira, T. 1991. Forest ecosystems of East and Southeast Asia in a global perspective. *Ecol. Research* (Japan), 6:185-200. Reprinted: *Vegetation Science in Forestry* (E. O. Box et al., eds.), pp. 1-21. Kluwer, Dordrecht.

Leemans, R., and W. P. Cramer 1990. The IIASA Data-Base for Mean Monthly Values of Temperature, Precipitation and Cloudiness on a Global Terrestrial Grid. Working Paper WP-90-41, Biosphere Dynamics Project. Internat. Inst. Applied Systems Analysis, Laxenburg (Austria). 28pp + CD-ROM.

Sakai, A. 1971. [Frost hardiness of evergreen and deciduous broad-leaved trees native to Japan]. *Low Temperature Science* (Japan), series B, 35:15-43 (in Japanese, with English summary).

Troll, C. 1961. Klima und Pflanzenkleid der Erde in dreidimensionaler Sicht. *Die Naturwissensch.*, 48:332-348.

Ugurlu, E., and S. Gökhan Senol 2005. *Quercus*-dominated vegetation units in the Aegean region of Turkey. *Botanika Chronika*, 18 (1):283-291.

Walter, H. 1968. *Die Vegetation der Erde in öko-physiologischer Betrachtung*. Vol. II: Die gemäβigten und arktischen Zonen. Jena: VEB Gustav- Fischer-Verlag. 1002 pp.

Walter, H. 1970. *Vegetationszonen und Klima*. Verlag Eugen Ulmer, Stuttgart. 382 pp (3rd ed. 1977, 309pp).

Walter, H. 1985. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*. 3rd edition. Springer-Verlag, New York. 318 pp (1st edition 1970).

Woodward, I. 1987. *Climate and Plant Distribution*. Cambridge University Press. 174 pp.

Zobel, D. B., and S. P. Singh 1997. Himalayan forests and ecological generalizations. *BioScience*, 47:735-745.

Appendix: Climatic Data for Representative Humid-Temperate Sites Around the Northern Hemisphere, with Climate Type Predicted from an Envelope Model and Mapped

E.O. Box and K. Fujiwara (eds.), *Warm-Temperate Deciduous Forests around the Northern Hemisphere*, Geobotany Studies, DOI 10.1007/978-3-319-01261-2,

	Lat	Elev	Tmax	Tmin	Tabmin	BT	WI	CI	Lwarm	MIy	Pmin	Mapped Type
Hokkaidô												
Asahikawa	43.8	114	20.8	−9.2	−41.0	8.0	60	−50	5	2.01	54	Cool
Obihiro	42.9	38	20.8	−10.0	−38.2	8.2	61	−50	5	1.73	44	Cool
Sapporo	43.0	17	21.4	−5.5	−28.5	8.7	65	−35	6	1.91	59	Typical
Hakodate (S peninsula)	41.8	33	21.9	−3.7	−21.7	9.0	68	−27	6	2.00	57	Typical
Pacific Japan												
Aomori	40.8	3	23.5	−2.7	−24.0	10.0	79	−23	6	2.22	67	WT-decid
Sendai	38.3	39	24.7	0.7	−20.2	12.0	94	−10	6	1.74	38	WT-decid
Fukushima	37.7	67	25.8	0.7	−18.5	12.6	101	−10	7	1.62	51	WT-decid
Mito	36.4	32	25.5	2.7	−12.7	13.5	105	−4	8	1.69	46	EG-BL
Yokohama	35.4	39	26.5	4.6	−8.2	15.0	120	−0.5	8	1.92	58	EG-BL
Matsuyama, Shikoku	33.8	32	27.4	5.1	−8.3	15.6	128	0	8	1.45	44	EG-BL
Interior Honshû and Japan Sea												
Hakone-san	35.2	938	20.3	−1.3	−14.3	9.8	73	−17	6	4.42	53	Cool
Karuizawa	36.3	999	21.2	−4.0	−20.3	8.8	66	−29	5	2.25	28	Typical
Nagano	36.7	418	25.6	−1.3	−17.0	11.9	98	−16	7	1.41	53	WT-decid
Takayama	36.1	560	24.4	−2.4	−25.5	11.2	91	−20	6	2.78	87	WT-decid
Niigata	37.9	2	25.7	1.3	−13.0	12.8	101	−8	7	2.37	93	EG-BL
Tôyama	36.7	9	26.5	2.0	−13.1	13.7	110	−5	8	2.90	123	EG-BL
Matsue	35.4	17	26.8	4.1	−8.5	14.7	118	−1.3	8	2.21	117	EG-BL
Kyôto	35.0	41	26.8	2.9	−11.9	14.2	114	−3	8	1.87	53	EG-BL
Okayama	34.6	3	27.6	3.8	−8.9	15.0	122	−2	8	1.38	29	EG-BL
Tsû	34.7	3	27.0	4.4	−7.8	15.1	122	−0.7	8	1.92	47	EG-BL
Kôbe	34.7	58	27.8	4.7	−7.0	15.7	128	−0.2	8	1.50	39	EG-BL
Hiroshima	34.4	4	26.7	3.9	−8.6	14.6	117	−1.6	8	1.80	46	EG-BL
Kyûshû to Okinawa												
Fukuoka	33.6	3	26.9	5.2	−8.1	15.5	126	0	8	1.79	70	EG-BL
Nagasaki	32.7	27	27.4	6.3	−4.3	16.4	137	0	9	2.04	75	EG-BL
Kagoshima	31.6	4	27.3	6.9	−6.7	17.0	144	0	9	2.24	79	EG-BL
Yakushima	30.4	36	27.4	11.1	−0.2	19.3	171	0	12	3.53	149	Subtropical
Naze, Amami Islands	28.4	3	28.1	14.2	3.1	21.1	193	0	12	2.40	151	Subtropical
Naha, Okinawa	26.2	28	28.2	16.0	3.4	22.2	207	0	12	1.62	108	Subtropical
Taiwan												
Taipei (northern)	25.0	8	28.4	15.0	−2.0	21.9	203	0	12	1.58	76	Subtropical
Tainan (central)	23.0	13	27.9	17.0	2.4	23.3	220	0	12	1.32	15	Subtropical
NE Siberia												
Sredne-Kolymsk	67.5	23	13.6	37.6	57.9	3.1	19	−229	2	0.63	5	Boreal
Yakutsk/Lena	62.1	102	19.0	42.5	64.0	5.1	36	−221	3	0.48	4	Boreal

	Lat	Elev	Tmax	Tmin	Tabmin	BT	WI	CI	Lwarm	MIy	Pmin	Mapped Type
Okhotsk-Kamchatka												
Okhotsk	59.4	6	13.1	22.5	45.0	3.4	20	−136	2	1.10	6	Boreal
Klyuchi (E Kamchatka)	56.3	30	14.5	−16.2	−48.3	4.5	28	−98	3	1.43	27	Boreal
Petropavlovsk-Kamchatsk	53.0	102	12.5	−8.7	−36.3	4.0	21	−64	2	1.98	47	Boreal
Amur-Primorye												
Nikolayevsk-na-Amurye	53.1	47	16.7	−23.6	−47.0	5.1	35	−124	4	1.16	18	Cool
Aleksandrovsk-Sakhal	50.9	16	16.4	−18.2	−37.0	5.4	35	−91	4	1.34	22	Cool
Blagoveshchensk	50.3	132	21.5	−23.9	−45.0	7.3	57	−114	5	0.97	3	Cool
Khabarovsk	48.5	86	21.2	−21.8	−43.0	7.7	59	−100	5	1.11	7	Cool
Yuzhnoye (S Sakhalin)	46.3	21	17.4	−8.3	−24.0	6.2	42	−52	4	1.90	24	Cool
Nikolsk-Ussuriysk	43.8	46	21.1	−19.8	−36.8	7.9	59	−85	5	1.16	6	Typical
Vladivostok (Primorye)	43.1	138	20.3	−13.7	−31.0	7.5	56	−63	4	1.39	10	Cool
Korea												
Hyesan (N Korea)	41.4	714	20.6	−16.7	−35.8	7.7	58	−74	5	1.13	5	Cool
Kimchaek (N Korea)	40.7	19	22.1	−5.8	−23.8	9.1	70	−33	6	1.21	13	Typical
Pyongyang (N Korea)	39.0	36	24.3	−7.8	−30.0	10.9	90	−36	6	1.40	11	Typical
Seoul Airport (Korea)	37.6	18	25.3	−3.6	−24.4	12.0	100	−21	7	1.92	21	WT-decid
Ulleung-Do (East Sea)	37.5	221	24.2	0.8	−13.6	12.2	95	−9	7	2.06	71	WT-decid
Daegu (Korea)	35.9	58	26.3	−1.4	−20.2	12.9	108	−14	7	1.28	20	WT-decid
Pusan (S Korea)	35.1	69	25.8	2.4	−14.0	14.1	113	−4	8	1.75	29	EG-BL
Mokpo (S Korea)	34.8	53	26.2	1.1	−14.2	13.4	109	−7	8	1.39	34	EG-BL
Jeju-Do (S Korea)	33.5	22	26.2	4.9	−6.0	14.9	119	0	8	1.56	49	EG-BL
Manchuria (Chinese)												
Yitulihe (Da Xingan L.)	50.5	994	16.3	−28.8	−50.2	4.8	33	−148	3	1.07	4	Boreal
Hingan (Da Xingan Ling)	48.8	982	17.3	−27.1	−45.7	5.1	37	−135	3	1.40	5	Boreal
Hailar (Da Xingan Ling)	49.2	650	20.2	−27.3	−49.3	6.4	50	−134	4	0.69	4	Cool
Qiqihar (W Manchuria)	47.4	150	23.3	−19.6	−38.0	8.6	69	−88	5	0.71	2	Typical
Harbin (Heilongj.)	45.7	151	23.1	−19.6	−42.4	8.7	69	−87	5	0.92	3	Typical
Changchun (Jilin)	43.9	216	23.2	−16.6	−36.5	9.0	73	−75	5	1.02	4	Typical
Shenyang (Liaoning)	41.8	45	24.7	−12.3	−33.1	10.2	87	−55	5	1.09	5	Typical
Dalian (S Liaoning)	38.9	97	24.2	−5.0	−21.1	11.2	92	−28	6	0.92	7	WT-decid
China (northern)												
Beijing	39.9	52	26.1	−4.5	−27.4	12.6	107	−25	7	0.83	3	WT-decid
Qingdao (Shandong)	36.1	79	25.2	−1.3	−17.6	12.3	101	−15	7	0.95	9	WT-decid
Xian (Shaanxi)	34.3	412	27.0	−0.6	−20.6	13.7	116	−12	7	0.72	6	WT-decid
Tianshui (SE Gansu)	34.6	1174	22.8	−2.3	−14.1	11.2	89	−18	7	0.81	3	Typical
China (southern)												
Xuzhou (Jiangsu)	34.3	4	27.3	−0.2	−18.3	14.3	122	−11	7	0.93	15	WT-decid
Nanjing (Jiangsu)	32.0	15	27.9	2.3	−13.8	15.4	129	−4	8	1.11	31	EG-BL
Shanghai	31.2	12	27.6	3.3	−12.1	15.5	128	−2.3	8	1.25	37	EG-BL

(continued)

	Lat	Elev	Tmax	Tmin	Tabmin	BT	WI	CI	Lwarm	MIy	Pmin	Mapped Type
Wuhan (Hubei)	30.6	23	28.9	3.5	−13.0	16.6	141	−1.5	9	1.23	29	EG-BL
Hangzhou (Zhejiang)	30.2	5	28.6	4.1	−10.5	16.2	136	0.9	8	1.51	54	EG-BL
Wenzhou (Zhejiang)	28.0	20	28.3	7.8	−5.7	18.1	157	0	10	1.60	43	EG-BL
Fuzhou (Fujian)	26.1	20	29.0	11.1	−6.0	20.0	180	0	12	1.17	38	EG-BL
Guangzhou (Guangdong)	23.1	18	28.5	13.5	−2.0	21.9	203	0	12	1.29	30	Subtropical
SW China												
Chengdu (Sichuan)	30.7	498	25.8	5.8	−6.0	16.4	137	0	9	0.99	6	EG-BL
Chongqing	29.6	259	29.2	8.1	−3.1	18.8	165	0	9	0.99	18	EG-BL
Kunming (Yunnan)	25.0	1893	19.9	8.4	−7.0	14.9	119	0	10	1.12	11	EG-BL
Simao (S Yunnan plat.)	22.8	1300	22.5	12.8	−2.5	18.6	163	0	12	1.35	14	Subtropical
Northern Europe												
Kiruna (N Sweden)	67.8	442	12.3	−13.5	−32.7	3.3	17	−97	2	1.39	22	Boreal
Trondheim (W Norway)	63.4	115	14.4	−3.2	−26.0	5.6	33	−34	3	1.75	42	Boreal
Bergen (W Norway)	60.4	39	14.6	1.2	−20.4!	7.4	41	−13	4	3.73	97	Cool
Helsinki (Finland)	60.3	51	17.0	−6.6	−36.0	6.2	41	−47	4	1.28	34	Cool
Tallinn (Estonia)	59.4	30	16.6	−5.7	−32.0	6.3	41	−42	4	1.15	23	Cool
Riga (Latvia)	57.0	15	17.7	−5.0	−35.0	7.1	49	−37	5	1.06	23	Cool
Uppsala (Sweden)	59.9	21	16.6	−4.6	−39.5	6.3	42	−40	4	1.08	25	Cool
Göteborg (S Sweden)	57.8	20	16.5	−1.3	−26.0	7.7	50	−20	5	1.35	38	Cool
København (Denmark)	55.7	22	17.1	−0.5	−24.2	8.0	53	−19	5	1.04	34	Cool
Edinburgh (Scotland)	55.9	134	14.8	2.9	−17.0	8.4	46	−5	5	1.13	38	Cool
Greenwich (London)	51.5	7	17.1	4.0	−14.1!	10.0	61	−1.9	6	0.98	38	Cool
Berlin-Tempelhof AP	52.5	50	18.6	−0.9	−31.0	9.0	64	−17	5	0.95	32	Cool
Hannover (N Germany)	52.5	56	17.5	0.8	−25.0	8.9	59	−12	5	1.03	37	Cool
Krakow (S Poland)	50.1	213	19.4	−3.0	−26.6	9.0	66	−23	5	1.06	34	Cool
Praha (Czechia)	50.1	197	18.0	−2.7	−27.1	8.3	59	−24	5	0.87	23	Cool
Frankfurt/Main (Germany)	50.1	109	19.0	0.2	−28.0	9.8	69	−11	5	1.01	37	Cool
Stuttgart (SW Germany)	48.8	314	19.2	0.3	−25.0	9.9	69	−11	6	1.05	35	Cool
Freiburg (SW Germany)	48.0	269	20.7	1.8	−21.7	11.3	81	−6	7	1.45	47	Cool
Paris-Le Bourget	49.0	66	18.7	2.6	−17.0	10.6	72	−5	7	0.94	37	Cool
Dijon (Bourgogne)	47.3	222	19.8	1.7	−22.0	10.4	73	−8	6	1.10	43	Cool
Wien (Vienna, E Austria)	48.2	203	19.6	−1.4	−22.6	9.6	71	−17	5	1.02	37	Cool
Innsbruck (Tirol, W Aus)	47.3	581	18.2	−2.3	−30.0	9.1	66	−19	5	1.44	39	Cool
Genève (W Switzerland)	46.2	416	18.7	−0.6	−18.4	9.1	62	−14	5	1.46	51	Cool
Lyon (Rhône/France)	45.7	200	20.5	2.1	−24.6	11.0	79	−7	7	1.18	41	Cool
Western Mediterranean												
Trento (N Italy)	46.1	312	22.8	0.8	−16.5!	12.4	97	−8	7	1.35	47	Typical
Torino (NE Italy)	45.2	301	22.7	0.2	−16.2!	11.8	92	−10	7	1.22	40	Typical
Lugano (Ticino, S Switz)	46.0	275	21.6	2.6	−14.0	11.9	87	−5	7	2.41	63	EG-BL
Milano (N Italy)	45.4	107	23.9	1.1	−16.2!	12.7	100	−8	7	1.31	58	EG-BL

	Lat	Elev	Tmax	Tmin	Tabmin	BT	WI	CI	Lwarm	MIy	Pmin	Mapped Type
Avignon (Rhône/S France)	43.9	20	23.4	5.2	−16.0	14.0	107	0	7	0.75	22	EG-BL
Montpellier (S France)	43.6	80	23.0	6.0	−15.0	14.1	109	0	7	0.88	27	EG-BL
Nice (Provence)	43.6	4	22.9	7.3	−7.5	14.8	118	0	9	0.92	18	EG-BL
Toulouse (S France)	43.6	152	21.2	4.6	−19.2	12.5	91	−0.4	7	0.92	45	Typical
Marseille (Provence)	43.4	6	22.8	6.5	−16.8	14.3	111	0	8	0.69	15	EG-BL
Firenze (Toscana)	43.8	40	24.9	5.4	−10.6	14.7	116	0	8	0.97	34	EG-BL
A Coruña (Galicia)	43.4	58	18.8	10.2	−5.5	14.1	109	0	12	1.20	28	Cool
Bilbao (N Spain)	43.3	34	20.0	8.8	−10.8!	14.0	108	0	9	1.47	54	EG-BL
Vitoria (N Spain)	42.8	550	19.2	4.7	−17.8	11.5	79	−0.3	6	1.29	35	Cool
Leon (N Span. meseta)	42.6	913	19.4	2.8	−17.4	10.6	72	−4	6	0.87	17	Cool
Burgos (N Span. meseta)	42.4	894	18.8	2.4	−22.0	10.1	67	−6	6	0.92	23	Cool
Soria (Spanish meseta)	41.8	1080	20.0	2.7	−16.4	10.5	71	−5	6	0.86	27	Cool
Valladolid (meseta)	41.6	734	21.4	3.4	−18.0!	12.0	86	−2.6	7	0.53	11	Typical (dry)
Salamanca (meseta)	41.0	782	21.6	3.9	−18.1!	12.1	86	−1.5	7	0.57	10	Typical (dry)
Segovia (central mtns.)	40.9	1005	21.5	3.2	−13.2	11.5	82	−3.4	6	0.72	14	Typical
Madrid (meseta)	40.4	657	24.8	5.0	−10.1	13.9	107	0	7	0.52	10	WT-decid (dry)
Cuenca (meseta)	40.1	945	22.1	3.6	−17.8	11.9	85	−2.3	6	0.77	15	Typical
Barcelona (Cataluna)	41.4	175	24.3	9.2	−6.7	16.2	135	0	11	0.62	28	EG-BL
Roma (Italy)	41.9	45	25.0	6.7	−5.4	15.4	125	0	9	0.91	17	EG-BL
Bragança (N Portugal)	41.8	691	21.2	4.6	−12.0	12.2	87	−0.4	7	1.02	12	EG-BL
Lisboa (W Portugal)	38.7	95	22.0	10.6	−1.7	16.0	132	0	12	0.74	4	Mediterranean
Evora (central Portugal)	38.6	321	23.9	8.9	−3.6	15.7	129	0	10	0.68	4	Mediterranean
Córdoba (Andalucia)	37.8	91	27.5	9.0	−8.2	17.6	151	0	10	0.62	1	Mediterranean
Balkan Peninsula												
Cluj-Napoca (Transylvan)	46.8	410	19.2	−4.4	−29.8	9.0	66	−27	5	0.98	24	Cool
Ljubljana (Slovenia)	46.2	385	19.2	−1.1	−23.0	9.3	68	−17	6	2.32	71	Cool
Zagreb (Hrvatska/Croat.)	45.8	163	21.4	−0.1	−30.5	11.1	85	−11	7	1.31	48	Typical
Novi Sad (Serbia)	45.3	80	23.1	−0.2	−26.0	11.8	94	−13	7	0.87	29	WT-decid
Beograd (Serbia)	44.8	132	22.1	−0.2	−25.5	11.7	91	−11	7	0.94	38	Typical
Bucuresti (Romania)	44.4	82	22.9	−2.9	−30.0	11.1	89	−19	7	0.85	32	Typical
Sofiya (Bulgaria)	42.6	586	20.2	−1.1	−27.5	10.1	74	−14	7	0.91	31	Cool
Plovdiv (Bulgaria)	42.1	179	23.3	1.0	−31.5	12.3	97	−8	7	0.72	29	WT-decid
Skopje (N Makedonia)	42.0	238	23.3	0.3	−25.0	12.2	97	−10	7	0.71	28	WT-decid
Split (Dalmatian coast)	43.5	122	25.6	7.4	−11.4!	16.0	132	0	9	0.87	28	EG-BL
Burgas (Black Sea coast)	42.5	16	22.6	2.6	−15.0	12.6	95	−3.9	7	0.76	26	EG-BL
Ioannina (NW Greece)	39.7	466	24.7	5.1	−10.0	14.4	113	0	8	0.41	13	EG-BL
Russia - Caucasus												
Sankt-Peterburg (Russia)	60.0	6	18.4	−8.1	−36.0	6.8	48	−52	5	1.04	25	Cool
Moskva (Russia)	55.7	156	18.5	−10.2	−42.0	7.0	50	−59	5	1.13	29	Cool
Kazan' (E Eur Russia)	55.8	35	19.7	−13.2	−44.0	7.2	53	−73	5	0.83	18	Cool

(*continued*)

	Lat	Elev	Tmax	Tmin	Tabmin	BT	WI	CI	Lwarm	MIy	Pmin	Mapped Type
Kyyiv (Kiev, Ukraine)	50.4	180	20.5	−5.5	−40.0	8.8	69	−37	5	0.97	34	Cool
Rostov-na-Donu (S Russ)	47.2	77	23.0	−5.4	−33.0	10.0	82	−34	5	0.81	34	Typical
Yalta (S Crimea)	44.5	14	23.7	3.8	−14.5	12.9	98	−2.3	7	0.71	27	EG-BL
Sochi (Black Sea)	43.6	50	23.0	5.7	−14.0	14.0	108	0	8	1.93	83	EG-BL
Kutaisi (W Georgia)	42.3	156	23.9	4.3	17.0	14.6	115	−0.6	8	1.54	70	EG-BL
Tbilisi (Georgia)	41.7	404	24.4	0.9	23.0	12.7	101	−9	7	0.66	16	WT-decid (dry)
Western Asia												
Zakataly (Azerbayjan)	41.6	500	24.8	2.9	22.0	13.2	103	−5	7	1.27	35	WT-decid
Istanbul (NW Türkiye)	41.0	40	23.6	5.4	16.1	14.2	110	0	8	0.83	24	EG-BL
Trabzon (N Türkiye)	41.0	35	23.2	7.7	7.2	14.8	118	0	9	0.92	34	EG-BL
Bursa (Marmara Sea)	40.2	101	23.9	5.2	−19.4	14.2	110	0	8	0.81	14	WT-decid
Izmir (W Türkiye)	38.4	25	27.2	8.1	−11.1	17.2	146	0	9	0.66	2	EG-BL
Rasht (N Iran)	37.2	−9	24.8	6.8	−9.0	15.8	130	0	8	1.27	19	EG-BL
Canada (eastern)												
Québec (SE Québec)	46.8	90	19.5	−11.8	−36.7	7.2	54	−64	5	2.15	74	Cool
Ottawa (Ontario)	45.4	79	20.7	−11.1	−38.9	8.3	64	−57	5	1.51	58	Cool
Montréal (S Québec)	45.5	57	21.2	−9.9	−33.9	8.6	67	−51	5	1.77	72	Typical
Halifax (Nova Scotia)	44.6	8	18.9	−3.7	−29.4	8.1	58	−28	5	2.51	93	Cool
Toronto (Ontario)	43.7	116	20.8	−5.1	−32.8	8.8	67	−35	5	1.40	60	Cool
Northeastern USA												
Syracuse, New York	43.1	128	21.7	−4.5	−32.2	9.6	75	−31	6	1.53	63	Typical
Boston, Massachusetts	42.4	6	21.8	−2.6	−27.8	9.8	76	−23	6	1.73	79	Typical
Hartford, Connecticut	41.9	53	23.0	−3.5	−32.2	10.5	84	−24	6	1.73	79	WT-decid
New York (city)	40.8	39	24.3	−0.4	−26.1	11.8	95	−15	7	1.62	79	WT-decid
Pittsburgh, Pennsylvania	40.5	367	23.2	−1.1	−30.0	11.3	90	−16	7	1.36	62	WT-decid
Midwestern USA (northern)												
Madison, Wisconsin	43.1	263	22.4	−8.2	−38.3	9.4	76	−43	6	1.29	32	Typical
Omaha, Nebraska	41.4	399	25.3	−5.5	−35.6	11.5	96	−29	7	1.04	19	Typical
Indianapolis, Indiana	39.7	243	24.0	−2.9	−32.8	11.6	94	−19	7	1.46	62	WT-decid
Cincinnati, Ohio	39.1	232	24.5	−1.4	−27.2	12.5	103	−15	7	1.42	65	WT-decid
Kansas City, Missouri	39.3	312	25.7	−2.5	−30.6	12.2	101	−18	7	1.28	32	WT-decid
St. Louis, Missouri	38.7	174	26.3	−0.4	−30.6	13.3	112	13	7	1.24	55	WT-decid
Lexington, Kentucky	38.0	298	24.6	0.5	−29.4	12.8	105	10	7	1.49	63	WT-decid
Southern Appalachians												
Burkes Garden (Virginia)	37.1	1006	19.4	−1.2	−32.8	9.3	68	−18	5	1.95	74	Cool
Banner Elk (N Carolina)	36.2	1143	19.1	0.5	−35.0	9.9	70	−12	6	2.20	87	Cool
Bluefield (W Virginia)	37.3	881	21.3	−0.7	−29.4	11.2	86	−13	7	1.48	64	Typical
Waynesville (N Carolina)	35.5	810	21.4	2.6	−30.0	11.9	89	−6	7	1.67	70	Typical

	Lat	Elev	Tmax	Tmin	Tabmin	BT	WI	CI	Lwarm	MIy	Pmin	Mapped Type
South-Atlantic USA												
Baltimore, Maryland	39.3	4	25.7	1.5	−21.7	13.5	110	−8	7	1.35	76	WT-decid
Charlottesville, Virg.	38.0	265	24.7	2.0	−23.3	13.6	110	−7	7	1.45	74	WT-decid
Raleigh-Durham, N Car.	35.9	132	25.6	4.7	−22.8	15.3	123	−0.3	9	1.28	68	WT-decid
Columbia, S Carolina	34.0	74	27.1	7.9	−18.9	17.7	152	0	9	1.08	58	WT-decid
Athens, Georgia	33.9	246	26.5	5.7	−20.0	16.5	138	0	9	1.27	76	WT-decid
Cape Hatteras, N Carol.	35.3	2	25.6	7.7	−14.4	16.7	140	0	9	1.44	87	EG-BL
Charleston, S Carolina	32.8	3	27.7	10.1	−12.2	19.0	168	0	12	1.09	61	EG-BL
Savannah, Georgia	32.1	15	27.6	10.5	−16.1	19.3	171	0	12	1.08	50	EG-BL
Tallahassee (NW Florida)	30.4	25	27.3	11.5	−18.9	19.8	177	0	12	1.29	71	WT-decid
Pensacola (NW Florida)	30.5	36	27.5	11.4	−15.0	19.9	179	0	12	1.30	93	EG-BL
Gainesville (N Florida)	29.6	29	27.3	12.7	−14.4	20.6	187	0	12	1.08	44	EG-BL
Tampa (mid-Gulf Florida)	28.0	8	27.9	15.9	−7.8	22.2	206	0	12	0.96	43	EG-BL
Miami (S Florida)	25.8	3	28.2	19.8	−2.8	24.2	231	0	12	1.03	48	Subtropical
Interior South (USA)												
Nashville, Tennessee	36.1	180	26.7	4.3	−27.2	15.7	129	−0.7	8	1.28	63	WT-decid
Little Rock, Arkansas	34.7	78	27.7	3.9	−25.0	16.5	139	−1.1	9	1.31	78	WT-decid
Oxford, Mississippi	34.4	116	26.7	5.2	−25.0	16.4	137	0	9	1.39	70	WT-decid
Montgomery, Alabama	32.3	67	27.6	8.1	−20.6	18.3	160	0	10	1.23	61	WT-decid
Mobile, S Alabama	30.7	66	27.3	10.6	−18.3	19.4	173	0	12	1.40	84	WT-decid
Biloxi, S Mississippi	30.4	5	27.8	10.9	−17.2	19.8	177	0	12	1.31	80	EG-BL
Baton Rouge, Louisiana	30.5	20	27.8	11.3	−16.7	20.0	180	0	12	1.25	83	EG-BL
Texas-Oklahoma												
Tulsa, Oklahoma	36.2	206	28.5	2.2	−26.7	15.8	133	−4	8	1.06	36	WT-decid
Dallas, N Texas	32.8	134	30.0	7.2	−22.2	19.0	168	0	9	0.82	47	WT-decid
Waco, central Texas	31.6	157	30.0	7.8	−20.6	19.4	173	0	10	0.70	42	WT-decid
Austin, central Texas	30.3	193	29.3	9.7	−18.9	20.2	182	0	11	0.68	46	WT-decid
Houston, SE Texas	30.0	30	28.7	11.2	−15.0	20.5	186	0	12	0.98	72	EG-BL
Mexico (upland)												
Xilitla, Sa. Madre Orien.	21.4	1035	24.5	15.6	1.0	20.9	191	0	12	2.06	37	Subtropical

The data and abbreviations for this larger set of sites are as in the "Overview" chapter (see Tables 7, 8 and 9; Box and Fujiwara, herein), with the addition of annual biotemperature (BT: sum of positive mean monthly temperatures, divided by 12) and the average precipitation of the driest month (Pmin). Unlike the tables in the "Overview" chapter, however, the climate types shown here are those predicted by the envelope model (Table 2) and mapped (Fig. 1) in the last chapter, "Projecting Warm-Temperate Deciduous Forest Areas" (Box, herein).