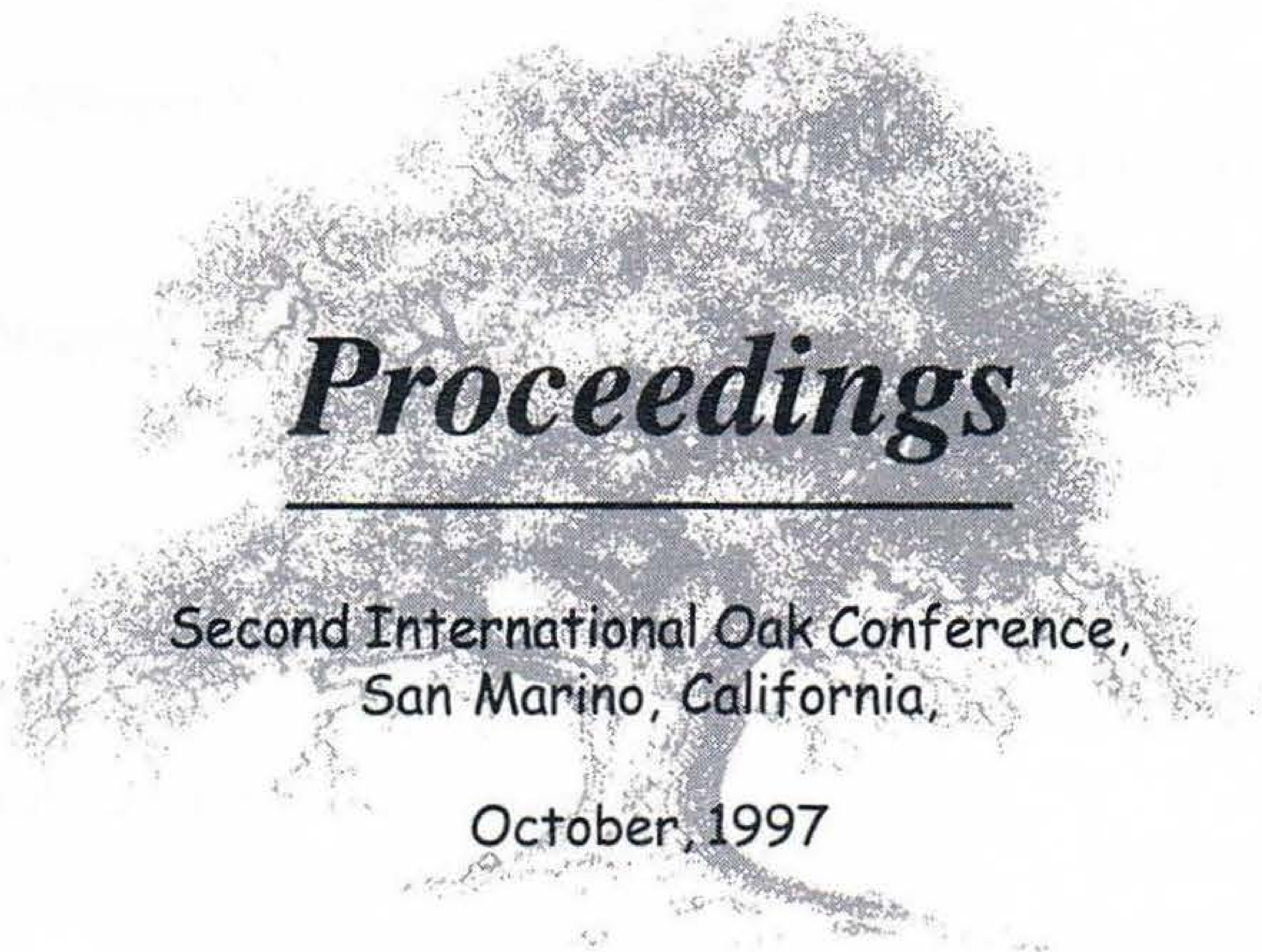
Proceedings

Second International Oak Conference
San Marino, California
October, 1997

Journal #9

International Oaks
The Journal of the International Oak Society



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About the cover

Participants in the Second International Oak Conference hike through scenic old groves of the island endemic oak species* Quercus pacifica *Nixon and C.H. Mull. on Santa Cruz Island, off the coast of southern California near Santa Barbara, on Friday, 24 October 1997.

Cover Illustration:

Photograph © Guy and Edith Sternberg

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Anyone interested in joining the International Oak Society or ordering information should contact Richard Jensen at the membership office.

Membership dues are U.S. $15 per year, and benefits include publications, conferences, and exchanges of seeds and information among members from 30 nations on six continents.

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Introduction to Proceedings

by Amy Larson
Conference Chairperson
California, USA

On behalf of the Board of Directors of the International Oak Society, it is my privilege to introduce the Proceedings of the Second International Oak Conference. This conference was held on October 21-23, 1997 at the beautiful Huntington Botanical Gardens and Library in San Marino, California, USA.

The International Oak Society, the Huntington, the California Oak Foundation, and the University of California Cooperative Extension were honored to host more than 100 people from 12 countries — possibly the largest and most diverse group of oak experts and enthusiasts ever assembled in the world. Participants enjoyed oral presentations, a poster session, the triennial seed exchange, a wine tasting from oak barrels, and a presentation on oak lore. Those who opted to take a field trip traveled by land and/or by sea to study native California oaks and collect their seeds.

From its humble beginnings as an informal seed exchange organization, the International Oak Society has grown to more than 500 members from nearly three dozen nations. The Society began to formalize itself at the First International Oak Conference, which was held in 1994 at the Morton Arboretum in Illinois. An interim Board of Directors, elected by the membership, incorporated the International Oak Society and obtained its nonprofit organization status.

Why all this fanfare around oaks? Traditionally, people went into forests to hunt and gather food and to celebrate the abundant resources that the forests provide. Today, International Oak Society members collectively study *Quercus* throughout the world; collect, exchange, propagate, and cultivate oak seeds; and share information about this diverse genus with one another and the botanical community. These activities are dwarfed, however, by the deep and global connections made between people, both personally and professionally, through the love of oaks.

It is this human perspective of our organization that is most critical. Sadly, forests and woodlands in many parts of the world — to their detriment — are being over-harvested for wood products and are being cleared for development or agriculture. Oak Society members recently helped rally support for a local initiative to protect oaks in Santa Barbara County, California. We hope that the International Oak Society and its many members will continue to spearhead efforts to preserve and enhance oaks throughout the world, and catalyze public opinion on issues related to oaks and oak conservation.

In the meantime, I invite you to go into an oak forest, and, for a change, do nothing. Stand still. Listen to water droplets falling into streams trickling into rivers, bays, and oceans. Remember that these forests filter our water and provide sustenance. Breathe the fresh air deep into your lungs. Be cool. Imagine all of the people who for centuries have felt renewed by doing absolutely nothing under a tree.

Be proud of your efforts on behalf of oaks.

I would like to acknowledge these helping hands to the Second International Oak Conference ...

Recognition and Thank You

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Huntington Botanical Gardens - Conference Host

- Jim Folsom, Director
- Jerry Turney
- Kathy Musial
- Danielle Rudeen
- Peggy Kelley
- Evie Cutting
- Fernando Montes de Oca

...and everyone at the Huntington who made this conference possible.

California Oak Foundation - Conference Registration

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- Mitch Weltbach

...and all of our presenters and those who contributed seeds to the seed exchange.

Amy Larson - Conference Chairperson
December 2, 1998

Editor's Note

by The Editorial Committee
Proceedings
International Oak Society

This issue of *International Oaks* is the Proceedings of the Second International Oak Conference, held in October, 1997, in San Marino, California. The following pages contain the papers that were presented at that meeting. It has taken many months to get these Proceedings published and for that we apologize, but we hope the wait will prove to be worth it.

Part of the reason for the delay is that we had all of the papers reviewed by external reviewers prior to publication. Originally, our goal was to establish a rigorous peer review process to insure that everything in these Proceedings met the standards of a scientific publication. But it soon became clear that it was neither possible nor appropriate to apply such criteria to all of the manuscripts. Many of the papers presented at the Conference were never intended to be scientific publications. They reported on arboreta collections, or summarized work in a particular area of oak taxonomy or management. And others were thought pieces that speculated about such things as global climate change or isoprene emissions, and what the long-term implications might be for the genus *Quercus*. Only a handful of the papers actually reported on research projects. The Editorial Committee therefore decided to set different review criteria for different types of papers.

For research papers, we required the authors build on previous research in the subject area and demonstrate that they had utilized appropriate scientific methods. For other papers, we sought to ensure that they were informative, well written and of interest to the readers of this Proceedings. We are pleased with this process and the results and hope that you, the readers, are pleased also.

We especially want to thank the following individuals for their time and energy in the review process: Hugh Angus, Allen Coombes, Rosi Dagit, Tom Gaman, Richard Jensen, Amy Larson, Rudolph Light, Doug McCreary, Charles Nelson, Mike Reichenbach, Rick Standiford, Guy Sternberg, Kareen Sturgeon, Ted Swiecki, and Jerry Tecklin.

A final note: We did find that even with the common language of English, not everyone in the world spells things quite the same. But instead of Americanizing all of the words that have different spellings, we decided that while (or perhaps "whilst"?) American trees may hybridize, those in the U.K. apparently only hybridise, so we left those spellings as we found them. Enjoy your reading...

Oaks at the Hillier Arboretum

by Allen J. Coombes
Sir Harold Hillier Gardens and Arboretum
Romsey, Hampshire, UK

The Sir Harold Hillier Gardens and Arboretum has long had a tradition for planting oaks. Occupying 184 acres near the village of Ampfield in Hampshire, southern England, it was founded in the early 1950s by Sir Harold Hillier who gave the Gardens to the Hampshire County Council in 1977. Sir Harold was interested in all woody plants but we know that oaks were high among his favourites and in his latter years he collected in many parts of the world, including the southern United States, Mexico, Japan and Korea. The oaks now form one of our 11 National Collections and contain some 150 species, about 70 cultivars, and many hybrids.

Some of the more interesting and unusual recent introductions from North America include *Q. acerifolia*, introduced from the type locality in Arkansas by the Morton Arboretum in 1989. It is growing extremely well here and because of its moderate size and splendid autumn colour, could be recommended as an ornamental tree. Oglethorpe oak (*Q. oglethorpensis*), first came to us in 1978 as scions, and after being grafted onto English oak (*Q. robur*), has grown slowly. We also have younger plants from wild-source seed but cool summers here result in frost damage to the young shoots in winter. *Q. myrtifolia*, introduced by Sir Harold from sand dunes on the Gulf Coast of the Florida pan-handle, is surprisingly hardy here.

In the last few years we have introduced many species from Mexico, but as yet these are largely untried outside. Several Mexican species survive here from earlier introductions, however. In 1979, Sir Harold visited Mexico for a few days and was remarkably successful in finding seed. His introductions of *Q. hypoxantha* and *Q. greggii* from Cerro Potosi, were probably the first to this country, and remain very rare, but both species are proving hardy. *Q. hypoxantha* produced several good acorns this year and we will wait with interest to see the progeny of these. It is another of Sir Harold's collections, however, that is causing great interest here. Sir Harold did not actually collect the first introduction of the magnificent Loquat oak (*Q.*

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Hillier Arboretum . . .

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rhysophylla) because in 1978 he received seed from his nurseryman friend in Alabama, Tom Dodd. Lynn Lowrey had collected this above Horsetail Falls, near Monterrey (Nuevo Leon, Mexico). However, Sir Harold visited the site the following year and made another collection. Although only 20 years old, one of these trees is already about 35 ft tall and the largest of this species in Britain. It produced its first acorns a year ago.

While we are actively seeking new hardy oaks from Mexico, another rich area that has been neglected is China. With more than 120 species, relatively few of them in cultivation, there is great opportunity for new introductions. Two particularly interesting evergreen species that have been introduced recently, both by Roy Lancaster, are *Q. longispica*, collected at 3,800 m in W Sichuan, *and Q. monimotricha*, from 2,700 m in NW Yunnan. *Q. longispica* is related to the better known *Q. semecarpifolia*, a large and fairly hardy evergreen tree, which the cultivated plant was originally thought to be. When it started to flower and fruit, however, the remarkably long peduncles showed it to be *Q. longispica*.

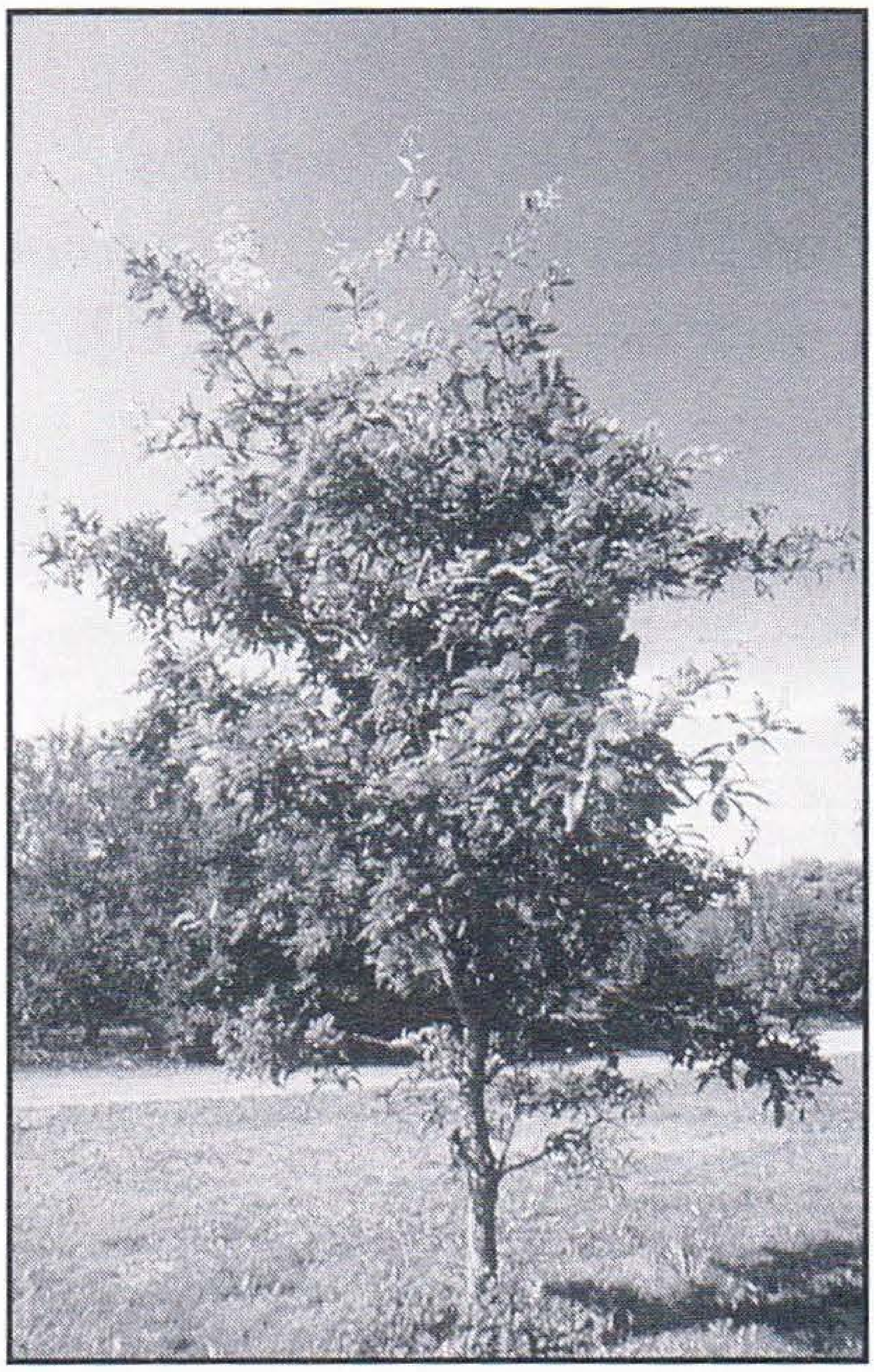

Photo by A. Coombes

Quercus oglethorpensis *W. H. Duncan, a rare oak from the southeastern United States, shown in cultivation at the Sir Harold Hillier Botanic Garden and Arboretum in Hampshire, England.*

Q. monimotricha is the smallest oak we have, making a low mound about a foot tall so far, with small, spine-toothed leaves. An interesting point about these species is that they both produced acorns when young plants, and seem to come true from seed without hybridisation.

Rare in cultivation, probably because of the difficulty in obtaining seed is the Golden oak of Cyprus, *Q. alnifolia*. This is a relative of the European Holm oak, *Q. ilex*, but is restricted to the mountains of Cyprus. A small, evergreen shrubby tree to about 15 ft or so, this very ornamental species is characterised by a mustard yellow felt on the underside of the leaf. Even nearer to home is a shrubby semi-evergreen species, *Q. lusitanica*, from Spain and Portugal. Because of confusion with other species, this is rare in gardens and seed under this name will often produce a large tree. We do appear to have a plant, however, which was received under another name. Eliot Hodgin collected seed in Spain and believed his plant to be a form of *Q. pubescens*, a large, deciduous tree. Harold Hillier, showing typical enthusiasm to

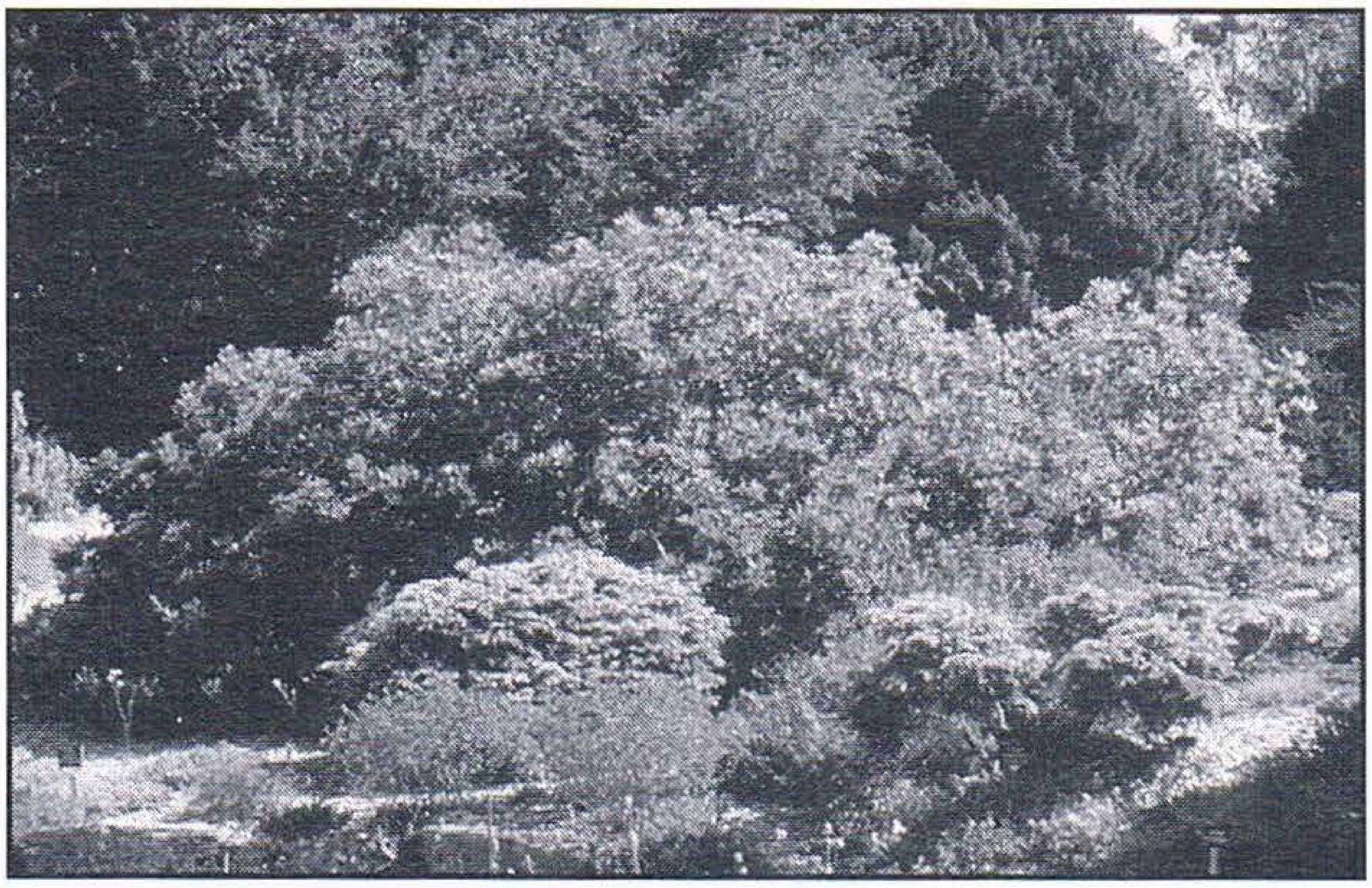

Photo by A. Coombes

Quercus lusitanica *Lam (syn.* Q. fruticosa *Brot.), a shrubby oak species from the Mediterranean region, shown in cultivation (the large mounded plant at center) in front of the Jermyns House at the Sir Harold Hillier Botanic Garden and Arboretum in Hampshire, England.*

obtain a new plant, collected scions from the original introduction and they were grafted. The resulting plant, now about 5 ft tall and 10 ft across, is typical *Q. lusitanica*, and has already borne fruit. It is now being propagated from seed to discover whether it will hybridise with other species.

Knowledge of whether a species will or will not hybridise if raised from seed is important, as collectors are (or should be!) wary of garden collected seed, and most species, given the chance, will probably cross with something else. With the difficulty in propagating oaks vegetatively, it is therefore advantageous if a species can be safely seed-raised from a cultivated plant.

In my opinion, hybrids have great value in gardens, both for their ornamental features and botanical interest. As we all know, many hybrids occur naturally, and as such, they are just as important as their parent species. Some of the work we are doing in Mexico involves raising seedlings of trees that are suspected hybrids. Many other hybrids, of course, only occur as a result of species being brought into contact in gardens, and are only of use, or interest (in botanic gardens at least) if their origin is known. Where an exotic species crosses with a native one, the result may be an increase in vigour, hardiness or both. The hybrid between *Q. pontica* and *Q. robur* (*Q.* x *hickelii*), has the advantage of being much more vigorous and a larger plant than *Q. pontica.* It does not have the large, bold leaves of *Q. pontica*, but the original tree at the Arboretum des Barres in France, shows that it can make a fine specimen.

Other species frequently grown in Europe that commonly cross with *Q. robur* include *Q. macranthera and Q. canariensis*. It is not too difficult to spot these in the first generation but back crosses would be not as distinct. If an exotic oak hybridises here it is usually easy to

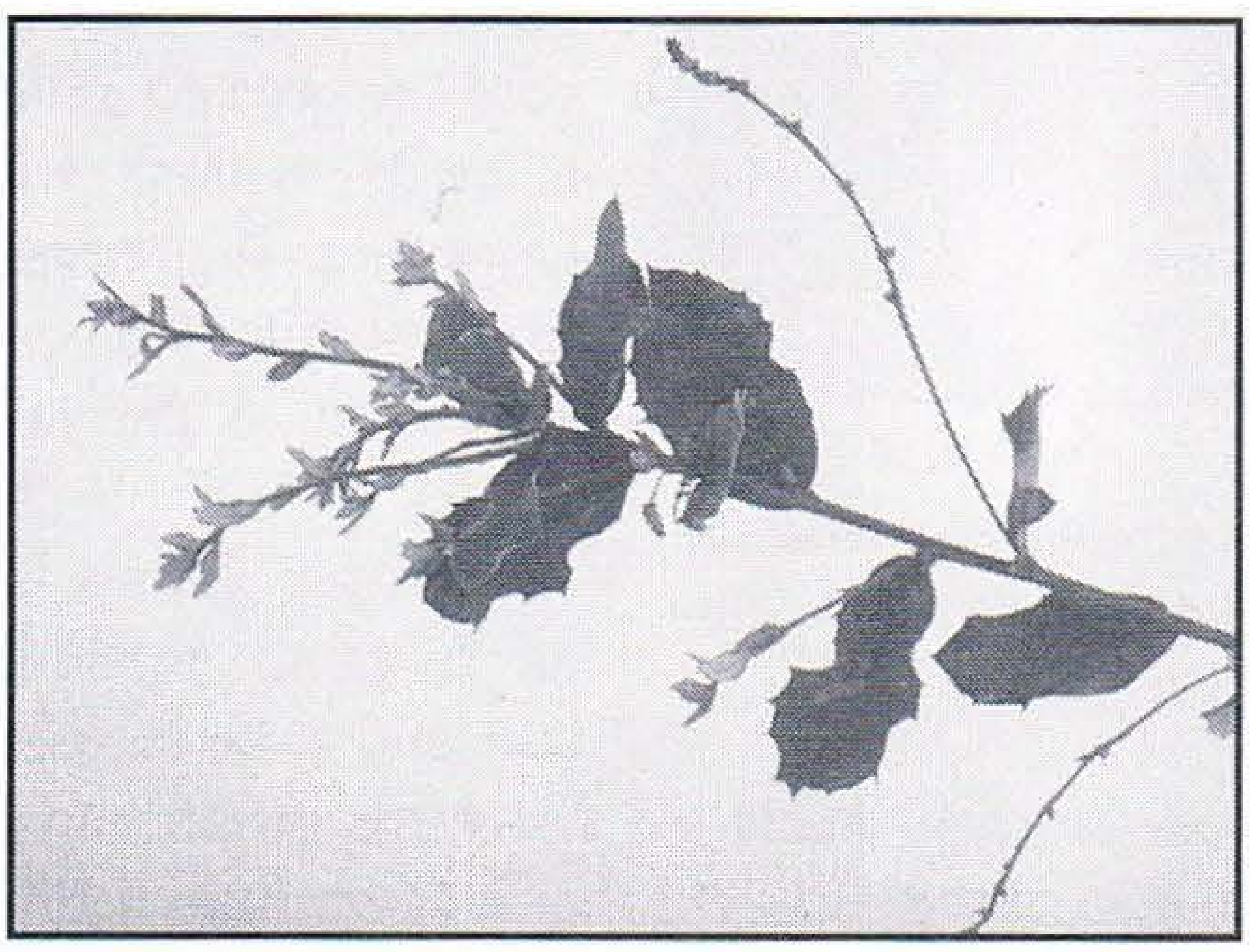

Photo by A. Coombes

Quercus longispica *A. Camus showing new spring growth and the long flower catkins for which the species was named.*

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determine the other parent. The white oaks will normally cross with *Q. robur*, except for the relatives of *Q. cerris*. There has been some debate in this country on whether *Q. robur* and *Q. cerris* cross, but I have yet to see a specimen that definitely proves it, and as both are very common trees in this country, it seems unlikely that they do hybridise. We recently raised seedlings here of several exotic species which bore fruit. Q. *macrocarpa* appears to have produced only hybrids with *Q. robur*. *Q. castaneifolia*, on the other hand, crossed exclusively with *Q. cerris*.

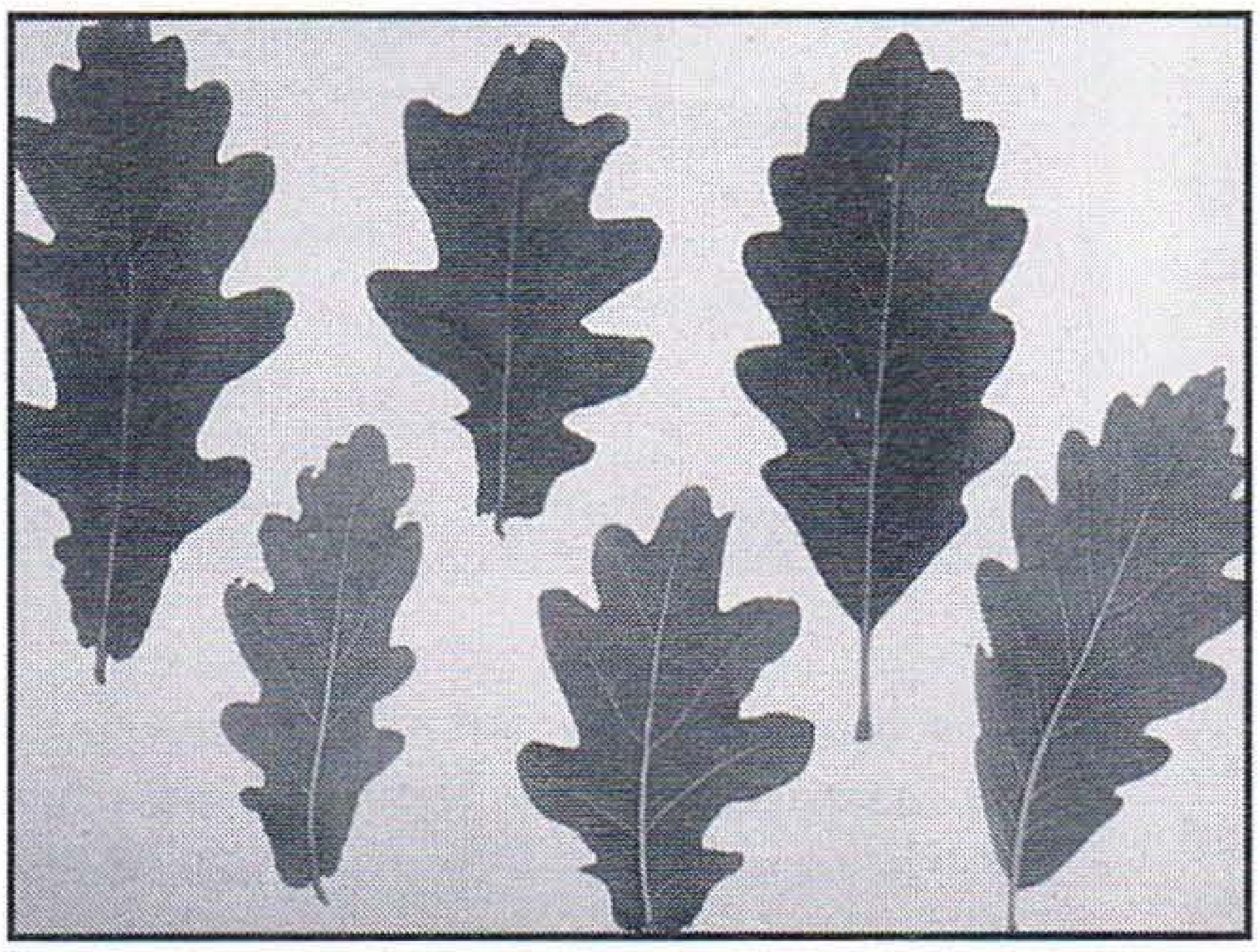

Photo by A. Coombes

Quercus macranthera xQ. robur *(left) with the parent species* Q. robur *L. (center) and* Q. macranthera *Fisch, & C.A. Mey. ex. Hohen (right).*

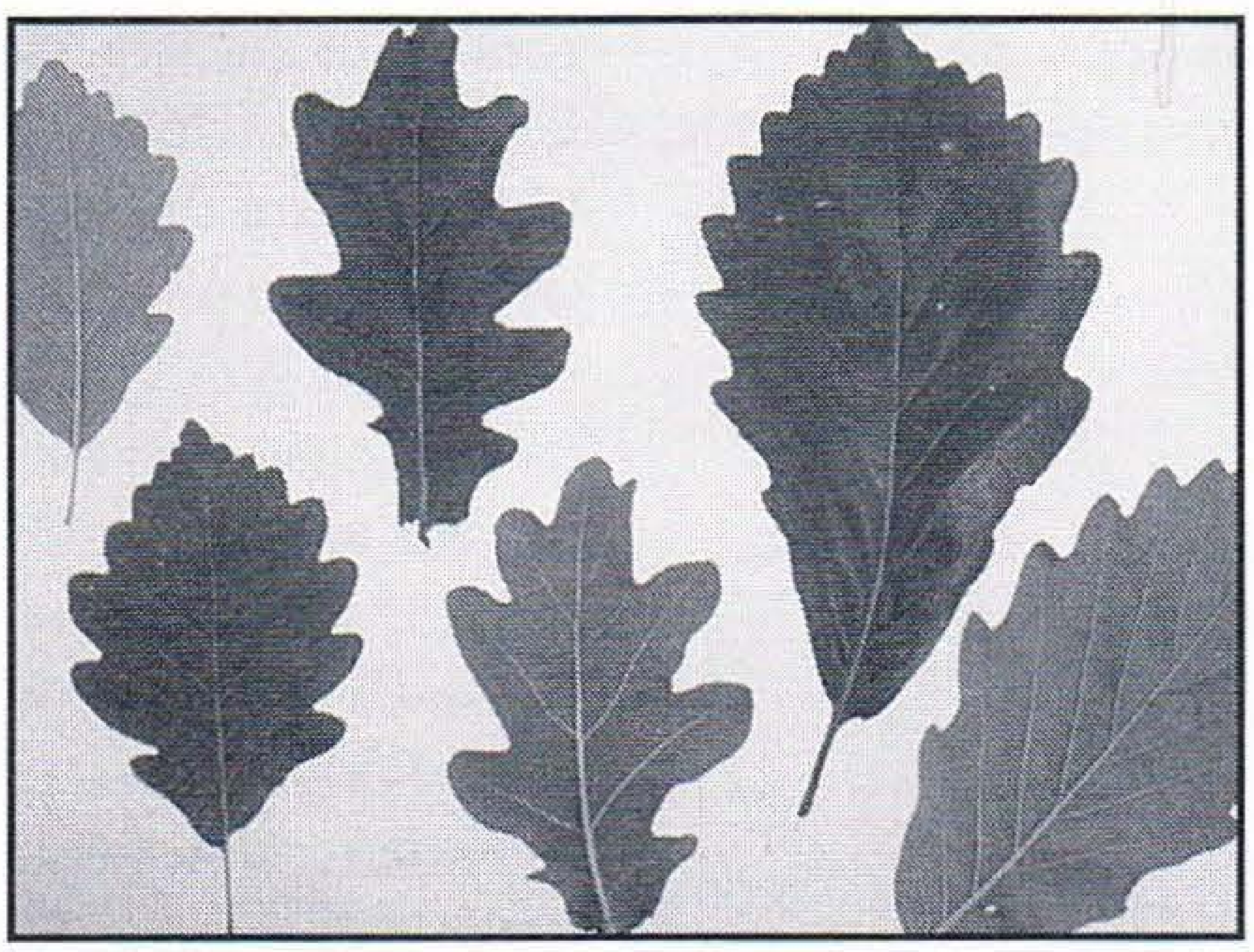

Photo by A. Coombes

Quercus canariensis xQ.robur *(left) with parent species* Q. robur L. *(center) and* Q. canariensis *Willd. (syn.* Q. mirbeckii *Durieu) (right).*

Seed received from North American gardens may give plants which are more difficult to determine. A plant originally grown as *Q. macrocarpa* here seems to be a hybrid with *Q. alba*, while a tree originally called *Q. hypoleucoides* appears to be a hybrid with *Q. emoryi*. We are already getting hybrids of Mexican oaks arising in gardens. Indeed there is one probable hybrid that has been in cultivation for many years. *Q. warburgii* was described in 1939 from a plant that had been grown in this country since 1870. It was raised from seed received from Italy as *Q. rugosa* but was later thought to be *Q. obtusata*. In my opinion it is a hybrid of a Mexican species with *Q. robur*. Judging by the long fruiting peduncles produced by *Q. warburgii*, I suspect *Q. rugosa* of being the other parent. We should therefore expect any seed of cultivated source to give hybrids, unless we know there is a reason to doubt this. A specimen sent to me recently of *Q. rhysophylla* grown in an English garden, and said to be of wild source seed, made me doubt the origin and I eventually discovered that it came from a cultivated source in Texas. It may not be possible to determine the other parent of this tree, but seedlings raised recently from one of our *Q. rhysophylla* trees appear also to be hybrids.

The Oaks of China

by Zhou Zhekun, Sun Hang and Fei Yong
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the Chinese Academy of Sciences
Peoples Republic of China

China has a flora very rich in oaks with more than 125 species recognized so far, nearly 25 percent of the world total. Apart from the number of species, the biodiversity of oaks is very important in China. Chinese oaks have a very wide distribution, and the genus is spread over the whole country except Xinjiang, (northwest China). They occupy various habitats and can be found from tropical, and subtropical to temperate zones, and from sea level to very high in the mountains. They have various habits, and can be evergreen, semi-evergreen, or deciduous trees, shrubs and stoloniferous shrubs. Oaks have become a large and important genus in Chinese broadleaf forests since the Tertiary and remain some of the most important trees in Chinese forests.

Chinese oaks are classified into two subgenera: *Quercus* subg. *Quercus,* and *Quercus* subg. *Cyclobalanopsis.* Circumscription of the subgenera, and relationships and phylogeny in the genus, have always been debated issues in China, and have been researched for many years. Different authors using different materials have expressed different opinions (Hsu & Jen, 1976, 1985; Hsu, 1990; Huang and Zhang, 1992; Zhou, 1992, 1993, 1995, 1996). However, most of these papers were published in Chinese, making it difficult for those who cannot read Chinese to understand their opinions. In the present paper, we have attempted to approach these problems and we present a very brief review of Chinese oaks. The common synonyms in Chinese literature are given, and we have attempted taxonomic clarification of Chinese oaks. Their relationships and distributions also are discussed in this paper.

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Project supported by National Natural Science Foundation of China

Oaks of China . . .

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Quercus subg. Cyclobalanopsis (Oerst.) Schneid.

Quercus subg. *Cyclobalanopsis* contains about 150 species mainly distributed in tropical and subtropical areas of east and southeast Asia. China includes 77 of these species (Table 1). Oaks in this subgenus provide one of the main Chinese subtropical forests. All of them are small to large evergreen trees 10 to 40 m tall, with smooth, occasionally fissured bark. The leaves are leathery, lanceolate or elliptic, deep bronze-red or red when young becoming blue-green with a glabrate adaxial surface and toothed or entire margins. Acorn cup scales are lamellate and most mature in one year. These oaks are easy to distinguish from those of *Quercus* subg. *Quercus* by their leaf and acorn morphology. Therefore it is not surprising that *Cyclobalanopsis* was considered as a genus by Ørsted and is still recognized as such by some Chinese oak experts (Hsu & Ren, 1975, 1985, 1990; J. C. Liao, 1991). However, *Cyclobalanopsis* appears as a subgenus of *Quercus* in nearly half of the Chinese taxonomic literature (Huang, 1992; Wang and Zhang, 1986; Liu & Fang, 1986; Zhou, 1992, 1993, 1995, 1996). Pollen morphology, leaf and wood anatomy, molecular biology and cladistic analysis all suggest that the true phylogenetic position of *Cyclobalanopsis* is as a subgenus of *Quercus* (Menitsky, 1984; Nixon, 1989; Soepadmo, 1972; Zhou, 1992, 1995, 1996). Taxonomic confusion arises for this reason. Botanists and horticulturists and even taxonomists who are not experts in Fagaceae have long suffered from using the scientific name of this subgenus. For example, *Quercus schottkyana* can be called *Cyclobalanopsis glaucoides* or *Quercus glaucoides* Koidz.[1] and a new name, *Q. yongchuniana* Z. K. Zhou has to be given to *Cyclobalanopsis longifolia* Y. C. Hsu & Q. Z. Dong because the name *Q. longifolia* has existed for a long time. The correct scientific name and common synonyms found in Chinese botanical literature are given in table 1. We have tried to clear up the taxonomic confusion.

Many attempts have been made to establish a systematic division of subg. *Cyclobalanopsis*. However, there is no universally accepted system. Camus (1936-1954) founded a classification of *Quercus* in her monograph. She divided *Quercus* into subg. *Quercus* and subg. *Cyclobalanopsis*. Six sections of subg. *Quercus* were founded in this work but no further division for *Cyclobalanopsis* was made. Menitsky established the classification of *Quercus* subg. *Cyclobalanopsis* (1976,1977) mainly based on hair type, length of style and shape of acorn. He treated *Quercus* subg. *Cyclobalanopsis* as containing nine sections. Menitsky later modified his system (1984). In his new system, subg. *Cyclobalanopsis* is divided into eight sections but because it was published in Russian, it was not understood by Chinese taxonomists. Also, many species of subg. *Cylobalanopsis* from China were not included in Menitsky's classification. In addition, characters employed to define sections by Menitsky are difficult to find on herbarium sheets and to deal with. Therefore Menitsky's system is not the best for the treatment of Chinese *Cyclobalanopsis* oaks. Several attempts on this subject have also been made by Chinese taxonomists. For example, Sheng Chung-Fu who tried to divide Chinese *Cyclobalanopsis* oaks into two groups and four subgroups. However, his work was not published officially and the details of his divisions were not made available. We treat *Cyclobalanopsis* as a subgenus of *Quercus* and try to classify species of subg. *Cyclobalanopsis* from China as three groups based on the shape of the nuts (Table 2). Group 1, the long acorn group, has elliptic acorns with the ratio of width to length of nuts less than 1 and includes 40 species. Group 2, the round acorn group has spherical acorns with the ratio of width to length close to 1 and includes 15 species. Group 3, the oblate acorn group has oblate acorns with the ratio of width to length more than 1 and includes 18 species. This is a temporary treatment, and more work is needed to establish a universally acceptable classification of *Quercus* subg. *Cyclobalanopsis.*

Oaks of this subgenus play a very important role in the ecosystem of tropic, tropic mountains and subtropical areas. They occur in several subtropical forest types, called subtropical evergreen broad-leaf forests, where many of them are the dominant elements. *Quercus glauca* forms pure blue Japanese oak forest in

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Key to subgenera, sections and groups of *Quercus* from China

1. Evergreen trees, leaves coriaceous, scales lamellate, forming distinctive ringed acorn cups (go to 2)

Subgenus *Cyclobalanopsis*

- 2. Nut cylindrical, diameter/height < 1 -- **long acorn group**
- 2. Nut spherical or oblate, diameter/height = 1 (go to 3)
  - 3. Nut spherical, diameter/height = 1 -- **round acorn group**
  - 3. Nut oblate, diameter/height > 1 -- **oblate acorn group**

1. Evergreen tree or shrubs or deciduous trees, leaves chartaceous or coriaceous, scales not lamellate, not forming ringed acorn cups (go to 4)

Subgenus *Quercus*

- 4. Evergreen trees or shrubs, leaves coriaceous (go to 5)
  - 5. Leaves with adaxial hypodermis, leaf apex rounded or obtuse, with fasciculate hairs, primary vein ± zigzag, branched at the top -- sect. *Brachylepides*
  - 5. Leaves without adaxial hypodermis, leaf apex acute, attenuate, primary vein straight, not branched (go to 6)
    - 6. Leaves with stalked fasciculate hairs -- sect. *Engleriana*
    - 6. Leaves with stalked stellate hairs -- sect. *Acrodonta*
- 4. Semi-evergreen or deciduous trees, leaves chartaceous (go to 7)
  - 7. Semi-evergreen trees, leaves 6 cm long with spiral stellate hairs -- sect. *Echinolepides*
  - 7. Deciduous trees, leaves at least 7 cm long with stellate hairs (go to 8)
    - 8. Leaves narrow ovate to lanceolate with long-spined teeth -- sect. *Aegilops*
    - 8. Leaves obovate, occasionally elliptic, with rounded teeth, or lobed -- sect. *Quercus*

Table 1. List of *Quercus* subg. *Cyclobalanopsis* of China

#	Scientific Name	Common synonym in Chinese botanical literature (*C.* = *Cyclobalanopsis*)	Natural range	Altitude range (m)	Fruit size (d/h) mm	M*
1.	*Q. albicaulis* Chun & Ko	*C. albicaulis* Hsu & Jen	Hainan, China	250-600	20-30/40	2
2.	*Q. annulata* Smith	*C. annulata* Oerst.	Yunnan & Sichuan,		11-14/12-15	1
3.	*Q. argyrotricha* A. Camus	*C. argyrotricha* Chun & Chang	Guizhou	1600	8-15/8-15	1
4.	*Q. augustinii* Skan	*C. augustinii* Schott.	SW China, Vietnam	1200-1700	8-12/10-17	2
5.	*Q. austrocochinchinensis* Hickel & A. Camus	*C. austrocochinchinensis* Hjelmq.	Xishuangbanna, Yunnan, Vietnam	760-930	13-18/11-14	?
6.	*Q. austroglauca* Chang	*C. austroglauca* Hsu & Jen	Xichou, Yunnan	850-1500	20-22/20-22	?
7.	*Q. bambusifolia* Hance	*C. bambusifolia* Hsu & Jen	S China, Vitenam	500	10-16/15-25	1
8.	*Q. bella* Chun & Tsiang	*C. bella* Chun	S. China	200-700	22-30/15-15-20	1
9.	*Q. blakei* Skan	*C. blakei* (Skan) Schott.	S & SW China, Laos	100-2500	15-3/2.5-3.5	1
10.	*Q. breviradiata* Huang	*C. breviradiata* Cheng	C & SW China	1100-1850	12/15	1
11.	*Q. camusiae* Trel. ex Hickel & A. Camus	*C. camusiae* Hsu & Jen, *C. faadoouensis* Hu	Xichou, Yunnan	1400-2000	17/17	?
12.	*Q. championii* Benth.	*C. championii* Oerst.	S & SE, China, Yunnan	800-1400	10-15/15-20	1
13.	*Q. chapensis* Hickel & A. Camus	*C. chapensis* Hsu & Jen; *C. koumeii* Hu; *C. shianpyngensis* Hu	S & SE Yunnan; Vietnam	1300-2000	15-27/10-22	?
14.	*Q. chevalieri* Hickel & A. Camus	*C. chevalieri* Hsu & Jen; *C. nigrinux* Hu	Guangxi, Guangdong, Yunnan, Vietnam	650-1500	6-8/10-15	?
15.	*Q. chrysocalyx* Hickel & A. Camus	*C. chrysocalyx* Hjelmq.	Luchun, Yunnan, Indochina	1200	25-35/15-25	1

Table 1. contd.

#	Scientific Name	Common synonym in Chinese botanical literature (*C.* = *Cyclobalanopsis*)	Natural range	Altitude range (m)	Fruit size (d/h) mm	M*
16.	*Q. chungii* Metc.	*C. chungii* Hsu & Jen	S & SE, China	200-800	14-17/15	?
17.	*Q. ciliaris* Huang & Chang	*C. gracilis* Cheng & T. Hong; *Q. glauca* var. *gracilis* Rehd. & Wils.	south of Yangtze river	500-2600	10/15-20	1
18.	*Q. daimingshanensis* Huang	*C. daimingshanensis* S. Lee	Wumin, Guangxi	1400	13/20-22	1
19.	*Q. delavayi* Franch.	*C. delavayi* Schott.	SW China	1000-2000	10-15/18	2
20.	*Q. delicatula* Chun & Tsiang	*C. delicatula* Hsu & Jen	Guangxi, Guangdong	300-700	15/20-25	1
21.	*Q. dinghuensis* Huang	*C. dinghuensis* Hsu & Jen	Gaoyao, Guandong	950	17-22/30-35	?
22.	*Q. disciformis* Chun & Tsiang	*C. disciformis* Hsu & Jen; *Q. shingjenensis* Cheng	Guangxi, Guangdong, Guizhou	200-1500	20/15-20	1
23.	*Q. dongfangensis* Huang		Hainan	1500	11/13	?
24.	*Q. edithiae* Skan	*C. edithiae* Schott.; *Q. tephrosia* Chun & Ko	S China, Vietnam	400-1800	20-30/30-45	1
25.	*Q. elevaticostata* Huang	*C. elevaticostata* Hsu & Jen	Ningjiang Hujiang	600-1000	10-21/15-22	1
26.	*Q. fleuryi* Hickel & A. Camus	*C. fleuryi* Hsu & Jen; *C. austro-yunnanensis* Hu, *Q. tsoi* Chun	C & S China, Tibet, Vietnam	500-1500	20-30/30-45	1
27.	*Q. fulvisericea* Z. K. Zhou	*C. fulvisericea* Hsu & D. M. Wang	SE Yunnan	1200	12/12	?
28.	*Q. gambleana* A. Camus	*C. gambleana* Hsu & Jen	C & SW China India	1100-3000	15/20	1
29.	*Q. gilva* Bl.	*C. gilva* Oerst.; *Q. hunanensis* H.-M.	E, S & C China	300-1500	10-13/15-20	1
30.	*Q. glauca* Thunb.	*C. glauca* Oerst.; *Q. sasakii* Kanehira; *Q. longipes* Hu	China, Japan, Korea & India	60-2600	9-14/10-16	1

Table 1. contd.

#	Scientific Name	Common synonym in Chinese botanical literature (*C.* = *Cyclobalanopsis*)	Natural range	Altitude range (m)	Fruit size (d/h) mm	M*
31.	*Q. helferiana* A. DC.	*C. helferiana* Oerst	S & SW China, India, Thailand, Indochina	900-2400	15-22/10-16	1
32.	*Q. hui* Chun	*C. hui* Hsu & Jen	C & S, China	250-1250	15-25/15-20	1
33.	*Q. hypophaea* Hayata	*C. hypophaea* Hayata	Taiwan	50-800	12-18/17-21	1
34.	*Q. hypargyrea* Huang & Cheng	*C. multinervis* Cheng & T. Hong, *C. hypargyrea* Hsu & Jen, *Q. hypargyrea* (Seem.) Huang & Cheng, *Q. glauca* var. *hypargyrea* Seem.	C China	1000-2000	10/18	2
35.	*Q. jenseniana* Hand.-Mazz.	*C. jenseniana* Cheng & T. Hong	C & S China	300-1700	13-15/17-22	2
36.	*Q. jinpinensis* Huang	*C. jinpinensis* Hsu & Jen	Jinpin, Yunnan		15/18	
37.	*Q. kerrii* Craib	*C. kerrii* Hu	S & SW China Vietnam, Thailand	160-1800	20-28/7-12	1
38.	*Q. kiukiangensis* Cheng	*C. kiukiangensis* Hsu & Jen; *Q. xizangensis*	Yunnan, Tibet	1800-2700	14-17/15-17	1
39.	*Q. kontumensis* A. Camus	*C. kontumensis* Hsu & Jen	Guannan, Yunnan	1700	15/20	?
40.	*Q. kouangsiensis* A. Camus	*C. kouangsiensis* Hsu & Jen; *Q. fengii* Hu & Cheng, *Q. nemoralis* Chun	C S & SW China	200-2000	25/50	1
41.	*Q. lamellosa* Smith	*C. lamellosa* Oerst.	Guangxi, Yunnan, India, Burma, Nepal	1300-2600	30-40/20-30	1

Table 1. contd.

#	Scientific Name	Common synonym in Chinese botanical literature (*C.* = *Cyclobalanopsis*)	Natural range	Altitude range (m)	Fruit size (d/h) mm	M*
42.	*Q. liboensis* Z. K. Zhou	*C. pseudoglauca* Y. K. Li & X. M. Wang	Guizhou	530	?	?
43.	*Q. litseoides* Dunn	*C. litseoides* Schott.	Guangdong, Guangxi	700-1000	10-15/18	?
44.	*Q. lobbii* Etting.	*C. lobbii* Hsu & Jen	Yunnan & Burma	2800-3300	12/15	?
45.	*Q. longinux* Hayata	*C. longinux* Schott.; *Q. pseudomyrsinifolia* Hayata	Taiwan	500-2500	10-12/8-9	1
46.	*Q. lungmaiensis* Huang & Cheng	*C. lungmaiensis* Hu	Huning, Yunnan	1100-1300	15-20/15-20	1
47.	*Q. meihuashanensis* Huang	*C. meihuashanensis* Q. F. Zheng	Shanhang, Fujian	1600	12-15/13-18	1
48.	*Q. morii* Hayata	*C. morii* Schott.	Taiwan	600-2600	10-18/15-25	1
49.	*Q. motuoensis* Huang	*C. motuoensis* Hsu & Jen	Motuo, Tibet	1700	10-13/14-18	1
50.	*Q. myrsinifolia* Bl.	*C. myrsinifolia* Oerst.	South of Yangze river	200-2500	10-15/14-25	1
51.	*Q. nanchuanica* Huang	*Q. lineata* var. *macrophylla* Seem.	Nanchuan, Sichuang		12/25	?
52.	*Q. ningangensis* Huang	*C. ningangensis* Cheng & Hsu	C. China		8-12/15-20	1
53.	*Q. obconica* Z.K. Zhou	*Q. hainanica* Huang & Y. T. Chang; *C. litoralis* Hsu & Jen	Hainan	900-1000	25-28/45	2
54.	*Q. obovatifolia* Huang	*C. obovatifolia* Hsu & Jen	C & SE, China	1500-1800	10-16/8-20	1
55.	*Q. oxyodon* Miq.	*C. oxyodon* Oerst., *Q. fargesii* Franch., *Q. lineata* var. *grandifolia* Skan	C, S, CW China Tibet, India, Burma	700-2800	14-17/16-22	1

Table 1. contd.

#	Scientific Name	Common synonym in Chinese botanical literature (*C.* = *Cyclobalanopsis*)	Natural range	Altitude range (m)	Fruit size (d/h) mm	M*
56.	*Q. pachyloma* Seem.	*C. pachyloma* Schott.; *Q. conduplicans* Chun; *Q. gracilenta* Chun	C & E China	150-850	15-30/20-30	1
57.	*Q. pentacycla* Chang	*C. pentacycla* Chang	Guizhou	1600	8-15/8-15	1
58.	*Q. petelliformis* Chun	*C. petelliformis* Hsu & Jen	Jiangxi, Guandong	400-1000	25-28/20-25	1
59.	*Q. phanera* Chun	*C. phanera* Hsu & Jen; *Q. basellata* Chun & Ko; *Q. insularis* Chun & Tam	Hainan & Guangxi	900-2400	20-2.5/3-4	1
60.	*Q. pinbianensis* Huang & Y. T. Chang	*C. pinbianensis* Hsu & Jen	Pingbian, Yunnan	1300-1700	8/20	?
61.	*Q. poilanei* Hickel & A. Camus	*C. poilanei* Hjelmq.	Guangxi, China; Vietnam	1300	13-15/18-15	?
62.	*Q. rex* Hemsl.	*C. rex* Schott.	SW Yunnan, Vietnam, Burma, India	1100-1800	35-5/25-35	1
63.	*Q. salicina* Blume	*C. salicina* Oerst.	Taiwan, Japan	200-700	10-13/15-18	1
64.	*Q. schottkyana* Rehd. & Wils.	*C. glaucoides* Schott.; *Q. glaucoides* Koidz.	SW China	1500-2500	7-10/10-14	1
65.	*Q. semiserrata* Roxb.	*Q. semiserratoides* Huang & Y. T. Chang; *C. semiserratoides* Hsu & Jen	Yunnan & Tibet, China, Indochina, India, Burma	650	12-20/40	1
66.	*Q. sessilifolia* Bl.	*C. sessilifolia* Schott.	South of Yangze, China	250-600	8-15/17-24	1

Table 1. contd.

#	Scientific Name	Common synonym in Chinese botanical literature (*C.* = *Cyclobalanopsis*)	Natural range	Altitude range (m)	Fruit size (d/h) mm	M*
67.	*Q. shennongii* Huang & Fu	*C. shennongii* Hsu & Jen	Hubei	700	10/6	?
68.	*Q. sichourensis* Huang & Chang	*C. sichourensis* Hsu & Jen	Xichou, ling,Yunnan	850-1500	30-40/20	?
69.	*Q. stewardiana* A. Camus	*C. stewardiana* Hsu & Jen	E & C China	100-2400	8-15/8-15	2
70.	*Q. subhinoidea* Chun & Ko	*C. subhinoidea* Hsu & Jen	Hainan	380-500	25-3/10-15	1
71.	*Q. tenuicupula* Huang	*C. tenuicupula* Hsu & Jen	Jinping, Yunnan	122	25-30/20-25	1
72.	*Q. thorelii* Hickel & A. Camus	*C. thorelii* Hsu & Jen; *Q. hsiensiui* Chun & Ko; *Q. chingsiensis* Chang; *C. chingsiensis* Chang	S Yunnan & Guangxi	1000	25-30/10-15	1
73.	*Q. tiaoloshanensis* Chun & Ko	*C. tiaoloshanensis* Hsu & Jen	Hainan, China	900-1400	14-16/20-22	1
74.	*Q. tomentosinervis* Huang	*C. tomentosinervis* Hsu & Jen	Jinping, Yunnan	2300	13-15/15-17	1
75.	*Q. xanthotricha* A. Camus	*C. xanthotricha* H. & J.; *C. fuhsingensis* Chang; *Q. fuhsingensis* Chang	SW Yunnan	800-1300	7-10/9-13	1
76.	*Q. yingjiangensis* Govaerts	C. *yingjiangensis* Hsu & *Q.* Z. Dong	Yingjiang, Yunnan	2000	30/20	?
77.	*Q. yonganensis* L. Lin & Huang	*C. yonganensis* H. & H	Yongan, Hujian	100-1370	12-15/14-18	?
78.	*Q. yongchuniana* Z. K. Zhou	*C. longifolia* Hsu & Dong	Yingjiang, Yunnan		15/7	?

*M: acorn maturation - 1 or 2 years

Oaks of China . . .

text contd. from pg. 15

south to central China, or can be associated with other subtropical trees such as: *Lithocarpus, Castanopsis, Lindera, Litsea*, etc. *Q. schottkyana* (*Q. glaucoides*) is endemic to central Yunnan, where it comprises pure or mixed Schottky oak forest. This is a typical forest in central Yunnan, China. *Q. oxyodon, Q. kiukiangensis,* and *Q. lamellosa* are the main oak trees in eastern Himalayan areas. They grow at altitudes of 1,500 to 3,000 m and comprise pure- or mixed-oak forests. These oaks are totally deciduous in the season April to May, before the new leaves develop. These forests are called semi-evergreen forests by some authors (Li, 1985). *Q. myrsinifolia* forms the oak forest mainly in central west China. *Q. nubium, Q. fleuryi, Q. bambusifolia, Q. rex* and *Q. edithiae* form the oak forest in subtropical regions of southern China.

Quercus subg. *Quercus*

Quercus subg. *Quercus* has about 47 native oak species distributed in China. They are classified into six sections: *Brachylepides, Engleriana, Echinolepides, Acrodonta, Quercus* and *Aegilops* (Table 3). This subgenus has the widest ecological range and the most diverse morphology and habits. Oaks of subg. *Quercus* are found growing in four different forest types in China: evergreen oak forest, evergreen sclerophyllous oak forest, semi-evergreen oak forest and deciduous oak forest.

I. Sect. *Brachylepides*

Section *Brachylepides* has 11 or 12 species and forms evergreen sclerophyllous oak forest. They are distinguished easily from other Chinese oaks by their obovate, occasionally elliptic leaves with round or occasionally obtuse apexes and variable margins, mainly entire or revolute, or with few to many spinose teeth in some species. Leaf blades are very thick and leathery, with yellow or gray fasciculated hairs (Jones, 1986) and adaxial hypodermis; the primary vein is more or less zigzag and branched at the top, Acorns mature in one year for most species, two years for three species. Oaks of this section range from Chiang Mai in Thailand to southwest China, Burma, India, Bhutan, and Nepal to Afghanistan. However, these oaks are mainly concentrated in eastern Himalayan areas, particularly northwest Yunnan and southwest Sichuan, China in the Hengduan Mountains. All species of this section can be found in these regions. Seven oaks, *Q. fimbriata, Q. gilliana, Q. guyavifolia, Q. longispica, Q. pannosa, Q. pseudosemecarpifolia* and *Q. rehderiana* are endemic to the Hengduan mountain areas. Their altitude range is from 1,700 to 4,800 m, but they occur mainly from 2,400 to 3,600 m. They have various growth habits. *Q. monimotricha* is a stoloniferous shrub only 0.2 to 1 m tall, mostly in open areas or at the tops of mountains, usually occupying a large area. Other species are small or large trees, 7 to 30 m tall in undisturbed forests, but they become shrubs, even stoloniferous, under excessive human activity when they are frequently cut for their wood and foliage. The tree oaks in this section form pure evergreen sclerophyllous oak forests or occur mixed with pines. This is a dominant forest type in the Hengduan Mountain areas of northwest Yunnan and west southwest Sichuan, and is very important in the high mountain ecosystem. These areas have a high altitude, cold and dry weather and poor soils and it is very difficult for most angiosperm

Table 2. A proposed systematic treatment of Chinese *Cyclobalanopsis*

Round Acorn Group	Oblate Acorn Group
Q. annulata	*Q. austrocochinchinensis*
Q. argyrotricha	*Q. bella*
Q. austroglauca	*Q. chapensis*
Q. camusiae	*Q. chrysocalyx*
Q. chungii	*Q. disciformis*
Q. elevaticostata	*Q. helferiana*
Q. fulvisericea	*Q. hui*
Q. glauca	*Q. kerrii*
Q. kiukiangensis	*Q. lamellosa*
Q. lungmaiensis	*Q. longinux*
Q. meihuashanensis	*Q. petelliformis*
Q. pachyloma	*Q. rex*
Q. schottkyana	*Q. shennongii*
Q. stewardiana	*Q. subhinoidea*
	Q. tenuicupula
	Q. thorelii

Long Acorn Group		
Q. albicaulis	*Q. fleuryi*	*Q. ningangensis*
Q. augustinii	*Q. gilva*	*Q. obconica*
Q. bambusifolia	*Q. hyophaea*	*Q. obovatifolia*
Q. blakei	*Q. hypargyrea*	*Q. oxyodon*
Q. breviradiata	*Q. jenseniana*	*Q. phanera*
Q. championii	*Q. kontumensis*	*Q. pinbianensis*
Q. chevalieri	*Q. kouangsiensis*	*Q. salicina*
Q. daimingshanensis	*Q. litseoides*	*Q. semiserrata*
Q. delavayi	*Q. lobbii*	*Q. tiaoloshanensis*
Q. delicatula	*Q. morii*	*Q. tomentosinervis*
Q. dinghuensis	*Q. motuoensis*	*Q. xanthotricha*
Q. dongfangensis	*Q. nanchuanica*	*Q. yonganensis*
Q. edithiae		

trees to grow there. However, oaks in this section have obvious xerophytic characters such as dense hairs, thick cuticles, lignified epidermal cell walls and cuticles, and low stomatal density (Zhou et al, 1995), and are adapted to such an environment. Therefore, they become dominant trees and form one of the most attractive landscapes of the high mountains.

Oaks of this section are very similar to some of the Mediterranean oaks such as *Q. ilex* and *Q. suber* and some more distantly related American evergreen oaks such as *Q. myrtifolia* and *Q. wislizeni* etc. It would be very interesting to research their relationships and distribution patterns.

II. Sect. *Engleriana*

The original section *Engleriana* was founded by Prof. Hsu Yongchun (1985), a taxonomist and expert on Chinese oaks who died in 1993. It included about 20 species. This is a confusing section. The characters used by Hsu to establish sect. *Engleriana* are: mature leaf toothed or sometimes entire; leaf apex acute or acuminate; primary vein straight (Hsu, 1985). However, these characters are shared by other sections of *Quercus*. For example, the leaves of most species are toothed, and the primary vein is straight in all sections of *Quercus* except

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Table 3. List of *Quercus* subg. *Quercus* from China

#	Scientific Name	Common synonym in Chinese botanical literature	Natural range	Altitude range (m)	E*	M*
	Sect. *Brachylepides*				E	
1.	*Q. aquifolioides* Rehd. & Wils.		Tibet, SW China	2700-4800	E	1
2	*Q. fimbriata* Chun & Huang		Sichuan, Yunnan	2800-3100	E	1
3	*Q. gilliana* Rehd. & Wils.		Tibet, Shangxi, SW China	1900-3100	E	1
4	*Q. guyavifolia* Levl.	*Q. pileata* Hu & Cheng	Yunnan, Sichuan,	2500-4000	E	1
5	*Q. longispica* A. Camus	*Q. semecarpifolia* Sm. var. *longispica* H.-M.	Yunnan, Sichuan,	2260-3800	E	1
6	*Q. monimotricha* H.-M.	*Q. spinosa* David var. *monimotricha* H.-M.	Yunnan, Sichuan,	2600-3500	E	2
7	*Q. pannosa* H.-M.	*Q. ilex* L. var. *rufescens* Fr.	Yunnan, Sichuan	2000-3900	E	2
8	*Q. pseudo-semecarpifolia* A. Camus	*Q. semecarpifolia* Sm. var. *glabra* Fr.	Yunnan, Sichuan	1500-4000	E	1
9	*Q. rehderiana* H.-M.		Yunnan, Sichuan,	1500-3800	E	1
10	*Q. semecarpifolia* Sm.	*Q. obtusifolia* D. Don	Thailand, Burma, Northern India, Tibet, China, Nepal, Bhutan, Pakistan, Afghanistan	2100-3600	E	1
11	*Q. sensecens* H.-M.		SW China, Tibet	2200-3500	E	1
12	*Q. spinosa* Fr.	*Q. semecarpifolia* Sm. var. *spinosa* Schott. *Q. taiyunensis* Ling	South of Yangtze river China	1700-2900	E	2
	Sect. *Engleriana*					
13	*Q. bawanglingensis* Huang et al.		Hainan, China	900	E	?
14	*Q. cocciferoides* H.-M.		Yunnan, Sichuan,	1000-2500	E	1

Table 3. contd.

#	Scientific Name	Common synonym in Chinese botanical literature	Natural range	Altitude range (m)	E*	M*
15	*Q. dolicholepis* A. Camus	*Q. spathulata* Seem.	South of Yangtze river China	500-2800	E	2
16	*Q. engleriana* Seem.		South of Yangtze river China	700-2700	E	2
17	*Q. franchetii* Skan		Yunnan, Sichuan	800-2600	E	1
18	*Q. kingiana* Craib		Yunnan, China, Burma, Thailand		E	
19	*Q. lanata* Sm.	*Q. tungmaiensis* Y. T. Chang, *Q. kongshanensis* Hsu & Jen.	Vietnam, Thailand Burma, Northern India, Nepal, Bhutan, Tibet,Yunnan, China	1600-2800	E/S	2
20	*Q. lodicosa* O.E. Warb.		India, Burma Tibet, China	1800-2400	E/S	1
21	*Q. marlipoensis* Hu & Cheng		SE Yunnan, China	1100	E	?
22	*Q. oxyphylla* H.-M.		South of Yangtze river China	200-2900	E	2
23	*Q. setulosa* Hickel & A. Camus	*Q. sinii* Chun	Thailand, Vietnam, Yunnan, China	130-1300	E	1
24	*Q. shangxiensis* Z. K. Zhou	*Q. lanceolata* S. Z. Qu & W.H. Zhang	Shangxi, China	1130	E	?
25	*Q. tarokoensis* Hayata		Taiwan	350-1250	E	1
26	*Q. utilis* Hu & Cheng		Kuangxi, Guizhou, Yunnan, China	1000-1500	E	1
27	*Q. yiwuensis* Huang		Yunnan, China	1000	E	?
	Sect. *Acrodonta*					
28	*Q. acrodonta* Seem.	*Q. parvifolia* H.-M. *Q. handeliana* A. Camus	Shangxi, Gansu, Henan, Fubei, Sichuan, Guizhou Yunnan China	300-2300	E	1

Table 3. contd.

#	Scientific Name	Common synonym in Chinese botanical literature	Natural range	Altitude range (m)	E*	M*
29	*Q. phillyreoides* A. Gray	*Q. ilex* L. var. *phillyreoides* Fr. *Q. fokienensis* Nakai *Q. singuliflora* A. Camus *Q. lichuanensis* Cheng *Q. fooningensis* Hu & Cheng, *Q. myricifolia* Hu	South of Yangtze river China	300-1200	E	1
	Sect. *Echinolepides*					
30	*Q. baronii* Skan	*Q. pseudoserrata* Liou	Shanxi, Shaanxi, Gansu, Henan, Fubei, Sichuan, Yunnan	500-2700	S	2
	Sect. *Aegilops*					
31	*Q. acutissima* Carruth	*Q. lunglingensis* Hu	Whole of China except Xinjiang, Vietnam,Burma,India,Bhutan,Nepal,Japan	60-2300	D	2
32	*Q. chenii* Nakai	*Q. acutissima* Carr. var. *brevipetiolata* Hoo, *Q. acutissima* Carr. var. *chenii* Menits.	C & E China	0-600	D	2
33	*Q. variabilis* Bl.	*Q. chinensis* Bunge	Whole of China except Xinjiang, Vietnam, Korea, Japan	500-3000	D	2
	Sect. *Quercus*					
34	*Q. aliena* Bl.	*Q. hirsutula* Bl.	South of Yellow river China, Thailand, Japan, Korea	100-2000	D	1
35	*Q. dentata* Thunb.	*Q. obovata* Bunge, *Q. dentata* subsp. *eudentata* A. Camus	Whole of China except Xinjiang, Guandong,Guanxi,China,Korea,Japan	50-2700	D	1
36	*Q. fabri* Hance		South of Yangtze rvier China	50-1900	D	1

Table 3. contd.

#	Scientific Name	Common synonym in Chinese botanical literature	Natural range	Altitude range (m)	E*	M*
37	*Q.* x *fenchengensis* H. W. Jen & L. M. Wang		Liaonin Shangxi, China	200-2000	D	1
38	*Q. griffithii* Miq.	*Q. aliena* Bl. var. *griffithii* Schott.	Yunnan, Sichuan, Guizhou, China Burma and India	700-2800	D	1
39	*Q.* x *hopeiensis* Liou		North China	50-900	D	?
40	*Q. malacotricha* A. Camus	*Q. griffithii* var. *urticifolia* A. Camus, *Q. aliena* Bl. var. *urticifolia* Skan	Yunnan, Sichuan, Guizhou	1500-2800	D	1
41	*Q. mongolica* Ledeb.	*Q. sessilifora* var. *mongolica* Fr.	N & NE China, Korea Japan,	350-1400	D	1
42	*Q.* x *mongolico-dentata* Nakai		Northeast China, Korea	100-200	D	?
43	*Q. monnula* Hsu & Jen		Sichuan	99-103	D	
44	*Q. serrata* Thunb.	*Q. glandulifera* Bl.	Whole of China except Xinjiang, Japan, Korea	200-2000	D	1
45	*Q. stewardii* Rehd.		C & E China	1000-1750	D	1
46	*Q. wutaishanica* Mayr	*Q. liaotungensis* Koidz., *Q. mongolica*	N NW & NE China, Korea Ledeb. var. *liaotungensis* Nakai	600-2500	D	1
47	*Q. yunnanensis* Fr.	*Q. dentatoides* Liou, *Q. yui* Liou, *Q. dentata* subsp. *yunnanensis* Menits. *Q. dentata* Thunb. var. *oxyloba* Fr.	C S & SW China	1000-2600	D	1

E: evergreen, S: semi-evergreen, D: deciduous, M: year the acorns mature

Oaks of China . . .

text contd. from pg. 23

Photo by Zhekun Zhou

Mixed oaks at 2,700 m elevation on Jizu Mountain above the temple at Bichuan, Peoples Republic of China.

those in the section *Brachylepides*. On the other hand, oaks of sect. *Engleriana* have different anatomical and morphological characters, particularly in hair types. *Q. baronii*, has spirally stellate hairs, *Q. acrodonta* and *Q. phillyreoides* have stalked stellate haris and other oaks of this section have columnar fasciculate hairs. According to Hardin (1976,1979), columnar fasciculate, spirally stellate and stalked stellate hairs are not only anatomically different but also represent different evolutionary stages. Therefore, sect. *Engleriana* (sensu Hsu and Jen) can be divided into three sections based on hair types (Zhou et al., 1995).

Now, sect. *Engleriana* includes 15 species (Table 3). All of them are medium to large evergreen trees 15 to 35 m tall. Their leaves are leathery, ovate to narrowly oblong, and toothed. They fall into of the modified urticoid type (Hickey and Wolfe, 1975; Zhou et al., 1995), with apex acute, occasionally mucronate, and base acute to obtuse and with columnar fasciculate hairs, the primary vein straight, and acorn maturing in one year or two years. Oaks in this section are distributed from Chiang Mai, Thailand in the south, north to the Qingling mountains, central west China, and from the east Himalayas to Taiwan. They can grow from sea level to 2,800 m. The best growth, however, can be found at around 2,000 m. They occupy different ecological sites to the oaks of sect. *Brachylepides*. Oak trees in this section form evergreen oak forests in subtropical areas of China.

III. Section *Echinolepides*

Section *Echinolepides* has only one species, *Q. baronii*. This is a semi-evergreen tree or shrub oak up to 15 m tall. Its leaves are dry in winter but do not drop off until the next year when the new leaves develop. They are narrow lance-ovate in shape, 3-6 cm long and 1.3-2 cm wide with yellow spirally stellate hairs, toothed in the distal two thirds, the apex is acute and the base acute to obtuse. The acorns mature in two years. One variation is recognized which has more dense, white, spirally stellate hairs. It is distributed in Henan, Shaangxi, Shangxi, and Sichuan, west central China. *Q. baronii* is found at the boundary of evergreen and deciduous oak forests, usually on limestone hillsides. It forms pure semi-evergreen oak forest in Henan, mixed with *Pinus armandii*. Its altitude distribution is from 500 to 2,700 m but it is most common below 2,000 m in the mountains.

IV. Sect. *Acrodonta*

Two oak species, *Q. acrodonta*, and *Q. phillyreoides* are included in this section. Sect. *Acrodonta* is very similar to Sect. *Engleriana* except that sect. *Acrodonta* has stalked stellate hairs and sect. *Engleriana* has columnar fasciculate hairs. Both oaks in this section are small evergreen trees, 10 to 15 m tall, sometimes shrub-like. The leaves have a few teeth on the distal portion of the blade, with more or less yellow hairs on the abaxial surface. The acorns mature in one year. *Q. acrodonta* is distributed in Shangxi, Gansu, Henan, Hubei, Sichuan, Guizhou and Yunnan, China. *Q. phillyreoides* ranges from Shangxi east to Japan and south from Guandong to Anhui. Both species grow in limestone mountains, from 300 to 2,300 m altitude. *Q. acrodonta* forms pure oak forest in southeast Yunnan. *Q. phillyreoides* is a tree in forests but becomes shrubby in areas of severe human impact.

V. Sect. *Aegilops*

This is a deciduous oak section. Only three oak species are recognized in China. They can be distinguished from the other deciduous oaks by their leaf outline and tooth type. All of them are large trees 30 m tall with a well developed crown. The bark is gray and gray-brown, deeply fissured in *Q. acutissima* and *Q. chenii*, thick and corky in *Q. variabilis*; leaves are narrow ovate to lanceolate, narrow-oblong to narrow-ovate, densely but thinly gray-hairy beneath in *Q. variabilis*, smooth on both side in *Q. acutissima* and *Q. chenii*. The toothed leaves have long spine-tipped teeth, and the acorns mature in two years. *Q. chenii* can be distinguished from *Q. variabilis* by the leaves being smooth beneath and from *Q. acutissima* by the linear, straight cupule scales slender at the top and the small nuts and leaves. The nuts of *Q. chenii* are usually less than 15 mm in diameter while the leaves are 7-12 cm long. *Q. acutissima* has long slender scales. The nuts of *Q. acutissima* are usually 15 to 20 mm in diameter, and its leaves are 9 to 18 cm long.

These oaks have very wide distribution ranges and can be found in all of China except Xinjiang province, northwestern China. They also can found in Vietnam, Burma, India, Nepal, Bhutan, Korea and Japan. They grow well in temperate areas and form pure oak forests there. No hybrids are recognized in this section. It is interesting that chemical and DNA evidence has shown that section *Aegilops* is most closely related to section *Brachylepides*.

VI. Sect. *Quercus*

This is the other deciduous oak section with 14 species recorded in China. All of them are small to large trees 12 to 30 m tall, with dark brown or gray bark, fissured or split into deep vertical cracks. They have obovate, occasionally elliptic leaves with round teeth or numerous untoothed lobes, more or less stellate-hairy on the abaxial surface and with irregularly arranged wax flakes on the adaxial surface, a unique character of this section. The acorns mature in one year. These characters make the sect. *Quercus* a natural group easily distinguished from the other deciduous oak section in China, sect. *Aegilops*.

Oaks in this section can grow on sunny hillsides, open mountains or in forests. They can grow in different soils and grow well in poor or rocky soils. They are widespread throughout China, and also in Japan, Korea and Russia .

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Oaks of China . . .

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One species, *Q. griffithii* can be found in Thailand, Laos, Burma, India and Nepal. Most species of this section are concentrated in forest regions where they reach their greatest development. Here they occur in several forest types. *Q. mongolica* and *Q. wutaishanica* (*Q. liaotungensis*) are dominant species in temperate forests and usually occur in pure oak forests or associated with other trees such as *Populus Butal*, *Pinus* and other oaks. *Q. malacotricha*, *Q. fabri* and *Q. aliena* are usually found in upland subtropical areas and occur in pure forests or associated with *Liquidambar*, *Schima*, *Acer*, *Pinus* and other oaks.

Several hybrids oaks are recognized in this section. They are *Q.* x *mongolico-dentata* (*Q. dentata* x *Q. mongolica*), *Q.* x *fenchengensis* (*Q. aliena* x *Q. dentata*), *Q.* x *fangshanensis* (*Q. dentata* x *Q. mongolica* subsp. *crispula*), and *Q.* x *hopeiensis* (*Q. dentata* x *Q. wutaishanica*)

In all, 125 oaks species are recognized in China. They are treated as two subgenera, *Quercus* subg. *Cyclobalanopsis* and *Quercus* subg. *Quercus*. The former can be temporarily divided into three groups based on the shape of their acorns, and the latter into six sections based on hair types, leaf shape and morphology. The main differences between subgenera and sections are given in thekey to subgenera and sections of *Quercus*, which is found on page 15 of this publication.

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2. The name *Q. glaucoides* Martens & Galeotti applies to a Mexican species

Rare Oaks of the Riviera

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Since the glaciations, the richest flora in France has been found in the Mediterranean region. Considering only the oaks (genus *Quercus*), 9 of the 11 French species are found there. *Quercus coccifera* and *Quercus suber* are exclusively Mediterranean. *Quercus cerris,* whose presence is certainly linked to an introduction, also grows there, as does *Quercus ilex* and its *ballota* form. *Quercus pubescens*, *Quercus petraea* and *Quercus robur* are also present. *Quercus faginea* deserves particular mention, as one single small stand has been reported in France, close to the Spanish border. *Q. petraea* is quite infrequent, and *Q. robur* even rarer, but only two Atlantic oaks are absent from the area, *Q. suber* var. *occidentalis* and *Q. pyrenaïca.*

Growing among these species in a small area between the Lion Gulf and the Italian border called the "French Riviera," a population of rare chance

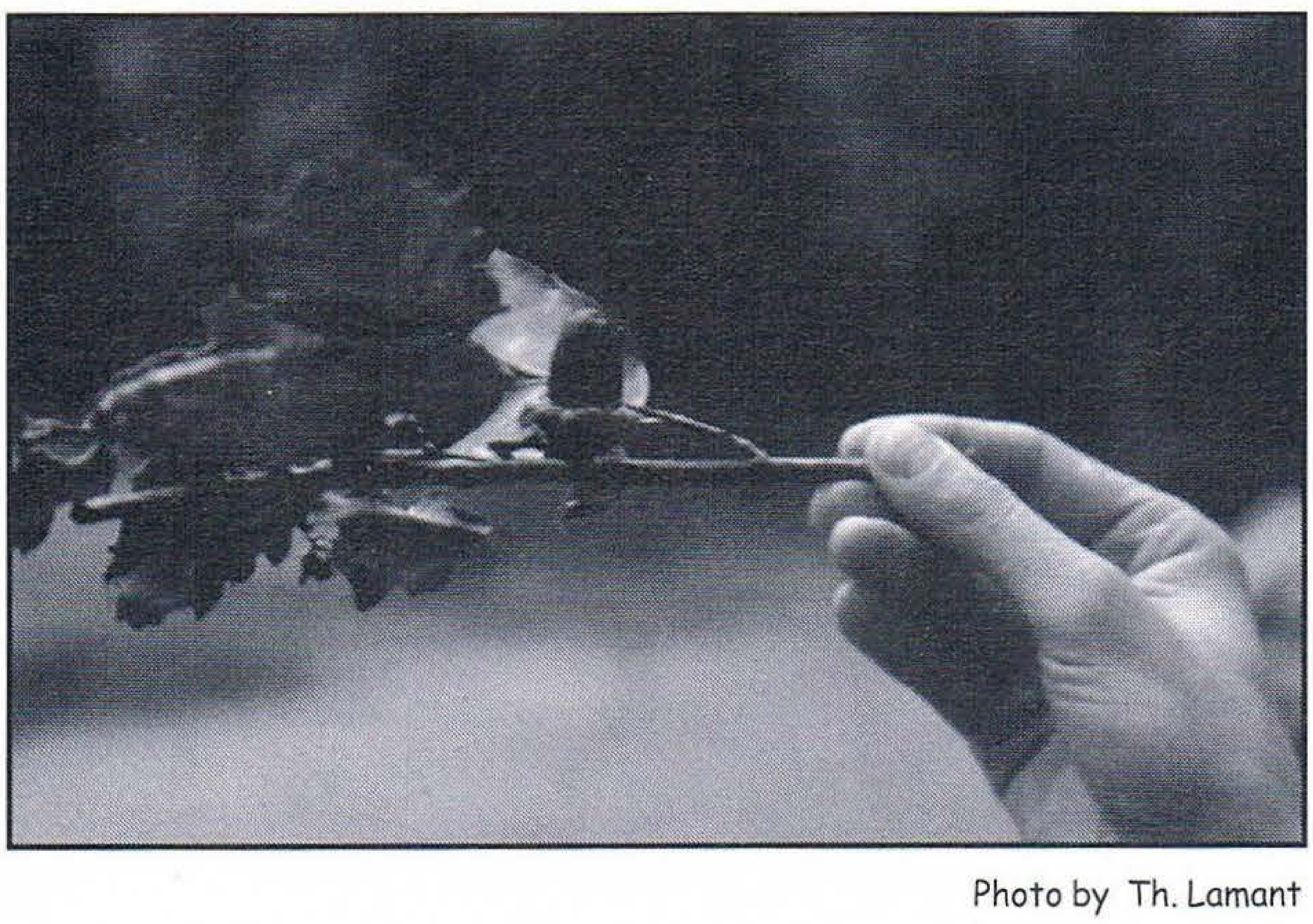

Photo by Th. Lamant

Quercus ×hispanica *Lam. (syn.* Q. crenata*) twig and acorn.*

hybrids (= "essaim d'hybrides fortuits") can be found. Their origin is due mostly to the close cohabitation of the parents. Several of these hybrids are discussed below.

Quercus x*hispanica* Lam. (=*Q. pseudosuber* Santi, *Q. crenata* Lam., *Q. fontanesii* Guss.); false cork oak.

This hybrid between *Q. cerris* and *Q. suber*, is known in Great Britain as "Lucombe oak", from the Lucombe nurseries in Exeter which had collected acorns from *Q. cerris* in 1762.

Chorology:

Found only sparsely as isolated trees in the Var and Alpes maritime departments, the origin of these populations may be explained by the introduction of six plants in 1789 which later spread. These six original trees were derived from seeds and a few grafts obtained from the two trees first introduced to France. The high proportion of individuals borne from seeds may explain the variability in the foliage.

Around Saint Cassien Lake, a few beautiful two-centuries-old trees are growing with rather fastigiate crowns and semi-deciduous foliage. At the photographed site, *Q. suber* is absent, but M. Barbero, R. Loisel and P. Ozenda mention it at other places around the lake. However, there are other locations where both parents coexists with the hybrid. Antoinette Camus, in her monograph of the genus *Quercus*, distinguishes two forms of the hybrid following the parentage. However, there is no categorical proof to back up this theory.

Photo by Th. Lamant

Quercus xhispanica *Lam. (syn.* Q. Crenata*) near Saint Cassien Lake, Departement Var, France, with Yves Chalamel of Arboretum Vallauris.*

***Q. suber* pollinated by *Q. cerris*.**

These trees reach 25 m in height, with an open crown of ascending branches. The upper part of the crown is rounded. The bark, at first smooth, becomes a pale brown-grey when older, forming many small non-suberous plates. The terminal bud is of a brown-reddish color, edged with scales, while the axillary buds lack them. The foliage does not remain until the spring, although sometimes a few brown leaves will cling unless the winter has been cold. The leaf blade is coriaceous, oblong-elliptic, 10 to 12 cm long by 3 to 4 cm wide, and is composed of 3 to 7 irregular lobes that end in a small spine. The sinuses are large and deep and the base is slightly rounded or heart-shaped. The color is a brilliant green on the upper leaf surface, and has a greyish tint beneath. Most of the time, only the midrib is hairy on the upper side. The petiole is 1/2 to 2 cm long. The lateral stipules are soon deciduous. The staminate flowers are borne in dense slender catkins 4 cm long and crimson in color before opening. The pistillate flowers do not exceed 2 mm long and are attached at the base of the terminal leaves on the current year's twig. They are solitary, rarely in pairs, supported by a 1 cm long peduncle and

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covered with a white flush. Additionally, they are edged with thin, numerous, imbricated red scales. Each flower has 4 to 6 styles. The acorns, rarely abundant, mature the second fall after flowering. They are held in a cup with a velvety inside, and many gray, prominent, and somewhat curved scales. This feature allows it to be distinguished from the cup of *Q. cerris*. The scales are shorter the closer they are to the peduncle. The cups measure 2.5 cm in length and 2 cm in diameter.

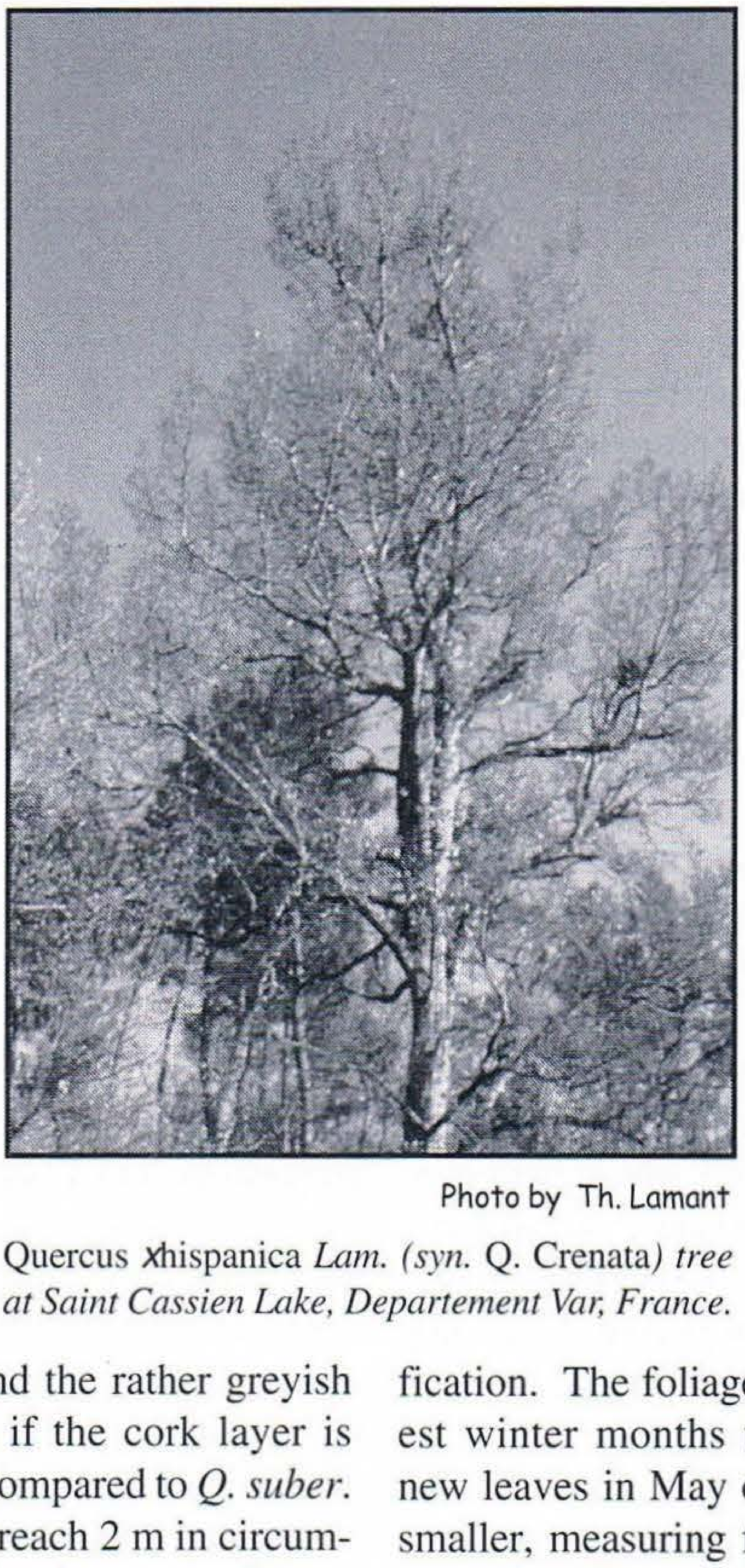

Photo by Th. Lamant

Quercus xhispanica *Lam. (syn.* Q. Crenata*) tree at Saint Cassien Lake, Departement Var, France.*

The trees observed close to the St. Cassien Lake are similar. What is striking about them is their fine slender trunk and the rather greyish and suberous bark, even if the cork layer is weak and of poor quality compared to *Q. suber*. The most handsome trees reach 2 m in circumference and 18 m in height. A group of three trees probably borne from the same trunk are 1.6 m in diameter and 14-m tall.

Distinguishing features:

The dense flush of the young twigs and the underside of the leaf, as well as its grayish and somewhat suberous bark, allow it to be differentiated from *Q. cerris*. The leaf is also more coriaceous and larger, and the axillary buds do not have any scales. It differs from *Q. suber* in being semi-evergreen and deciduous.

Q. cerris* pollinated by *Q. suber

This description is quite similar to the previous one, except for the following features. The hybrid is sometimes more shrubby, with dark grey bark sinuated with dark cracks isolating non-suberous smooth plates. The bark is seldom of a yellow-grey colour, thinly cracked and suberous as in the first type. Its crown is narrower and reminiscent of *Q. ilex* in its dense and tortuous ramification. The foliage remains during the hardest winter months until the development of new leaves in May or June. The leaf blade is smaller, measuring from 4 to 6 cm long by 2 cm wide. The 4 to 5 lobes are triangular with small spines. The spring color is silvery white.

The blooming of both types occurs in April and May and they bear fruit from September to December the following year. The seeds are disseminated by rodents. The root system is generally deep. However, the hypothesis of two distinct types following the parentage is often debated, and it is possible that there might be only one hybrid with a strong morphological diversity.

Ecology :

Q. x*hispanica* grows mostly under 500 m in altitude, often in deep fresh clay, sandy soils or slightly acid to weak active calcareous soils. It does not do well in too dry soils or superficial ones, and will be found in regions with high rainfall and hygrometry. It is hardy to European zone 6 (from - 17 °C to - 23°C). At St. Cassien Lake, it grows associated with *Q. suber*, *Q. ilex* and *Q. pubescens,* but *Q. cerris* is completely absent, suggesting that the hybrid was introduced. *Q.* x *hispanica* also grows associated with *Ostrya carpinifolia*, *Pinus pinaster*, *Phillyrea angustifolia* and *P. media*, *Paliurus aculeatus*, *Cornus sanguinea*, *Rhamnus alaternus*, and *Cistus salviifolius*. In other sites, it grows close to *Q. cerris* but without *Q. suber*.

***Quercus* x*morisii* Borzi**

(= *Q.* x *mixta* Villalobos, *Q.* x *bertrandii* Albet & Reyn, *Q. hispanica* Colm & Bout):

This very rare oak, described in 1880, is a hybrid between *Q. ilex* and *Q. suber*.

Description :

This small tree measures 5 to 20 m in height and has a crown aspect similar to *Q. ilex*. The young shoots are densely white The foliage is lanceolate, oblong-ovate or oblong-lanceolate. The leaf blade has a rounded or cordate base, seldom cuneate, with a sharp end. It measures 3 to 5 cm long, with a glabrous upper surface covered with a white flush beneath. The blade is edged with mucronate lobes, but only from its middle to its top. The veins of the lower face are prominent. The stalk reaches a fifth of the whole blade length. The male catkins bear 4 to 5 slightly pubescent anthers. The pistillate flowers are held on a 1- to 2-cm long tomentose stalk. The acorn matures in one year and is half enclosed in a cup that has a velvety inside. The cup has a flattened bottom and densely velvety, obtuse ovoid scales, which are closely appressed and erect, but longer than in *Q. ilex*.

Distinguishing features:

The foliage reminds one much of *Q. suber,* but the lower leaf surface is only slightly pubescent. The cups have the hemispheric shape of *Q. ilex* but are clearly less fringed than those in *Q. suber*. Bark observation is determinant for this hybrid: it is not suberous as for *Q. suber*, but thick, smooth, and above all, deeply cracked into large plates with more or less recurved edges. Because of this, the bark is not similar to that of *Q. ilex*.

Chorology:

A specimen is located next to St. Cassien Lake, not far from the *Q.* x*hispanica* station. It grows in a cool and shaded thalweg (valley) on the northern slopes, associated with *Q. ilex*, *Q.* x*hispanica* and *Castanea sativa*. It has also been located in the Var department as a multiple-trunk example, associated with *Q. ilex* and *Q. suber*, which were found close to the hybrid this time. The hybrid has also been located next to Parpaillon, Var Department, and also near Santa Lucia, Bastia, in Corsica. These last observations should be checked, since the reports are 50 years old.

Ecology:

Its distribution depends directly on the ecological needs of one of the parents, *Q. suber*. This hybrid is not suitable for chalky soils. *Q.* x *morisii* will be found upon a silice, gneiss or shists, and also soils of granitic origin. It grows associated in particular with *Castanea sativa*, *Erica arborea* and *Arbutus unedo*.

***Quercus* x*auzandri* Gren. & Godr.**

(= *Q. auzendi* Gren. & Godr. , *Q. ilex* var. *agrifolia* DC. , *Q.* x*catalaunica* Sennen,

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Quercus airensis Franco & Vasc. , *Q. coccifera ssp. auzandri* Batt. & Trabut.

This oak, described in 1855, is a hybrid between *Q. coccifera* and *Q. ilex*. It is rare, although it is more frequent where the two parents grow together.

Description:

Its dimensions and crown habit are reminiscent of both *Q. coccifera* and *Q. ilex*. In the first case, it can be a small, dense, bushy shrub never growing above 2-m tall, while it can also take the aspect of a tree or shrub with dimensions of 10 - 15 m in height in the second case. The leaf is coriaceous, oblong and attenuated at the two ends, with a wavy margin and a few pointed prickly lobes, glossy on the upper side and covered with a sparse or continuous tomentum beneath. The acorns mature in one year. They are of an ovoid - oblong obtuse form, in a cup that covers two fifths of the acorn base. The cup itself is rounded at its base and bears sharp lanceolate scales, light tomentose and appressed, slightly uneven on their upper side.

Distinguishing features:

This hybrid has extremely variable leaves, like *Q. ilex*, and sometimes even resembles that parent. The lateral twigs are not divaricated (that means, inserted at right angles) like *Q. coccifera*, but rather ascending similar to *Q. ilex*, sometimes even drooping. The leaves are always more or less covered with a starry tomentum beneath, in contrast to *Q. coccifera,* whose leaves are greenish underneath. Also, and this is a very helpful clue, they have a distinctive character most often lacking in *Q. ilex*: the veins end in a prominent prickle like *Q. coccifera*. The cups are similar to those of *Q. ilex*. However, the scales of *Q.* x *auzandri* are longer, larger, and their tip is generally more or less divergent and never appressed against the cup.

Chorology:

This hybrid has also been mentioned in other places in the Var department. Some examples with shorter cups, sharper acorns and truncate or emarginate leaves have been described next to Maraval. A tree with little rounded and mostly oval leaves has been observed

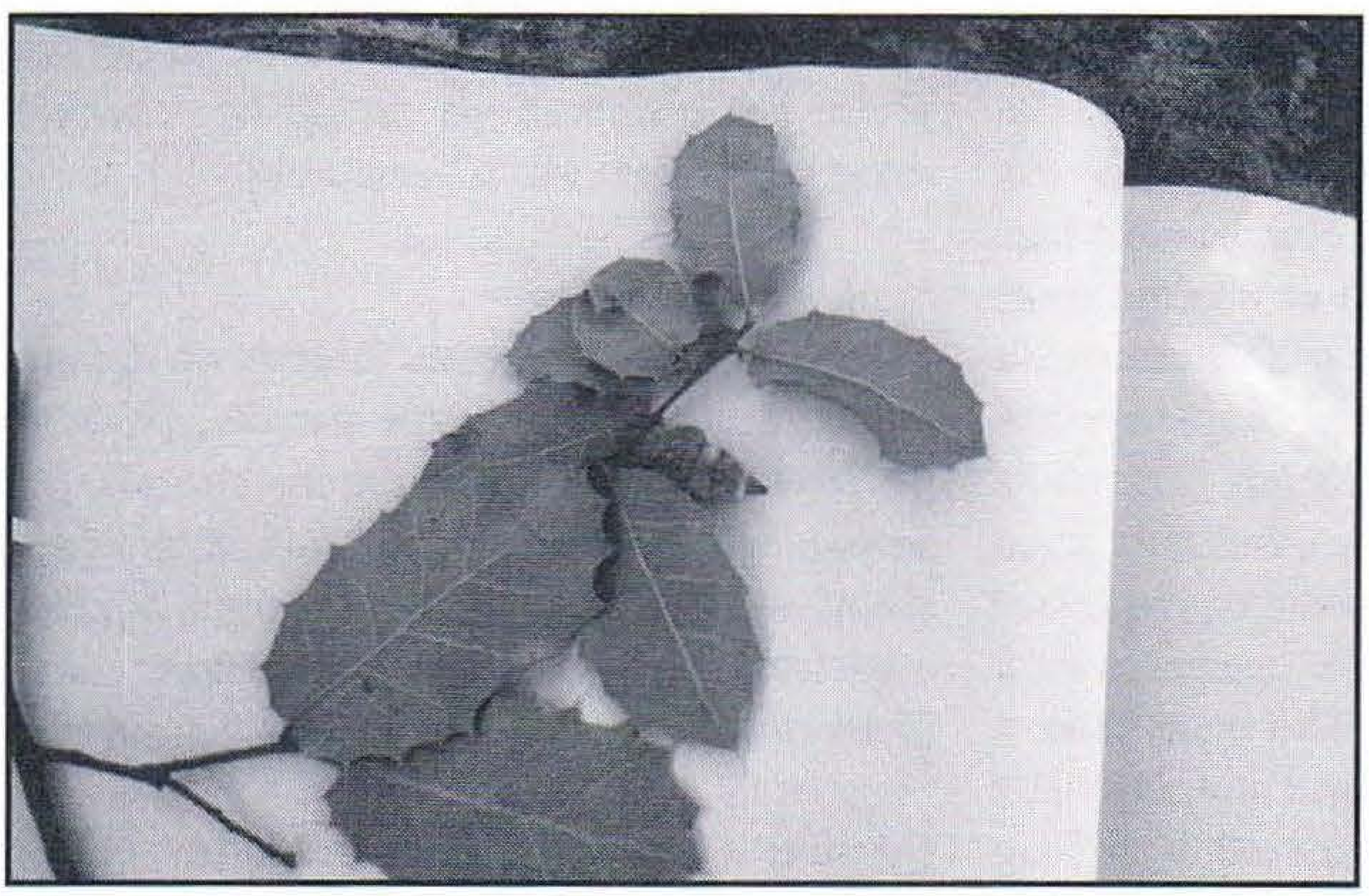

Photo by Th. Lamant

Quercus xauzandrii *Gren. and Godr. (syn.* Q. auxandrii*) herbarium specimen from Cadolive, Departement Bouches du Rho. Specimen courtesy of Pierre Lieutaghi.*

next to St. Zacharie. Other specimens have more recently been found in the neighboring departments, next to Cap d'Antibes, in the Bouches-du-Rhône, Vaucluse, Provence Alps.

Ecology:

This oak, like *Q. coccifera*, grows in dry, warm bushy formations called "guarrigues" (with a more or less compact and calcareous soil) together with *Pinus halepensis* and sometimes only *Q. ilex*. In other localities, it grows in warm, dry rocky places with good light. It is interesting to note that *Q. coccifera* has not been confirmed everywhere the hybrid is found. Associated plants are *Phillyrea angustifolia* and *P. media*, *Lonicera implexa*, *Rhamnus alaternus*, *Rosmarinus officinalis*, *Cistus albidus*, *Viburnum tinus* and *Pistacia teribenthus*.

Finally, we are still in search of examples of ***Quercus.* x*albescens* A. Camus** (*Q. ilex* x *Q. pubescens*), described by Antoinette Camus in her monograph of the genus *Quercus* at the beginning of the century. This hybrid was mentioned as occurring at a location in the Maritime Alps.

Description:

The twigs are densely tomentose but become glabrous at the end of the season. The buds are equally hairy but bear more scales than *Q. ilex*. The semi-deciduous foliage is characterized by small short-stalked leaves (stalk 0.3 to 1 cm long), of an obovate form with rounded or obtuse tips and a truncate or somewhat rounded base. The leaf blade measures 4 to 7 cm long by 2 to 3 cm wide, with thick texture (except when young) and is edged with coriaceous and often mucronate teeth, at the end of the veins. The teeth in the middle of the leaf are sometimes slightly lobed. The middle vein is rather prominent.

These chance hybrid populations have no genetic stability, as the second generation's diversity is increased by backcrosses with the parents. Their future is strictly linked to their ability to fit their environment, in particular to a strong initial growth. Most often these chance hybrids are not favoured by the selective pressure of nature. If ever they would persist and become well adapted to their environment, these hybrids could become true species (as in the example of *Abies borisii-regis*, borne from an introgressive zone between *A.. alba* and *A. cephalonica*).

Conclusions

The Mediterranean forest has been strongly degraded by human intervention. But Man is also sometimes responsible for causing hybridization by inducing artificial cohabitation between two species. Unfortunately, the Mediterranean hybrids are still poorly known and the botanical descriptions do not always match from one book to another. As usual, careful field observations often reveal the distinguishing features of these hybrids. However, the extreme foliar diversity of *Q. ilex* (one of the parents of these hybrids), influenced partly by various conditions of climate and site, make the identification of the hybrids difficult. In spite of this, the main difficulty is the chorology. An enormous effort of inventory should be undertaken, followed by measures of preservation at least for the most endangered trees. A few people are working for that purpose. Pierre Leuthaghi is one of these and thus deserves great thanks.

The Mediterranean forest is fragile and threatened. The knowledge of rare hybrids, their preservation, and multiplication in specialized collections or as small forest stands could help, in a way, protect it. If these hybrids are to become efficient (that means, well adapted to their environment), it would be interesting to promote them and recreate the Mediterranean forest that Man helped destroy.

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Table 1. Comparative features of *Q.* x *hispanica* and its two parents.

Species	Features Habit	Bark	Twig	Bud	Leaf	Fruit	Maturity	Ecology
Q. suber	Tree >20 m, open crown rounded	suberous and very thick	hairy	tomentose	evergreen, margins wavy and armed, dark green glabrous above, tomentose grey bluish below	solitary or on pair, short stalk, scales villous & erected, acorn half enclosed in the cup	one year	not chalky soils, high hygrometry
Q. cerris	Tree >35 m, large crown rounded	dark grey with greyish longitudinal ridges separated with orange deep fissures	brown and hairy	brown, sharp with long scales	deciduous, very coarsely thooted or lobed, glabrous above, hairy below becoming glabrous	solitary or till 4, very short stalk, scales villous & curved, acorn half enclosed in the cup	two years	neutral, loamy, chalky soils & calcareous sands
***Q.* x *hispanica* (= *Q. suber* x *Q. cerris*)**	Tree >25 m, open crown rounded	Dark grey and somewhat suberous	reddish-brown & very hairy	Brown, with long scales only on terminal buds	subevergreen, tough, nearly glabrous above, tomentose below	solitary or in pair, short stalk, scales tomentose, acorn half enclosed in the cup	two years	loamy, sandy soils, without active chalk, high hygrometry

Table 2. Comparative features of *Q.* x *morisii* and its two parents.

Species	Features Habit	Bark	Twig	Bud	Leaf	Fruit	Maturity	Ecology
Q. ilex	Tree >20 m, densely branched, globose or ovoid crown	longitudinally furrowed in little thin scaly grey dark plates	greyish, hairy when young becoming more or less hairy	little & globose	evergreen, tough, more or less remotely toothed, dark green shiny & glabrous above, greyish tomentose below	solitary or till 3, short stalk, short appressed tomentose scales, acorn nearly half enclosed in the cup	one year	limestone to sandstone
Q. suber	Tree >20 m, open crown rounded	suberous and very thick	hairy	tomentose	evergreen, margins, wavy and armed, dark green glabrous above, tomentose grey bluish below	solitary or on pair, short stalk, scales villous & erected, acorn half enclosed in the cup	one year	not chalky soils, need high hygrometry
***Q.* x *morisii* (= *Q. ilex* x *Q. suber*)**	shrub or little tree (5 to 20 m)	thick, deeply furrowed in large plates with more or less curved edges	densely white tomentose when young	petits et tomenteux	evergreen, glabrous above, white tomentose below, upper half with toothed margin	solitary, short stalk, long appressed tomentose scales, acorn half or more enclosed in the cup	one year	calcifuge, silice, gneiss, shists & granitic origin soils, need high hygrometry

Table 3. Comparative features of *Q.* x *auzandri* and its two parents.

Species	Features Habit	Bark	Twig	Bud	Leaf	Fruit	Maturity	Ecology
Q. ilex	Tree >20 m, densely branched, globose or ovoid crown	longitudinally furrowed in little thin scaly grey dark plates	Greyish, hairy when young becoming more or less hairy	little & globose	evergreen, tough, more or less remotely toothed, dark green shiny & glabrous above, greyish tomentose below	solitary or till 3, short stalk, short appressed tomentose scales, acorn nearly half enclosed in the cup	one year	limestone to sandstone
Q. coccifera	bushy shrub, 0.5 to 4 m, densely branched	grey dark & smooth	Tough, often divaricated, greyish & hairy	brown & ovoid	evergreen, little, coriaceous, margin very spiny, glabrous & shiny on both faces	solitary, short stalk, sharp lanceolate & erected scales, acorn more than half enclosed in the cup	two years	warm, dry and compact chalky soils
***Q.* x *auzandri* (= *Q. ilex* x *Q. coccifera*)**	Bushy shrub > 2 m or small tree > 15 m	indifferently like one or the other of the 2 parents	hairy, erected or drooped but never divaricated	brown & ovoid	evergreen, margin slightly toothed, glabrous above & more or less tomentose below	solitary, short stalk, long scales never appressed, acorn more than half enclosed in the cup	one year	warm, dry and compact chalky soils

Rare Oaks . . .

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Oak Management at Westonbirt Arboretum

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Westonbirt Arboretum was founded in 1829 by Robert Holford. Today it extends to 600 acres and has in excess of 18,000 numbered trees and shrubs, many dating back to this period. The collection was centered around the current site due to the occurrence of two pockets of acid soil. These are situated in Savill Glade and the Sand Earth area of Silk Wood. These pockets of acid soil can support a much greater diversity of trees and shrubs. When Robert Holford was planning the Arboretum his main aim was to create the biggest collection of trees in the United Kingdom. Subsequent generations of the Holford family have continued to plant trees with the same passion and commitment. In 1956 the collection passed to the Forestry Commission who have been managing it ever since.

The area just north of the visitor center is where the Arboretum was started and all the ground north and east of this area was open fields in the 1820's, with only a few hedgerow trees which still remain today. The next area, developed in the 1850's, was that around 'The Pool' and then in the 1870's, Jackson Avenue.

In 1875 Robert Holford was joined by his son Sir George Holford and his first job was to start on the development of Silk Wood. Silk Wood was all semi-natural woodland at this time and has a history dating many centuries. The main crop is *Quercus robur* with an understorey of *Corylus avellana*. The first job Sir George undertook was to cut through this woodland and create Willesley, Broad and Waste Drives. Sir George was also responsible for the original maple plantings both in this area and in the Old Arboretum. Many of the trees still growing in this area date back to this period.

In 1956 the estate passed to the Forestry Commission and we carry on the Holford's work, albeit from a much more scientific viewpoint. Our main objectives today are conservation, education and recreation. All these objectives are of equal importance and the skill of management today lies in getting the correct balance between them.

The conservation side of our work is the collection of trees themselves and the information that we collect about our 18,000 numbered individuals. We are basically plotting the life history of every tree from the time that it arrives in the Arboretum until its death. This means that we record anything of significance that happens to each one. All records are kept on a computer database and the information is recorded in the International Transfer Format. This will allow us, at some time in the future, to communicate more effectively with other collections around the world. Today the greater percentage of species added to the collection are of documented wild origin. We currently list some 63 species that are regarded as rare and endangered in the wild.

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*Former director John White examining a declining English oak (*Quercus robur *L.) at Westonbirt dated by White to the year 1665.*

To look after our educational responsibilities we employ a full time Education Officer who is supported by a number of part time staff. We offer a wide range of activities ranging from half-hour introductory talks to a full-day programs, depending on the needs of the particular group. We have concentrated our activities towards the younger age groups and 95% of our work today is with 5- to 11-year olds. During most years around 12,000 children visit and use our facilities. We are also developing a number of Botanical Workshops through our events program. These involve a number of activities such as Fungal Forays, Identification of Conifers, Tree Gazing and Propagation.

The Arboretum has been open to the public since 1956 but it is only in the last few years that visitor numbers have reached about 250,000. Of these, up to half come to see our displays of autumn color during the month of October. However it is the variety of fungi, birds, flowers and insects, as well as the trees and shrubs, that makes Westonbirt such a special place to so many people. Visitors now provide us with enough income to cover all our expenditures.

This has enabled us to start looking at expanding the collection. A project team is currently involved in looking at this and hopes to draw up some objectives and plans within the next few months. Some of our current thinking revolves around strengthening our maple and native species collections. We shall also look at our current management of the semi-natural woodland, although this will involve more active management.

The greater part of our work at Westonbirt involves the active management of trees and we have several hundred oaks that we look

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after for different reasons. These are spilt into five different management types.

1. Oaks used in the shelter matrix.
2. Veteran oaks - trees greater than 200 years old.
3. Oak standards with hazel coppice.
4. Oak collection.
5. Expansion plans.

Westonbirt Arboretum is 400 ft. above sea level. It has no natural shelter and is open to all elements so it was essential to establish some shelter before starting to plant the collection. This was recognized by Robert Holford and his first job was to plant a matrix of trees on the open ground. The main species that he planted were *Quercus robur*, *Quercus ilex*, *Taxus baccata* and *Pinus sylvestris*. Once these trees became established, he then began to cut out pockets and plant them with the new plants that were coming into the country at that time.

Quercus robur forms 70 percent of these shelter plantings and is by far the most important of the overstory species. The characteristics of *Quercus robur* that interest us most in this situation are that : it makes a large tree; it is long lived; it has a good rooting system and is relatively wind firm. Growing into a large tree is very important as many of the specimen trees needing shelter also have the potential to grow very big. Therefore the trees put in to provide shelter also need to be large.

It is also advantageous if these trees are long lived, since this avoids re-planting and gives a greater continuity of shelter. This in itself is of great importance. Using *Quercus robur* will hopefully mean that we have the right tree in the right place for at least 200 to 300 years. Being on an exposed site means that we are buffeted by a number of strong winds every year. It is inevitable that we will lose some trees, but having a tree that is wind firm within the shelter system means that the losses are much reduced.

The importance of continuity in a shelter system has been mentioned already. This can not be over stressed and can only be achieved by the active management of those trees used to provide shelter, in conjunction with good

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*A healthy English oak (*Quercus robur *L.) planted at Westonbirt in 1829.*

choice of species. This means that we can not wait until the trees die of old age, as this means that a large percentage of a particular species is liable to die within a relatively short period of time. The consequences of this can only be imagined but would, without doubt, have a catastrophic effect upon a collection like Westonbirt. To minimize this we have established an active policy of removing relatively young trees and planting new ones. Over the next hundred years or so the age structure of the shelter plantings will be much more continuous, resulting in the whole collection being less prone to wind damage.

I mentioned the removal of trees at a relatively young age. By this we are not talking about plants less than 100 years old. It is also important to stress that with a continuous age structure there will be room for 500-year-old trees alongside the one- and two-year olds. The aim is to achieve this continuous age structure throughout the whole collection.

Careful management of our older trees is essential, especially with the large number of visitors present in our grounds. Accidents caused by falling trees and branches must be avoided. First, it is essential that we know where all the older trees are. This is achieved by having every one of our trees mapped. An active mapping program is essential to ensure that maps are kept up to date.

Once these trees are identified they go onto our "trees for regular inspection" list and they are looked at once during every six month period. During this inspection we determine if the tree looks healthy, and also if there are any potential problems from a public safety viewpoint. All details from these inspections are recorded on our database. The location of the tree will also determine what type of action we take. For instance if the tree is in an area of high public access then we would remove any deadwood as a matter of routine. However if it is well away from the public areas we may not take any immediate action.

If we decide that a tree is inherently unsafe, then we must consider the type of action most appropriate. In the case of a large old oak in the vicinity of our Visitor Center we decided that something had to be done before it became a real hazard. The tree was around 300 years old and had some very big scars from previous tree surgery work. In addition, at least one very large limb was overhanging a main path. Our first thoughts were that the tree would need to be removed. This was a difficult decision, but we felt that we had no choice because of its position. At this point we came up with the alternative idea of pollarding the tree. This involved removing all the large diameter limbs about four meters from the ground. This addressed the public safety concerns while retaining the genetic material. Concerns about the appearance and life expectancy of the tree after the work had been done were unfounded, part of the success being due to our highly skilled tree team. Five years later I am pleased to say that the tree appears to have recovered well and has a very satisfactory appearance.

If the only thing to do is to remove a tree, then we ask if that particular tree has any genetic value to the collection ? If the answer is "yes," then the tree will immediately go to a category one status on our "trees for propagation" list. This basically means that we shall propagate from the tree before it is removed. Having done this means that we retain the genetic material, albeit in the form of a 10-cm plant rather than a 30-m tree.

Our next management category is our "oak standards and hazel coppice." These areas at one time covered the whole of Silk Wood. This area of woodland has a history of being sold to the peasants dating back to the twelfth century and was actively worked up until 60 years ago. However we are now trying to bring all the remaining areas back into rotation. To

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date we have re-cut some 25 percent of the 30 hectares remaining. It is important with any areas like this to be sure of the objectives before starting any work. I would also stress the importance of recording this information for future reference. Our main objectives with these areas are to:

1. Increase visitor enjoyment by seeing active hazel coppicing in action.
2. Increase the ecological value of the area.
3. Create a sustainable market for the hazel coppice.
4. Enhance the educational value of the area.
5. Re-cut all the areas of hazel coppice.

Oak trees are a key element in these areas. The main consideration is the number of trees to grow on any particular area. Generally speaking the more oaks there are, the less hazel. It is necessary to know what sort of market you have for the hazel, since this dictates how long to leave the hazel between cuts. The better the market for hazel, the fewer oaks will be needed on a given area.

It is important to remember that good management of this woodland type dictates the removal of trees as an essential part of the process. If the oaks are left to grow indefinitely, eventually they will shade out the hazel coppice. This means that every time the hazel is cut it is essential to evaluate the crop of oaks and make an assessment on the number to be left. Any trees that are deemed surplus can then be removed. At the same time it is essential to plant and maintain new trees. Traditionally any type of oak planting stock was used in an arboretum of this nature. However, it is a lost opportunity not to plant something of greater genetic value. It may be possible to plant the progeny from an old tree that had to be removed from somewhere else in the collection. When no local stock is available it is possible to use stock from other areas. Whatever the decision, good record keeping is a key element of this work.

When trees have been felled we are always looking for an innovative use for the timber. Most tend to be sold into the timber trade and are probably sawn up into planks. However at Westonbirt we hold an annual large tree carving event which makes good use of some of the trees. This is a week-long event and finishes with the completed pieces being auctioned and a percentage of the money raised going to 'Tree Aid'. This is a charity committed to planting trees throughout Central Africa.

The oak collection at Westonbirt is centered around the northern end of Broad Drive. It incorporates both the old and new collection. The old collection was started by the Holfords, but the lack of species would suggest that they had no real enthusiasm for this particular genus. The current collection has 105 taxa divided into 68 species, 24 cultivars and 13 others. Out of our 108 trees that are the biggest in the British Isles, only three are oaks. This again indicates the lack of interest shown by the Holfords for this genera.

The area of scrub woodland, adjacent to this collection will be used once we start to expand the collection. For this reason the time has come to re-assess our reasons for having an oak collection. We need to set objectives whether we are re-evaluating an old collection or starting a new one. Then it is important to decide why to have a collection of oaks. There may be a variety of reasons including:

1. Timber production.
2. Scientific research.
3. Conservation.
4. Aesthetic/Landscape.
5. Educational.

Once the objectives are decided upon, the next step is to decide which oaks will best meet them. First, since *Quercus* is such a large genus, it is unlikely that any one site could accommodate all the species. As an example, if conservation is the main objective, then we would probably want to collect the rare and endangered species from around the world. It would also be essential to ensure that the soils and climate are suitable for the type of oaks that we want to grow. As an example, most of the Mexican oaks are not going to survive in Northern England and Scotland, so it would be a waste of resources to consider plants from this area.

Obviously it is not possible for us to grow all oak species at Westonbirt. However, it is important that we assess our current strengths and build on them, including our current maple collection. It therefore seems likely that we shall not be concentrating particularly on oak species. However *Quercus robur* will always be an important tree to the Westonbirt collection, particularly from a wind protection viewpoint. This means that, without doubt, we shall be planting good numbers of oaks throughout our expansion area. If we are going to do this anyway then it makes sense to use plants that have a genetic value. This means that we shall have to consider some sort of propagation program. Planting oaks from this type of material would mean that we would meet a conservation objective as well as providing good wind protection.

To summarize I would like to recap the five different management approaches for oaks at Westonbirt.

1. Quercus robur is one of the essential species in protecting other plants from strong winds. Continuity of shelter is an important element in any plantings and an active management regime of felling and planting is necessary to achieve this. This helps to create a continuous age structure of wind firm trees for long periods of time.

2. Ecologically old oaks are very desirable, but can be a problem from a public safety viewpoint. Hazardous trees must be identified, problems addressed and solutions found. This does not always lead to felling the tree in question and should certainly not lead to any loss of genetic material.

3. Continuity of a good crop of different aged oaks is only achieved by a good felling and planting program. We also look for good ways to use any felled trees. More oaks means less hazel. You need to know your markets and grow the crop that meets that demand.

4. It is essential to define objectives for starting any collection of plants and to state these in a written document ensuring they are revisited at regular intervals. If this is not done, then plants tend to be collected in a very random fashion.

5. Oaks are an essential element to any expansion plans at Westonbirt and it is difficult to imagine Westonbirt without them.

California Oaks and Environmental Education

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In 1990, California celebrated the "Year of the Oak," a statewide aware ness campaign to arouse the public's concern for local and statewide oak issues. At that time, the State Board of Forestry adopted a non-regulatory resource management policy for native oaks that included both research and public education. Recognizing that in the long run, children are an important part of this strategy, many organizations such as the University of California Cooperative Extension and the Sacramento Tree Foundation, began to develop materials and programs for teachers and youth-group leaders focusing on California's oaks and their habitat. As a result, in many parts of the state where oaks are a part of the landscape, some youth have been involved with gathering acorns, planting oak seedlings, and learning about the stewardship issues of oak habitat conservation (Antunez de Mayolo, 1990).

During this past decade, some of these programs, especially those offering curriculum materials for educators and field trips for children, have continued to be used and have also helped educators meet important educational goals. Those that assist teachers comply with the current education reform efforts, such as programs that involve youth in "hands-on" educational experiences that help develop students' analytical and problem-solving skills, are welcomed by educators who are looking for ways to supplement textbook based teaching (California Department of Education, 1995). But many of these programs have been "one-time events." Often they lack support, both the funding and leadership needed to promote them, and have not been sustained or reached the potential to educate enough of California's six million school-age youth. And, if children are considered to be part of the plan to educate the public in an overall non-regulatory resource management strategy that will effectively protect and sustain native oak populations, coordination of an educational outreach program needs to be taken more seriously. Without a systematic and coordinated approach to reach educators , one of the critical links in this conservation strategy — the recruitment of the next generation's concern for the care and protection of California's oaks — may be in jeopardy.

1997 Survey of Oak Education Programs

As a follow-up to a previous informal study of native oak educational programs for school-age youth, a new survey was conducted during 1997. Seventy educators and organizations known to have been involved for the past eight years in youth programs that included some information about oaks, were asked to complete a 2-page survey that requested information about their particular oak education program. A review of 28 of the 34 programs and educators that responded is summarized in Table 1. This sample demonstrates that there has been continuous interest to provide educational opportunities for students to learn about oaks and oak issues. Lessons learned from an evaluation of the responses are provided in this paper.

Educational Strategies

The types of oak education programs reported can be grouped into three categories: curriculum and project activity guides for teachers and youth group leaders; hands-on horticultural lessons; and field trip experiences for children.

Curriculum such as *Seed to Seedling* (Antunez de Mayolo, 1990), developed and currently distributed by the Sacramento Tree Foundation and the California Oak Foundation, continues to be used by teachers. This curriculum was evaluated by a team of environmental educators in 1995 and described in *Environmental Education: Compendium for Natural Communities* (California Department of Education, 1995). Inclusion in this document indicates that the materials meet certain educational criteria and are recommended for use in classrooms. In addition, the student pages for *Seed to Seedling* have been translated into Spanish, Russian, Vietnamese, and Lao languages.

Other examples of curriculum are *Youth Oak Project* (1992) and *Oak Woodland Wildlife and Habitat Project* (1992) sponsored by the University of California Cooperative Extension. Both programs are used within the 4-H Program. In Redding, the Carter House Museum's *Autumn Oaks* (1995) curriculum provides teachers with a regional focus on oak ecology and issues.

Acorn gathering and propagation, and oak seedling and tree planting are popular educational activities organized for students. A number of individual teachers and several organizations, such as the 4-H programs, continue to engage youth in propagating and planting oak trees. Many provide care for the trees planted, yet it is clear that without someone "championing" oaks, these projects often do not continue nor achieve the purpose of restoring oaks to an area. One teacher reported that after her retirement, the oak tree planting project she developed and sustained for seven years was eliminated by a school administrator who located portable classrooms on the oak restoration site. Other programs, such as the "New Oaks Project," developed and maintained by the San Juan Water District in Sacramento County, demonstrates that the longevity of a

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Table 1- Summary of a 1997 survey of oak education strategies used with school-age children.

Program Objectives:

- 1. - General awareness and appreciation of California's oaks.
- 2. - Knowledge and understanding of oaks (botanical-historical)
- 3. - An understanding of oaks and oak habitats; environmental and resource management issues.
- 4. - Cultivating a stewardship ethic by providing opportunities for youth to plant trees, assist with oak woodland restoration, etc.

Program	Objectives	Methods/Tools	Audience (age, no., status)
Adopt-a-Watershed Hayfork, other sites	1,2,3,4	Curriculum materials on-going restoration projects	Grades K-6 1250; on-going
Carter House Museum Redding	1,2,3	*Autumn Oaks* curriculum	100 teachers, 4-8 on-going
University of California, Integrated Hardwood Range Management Program, Brown's Valley	1,2,3,4	Field tours, slides shows acorn gathering, planting teacher workshops	hundreds, ages 6-18 on-going
Sacramento River Discovery Center Red Bluff	1,2,3,4	oak tree propagation and planting	new, 1997
Folsom Unified School District, Folsom	1,2,3,4	*Seed to Seedling*	150, grade 2 on-going
"New Oaks" Project Granite Bay, Sacramento	1,2,3,4,	Acorn gathering, seedling care, transplanting	1176, ages 3-18 on-going
Placer Nature Center Auburn	1,2,4	Thematic trail featuring oaks *Seed to Seedling*	7500, grades 1-4 on-going

Table 1- contd.

Program	Objectives	Methods/Tools	Audience (age, no., status)
American River Conservancy, Coloma	1,2,3,4	School programs featuring oaks acorn gathering, propagation, Planting	2000, grades K-6 on-going
Oak Hill Elementary Antelope, Sacramento Co.	1,2	*Seed to Seedling*; gather and propagate acorns, plant seedlings	350, grades 4-6 on-going
Sacramento Tree Foundation	1,2,3,4	*Seed to Seedling* curriculum Educator workshops, classroom Presentations, oak tree planting	2000, grades 4-8 on-going
Cosumnes River Preserve Galt	1,2,4	School programs, students gather and propagate acorns Educator materials	3000, grades K-12 on-going
University of California Davis, Arboretum	1,2	School programs featuring oaks	40,000 grades K-6 on-going
Orchard Elementary School Vacaville	1,2,3,4	*Seed to Seedling* propagate acorns, care	90, grades K-1 on-going
Park Day School Oakland	1,2,3,4	Seed to Seedling propagate acorns to plant after Oakland fire	600, grades K-6 one-time event
California State University, Hayward	1,2,3,4	New teacher discussions about oaks, field trips	900 pre-service on-going
Ormondale School Portola Valley	1,2,3,4	Acorn gathering, propagation planting, native oak study	70, grade 1 discontinued

Table 1- contd.

Program	Objectives	Methods/Tools	Audience (age, no., status)
Return of the Native Restoration Project Seaside, Monterey Co.	4	Restoration of oak woodlands oak seedling planting	5,000, grades K-12 on-going, 50 schools
Cooperative Extension Calaveras County, 4-H San Andreas	1,4	Youth Oak Tree Project video and study materials	700, grades 7-12 on-going, occasional
Yosemite National Park	1,2,3,4	Oak tree planting	40, grades 4-8, One-time event
Orosi High School Sanger	1,2,3,4	Agricultural Education program, oak propagation Identification	400, grades 9-12 on-going
Tule River Parkway Association, Porterville	1,2,3,4	Oak propagation planting, inventory	150, grades 6-8 new, 1997
Cooperative Extension, 4-H San Luis Obispo	1,2,3,4	*Oak Woodland Wildlife Habitat* Project	100, grades 2-10 on-going
Cooperative Extension, 4-H Santa Barbara	1,2,3,4	*Oak Woodland Wildlife Habitat Project*	500, grades 3-12 on-going
Tehachapi Resource Cons. Dst. / Kern County	3,4	Oak tree planting in native gardens	50, grades K-6 one-time event
Riverside-Corona Resource Conservation District, Riverside	1	Oak tree planting at schools	3,600, grades K-6 occasional
Live Oak Park Coalition Fallbrook	1,2,3,4	Teacher and docent guide book, nature trail programs	300, grades 3-4 new 1997

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program often depends on continuous commitment and leadership. In this case, a board member continues to oversee that an annual event, involving hundreds of scouts in the propagation and planting of oak seedlings, that is supported by the agency's staff, with the help of community volunteers.

Interpretative tours and field trips to view oaks and oak woodlands continue to be provided by nature centers and arboreta. These often include acorn gathering and propagation, tree planting activities, discussions of the natural history of native oaks, Indian uses of acorns, and oak folklore. For many years, the arboretum at the University of California, Davis, which has many old oaks, has offered these types of tours and programs for school groups.

Educational Considerations

For several decades, proponents of conservation and environmental education have seriously debated how to educate the public to value the environment in order to conserve and protect natural resources (Hungerford and Volk, 1990.). After the 1992 "Earth Summit" in Rio de Janeiro, an additional emphasis was placed on managing resources to achieve environmental "sustainability". (President's Council on Sustainable Development, 1994). Currently, the California Department of Education is developing and plans to publish a document titled, "California Guide to Environmental Literacy", a blueprint to help schools integrate environmental education into all areas of study, to insure that students arrive at graduation with a comprehensive understanding of ecological principles (California Department of Education, draft).

To accomplish these goals, teachers and their students are encouraged to study ecological principles and help nurture interest in "earth stewardship" values. Yet, in California, with over 6-million students and 200,000 teachers in public schools alone, there is little effort to coordinate environmental education programs or provide adequate funding to help accomplish these goals. It is no mystery why oak education has been limited and difficult to sustain!

Yet despite these hurdles, there are ways to continue to impact California's educators and youth and involve them in learning and caring about native oaks. For example, many teachers have begun to look for ways to involve students in educational activities that may also offer oak educators new opportunities. "Service-learning" programs that combine classroom lessons with community service projects or other types of project-based learning experiences, can easily be centered on oak issues. Teaching issue analysis by using "case studies" that investigate land-use and natural resource issues are popular with middle and high school teachers. Field work to inventory and monitor sample plots within stands of native oaks, habitat restoration and other types of stewardship projects can offer students valuable first-hand information and understanding about oaks. Community organizations and educators interested in supporting these types of educational efforts should consider adapting their programs to complement these types of changes in the classroom curriculum. In doing so, they will educate about oaks and contribute to many of the goals of education reforms (Goals 2000).

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Conclusion

During the last decade, a number of oak education programs have been developed and used by California educators and organizations. To some degree, these efforts continue to help foster the development of children's knowledge and understanding of native oak conservation. Yet, as noted by this survey, there is little effort to coordinate or support these programs, and as a result, many have been discontinued or are "one-time efforts."

Challenged by the state's non-regulatory policy to conserve native oak populations, resource managers and environmental educators should make a serious effort to prepare the state's future decision-makers. It would make sense to expand the support and coordination of oak education within California's schools and in informal educational programs. Organizations and agencies such as the California Oak Foundation, the University of California Integrated Hardwood Range Management Program, the California Department of Forestry and Fire Protection and others could work more closely together, and with educators, to support and sustain these programs. With millions of school-age youth, many living within or nearby regions that are rapidly urbanizing and engulfing oak woodlands, the potential for educating future voters has been significantly under-utilized. To sustain oak education efforts, every year should be the "Year of the Oak". Leadership and coordination of youth involvement should become an important priority and component of the statewide strategy to conserve this precious part of California's natural landscape and valuable natural resource.

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Oaks in Environmental Education in California

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Of the over two hundred identified habitat types in the state of California, 80 percent are threatened by anthropogenic sources. Ninety percent of California's coastal wetlands have been partially or totally destroyed; the State's montane forests are suffering from overexploitation and overmanagement; and our scrubland habitats are being bulldozed to make way for malls and suburban development (Barbour et al. 1993; Jensen et al.1993). Oak habitats are not immune to these pressures.

Throughout many areas of the state, oak and other hardwood rangelands are rapidly giving way to residential and commercial development, golf courses and malls. The fact that the various oak woodland, riparian and forest habitats are largely in private hands has hastened the concern of many. A recent statewide public opinion poll conducted for the California Oak Foundation demonstrated that, *when informed about the issues* affecting oak trees, almost 70 percent of the respondents supported protection of California's native oaks (85 percent of the urban respondents, 45 percent of the rural respondents: J. Cobb, personal comm.). Clearly education has a tremendous role to play in the development of attitudes of stewardship toward our native oaks.

Long-term attitudinal shifts towards stewardship are most likely to resonate throughout a population if successive cohorts of younger people are continuously exposed to and engaged by the messages coming out of ecological science and conservation biology. The California Institute for Biodiversity is a nonprofit, nongovernmental, organization dedicated to providing educational resources in the field of biological diversity. This article reports on an interactive multimedia software program, called *Cal Alive! —Exploring Biodiversity*, targeted for classroom use for young people ages 10 to 15 years. In this paper we focus especially on the formative

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assessment of its Oak Story subprogram. Because of its success here in California, oak enthusiasts around the world are encouraged to consider developing similar resources that embody images and stories about local/regional oak habitats, using software technology as a tool for dissemination.

Methods and materials

Background and local focus of the program

Educators from primary schools all the way to the colleges and universities of California agree that there are scant materials, including textbooks and posters, that directly relate to California's natural environment. Teachers are inundated with resources focusing on the tropics, or on eastern U.S. animals and plants. In desperation, many teachers even try to produce their own pamphlets and handouts because students respond more readily to local and regional references than exotic ones (Fuentes, 1996; Rigby 1997). Our CD-ROMs focus on California biological diversity, and are popular among teachers and professors for that reason above all.

Biodiversity exploration

Cal Alive! —Exploring Biodiversity gives the instructor the option to explore the state's tremendous biodiversity (6000 native vascular plant species, 1000 wildlife species, colossal marine and insect diversity) either *geographically* (by region) or *ecologically* (by biome). Each habitat is thus assigned to both a region and a biome. *Cal Alive!* includes tutorials that relate to the sources of richness of the state's biota. There are panoramas, digitized satellite maps, and activities and stories that link several habitats together into a landscape or representative biome. Since California has a huge number of native oak species (24), oaks are featured in the subprogram "Oaks in California" and also represented in 14 of the 50 total habitats considered by *Cal Alive*.

Science bias

The educational curriculum is science-based, but cross-disciplinary. Much of its science content is quite rigorous and rich. Recently California (and the U.S. in general) has come under criticism for poor performance on standardized science and math exams. Considering that several different measures of intelligence and intellectual ability suggest that California students are more *capable* than ever, one might conclude that, at least in part, schools have failed to engage students in these subjects. Our current program strives to excite students about science and doing science, while allowing them to control and interact with the material. This study focused on an activity that uses constructivist learning strategies when presenting science information to young students.

The medium

Multimedia computing adds a new dimension to learning, by engaging students' spirit of inquiry, stimulating their imaginations through visual/auditory inputs, and providing the potential for one-on-one experimentation and stepwise learning. If used appropriately, multimedia CD-ROMS (and web sites) offer intellectual challenges at the same time that they provide a concise and holistic summary of the discipline.

Instructional objectives and cognitive tasks

A clear objective of the oak study was to engage students' interest and illustrate the consequences of poor management decisions on this habitat. The curriculum uses the resident acorn woodpecker as a faunal mascot to grab the students' interest and illustrate the tight interconnection of life in the oak woodland/forest/savanna. Since these birds harvest acorns for food (highly unusual among woodpeckers), and later store the acorns, they capture the student's attention. As the subject of an activity, the oak/woodpecker relationship points out many interesting facts relating to the ecological value of oak woodlands.

An interactive activity was placed in the oak story segment. Following a constructivist learning strategy, the material (**a**) allowed students to participate in their own learning experience by placing them in control of the navigational options; (**b**) provided navigational tools that allowed students to control content; (**c**) and designed a user-friendly interface that stimulated inquiry learning.

Briefly, the student enters an oak-tree-studded landscape, presumably an "oak savanna". He has learned that acorn woodpeckers (delightful birds with clown-like "faces") feed on acorns and store them for later use. He is given a shovel to plant more oak trees; in planting virtual trees, he sees how, with a larger acorn crop, many new birds are then attracted to the landscape. A second activity relates to the value of leaving dead oaks (snags) in place to serve as storage granaries for the woodpeckers (hatchets allow the student to remove snags, and then observe the decline in woodpeckers.)

Integration with curriculum

The *Cal Alive* oak subproject interweaves well with the major themes of the Science Framework for California Schools (California Department of Education, 1990), especially the sections relating to ecology, ecosystems, geophysics and biology. The CD-ROM's oak story segment also includes interdisciplinary activities that connect with the themes of the Mathematics Framework. For instance, in the woodpecker activity (with visuals of bar charts that animate as the number of acorns, of trees, of snags and of woodpeckers increase or decrease), the student is challenged to describe with words each mathematical effect of each manipulation. Teachers are also thrilled that the CD includes some material on native Indian uses of California oak trees (a photo-essay), as it connects very well with the state's History-Social Science Framework.

Formative assessment

Between October 29 and November 19, 1996 we conducted a formative assessment of the oak story segment in eight schools. The total sample population, drawn from five grade levels, was 160 students. Both pre-testing and post-testing were conducted using formal questionnaires. The study emphasized the central role oaks play in the life cycle of the local oak fauna, and students' understanding of the importance of oak tree habitats in the state.

In addition, we analyzed the response of the students to the use of the CD on videotaped interviews with well-known personalities who shared their feelings about California's oaks, and of animal video. There was a series of questions that were designed to solicit student comment on overall response to the oak story. We included detailed questions about specific aspects of the oak story program, as well as reactions to the computerized format.

Responses to the student questionnaire were recorded, codified and analyzed. Quantitative assessment of content knowledge was based on scoring correct answers. Qualitative data results were synthesized into coherent summaries. Descriptive statistical procedures were used to illuminate specific results. Some of the significant findings are conveyed to the reader in narrative mode (Renn 1996).

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Results

Content

Comparisons of factual material about oaks known or understood by students before and after they went through the oak story segment showed that overall, close to 95 percent of all students had gained a great deal of information about California oaks from the experience. While there were between-school differences in pre-test knowledge about the trees themselves, all schools showed a significant increase in understanding of the ecological material, including issues involving oak conservation, as given by post-test scoring. Follow-up tests administered three months later confirmed retention of, on average, 85 percent of the information tested.

Use of computers in learning

When asked if they like using a computer to learn about native plants and animals, 83 percent responded very positively ("yes, this is the best learning method"). And over 75 percent of the respondents found that exploring on their own, through the interactive navigational instrument found in the oak activity section, was a very good way to learn and get information. Only 1% found that they did not like that mode of learning. (The remainder checked middling categories on their questionnaires.)

One question on the questionnaire asked the students if this was the first time they had used a CD-ROM to learn. Only 24 percent responded that it was their first time. There was an even distribution between boys (12 percent) and girls (12 percent). In a related question, students were asked if they used computers at home; 45 percent of the sample did use computers at home. A closer examination of the data showed that 23 percent of fourth graders used computers at home, while 79 percent of eighth graders did.

Interest level

The most relevant data gleaned from this student survey focused on the interest level of the students. Overall, they were most interested in the acorn woodpecker activity and had learned a great deal about oaks and woodpeckers from it. The interview with Malcolm Margolin was popular too. We compared the level of interest with the interest level in textbooks about California habitats, and found that many more of these students (89%) were excited and motivated by the computer presentation than by textbook presentation of similar material.

Conclusions

Many Californians are unaware of the remarkable biological diversity of their state, and of the great diversity and importance of oaks within its borders. Formal education can be used in helping people become more aware of the status of oaks in their region. One very effective tool in this process of reaching out to young people is through the use of computer technology. Multimedia CD-ROMs can effectively convey information and images to large numbers of students, who then create their own learning regime. *Cal Alive!—Exploring Biodiversity* is a new, high-quality CD-ROM title for 4th to 8th grade levels, that focuses on oaks.

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Back Issues

The following back issues of this journal are available at the prices indicated:

#2, fall/winter 1992
U.S. $5.50
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#3, summer/fall 1993
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(oak hybridization, oaks for urban sites, bur oaks, kermes oak, oaks in philately)

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#5, fall 1994
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(conference proceedings)
U.S. $9.50
(13 papers presented during the 1994 conference)

#7, winter 1996
U.S. $5.50
(Spanish moss, pollen, oak reproduction, oaks of Kaliningrad, Oglethorpe oak, oaks in Sweden)

(NOTE: Proceedings issues #8 and a reprint of issue #1were published in 1999.)

The new book "The Life of an Oak" by Glenn Keator is now available for U.S. $17.95 plus U.S. $3 domestic shipping, or U.S. $5 foreign shipping (surface mail).

The Ecology of Blue Oak (*Quercus douglasii*) Acorn Production

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Acorn production by trees of the genus *Quercus* is highly variable from tree to tree, year to year and site to site. Such variability, particularly among years, is so common among temperate-zone trees that it is generally known as "mast fruiting" or simply "masting" after the old English word the seeds of forest trees. Although oaks may be the most widely distributed genus of tree in the world (Critchfield and Little 1966), their patterns of masting are poorly understood. This is nowhere more evident than in California, where nine species of tree oaks dominate over 3.1 million hectares of woodland throughout the foothills of the state. Acorns produced by these oaks provide a major portion of the food supply for a vast array of wildlife from acorn woodpeckers (*Melanerpes formicivorus*) to turkeys (*Meleagris gallopavo*) and from mule deer (*Odocoileus hemionus*) to wild pigs (*Sus scrofa*) (Verner 1980, Barrett 1980). Acorns have also been estimated to have constituted up to half the diet of most tribes of California Native Americans (Pavlik et al. 1991). Thus, understanding patterns of acorn production is likely to lead to insights into the population dynamics of an important fraction of California's wildlife species and prehistoric native peoples.

Here we summarize some of our research on the causes and consequences of variation in acorn production by California oaks, thus updating earlier publications on this project (Koenig et al. 1994a, Koenig et al. 1994b, Koenig et al. 1996, Koenig and Knops 1995, Koenig and Knops 1997). This has been initiated in stages starting with annual surveys of five species at Hastings Reservation in central coastal California. We later became interested in geographic patterns of acorn production and in 1989 began comparable surveys in two other localities in the central coast ranges. Finally, in 1994, we initiated a statewide acorn survey encompassing 34 populations of 6 species located at 14 different sites between Shasta County in the north to San Diego County in the south. With only four years of data for the statewide survey as of this writing, we can only offer preliminary results on this aspect of the study.

One clear finding of our surveys is that there are significant differences between the acorn production pattern of the species (Koenig et al. 1994a). Here we focus on results from the blue oak *Quercus douglasii*, a species of particular economic and conservation interest due to the fact that it appears to be regenerating poorly throughout much of its wide range in California (Pavlik et al. 1991).

Materials and Methods

The blue oak is the most abundant oak species throughout the foothill regions of California, ranging from Shasta County in the north, encircling the Central Valley, and ending in Los Angeles and Santa Barbara Counties in the south (Griffin and Critchfield 1972), a distance of nearly 800 km. Within this range, it covers an estimated 1.2 million hectares of woodland (Bolsinger 1987).

Blue oaks are a member of the "white oak" subgenus *Quercus* and occasionally hybridize with valley oaks, the other major member of this subgenus in California. Both these species are deciduous and require a single year to mature acorns. That is, flowers produced in spring (March and April) are fertilized and grow into mature acorns several months later in the following autumn (September and October).

Our primary study site is Hastings Reservation, a field station run by the University of California, Berkeley, located in the upper Carmel Valley, Monterey County, in central coastal California. Starting in 1980, we surveyed 56 individually marked blue oaks at this site, all within 3.5 km of each other. We used visual acorn surveys (Koenig et al. 1994b) modified from the original method proposed by Graves (1980). Briefly, each tree is visited in September prior to acorn fall. Two individuals visually survey different parts of the tree and count as many acorns as they can in 15 seconds. These counts are then added to yield "N30," the number of acorns counted in 30 seconds. We also give each tree a score of between 0 (no acorns seen) and 4 (a bumper crop). For statistical analysis, N30 values are generally log-transformed [log(N30+1)]; these values will be referred to as "LN30." Log-transformation compensates for the fact that differences between large N30 values (i.e., between 100 and 110) are intuitively much less than differences between small N30 values (i.e., between 0 and 10). LN30 values are averaged across all individuals to obtain an estimate of the mean annual crop.

For study of geographic synchrony in acorn production, we obtained data from eight additional sites throughout California (see Fig. 6). Two of these (Jasper Ridge and Pozo) were first surveyed in, while the other six were first surveyed in 1994. Methods used were identical to those used at Hastings Reservation.

Results

Annual variation

Acorn production by blue oaks shows considerable variation from year to year (Fig. 1). At Hastings Reservation, the mean number of acorns counted per tree has ranged from less than 1 in 1986 to just over 70 in 1985. Effectively, these correspond to years when it is very difficult to find an acorn and years when almost every blue oak tree produces a bumper crop.

These data raise several issues of interest. First, do these data correspond to what we would expect if acorn crops occur primarily as "boom"

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and "bust" crops? That is, are most years either excellent or poor years for blue oak acorns, with relatively few intermediate years? One way to examine this hypothesis is to compare the frequency distribution of the mean acorn crops against that expected by a normal distribution. If we are unable to reject the hypothesis that the distribution of mean acorn crops is normally distributed, then the data fail to support a bimodal pattern in which most years are either very good or very poor. This is done in Fig. 2 by plotting the actual values versus those expected if mean acorn crop size follows a normal distribution. The observed values match the expected distribution very closely and is not significantly non-normal by a Kolmogorov-Smirnov one-sample test ($z = 0.5$, $P > 0.9$). Thus, the distribution of acorn crop size across years is not strongly bimodal, but rather corresponds to that expected under a (log-) normal distribution, with most years being intermediate in size and relatively few years being either very good or very poor.

What determines the mean acorn crop in any particular year? Previous work has suggested three potentially important variables: (1) rainfall, (2) conditions during flowering and pollination in the spring, and (3) the acorn crop in the prior year. The first pair of these variables tests for correlation between weather conditions and the subsequent acorn crop, while the last postulates significant autocorrelation between the acorn crop in one year and that in the subsequent year.

Pearson correlation coefficients between each of these three variables and the blue oak acorn crop are all significant or nearly so (rainfall during the prior year: $r = -0.52$, $n=18$ years, $P = 0.026$; mean April temperature: $r = 0.75$, n = 18 years, $P < 0.001$; prior year's acorn crop: $r = -0.45$, $n = 17$ years; $P = 0.07$). That is, blue oak acorn crops at Hastings tend to be larger in years when April temperatures are warm and smaller when the prior winter was wet or the prior year's acorn crop was large. However, in a multiple regression including all three of these variables as predictors, only mean April temperature is significant ($F_{1,15} = 3.45$, $P < 0.005$). Using only this variable, we are able to explain 56 percent of the variance in mean annual acorn production by blue oaks at Hastings Reservation. Examination of data suggests that

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Quercus douglasii *Hook and Arn. woodland in the foothills of the Tehachapi Mountains in southern California.*

the main predictive power of this relationship is at the extremes of the spectrum. That is, when mean spring temperatures are very low (<10°C) or very high (>13.5°C), we can confidently predict that the subsequent acorn crop will be correspondingly poor or very good. However, when spring temperatures are intermediate, it is more difficult to be certain what the subsequent acorn crop will be other than that it is unlikely to be unusually large.

One further descriptive issue of interest is the extent to which mean annual acorn production cycles in a predictable way. We have already mentioned that there is a nearly significant negative autocorrelation between the acorn crop one year (year x) and the next year (year $x+1$). However, there is no significant correlation between the acorn crop in year x and in any other subsequent year (Pearson r values for x with $x+2$ through $x+9$ all yield P-values > 0.05). A more precise way to search for cyclicity is to perform time-series analysis. Based on results using the spectral density indicating the relative strength of cycles of the length shown along the x-axis, there is a statistically significant tendency for a cycle of between 2 and 4 years in length with a peak at a period of 2.25 years. Thus, there is significant cyclicity to the mean acorn crop data, but it tends to be obscured by the fact that it is not an integral number of years in length. Data from this testing can only be considered preliminary due to the relatively short (18 year) length of the data set,

Individual variation

Mean annual acorn productivity is a standard measure but sidesteps the considerable variation among individual trees that occurs within the population. For example, one of the 56 trees at Hastings never produced a single acorn as far as we know, while another never had a year in which it did *not* produce at least a detectable. Conversely, 11 trees never produced a "very good" crop defined as having a score of 3 or 4, while the most productive tree in the study was classified as having a very good crop in 13 of the 18 years.

Averaging the LN30 values across all years for each tree, the distribution of the mean productivity of the 56 trees in the Hastings study site can be graphed overlaid with the expected distribution under the null hypothesis that the distribution is (log-) normal across trees. And again, as before, there is no significant difference in the distributions (Kolmogorov-Smirnov test, $z = 0.8$, $P > 0.4$), indicating that, like mean annual productivity, mean individual productivity of blue oaks at Hastings is normally distributed. That is, there are a few extremely productive trees and a few very unproductive trees, but on average, most trees produce, over time, an intermediate number of acorns.

Prior analyses have demonstrated that among-year patterns of acorn production are similar within species (Koenig et al. 1994a). In other words, although individual trees vary widely in their productivity, they are synchronized in their relative productivity; in good years virtually all trees do relatively well and in poor years virtually all trees do relatively poorly. For example, of the 56 trees in our sample, 41 (73%) produced as many acorns as they did during any year of the study in 1985 or 1987, the two best years overall. Conversely, 48 (86%) experienced their worst year in either 1983 or 1986, the two poorest years overall during the study.

What causes individual variation in long-term productivity of individual trees? To address this issue, we measured several variables characteristic of individual trees, including size (DBH), elevation, slope, xylem water potential (Knops and Koenig 1994), leaf nutrient concentrations, and soil nutrient concentrations (Knops and Koenig 1997). Xylem water potential was measured in September and October 1991. Leaves were collected in summer and fall of 1992. Available soil nitrogen and phosphorus were measured using ion exchange

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resin bags buried in the soil around each tree during the winter of 1992-1993, while total soil nitrogen and phosphorus were measured in the summer of 1992. Additional analyses are forthcoming; in particular, we have not yet completed an analysis of monthly nutrient flux and litterfall underneath a subsample of our trees that we conducted over a five-year period. However, results based on this preliminary data set yield no significant correlation between long-term mean acorn production by individual blue oaks at Hastings and the majority of variables we have measured, including DBH, elevation, and slope. Variables that correlate significantly with mean long-term acorn productivity include predawn xylem water potential, total soil nitrogen, and specific leaf mass, the latter both measured in July 1992. These relationships suggest the following correlates of good long-term acorn production:

(1) *Predawn xylem water potential.* —Trees with better access to ground water have higher predawn xylem water potential values and greater long-term acorn productivity.
(2) *Total soil nitrogen.* —Trees growing in soil containing greater concentrations of nitrogen produced more acorns over the long term.
(3) *Specific leaf mass.* —Trees with tougher, more sclerophyllous leaves tend to produce more acorns, possibly because these trees are also better at conserving water.

How well can we predict long-term acorn productivity based on these values? Including all three of the significant variables in a multiple regression, only predawn xylem water potential variables come out to be significant ($P < 0.05$), explaining 20% of the variance, compared to the 56 percent of the variance in mean among-years productivity we are able to explain with April temperatures. Thus, we are currently able to explain only a relatively small proportion of the variance in productivity among individual trees.

Geographic variation

Masting fruiting is a population phenomenon (Kelly 1994). That is, an individual tree may produce a variable number of seeds from year to year, but masting only occurs when a group or population of many trees together produce (or fail to produce) seeds synchronously from one year to the next. How large is the population of trees that produce acorns synchronously? Most studies of seed production have focused on relatively small areas and there are few data with which to examine this important question.

We now have data on blue oak acorn production over a period of four years by 20 or more individual trees at nine sites throughout California. Although preliminary, the results appear clear. First, the overall trend is for correlation between the mean acorn crops of the various sites to be very high; of the 36 pairwise correlation coefficients, all but one (97 percent) is >0.70. There is also no apparent decrease in synchrony with distance; in fact, using a Mantel test, which tests for a relationship between mean r values and distance, the correlation increases with distance (overall z-value = 0.3, P = 0.04).

Many of the correlations are high due to the fortunate circumstance that the first year of the survey (1994) was an extremely good year throughout the state whereas the second year (1995) was extremely poor (Koenig and Knops

1997). Values are likely to decrease as we accumulate more data, as suggested by the single relatively small value (0.42) which is the correlation between Jasper Ridge and Pozo based on nine years (1989 - 1997) rather than only four years of data. In any case, it appears that blue oaks are clearly synchronized, at least to some extent, in their annual acorn production throughout their range.

Discussion

Our results suggest several important conclusions about acorn production patterns by blue oaks. First, annual crop size correlates strongly with conditions during the spring pollination and fertilization period: relatively dry, warm conditions are presumably favorable for fertilization and are generally followed by larger autumn acorn crops. Second, the distribution of mean annual acorn crops is normally distributed, with most years experiencing intermediate acorn crops rather than "boom" or "bust" crops. Third, there is a significant cyclic period in mean annual acorn production of between 2 and 4 years with a peak at 2.25 years.

As with mean annual productivity, the productivity of individual blue oak trees is normally distributed; most trees produce an intermediate number of acorns over the long term. Several variables correlate with long-term productivity of individual trees, including their access to ground water (as indicated by xylem water potential), total soil nitrogen where they are growing, and the specific leaf mass of their leaves during the summer. However, even in combination, these variables are able to explain only a relatively small proportion of the variance among trees. Currently we have a good idea of what makes for a good and a bad blue oak acorn year, but we know very little about what makes for a good and a bad blue oak acorn tree, other than that differences in productivity are consistent across years.

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Guy Sternberg examining an old Quercus douglasii *Hook and Arn. in the Los Padres National Forest during the Ventura County field trip of the Second International Oak Conference.*

Although results are preliminary, thus far our statewide acorn surveys suggest that the mean annual blue oak acorn crop is geographically synchronous throughout their range, which extends over nearly 800 km. Apparently the population involved in mast fruiting by blue oaks is very large, covering most, if not all, of the range of the species. Even more extensive geographic synchrony in seed production has been found in boreal trees (Koenig and Knops 1998).

Why do blue oaks exhibit variable acorn production? Like most evolutionary questions, this must be addressed at several levels. Proximately, varying acorn crops by individual trees are the products of ecological differences between trees, including their access to ground water and the nutrient conditions of the soil in which they are growing. Virtually nothing is known con-

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cerning the possible effects of genetic differences between trees or of the role that parasites, predators, or other organisms may play in the long-term success of individual trees in producing acorns. Even less is known about how differences between individual trees in their acorn production patterns may translate into subsequent fitness differences in terms of the probability (which is always very low) that acorns produced by a tree may ultimately survive to grow into a reproductive adult.

Between years, the size of the crop produced by trees within the population at large is correlated with weather conditions during the spring; warm, dry springs are apparently more conducive for pollination and fertilization of flowers. At this point, however, relatively little is known about this important aspect of the life history of blue oaks, or any species of California oak.

Ultimately, the question is one of the fitness consequences of variable acorn production: presumably, trees that produced many acorns some years and few acorns in other years are more successful at leaving progeny than trees that do not vary their acorn production from year to year. Furthermore, trees that vary their patterns of acorn production in synchrony with other trees in the population are also more successful, leading to the pattern of relatively synchronous mast fruiting over the entire range of the species.

Data from our surveys at Hastings Reservation also indicate that species requiring the same number of years to mature acorns produce crops are positively correlated, while those that require different numbers of years to mature acorns are not. For blue oaks, this shows up as a significant positive correlation with both valley and coast live oaks and negative (but non-significant) correlation with both canyon live and California black oaks. This means that acorn availability within many sites throughout California are moderately synchronized, since valley, blue, and coast live oaks are the three common constituents of many coast range communities throughout the state. However, most sites in California are topographically quite diverse and species requiring two years to mature acorns are frequently either present or growing less than a few miles away. Thus, in general, it is rare in California for acorn production by all species of oaks at a site to fail simultaneously.

This puzzling aspect of oak biology may be partially explained by the curious fact that some of the major vertebrate predators of acorns, particularly California scrub-jays (*Aphelocoma californica*), are simultaneously the primary dispersers of acorns throughout much of California, caching large numbers of acorns in the ground where they are offered a relatively good chance of surviving and germinating (Grinnell 1936). From an evolutionary standpoint, this places many species of California oaks in something of a dilemma. From a pure standpoint of predator satiation, the more synchronized all trees in the community are the better. However, to maximize dispersal of acorns, trees probably benefit by maintaining a moderately large, healthy population of scrub-jays. Perhaps the observed result, which is a population of predators sustained sufficiently by acorns that they are able to harvest the entire crop in most years but are overwhelmed in very good years, is exactly the compromise we would expect given the conflicting roles of many of these major acorn predators.

Conclusion

The acorns produced by California oaks offer both a vast wealth of food for wildlife and a nearly limitless source of variation begging to be explained. We are just now beginning to describe and understand the complex patterns of acorn production, both across individuals, species, years, and sites. Yet many questions remain. We still know very little about what goes on prior to the maturation of a particular year's acorn crop. The extent to which the production of female flowers or varies in synchrony with subsequent acorn production is largely unknown, in part because of the relative difficulty of censusing female flowers. We know surprisingly little about the effects of predators on patterns of acorn production and even less about the causes of variation in the life-history strategies of individual trees. We are able to explain a high proportion of annual variation in some species but relatively little in others (Koenig et al. 1996).

Particularly notable is the all but complete absence of information on catkins production or on pollen dispersal by oaks; only recently with the development of molecular DNA markers has it become possible to determine paternity of acorns (Dow and Ashley 1996). Although few data are available spatial patterns of acorn production, ongoing work promises to make a significant inroads in this field as well. Ultimately, we look forward to a day when we are able to explain a much higher proportion of the variation in acorn production by California oaks at all levels than is currently within our grasp.

Acknowledgements

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Artificially Regenerating Native Oaks in California

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Since the turn of the century, there have been persistent reports that the natural regeneration of several species of native California oaks is inadequate to sustain their populations. The primary species of concern are blue oak (*Q. douglasii*), valley oak (*Q. lobata*) and Engelmann oak (*Q. engelmannii*). These are all deciduous white oaks, endemic to California, that grow primarily in the foothills or lower elevation valleys. Unlike many oaks in other parts of the United States, these species have little commercial value other than for firewood. As a result, there has been little economic incentive to study them. Interest in their ecology and management has sprung up in the last two decades. Fear has arisen that important aesthetic and wildlife values associated with these species will be depleted or lost if we don't understand the factors contributing to poor regeneration and take steps to enhance regeneration through artificial means. Unfortunately, until recently, few native oaks were produced in the state and relatively little research was directed towards growing vigorous, healthy stock, or to understanding factors which influence field performance. To help develop guidelines for successfully artificially regenerating native California oaks, research projects have been undertaken during the last ten years. Projects at the University of California's Sierra Foothill Research and Extension Center, 30 km northeast of Marysville, and at the California Department of Forestry and Fire Protection nurseries at Davis and Magalia have focused on developing practical, low-cost techniques for producing, planting and protecting oak seedlings. Hopefully this information will promote greater success in regeneration plantings and help ensure the long-term conservation of these important indigenous species.

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Acorn Projects

Several studies have examined acorn collection, handling, storage and planting, including the best time to collect blue oak acorns and the effect various pre-storage treatments have on germination. Results have indicated that acorns can be successfully collected over a fairly wide interval, extending from late August until late October. Acorns from these harvest dates had high germination, as long as they were not allowed to dry out before storage. However, the earlier the acorns were collected, the earlier they tended to germinate. Soaking acorns for a day prior to storage had little effect. Drying acorns, however, reduced both the rate and amount of germination. A 10 percent reduction in moisture content resulted in almost 40 percent less total germination, and all acorns that lost 25 percent or more of their moisture after harvest failed to germinate during the 10-week test interval.

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An ancient, picturesque specimen of Quercus douglasii *Hook and Arn. in Oak Creek Canyon, southeastern Kern County, California.*

Another project examined the effect of trimming acorn radicles on field growth and survival of blue oaks. For this study, a large group blue oak acorns were pregerminated by placing them in moist vermiculite at room temperature. They were then divided into treatments including acorns whose radicles were left intact, and acorns whose radicles were partially cut off. While radicle trimming tended to promote multi-branched root systems, it had no effect on field performance. Another study examined sowing date. In this project, the date acorns were outplanted greatly influenced seedling emergence, as well as survival and height growth. Sowing in the early fall (October 10 or November 10) resulted in earlier emergence, greater survival and increased height growth, compared to sowing in the late winter (March 10) for both blue and valley oaks. In the Mediterranean climate of California, where there is often little rainfall after April, early acorn sowing apparently gives seedlings a better chance to become established before soil moisture becomes limiting.

Producing Oak Seedlings

Several methods of growing native California oak seedlings, including both bareroot and container production, have been evaluated.

This research has demonstrated that there are a variety of oak seedling stock types that can be successfully propagated and outplanted. The type of stock best suited for a particular planting will depend on a host of factors, including costs, seedling availability, and conditions at the planting site. One-year-old bareroot blue and valley oak seedlings have had high survival and vigorous growth after outplanting, as long as the roots were undercut early enough in the nursery to promote the development of a fibrous root system, and the seedlings were lifted and planted in the field by mid-March. Similarly, blue oak seedlings grown for one year in a wide range of container sizes have performed well in the field. While seedling size at outplanting was directly related to the size of the container they were grown in, by the end of the second field season, these differences had all but disappeared and seedlings from the container sizes tested grew about the same.

A study also compared the field performance of standard one-year-old blue oak container stock with that of seedlings grown for only 4 months and outplanted the spring after the acorns were collected. While the younger stock at outplanting was much smaller, after the first field season, survival and total height were significantly greater. This trend continued for the subsequent three years. Since 4-month old seedlings are far cheaper to produce, they may be a preferred stock type for future regeneration programs for this species.

Another study compared both standard container and bareroot nursery stock to a new stock type called mini-plugs, which are seedlings that are grown for several months in small, shallow containers and then transplanted to barefoot nursery beds in the spring. While in the containers, the oak's roots grow rapidly, but due to the shallow container depth, they repeatedly air-prune themselves. As a result, a highly branched root system with numerous growing tips develops. The mini-plug transplants in this study grew larger initially and performed better in the field during the first three field-growing seasons than the other stock types. By the fourth year, however, there were no significant differences in survival or diameter among any of the stock types evaluated. The mini-plug transplants were also considerably more expensive to produce, so at present, we cannot recommend this stock type for commercial production of oaks.

Finally, several studies have compared the field performance of directly sown acorns to that of transplanted container seedlings. In general, the direct-seeded acorns have performed as well or better than transplanted seedlings. The one exception has been in field sites where acorn depredation was a serious problem because of high populations of rodents. In such instances it can be difficult to successfully establish oak seedlings from acorns without somewhat heroic efforts to protect the seeds in the ground from animal depredation. Without adequate protection, a high percentages of the planted acorns will be eaten before they can grow into seedlings.

Seedling Planting and Protection

Many areas targeted for artificial regeneration of native oaks in California are on hardwood rangelands where dense annual vegetation, compacted soils, and animal herbivory, can limit recruitment success. Controlling competing vegetation through scalping, spraying or mulching can greatly improve the survival and growth of outplanted seedlings. In a study initiated several years ago, various levels of weed control (diameter of weed-free zones around seedlings) were compared. Results indicated that seedling height and diameter growth were strongly related to the diameter of the weed-free areas, up to a diameter of 1.8 m. In this same trial, we also compared the field performance of seedlings protected with treeshelters (double-walled plastic tubes) to those covered with aluminum screens. During

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the first season, seedlings in treeshelters had higher survival, more flushes, grew taller, and were more resistant to attack from small sucking insects, which were able to pass through the screens. By the second year, the seedlings in the tubes also had significantly greater diameter and diameter increment. Subsequent trials with treeshelters have also shown that they greatly stimulate height growth, even of seedlings several years old that have been stunted due to harsh field conditions. Treeshelters have also successfully protected seedlings from a wide range of animals, including deer, rabbits, cattle, voles and grasshoppers, and have had fewer maintenance problems over the long term.

Studies have also shown that augering holes prior to planting can improve field performance — especially on compacted sites — by allowing seedling roots to more easily penetrate downward and obtain soil moisture unavailable at shallower rooting depths. Fertilizing seedlings with slow release fertilizer tablets at the time of planting has also resulted in large short-term increases in both diameter and height growth in field trials.

Conclusions

These studies suggest that native California oaks can be successfully propagated and outplanted if sufficient attention is paid to maintaining the physiological quality of the acorns and seedlings, if they are planted properly, and if the plants are protected and maintained in the field. The survival and growth of oak seedlings in natural settings is often limited by harsh environmental conditions. By providing a more favorable environment through weed control, augering, fertilization and protection with treeshelters, rapid juvenile growth after outplanting can be stimulated. This should allow seedlings to quickly grow above the level where they are particularly vulnerable to browsing pressures, and help ensure the success of regeneration plantings. However, it is important to note that all of this research has been underway a relatively short time — at least compared to the life span of oak trees — so any conclusions regarding the long-term effectiveness of these treatments must be made cautiously. Also, while we have had considerable success in research plots under controlled conditions, we have also found that it is much more difficult "in the real world". Even at the Research Center we have had much greater difficulty getting oaks established in larger plantings where we have had less control of the environment.

Finally, to date, there have still been few large scale oak restoration plantings in the state due, primarily, to the high costs of maintenance and protection. The main groups actively planting oaks are developers, as part of mitigation for tree removal, and The Nature Conservancy, as part of riparian restoration projects along the Cosumnes and Sacramento Rivers. It is hoped that as awareness of the critical ecological role that oaks play in the natural environment of California increases, and the costs of artificial regeneration decline, more areas will be artificially regenerated with native California oaks.

The Ecology of Blue Oak Regeneration

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Blue oak (*Quercus douglasii*) is a drought-tolerant deciduous white oak that is endemic to California's Sierra Nevada foothills and Coast Ranges. Woodlands dominated by blue oak cover almost 1.2 million hectares in California and rank as the most abundant hardwood forest type in the state (Bolsinger 1988). Blue oak may occur in nearly pure stands, as a dominant in mixed stands that include foothill pine (*Pinus sabiniana*), interior live oak (*Q. wislizeni*), valley oak (*Q. lobata*), and/or coast live oak (*Q. agrifolia*), or as a minor component in mixed stands of oaks and other hardwoods.

Blue oak presents an apparent paradox because this common and well-adapted species is now regenerating poorly over much of its current range. In 1992, we surveyed 61-hectare sections of blue oak woodland at each of 15 locations distributed throughout the range of blue oak. Mortality of overstory blue oak trees had occurred within the past 30 years at all 15 locations, yet sapling recruitment was observed at only 11 locations (Swiecki et al 1993). When we examined the balance between plots with density losses due to mortality and plots with the potential for density gain due to sapling recruitment, we concluded that 13 of the 15 locations were losing blue oak density at the stand level due to unreplaced mortality. Consistent with our results, surveys by Bolsinger (1988) and Muick and Bartolome (1987) have also indicated that blue oak sapling populations are insufficient to maintain current stand densities.

The lack of a unifying model of blue oak regeneration has led to disagreement over the severity of the regeneration problem and conflicting recom-

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mendations for sustainable management of blue oak woodlands. In this paper, we seek to integrate recent experimental data with a century's worth of ecological observations to build a conceptual model of blue oak regeneration. The model we describe here allows us to develop reasonable explanations for both current and past regeneration patterns and points toward strategies for sustainable management of blue oak woodlands.

A model of blue oak regeneration

Quercus species produce seed crops that vary widely in quantity from year to year. Most acorns land under or near the canopy of the parent tree, although some are planted beyond the canopy by seed-eating animals. No long-term seed banks exist for oaks because acorns do not survive from year to year.

In place of a seed bank, most oaks regenerate from a bank of persistent seedlings beneath the canopy, which is also known as advance regeneration (Oliver and Larson 1990). The seedlings constituting advance regeneration are suppressed by competition from the overstory. These understory seedlings may survive for years, producing a strong root system but little shoot growth. Shoots of persistent seedlings may periodically die back to the ground, but new shoots later resprout from the root collar. When released from competition by the death or removal of the overstory, established persistent seedlings respond with relatively rapid shoot growth, and a pulse of regeneration results.

Blue oak regeneration fits this general model. Blue oak acorns germinate as soon as moisture is present. The food reserves in the acorn are translocated into the developing seedling, and most of the stored carbohydrate is invested in the seedling's large taproot. The energy reserves in the taproot make it possible for seedlings to resprout from the root crown following shoot loss.

Blue oak seedling advance regeneration is very small, typically less that 15 cm tall, and easy to overlook. Blue oak seedlings in this size class can persist in the understory for many years without any net gain in shoot height (Swiecki et al 1990, 1993, Phillips et al 1997). A stem may grow for one to several years, sometimes dying back part way, sometimes dying all the way back to the thickened shoot base. Many seedlings that appear dead and gone in August may well be back the following spring, a fact that has not been adequately accounted for in past seedling surveys (Bolsinger 1988, Muick and Bartolome 1987).

Persistent seedlings do not survive and resprout indefinitely. The mortality rate of natural seedlings which died back to the shoot base two years in a row was four times that of seedlings whose shoots persisted over the previous two years (Swiecki at al 1990). Among six natural blue oak seedling cohorts which we marked in 1988, survival after five years ranged between 6.5 percent and 83 percent. Seedling persistence is influenced both by site characteristics, such as microclimate, and damaging agents that destroy the shoot, including herbivores and fire.

As is typical of advance regeneration, almost all small blue oak seedlings are found beneath or near the edge of blue oak canopy. Besides being the landing zone for most of the acorn crop, conditions under the canopy are favorable for seedling establishment. Oak litter protects acorns from desiccation and provides a favorable seedbed for germination. Blue oak seedlings benefit from the moderate shade and elevated soil nutrient levels found beneath blue oak canopy. In xeric sites receiving full sun, blue oak seedlings typically succumb to drought within the first year or two (Muick 1997). Mycorrhizal colonization of seedling roots may also be favored beneath oak canopy. Although the blue oak canopy benefits early seedling survival, parent trees also compete with their understory progeny for soil moisture because their roots share the same soil volume. This competition is at least partially responsible for the dwarf stature of blue oak advance regeneration. In arid climates where blue oak achieves its greatest dominance, characteristics that reduce soil moisture competition between overstory trees and understory seedlings would have adaptive value. Intraspecific competition for soil moisture would be intense and detrimental if numerous large seedlings or saplings existed in the blue oak understory.


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Foliage of Quercus douglasii *Hook and Arn.*

For blue oak, we define the sapling stage as the transitional stage between seedling advance regeneration and overstory trees. This transitional sapling stage includes a size range from plants with basal diameters of 1 cm or more up to those with a DBH of 3 cm, a size range smaller than foresters would typically call saplings. Functionally, blue oaks have been recruited to the tree size class once they are safely beyond the browse line (typically about 150-170 cm). In many parts of its arid range, mature blue oak trees may be less than 9 m tall, and may require 50 to 100 years to attain a DBH of 10 cm (Kertis et al 1993).

Like mature trees, sapling blue oaks are intolerant of overtopping and will slowly decline in heavy shade. Thus, saplings and small trees are most commonly found in the open even though small seedlings are almost exclusively located adjacent to or beneath blue oak canopy (Muick and Bartolome 1987, Swiecki et al 1993). This shift in spatial distribution comes about through the removal or natural mortality of overstory trees and subsequent release of seedling advance regeneration.

Under favorable conditions, blue oak seedlings and saplings can grow rapidly. However, under the moisture-limited conditions found over most of the blue oak range, saplings are tenacious rather than fast growing. Several studies have shown that it has historically taken at least 10 to 30 years for blue oak stems to grow from ground level to a height of about 140 cm. This is an average of only 5 to 14 cm of height growth per year (Harvey 1989, Kertis et al 1993, McClaran 1986, Mensing 1992). The rate of sapling height growth is strongly affected by soil moisture and browsing.

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A second pattern of blue oak regeneration from seed can also be observed, and may have been more common in presettlement blue oak woodlands. Blue oak seedlings can become established from acorns transported by animals to lightly shaded or open mesic sites if plant competition and herbivory are limited. Pioneer colonization of this type most commonly occurs in sites such as roadsides beyond pasture fences, where browsing is minimal and road runoff provides additional soil moisture. Artificial methods for establishing blue oak from seed are essentially based on producing such favorable microsites through weed control and protective enclosures. As discussed below, such "safe sites" are relatively uncommon in grazed woodlands and consequently this pioneering type of reproduction is rare in grazed areas.

Blue oaks can also regenerate from stump sprouts if the cut trees are fairly young and vigorous (Jepson 1910). Sprout-origin trees are often multi-trunked, or may have a single trunk with a sweep at the base where the old stump has callused over. Such trees usually make up a small proportion of blue oak stands, but localized patches dominated by sprout-origin trees occur. Stands dominated by sprout-origin trees arise when uniformly young stands are cut or topkilled by fire. Uniformly young stands of blue oak were probably rare in the virgin woodland but became more common after cutting gave rise to young stands of second-growth. Hence, many of the stands dominated by sprout-origin trees probably represent third growth.

Effects of canopy and site conditions

In our survey, we found that most blue oak saplings are associated with canopy gaps created by cutting or natural overstory mortality occurring in the past 30 to 40 years (Swiecki et al 1993). This is what we would expect if advance regeneration is the typical source of saplings and sapling growth is slow. If blue oak typically pioneers into openings, saplings should occur with equal likelihood in both recent and older openings. However, blue oak saplings are rare in old clearings or openings. This indicates that pioneer reproduction by blue oak is uncommon in rangelands, at least under recent conditions, and that advance regeneration is the source of most saplings we observe.

Many of the natural openings in which blue oak saplings occur are small, such as would result from the death of a single mature tree. Consequently, on a local scale, saplings are usually associated with overstory canopy. Out of the 1500 0.1 hectare plots we surveyed, saplings were most abundant and most common in plots with 20 percent to 50 percent canopy cover even though they were normally in the noncanopied portions of these plots (Swiecki et al 1993). Saplings were uncommon in plots with little or no canopy, unless the lack of canopy was due to a recent canopy gap. Saplings were also less likely to occur in heavily canopied plots, as would be expected for saplings intolerant of overtopping.

At the most xeric locations we studied, blue oak saplings were most likely to be found in relatively mesic sites. These included north-facing slopes, patches of deeper soil, and topographic positions that tend to collect runoff. However, in mesic locations, these site factors are often associated with dense mixed hardwood canopy cover. Because blue oak saplings do not survive under dense canopy, blue oak saplings tend to occur in the more xeric and open sites within mesic locations. This sapling distribution mirrors the current distribution of mature blue oak along a xeric-mesic gradient.

Accounting for historical regeneration patterns

Several dendrochronological studies (McClaran 1986, Mensing 1992, Vankat and Major 1978, White 1966) and other lines of evidence indicate that regeneration of blue oak was locally abundant in numerous widely-separated locations between the 1850's and early 1900's but has been scanty since then. Most blue oak woodlands are dominated by second and even third growth trees established between the Gold Rush of the mid 1800's and the 1930's, although both older and younger trees are found in some areas.

Several possible explanations for this age structure have been advanced, the most common of which are variants of the "lucky coincidence" hypothesis. This hypothesis suggests that regeneration is a rare event occurring when several favorable conditions converge: a large acorn crop, favorable winter/spring precipitation, and low pressure from acorn and seedling herbivores. Some suggest that fire is also necessary in the mix. However, it is difficult to imagine that blue oak would be such a successful and widespread species if its regeneration depended on such rare alignments. This hypothesis also fails to explain why these rare convergences suddenly became common throughout California during the period starting with Gold Rush and have become scarce after the 1930's.

We believe that most of the historic pulses of regeneration in the last 150 years can be explained as the release of established advance regeneration. This release was mainly caused by the liberal cutting and burning of the presettlement blue oak overstory that occurred between the 1850's through the first decades of the 20th century. Vast areas of California oak woodland were cleared for fuelwood, agriculture, and range during this period. The extent of oak woodland clearing conducted prior to the 1940's is poorly documented, perhaps due to the fact that "clearing the wilderness" was such a mundane and normal practice among California's early settlers.

Lithographs of mining towns made in the mid to late 1850's by Kuchel and Dresel show that large areas around these settlements had been cleared by that time. Bancroft (1888) describes the aftermath of the gold miners' workings as "...shorn stumps, midst unsightly mounds of earth, despoiled river beds, and denuded slopes, the ghastly battle-field of Titanic forces." Although mining had its greatest impact in the Sierran foothills, mining occurred throughout the range of blue oak, as miners searched for deposits of any valuable material: gold, mercury, copper, even coal. At each site, local trees would be cut for timbers, fuelwood, and simply to make way. As miners moved on to fresh diggings, settlers remained behind in the newly opened areas and cleared more woodlands for agricultural pursuits.

Clearing and lumbering were so widespread that by 1870, the California State Agricultural Society warned that much of California's easily accessible tree resources "have been most recklessly and uselessly destroyed." By the 1880's, growing concern over the potentially adverse environmental consequences of deforestation prompted the California Board of Forestry to poll county officials about the status of forests and woodlands. The response from Placer County indicated that half to two-thirds of the foothill woodlands had been cut, with some oak and "nut pine" (*Pinus sabiniana*) left standing. The San Joaquin County respondent indicated that "a great deal" of the oak woodlands had been cut to clear for agriculture. The Sonoma County return suggested that half of the hardwood acreage had been cut off, and half of this was due to agricultural clearing.

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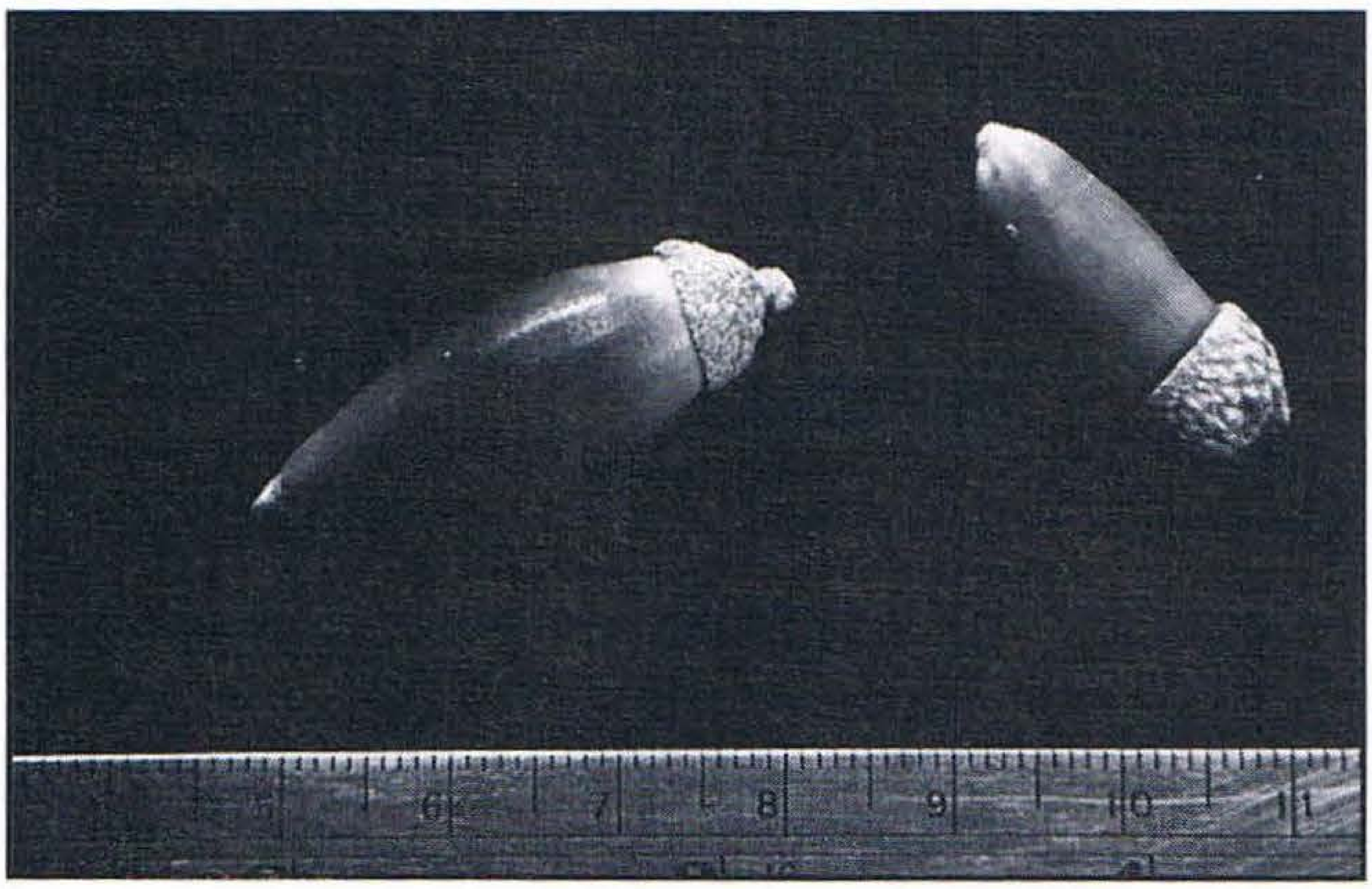
Because California lacks any substantial coal deposits, wood and charcoal were the primary fuels used for heating and cooking into the early part of the 20th century. A small ranch would commonly use 15 to 20 cords (about 36 to 48 m3) of wood per year for heating and cooking. This would require the annual clearing of between 0.4 and 1.6 hectares of moderately-stocked blue oak woodland (40-60 percent canopy cover). Jepson (1938) estimated that between 1860 and 1938, local ranchers had cut at least 200,000 cords of fuelwood from the hills around Vacaville, at that time a small town amid fruit orchards. This volume is roughly the equivalent of a 27 km2 clear cut assuming about 80 percent canopy (74 cords/ hectare). Large amounts of fuelwood were also required for industrial uses including railroads, steamships, and smelters. In the 1880's, an iron foundry near Auburn reportedly consumed 9,100 to 13,600 metric tons of charcoal annually, requiring the annual harvest of up to 30,000 cords of wood (Rossi 1980). By 1910, Jepson noted that "[blue oak] is used for fuel and has been so largely drawn upon for this purpose that the first-growth has quite disappeared from many sections of the Sierra foothills".



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Fruits of Quercus douglasii *Hook and Arn. collected at 750 m elevation on Mt. Diablo near Walnut Creek, California.*

Although many woodland and savanna stands were permanently obliterated during this period, blue oak clearly rebounded throughout the area that now constitutes its range. Especially after release, established blue oak seedlings exhibit a weedy tenacity because of their resprouting ability and are not easily eradicated. Lacking herbicides, early farmers could only kill established blue oak seedlings with deep cultivation, which was impossible on shallow and rocky soils, or through repeated shoot destruction by grazing, fire, or cutting. Redding (1878) noted that, "Ordinarily, the land has to be cleared of trees found upon it, and cultivation must be continuous, for on the [foothills along] the whole western face of the Sierra the mature trees, when cut or burned down, are rapidly replaced by a new growth of the same kinds." Jepson (1910) also noted that, "Young growth from seed is in many places fully replacing the cut trees" in cleared blue oak stands. Because oak fuelwood was viewed as a necessary resource, natural restocking of blue oak from advance regeneration was undoubtedly allowed to proceed in many areas. Thus, incomplete destruction of advance regeneration allowed blue oak to survive both short-lived attempts at agriculture and routine wood harvesting and gave rise to the stands that make up most of the current resource.

Oak fuelwood cutting diminished as other energy sources replaced wood, but clearing of oak woodlands was revived in the 1940's under the mantle of range improvement. Bolsinger (1988) estimated that California oak woodland cover was reduced by about 360,000 hectares between 1945 and 1973 due to rangeland clearing activities. With government subsidies and technical help from UC Cooperative Extension, ranchers used heavy equipment and herbicides to more efficiently eradicate both overstory trees and virtually all woody understory plants. Many of these efforts have resulted in essentially permanent vegetation type conversion to annual grassland.

Sustainable management of blue oak woodlands

Mechanical cutting and clearing, livestock grazing, fire, and the introduction of non-native grasses and forbs have been the most important management practices used in blue oak woodlands. These disturbances have altered the composition of the oak woodland understory, habitat for native herbivores and their predators, and soil conditions. As a result, the environment that blue oak advance regeneration must establish and persist in now may be vastly different from presettlement conditions. Unfortunately, baseline information on presettlement conditions is largely lacking, so the magnitude of these changes can only be inferred. Furthermore, there is clearly no way to return to pristine conditions, due to the ubiquitous presence of introduced vegetation. If blue oak woodlands are to survive, we must determine how to manage for regeneration in this altered ecosystem.

An understanding of advance regeneration and gap dynamics provides a framework for interpreting both current and past regeneration patterns in the light of management practices. According to the model, a narrow window of opportunity exists for sapling recruitment from advance regeneration when overstory mortality occurs. Advance regeneration must be adequate before canopy loss and must be allowed to grow after canopy loss. If these conditions are met, a pulse of regeneration can result. If the production, survival, and/or release of advance regeneration is inhibited, overstory mortality will result in stable openings that cause the stand to thin, eventually to the point of extinction.

The relatively even-aged stands now found in many blue oak woodlands represent an additional challenge for sustainable management. It is likely that presettlement stands were mostly uneven-aged, with scattered mortality and recruitment in canopy gaps. As current even-aged stands age, they will be much more susceptible to widespread declines affecting large blocks of trees, requiring regeneration of the entire stand over a short period of time if the stand is to remain viable.

Effects of grazing

Because most current blue oak woodlands are used as rangeland, grazing is a management factor that must be scrutinized. Long-term livestock grazing has more potential to adversely affect blue oak regeneration than any other factor. Cattle eat acorns, reduce or eliminate the litter layer beneath trees, and compact the soil, reducing the potential for initial seedling establishment. Surviving seedlings are repeatedly browsed and trampled. This damage shortens the life of individual seedlings and can deplete or eliminate the persistent seedling bank over time. Under even moderate stocking rates, livestock browsing severely inhibits

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sapling growth. Repeated cattle browsing reduces blue oak saplings to small shrubs which may survive as long as 80 to 100 years without growing above browse line (Harvey 1989). Thus, livestock impact the establishment, survival, and release of blue oak advance regeneration.

Livestock grazing severely constrained the regeneration of blue oak at most of the locations we studied (Swiecki et al 1993), but the impact of grazing is not limited to blue oak regeneration. Reproduction of most other woody species in the understory was also virtually eliminated under moderate to heavy grazing pressure. In such locations, blue oak saplings and juveniles of other palatable woody species are limited to areas where grazing pressure is reduced, such as on steep slopes and among rock outcrops. In some of these locations, only juveniles of less palatable woody species such as chamise (*Adenostoma fasciculatum*), manzanita (*Arctostaphylos* spp.), and live oak (*Q. agrifolia* and *Q. wislizeni*) were able to survive in the understory. The negative effects of grazing on palatable species were common knowledge over a century ago: "No fact is better established than that improper pasturage...kills out the useful fodder plants and all young growths of trees" (California State Board of Forestry 1886).

Blue oak regeneration does not generally respond quickly to a cessation of grazing because simply removing livestock does not cause the landscape to revert to its presettlement condition. Management inputs may be necessary to favorably alter the composition and density of herbaceous vegetation. Rodent populations may be high due to lack of predators and abundant introduced grasses. Many years may be needed to reestablish healthy populations of advance regeneration which are available to be recruited in new canopy openings. Even if a site is no longer grazed, old clearings are unlikely to be colonized, and saplings will not grow up under heavy tree canopy. If regeneration is being constrained by several factors, changing only one factor may not be sufficient to allow regeneration to proceed.

Why didn't livestock completely inhibit the release of advance regeneration in the last century? Various old clearings that date to the late 1800's and early 1900's probably do represent areas where regeneration was inhibited by grazing. However, the relatively consistent grazing regimes that now typify much of the blue oak range were not established in many areas until the first few decades of the 20th century or even later. In much of California, livestock were originally grazed on unfenced range. In the late 1800's, some huge herds of sheep and cattle were seasonally ranged in the Coast Ranges, the Central Valley, and the foothills and mountain meadows of the Sierra Nevada. Livestock populations were not stable, as herds were periodically decimated during episodes of drought. Parcels were subject to ownership disputes and changes, cycles of partitioning and consolidation resulting in a complex mosaic of grazing histories throughout the range of blue oak. Thus, regeneration was more common during a period when grazing impacts were more inconsistent and variable over time, but has become uncommon under the consistent seasonal and year-round grazing regimes of the past half century.

Grazing is a broad term that encompasses different types of animals and stocking rates, season and duration of use, and year to year consistency. The impact of grazing on regeneration is further influenced by the species composition and productivity of the herbaceous layer, soil types, weather conditions, distribution of water sources, and other factors. In almost any site, grazing will tend to reduce the reproductive potential of blue oak. Whether this reduction will critically limit regeneration will vary between locations, and may vary between years at a given location. Grazing impacts will be most pronounced in stands with less than about 25 percent canopy cover, in xeric sites, especially those at the edges of the current blue oak range, and in locations with gentle topography which are grazed very uniformly. Consistent grazing on an annual basis may inhibit regeneration more than rest rotations that periodically take parcels out of grazing for one or more years.

Deer can also negatively affect seedlings and saplings, but they generally cause less damage than livestock for several reasons. Cattle cause more shoot damage because they typically chew into larger-diameter stems than do deer. Cattle will also destroy the growing points of stouter saplings by scratching themselves against stems. Compared with deer, browsing pressure from fenced livestock is generally more intense, more consistent, and consequently more damaging to oak regeneration.

Effects of fire

Fire plays an important role in the maintenance of numerous plant communities in California and there has been considerable speculation that fire may favor blue oak regeneration. Fire scar and tree ring analyses have been used to document historical associations between fire and apparent tree age at several locations (McClaran 1986, Mensing 1992), but these studies are not evidence of fire-dependent regeneration. When topkilled saplings resprout after a fire, the resulting shoots date to the time of the fire. A correlation between fire and tree age will therefore exist whether fire's influence on recruitment is positive, negative, or neutral.

Based on our model of blue oak regeneration, it is possible that fire could promote sapling recruitment in some instances by killing decadent overstory trees and releasing advance regeneration. However, several studies have shown no positive effect of fire on seedling establishment or survival (Allen-Diaz et al 1990, Haggerty 1991, Schwan et al 1997) and our sapling survey data do not indicate that fire is requisite for sapling recruitment (Swiecki et al 1993).

In June 1997 and May 1998, we surveyed an oak stand with many small blue oak saplings that had burned in a September 1996 grass fire. In this relatively light fire, 6 percent of the saplings died and almost all saplings less than 150 cm tall and/or with basal diameters of less than 5 cm were completely topkilled. Nearly two years after the fire, post-fire shoot height, caliper, biomass were clearly much lower than prefire levels for all but the smallest topkilled saplings. At Pinnacles National Monument, we found that saplings were least likely to occur in plots that had experienced multiple fires over a five-year period (Swiecki et al 1993). Although mature blue oaks are relatively fire resistant, blue oak regeneration is not fire dependent and is actually inhibited by frequent fire.

Conclusions

Low sapling populations do not necessarily provide evidence of a regeneration problem. We must also determine levels of mortality in the stand and where saplings do and do not occur. According to the model of regeneration described here, saplings should be rare in densely canopied stands. Old clearings may represent past failures of regeneration, but we should not expect that blue oaks will now aggressively invade these openings. However, we should find saplings in recent openings caused by mortal-

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ity of mature overstory oaks. This is not the case in many locations, and this is evidence that blue oak regeneration is failing.

In most sites, it is not possible to meaningfully interpret current patterns of regeneration without considering at least 30 years of site history. The process of blue oak regeneration typically occurs over a period of many years, and current site conditions do not tell the whole story. Similarly, one must look forward in time 30 to 50 years when considering how current management practices will affect the future stand.

It is unlikely that all blue oak woodlands will completely disappear soon. However, many blue oak stands are headed for extinction if current management practices persist. In many areas, blue oak savanna is slowly being converted to annual grassland as old trees die out. In some of these very open stands, planting may be the only way to regenerate blue oaks. In many other areas, natural regeneration may still be possible. If blue oak is to be managed as a sustainable resource, grazing practices will need to be modified in many areas. Efforts must also be made to monitor the status of advance regeneration before, during, and after canopy or understory manipulations.

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Irrigation and Rangeland Oaks

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The problem of oak tree regeneration and recruitment has been the focus of much research in California in recent years. The University of California and the U.S. Forest Service have sponsored four comprehensive symposia devoted to the subject of oaks and hardwoods, and many scientists and concerned citizens have sought answers and remediation. Concern has led individuals to form the California Oak Foundation, dedicated to the preservation and regeneration of oaks and their habitats.

That some species of native California oaks are not reproducing well was observed nearly 90 years ago (Sudworth, 1908; Jepson, 1910). More recently Griffin (1971, 1973) called attention to the lack of regeneration in blue oaks and valley oaks. Replacement rates are especially low in the coastal ranges and foothill regions of the state (White, 1966; Steinhart, 1978). When a blue oak sapling is found, it is likely to be in a relatively moist habitat (Bolsinger, 1988). Callizo (1983) suggests that newly emerged valley oak seedlings will not survive their first year without one or two summer rainstorms, and because these happen so seldom in a century, one sees even aged stands and few young trees. McCreary (1990) discusses the "pulse" theory of several necessary contemporaneous factors for regeneration to take place.

Bartolome et al. (1987) state that the more successful regeneration is occurring at upper elevations. When a rainfall map is consulted, it is clear that these are areas of greater precipitation, especially in the spring and summer. Soil moisture depletion caused by a five to eight month dry period can cause deaths of seedlings (Pancheco, 1987; Larson and Whitmore, 1970; Lathrop and Osborne, 1990).

Acorns germinating on north facing sites or in shade are more likely to survive than those in the open (Barbour, 1987). Thus, we view desiccation as a major potential cause of early mortality. There are some published reports on the effects of supplemental irrigation on oak seedling survival and growth.

McCreary (1990a) found more frequent watering was beneficial at least during the first year, but he used small volumes. Bernhardt and Swiecki (1991) reported only 4 percent of valley oak seedlings planted under irrigation died, while 43 percent of non-irrigated seedlings died their first year. Meyer (1991) found that well watered seedlings grew taller and had more leaves than seedlings without supplemental water. Costello, Schmidt and Giusti (1991) working at a site 40 kilometers south of our study site found the growth of irrigated oak seedlings to be about five times that of those left to nature.

Another experiment by Costello et al. (1996) at the same location with blue oak, interior live oak, valley oak and Douglas fir reported much better growth and survival rates for irrigated seedlings.

Summary of Species Characteristics Used in this Experiment

This study used four species of oaks common to the Northern California Coast Ranges: blue oak (*Quercus douglasii* H. & A.), California black oak (*Q. kelloggii* Newb.), Oregon white oak (*Q. garryana* Dougl.) and interior live oak (*Q. wislizeni* A. DC.). Each of the four species selected for this study grows well in the study area, although seedlings of all but interior live oak are uncommon to rare. Blue oak generally lives in drier, hotter areas of lower elevations and while it can survive with only 35 cm of annual precipitation, it does better in areas where rainfall is about 65 cm. California black oak is found at higher elevations than blue oak and does better with 90 cm of rain than 65 cm. The live oaks do well on hillsides, but better on north-facing slopes or in canyons and near stream beds where water is available later into the summer. Oregon white oak requires more moisture than the others and this study site is near the southern limit of its distribution.

Questions and Hypotheses

The normal summer dry period in the study area lasts five to eight months, and there is added moisture stress due to the competition from grasses. In this study we wanted to find out what happens to the survival and growth of oaks under differing watering conditions throughout several summers. We were also interested in determining if there is an optimum amount of irrigation to apply for each species, an amount below which survival is in serious jeopardy, and an amount above which growth is retarded. We hypothesized for all but the Oregon white oak that there would be some range of water providing maximum growth over a summer, and with more or less applied water, there would be a decrease in relative growth.

We hypothesized that the Oregon white oak would grow best with a high amount of water.

Methods and materials

Site

The study area is located in Redwood Valley, 18.9 km north of the city of Ukiah in Mendocino County, CA at an elevation of 270 meters. The site is covered with grasses and forbs and has not been grazed for over 10 years. This site was chosen because it receives full sunlight and becomes very dry during the summer. This land has a 9 percent slope with a northwest aspect, and the soil type is Pinole loam.

Experimental Design

Acorns were collected from healthy trees all within 0.6 km of the study site and were picked in October, 1991. On 13 December the acorns were planted in 38 cm long planting tubes. Many of the blue oak and some of the Oregon white oak acorns were already sprouting. All acorns were positioned on their side, and any visible radicles were pointed down.

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A rectangular grid was laid out at the site (Fig. 1) and water collecting cans were placed in four rows of seven cans each. The distance between cans in a row and between rows was 4 m. Three overhead irrigation sprinkler heads were placed so that some cans received no water at all and some cans a great deal of water (Table 1). The sprinkler placements were arranged to provide a smooth continuum from no water to maximum water. With an array of 28 irrigation measuring cans, we chose 42 seedlings of each of the four species and assigned six seedlings to each can. The seedlings were planted in a hexagonal arrangement 1 m to aside and 1 m from the measuring can. The assignment of trees to cans was random to the extent that each can received at least one tree and no more than three trees of each species.

The test plot was fenced to prevent deer and rabbits from entering the exclosure. We provided no other assistance to the oak trees. In order to maintain reasonably natural field conditions, we did not scrape or mulch the soil around the trees but did mow the area twice each summer to provide access.

Measurement of Soil Moisture

We buried gypsum based soil moisture sensors and temperature probes at depths of 30 cm, 90 cm and 150 cm in different locations, corresponding to sites receiving varying amounts of irrigation. After calibrating the sensors to this soil, measurements were made with an electrical resistance soil moisture meter. Readings corrected for temperature were taken every four days beginning in March.

Experimental Procedure

We planted the seedlings on 13 March 1992. We used a bimonthly measuring schedule beginning 15 March. Height was taken to the tip of the main leader. Seedlings were eventually placed into one of three categories. The first was that of continuously living seedlings which had retained the original growing leader and growth results are presented only for this group. This group was analyzed for growth using descriptive statistics and one way analyses of variance on the log transformed data. The second group consisted of trees which survived but lost their main stems; analysis is restricted to survivorship because they could provide no growth information. The third group consisted of trees that died.

Results

Annual Growth Patterns in Trees with Original Leaders

1) Phase 1—Irrigation with Overhead Sprinklers

The seedlings of each species of oak demonstrated a characteristic optimal range of water needs each summer. For both blue oak and California black oak the medium amount of water from irrigation and rainfall (approximately 42-63 cm each summer) resulted in significantly better growth than either lower amounts (23-41 cm) or higher amounts (>64 cm).

The heights over time of the California black oak are shown in Fig. 2, a nearly identical pattern was shown by the blue oak, and a similar one by the interior live oak. The growth dif-

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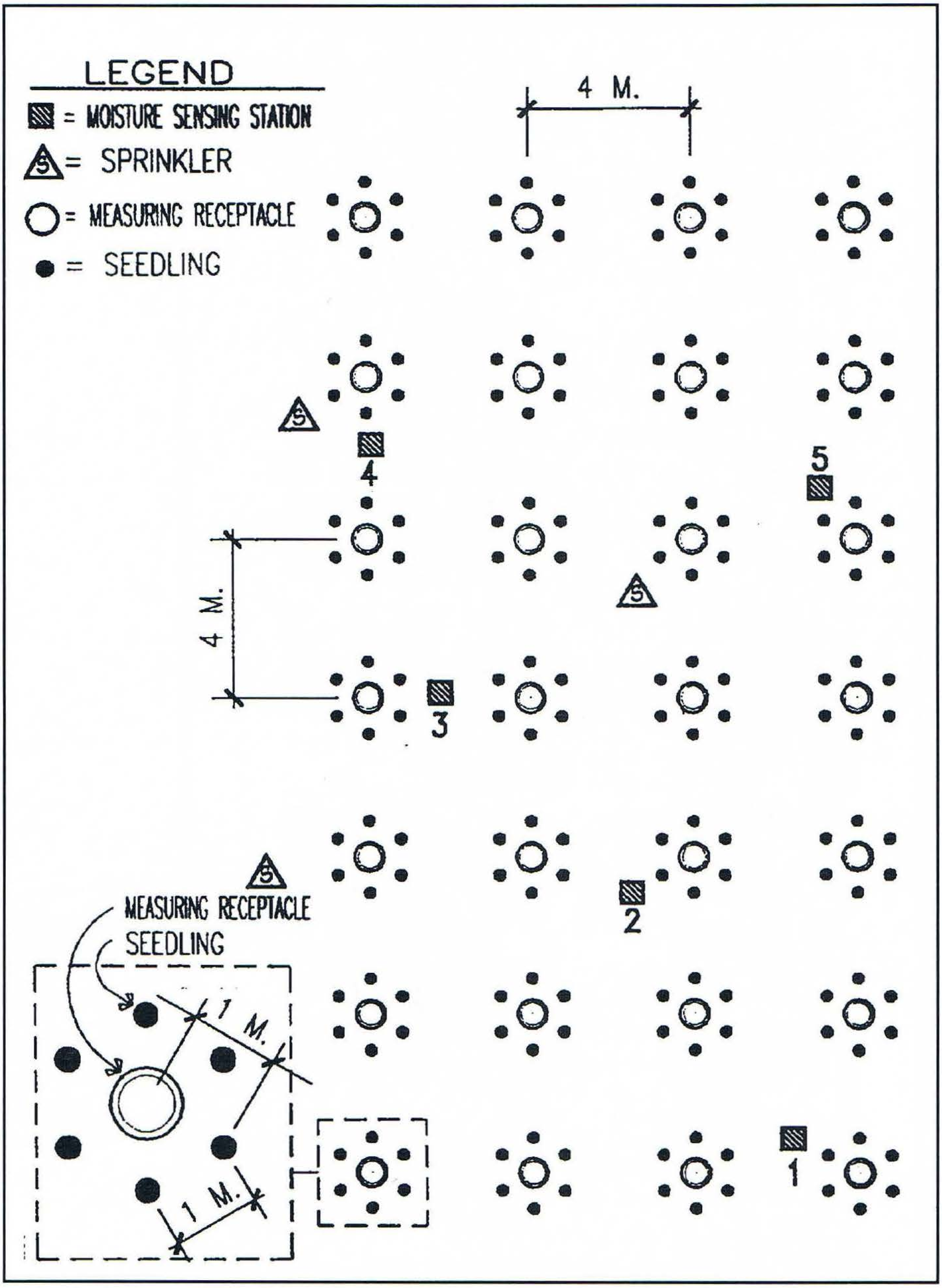

by R.H. Light and T.R. Buckner

Figure 1. Experimental layout showing arrangement of collecting cans, 168 oak seedlings, soil moisture stations and sprinklers.

Table 1. Amounts of water received by 4 species of oak seedlings during 4 years (15 March through 15 November). Mean values followed by ranges in parentheses, and measurements in cm. The 15 March - 15 November rainfall was 23.1 cm in 1992, 33.5 cm in 1993, 24.6 cm in 1994, and 42.2 cm in 1995. Subtract these from tabulated figures to determine irrigation water.

Year	Low	Medium	High
1992	30.5 (23-41)	44.7 (42-51)	64.8 (52-75)
1993	42.6 (34-50)	57.3 (51-63)	70.5 (64-79)
1994	34.8 (25-46)	54.0 (47-61)	72.3 (62-85)
1995	50.2 (42-62)	66.3 (63-71)	78.1 (72-88)

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ferences showed up statistically in the third year for blue oak ($p<.01$) and in the fourth year for California black oak ($p<.05$). The blue oak trees receiving the low irrigation scheduling grew from an average height of 17 cm to an average height of 31 cm in four years, while those in the medium irrigation scheduling went from 15 cm to 68 cm. Those receiving high amounts of water grew from 12 cm to 43 cm. For the interior live oak, both medium amounts of water (42-63 cm) and high amounts of water promoted significantly greater average growth than the low water (23-41 cm) scheduling ($p<.01$). This difference showed up in the third year. There was no significant growth difference between the medium and high water conditions. Growth after four years in the low water scheduling was from 22 cm to 88 cm, in the medium water condition from 27 cm to 216 cm, and in the high water condition, from 24 cm to 188 cm. While the survival rate of interior live oak was significantly less than the other three species, those which did survive grew very fast under optimal conditions.

The pattern for the Oregon white oak differed from the others in that the trees with the most water each year grew somewhat taller than those with either medium or low irrigation, and although differences showed a clear trend (Fig. 3), they were not statistically significant.

2) Phase 2— With Drip Irrigation

In 1996, we switched irrigation scheduling, so the blue oak, California black oak and interior live oak trees which had been getting a medium amount of water now received a low amount, and vice versa. The trees going from medium to low were well enough established so the reduced irrigation slowed the growth rate only moderately. But there was a dramatic increase in growth when going from low to medium irrigation. For the interior live oak, the change was little short of miraculous. In four years of growth under low irrigation, the average height was 88 cm; the next year, with more water they grew an additional 63 cm, and through September 1997 achieved a mean height of 178 cm. The Oregon white showed a dramatic increase when changed from a low water to a high water regimen. In the first four years of low water, average height increased from 10 cm to 36 cm; in the last two years with enough water, they more than doubled their height to 77 cm, and are now nearly as tall as the trees which had first received high water and were changed to the low water sched uling.

Mortality

As anticipated, some trees died during the experiment. Twenty-three of the 168 healthy seedlings planted succumbed during the first four years, and one more died in the fifth year. While the distribution of dead trees was uneven with respect to species, time and amount of water received, the cause of death in all cases appeared to have been desiccation. None was lost to mammals, birds or insects.

With respect to time, 16 trees died in 1992, five in 1993, two in 1994 and one in 1996. Mortality was clearly seasonal, with 17 deaths in the hot period. Mortality was also dependent on irrigation scheduling, for 16 of the 23 trees that died were in the group receiving the least water during phase 1. This was highly

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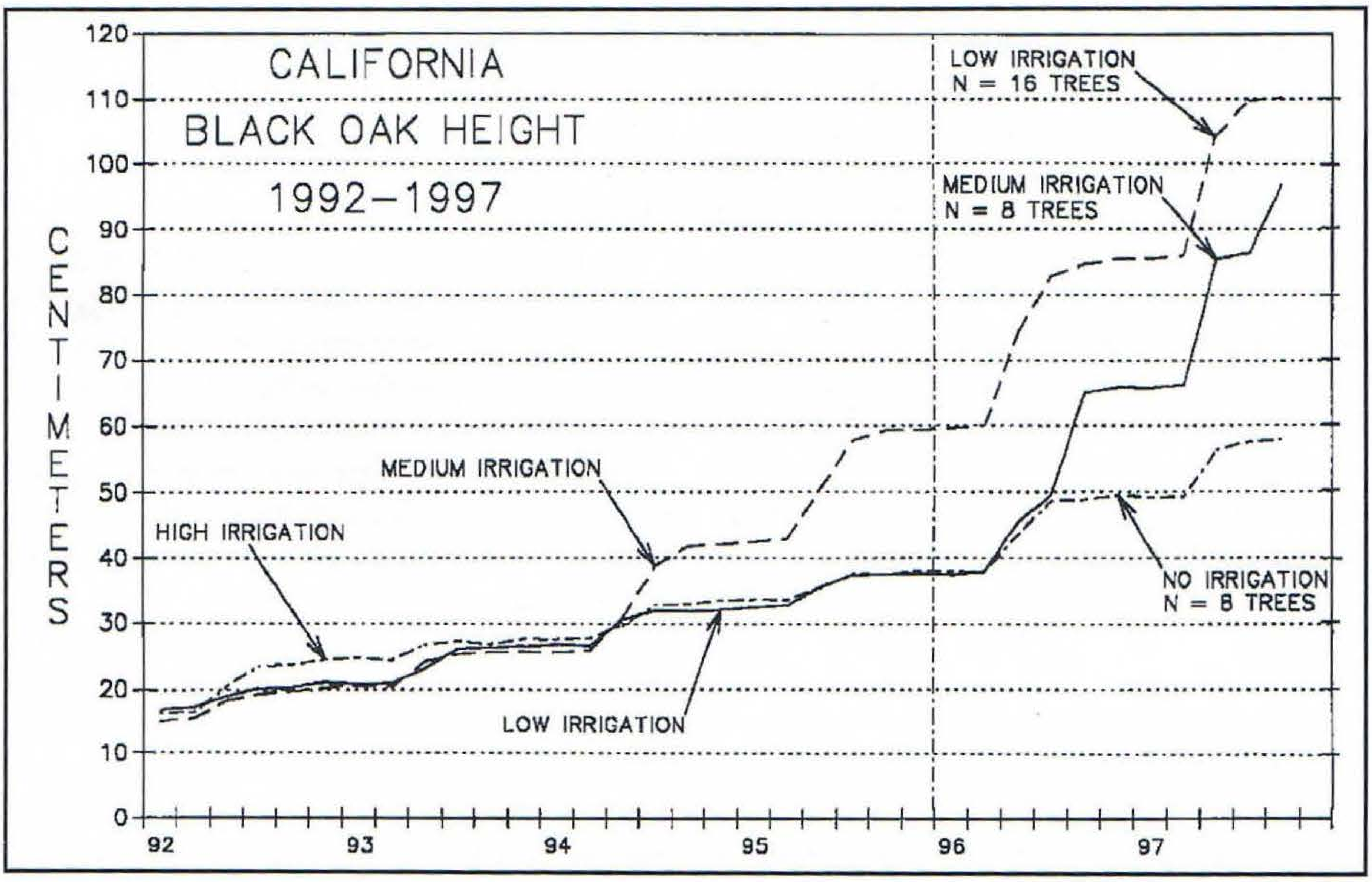
significant (chi-square = 13.6; $p<.005$). This finding underscores the importance of maintaining sufficient water throughout much of the summer.

Discussion

By the end of Phase 1 of the experiment, the growth of all four species was least under the lowest irrigation scheduling, and best under medium irrigation for three of them. For blue oak and interior live oak height differences were highly significant ($p<.01$) by the third year. For California black oak statistical significance was obtained in the fourth year. The Oregon white oak seedlings showed a clear trend for maximum height under a high water regime. Phase 2 changed irrigation from low to medium, or in the case of Oregon white oak from low to high, which resulted in a dramatic increase in seedling heights, and demonstrated the importance of abundant supplemental irrigation. Where there was low supplemental water, soil moisture from the surface to a depth of 30 cm was rapidly depleted by early summer. At 90 cm deep, the depletion rate was slow until mid July when the depletion rate rapidly accelerated and the soil became very dry by early September. At a depth of 150 cm deep, the soil stayed nearly at field capacity until mid July, then gradually dried for the rest of the



by R.H. Light and T.R. Buckner

Fig. 2. Mean heights of 32 California black oak seedlings 1992-1997. Note changes in irrigation scheduling in 1996.

summer.

First year seedlings are at great risk with little or no irrigation. In fact, five of the six seedlings near the driest moisture site died and after four years the single living specimen (a blue oak) has grown only 10 cm. When this blue oak received adequate water by drip during the next two years, it grew an additional 12 cm.

For the medium irrigation, soil moisture values at the 30 cm depth went very low during the summer, but this happened late enough not to cause damage. At the 90 cm depth, the soil contained water until September or later. At the 150 cm depth, the added water at the medium irrigation sites served to keep the soil not far below field capacity. The wettest areas received from 52-88 cm of water, and about half was after July. The soil never dried out at 90 cm deep or at 150 cm deep, never aerated properly, and kept roots very wet. Even at 30 cm deep, there was no drying cycle, only a cycle from field capacity to moderately wet and back to field capacity. There was no mortality at this level of irrigation but seedlings did not grow well, the Oregon white oak excepted.

The shorter heights of seedlings in the high water conditions has alternate explanations than just too much water. Very heavy application of water supports a lush grass cover, and the grass may in part be responsible for the slowed growth due to competition for nutrients or production of allelopathic chemicals. Excess water probably causes oxygen deprivation in the soil, and as Costello, MacDonald and Jacobs (1991) demonstrated, blue oak is highly sensitive to an hypoxic condition. Water stress in some plants results in better root exploration of the soil and more root proliferation (Hsiao and Acevedo, 1974).

Under natural conditions better regeneration has been found with trees in moister conditions such as the higher mountains, north exposures, and where the water table is reasonably shallow, such as river bottomland soils. Extra water is imperative for good growth; supplemental irrigation extends the growing season, mimics late spring and early summer rains and counteracts the desiccating effects of introduced annual grasses. Typically, this area of the north coast receives 11 cm of precipita tion from mid-March to the end of July, so irrigation is important. In our experiment eight of the ten trees which died by 15 July of the first year had received less than 21 cm of combined rain and irrigation. This strongly suggests they need at least 25 cm of water by that date, or seedling survival is in jeopardy. If more than 60 cm of water is applied from March through November growth suffers, although the effects of the surplus water are not fully known; perhaps there is no harm to young trees. We do not advocate watering trees all summer into fall. We do advocate extending the spring and summer wet period at least through July.

Under natural conditions, seedling growth extends from March through June and part of July, with very little growth afterward. Further growth adds leaves but little height. With supplemental water, the growing season is extended significantly, and there is still modest growth into September.

We have shown that the growth differences under varying irrigation schedules appear in the second year, and by the third and fourth years, may be quite dramatic. There is no doubt that the added water is the extra factor. In subsequent years, less water may be preferable. In the fifth and sixth years, we altered the irrigation schedule. Only one tree died, but the changed schedule showed different growth patterns (Figs. 2 and 3). The trees which first received low water and then were shifted to a medium amount began to thrive and show a growth curve similar to those which initially received a medium amount of water. Those which had initially received a medium amount and then were given a low amount slowed their growth rate. The condition of global warming has come to be widely accepted. If the amount

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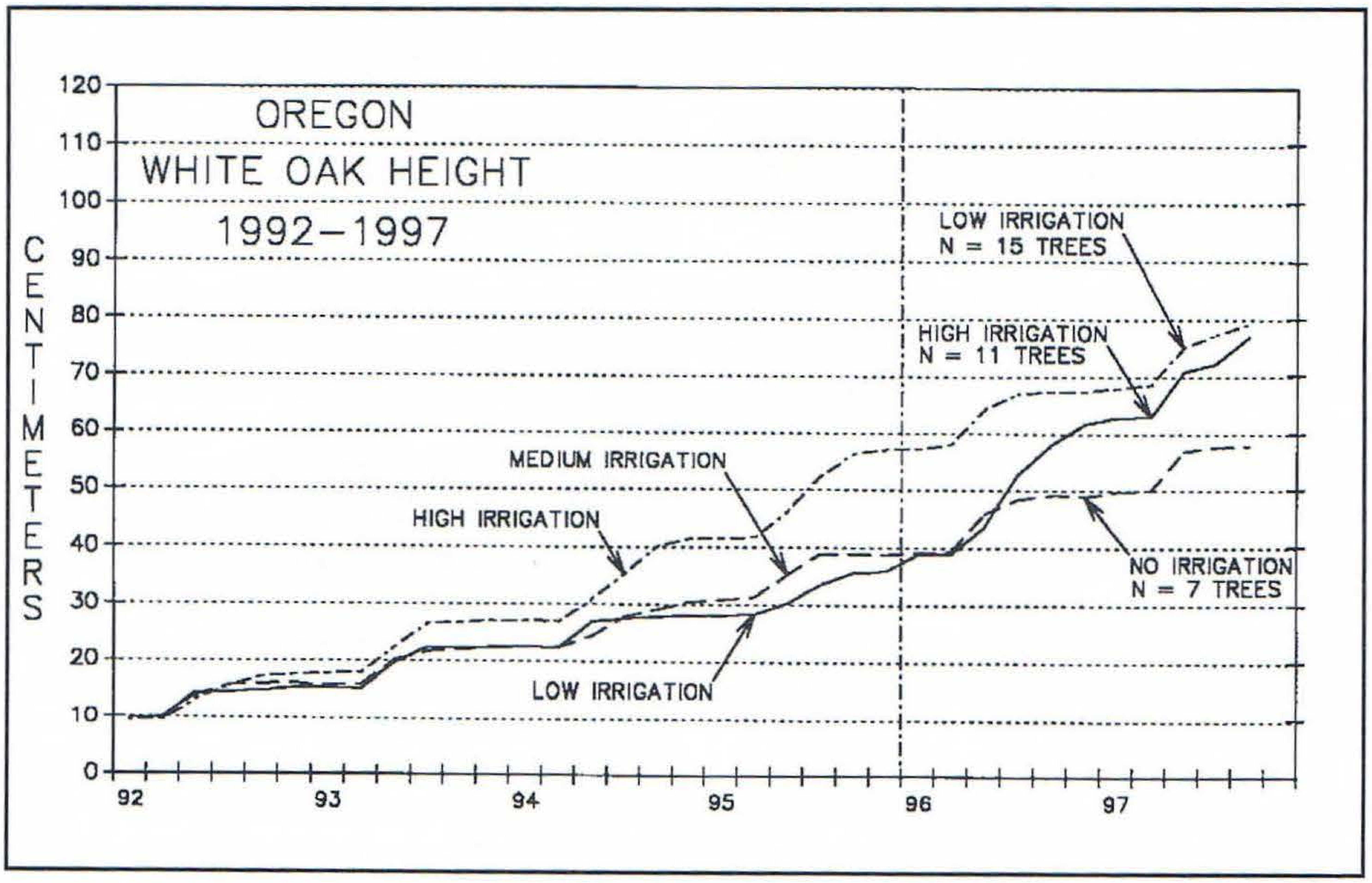
of available soil water has indeed decreased over time due to climate change or groundwater pumping, then the supplemental water given to seedlings effectively restores the more "normal" conditions of the past. The acorns and seedlings may require more water than is naturally available now. Use of supplemental irrigation of seedlings may in many areas be necessary for successful regeneration, in spite of considerable added cost.

Conclusions

The results from this study demonstrate that for oak seedlings to thrive, they need appreciably more water than is generally available by rainfall alone, and more than is applied in most oak regeneration experiments. Survival is highly dependent on adequate water during the first year.

Growth, on the other hand, is far more dependent on adequate water during the warm season for at least several years. To ensure survival of planted oak seedlings, one must provide about 40-50 cm of water from March through November, and to obtain good growth, it is necessary to apply about 25-30 cm from March through the end of July, through rain or irrigation.



by R.H. Light and T.R. Buckner

Fig. 3. Mean heights of 33 Oregon white oak seedlings 1992-1997. Note changes in irrigation scheduling in 1996.

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The Emission of Isoprene From Oak Leaves

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The oaks of the world are a complex group. Determining which oak species throughout the world release isoprene to the atmosphere is also complex. Isoprene is produced in oak leaves only when the leaves are in sunshine, and is not produced in the dark. All of the oaks of North America release large quantities of isoprene to the atmosphere, and as much as 2 to 10 percent of the carbon fixed during photosynthesis is lost this way.

Isoprene is a C_5H_8 hydrocarbon that has two unsaturated bonds, allowing it to react very quickly in the atmosphere. It is the most reactive hydrocarbon released into the air in large quantities. Essentially, all of the isoprene emitted into the atmosphere comes from plant foliage during the daylight hours. Isoprene participates strongly in smog-type chemical reactions and one of the byproducts of these reactions in urban areas is the formation

Table 1. The Status of Isoprene Emissions for Oaks from China and Japan.

Species	Isoprene Emission
Quercus acuta	NO
Q. acutissima	NO
Q. aliena	YES
Q. aliena Var. *Acutaserrata*	YES
Q. acutadentata	YES
Q. bambusaefoila	NO
Q. chenii	NO
Q. dentata	YES
Q. elmerii	NO
Q. gilva	NO
Q. glandulifera	YES
Q. glauca	NO
Q. leucotrichophora	NO
Q. liaotungensis	YES
Q. mongolica	YES
Q. myrsinaefolia	NO
Q. phillyraeoides	NO
Q. stenophylla	NO
Q. variabilis	NO/YES

Table 2. The Status of Isoprene Emissions for Oaks from Europe and the Middle East

Species	Isoprene Emission
Quercus Brantii	NO
Q. boisseiri	YES
Q. caliprinos	NO
Q. canariensis	YES
Q. castaneifolia	NO
Q. cerris	NO
Q. coccifera	NO
Q. faginea	YES
Q. haas	YES
Q. iberica	YES
Q. ilex	NO
Q. ithaburensis	NO
Q. libani	NO
Q. macrolepis	NO
Q. petraea	YES
Q. pontica	YES
Q. pubescens	YES
Q. robur	YES
Q. x*turnerii*	YES
Q. suber	NO
Q. trojana	NO
Q. vallonea	NO
Q. x*hispanica*	NO

of excess ozone, on a scale comparable to that produced from auto exhaust. Along the eastern seaboard and Appalachian highlands, where the oaks have replaced the American chestnut tree, the oaks contribute especially large amounts of this very reactive hydrocarbon to the air corridors of the local urban areas. Current photochemical models suggest that these summertime emissions from the forests interfere with the achievement of the Environmental Protection Agency (EPA) mandated ozone standard in and between the urban airsheds in Pennsylvania, New Jersey, New York, Connecticut, Rhode Island and Massachusetts.

But not all of the oaks of the world release isoprene to the atmosphere. The oaks of China and Southeast Asia that belong to the *Cyclobalanopsis* section in the genus *Quercus* do not produce isoprene (Table 1). However the white oaks in these regions do produce isoprene at rates similar to those produced by the *Lepidobalanus* and *Erythrobalanus* oaks in North America. Throughout northern Europe the high production of isoprene from the white oaks occurs as well. However, in the Mediterranean area many deciduous and live oak species do not produce isoprene (Table 2). This is highly unusual since, in the Mediterranean regions of the world, the occurrence of isoprene-emitting plants is very high. The deciduous species around the Mediterranean that do release isoprene seem to be more closely related to the common white oak of Europe, *Q. robur*. The dominant deciduous species that release very little to no isoprene are *Q. castaneifolia*, *Q. cerris*, *Q. trojana* and sometimes *Q. petraea*. None of the evergreen oaks (*Q. calliprinos*, *Q. coccifera*, *Q. ilex*, *Q. ithaburensis* and *Q. suber*) produce isoprene. A very interesting twist is that both *Q. ilex* and *Q. suber* have monoterpene ($C_{10}H_{16}$) emissions instead (Table 3), similar to those from pine trees, but at much higher rates and only when the foliage is in sunshine. This is also observed in the deciduous foliage of *Q. cerris*.

The hybrid oak *Q.* x*turneri* - a cross between *Q. ilex* and *Q. robur* - produces moderate amounts of both isoprene (inherited from *Q. robur*) and monoterpene (inherited from *Q. ilex*). In the case of the hybrid *Q.* x*hispanica*, a cross between *Q. suber* and *Q. cerr*is, no isoprene is produced. This active physiological emission of oaks is very different from the more passive thermal emission of monoterpenes from pines.

In my surveys exploring for plants that produce isoprene, a fascinating array of physiological and taxonomic relationships has been observed. Currently we have identified with gas chromatography and mass spectrometry measurements more than 280 compounds emitted from the intact foliage of several dozen tree species. Surprisingly, biogenic sources of monoterpene hydrocarbons have been observed

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Emission of Isoprene. . .

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being released in other tree species not known for having terpenoid oils in their leaves. These emissions occur under physiological conditions similar to the light-dark regimen required for the on-off production of isoprene, and in a variety of important forest broadleaf genera including *Acer, Betula,* and *Lithocarpus*, in addition to *Quercus*. How these studies relate to the oaks and their close relatives is very interesting. For example, the volatile organic compounds in the foliage emissions from *Q. robur* are 97 percent isoprene, with almost no monoterpenes. However, the foliage actively emits higher molecular weight sesquiterpene ($C_{15}H_{24}$) compounds like beta bourbonene, which are normally beyond the range of routine measurement of the volatile emissions. But it is these higher molecular weight hydrocarbons and their oxygenated products that most probably have a role in the communication between plants through their volatilized emissions. To my knowledge isoprene does not function in this role, but rather is believed to protect the photosynthetic apparatus in the leaf from short- term high temperatures. Clearly, oaks continue to be the most interesting of trees.

Table 3. The Status of Monoterpene Emissionsof Oak Species that do not release Isoprene.

Section Cerris	**Isoprene Emssion**	**Monoterpene Emission**
Q. acutissima	NO	SOME
Q. castaneifolia	NO	NO
Q. cerris	NO	YES
Q. macrolepis (*Q. aegilops*)	NO	NO
Q. ithaburensis	NO	YES
Q. trojana (*Q. macedonica*)	NO	NO
Q. variabilis	NO/YES	NO/YES
Section Suber		
Q. calliprinos	NO	?
Q. coccifera	NO	YES
Q. suber	NO	YES
Q. X*hispanica* (*Q. cerris* X *suber*)	NO	YES
Section Ilex		
Q. chrysolepis	YES	NO
Q. ilex	NO	YES
Q. phillyraeoides	NO	YES
Q. virginiana	YES	YES/NO

Seedling Performance in Two Oak Species

The Effects of Seed Size, Cotyledon, Reserves, and Herbivory

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The role of seed size in seedling performance has received consider able attention (Foster, 1986; Mazer, 1989; Seiwa and Kikuzawa, 1991; Westoby, Jurado, and Leishman, 1992), and differences in seed size among species have been found to relate to the ecological conditions in which plants establish.

Some of the patterns detected in comparisons among species are also found within species. A positive relationship among seed size and seedling establishment and growth has been reported in a variety of species (Weis, 1982; Stanton, 1984; Weller, 1985), including oaks (McComb, 1934; Tecklin and McCreary, 1991), but there have been few attempts to explore the relationship between seed size and the performance of oak seedlings under a variety of ecological conditions.

Oaks are frequently dispersed by jays and small rodents, which are also their main seed predators. It has been argued that the rapid germination (nondormancy) and establishment of white oaks is a mechanism that allows escape from post-dispersal seed predation, since it permits the seedling to escape seed recovery by caching animals (Barnett, 1977; Fox, 1982). However, the probabilities of survival and continued growth of a seedling after detachment of the acorn (cotyledons) may be affected by the amount of reserves originally available to the seedling. Herbivory, frost, drought, and pathogens are other common challenges facing a seedling early in its life and its ability to cope with them is likely affected by the presence or absence of cotyledons, the size of the seed from which it originated, and the time elapsed since germination.

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Seedling Performance . . .

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Quercus rugosa (subgenus *Leucobalanus*, *Quercus*) is a 15-20 m tall tree, widely distributed in Mexico, that frequently coexists with *Q. laurina* (subgenus *Erythrobalanus*), a 15-30 m tall tree (González-Villareal, 1986; Bello and Labat, 1987). Both species can be found in pure oak stands or intermingled with pines at higher elevations.

In this study the effects of seed size and presence or absence of cotyledonary reserves on survival and growth of *Q. rugosa* and *Q. laurina* seedlings were evaluated, both in presence and absence of simulated herbivory. The objectives were to determine (1) whether differences in the ability of one-month-old seedlings to survive detachment of cotyledons are related to seed size, (2) whether reserves remaining in the cotyledons at time of detachment still contribute to survival and growth, (3) the interaction of herbivory and seed size on seedling survival and growth, and (4) the consequences of cotyledon removal on the response of the seedlings to simulated herbivory.

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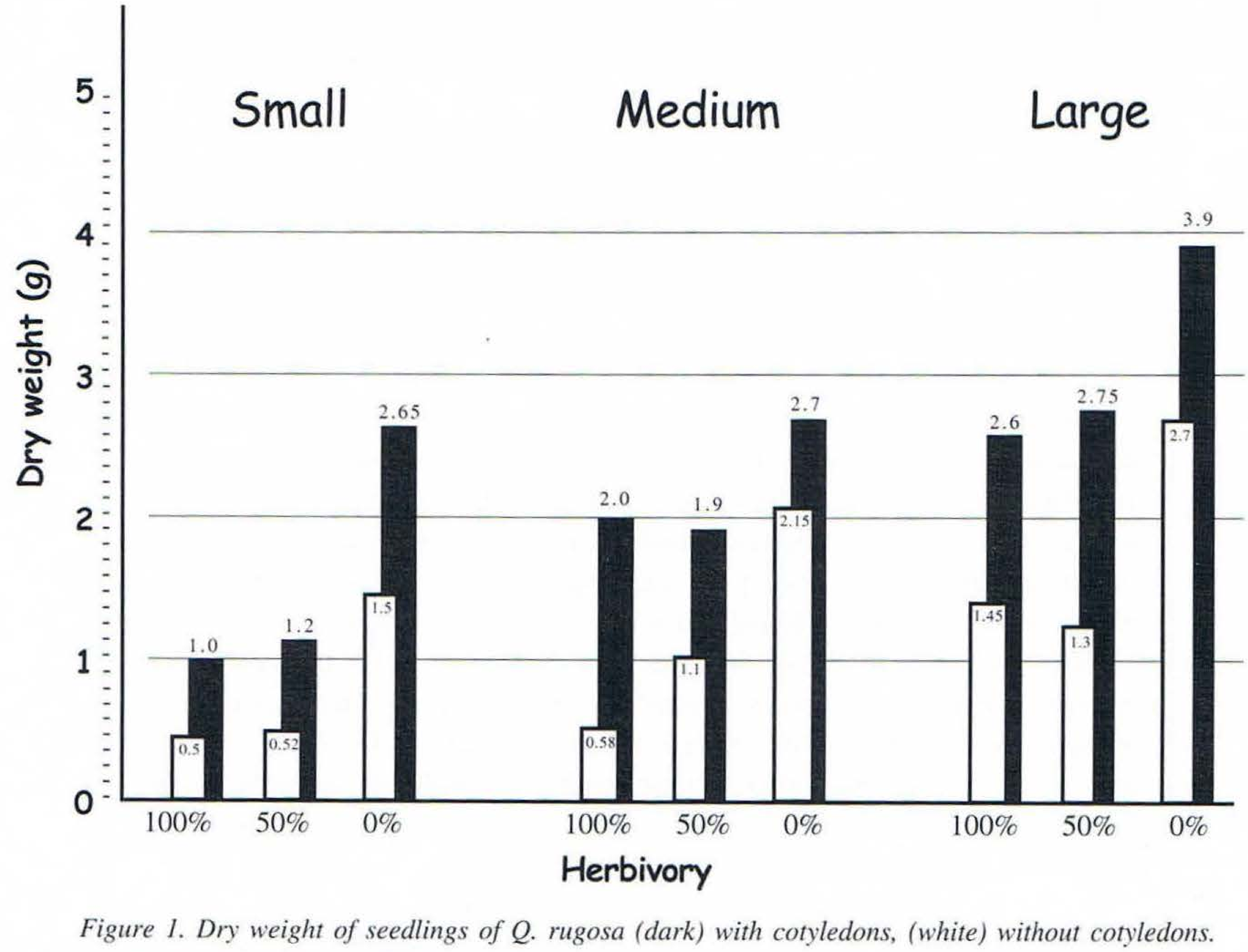

Figure 1. Dry weight of seedlings of Q. rugosa (dark) with cotyledons, (white) without cotyledons.

Table 1. Survival (proportion) of *Quercus rugosa* and *Quercus laurina* seedlings in the presence and absence of cotyledons (+/- cot.) at three levels of simulated herbivory. The numbers in parentheses indicate the expected values of the logistic model. Since herbivory did not have a significant effect in *Q. laurina*, the expected values are the same for all three herbivory levels.

	Seed size					
	Small		Medium		Large	
Herbivory	+ cot.	- cot.	+ cot.	- cot.	+ cot.	- cot.
			Quercus rugosa			
0 %	1.00	0.81	1.00	0.95	1.00	0.96
	(0.98)	(0.81)	(0.99)	(0.94)	(1.00)	(0.99)
50 %	0.91	0.52	1.00	0.73	1.00	1.00
	(0.92)	(0.51)	(0.98)	(0.80)	(1.000)	(0.96)
100 %	0.80	0.36	0.95	0.71	1.00	0.92
	(0.85)	(0.34)	(0.96)	(0.67)	(0.99)	(0.93)
			Quercus laurina			
0 %	0.75	0.22	0.69	0.23	0.83	0.35
50 %	0.85	0.21	0.67	0.07	0.83	0.06
100 %	0.50	0.11	0.56	0.00	0.95	0.06
	(.74)	(0.14)	(0.65)	(0.09)	(0.82)	(0.21)

Seedling Performance . . .

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Materials and Methods

During January 1993, acorns were collected from below six different trees of both *Q. rugosa* and *Q. laurina* in the Ajusco Hills, south of Mexico City. Each viable acorn was marked with a number and its individual weight recorded. A subsample (N = 62 for *Q. rugosa*, N = 54 for *Q. laurina*) was oven dried for 48 hours at 80°C and used to evaluate the relationship between fresh and dry weight and the proportion of dry weight in the cotyledons. Fresh-weight data of all the seeds (1185 for *Q. rugosa*, 1075 for *Q. laurina*) were used to assign each seed to one of three size categories, small (<1.5 g), medium (1.5 - 2.5 g for *Q. rugosa*, 1.5 - 2.0 g for *Q. laurina*), and large (>2.5 g for *Q. rugosa*, >2.0 g for *Q. laurina*) within each species.

In May 1993, the seeds were soaked for 24 hours in a 1 g/L giberellic acid solution in order to synchronize germination, and placed horizontally on trays containing agrolita. Every other day the trays were watered and the seeds inspected to record the date of germination.

Two weeks after germination, seedlings were carefully transplanted to black plastic bags filled with homogenized soil from the study site. When seedlings were one-month old, each member of the three seed size classes was randomly assigned to one of six experimental combinations for a total of 18 treatments: three seed sizes (small, medium, and large), three levels of simulated herbivory (O, 50, or 100% of shoot length removed) and two levels of cotyledons (presence-absence). Cotyledon excision and simulated herbivory were applied simultaneously, at which time all seedlings had completed their first burst of shoot elongation and had expanded leaves.

Twenty-five seedlings of *Q. rugosa* were assigned to each of the 18 treatment combinations. Due to poor germination, only 17 *Q. laurina* seedlings were available for each treat-

Table 2. *Quercus rugosa*: F statistics and probabilities for ANOVAs.

Variable	Seed size		Herbivory		Cotyledons		Size x Herb.		Size x Cot.		Herb x Cot.		S x H x C	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
df treatment [a]	df 2		df 2		df .		df 4		df 2		df 2		df 4	
Shoot height	22.81	< 0.00001	274.75	< 0.00001	98.32	< 0.00001	1.01	NS	3.45	0.033	6.46	0.002	2.50	0.043
Leaf area	28.76	< 0.00001	63.86	< 0.00001	97.56	< 0.00001	2.31	NS	0.27	NS	3.72	0.03	1.86	NS
Diameter	69.36	< 0.00001	111.45	< 0.00001	139.78	< 0.00001	5.03	0.006	0.96	NS	0.35	NS	3.32	0.01
No. leaves	3.89	0.02	33.47	< 0.00001	7.46	0.007	6.81	0.00003	2.44	NS	6.93	0.001	2.07	NS
Mean area per leaf	31.86	< 0.00001	.7.72	< 0.00001	96.09	< 0.00001	0.72	NS	0.31	NS	3.44	0.03	1.89	NS
Biomass														
Shoot	86.83	< 0.00001	186.45	< 0.00001	251.25	< 0.00001	2.68	0.03	0.89	NS	5.50	0.005	4.38	0.002
Leaves	48.97	< 0.00001	70.57	< 0.00001	141.89	< 0.00001	4.39	0.002	0.26	NS	4.06	0.02	3.24	0.01
Root	90.49	< 0.00001	86.60	< 0.00001	145.76	< 0.0001	4.37	0.002	0.48	NS	6.01	NS	3.12	0.02
Total	101.41	< 0.001	123.25	< 0.00001	219.18	< 0.0000.	6.12	0.001	0.89	NS	10.34	0.00005	4.68	0.043

[a] df error: 235 for size variables, 233 for biomass variables

ment. During application of treatments, shoot height and number of leaves were recorded and those seedlings that kept their cotyledons were superficially unearthed and reburied in the same way as those from which cotyledons were removed.

Seedlings were placed on wire-mesh tables in a nursery covered with green plastic mesh in a completely randomized design, with a border row of extra seedlings around each table to minimize edge effects. Rainfall was supplemented by watering to maintain soil moisture. Beginning 3-4 weeks after application of treatments, seedling height and number of leaves were recorded twice a month and the length of each leaf was measured once a month. Total leaf area was estimated by means of a previously developed regressions of leaf area versus leaf length. Seedlings were harvested 5 months after treatments, and shoot length, basal diameter, and leaf area were measured. Seedlings were oven dried for 48 hours at 80°C and each seedling part (root, shoot, and leaves) was individually weighed.

Survival data was analyzed by means of logit analysis for binomial data (i.e., proportions). Variables measuring final size and biomass of each seedling part were analyzed by means of ANOVA. When necessary, data were transformed in order to fulfill the requirements of homoscedasticity for the ANOVAs. Relative height growth rate (RGR) was also analyzed. This was the height growth of each seedling relative to its initial height at the time the treatments were applied.

Results and Discussion

Seed weight

The two species differed significantly in their mean seed weights. The range of variation of seed sizes was quite different in the two species (mean = 1.99 g, SD = 1.14 for *Q. rugosa* and mean = 1.75 g, SD = 0.48 for *Q. laurina*). There was a strong correlation between acorn fresh and dry weights for both species (r^2 = 0.998 for *Q. rugosa*, r^2 = 0.997 for *Q. laurina*), as well as between total fresh weight and cotyledon dry weight (r^2 = 0.995 for *Q. rugosa*, r^2 = 0.992 for *Q. laurina*), suggesting that seed fresh weight is a good indicator of the amount of reserves available for seedling growth.

Quercus rugosa establishes in a broader range of microsites than *Q. laurina.* The larger seed-size variation of *Quercus rugosa* may partially account for its ability to establish in a mosaic of microsites with different physical and biotic conditions, and thus broaden its regeneration niche (sensu Grubb, 1977).

Seedling survival

Seed size had a clear effect on survival of *Q. rugosa*, with seedlings from large seeds having the highest survival and seedlings from small seeds the lowest (Table 1). Within each size class, survival was reduced by removal of the cotyledons and by increasing levels of shoot removal. The effects of cotyledon removal, seed size, and herbivory were highly significant, and the interactions between these variables were not.

Cotyledon loss caused greater mortality in *Q. laurina* and seed size did not compensate for this loss (Table 1). The effects of seed size and cotyledon removal were significant, with the predicted drop in survival due to cotyledon loss 60% in both large and small-seeded seedlings. Herbivory and the interactions among variables were not significant. Results for *Q. laurina* must, however, be treated with caution because some seeds and seedlings showed evidence of pathogen attack (probably a fungus), reducing survival even in seedlings from the control group.

The large drop in survival as a consequence of cotyledon removal in both species shows that cotyledons still contribute to seedling survival one month after germination, while the higher survival after cotyledon removal in *Q.*

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rugosa than in *Q. laurina* may indicate a more extended dependence on these reserves in the latter.

The results for *Q. rugosa* have implications for the hypothesis of non-dormancy as a means of escaping post dispersal seed predation, as the probabilities of surviving cotyledon detachment are significantly higher in large-seeded seedlings. Although predators would prefer to excise the cotyledon as early as possible, before its food reserves are consumed by the seedling, early excision of the acorn greatly reduces its chances of surviving, especially for small-seeded seedlings. Previous trials showed that seedlings are unable to survive if cotyledons are removed 7-15 days after germination.

Seedling growth

Quercus rugosa. The effect of seed size on height was evident throughout the growing season regardless of the level of herbivory. At the time the treatments were applied, there were already significant differences in height and number of leaves between seedlings coming from different seed sizes. Leaf development was greater in seedlings from medium and large seeds (median = 5 leaves) than from small seeds (median = 3 leaves).

There was a highly significant effect of the three factors studied on final shoot height, leaf area, basal diameter, number of leaves, and mean area per leaf (Table 2). The herbivory-

Table 3. ANOVAs on relative growth rates.

Effect	F	df	p
Q. rugosa			
Size	12.28	2	<0.001
Herbivory	792.57	1	<0.001
Cotyledons	59.65	1	<0.001
Size x Herb.	8.65	2	<0.001
Size x Cot.	4.34	2	0.014
Herb x Cot.	15.79	1	<0.001
S x H x C.	1.76	2	0.173
Error		215	
Q. laurina			
Size	1.03	2	0.362
Herbivory	59.95	1	<0.001
Size x Herb.	0.29	2	0.747
Error		62	

cotyledon interaction was significant for almost all variables, because the effect of increasing levels of herbivory was amplified by the absence of cotyledons.

The conspicuous effect of herbivory on shoot height persisted until the end of the experiment. It also reduced leaf area in all seed sizes, although little difference was observed between 50 percent and 100 percent herbivory. In large-seeded seedlings that kept their cotyledons, there was a noticeable recovery in leaf area towards the end of the growing season. The effects of herbivory were always mitigated by the presence of cotyledons, with 50-150 percent more final leaf area relative to seedlings without cotyledons.

The three variables studied had a significant effect on total, root, shoot, and leaf dry weight (Table 2). In all cases, the most conspicuous effect was due to cotyledon retention, followed by herbivory and seed size. The seed size-herbivory interaction was significant in all cases, due to the greater impact herbivory had on dry weight of small-seeded seedlings. Mean total dry weight responded in a manner similar to that of seedling parts. In general, the two levels of herbivory had a similar effect, but were clearly different from the control group (Fig. 1). There was also a trend for the effect of cotyledon retention to be more conspicuous when herbivory occurred.

Seed size, herbivory, and cotyledons, as well as all second-order interactions, had a significant effect on the relative growth rate (RGR) of *Q. rugosa* (Table 3). This analysis excluded seedlings without herbivory, due to differences in variability in the response of seedlings with and without herbivory. In general, seedlings with 100 percent herbivory had higher RGRs than those with 50 percent, and RGRs increased with seed size. The lack of cotyledons caused a reduction in RGRs in all cases, although this reduction was smaller in seedlings from large seeds. Differences between seedlings with and without cotyledons were more pronounced in the 100 percent than in the 50 percent shoot loss.

The proportion of dry weight accounted for by the root (root-weight ratio) in seedlings of *Q. rugosa* that did not experience herbivory differed significantly with seed size (small = 0.47, medium = 0.48, large = 0.53). The presence or absence of cotyledons did not affect this relationship. This result reinforces the view that in oaks the seed reserves are quickly directed to the root (McComb, 1934; Grime and Jeffrey, 1965), where they remain available for seedling resprout (Matzuda and McBride, 1986; Crow, 1988; Walters, Kruger and Reich, 1993) after disturbance-caused death of aerial biomass. The fact that root biomass was reduced by herbivory may reflect the utilization of stored reserves in the production of a new shoot.

Quercus laurina

The low number of seedlings surviving cotyledon detachment did not allow a sound comparison between the growth parameters of seedlings with and without cotyledons, so comparisons were made only among those treatments with cotyledons. As with *Q. rugosa*, one month after germination there were already significant differences in height and leaf number among seedlings from small, medium, and large seeds.

Differences in height due to herbivory were maintained in seedlings of the three size classes throughout the growing season. Relative height growth rates were not significantly affected by seed size (Table 3). The growth of seedlings without cotyledons could only be observed in a few individuals but the results suggest that cotyledon loss had a great impact on both seedling height and leaf area, as was the case for *Q. rugosa*.

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Seedling Performance . . .

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Final leaf area and basal diameter of *Q. laurina* were both significantly affected by seed size and herbivory (Table 4). Total number of leaves was significantly affected by seed size, and seedlings from large seeds had an average of 3.5 more leaves than seedlings from small- or medium-sized seeds. Mean area per leaf was affected by herbivory, and seedlings without herbivory had larger leaves.

With the exception of shoot weight, seed size was more important than herbivory in the biomass attained at the end of the season, although both variables had significant effects on almost every seedling part (Table 4). The strong effect of herbivory on shoot weight, as on height, indicates that seedlings are unable to recover from loss of aerial tissue in one growing season.

As with *Q. rugosa*, *Q. laurina* seedlings from large seeds had a clear advantage in most cases, while there were not always differences between seedlings from small- and medium-sized seeds. Herbivory resulted in a clear decrease in total dry weight. Seed size did not have a significant effect on root-weight ratio in *Q. laurina*.

Conclusions

In both species there was a clear effect of seed size on seedling growth, both initially and at the end of the growing season. In *Quercus rugosa*, the consistent increase in RGRs with seed size both in seedlings with and without cotyledons shows the importance of having a large supply of reserves from the very start. The fact that seed-size did not affect RGR in *Q. laurina* suggests that differences among seed size classes in height at 6 months are determined principally during the first month.

In both species the removal of 50 percent of the shoot resulted in the loss of most leaves and frequently produced shoot dieback. This, combined with the higher subsequent RGR of plants in the 100 percent shoot loss treatment, resulted in seedlings from both levels of herbivory having similar final size and biomass.

The relationship between seed and seedling size in oaks has been described before (McComb, 1934; Triphati and Kahn, 1990; Tecklin and McCreary, 1991). This study shows that in *Q. rugosa* the capacity of seedlings to recover from herbivory is mediated by seed size. Nevertheless, differences in height and biomass

Table 4. *Quercus laurina*: F statistics and probabilities for ANOVAs.

Variable	Seed size		Herbivory		Size x Herb.	
	F	p	F	p	F	p
df treatment [a]	df 2		df 2		df 4	
Leaf area	9.97	0.0001	4.14	0.02	1.89	NS
Diameter	7.25	0.001	4.43	0.015	1.56	NS
No. leaves	3.78	0.03	0.57	NS	0.89	NS
Mean area per leaf	2.10	NS	4.14	0.02	0.55	NS
Biomass						
Shoot	18.22	< 0.00001	42.27	< 0.00001	2.19	NS
Leaves	12.76	0.00002	4.02	0.02	1.00	NS
Root	19.98	< 0.00001	1.99	NS	1.22	NS
Total	26.09	< 0.0001	15.11	< 0.00001	1.94	NS

[a] df error: 77

between uncut seedlings and those that suffered artificial herbivory were maintained until the end of the study period. Welker and Menke (1990) also found that severely defoliated *Quercus douglasii* seedlings did not accumulate biomass to levels that approached non-defoliated seedlings.

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Conservation and Ecological Reconstruction of Oak Forests in Romania

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Nine *Quercus* species grow spontaneously in Romania: *Q. petraea* Liebl., *Q. robur* L., *Q. polycarpa* Schur., *Q. dalechampii* Ten., *Q. cerris* L., *Q. frainetto* Ten., *Q. pedunculiflora* C. Koch, *Q. pubescens* Willd., and *Q. virgiliana* Ten. In ancient times, when forests covered more than 75% of the country's territory, oak forests had a considerably greater extent. The pedunculate oak (*Q. robur*) stands alone occurred on more than two million hectares. Large, compact, monumental forests of *Q. petraea*, *Q. cerris* and *Q. frainetto* were common on hills, plains and plateaus.

Due to historical conditions, oak forests today occur only on a small area (1,139,000 hectares, or 19 percent of the country's forested land). But in spite of this severe reduction, they continue to be of great economic and ecologic importance, because most of these species produce high quality timber. Also, all of them have multiple useful and protective functions in relation to climatic, hydrological, erosion control, scenic, and other values. As a result of Romania's varied relief and climatic conditions, a great biodiversity exists in these oak forests, confirmed by the fact that there are 141 forest types and 74 forest ecosystems in 104 different site types (Radu, 1993, 1995).

Over the centuries, the extended natural oak forests have endured a strong anthropic pressure. Deforestation for agriculture, incorrect practice of coppice systems, abusive grazing, air pollution and acid rains, coupled with prolonged droughts and occasional severe defoliation by insects, led to a dangerous reduction and fragmentation of ancient, large and durable stands. Today, we are confronted with fragile, destructured and simplified stands that are susceptible to ecological problems. The reduction of ranges is connected to the change of species area hierarchy, as today the sessile oak

(*Q. petraea*) stands are more abundant (on 11.6 percent of forest land) than those of *Q. cerris* (2.9 percent), *Q. robur* (2.4 percent), *Q. frainetto* (2.0 percent) and *Q. pedunculiflora* - *Q. pubescens* (0.4 percent).

The forest decline recorded during recent decades elsewhere in Europe also is noted in Romania, particularly in pedunculate and sessile oaks, but also in other oak species. Unfortunately, the aggressive pressure on all forests, including oak stands, is continuing today because of economic difficulties and poverty. In the absence of an effective and practical means of forest protection during the transition to a market economy, the change of the ownership status of forests from state to private property may unleash a new wave of deforestation and illegal cutting on considerable areas. Should this occur, it could result in ecological and economic disaster.

In order to stop the decline and to preserve these valuable forests, considerable silvicultural interventions have been undertaken during the last 50 years. This work had been initiated earlier by the State Forest Service on the basis of scientific research done by the National Forest Institute. These actions were aimed at the reduction of cutting volumes and the preservation of oak stands as protected forests or reserves; the practice of more sophisticated silvicultural systems to assure natural regeneration; the return of coppices to former high forests; reforestation; and, recently, ecological reconstruction (here called "restoration forestry").

In my opinion, it is necessary at this time also to mention other measures taken by Romanian silviculturists and scientists for the conservation of biodiversity in oak forests, *in situ* and *ex situ*. In order to preserve the country's genetic resources and to assure high quality seed production for reforestation, a seed stands catalogue was drawn up for all 29 primary tree species by Enescu in 1986. This catalogue includes a total area of 26,000 hectares of approved (certified) valuable seed stands for oak species in the following proportions: *Q. petraea*, 67 percent; *Q. robur*, 20 percent; *Q. frainetto*, 7 percent; *Q. cerris*, 3 percent; *Q. pedunculiflora*, 3 percent; and *Q. pubescens*, 0.1 percent. At present, a program for the revision and updating of this national inventory of forest genetic resources is underway by the staff of the National Research Institute. In addition, the production of genetically improved seeds is realized in 83 hectares of clonal seed orchards, mainly for rare native oaks.

The selection and establishment of protected areas (national parks, forest reserves, monuments of nature and other protective categories) was another effective measure to protect and conserve *in situ* valuable forests. Between 1932, when the first forest reserve for an authentic oak ecosystem (Forest Mociar) was set up, and the present day, a considerable number of valuable forest areas were established, managed or proposed as protected areas. Table 1 shows the occurrence of oak species in 34 forest reserves in Romania. In spite of the dispersed locations and, in some cases, reduced area of these reserves, the data reveal the large biodiversity of oak reserves in this country and their uniqueness and scientific importance in a framework of a future European network of forest reserves.

In order to avoid the extinction of some rare oak species, *Quercus virgiliana* Ten. was included (Radu, 1995) in the "Red List" of threatened plants as a rare species. But efficient protective measures must be taken as well for the stands with *Q. pubescens* Willd. and *Q. pedunculiflora* K.Koch.

Like other trees, oak taxa (species, subspecies, ecotypes, valuable populations, biotypes, cultivars, etc.) can be preserved *ex situ* in arboreta, according to their ecological requirements, using generative (seeds) or vegetative propagation. Until recently this kind of conservation was used mainly for introduced (exotic) species, and only occasionally for native oaks.

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Table 1

OCCURRENCE OF OAK SPECIES IN SOME FOREST RESERVES IN ROMANIA

(Excerpt from: Radu, 1994. *Inventory of natural and semi-natural forest in Romania*)

No.	Name of Reserve	Location (County)	Area of Forests (hectares)	Short Description - Importance
1	NP Cozia	Vîlcea	6747	— Natural and quasi-virgin forests of beech, sessile oak, spruce and fir. Occurrence of *Q. robur* at high altitudes (1800 m).
2	Nat. P. Portile de Fier	Mehedinti	423	— Semi-natural stamds on limestone along the Danube, with *Fagus* (*F. sylvatica, F. taurica, F. orientalis*) and Quercus (*Q. cerris, Q. pubescens, Q. virgiliana, Q. polycarpa* and *Q. dalechampii*).
3	FR Bavna (Fersig)	Maramures	26	— Old virgin oak forest (*Q. robur*).
4	FR Dumbrava - Vîna-toril Neamtului	Neamt	866	— Old oak natural forest (*Q. robur*).
5	FR Runcu-Grosi	Arad	932	— Old quasi-virgin and natural sessile oak forests.
6	FR Domogled	Caras-Severin		— Natural stands with *Q. pubescens, Q. cerris, Q. frainetto*, and other submediterranean broadleaved species on limestone in Domogled Mts. Occurrence of Pinus nigra var. banatica.
7	FR Tudora	Botasani	126	— Remnants of old natural beech-hornbeam-sessile oak forest preserving scattered *Taxus baccata*.
8	FR Uricani-Ciurea	Iasi	63	— Natural oak forest (*Q. robur, Q. petraea*).
9	FR Hârboanca-Brahasoaia	Vaslui	70	— Natural oak forest (*Q. pedunculiflora, Q. pubescens, Q. dalechampii, Q. virgiliana*) in sylvic-steppe, with occurrence of their natural hybrid populations.
10	FR Calinesti	Vaslui	365	— Old natural sessile oak-beech forest.
11	FR Mociar	Mures	50	— Remnants of old natural oak forest (*Q. robur*) on heavy, moist soils.
12	FR Dalhauti	Vrancea	138	— Remnants of old sessile oak-beech forest.
13	FR Cristian	Brasov	372	— Natural sessile oak-fir mixed forest (azonal relict) at 900-930 m. elevation.
14	FR Prejmer	Brasov	252	— Natural oak (swamp ecotype of *Q. robur*) forest with other rare and endemic spp.
15	FR Dumbrava Vadului	Brasov	395	— Natural thinned oak forest, sheltering an abundant occurrence of *Narcissus stellaris*.
16	FR Spataru	Buzau	174	— Natural and semi-natural ash (*Fraxinus pallisae, F. angustifolia*) with oak on primary saline soils.

17	FR Gîrboavele	Galati	450	—	Remnants of natural *Q. pubescens* and *Q. pedunculiflora* forest. Occurrence of hybrids.
18	FR Caraorman	Tulcea	841	—	Semi-natural ash-oak (*Q. robur, Q. pedunculiflora*) and poplar forest on river-marine sand dunes, in Danube-Delta.
19	FR Letea	Tulcea	2746	—	Natural and semi-natural oak-ash and *Alnus* forests, on river-marine sand dunes in Danube delta.
20	FR Hagieni	Constanta	207	—	Natural forest of *Q. pedunculiflora* and *Q. pubescens* with *Carpinus orientalis*.
21	FR Ciornuleasa	Calarasi	254	—	Natural and semi-natural mixed oak forest (*Q. robur, Q. pedunculiflora*) with lime, ash and *Prunus mahaleb*.
22	FR Comana	Giurgiu	439	—	Complex natural oak (*Q. robur, Q. pedunculiflora, Q. pubescens, Q. frainetto, Q. cerris*) forest, which includes reserves for rare and threatened species (*Convallaria majalis, Paeonia peregrina, Ruscus aculeatus*).
23	FR Snagov	Ilfov	1727	—	Remnants of ancient natural Querceto-Carpinetum. Sporadic occurrences of beech species and *Q. petraea*.
24	FR Caldarusani	Ilfov	468	—	Old natural *Q. robur* forest with white poplar and willow.
25	FR Seaca-Optasani	Olt	434	—	Old remnants of ancient 2000-ha pure massif of *Q. frainetto*.
26	FR Topana	Olt	473	—	Remnants of mixed *Q. cerris-Q. frainetto* forest and of pure *Q. frainetto* natural stands.
27	FR Plopeni	Prahova	254	—	Old remnants of natural *Q. robur* forest with some endemic herbaceous species.
28	FR Tismana-Pocruia	Gorj	220	—	Remnant groups of natural *Castanea sativa*, dispersed in natural oak (*Q. petraea, Q. cerris, Q. frainetto*) or beech stands.
29	FR Bejan	Hunedoara	235	—	Natural occurrences of eight native oak species (all except *Q. pedunculiflora*) and famous genetic center for natural hybrids among these species.
30	F Drinova-Lugoj+)	Timis		—	Old growth mixture of *Q. petraea* and *Q. robur*; high quality ecotype of *Q. petraea*.
31	F Neudorf-Lipova+)	Arad		—	Old growth mixture of *Q. petraea* and *Q. cerris*.
32	F Labasint-Lipova+)	Arad		—	Old growth stand of *Q. petraea*.
33	F Bistra-Lunca Timisului+)	Timis		—	Old natural stand of *Q. robur* with other local broadleaved species.
34	F Cheveres-Lunca Timisului+)	Timis		—	Old growth *Q. robur* monumental stand, proposed as " monument of nature."

Legend: NP = National Park; Nat. P. = Natural Park; FR = Forest Reserve; F = Forest
+) = Forests described by Smejkal, Bîndiu and Visoiu, 1995, in "Benater Urwälder"

Oak Forests in Romania . . .

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Due to their size, longevity and durability in time, oaks play a significant role in the spiritual and cultural lives of peoples. Thus, many single oak specimens also are protected in this country as ancient, famous or historic trees. It is very important to keep records, on a national level, for all tree species and to protect them before their disappearance due to human ignorance or enmity.

Storing a great biodiversity, oak ecosystems changed in time their composition and structure. These changes resulted, unfortunately, in degradation and instability. During the last centuries, silviculturists attempted (through great efforts which often were misunderstood by the public) to save these ecosystems in order to make them vital and useful for society, from economic and (more recently) ecological points of view.

The latest research on causes of the decline of oaks stipulates, first of all, an analysis of the components of ecosystems which may influence the vitality and stability of trees. These components include climatic, site, silvicultural and biotic factors. To separate and establish the hierarchy of different factors in a particular local case is a very difficult task, demanding solid knowledge, due to the complexity of decline and the interference of provocative associated factors. Since the stand constitutes the basic component of a forest ecosystem, the decline affects the main characteristics of the stand: species composition, horizontal and vertical structure, soil-site complex, as well as other silvicultural characteristics.

The gradual (or rapid) and, in most cases, irreversible passage from a normal stand structure to successive ranks of deterioration (weak, moderate or intense) is accompanied by changes of main stand structural features characterized by the following:

- the decrease, inclining toward total extirpation, of valuable oak species (suitable to the site or to the climax stage) and their replacement by secondary or pioneer species or by grassland formations;
- the reduction of stand density and breaking of the stand layers, concomitant with the luxurious development of undergrowth, composed of light-demanding or fast-propagating shrub species;
- the gradual replacement of typical understory flora by a dense and compact carpet of grasses, which makes it very difficult to establish natural forest seed regeneration;
- the appearance of simplified, disturbed and chaotic structures, due to the disappearance of the superior stand layer and of the closed canopy profile;
- the drastic reduction of valuable timber volume by unit area;
- the reduction of soil depth and fertility due to rapid litter decomposition, leaching of the humus layer and erosion;
- the decrease of stand vitality, stability and resistance to different stresses; and
- the reduction of biodiversity for some categories of plants (trees, shade herbs) or animals (large mammals), and the temporary increase of others (certain insects and birds).

Of course, in a managed forest the owner cannot wait inactively until, after a long period of vegetation succession, he might record the spontaneous reestablishment of a more or less valuable forest. Economic necessities oblige him to interfere in the sense of an active forestry restoration. For these reasons, the ecosystem reconstruction includes a complex of actions to be applied in deteriorated stands, with the aim to realize a certain structure of sites able to assure an ecological equilibrium of ecosystems and the fulfillment of their multiple functions in the environment (Ianculescu, Donita, 1995; Stanescu, 1996).

Consequently, the works practiced in the frame of ecological reconstruction belong to a great variety of interventions suitable to the stage of the stand and the degree of its deterioration. If the stand is not affected by an intense dieback and the main oak species are still sufficiently represented, the stand gaps can be planted with associated broadleaved species and shrubs in order to insure an optimal stand density and to protect the soil. In extreme cases, completely destroyed stands must be replanted using species and technologies adequate for the site.

In so-called "derived stands" (second growth), with a predominance of hornbeam (*Carpinus*), lime (*Tilia*), maples (*Acer*) or other broadleaved associate species that appeared as a result of degradation in former mixed oak forests, the oak species can be reintroduced by planting of transplants in small groups. In many cases, direct acorn seeding is preferable, but frequent scarcity of fructification is limiting this method. Also, wild boars inflict serious damages to acorn seeding in autumn, and up until now no efficient repellant has been found to stop this.

In simplified pure oak stands, it is recommended, according to site conditions, to reintroduce the associated broadleaved species (*Fagus, Tilia, Acer, Fraxinus, Carpinus*) and for soil protection, to introduce different native shrubs in moderate density.

Because some stands have not lost their natural regeneration capabilities and produce small annual amounts of acorns, preparing the soil in small square or circular plots before seedfall can stimulate the establishment of young oak plants. Concomitantly, advance regeneration must be protected during logging and promoted by removal of competing vegetation. Tree shelters also can be an effective aid to oak establishment, particularly in areas exposed to grazing.

I think these considerations are not only of local importance, but can constitute a useful exchange of thoughts and experiences in our common efforts to save the oak, rightly called by the famous Romanian silviculturist, Dr. Martin Dr_cea, "the aristocrat of the forest and the diamond of woods."

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Using GIS Technology to Assess Potential Hardwood Loss

in the Northern Sacramento Valley, California

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Since early 1994, The Northern Sacramento Valley Sustainable Land scapes Project (SLP)[2] has focused on facilitating informed discus sions between public policy makers and resource stakeholders, including the general public, on long term management of the extensive oak woodland landscape (fig.1). As part of its goal to develop an acceptable framework for discussing issues related to sustainability, the SLP has chosen to utilize geographical information system (GIS) technology. By incorporating land use and population projections into a GIS, it is possible to begin a spatial assessment of present and future growth patterns.

Like most of California's inland valleys, the population of the northern Sacramento Valley is forecast to more than double by the year 2040 (California Department of Finance 1993). Population growth in the region typically takes the form of low density development (averaging 1 to 3 dwelling units per acre) within the planning areas of incorporated cities. In addition, rural residential lots of one to 40 acres per dwelling unit develop around farming communities and in oak woodland and timbered landscapes.

Increased growth implies that additional land will be placed under development pressure for urban and rural residential uses. If this pattern of lower density urban development and extensive rural residential development is

1This paper is the update to a paper by Nelson and Radabaugh (1996). Base information and data are the result of research conducted by Mark Radabaugh and are described in a report (Radabaugh 1995).

2The Northern Sacramento Valley Sustainable Landscape Project includes Butte, Colusa, Glenn, Shasta and Tehama Counties, California. These five counties contain approximately seven percent of California's land area. Oak woodlands cover approximately 21 percent of the landscape in the five county region and the region accounts for approximately 14 percent of the State's oak woodland inventory based on Pillsbury (Pillsbury 1991).

projected past the 15- to 20-year time frames of local area plans, significant oak woodland acreage will be affected.

Methodology

A review of past and present population patterns and growth trends in the five county SLP region resulted in a series of GIS coverages depicting future land use and population density (Radabaugh 1995). Land-use polygons were identified and population distribution forecasts were made based on key factors including:

- An estimate of existing population based on the 1990 Census, county assessors records and other data;
- An estimate of population build-out potential described in terms of average density; and
- The estimated average annual population growth rate to be expected within each polygon.

TABLE 1-TOTAL ACREAGE OF HARDWOOD RANGELANDS

County	Total Acreage of Hardwood Rangelands	Percent of County
Butte County	242,771	22.6
Colusa County	158,881	21.5
Glenn County	142,646	16.8
Shasta County	304,849	12.4
Tehama County	672,189	35

Paper maps of each of the five counties were prepared and digitized using one of five general land use categories. These categories included:

- *Incorporated city spheres* of influence or areas specifically designated for future urban growth and expansion;
- *Unincorporated communities* where water and/or sewer services are provided and residential build- out density is less than one dwelling unit per acre;
- *Rural residential lands* where build-out density is between one and 40 acres per dwelling unit and resource production from the parcel is not the primary land use. They are generally located on agricultural, grazing and range, and timber producing land;
- *Agricultural lands* were divided into small-scale agriculture (less than 20 acres per dwelling unit) and large- scale agriculture (greater than 20 acres); and

- *Other resource producing lands* including lands utilized for grazing, timber production, mining, wildlife habitat and open space. Resource lands were divided into foothill rural and timber. Acreages are greater than 40 acres per dwelling unit.

For the purposes of assessing impacts in the oak woodland interface, the first three categories were considered sensitive to population change. As more information like riparian data along the Sacramento River and its tributaries becomes available, impacts in the valley oak areas along the river can be added as well.

Information from data collection was digitized using ArcInfoÓ software, a GIS product developed by Environmental Systems Research Institute (ESRI) in Redlands, California. ESRI desktop GIS software, ArcViewÓ, was utilized for plotting maps and for statistical analysis.

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Using GIS Technology . . .

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GIS Analysis

A geographical information system (GIS) is best defined as the marriage of the map and the database. GIS technology combines the qualities of a mapping system with the ability to analyze geographic locations and and information linked to those locations. GIS information is database driven. Results can be accessed from the map or from the database (ESRI 1995).

TABLE 2 -TOTAL ACREAGE IMPACTED BY DEVELOPMENT

County	Total Acreage Impacted By Development	Percent of County
Butte County	117,972	48.6
Colusa County	535	0.3
Glenn County	68	0.05
Shasta County	166,929	54.8
Tehama County	33,392	4.9

Map information compiled by Pillsbury (Pillsbury 1991) showing California hardwood types was obtained from the California Department of Forestry and Fire Protection (CDF) as a digital file (fig.2). Using ArcView software, it was easy to generate statistics showing the total acreage of hardwood rangelands in the five county SLP region.

Examination of the potential impact of population growth on the oak interface requires overlaying Radabaugh's land use layer (coverage) with the Pillsbury's hardwood coverage. Incorporated city spheres, unincorporated communities, and foothill rural residential area were used as they are population sensitive and have the greatest impacts in the oak woodland interface. Those land-use areas not within the hardwood region were deleted; i.e., the agricultural areas on the valley floor were skipped. In addition, the timber and foothill rural resource areas were deleted if their densities were greater than 40 acres per dwelling unit.

When this step is completed and statistics are generated, the impacts of potential build out within the oak woodland interface become very apparent and the true extent of the foothill rural residential area becomes defined (fig. 3). Further, when examined on a regional scale, it becomes apparent that not all of the counties are significantly impacted.

One of the advantages of using GIS technology as a tool to examine impacts is that it gives the user the opportunity to quickly see which areas are impacted and to ask "why?". In this case, it becomes obvious that the major impacts are tied to land use and will occur where major growth is projected; i.e., in Butte and Shasta Counties.

Butte County is the most populous of the five-county SLP area. Although this county contains the region's largest urban area population, the population of its unincorporated community centers and towns is the smallest

TABLE 3 -TOTAL ACREAGE OF HARDWOOD RANGELANDS BY TYPE

Hardwood Type	Butte County (in acres)	Shasta County (in acres)
Blue Oak/Foothill Pine	82,765	212,187
Blue Oak woodlands	10,623	87,386
Montane Hardwoods	148,020	5,271
Other Hardwoods	1,364	16

of the five-county area. Nonetheless, Butte County has the second largest inventory of rural residential land and population, following Shasta County. The City of Chico accounts for roughly 44% of the county's population.

Shasta County is the second most populated county. It contains the largest inventory of rural residential land which has accounted for much of the past growth within the unincorporated area. The City of Redding and its sphere of influence account for over 50% of the county's population.

In order to better quantify impacts in these two counties, an examination of the Pillsbury's hardwood coverage gives the following breakdown of hardwood rangelands by type.

Examination of the impact of potential growth on the oak interface requires overlaying the land use coverage with the hardwood layer. When this step is completed and statistics are generated, a third set of data was generated illustrating potential vegetation loss by hardwood type. Percentages can be easily calculated and statistical summaries can be generated as needed, including number of new polygons created (fragmentation rate), average area, and percent of total area impacted. Below are the numbers of acres in each county impacted by the projected build outs.

Each impacted hardwood is the result of a land-use impact. Therefore, it is also possible to generate impacts by land-use type or by development density. From these figures, new questions can be formulated and new GIS inquiries made. Results can be viewed as a table or on maps. These maps help facilitate discussions which can lead to better decisions.

Implications

Impact statistics, while significant, can be misleading and are open to debate. For instance, resource professionals suggest that the impact of one dwelling unit per 40 acres may be significant to oak habitat. Others question this

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TABLE 4 – POTENTIAL BUILDOUT IMPACTS IN BUTTE AND SHASTA COUNTIES

Hardwood Type	Butte County (in acres)	Build-out Impact (in percent)	Shasta County (in acres)	Build-out Impact (in percent)
Blue Oak/Digger Pine	42,600	51.5	123,911	58.4
Blue Oak woodlands	4,828	45.4	38,219	43.7
Mixed Hardwoods	71,575	48.4	2,018	38.3
Other Hardwoods	330	6.0	7	45.9

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assumption. With a GIS, it is easy to re-evaluate impacts as new research becomes available or as policy shifts occur.

The information generated in this project was based on growth projections and should not be used to stop development in Butte and Shasta County or anywhere else in the five county region. Rather, it should be used to guide responsible growth. Maps and statistical information merely give planners, decision makers and the interested public the ability to examine potential impacts, initiate discussion, and try to formulate workable growth strategies.

Further, techniques used to do the above analysis are general in nature and assume a level plane with little or no regard to local development policies and practices. While this works well on a regional level, clearly a more sophisticated GIS approach is needed before major policy decisions are made. These decisions should be made using large scale parcel level maps and the best environmental information available within each local jurisdiction.

Conclusions

The ability to graphically illustrate growth projections in a GIS gives the SLP an important planning tool. Some of the potential uses for this type of data are:

- The improved ability to assess changes in the oak woodland landscape on a comparative basis with other resources can lead to new or expanded ideas regarding oak woodland sustainability. Digital maps and statistical information can be used as tools to help counties formulate general plan policy in the hardwood rangelands.
- New thematic digital map layers including riparian, wetlands, vernal pool, deer herd, and land ownership are available for many of the SLP counties and have been incorporated into a map data base developed by the Geographical Information Center at California State University, Chico (GIC);
- The GIC has begun making SLP data available via the Internet (http://phobos.lab.csuchico.edu/ hosted/sustainable/index.html). Maps can be obtained as .pdf files which can be loaded at scale, viewed and printed using Adobe Acrobat ReaderÓ. Acrobat Reader is a shareware product linked to the GIC's download site or available free of charge from Adobe ;
- Inclusion of a method to spatially assess population growth impacts on a variety of other natural resource components will likely lead to more related research in the region;
- A GIS data system is adaptable and can be easily updated to accommodate new spatial information. Monitoring and classifying California's rangelands is an ongoing endeavor. As new digital maps are developed, information can be used to update existing oak woodland or land use statistics. In fact, a new digital hardwoods layer has recently been completed by CDF; and
- Mapping provides a clear visual format for area residents to understand relationships between land use and population growth. Low cost software like ArcView makes desktop GIS and SLP data readily available to local decision makers who will ultimately decide the fate of the oak woodland interface.

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Soil Microbial Ecology of Oregon White Oak in an Urban Landscape

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In a series of storms during the winter of 1995, several trees were lost from a grove of approximately 100 native Oregon white oaks (*Quercus garryana* Dougl.) on the Linfield College campus in McMinnville, Oregon. Inspection of the fallen trees revealed the absence of major structural roots, suggesting infection by *Inonotus dryadeus*, and evident symptoms of *Armillaria* root rot. Subsequently, horticultural practices within the grove were modified (summer irrigation and fertilization were eliminated and mowing was reduced to once/month) to minimize further damage by pathogenic fungi and to restore the health of the grove. In 1995, we began a study to quantify and describe changes in soil microflora as management practices were changed. Here, we describe baseline measurements of soil bacteria and fungi in the grove and adjacent sites. We describe antagonism of *Streptomyces* spp., which were isolated from the samples, against Armillaria, and mycorrhizal colonization of oak seedlings germinated in soil samples.

Materials and Methods

Collection of samples — Soil collections were made in December 1995 and January 1997 and in the summers of 1996 and 1997. We collected soil and root samples from six oaks located in the interior of the grove and along its perimeter. The specimens included one large savanna oak that serves as the visual symbol of the College (the "old oak"); two sites in a large lawn area (the "graduation green") lying between the grove and the savanna oak; and two oaks located downslope from the graduation green (Table 1). Except during January 1997, when the Cozine Creek, which runs through the campus, was flooded, we also collected from four oaks growing on banks alongside this creek. Here, the oaks are growing in an unmanaged, relatively undisturbed riparian stand dominated by Oregon ash, *Fraxinus latifolia* Benth.

At each site, except the two in the graduation green where there are no trees, soil samples were taken from the base and six meters to the south of each tree. The two sites in the graduation green were chosen from the center of the lawn area away from any trees. Each sample consisted of five soil cores approximately 5-7 cm deep, which were mixed to give a composite sample of approximately 1,000 g of soil. Subsamples were combined again to form a total of 13 composited samples, which were stored at 5° C until processed (Van Elsas and Smalia 1997, Wollum 1994). Soil pH was determined using a Kelway® Soil pH and Moisture Tester. Soil types were obtained from the Soil Survey of Yamhill Area, Oregon (USDA SCS 1974).

Dilution plating — The soil was thoroughly mixed and sifted through a two mm screen to remove rocks and plant segments. Ten grams of each composite sample were added to 90 ml of sterile water, dispersed by agitation for 20 minutes, and serially diluted in deionized water. Triplicate samples of appropriate dilutions were made using the pour plate method (Wollum 1994, Zuberer 1994) in either tryptic soy agar (TSA) to isolate bacteria or rose bengal agar (RBA) containing chloramphenicol (0.1 mg/ml) to selectively isolate fungi (Atlas 1995). Plates were incubated at 25° C and counted after 48 hours. Counts were corrected for soil moisture content (Zuberer 1994).

Statistical analysis — All statistical analyses were performed using Microsoft Excel 5.0. Means of triplicate plate counts are expressed as colony forming units (CFU) per gram of dry soil. The 95 percent confidence intervals were defined as plus or minus two standard errors of the mean (± 2 SE). Standard regression analysis was used to test for relationships between plate counts and the environmental parameters of soil moisture and pH.

Mycorrhizal colonization bioassay — Attempts to use acorns from oaks collected from the oak grove for our mycorrhizal colonization bioassy failed when a hard winter frost killed every seedling. Subsequently, acorns collected from two sites within the city of McMinnville were obtained from the Oregon State University Extension forester and used to bioassay for mycorrhizal colonization. The acorns were surface-cleaned and sown in Monarch plant bands filled with soil from each site. The seedlings were harvested after seven months and measured for height and weight, number of leaves, number of root branches, and root biomass. Visual evaluation for the presence of ectomycorrhizae was conducted using a dissecting microscope. Root segments were removed from each seedling, thin sectioned, and stained with Trypan blue (Cox and Sanders 1974, Jarstfer and Sylvia 1997) in order to enable direct observation of ectomycorrhizal Hartig nets and mantles and arbuscular-mycorrhizal hyphae (AM) and arbuscules.

We searched for soil propagules (spores) of AM fungi by passing a slurry (100 g soil in 1 l water) through a nested series of sieves (1000 uM to 45?uM). Residues from the 350, 150, and 45 uM sieves were centrifuged in a sucrose gradient and the resulting pellet was searched under a dissecting microscope for the presence of spores in the AM fungal order *Glomales*.

Antibiosis — Actinomycete isolates were used in a cross-inoculation assay method (Hutchins and Rose 1984) to test for antagonism of *Streptomyces* spp. to the root rot fungus, *Armillaria mellea*. In December 1995, we isolated strep-

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tomycetes from the soil subsamples based on gross colonial characteristics (e.g., size of hyphae, size of colony, general colony appearance) and inoculated them onto sodium albuminate agar, a selective medium that allows for the rapid growth of *Streptomyces*. We grew *Armillaria mellea* for 10 days on yeast malt agar (YMA) and placed a subculture of the streptomycetes on the test plates. After incubation for two weeks at 25° C, we counted zones of inhibition between pathogen and antagonist and inspected the pathogen for hyphal abnormalities and altered morphology, which are indicators of antagonism between *Streptomyces* spp. and *Armillaria*.

Results

Soil bacteria and fungi — Total aerobic counts per gram of dry soil were approximately 107 CFU for bacteria and 105 for fungi (Figs. 1 and 2). No significant differences in microbial population counts were evident among sites (ANOVA $F = 1.29$, $p = 0.248$ for bacteria; $F = 1.36$, $p = 0.21$ for fungi) but significant seasonal differences were found for both bacteria and fungi ($F = 22.46$, $p < 0.05$ for bacteria; $F = 6.2$, $p = < 0.05$ for fungi). In both cases, microflora numbers were lower in winter than in summer. Low bacterial populations were also present in June 1997, when soil conditions were drier than in previous years.

The study area encompassed three soil types: Woodburn Silt Loam, Terrace Escarpment, and Wapato Silty Clay Loam. Soil pH averaged across the collection sites was generally lower in winter than in summer, averaging 5.6 in winter and 6.7 in summer ($t= 9.2$, $p<0.01$). Both bacteria and fungal numbers increased with increasing moisture content ($r2 = 0.08$, $p<0.05$ and $r2 = 0.07$, $p<0.05$ respectively). The relationship between pH and microflora populations depended on microfloral type: bacterial counts increased significantly with increasing pH ($r2 = 0.24$, $p<0.05$); fungal counts did not vary with pH ($r2 = 0.003$, $p = 0.67$).

Mycorrhizal colonization — Forty-one percent of the oak seedlings bioassayed supported ecotomycorrhizal fungal structures. None displayed any AM (endomycorrhizal) structures; however, soil sievings from all sites revealed spores from the AM genus *Glomus*.

Antibiosis — Twelve percent of our *Streptomyces* isolates displayed some antagonism toward *Armillaria*. However, we did not find a reduced incidence of antagonism in soils associated with diseased trees nor did we detect any relationship between the presence of antagonistic *Streptomyces* and site or management regime.

Discussion

The goal of our study was to quantify and describe soil microbiota in the rhizosphere of a grove of Oregon white oaks and in adjacent sites under different management regimes. The rhizosphere includes a narrow band (usually 5 mm) of soil surrounding plant roots where soil microorganisms, such as bacteria, fungi, algae and protozoans are found in higher numbers than in non-rhizosphere soil. We hypothesized that the total rhizospheric concentrations of soil bacteria and fungi would differ among sites and seasons, and change with improved horticultural practices in the grove.

The abundance and diversity of soil microorganisms reflects the species composition of above-ground vegetation, and the microorganisms affect growth and development of the plants. For example, bacteria and fungi play a critical ecological role as decomposers in ecosystems, and approximately 90 percent of all plants assessed thus far support mycorrhizal fungi, indicating the important role they play in plant nutrition (Gray and Williams 1971, Sylvia et al. 1998). On the other hand, some microorganisms, such as *Armillaria*, are pathogenic. Actinomycetes are aerobic soil bacteria that form a mycelium composed of branching filaments, and **Streptomyces**, which produce antibiotics that can inhibit plant pathogens such as *Armillaria,* are often dominant members of the actinomycete population (Hutchins and Rose 1984).

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Quercus garryana *Douglas ex. Hook*

Soil type and other environmental factors may affect the distribution and diversity of microorganisms. Environmental influences on microbial diversity and distribution include season, temperature, pH, and soil depth and moisture (Alexander 1977, Killham 1994). In western Oregon, where winters are very wet and summers are essentially rain free (Franklin and Dyrness 1973), one would expect to find seasonal differences in soil microbiota. Horticultural practices may also affect the distribution and types of soil microorganisms. Native species, such as Oregon white oak, are adapted to summer drought and suffer in environments where summer watering, fertilizing, and mowing are common horticultural practices (Hopkins 1998). Such was the case in the oak grove on the Linfield College campus where the lawn underlying the oaks was irrigated for 14 weeks during the summer (June through September) with one inch of water per week. Subsequently (June 1995), summer watering, fertilizing, and mowing have been halted within the grove, but they continue in the graduation green, which affects both the large savanna oak and the oaks situated downslope from the graduation green.

Soil bacteria and fungi — Colony forming units of 107 for bacteria and 105 for fungi are within the range of values commonly reported for soil bacteria and fungi; bacteria are typically 100 times more numerous than fungi (Alexander 1977, Tate 1995). Although soil microflora varied considerably in space and time, we were unable to detect consistent significant differences in microbial population counts among sites. For example, no differences were detected between the microflora at sites along the periphery of the oak grove (with summer irrigation) and sites in the interior of the grove (without summer irrigation). Several years of sampling may be necessary to discern changes in the soil microflora in those sites where horticultural practices have improved recently. The highest numbers of bacteria were found at those sites where no changes have been made in horticultural practices, such as along the periphery of the grove and beneath the Old Oak.

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Bacterial populations were generally lower in June 1997, when soil conditions were drier than in previous years, suggesting that microflora at our sites may eventually respond to reduced summer irrigation.

Surprisingly, despite the differences in soils in the study area and the fact that both fungal and bacterial counts increased with increasing moisture, we were not able to detect differences in soil microflora associated with the three soil types. Woodburn Silt Loam is the most extensive soil found on Willamette Valley terraces and is moderately well-drained. Terrace Escarpments are found along small streams, such as the Cozine Creek, that have cut deeply into Willamette Valley terraces. Like Woodburn Series soils, Terrace soils are well drained, but tend to be more sloping and to include small seep spots. Both of these soil types typically support Oregon white oak. On the other hand, Wapato Silty Clay Loam consists of poorly drained soils in bottom lands along streams and supports a vegetation consisting primarily of Oregon ash (USDA SCS 1973). Thus, we anticipated that summer bacterial and fungal counts in Wapato soils would differ from those in Woodburn and Terrace soils. Because winter precipitation in Oregon is abundant and all soils are saturated, we did not expect to detect microflora differences in this season.

The dilution plate method detects only those microorganisms capable of multiplying in TSA and RBA culture media, aerobic conditions, and within 48 hours at 25° C (Johnson 1998, Tate 1995). Thus, the cultural conditions under which our study was performed precluded our detecting certain microflora, such as anaerobic bacteria that likely are present in greater numbers in the hydric Wapato soils. These same conditions may contribute to inflated estimates of fungal numbers in winter soils because spores, dormant in anaerobic soils, would germinate under the conditions of this experiment.

Correlations with soil pH — Johnson (1998) compared seasonal differences at our sites and two additional sites for one year (June 1997 and January 1998). She also found that bacteria were more abundant in winter than in summer possibly because they prefer a pH range of 6.5 to 7.5, which is well above the average winter pH of 5.6 that we document at our sites. In contrast to our findings, she did not detect any seasonal differences in numbers of fungi, which she attributes to their ability to remain functional over a wide range in pH and, thus, make up a larger percentage of the microflora community than bacteria in winter (Griffen 1972, Alexander 1977).

Mycorrhizal colonization — More than 95 percent of all plants support mycorrhizae, and roots colonized by mycorrhizal fungi are less susceptible to infection by root pathogens than non-mycorrhizal roots (Marx 1971). Although most of their interactions are with ectomycorrhizae, oaks support AM (endo-) and ectomycorrhizae (Bagyaraj 1991, Johnson 1998). Our finding that 41 percent of the oak seedlings bioassayed supported ecotomycorrhizal fungal structures is within the range of colonization detected in greenhouse experiments in oaks (Riffle and Tinus 1979). Arbuscular mycorrhizae do not grow well in culture (Bowen 1987) even though their spores are often isolated from soil samples (Johnson 1998). Thus, it is not surprising that we were unable to detect AM structures on our oak seedlings even though were able to identify spores from the AM genus *Glomus* in our soil sievings.

We did not examine mature oaks for mycorrhizal structures, but a single observation of the root system of a fallen oak revealed dichotomously branding roots typical of ectomycorrhizae and rhizomorphs characteristic of *Armillaria*. Thus, both symbionts are most likely present at most, if not all, of our sites.

Antibiosis — Actinomycetes numbers are typically higher in summer when conditions are dry (Sylvia et al. 1998) and the pH is 6 or above. Thus, our winter soil samples, which were collected from wet, acidic soils, probably represent a low estimate of the total numbers present throughout the year. On the other hand, horticultural practices may, in fact, reduce actinomycete abundance in summer. In addition to increasing the presence of pathogens, such as *Armillaria* and to adversely affecting the inoculum potential of mycorrhizal fungi, intensive fertilizer use, which was typical in our study sites, decreases antagonist abundance (Sylvia et al. 1998).

A number of studies have reported actinomycete antagonism to root pathogens found in our region (Hutchins and Rose 1984) and have demonstrated their ability to inhibit the growth of *Armillaria mellea* and *Fomes annosus* under laboratory conditions (Gunderson 1963). Although we found that 12 percent of our *Streptomyces* isolates displayed some antagonism toward *Armillaria mellea* cultures, we do not know if this antagonism occurs at our study sites, nor do we know if the antibiotic substances are stable under field conditions. We are now attempting to isolate water soluble antimicrobial substances from the antagonistic *Streptomyces*, and we are using SEM and biochemical tests to identify the species.

In addition to antagonistic *Streptomyces*, mycorrhizal fungi may also inhibit *Armillaria mellea*. In healthy stands, mycorrhizal fungi compete favorably with root pathogenic fungi for colonization zones on the root surface.

Summary

In this paper, we discuss preliminary results of a long-term study to quantify and describe seasonal and site diifferences in soil microflora in a grove of Oregon white oak and adjacent sites under different management regimes. Although the results of our study have not yet been fully analyzed, we report the following preliminary findings:

-Total aerobic counts per gram of dry soil are within the range typically reported for soil microflora (107 CFU for bacteria and 105 for fungi). We found no statistically significant differences in microflora numbers across sites, but both fungal and bacterial counts are lower in winter than in summer. The highest numbers of bacteria were found at those sites where horticultural practices remain unchanged.

-Soil pH was generally lower in winter than in summer, averaging 5.6 in winter and 6.7 in summer. The relationship between pH and microflora populations depended on microfloral type: bacterial counts increased significantly with increasing pH; fungal counts did not vary with pH. Soil moisture varied seasonally and among sites. Both bacteria and fungal numbers increased with increasing moisture content.

-Forty percent of oak seedlings surveyed supported ectomycorrhizae, but we were unable to detect any AM structures. However, spores of the AM genus *Glomus* were found in all soil samples. Thus, mycorrhizae are present in the study area.

-Twelve percent of the *Streptomyces* isolated from the soil samples displayed some antagonism against *Armillaria*. Although we did not find a correlation of antagonistic *Streptomyces* to diseased trees, we suspect that the change in horticultural practices will benefit the oaks by altering the relationship between the root pathogen *Armillaria*, mycorrhizal fungi, and the *Streptomyces* populations.

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We plan to continue monitoring these sites over the next several years, comparing soil microflora between seasons and among sites where managment conditions differ or change over time.

This paper is based on a poster reporting on preliminary results. A manuscript, which will include an additional year of data and a complete analysis of our results, is in preparation.

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Sustaining Oak Woodlands in California's Urbanizing Environment

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California's oak woodlands, also known as hardwood rangelands, cover 10 million acres, or ten percent of the state (Bolsinger 1988; Greenwood et al. 1993; Pacific Meridian Resources 1994). These areas have an overstory tree canopy, predominantly in the oak genus (*Quercus spp.*), and an understory of exotic annual grasses and forbs, and occasional native perennial grasses (Griffin 1973; Bartolome 1987; Holmes 1990; and Allen et al. 1991).

Since European settlement of California, oak woodlands have been managed primarily for livestock production. These areas have taken on a new importance because of the recognition that they have the richest species abundance of any habitat in the state, with over 300 vertebrate species, 5000 invertebrate species, and 2000 plant species found on oak woodlands (Verner 1980; Barrett 1980; Garrison 1996). Oak woodlands also provide water quantity and quality, outdoor recreation, and aesthetics. Over 80 percent is in private ownership (Greenwood et al. 1993).

The five major oak species occurring on oak woodlands include three deciduous white oak species – blue oak (*Quercus douglasii*), valley oak (*Quercus lobata*), and Engelmann oak (*Quercus engelmannii*); and two evergreen oaks – coast live oak (*Quercus agrifolia*) and interior live oak (*Quercus wislizeni*).

California has one of the most rapidly growing human populations in the world. The state's population has grown from less than 100,000 people in 1850, to over 31 million people today (an average annual rate of growth of 3.4 percent) to a projected 63 million people in the next 50 years (Medvitz and Sokolow 1995). This population growth is having an impact on oak woodlands. A survey of oak woodland owners showed that the majority of all owners now live less than 5 miles from a subdivision (Huntsinger and Fortmann 1990; Huntsinger 1992). These surveys also showed that approximately one-third of the properties changed owners between 1985 and 1992, and 5 percent were subdivided for residential development. The urban interface with oak woodlands, once confined to the major population centers of the San Francisco Bay, Sacramento, and the Los Angeles basin, now extends throughout the entire state.

Oak woodland conservation strategies must recognize the widespread extent of this broad habitat type, its role in the state's economic livelihood, and its important ecological values. This paper assesses how urbanization affects oak woodland sustainability, which includes maintaining:

- ecosystem processes at multiple scales;
- the existing diversity of biological organisms;
- economic viability over the long-term.

Each of these items will be discussed in some detail below, as well as some of the conservation policies being implemented in the state.

Spatial and Temporal Aspects of Sustainability

Landscape-Level Sustainability

Landscape factors affecting oak woodland distribution include long-term climatic factors, and more recently, human-caused events. Pollen analysis shows shifts in distribution of oak stands along altitudinal gradients (Byrne et al. 1991). Over the past 40 years, California's oak woodlands have decreased by over one million acres on a statewide scale (Bolsinger 1988) due to human-induced factors. Major losses from 1945 through 1973 were from rangeland clearing for enhancement of forage production. Major losses since 1973 were from conversions to residential and industrial developments. Regionally, some oak woodlands have decreased due to urban expansion (Doak 1989), firewood harvesting (Standiford et al. 1996), range improvement (Bolsinger 1988), and conversion to intensive agriculture (Mayer et al. 1985). Habitat fragmentation, increased conflicts between people with different value systems, predator problems, and soil and water erosion have resulted.

Stand Level Sustainability Considerations

From 1932 to 1992, blue oak woodland canopy density and basal area increased under typical livestock grazing, and fire exclusion policies (Holzman 1993). This indicates that many oak stands are stable to increasing over a moderately long period, despite perceived natural regeneration problems (Muick and Bartolome 1986; Bolsinger 1988; Swiecki and Bernhardt 1993). However, more than 20% of the study sites were converted to other land uses, primarily residential subdivisions, during this period (Holzman 1993). A similar study of changes in tree and total woody cover of foothill oak woodlands from 1940 to 1988 found these areas were relatively stable (Davis 1995).

Pollen analysis studies document the dynamics of hardwood rangeland composition over a very long-term period and highlight the changing influence of human populations (Byrne et al. 1991). Oak woodlands were relatively stable during the long period of use by Native Americans. Following European settlement, livestock introduction, and clearing for intensive agriculture approximately 150 years ago, oak densities declined. Exotic annuals first show up in the pollen record at this same time. Since this initial exploitation of the oak resource in this early settlement period, oak cover has increased dramatically. Current oak densities derived from the pollen record are at their highest level, due to fire exclusion policies of the last 50 years,

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and low intensity, extensive management practices associated with ranching uses.

Maintaining Ecosystem Processes

Beginning with the introduction of domestic livestock and exotic annuals by European settlers, oak woodland ecosystems have changed dramatically. Herbaceous composition has changed from perennials to annuals (Holmes 1990). Fire intervals and intensity have increased (McClaren and Bartolome 1989). Overstory cover, if not converted to another land use, has generally increased (Holzman and Allen-Diaz 1991). Soil moisture late in the growing season has decreased, and soil bulk density has increased due to compaction from higher herbivore densities (Gordon et al. 1989). Riparian zones are now less dense and diverse (Tietje et al. 1991). A general summary of the changes in ecosystem inputs from pre-settlement conditions to the current time is shown below (Table 1). These ecosystem process changes are discussed below.

Herbaceous Composition

The pre-European herbaceous community in oak woodland understory included native perennial bunchgrasses and forbs (Holmes 1990). Native species were displaced by alien annuals from Europe, Asia, Africa and South America with arrival of European settlers (Burcham 1970). Urbanization is accelerating exotic invasion, although mitigation projects often require restoration with native grasses.

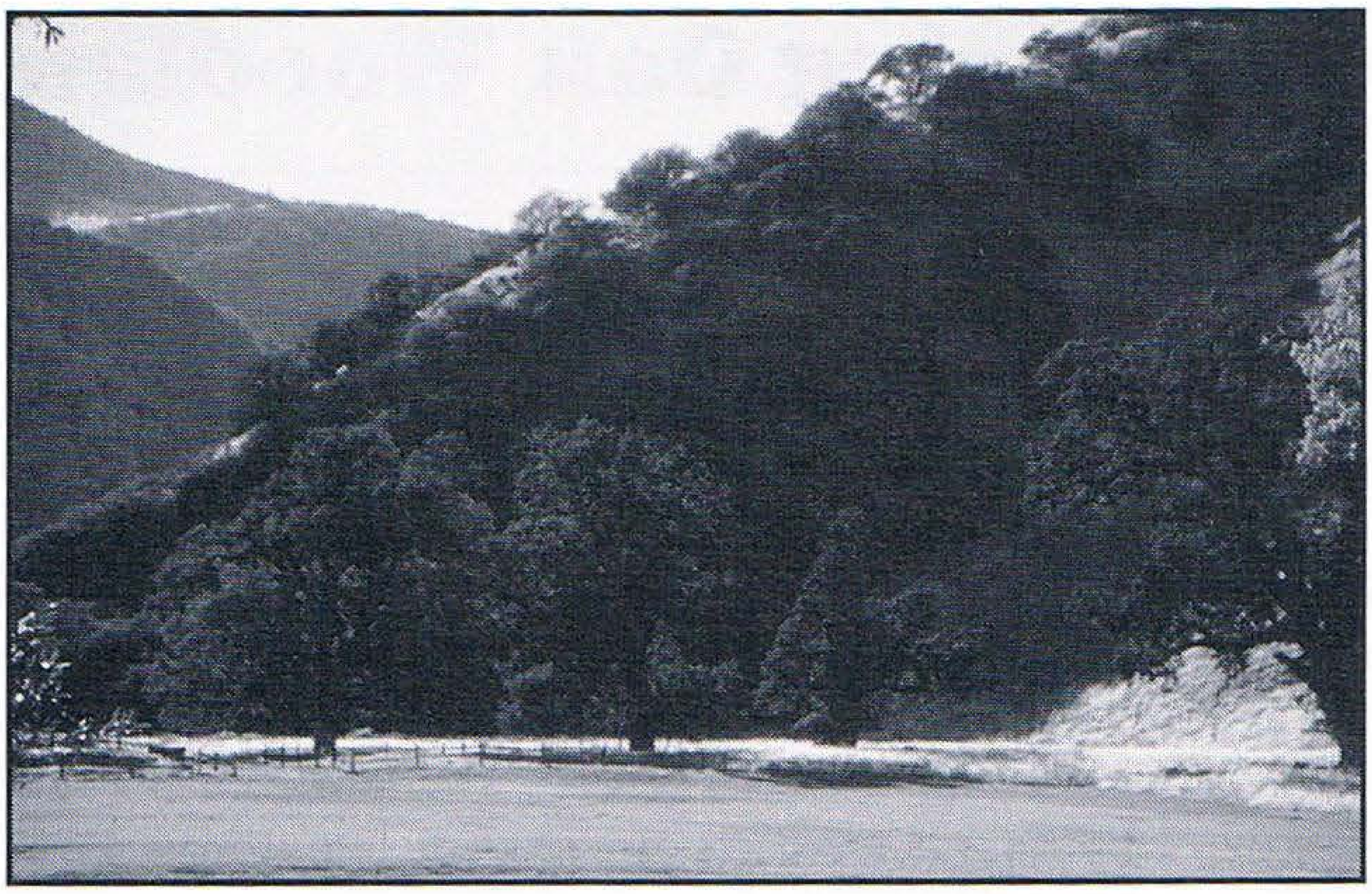
Soil Processes and Nutrient Cycling

Soils under oak canopies have higher organic matter, greater cation exchange capacity, lower bulk density and greater concentrations of some nutrients than open grasslands due to organic matter input from oak leaf litter and nutrient leaching from rainwater drip (Jackson et al. 1990; Frost and Edinger 1991; Firestone 1995). This nutrient effect from oak cover gradually dissipates after tree removal (Kay 1987). Woodlands with native perennial grasses have higher soil moisture later in the growing season than those with exotic annual grasses (Gordon et al. 1989). Exotic invasions and the resulting decrease in available water later in summer months may explain some of the observed lack of sapling recruitment in oak woodlands. Removal of oaks in the development process depletes the reservoir of soil organic matter and disrupts nutrient cycling. Adjacent interface areas retaining oak cover help to maintain nutrient cycling processes.

Grazing Processes and Forage Production

Livestock grazing has had a major impact on California's oak woodlands. By 1880, Spanish coastal missions had four million sheep and one million cattle (Holmes 1990) fostering a large demand for forage and oak browse. Currently, two-thirds of all woodlands are grazed (Huntsinger 1992). In addition to domestic livestock grazing, feral hogs consume acorns while rodents such as ground squirrels and pocket gophers utilize large quantities of acorns and seedlings.

Grazing has both positive and negative effects on oak woodland sustainability. Positive grazing effects include: reduced moisture competition between oaks and herbaceous material (Hall et al. 1992); reduced leaf area in seedlings, which may help conserve moisture late in the growing season (Welker and Menke 1990); habitat for rodents who consume acorns and young seedlings may be reduced; and fuel ladders are eliminated, reducing the probability of crown fires in grazed woodlands. Some of the negative effects of livestock grazing include: livestock and other grazing animals consume oak seedlings and acorns (Swiecki and Bernhardt 1993; Adams et al. 1992 ; Hall et al. 1992); grazing may increase soil compaction, making root growth for developing oak seedlings more difficult (Gordon et al. 1989); and soil organic matter may be reduced.



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*Oak woodland clothes the hillside above large valley oaks (*Quercus lobata *Nee) on the valley floor at 1,000 m elevation at Fort Tehon State Park, California, as seen during the Ventura County field trip of the Second International Oak Conference.*

The effect of oak canopy on forage quantity and quality vary depending on precipitation, oak species, and amount of cover (George 1987; . Kay 1987; Jansen 1987; Holland and Morton 1980; Frost and McDougald 1989; Ratliff et al. 1991; Holland 1980). Oaks compete with the forage understory for both sunlight and moisture, and alter the nutrient status of the site because of the deep rooting of oaks and nutrient cycling from litter fall.

Urbanization has decreased livestock grazing in interface areas due to high land prices, conflicts with urban neighbors, and reduced market access. This results in higher fuel accumulation and increased fire risk to both habitats and residential structures. Grazing pressure on oak regeneration and riparian habitats may be reduced, however.

Oak Regeneration and Recruitment Processes

There is concern whether adequate oak regeneration exists to sustain current stand structure. Oak regeneration surveys (Bolsinger 1988; Muick and Bartolome 1987; Standiford et al. 1991; Swiecki and Bernhardt 1993) have shown a shortage of sapling trees for certain species (especially blue oak, Engelmann oak, and valley oak) in certain regions of the state (low elevation, south- and west-facing slopes, shallow soils, high natural or domesticated herbivore populations). This shortage of small trees may result in loss of oak stands as natural mortality factors or tree removal eliminate large, dominant trees in the stand.

Blue oak recruitment may arise from a gap mechanism where an understory seedling bank persists until a moderate stand disturbance (such as clearing, fire or natural tree mortality) occurs, after which sapling recruitment proceeds (Swiecki and Bernhardt 1993). Valley oak has experienced inadequate regeneration since the last century (Griffin 1973; Bernhardt and Swiecki 1991; and Danielsen and Halverson 1991). Alien annual grasses, which make less water available to oaks than native perennial grasses, may be one cause of this effect.

Stump sprouting has been widely observed in most oak woodland species. Studies have shown a high probability of achieving stump sprouting for blue and live oak species. This observa-

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tion reduces the concern that a lack of sapling trees once suggested (McCreary et al. 1991; Standiford et al. 1996).

In urbanizing areas, the trend of increasing tree density will continue to lead to conditions where poor sapling recruitment will occur. This is only a problem if mortality of overstory trees exceeds recruitment of seedlings into larger tree sizes.

Oak Restoration and Planting

Planting acorns or seedlings is necessary where recruitment is inadequate to maintain desired oak cover. However, the same factors limiting natural oak regeneration makes it difficult to artificially regenerate native oaks. Substantial care must be taken to plant, protect and maintain young oaks in the field. Techniques for establishing oaks have been well-described and success of over 90 percent is not uncommon (McCreary 1996). Currently, over one million oak seedlings are planted annually in California (IHRMP 1994). A very large proportion of these seedlings are planted as part of restoration projects required as mitigation for various urban development projects. Costs per surviving seedling are quite high (Standiford and Appleton 1993). However, the urbanization process and its associated environmental regulations has created the capital, and the economic justification, to accomplish restoration of large areas of oak woodlands, partially reversing the negative impacts of the development process.

Riparian Management Processes

Although a small percentage of the state's water supply originates on hardwood rangelands, virtually all of it flows through oak woodland riparian zones (CDF 1988). Also, most of the state's major reservoirs are located on oak woodlands. Riparian zones provide important habitat for wildlife and aquatic organisms. Management activities influence water quality, and wildlife and fisheries habitat. Yet, removal of up to one-third of the oak canopy had little effect on water quality and yield in one regional study (Epifanio et al. 1991). New efforts have been started to develop rangeland management practices to minimize erosion as part of the state's water quality management plan (Humiston 1995). In urban interface areas, riparian zones are often subject to very high levels of human use for recreational purposes. Scott and Pratini (1996) documented how urban development increases human use of riparian areas, lowering the habitat value for various wildlife species and decreasing overall biological diversity.

Fire Ecology Processes

Fire is a natural part of California's oak woodland ecosystem and has been an important management tool since Native Americans inhabited these areas. Fire influences oak woodland stand structure, regeneration, wildlife habitat, nutrient cycling, and economic uses. Fire also creates significant health and safety risks to people living in oak woodlands and the interface area.

The ecological effects of fire depend on their frequency, intensity, and size of patches that occur from fire-induced tree mortality. Recent increases in the acreage of stand destroying

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Table 1. Comparison of oak woodland conditions before European settlement, during extensive ranching period, and in urban interface areas.

Pre-European Settlement Conditions	Extensive Ranching Period	Current Urban Influence
Perennial herbaceous layer	Exotic annual invasion	Increasing annual invasion, especially noxious weed
Regular fire interval	Continuation of regular fire interval	Fire suppression policies and long fire interval and increased intensity
More open overstory layer	Range clearing and tree thinning	Increased overstory layer of unconverted stands
Soil moisture higher, later into growing season	Soil moisture late in growing season decreased due to exotic annuals	Decreased soil moisture late in growing season due to exotic annuals
Lower soil bulk density	Increased soil bulk density	Increased soil bulk density
Snags, large woody debris	Snags, woody debris cleaned up in typical management activities	Less attention to clean-up; increased snags and woody debris
Dense, diverse riparian zone	Riparian zones less dense and diverse	Higher human use of riparian zones, and increased storm runoff from urban areas
Lower herbivore densities	Higher herbivore density, primarily domestic livestock	Decrease in domestic livestock

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fires has resulted from decades of attempting to exclude fire from woodlands.

McClaren and Bartolome (1989) have shown fire frequencies in oak woodlands of 7 to 25 years during occupation by Native Americans and early ranchers. Fire was a common management tool until the 1950's, when fire suppression became the dominant practice. These past higher fire frequencies may have created conditions more conducive for oak regeneration. McClaren and Bartolome (1989) showed that oak recruitment was associated with fire events, and has been rare since fire suppression. The importance of fire on oak regeneration may be due to: enhanced postfire oak sprout growth; improved seedbed for acorns; reduced moisture competition from herbaceous species; and reduced habitat for wildlife species that feed on acorns and seedlings. Fire also kills diseases and insects, such as the filbert weevil (*Cucurlio occidentalis*) and the filbert worm (*Melissopus latiferreanus*), which can infest the acorn crop (Lewis 1991). High frequencies of low intensity fires also reduce fuel ladders under oak canopies preventing high intensity crown fires.

Maintaining Biological Diversity

A second way that urbanization influences the sustainability of oak woodlands is through its effects on biodiversity. Oak woodlands provide habitat for over 300 vertebrate wildlife species, 2000 plant species and 5000 insect species. Favorable woodland habitats supply food, water, and cover to sustain wildlife species. Each habitat element provides unique niches, favoring particular wildlife species. Conversely, the absence of a particular element in a habitat may limit species diversity. Examples of oak woodland habitat elements that are important to consider include riparian zones, vernal pools, wetlands, dead and downed logs and other woody debris, brush piles, snags, rock outcroppings, and cliffs.

Riparian habitat elements are used by almost 90 percent of all hardwood rangeland wildlife species, illustrating the importance of conserving this habitat element where present. Over one-third of all oak woodland bird species use snags, suggesting that strategies to maintain snags will result in greater wildlife species diversity. Downed woody debris from fallen limbs or dead trees, provide an extremely valuable habitat for most reptiles and amphibians, as well as for many bird species. Oak woodland management for wildlife must include these trees as well as trees in various stages of vigor in order to maintain critical wildlife habitat (Block and Morrison 1990). Mid-elevation hardwood rangeland habitats, with several oak species, vertical diversity in vegetation structure, and diverse riparian zones, have the richest diversity of wildlife (Motroni et al. 1991).

The threats of urbanization to biodiversity on oak woodlands include: 1) fragmentation of large blocks of extensively managed hardwood rangelands; 2) reduction in important habitat elements such as snags, woody debris, and diverse riparian zones; and 3) increasing interface with urban areas, bringing household pets, humans, and fire suppression policies into contact with hardwood rangeland habitats. These threats to biodiversity can be reduced by encouraging cluster development and conservation of connecting corridors between large hardwood rangeland habitat blocks in developing areas (Giusti and Tinnin 1993).

Maintaining Economic Viability and Utilization of Oak Woodlands

Oak woodlands have been important to humans living in California for centuries. Management practices utilized by Native Americans and the ranching community maintained large blocks of habitat that supported ecosystem processes at a variety of scales. However, as people have left the major urban areas of the state to seek the aesthetic and amenity values of oak woodlands, these areas are being converted to residential and industrial uses. Some of the economic and utilization issues from these land use changes are discussed below.

The original human inhabitants of oak woodlands were Native Americans. Acorns were the dietary staple for three-fourths of all Native Americans in California, and sustained their cultures (Pavlik et al. 1991; McCarthy 1993). Many cultural traditions and celebrations focused on oaks. Oaks and acorns were also used as medicines and dyes. Burning was the most prevalent and effective management tool used by Native Californians to manage the oaks and the acorn crop (McCarthy 1993) and to keep prized oaks from being dominated by conifer species.

Since the 1800s, oak woodlands have been used mainly for domestic livestock products. Dramatic annual fluctuations in livestock markets, coupled with risk from forage shortages due to high variability in annual rainfall, has made many livestock operations marginal. There is also a high opportunity cost to extensively managed livestock operations from high value land uses such as suburban developments or intensive agricultural products such as wine grapes. One study shows land value for grazing represents only 20 percent of the current total land value for residential development in the central Sierra Nevada (Johnson 1996). Uncertainty about federal grazing policies, inheritance taxes, the pyramid of heirs, low profitability, high risk, and high opportunity cost have accelerated conversion of extensively managed private ranches to suburban developments.

Historical efforts to increase ranch profitability focused on enhancing forage production through removal of the oaks. This simplification of the ranch ecosystems paid short-term dividends in improved forage yields, but risk from fluctuating product markets and weather variability continued to make ranching a low profitability enterprise.

New markets developed in the last 20 years for the oaks on hardwood rangelands for firewood and as habitat for commercial hunting enterprises. This diversified economic portfolio has helped to enhance the economic sustainability of these areas by spreading risk out over several enterprises, increasing overall returns per acre, and providing an economic incentive to conserve more diverse woodlands (Standiford and Howitt 1990; Standiford and Howitt 1993). Diversified markets have reduced tree harvesting and intensity of livestock use.

Historically, the market value of oak woodlands for subdivision near urban areas has exceeded their value for amenities and ecological functions. Recent human population increase in these areas, however, has raised the potential values of woodland amenities to a point where they may be a financially viable alternative to land development (Scott 1996). Woodlands provide a large component of the quality-of-life sought by many relocating industries, and the relatively low cost of industrial sites in these woodlands is equally appealing. Woodland owners along the wildland urban interface often find that their management options track public demand for specific values. If woodland conversions trigger a public demand for amenity protection, the solutions typically must be found on private lands. Open space easements, and other deed restrictions provide financial, tax, or development incen-

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tives for the voluntary maintenance of public amenity values on private lands (Duwe undated). Mitigation banking provides another economic value for hardwood rangeland in urban interface areas (Reyes-French and Cohen 1991).

Conservation Policies and Strategies

A series of policy instruments to conserve oak woodlands have evolved in California against the backdrop of the ecological and economic factors described above. Various interest groups have expressed concerns about oak woodlands to the California State Board of Forestry (BOF), the state regulatory and policy-making body responsible for forest and rangelands. In response to these concerns, the BOF asked the University of California (UC), the California Department of Forestry and Fire Protection (CDF), and the California Department of Fish and Game (CDF&G) to develop a program of research, education, and monitoring to conserve hardwood rangelands (Passof and Bartolome 1985). This program is known as the Integrated Hardwood Range Management Program (IHRMP). With the development of the IHRMP, the BOF decided that an intensive educational program, problem-focused research, and frequent monitoring of the resource was the most effective way to work with landowners and local governments to resolve hardwood issues.

The IHRMP has funded 66 research studies over ten years, which in turn has stimulated additional research on various aspects of hardwood rangelands. These research studies, resulting in over 250 new scientific articles, contribute to the base of understanding of the ecological and managerial processes extent on hardwood rangelands (IHRMP 1992). Research results have been disseminated in IHRMP-sponsored symposia and workshops and incorporated directly into educational documents and newsletters.

Surveys were implemented to evaluate the effectiveness of education as a conservation policy (Stewart 1991; Huntsinger and Fortmann 1990; Huntsinger 1992). These showed that individuals who participated in IHRMP educational programs were more likely to carry out oak enhancing management activi-

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*A preserved natural woodland of Engelmann oak (*Quercus engelmannii *Greene) at Arcadia, near Los Angeles, California.*

ties practices (protect sprouts, maintain fixed oak canopy levels, thin softwoods to promote oak growth, planting oaks) than non-participants. After a seven year period of intensive educational outreach, oaks were more valued by landowners for wildlife habitat, soil protection, enhancement of property values, and for browse and mast production. The number of large owners selling firewood or cutting trees for forage enhancement decreased. During this same time period, the number of owners who conducted wildlife habitat improvements increased.

Local Policy Initiatives

In May, 1993, the BOF held hearings to evaluate the effectiveness of seven years of research and education as an approach to oak woodland conservation. These hearings showed strong support for the continuation of research, outreach, and monitoring, and revealed a large number of threats facing hardwood rangelands. Firewood harvesting was recognized to be a concern only in the northern Sacramento Valley, while conversion to subdivisions was important in the central Sierra Nevada, San Francisco Bay Area, Central Coast, and Southern California (IHRMP 1994). These findings confirmed that statewide regulations would not be able to effectively address the wide diversity of conservation issues. The BOF decided to intensify its outreach to local governments, and encourage their participation in local policy development with the assistance of the IHRMP. The IHRMP has worked closely with local governments to encourage the development of local policies to conserve hardwood rangelands. Currently, 37 counties have adopted or started the process of adopting local conservation strategies. These strategies fall into three categories, namely: county voluntary guidelines; land use planning; and tree harvesting ordinances. Each of these are discussed below.

County Voluntary Guidelines

At the 1993 BOF Hardwood Hearings, political and agricultural leaders from a northern Sacramento Valley county volunteered to initiate a county-based effort to address concerns about widespread oak firewood harvest. A county oak committee composed of various resource agencies, environmental groups, and agricultural groups was appointed. They developed a set of voluntary oak retention guidelines to maintain economic viability of grazing and ecological values of hardwood rangelands, which was passed by the county Board of Supervisors, and mailed to all landowners in the county (Gaertner 1995). With this successful pilot project, several other counties began to develop voluntary guidelines. Currently, 12 counties are in various stages of developing voluntary guidelines. Each effort addresses important local issues, and includes education and monitoring. For example, several of the voluntary guidelines in the northern Sacramento Valley address impacts from firewood harvest, while biomass harvest, fire protection, and soil erosion were important issues addressed in southern Sierra guidelines. Most of the guidelines also have general recommendations on urban development patterns to help guide local land use policies.

General Planning Process

' The county General Plan sets policies governing land use. Sample language on the importance of oak woodlands have been developed by the California Oak Foundation for possible inclusion in individual county general plans, and mailed to all county planning departments. Pilot educational activities have started in several Central Coast counties to utilize overlays of hardwood habitat maps and parcel maps in a geographic information system (GIS) to implement landscape-based oak conservation strat-

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egies in the county planning process (Tietje and Berlund 1995). In southern California, the IHRMP has worked closely with three county planning offices and Boards of Supervisors in the design of a corridor system to minimize the effects of habitat fragmentation. General regional and county-wide habitat conservation plans (HCP) have been coordinated with the goals of the IHRMP in Southern California.

Ordinances

Some areas have utilized ordinances to protect oaks. Ordinances create a regulatory environment at the county or city level, and usually involve a permitting process for the removal of any tree over a certain size class, and mitigation standards where tree removal is allowed. Most tree ordinances have focused on the single tree rather than at a broad habitat scale. CDF has developed an educational book on ordinances which describes the importance of setting objectives for an area prior to writing an ordinance, and monitoring whether the objectives have been accomplished (Bernhardt and Swiecki 1991). This book has been distributed to all counties in the state. At this time, there are 11 counties which have ordinances designed to protect oak trees.

Conclusion

Oak woodlands are an important ecological component in California. Sustainability of ecological values is of concern due to rapid population growth, and the resulting conversion and fragmentation of hardwood rangeland habitats. Important information has been developed on the ecology and sustainable management of hardwood rangelands through activities of the IHRMP. Sociological and biological monitoring shows that diverse audiences have accepted and acted on educational information. A large number of counties have started the process of adopting local conservation strategies to conserve hardwood rangelands. Education and research have played a major role in conservation. Major accomplishments have been made in rural areas of the state, where livestock and natural resource management are the predominant land use. Where individual landowners have the ability to implement management activities that affect large acreages, education and research has contributed to decisions that favor conservation of oak woodlands.

However, for much of California, conversion of oak woodland habitats to urban or suburban land use is having the largest impact on sustainability of resource values. Educational materials developed on hardwood rangeland conservation in land use planning have been widely accepted by professionals working in the land use arena. However, incorporating these educational materials into successful land use plans adopted by the county government is only beginning. Since conversion to residential and industrial uses is ultimately a land use decision, it is a political process involving action by elected officials with input from different constituencies. The political and economic forces vary greatly in different parts of the state. Since "success" in this area involves multiple individuals agreeing on a political course of action, this issue will present the largest challenge for a research and education strategy. It needs to be evaluated very carefully over the next several years to determine if education and research alone are sufficient to sustain the ecological values of hardwood rangelands.

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Developing a Digital Atlas of the Natural Ranges of Oaks of the World

by Thomas H. Gaman
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Worldwide forest resources are being digitally mapped by agencies and universities everywhere. A few programs are making efforts to draw together information on international forest resources and support for those programs is growing as recognition of the importance of global forests broadens. Here in California our native oak forests have been mapped twice in the past decade. We can present accurate maps showing local and statewide forest resources, alone, or with reference to other digital data.

Mexican forests, which include approximately 200 species of oaks, are also being mapped and assessed. Existing paper maps can be digitized, or GIS (Geographic Information Systems) coverages can be created directly from GPS (Global Positioning Systems), satellite or other remote sensing media. The Eastern United States is home to extensive native oak forests. The FNA (Flora of North America, Volume 3) project of the Missouri Botanic Garden has just published the authoritative flora of the *Fagaceae* for the US and Canada, including 97 (62 endemic) species, 90 of which are in the genus *Quercus*. A fairly good-quality graphic showing the range of each of the oak species is available on-line, but not geo-referenced. The World Conservation and Monitoring Center (Cambridge, UK) has recently published a CD of assembled GIS coverages of world forest resources, and presented this at the World Forest Congress in Ankara. A new Hammond Atlas of the World, the first atlas completely based on digital maps, has just been published and includes good climatic information. A digital atlas of the world has also been developed. The University of California at Santa Barbara has initiated a project known as the "Alexandria project" which includes a digital GIS library

Proposed Mapping Effort

I am proposing a project to map and develop a digital atlas of the approximately 400 species of *Quercus* worldwide. Although I can initially lead this effort, the project needs broad involvement and support, and perhaps leadership provided by an agency or university. In order to get things underway. I am soliciting ideas, assistance and information. A metadata form is included in this paper, with which contributors may submit their data, information on existing datasets, or other relevant information. The information supplied becomes "metadata" or descriptive information about the structure and applicability of each GIS database or digital atlas contribution. The metadata text file contains information on the species, resolution, geographic extent, accuracy, tabular data, and nature of available datasets. I expect that applicable metadata and datasets could be made available online via Alexandria (UCSB) or another institution.

I have already found that information on oak forests, derived from so many sources, is highly variable. Although defined in the metadata and quite useful as stand-alone information, datasets may not be directly applicable to the Digital Oak Atlas project. As part of the effort to develop a digital oak atlas, I have adopted certain standards. The initial effort, for instance, is going to map the native ranges of the oak species, not the extent of oak forests. The Atlas is intended to provide a global and regional/national perspective on oak ranges, and therefore low resolution data is fine, presentable at a scale of 1:3000000 or better. Although a variety of coordinate systems and map projections can be accommodated, the Digital Oak Atlas database will be constructed interchangeably using the geographic (latitude/longitude) and UTM (Universal Tranverse Mercator) coordinate systems. Data should be developed using a vector format compatible with GIS standards. I am most interested in receiving raster datasets, which may be converted to vector formats as necessary and applicable.

Accuracy is a matter that is somewhat subjective. Rather than set standards at this time, a statement of the source and anticipated accuracy of any submitted data should be attached (in a text file) to the metadata.

Presentation of maps will be feasible using ArcViewÓ, Arc-InfoÓ, BaseMap2000 GISÓ, or with a variety of Internet map query and presentation systems presently under development. Maps and datasets will be accessible using the Internet. Sources will be recognized in every instance.

Once the home range digital mapping is underway, I propose creating another adjunct dataset — a mapping of the oak forests of the world. This addition requires that another set of standards be developed in order to describe and define an "oak forest". For instance what is the species composition? What is the density? As many of our North American oaks are actually scrub species, it even becomes necessary to define a forest! Here in southern California many of the oaks grow in the chaparral and are not accurately mapped. How then to map these oaks? This is a subject that I will leave until later.

The overall goal of the program is to satisfy a curiosity, educating others and ourselves and, over the long-term, to promote monitoring of the oak forest resources of the world. Techniques in the use of Geographic Information Systems, Global Positioning Systems and remote sensing technologies are constantly changing and improving. As we enter the 21st century, technology is providing the opportunity to promote stewardship of natural resources. I strongly recommend that oak enthusiasts, and admirers of natural systems, move to embrace these technologies as tools for educating people, and that we use the information to service our needs. I do hope that pursuit of this project will lead to increased recognition of the importance of resource protection, inventory and monitoring.

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References and Project citations

Alexandria Digital Library Web Interface. The Alexandria Digital Library includes substantial information, including hundreds of GIS coverages, on California forests and natural systems. Alexandria seeks to build a worldwide digital atlas. ***Contact:*** *Jason Simpson: simpson@alexandria.ucsb.edu http://alexandria.sdc.ucsb.edu/*

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Organization: Center for Botanical Informatics, Subject: Re: FNA maps (Oaks, volume 3) http://www.fna.org/Libraries/plib/WWW/temp/online.html

Forest Conservation IUCN Programme. BIODIVERSITY CONSERVATION INFORMATION SYSTEM is a joint initiative of 11 partner organizations. IUCN maintains information and biodiversity, landscape and forest and seeks to identify key data sources using globally accepted standards. ***Contact:*** *Don Gilmour, IUCN Switzerland.* Tel: +41.22.999.0263; Fax: +41.22.999.0025; *E-mail: dag@hq.iucn.org***2.**

World Conservation Monitoring Centre (WCMC) and the Center for International Forestry Research (CIFOR). The World Conservation Monitoring Centre (WCMC) and the Center for International Forestry Research (CIFOR) maintains world forest maps, including data on forest location, by type, and protection status. A new (10/97) CD-ROM product contains GIS spatial data files on forests, protected areas and ecological zones, contributed from a variety of sources with extensive documentation. ***Contact:*** info@wcmn.org.uk or http://www.wcmc.org.uk/forest

Digital Atlas Metadata Form

(Natural Home Range of Oak Species *or* Extent of the Oak Forests the World)

Please list the following in your metadata submission:

1. Oak species.
2. Coverage name.
3. Brief description (including type of coverage and attribute data – species, density, size, forest type, etc.). Particularly note whether the coverage describes the home range of a species, or extent of oak forest(s). Please note mapping criteria & variables.
4. Organization/Individual from whom the coverage can be obtained.
5. Date of coverage.
6. Geographic extent of coverage: (Lat./Long.).
7. Scale /Coverage projection/units.
8. Path of coverage on local system or internet availability via FTP or Website address.
9. Software with which the coverage was developed.
10. Notes/comments

Please e-mail to: Tom Gaman, forester@compuserve.com. Tel/fax: 415 669 7426.

Transplanted Live Coast Oaks (*Quercus agrifolia*) in Southern California

by Rosi Dagit, Conservation Biologist
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and
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Ventura, California, USA

During the late 1980's it became increasingly common to transplant large coast live oaks (*Quercus agrifolia*) to mitigate for the loss of oak woodland due to development. Developers loved the idea of being able to "save" the trees and incorporate them into their new landscapes. Tree moving companies became expert at the extremely difficult technique of moving a boxed tree weighing many tons. New homeowners paid as much as 30 percent more for lots having a mature transplanted tree. The decision makers felt that they had required adequate mitigation for the loss of native oak woodlands and required two to five year monitoring for survival. The long term survival rates (over 5 years) of transplanted trees has not been documented.

To date, few studies have focused on the success of transplantation, the physiological responses of the trees to drastic root loss, or the cost effectiveness of moving trees in light of their long term maintenance and survival. Roberts and Smith (1980) did a one year study of water potential and stomatal conductances of oak trees impacted by root injury from trenching. Scott and Pratini (unpublished data) followed the health and vigor of 593 transplanted coast live oaks in Orange County, CA for more than 4 years. Neither of these studies evaluated quantitative responses. Our study combined both quantitative and qualitative observations over 5-6 years in an effort to better understand the response of the trees to transplantation.

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One of the oldest documented transplantation in California of coast live oaks took place from 1938-1941 at Hearst Castle in Cambria, CA where 6 trees were boxed in concrete. While no formal study of these trees took place, review of the gardener's notes and inspection of the 2 trees partially remaining in 1995 indicated that the trees slowly declined over the years, required continuing maintenance and were barely alive.

As part of an effort by the City of Calabasas to discourage oak tree transplantation, the City required that any transplanted oak trees be monitored for 5 years. Three sites in the City had a total of 25 mature coast live oaks which were moved. Starting in January 1992, monitoring of 10 transplanted trees began at Site 1, followed by the addition of eight trees at Site 2 and seven transplants at Site 3 in April 1993, either as the trees were being boxed or shortly thereafter. Monitoring concluded in October 1997.

Transplantation methodology

All portions of the sites to which trees were moved experienced extensive grading and drainage changes before replanting. Sites 1 and 2 were originally north-facing hillside drainages with intermittent streams, clay soil, and mixed chap-

Table 1. Vigor rating scale.

Vigor rating	Description	Criteria for evaluation
1	Dead	No living canopy, severe root and trunk defects, severe infestation or disease
2	Nearly dead	Less than 25% growing canopy, major root and trunk defects, severe pest infestation or disease
3	Decline	25-50 % growing canopy, some root and trunk defects, moderate pest infestation or disease
4	Stable	Greater than 50 % growing canopy, few root or trunk defects, minor infestation or disease
5	Improving	Greater than 75 % growing Fairly healthy canopy, no root or trunk defects, minimal pest infestation or disease
6	Very healthy	Well balanced, symmetrical canopy, no root or trunk defects, very little pest

Table 2. Vigor Rating of 25 Transplanted Oaks 5 years post-transplanting (October 1997)

Vigor Rating	Site 1	Site 2	Site 3	Percentage
1 Dead	4	3	0	28%
2 Nearly Dead	1	1	4	24%
3 Decline	3	4	1	32%
4 Stable	2	0	2	16%
5 Improving	0	0	0	0%
6 Very healthy	0	0	0	0%

arral vegetation. Following grading, they were 95 percent compacted cut and fill pads which maximized development opportunities. Site 3 was initially a level riparian area that was transformed into a freeway interchange.

Trees from hillside areas were selected for transplanting by the tree-moving company and their associated arborists. Trees selected ranged in size from 15 to 100 cm Diameter Breast Height (DBH). Some were single trunk, but most were multi-stemmed. Height ranged from 4 - 15 meters. Crown diameter varied as well, from 4 to 25 meters. Concurrent with root pruning and side boxing, the canopies of the selected trees were pruned, removing 30 to 70 percent of living tissues. Deadwood, inner foliage, and terminal buds were trimmed, leaving a thin shell of foliage on the perimeter of the canopy.

A backhoe was used to trench all four sides at once around each tree. Plywood box sizes ranged from 1.5 to 8.5 meters wide, and 1 to 2.5 meters deep. Bottom boxing was completed 3 to 6 months later. After boxing, trees were irrigated weekly by water trucks, as directed by the tree-moving company. All trees were planted in holes dug by backhoes, usually 1 to 2 meters wider than the box and approximately the same depth as the root ball. The plywood box bottoms were left in place, the sides removed, and backfilling done by backhoe and hand tools. Sprinklers were installed at Site 2 and irrigation was modified seasonally. The other two sites continued to be watered by truck from one to three times weekly. By coincidence, a total of 3 trees were planted in the same orientation as they had originally grown.

Monitoring

The monitoring protocol included quantitative and qualitative observations of both transplanted and control trees on a quarterly, then on a semi-annual basis. At each site, 1-8 control trees were selected from undisturbed areas on the development parcel having soil type, orientation, slope conditions, and sizes comparable to the transplanted trees. Every time the trees were observed, each tree was given a vigor rating from 1 (dead) to 6 (very healthy). The rating was modified from the International Society of Arboriculture standard condition evaluation for landscape trees which includes evaluation of canopy, foliage, trunk, and root condition (table 1).

Water potential was measured to monitor tree water stress quarterly, then semi-annually. On each tree, mid-day readings of five sample twigs (5 to 13 cm long) taken from four cardinal directions in full sun were followed by five predawn samples, using either a PMS Scholander Pressure Chamber (PMS Instrument Company, Corvallis, Oreg.), or Model 3005 Plant Water

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Status Console (SoilMoisture Equipment Co., Santa Barbara, Calif.).

Soil probing to examine roots down to 30 cm depth started one meter from the trunk of both control and transplanted trees. Probes were also done at mid-canopy, at the dripline, at the perimeter of root ball, just outside the box edge, and 1.5 meters farther out. Samples were qualitatively examined in the field, noting presence, size (mm), and density of roots (number per cm). At Site 2, non-woody root samples (less than 5 mm width, 5 cm length) were taken from the top 15 cm of soil at four cardinal points around the mid-dripline of the trees in October 1997 and plated to identify any infection by *Armillaria sp.* and *Phythopthora sp.*

Each spring and summer, shoot length, number of leaves and shoots per terminal bud were measured from 5 randomly selected samples within reach of the ground on each tree. Presence of flowers and acorns was also recorded.

Results

Control trees at all sites maintained a stable, healthy condition during the study. Despite several stretches of drought, some exceeding 200 days (Tietje, 1993), the 15 control trees had vigorous shoot growth and full canopies. However, by October 1997, transplanted tree condition had declined severely (figure 1 and table 2).

Control trees maintained a dense canopy and normal branching structure, with few epicormic sprouts. Transplanted trees had little apical growth and their canopies remained characteristically thin, open, and often chlorotic. Trees showing improvement had epicormic growth clustered densely in the center of the tree, thinning out towards the dripline. Transplanted trees chronically suffered from twig girdlers (*Agrilus angelicus*) and whitefly (*Aleuroplatus coronatus*) infestations.

The control trees typically had 2-4 new shoots per sample that ranged in length from 5-30 cm, while transplants had fewer new shoots (1-3 per sample) which did not exceed 12 cm. The number of leaves per shoot (6-18) was consistently higher than that found on the transplants (5-10). Most notable was the difference in distribution of shoots. While the control trees grew in a normal branch pattern, the transplants produced primarily epicormic sprouts from the scaffold branches and trunk, with few shoots emerging from terminal buds.

Most control trees had visible growth cracks in the trunk bark, indicating active radial growth. Such cracks on the transplants, if present at all, were smaller and fewer in number. From 1992 - 1997, the diameter of 10 control trees increased, while 3 remained the same. Transplanted trees had 7 trees showing slight expansion, 9 remained the same size and 9 shrunk (table 3). In the case of one large, declining tree, the diameter lost 18 cm in 5 years.

Soil probe observations indicated that only 2 transplanted trees had roots extending outside the planting hole. Most transplanted tree roots were sparse. By contrast, the control trees had dense mats of roots at all areas probed. *Phytophthora cinnamomi* was isolated from the roots of 6 transplanted trees at Site 2, but not from the 4 control trees sampled.

Water potentials of transplanted trees were not correlated with final vigor ratings (r^2= 0.0008). However, a few trends were apparent. Variability in readings was greater in the transplants, with control trees remaining more consistent at any given time (figure 2). No statistical comparisons were made for individual data from same dates. Control trees (receiving no irrigation) did show lower summer/fall water potential (July and October), but they rarely dropped below a pre-dawn potential of -2.5 MPa. By contrast, declining transplanted trees routinely exceeded that limit. In nearly-dead trees, pre-dawn water potentials exceeded those at midday.

Discussion

After 5 years, only 16 percent of transplanted trees in this study showed signs of establishment. The remaining 84 percent were declining or dead. All continued to require extensive maintenance. Thus it appears that long-term survival for these transplants would be no more than 20 percent, and perhaps considerably less.

This is consistent with trends documented by Scott and Pratini (unpublished data) for an oak transplant project in Orange County, CA. Two methods of moving trees were used at that site in 1989. Some trees were dug up by a bulldozer, with 100% mortality resulting within 6 months. Of the additional trees that were boxed, 50% had also died within the first 6 months. Mortality among those that survived the first 6 months had reached 71percent by 1996, 6 years following transplantation. This initial mortality of trees immediately following boxing is frequently ignored when tree moving companies quote statistics about tree survival. Most important to note is that once the trees began to decline, they were not able to recover.

We observed steady tree decline resulting from transplantation. Impacts from removing the majority of the root system and canopy were manifested in disrupted water relations (Tyree, et al. 1994), loss of internal hormone relationships (Coder, 1994), carbohydrate balance (Hollinger, 1992), and stress-induced pest/disease problems (Hagen, 1989) found in the transplants. Regeneration of root and canopy tissue is related to tree size and maintenance conditions (Watson, 1994). Even with improvements to the transplanting procedure, such as boxing one side at a time over 12 months (Himelick, 1991), it may be that the highest attainable level of care would not be sufficient to overcome the trauma of transplantation for mature coast live oak trees. While transplanted trees remained alive, they were no longer self-sustaining natives, but rather high-care exotics that required intensive, long-term maintenance.

Table 3. Average trunk growth of *Quercus agrifolia* after boxing
(1992/93 - Oct. 1997)
Change in surface area diameter at breast height (cm^2)

Treatment	Site 1	Site 2	Site 3
Transplants	-0.25	0.541	-1.325
Controls (not moved)	0.45	0.1	2.6

The cost of boxing each tree in this study varied from $1,000 to over $100,000, totaling $450,000 for all 25 trees. Given the high cost of moving, maintenance and monitoring (approximately $40,000 per year), it appears that a low 5-year survival rate fails to justify the expense. After 5 years, 28 percent of these trees are already dead, the rest are in decline.

If the goal of mitigation is to replace lost resources, then the cost-effectiveness of transplanting oaks needs to be carefully examined. The impetus for moving large oaks comes from the increased property value associated with mature landscapes and the desire of developers to appear to be environmentally conscious. However, isolated trees distributed throughout a suburban development do not have the same eco-

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logical value as a grove of undisturbed trees with the associated complex suite of organisms found with them. Use of transplantation funds for purchasing existing oak woodlands and dedicating them to the public trust would provide a more realistic mitigation. While there may be a few instances where moving an individual tree is warranted, all involved should be aware of the high long term costs involved in supporting a severely damaged tree.

Another consideration should be the placement of the tree in the landscape. By definition, transplanted oaks are considered to have high hazard potential associated with the drastic root loss. Placement of trees in open space areas away from possible "targets" (such as picnic benches, walkways, buildings and roads) should be required. Oaks are also highly susceptible to infection with *Phytophthora cinnamomi,* a common landscape pathogen. Severely stressed transplants needing continued summer watering provide ideal hosts for the pathogen.

The results of this study indicate that transplanting success is minimal, the physiological response of the trees to the trauma is extreme, recovery is limited, and the costs are high. Transplanting coast live oaks does not appear to be an effective mitigation practice to replace lost oak woodlands.

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Oaks and Oak Hybrids at Arboretum Trompenburg

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The collection of oaks in the Arboretum Trompenburg originates from 1925 and continues to develop today. Apart from some *Quercus robur* remaining from the original layout of 1820, the oak collection could be built only after the Dutch elm disease cleared the area. More than 400 huge elms had to be cut down. At the time, we considered it to be a disaster; now, we see it as a blessing, because my father was granted the opportunity to develop Trompenburg into the arboretum for the City of Rotterdam, Holland.

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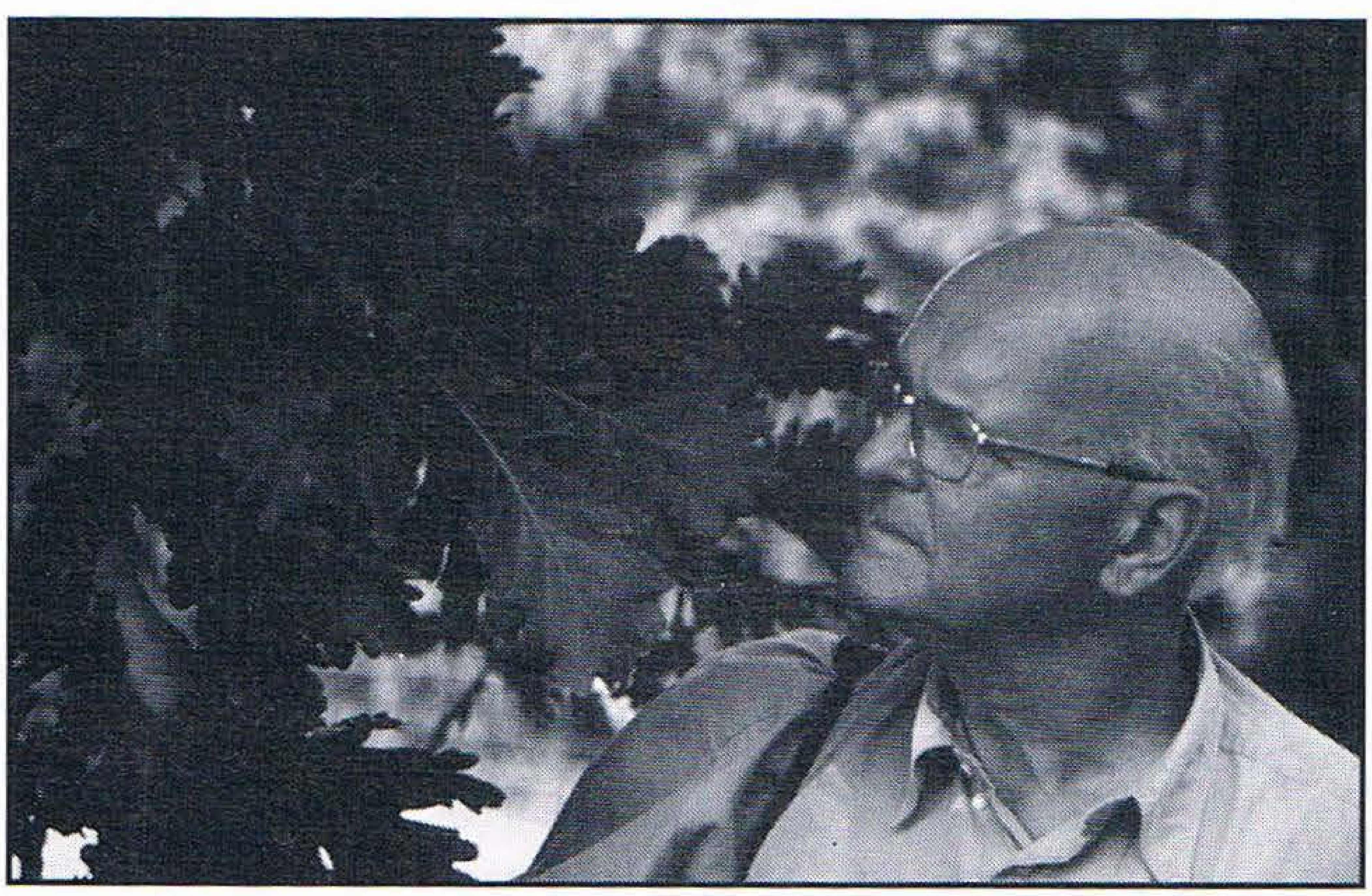

J.R.P. van Hoey Smith with his introduction, Quercus macranthera x Q. frainetto *(cutlivar 'Macon') at Arboretum Trompenburg.*

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Quercus robur *'Cristata' (left) and* Quercus frainetto *Ten. (right) at Arboretum Trompenburg.*

To fill the gaps created by the removal of the dead elms, he traveled across Europe to buy trees and shrubs, visiting (among others) the Hesse Nursery in Germany near the Dutch border. This nursery had propagated the oak collection of the famous estate of Muskau, situated on both sides of the Oder River, the international border between Germany and Poland. Owing to the Second World War, not much is left at Muskau today. On the German side, a nice landscape with a few trees still exists; on the Polish side little remains. My father bought 15 of the Muskau oaks from the Hesse Nursery to start our present oak collection. These he planted between 1930 and 1940.

During the Second World War, nothing further could be done. After that war, I assumed management of the arboretum. As soon as travel again was possible, I went to the Royal Botanic Garden Kew in London during half of October to collect acorns from the extensive collection there. It is astonishing to note that, apparently owing to different times of flowering, most species came true from seed and were not hybridized. I returned with a suitcase full of acorns in bags precisely labeled with the species (but not the genus, since all were *Quercus*).

Acorns were, and are still, forbidden to import into Holland. Upon opening my bag, I suggested to the customs official it contained a sample collection of hazelnuts. This worked, and for years on end they accepted the explanation! This was the start of expanding our oak assortment, which now comprises more than 250 taxa including 110 species and 140 cultivars and hybrids. Of these, 25 are evergreen. We are able to grow these 25 tender evergreen oaks due to the fact that we learned, with practice, that if the plants can be protected during their first five years until the vigorous juvenile growth slows, the plants then begin to harden earlier in the fall and can withstand cold better.

Having only five hectares (12.5 acres) at our disposal, we must specialize. So we have chosen to feature oaks, beeches, and rhododendrons. I cannot even grow all oak species and cultivars in our limited space, so we concentrate upon those which are conspicuously different. Thus, many common varieties are missing. In order to make the arboretum interesting also for the general public (which pay the majority of our expenses), we also plant other genera, but only the raisins from the cake, which help to make the arboretum attractive for everyone.

We have found that sowing acorns is fascinating and can produce unexpected results. We normally would predict the progeny from hybrid oaks to Mendel back 25% to each parent and 50% intermediate for each characteristic, but this is seldom true. The seedling progeny from cultivars may yield very few interesting specimens. For instance, 1000 acorns from *Quercus robur* 'Pendula' yielded not a single pendulous plant, while 100% of a sowing of *Q. robur* 'Salicifolia' were true to type. From *Q. robur* 'Cristata' 50% were true and the rest reverted to plain *Q. robur*. Finally, from 1000 acorns of *Q. robur* 'Pectinata' we found not a single progeny true to type. We continue to ponder the cause of this different behavior.

A selection of oaks at Arboretum Trompenburg

Quercus acuta
Q. alnifolia
Q. x*brittonii* (*Q. ilicifolia* x *Q. marilandica*)
Q. x*bushii* (*Q. marilandica* x *Q. velutina*)
Q. castaneifolia
Q. cerris 'Argenteovariegata'
Q. cerris 'Laciniata'
Q. cerris 'Marmorata' (a Trompenburg introduction)
Q. coccifera
Q. dentata
Q. dentata 'Pinnatifida'
Q. frainetto
Q. hartwissiana
Q. x*hispanica* 'Lucombeana' (*Q. cerris* x *Q. suber*)
Q. ilex
Q. ilicifolia
Q. macrolepis
Q. x*kewensis* (*Q. cerris* x *Q. wislizeni*)
Q. lamellosa
Q. semecarpifolia
Q. libani
Q. x*libanerris* 'Rotterdam' (*Q. libani* x *Q. cerris*)
Q. lusitanica
Q. macranthera
Q. (*macranthera* x *Q. frainetto*) 'Macon'
Q. mongolica var. *grosseserrata*
Q. myrsinifolia
Q. (*petraea* 'Mespilifolia' x *Q. robur* 'Fastigiata') 'Columna'
Q. (*petraea* 'Mespilifolia' x *Q. robur* 'Fastigiata') 'East Column'
Q. (*petraea* 'Mespilifolia' x *Q. robur* 'Fastigiata') 'West Column'
Q. petraea 'Laciniata Crispa'
Q. petraea 'Mespilifolia'
Q. phillyreoides
Q. pontica
Q. (*pontica* x *Q. dentata*) 'Pondaim'
Q. x*hickelii* (*Q. pontica* x *Q. robur*)
Q. x*turneri* 'Pseudoturneri' (*Q. ilex* x *Q. robur*)
Q. pyrenaica
Q. robur 'Atropurpurea'
Q. robur 'Concordia'
Q. robur 'Cristata'
Q. robur 'Pectinata'
Q. robur 'Pendula'
Q. robur 'Salicifolia'
Q. rubra 'Aurea'
Q. rubra 'Miki'
Q. rubra 'Regence'
Q. sadleriana
Q. x*tabajdiana* (*Q. frainetto* x *Q. petraea*)
Q. trojana
Q. variabilis
Q. x*vilmoriniana* (*Q. petraea* x *Q. dentata*)
Q. vulcanica
Q. warburgii (doubtful species – possibly hybrid origin)

Global Climate Change and California Oaks

by Robin Bayer, David Schrom, Joan Schwan
Magic Box
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For nearly 20 years, the authors have monitored, planted, and cared for native oaks (*Quercus agrifolia, Q. douglasii, and Q. lobata*) on more than a thousand semi-rural acres on the San Francisco Peninsula. By guarding oaks against unsustainable grazing, urban sprawl, and firewood cutting, and by suppressing competing exotic vegetation, we have conserved the habitat—and perhaps increased the vigor—of many thousands of trees. By planting and nurturing acorns and seedlings among populations that appeared to be failing to regenerate naturally, we have established more than 2,000 new saplings. Despite these gains, we are concerned that our actions may prove inadequate to our objective: self-sustaining oak populations on the land we steward. We perceive that ongoing anthropogenic global climate change is a challenge of a new genre, destined possibly to reverse our own and others' oak protection achievements to date, and perhaps even to inflict additional losses far greater than any previously endured.

We undertook a review of literature on global change and its implications for plants in general and oaks in particular. These studies ranged from assessments of known atmospheric changes, to probable effects on climate, to possible effects on California oaks, moving further into indeterminacy with each narrowing of focus. Thus, this paper is less an effort to predict in detail the consequences of climate change for California oaks than an argument that we already have sufficient information to warrant responding vigorously to this threat. To frame the issue, we begin with a summary of recent and projected human alterations to the gaseous composition of the atmosphere, and with an overview of appraisals of resultant effects on climate, and on ecosystem elements like soils and water. Next we review some of the literature examining possible impacts of sudden climate change on oaks and other biota. Then we discuss how we are adapting our own research, advocacy, and field work to the accumulating evidence of human-driven global climate change, noting obstacles that we have encountered and offering our thoughts about their underpinnings and ways to surmount them. Finally we suggest how people may husband oaks through what appears likely to be at least a difficult transitional period, and how we may reduce human threats to their longer-term well-being.

Human Impacts on Atmospheric Composition & Climate

The gaseous composition of Earth's atmosphere was relatively stable from the end of the last ice age, about 10,000 years ago, until the 1800s. Over the past century or so, people have substantially altered this long-standing balance (Vitousek, 1994). By burning fossil fuels, clearing forests, increasing domesticated livestock populations, and processing industrial materials, we have added to the amounts of carbon dioxide, nitrous oxide, and methane in the air. In addition, we have released artificial chemicals heretofore absent from the ecosphere, such as chlorofluorocarbons (CFCs), which alter atmospheric composition both by their presence, and by their diminution of other components (e.g. stratospheric ozone) (Mitchell, 1989; Rowland, 1989).

These changes are already measurably affecting temperature, precipitation, insolation, and wind. The Intergovernmental Panel on Climate Change (IPCC) recently concluded that human disturbance of the atmosphere will likely cause global average temperatures to rise at an accelerating rate, producing overall warming of 0.9-3.5 degrees C by the end of the 21st century. During the last ice age, the Earth was only about 5 degrees C cooler than it is today (Goudie, 1992).

In California, because of maritime influences and variations in topography, local results of warming will vary. For example, a strengthened California current—one possible effect of overall warming—may yield increased fog with resultant cooling of the coast during summer. Alternatively, global warming may weaken the California current. Even if this occurs, higher overall temperatures may make coastal California cooler and wetter by inducing greater and more frequent inland movement of the marine layer (Knox, 1991, Botkin et al. 1991).

Warming is projected to increase precipitation globally by 10 percent, and may significantly alter its form, timing, intensity, and distribution (Knox, 1991). Seasonal shifts are possible, and wider fluctuations from norms are likely (Vaux, 1991). An overall increase in California precipitation is expected, but changes for particular locales fall in the range of ±20 percent (Vaux, 1991). More certain is that rain will replace snow over 100-150 m of elevation for each 1 degree C of warming (Gleick, 1987). By reducing upper atmosphere concentrations of ozone, humans have allowed more biologically damaging high-frequency UVb to reach Earth's surface (de Gruijl, 1994). In 1991, UVb within California was estimated to be 10-20 percent above levels of mid-20th century (Knox, 1991). UVb is generally thought to be increasing about 2 percent for each 1 percent decrease in ozone, suggesting that it may peak at 20-40 percent above historic levels (Madronich et al. 1994). At the same time, some researchers expect that warming will increase cloud cover locally and seasonally, reducing the duration and intensity of sunlight, and further altering the proportions of solar energy of various frequencies which reach the Earth's surface (Westman and Malanson, 1992).

As additional heat energy is absorbed by the atmosphere, storm winds may increase in strength and frequency. Though much uncertainty remains, meteorologists are accumulating evidence for such a trend. For example, in 1995, the United States had the most active Atlantic hurricane season since the 1930s (Flavin, 1996; Botkin et al. 1991). Many parts of

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California are already regularly subjected to powerful winds. If the California current is strengthened by global warming, onshore winds will probably increase. In addition, overall warming may shift storm tracks northward, subjecting California to greater risk from high velocity wind (Knox, 1991).

Effects of Climate Change on Surface Features

Stream and river flows, lake levels and flushing, ocean levels, aquifer recharge, wetland functioning, and soil depth, texture, and nutrient content are all dependent upon climate and are being affected by the changes underway (Vaux, 1991; Botkin, 1991).

Increased precipitation, especially where peak hourly or daily rainfall is higher than it had been, may result in flooding (Watson et al. 1996). Evidence from the geological record of the past 7,000 years shows that changes in mean annual global temperatures of only 1-2 degrees C and increases in mean annual precipitation of only 10-20 percent can bring frequent floods of a magnitude that previously occurred only once every 500 years (Knox, 1993).

With a 2-4 degree C warming, California snowlines are expected to rise by 200-600 m vertically, and the snowpack will probably melt earlier (Gleick, 1987; Vaux, 1991). If this occurs, runoff will increase during winter and early spring, and decrease during late spring and summer. These changes may bring more frequent and extensive winter and spring floods; and they may also lessen the summer and autumn availability of surface water. The amount of water stored in snowpack is projected to drop 33 percent statewide in an average year, with Sacramento Basin losses projected to be at least 40 percent, and San Joaquin Basin losses about 25 percent (Knox, 1991; Vaux, 1991).

One researcher suggests that a 4 degree C rise in temperature will increase evaporative losses from lakes, rivers, streams, and soils enough to reduce overall annual run-off in northern California by 10 percent, with summer reductions as high as 62 percent (Gleick, 1988).

Groundwater drawdown and recharge may well be markedly different as a result both of climate change and of human action to compensate for it, and overall drop of groundwater levels is likely (Vaux, 1991).

Sediment burdens may increase as heavier storms augment runoff, as soils previously subjected primarily to snow are scoured by rain, and as those once protected by vegetative cover are left bare by the death of heat- and drought-stressed plants. Accumulation of water-borne sediment in artificial reservoirs and natural lakes and estuaries may further exacerbate flooding during peak flows (Vaux, 1991; Botkin et al. 1991).

Oceans have risen 10-25 cm in this century as warming seawater has expanded and polar ice has melted. If warming continues as projected, cumulative worldwide mean increases in sea levels by the end of the 21st century are predicted by the IPCC to be about 50 cm, with much local variation (Houghton et al. 1996). In 1989, the National Research Council estimated sea level rises during the next 50 years along California shores on the order of 0.2-1 meter. Intrusion of brackish water into coastal aquifers and surface waters, particularly in the San Joaquin/Sacramento delta, and flooding of low-lying areas around San Francisco Bay and in the Central Valley are likely (Vaux, 1991).

Increased temperatures, greater evapotranspirative losses, more severe storms and runoff, increased flooding, and higher winds will probably accelerate weathering and erosion, and may significantly alter soil moisture, aeration, nutrient levels, organic content, and soil organism populations. Loss of plant cover may reinforce these trends, and soil depth may be altered in many places (Botkin et al. 1991).

Impacts of Climate Change on California Oaks

As we have discussed alterations of atmospheric composition, climatological consequences, and impacts on soil and water, we have become progressively less certain of our predictions. In assessing how oaks will be affected by global climate change, we take a further step into indeterminacy. Researchers have widely differing views about the degrees to which oaks will expand beyond, persist in, or disappear from their current ranges. Though accumulating evidence will confirm some forecasts and strengthen our confidence in others, complexity of the ecosystem and limitations of our modeling ensure that much about impacts of anthropogenic global climate change on oaks will remain unknowable even after they occur. Our purpose here is to alert readers to possibilities of which many may have yet to become aware, and to stimulate consideration of costs and benefits of actions by which we may make various outcomes more or less likely.

Like all living things, oaks persist by maintaining a match between their internal information and the qualities of their environment. Raven and Axelrod (1978) assert that the pattern of Mediterranean climate characteristic of current California oak habitat—cool, wet winters and warm, dry summers—emerged in the Quaternary (1 my bp). California vegetation types with substantial oak components—including oak woodland, blue oak-gray pine woodland, inland prairie, and chaparral—are tightly coupled to both temperature and precipitation, and because the ecosystems in which California oaks grow are typically semi-arid, they may be particularly sensitive to warming (Watson et al. 1996). Human-induced global climate changes are now proceeding at a scale and speed that is unprecedented in oaks' history and will pose a challenge to their ability to adapt.

Mechanisms for Climatic Impact on Oaks

Oak species differ in sensitivity to CO_2, temperature, water, light, soil, and presence or absence of other species. Their response to each of these may fluctuate with stages in their life cycles, and will vary also with limiting factors at boundaries of particular habitats. Climate change may affect reproductive success, vigor, and mortality at many ages (Botkin et al. 1991).

Higher CO_2 levels may accelerate growth and improve efficiency of water use during photosynthesis. This is potentially an advantage to oak species that are metabolically active during summer (Woodward, 1992).

Untimely or excessive heat, cold, rain, or drought may impede flower development, pollination, acorn numbers and viability, and seedling establishment. Warmth may stimulate growth, but excessive heat decreases it, and if prolonged or intense enough can be fatal. Low temperatures may suppress insects and other organisms which can damage or kill oaks, but they also limit growing season. Even short periods of extreme heat or cold during critical times may injure or kill. Because temperatures are expected to become more volatile, damage arising from unseasonable or extreme heat and cold will likely become more common.

Reductions in snowpack and late-season runoff may diminish availability of water during the warmest months with the longest days, and may also bring saltwater intrusion into low-

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lying areas. Both types of change might prove devastating to oaks (Lewis et al. 1991; Botkin et al. 1991).

Increases or decreases in cloudiness and in stratospheric transparency to UVb will alter light energy available, possibly affecting photosynthesis and evapotranspiration. Ultraviolet radiation can damage many important biologically active molecules, including DNA. Current and expected UV levels are beyond anything oaks and many of their symbionts have previously endured (de Gruijl, 1994). Already ozone depletion and resultant rise in UVb have been implicated in damage to populations as disparate as ocean corals (Vitousek, 1993) and human beings (de Gruijl, 1994).

Die-off of understory plants may result in disruption of beneficial symbioses, reduced percolation—further limiting water availability, and heating of exposed soils to levels fatal to oak seedlings and damaging to mature trees. Colonization by invasive species may pose added obstacles to regeneration. Woodward (1992) has observed an 8% increase in plant family diversity for every 10 degree C increase in minimum temperatures. Warming is likely to lead to at least temporary increases in biodiversity, with persistence of oaks and their historical symbionts in their current ranges depending upon successful competition with new challengers in unfamiliar conditions.

Stressed oaks and other species may become more vulnerable to pests of all kinds. Standing dead biomass may fuel more frequent, more prolonged, and hotter fires, which kill additional seedlings or even mature trees (Botkin et al. 1991).

On the slopes of the Sierra foothills and the coastal ranges, erosion from the combined effects of understory species lossing to drought, fire, and increasingly violent storms may accelerate decline in older trees and make reseeding and seedling survival in situ, as well as migration to other areas, less likely (Botkin et al. 1991).

Once the fabric of life is rent, a cascade of unforeseen—or even difficult to imagine—effects may ensue. For example, extensive loss of northern and temperate boreal forests during the next few decades may release tens of billions of tons of additional carbon into the atmosphere. Warming of tundra, with attendant decay of long-frozen organic detritus, may generate immense quantities of methane and CO_2 (Woodwell and Mackenzie, 1995). Both of these processes may further accelerate warming and intensify resulting impacts on oaks and oak habitat.

Migration as an Adaptation to Climate Change

Obstacles to oaks' migration are many. Unsuitability of contiguous or proximate soils and slopes, momentum in existing plant communities, and competition by weedy species well-adapted to disturbance all pose challenges. Moreover, oaks themselves are in several important ways ill-equipped for rapid migration. They require several years to produce their first seed, and decades to reach reproductive maturity. Their seed production is modest by contrast to that of many plants, and often intermittent, and dispersal is limited by the sheer size of acorns (McBride and Mossadegh, 1990; Westman and Malanson, 1992; Woodward, 1992).

Although some may imagine oaks moving northward or upslope in response to warming, California's diverse physiography often bars such migration. For example, there are no geographic equivalents of the Salinas Valley or the Napa Valley anywhere between Santa Rosa and Washington State (Lewis et al. 1991). In addition, humans have fragmented oak populations and habitat, and have blocked many potential migration corridors with urban settlements and agricultural uses.

If warming stops within the limits of current projections, existing and potential future ranges of particular oak species may indeed overlap, and surviving populations may eventually be able to migrate into newly-available zones of favorable climate. Under transitional conditions, squirrels, jays, and other acorn-planting rodents and birds may increase their numbers, and become even more effective seed dispersers. In any event, oaks' genetic variability may afford them some advantage in competing (McBride and Mossadegh, 1990).

If warming continues beyond what is currently predicted, however, there may be no overlap between existing and future habitats. With each increment of distance, successful migration becomes less likely. Colonization of outlier patches is difficult in a landscape as topographically and geographically complex, and as thoroughly fragmented by humans, as California's.

Even where contiguous potential habitat allows for migration, we have posed an unprecedented challenge by the speed of the changes we have set in motion. During the last period of glacial retreat, sustained, globally-averaged warming of a few degrees occurred over thousands of years. We are projected to generate a shift of this magnitude in mere decades. With mid-latitude temperatures varying ~1degree C per 100 kilometers of north-south travel, a 2-4 degrees C warming corresponds to a 200-400 km poleward shift of thermal zones (Roberts, 1989). If such a warming occurs in a century, it will entail movement of kilometers each year, a rate which appears well beyond the capability of oaks, given the time they require to reach reproductive maturity, their seed dispersal ranges, and observed patterns of ecological succession.

Margaret Davis and Catherine Zabinski (1992) studied plant migration in response to warming at the end of the last ice age and concluded that individual species moved at different rates and even in different directions. Such migration can result in new, "no-analog" habitats depauperate in pollinators, dispersal agents, or other critical-link species (Schneider, 1997a).

Observed and Predicted Effects

California oaks may already be waning as a result of climate change. In recent decades, blue oak (*Q. douglasii*), the dominant native low-elevation tree in the state, has been failing to regenerate. While researchers typically attribute blue oaks' decline to grazing, to increases in populations of rodents resulting from extirpation of their predators, or to inability to compete with non-native annual grasses for limited water, Lewis et al. (1992) note that "the only [blue] oaks standing today are those that germinated during periods of 2 or 3 consecutive wet years. The last such period occurred about 60 years ago. A drier environment caused by global warming could conceivably bring about the elimination of the blue oak in California." Others have noted local disappearance of valley oak, and conjecture that this might be attributable to falling water tables (Schoenherr, 1992). This may partially be a result of prolonged drought linked to increased climate volatility.

Regardless of whether climate-induced changes have begun, and of how great they will ultimately prove, initial effects will probably be subtle, and most evident at the margins. Increases and decreases in seed production and seedling survival may be early indicators of climatological impacts where populations of mature trees appear little changed (Davis and

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Zabinski, 1992). If late-season stream flows diminish as projected, riparian habitat edges may contract inward and downstream. Also, streamside habitat may narrow if higher-volume winter and early spring flows accelerate bank erosion, or if floods prove directly fatal, or deposit intolerable sediment over root zones or crowns. Where saltwater intrusion currently limits oak survival, as it may in low-lying areas adjoining San Francisco Bay, rising ocean levels and wind-borne salt spray may further restrict their range (Botkin et al. 1991).

Oaks may benefit from some aspects of climate change. Increased warmth, and in some areas greater precipitation, may enable them to become more securely established or to expand their range where lack of heat or water are now constraints. McBride and Mossadegh (1990) assessed responses of California oaks to climate change using models developed at the Goddard Institute for Space Studies (GISS), Geophysical Fluid Dynamics Laboratory (GFDL), and Oregon State University (OSU). They concluded that because greater precipitation will offset higher temperatures in northern California, and because more efficient use of water resulting from elevated CO_2 and existing adaptations to drought will enable oaks to persist in the San Joaquin drainage, "distributions of arboreal species of oaks will not be significantly impacted."

Research by others suggests that where oak populations are at the threshold of their tolerance for dry conditions, the hotter, drier climate which may accompany global warming over parts of California may eliminate them. When Westman & Malanson (1992) applied the GISS and GFDL models, they found that expected alterations in temperature and precipitation were likely to lead to expansion of chaparral at the expense of southern oak woodland and blue oak-gray pine woodland. Neilson (1993) asserts that under most models, greater evapotranspiration more than offsets benefits from increases in precipitation and water use efficiency. Woodward (1992) notes that because gases besides CO_2 contribute to global warming, actual CO_2 will only be about 1.5 times historical levels when temperatures reach the level predicted for "doubled CO_2," and that as a result, models of plant response to a doubling of CO_2 and studies performed at these concentrations underestimate moisture stress.

T. Webb (1986) has proposed that the ratio of plant taxa response time (the time it takes to respond significantly to a given climate change by changing local abundance and/or geographic range) to the rate of climate change is a guide in assessing the likelihood of successful adaptation. If the ratio is small (e.g. 200 years/20,000 years) dynamic equilibrium can prevail. If it is larger (e.g. 200 years/200 years) then disequilibrium may exist. Response times for tree taxa are yet to be determined conclusively, but minimums on the order of 50-200 years have been estimated. These are fast enough for tree taxa to stay in equilibria with most major past climate changes, but are similar in length to the predicted time scale for current human-mediated climate change, and imply disequilibria. (Westman and Malanson, 1992)

S. P. Hamburg and C. V. Cogbill (1988) describe an example of disequilibrium for conifers when they report that as growing season has lengthened over the last 180 years in mixed boreal conifer and deciduous broadleaved forest of the eastern U.S. Canopy dominance by conifers has been gradually decreasing, and red spruce (Picea rubens) has been virtually extinguished.

Joseph Knox, Director of the National Institute for Global Environmental Change at UC Davis, and editor of Global Climate Change and California, described his group's work as "plausible estimates ... which have been made as consistent as possible with the current consensus understanding of the greenhouse effect." He reported that, "The panel estimates that 20-50 percent of the area occupied by natural ecosystems will no longer be suitable for the communities that exist there now ..." and concluded bluntly that, "Diebacks ... and loss of species could well prevail ..." (Knox, 1991).

McBride and Mossadegh (1990) cited a study conducted a decade ago to predict the impacts of global climate change on oaks. This study by Woodman and Furiness (1988) evaluated the effects of potential climatic change on the major commercial conifer species in California, and concluded that the state was "unlikely to experience significant large-scale reductions ... in the next century." Yet four of the 10 largest California wildfires of the past 60 years occurred between 1987 and 1996 (California Department of Forestry and Fire Protection, 1997). Exceptional heat and drought, and insect infestation of stressed trees were factors in these fires. A link to global climate change remains unproven, yet we may fairly ask whether this threat was accurately assessed.

EPA researchers have warned that, "[G]reenhouse warming will spell doom for many forests across the United States. ... [Total forested area in the West could be dramatically reduced. ... [Some species would go locally extinct." Even where they deemed dominant trees possibly able to adapt, they characterized chances of survival for many understory plants as "disappearingly small" (Roberts, 1989).

Though there are many grounds to assert that oaks will survive the next century, there is mounting evidence that they will be sorely tested by human-generated climate change.

Evolving Our Response to Global Climate Change

Nearly 20 years ago the authors observed that California native oaks on Stanford University lands were dying without successors. We began planting acorns in hopes of contributing to more stable oak populations. Our results were disappointing, so we sought advice from Stanford and UC Berkeley faculty, and from UC Extension and California Division of Forestry staff. From them we learned that oaks in many parts of California were apparently failing to regenerate, and with their guidance, we began a series of trials. When Stanford planners retained a forester and a landscape architect to prepare a vegetation management plan with special emphasis upon oak preservation and regeneration, we were contracted to implement it.

Both our own early activities and the vegetation management plan were founded on an assumption that proper local resource management was sufficient for oak regeneration. Our tools were prohibition of tree-cutting and of downed wood removal, modified grazing regimes, a moratorium on additional road and building construction, rodent suppression and exclusion, limited vehicular access, eradication of exotics, planting of natives, fire management, and regulation of recreational use.

Despite these interventions, we noted continuing adverse change on lands we stewarded. Erosion seemed to be accelerating, with gullies and slumps proliferating. Fox and coyote became rarer. Rodent populations burgeoned. Stands of exotics like mustard became denser and more extensive. Most oaks produced few or no acorns, and seedling recruitment was far from sufficient to maintain existing populations.

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Observers elsewhere noted similar departures from past patterns. Fire devastated forests across the western United States. Species ranging from Monterey Bay snails (Barry, 1995) to Edith's checkerspot butterflies (Parmesan, 1994) disappeared from habitats where they had long flourished. Record heat, cold, rain, drought, winds, and floods struck around the globe (Flavin, 1996). Scientists in diverse disciplines published a growing number of papers suggesting that these and other ecosystem disruptions were human-driven, and that remedying any of them successfully was likely to require addressing all of them.

As we have become more aware of possible linkages between oaks and global phenomena, our attitudes and strategies have evolved. We are now far less confident that our tree planting and care will have lasting or significant direct impacts on the landscape. We have supplanted promises about "restoring" nature, with which we once motivated ourselves and others, with cautions against such hubris. We have tempered dreams of returning to admire our handiwork in forty or fifty years with questions about what more we will do if oaks are to persist.

When we introduce new volunteers and community audiences to our project, we increasingly emphasize oaks' dependence upon integrity of a global ecosystem, and we outline unprecedented ways in which humans are disturbing that system. What once was primarily an oak project is now much more a people project. Metaphorically, at least, we now see oaks growing as much in human hearts and minds as in any other medium. To create suitable "habitat" there, we are becoming more attentive to—and teaching others about—laws of nature, consequences of human choices, and necessity for deeply and persistently questioning what we want, how we can get it, and above all, how we arrive at our conclusions about these things.

Why are so many only slowly acknowledging and rising to the challenge of anthropogenic climate change, which scientists worldwide have identified as one of the greatest threats to our own and our descendants well-being? We offer a few ideas, aware that they are but a partial explanation. For centuries, Europeans and North Americans have led the way in using the leverage of fossil fuel burning to realize a vision of progress based upon accelerating conversion of nature to artifact. As we have gained the equivalent of slave labor in the form of fossil fuel energy—and capital plant and equipment converted from it—we have also transformed political economy from a consciously communal enterprise to one much more readily imagined to be individualistic, and we have coerced people around the world to follow suit. Now belief, law, and custom are everywhere increasingly uniform, and reflect centuries of apparent success in improving upon nature by manipulating it, and in defining self-interest narrowly.

To adapt successfully in both near and longer term, we will become more cautious about imagining that we can manipulate what lies around us to good effect, and we will more fully appreciate benefits of cooperating to secure our common future. Substantially lessening our impacts on climate entails gross reductions in fossil fuel burning, deforestation, CFC releases, and other activities which are central to many of our lives. To reverse current trends towards devil-take-the-hindmost and move instead towards greater civility, some will lead in accepting very evident personal costs of addressing climate change, even though we lack guarantee of future reward for ourselves or anyone else. Our success will depend at once upon reducing our own direct impacts on climate, and upon convincingly demonstrating the advantages of such action to others.

As "winners" in the current order, many of us want it to continue and are eager to believe that it can and will. Even people who recognize an end to recent trends to be inevitable, and who see benefit in that occurring sooner rather than later, face obstacles to voicing or acting upon such views. In governmental agencies, private enterprises, non-profit organizations, and informal groups, we encounter many who are determined to carry on with business as usual—implicitly or explicitly denying past failures to accurately foresee consequences of our acts. Jobs, pay, authority, promotion, publication, and their collateral rewards are withheld from those who suggest that we are accumulating a vast ecological debt that will burden us and our heirs far into the future. Yet multinational agreements; local, state, and national government policies; and corporate and nonprofit organization operations all reflect and depend upon individual choices for their success. Each of us can lead.

Recommendations

Long-term welfare of oaks depends to a great extent upon short-term success in developing and implementing resource management policies that protect existing and potential oak habitats and that conserve and regenerate oak populations. Recommendations which follow are intended to complement rather than replace such activities, by securing their benefits against loss due to climate disruption and similar phenomena.

Each of us can reconsider in light of evidence for global climate instability our ideas about what we want and how to obtain it. These are our values, from which we generate our lives. With the fruits of introspection and study, we may reshape our behaviors to better reflect limits of the possible and our preferences within them. Though we have been conditioned to view our professional roles as those in which we exercise greatest influence, important changes requisite to slow or halt climate disruption lie outside this realm. We can effect greater change by modeling these as well.

We may encourage others to reflect upon their own ends and means, and to adjust their behaviors to match emerging realities. We may bring discourse about climate change and its connection to human values into community and professional forums. We may lobby for adoption and rigorous enforcement of local, state, national, and international policies to lessen human impacts on climate in particular and ecosystem stability in general. Specific ends we might pursue include decreasing release of greenhouse gases, balancing carbon budgets, and enforcing a ban on CFCs and other particularly potent greenhouse chemicals (e.g. methyl bromide). To avoid replacing current maladaptive behaviors with others similarly destructive, we will also find more fundamental ways to redistribute responsibility and privilege, so that we encourage behavior conducive to ecosystem integrity. Among the most critical issues are: setting limits upon reproduction, narrowing disparities in distribution of wealth, and establishing comprehensive limits, both qualitative and quantitative, on human-mediated matter-energy conversion.

In our field work with oaks we may study existing habitat with an eye to which portions may prove enduring; assess potential future habitat; lay plans to establish and/or sustain oaks where they appear more likely to survive a century or more of instability; collect, store, and plant seed from oaks in many locales to preserve genetic diversity and to learn which trees may be better suited to emerging conditions; more fully map biotic interactions to

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gain a better understanding of symbiotic and parasitic relationships sensitive to climate shifts; and conserve water and increase local surface storage and percolation.

Readers may find these recommendations somehow unsatisfying. Issues raised here are complex, broad, and deeply embedded in a host of others, and determining how to resolve them in advantageous ways is an evolutionary process in which all of us are engaged. The era of illusion about "simple things we can do to save the Earth" is drawing to a close.

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The Mexican Oak National Collection

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The role that every botanical garden plays in conservation is of vital importance when its collection policy is part of a National or Inter national conservation strategy. Although accurate accounts are not yet available, Mexico is considered one of the most bio-diverse countries in the world. This fact, coupled with the high rate of habitat destruction in many Mexican territories, makes it far more difficult to develop a conservation strategy that effectively maintains and protects this diversity.

In this context, the Mexican Association of Botanic Gardens decided in 1995 to invite all its garden members to support the establisment of

photo by Maricela Rodriguez - Acosta

Quercus germana *is one example of white oaks being cultivated in Mexico. White oaks show a better growth rate than some red oak species.*

National Plant Collections as a very specific way of contibuting to the conservation efforts taken by the Mexican goverment. The Louise Wardle de Camacho Botanic Garden decided to accept this invitation by starting the Mexican Oak Collection (Rodríguez, 1996), which has been established now for two years.

There are several reasons for supporting the idea of National Collections, however the following were some which apply specifically to the collection of *Quercus*.

a) In Mexico oak forests occupy an estimated 5.5 percent of the territory (Rzedowski, 1981).
b) There is a very high diversity of *Quercus*, calculated at between 150 and 200 species (Nixon, 1991; Rzedowski, 1981; Zavala, 1995)
c) There is a very strong relation between oak forest and human activity, which poses a threat to *Quercus* species in different regions of the country (Nixon, 1991).
d) Until 1994, *Quercus* were very poorly represented in Mexican Botanic Gardens (Razgado, 1994).
e) There is an enormous lack of knowledge regarding the cultivation of this group of plants.
f) There is a considerable amount of work to be carried out on the taxonomy of the genus.

The first step in this project was the herbarium work in the National Mexican Herbarium (MEXU) at the National University (UNAM), and the reviewing of previous papers and books about this genus by different mexican researchers, in order to develop a col-

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Table 2. *Quercus* cultivated in the Louise Wardle de Camacho Botanic Garden.

Q. acherdophylla	*Q. fusiformis*	*Q. peduncularis*
Q. acutifolia	*Q. germana*	*Q. polymorpha*
Q. acutifolia x *mexicana*	*Q. glabrescens*	*Q. praeco*
Q. affinis	*Q. glaucescens*	*Q. rugosa*
Q. candicans	*Q. glaucoides*	*Q. rhysophylla*
Q. candicans x *laurina*	*Q. hintonii*	*Q. sapotifolia*
Q. conspersa	*Q. insignis*	*Q. sartorii*
Q. convallata	*Q. laeta*	*Q.* aff. *sartorii*
Q. castanea	*Q. laeta* hybrid	*Q. sebifera*
Q. castanea x *eduardii*	*Q. lancifolia*	*Q. subspathulata*
Q. crassifolia	*Q. laurina*	*Q. scytophylla*
Q. crassipes	*Q. liebmannii*	*Q. striatula* x *tinkhamii*
Q. deserticola	*Q. magnoliifolia*	*Q. tinkhamii*
Q. deserticola x *laeta*	*Q. mexicana*	*Q. uxoris*
Q. x *dysophylla*	*Q. microphylla*	*Q. xalapensis*
Q. eugeniifolia	*Q. microphylla* hybrid	
Q. elliptica	*Q. obtusata*	

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lection strategy which could help us to increase our knowledge about Mexican oaks and to make the field work easier.

As a result of the herbarium work, around 3000 records were compiled containg 194 *Quercus* species. This work is not finished yet, however, we believe that the remaining 30 percent of the specimens are not going to change the results significantly. Regarding the actual topics studied by Mexican researchers, three are the most important: Taxonomy, Ecology and Wood technology.

After obtaining this information, it was possible to know all the *Quercus* species collected in Mexico together with their distribution. Using this information, it was possible to make a very artificial classification dividing the species into four groups:

Group 1. Species with a very restricted distibution area: *Q. hintonii* (Estado de México), *Q. hintoniorum* (Nuevo León, Coahuila) and *Q. hypoleuca* (Chihuahua).

Group 2. Species with a Central-North or Central-South distribution: *Q. tinkhamii* (San Luis Potosí, Hidalgo, Chihuahua), *Q. hypoleucoides* (Chihuahua, Sonora, Coahuila, Durango), *Q. liebmannii* (Oaxaca, Guerrero, Michoacán), *Q. insignis* (Veracruz, Jalisco, Chiapas, Guerrero)

Group 3. Species with a wide but disjunct distribution: *Q. hypoxantha* (Coahuila, San Luis Potosí, Nuevo León, Oaxaca), *Q. conzatti* (Oaxaca, Jalisco, Durango, Zacatecas), *Q. trinitalis* (Hidalgo, Tamaulipas).

Group 4. Species with a wide and continuous distribution: *Q. castanea* (21 states), *Q. laeta* (20 states) and *Q. crassifolia* (18 states).

Table 1. States with the highest *Quercus* diversity in Mexico.

State	Number of species	State	Number of species
Chihuahua	62	Coahuila	43
Oaxaca	62	Tamaulipas	43
Nuevo León	55	Puebla	42
Jalisco	55	Guanajuato	41
Durango	53	Michoacán	40
Veracruz	50	Estado de México	40
Hidalgo	48	Chiapas	40
San Luis Potosí	46		

The richest states in species diversity are: Chihuahua, Durango, Nuevo León, Coahuila, Tamaulipas, Jalisco, Guanajuato, Hidalgo, Michoacán, Estado de México, Puebla, Veracruz, Oaxaca and Chiapas (Table 1) , however, some of these differences may be due to lack of field work in some areas. Chihuahua in the north and Oaxaca in the south are far the most important with a total amount of 90 different species, 16 common to both states. These figures show that almost 50 percent of *Quercus* species can be found in only two states of the Mexican Republic. In addition, we can say that species which are located at the north have a more restricted distribution in comparison to those located in Oaxaca, which show a wider distribution in the rest of the country.

photos by Maricela Rodriguez - Acosta

Two examples of Quercus *cultivated at the Louise Wardle de Comacho Botanic Gardens: (top) Q. rugosa; (left) Q. magnoliifolia.*

Even though this information has been very useful in the establishment of our collection strategy, it is necessary to make some consideration to it.

1. There is an unknown number of synonyms in the 194 species recorded,. which makes it difficult to know the exact number of *Quercus* species in México.
2. Many of the herbarium specimens lack fruits, making identification difficult.
3. Exploration work in Mexico is incomplete.

These points make more urgent the necessity to work in the three directions: Taxonomy, collection and exploration. This is not always as easy as it seems. The need for collection permits, contacting local authorities, collection reports and financial support, make field exploration work more difficult. Even after these problems have been solved, there still exists one of the most important characteristics of oaks: that is the unpredictability in the fruiting times which means it is often necessary to visit a site over several years in order to obtain acorns.

After almost two years of work, 90 different *Quercus* species and hybrids have been found and a little more of 50 percent of them bearing fruit (Table 2). From the collections made, red and white oaks are now equally represented in the collection. They do not appear to have the same cultivation requirements, red oaks seeming to be a little more susceptible to pests than white oaks. They also show different growth

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under natural conditions. The white oaks, such as: *Q. germana*, *Q. lancifolia* and *Q. rugosa* show a better growth rate than the red oaks such as *Q. acherdophylla*, *Q. candicans* and *Q. affinis*. However, the collection is young and it is necessary to make observations over a longer period of time before we will know fully the growth characteristics and requirements of the species in the collection.

It is neccesary to say how important has been the collaboration we have established with different institutions interested in increasing the knowledge of *Quercus*. These have been invaluable to the development of the National Collection project. The Institutions which have participated with us in this are The Sir Harold Hillier Gardens and Arboretum, England; the Sciences Faculty Herbarium and National Herbarium in México; and the Puebla University Herbarium in Puebla, Mexico.

After the experience gained during these two years, the following activities should be given priority in order to improve the development of the National Mexican Oak Collection:

a) To strengthen our network at a national level.
b) To increase exploration and field work.
c) To attract financial support from a wider variety of sources.
d) To increase the number of collaborators in this project.

With these activities we believe it is possible to increase not only the number of species in the collection, but also knowledge of Mexican oaks. It is in this way that this Botanical Garden has responded to the Mexican Association of Botanic Gardens.

However, while more oak forests are explored, it is also necessary to carry out more research work in them. More hard work is needed before we can say that we have the National Mexican Oak Collection. At the moment the only thing we can say is that so far the Louise Wardle Botanic has the largest *Quercus* species collection in México.

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