Geobotany Studies
Basics, Methods and Case Studies

George Nakhutsrishvili

The Vegetation of Georgia (South Caucasus)

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Basics, Methods and Case Studies
Series Editor: Franco Pedrotti

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The Vegetation of Georgia (South Caucasus)

The book describes richness and diversity of Georgia's vegetation. Contrasting ecosystems coexist on the relatively small territory of the country and include semi-deserts in East Georgia, Colchic forests with almost subtropical climate in West Georgia and subnival plant communities in high mountains. West Georgia lacks xerophilous vegetation zone and mesophilous forest vegetation spreads from the sea level to subalpine zone. The Colchic refugium (West Georgia) ensured survival of the Tertiary's mesophilous forest flora. Vertical profile of the vegetation is more complex in East Georgia with semi-desert, steppe and arid open forest zone. In South Georgia the montane zone represented by montane steppe is devoid of forests.

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Geobotany Studies

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The Vegetation of Georgia (South Caucasus)

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Preface

Georgia, an ancient Christian country, occupies the central and southwestern parts of the Caucasus – an isthmus between the Black and the Caspian Sea. In the west, it is contiguous to the Black Sea, in the east to the intermountain depression of the River Mtkvari (=Kura) in the Caspian Lowlands (the Transcaucasian Depression), the northern border follows the high mountain tops of the Greater Caucasus, the southern one crosses the Lesser Caucasus (in the eastern part) and separates the Lesser Caucasus from the adjacent mountain ranges of northeastern Asia Minor. Politically, Georgia borders on the Russian Federation (to the north), Azerbaijan (to the east), Turkey (to the southwest) and Armenia (to the southeast). The borders have changed several times during the history of Georgia, especially in the earlier stages of the formation of the Georgian nation.

Kavkasioni, i.e. the Greater Caucasus range, rises up to 5,068 m (Mt. Shkhara, highest mountain within Georgia) and 5,633 m a.s.l. (Mt. Elbrus, in the Russian Federation), i.e. over 1,000 m above the eternal snow-line. Mountain passes at an altitude of 2,200–3,000 m a.s.l. were used as trade-routes from the earliest times. In the mountains of Kavkasioni, permanent settlements are found up to an altitude of 2,500 m a.s.l. Though the Lesser Caucasus mountains reach an altitude of 3,304 m a.s.l., there are no glaciers and no eternal snow.

The natural conditions of the so-called intermontane lowlands of Georgia, consisting of the Colchic Lowlands (adjacent to the Black Sea, in West Georgia) and the foothills between Kavkasioni (in the north) and the Lesser Caucasus (in the southwest), including the Mtkvari Valley (resp. Kura valley, in East Georgia), are favourable for settlement and mixed farming.

In the east, the Colchic Lowlands are surrounded by the Imeretian Elevation which connects the Greater Caucasus with the Lesser Caucasus. The highest part of it, the Surami range, divides the country into two major natural geographical regions: Eastern and Western Georgia, the first having been called Iberia and the latter Colchis by ancient Greek and Roman writers.

Diversity of climate and relief of Georgia has been highly important for its economic development since the early stages of human activities. Numerous rivers (more than 25,000), which promoted intensive agriculture, eliminated the need for irrigation systems, having proved so essential in the economy of the Ancient Eastt (Egypt, Babylon). Besides, these rivers served as trade routes. Due to their rapid current, the rivers were used for transportation of timber (especially in Colchis).

Georgia is rich in various mineral resources. In the mountains of Georgia, copper was extracted, essential for non-ferrous metallurgy, which by that time reached a high level of development. Rich iron deposits prompted the progress of ferrous metallurgy. Magnetic sands along the Black Sea were of particular importance. Rivers, containing gold dust, were known during the Greek Epoch.

Vakhushti Bagrationi, the prominent Georgian historian and geographer of the eighteenth century, distinguished two botanical and agricultural zones within Georgia: the mountainous and the lowland one. Since the Neolithic Revolution, these two zones represented one closely integrated system. The lowlands were characterized by rich harvest of grain crops, vineyards and orchards. In the mountainous areas, the harvest of grain crops was much poorer, and vineyards and orchards were absent.

Georgia covers an area of 69.500 km^2. The population is 5.5 million (two third being Georgians). The Georgians call themselves 'kartveli' (sing.) and 'kartvelebi' (pl.), hence the name of the country in Georgian language is 'Sakartvelo'. The Georgian language belongs to the group of Kartvelian languages, included in the family of Iberian-Caucasian languages. It is suggested that the Georgian language is related to Anterior-Asian languages, the Basque language (the Basque country lies partly in Spain, in the northern part of the Iberain peninsula, close to the Pyrenees). Connections to the Indo-European languages, however, are uncertain. Written Georgian dates back to the third century B.C. (to the reign of king Parnavaz).

Christianity, adopted as the official religion in 337 A.D., promoted the unification of Georgia and the development of written Georgian language.

In ancient times, Georgian tribes were known as skilful farmers, cattle-breeders and metallurgists. Various archaeological discoveries, as well as ancient oriental and Georgian manuscripts testify to an early economical, social, and cultural development of the Georgian people. According to these data, the leading branches of economy of the country must have been: (1) agriculture (field crop cultivation, vine making, horticulture, vegetable growing, etc.); (2) cattle breeding; (3) domestic craft (weaving, woodwork, blacksmith work, textile production, pottery, ceramics, etc.). Georgians developed plough-land cultivation and various forms of irrigation (especially in the mountain areas) aiming to increase crop capacity of natural grasslands (2–3 harvests per season). Of the 16 species of wheat, 11 are represented in Georgia.

Ancient Georgian manuscripts and special medical books ('Karabadini') contain information on various herbs. The first serious scientific information concerning the vegetation of Georgia was given by Vakhushti Bagrationi (eighteenth century). According to several historical sources and notes of foreign travellers, the plants from different parts of Georgia and from other countries were cultivated in the park of Georgian kings in Legvta Khevi (now Botanical Garden of Tbilisi). In the eighteenth century, foreign scientists became interested in the extreme diversity of Georgian vegetation and flora. In 1852, on the basis of rich collections of Caucasian plants, the Caucasian Museum was founded. In the beginning of the twentieth century, all the branches of botanical science (anatomy, physiology, taxonomy, floristics, phytosociology, etc.) started to develop in Georgia. The

Institute of Botany, which belongs to the Academy of Sciences, was opened in 1933. The book *Vegetation of Georgia* by N. Ketskhoveli was published in 1935 and 1960. Long-standing expeditions to different parts of the Caucasus and of Georgia, as well as monographic studies of separate taxa served as a basis for the eight-volume *Flora of Georgia*. In 1971, the first volume of the totally revised second edition of *Flora of Georgia* appeared (16 volumes (1971-2011) have already been published so far). Key to Plants of Adjara by Dmitrieva (1959) and four volumes of the Flora of Abkhazia by Kolakovsky (1980-1986) are also worth mentioning here. Later, it was decided to publish *The Vegetation of Georgia* under the editorship of the present author (Nakhutsrishvili 1990–1991). A brief description of the vegetation cover of Georgia by R. Kvachakidze was published in 2009. The books *Forest Vegetation of Georgia* by A. Dolukhanov and *The History of Flora and Vegetation of Georgia* by I. Shatilova et al. were published in 2010 and 2011, respectively. Until its complete publication, the author of the present book decided to characterize briefly the main types of vegetation of Georgia and to publish it in English. This present publication bears a special purpose: During the 75-year period of isolation of the USSR and of Georgia in particular, it was not so easy for foreign scientists to get adequately acquainted with the interesting plant life of Georgia and to compare the Caucasian flora and plant communities with those of other countries. Today, Georgian botanists are collaborating with scientists from many other countries.

The Number of Plant Taxa

The flora of Georgia comprises about 4,150 species of vascular plants, of which 260 species are endemic, while the flora of the Caucasus comprises 6,350 species of vascular plants, of which 1,600 species are endemic.

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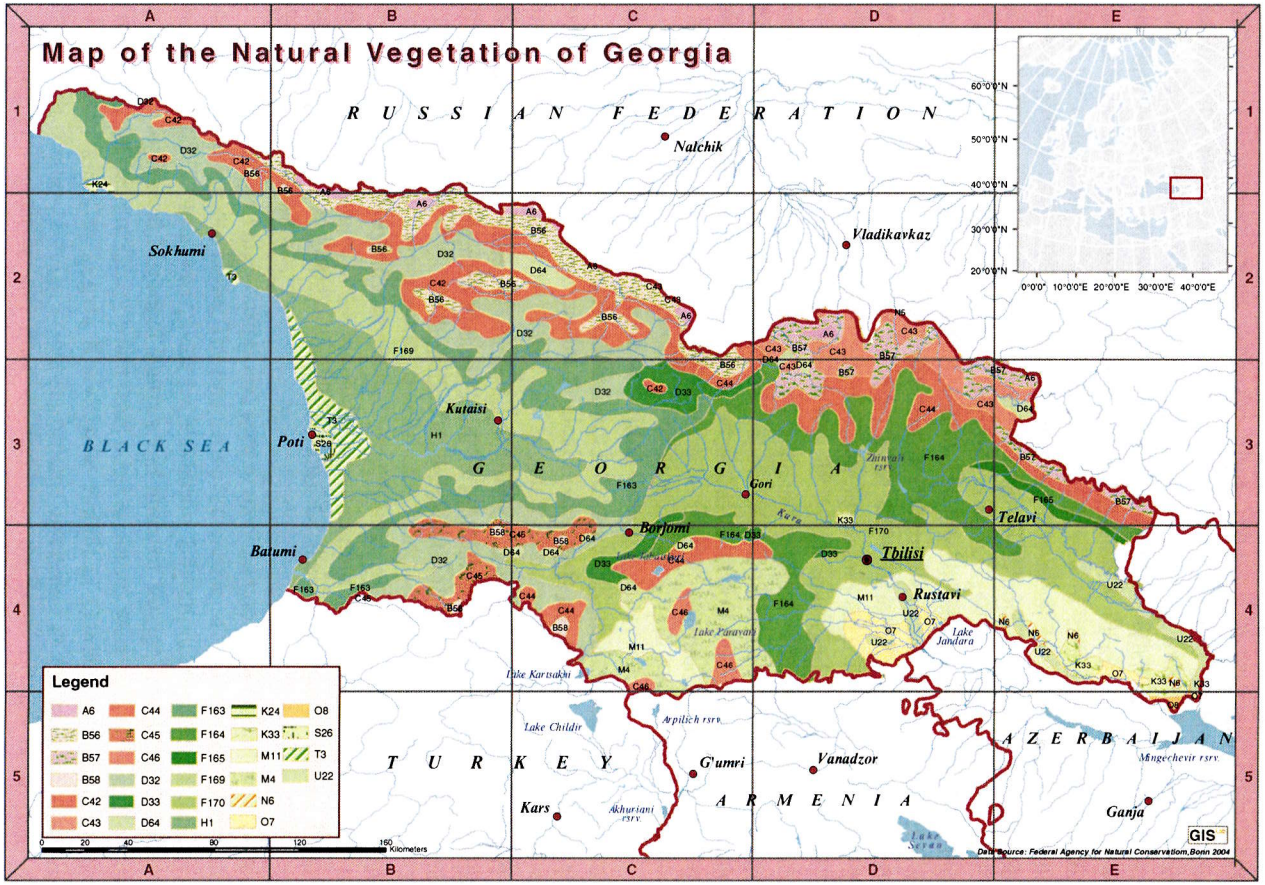
Map of the Natural Vegetation of Georgia
RUSSIAN FEDERATION
Nalchik
Vladikavkaz
Sokhumi
Kutaisi
Poti
BLACK SEA
GEORGIA
Gori
Borjomi
Telavi
Batumi
Tbilisi
Rustavi
Lake Paravani
Lake Jandara
Lake Karsakhi
Lake Childir
Akhuriani rsrv.
TURKEY
G'umri
Vanadzor
Kars
ARMENIA
AZERBAIJAN
Mingechevir rsrv.
Ganja
Lake Sevan
Legend
A6 B56 B57 B58 C42 C43 D32 D64 F163 F164 F165 F169 H1 K24 K33 M11 M4 N6 O7 O8 S26 T3 U22
0 20 40 80 120 160 Kilometers
GIS
Data Source: Federal Agency for Natural Conservation,Bonn 2004

Expanded Legend

A6 Caucasian open vegetation of lichens and mosses (*Rhizoplaca chrysoleuca, Thamnolia vermicularis, Pohlia elongata, Dicranum elongatum*), with scattered vascular plants on rocky habitats (*Saxifraga ruprechtiana, Primula bayernii*) and on screes (*Cerastium kasbek, Delphinium caucasicum, Symphyoloma graveolens, Scrophularia minima, Lamium tomentosum*)

B56 West Caucasian alpine grasslands (*Geranium gymnocaulon, Nardus stricta, Festuca djimilensis*), calcareous rocks with *Geum speciosum, Carex pontica* and small herb communities (*Sibbaldia semiglabra, Ranunculus brachylobus*), alternating with shrub (*Rhododendron caucasicum*), rock and scree vegetation

B57 East Caucasian alpine grasslands (*Festuca varia* subsp. *woronowii, Nardus stricta, Carex tristis, Kobresia capilliformis*) with *Alchemilla elisabethae* and small herb communities (*Sibbaldia parviflora, Campanula biebersteiniana*), alternating with shrub, dwarf shrub (*Rhododendron caucasicum, Dryas caucasica*), rock and scree vegetation

B58 North Lesser Caucasian alpine grasslands (*Festuca varia* subsp. *woronowii, Nardus stricta, Carex tristis, Bellardiochloa polychroa, Scabiosa caucasica*) with *Agrostis lazica, Bromopsis variegata* and small herb communities (*Carum caucasicum, Campanula tridentata*) with *Gentiana pontica*, alternating with shrub (*Rhododendron caucasicum*), rock and scree vegetation

C42 Southwest Caucasian krummholz and open woodlands (*Betula litwinowii, Fagus orientalis, Acer trautvetteri*) with *Betula megrelica, Quercus pontica*, scrub (*Rhododendron caucasicum*) with Rhamnus imeretina (on carbonate rocks with *Coryllus colchica*), tall-forb communities (*Heracleum ponticum*) with Delphinium pyramidatum (on carbonate rocks with *Heracleum aconitifolium, Ligusticum arafoe*) and grasslands (*Calamagrostis arundinacea, Betonica macrantha*, on carbonate rocks with *Woronowia speciosa, Carex pontica*)

C43 Northeast Caucasian krummholz and open woodlands (*Betula litwinowii, Acer trautvetteri, partly Pinus kochiana*) with *Betula raddeana*, scrub (*Rhododendron caucasicum, Juniperus communis* subsp. *hemisphaerica*), tall-forb communities (*Heracleum sosnowskyi, Delphinium flexuosum*) and grasslands (*Festuca woronowii, Bromopsis variegata*), alternating with dry grasslands (*Festuca ovina, Carex humilis*)

C44 Southeast and Lesser Caucasian krummholz and open woodlands (*Betula litwinowii, Acer trautvetteri, Quercus macranthera*), scrub (*Rhododendron caucasicum*), tall-forb communities (*Heracleum sosnowskyi, Aconitum orientale*) and grasslands (*Festuca varia* subsp. *woronowii, Calamagrostis arundinacea, Geranium ibericum*)

C45 West Lesser Caucasian krummholz and open woodlands (*Betula litwinowii, Fagus orientalis, Acer trautvetteri*) with *Quercus pontica, Betula medwedewii*, scrub (*Rhododendron caucasicum*) with *Rhododendron ungernii*, tall-forb communities (*Ligusticum alatum, Milium schmidtianum*) with *Heracleum cyclocarpum, H. mantegazzianum* and grasslands (*Agrostis planifolia, Geranium platypetalum*) with *Euphorbia oblongifolia, Astragalus bachmarensis*)

C46 East Lesser Caucasian krummholz and open woodlands (*Quercus macranthera, Acer trautvetteri, Betula litwinowii*), scrub (*Juniperus communis* subsp. *hemisphaerica*, J. sabina), grasslands (*Festuca varia* subsp. *woronowii, Bromopsis variegata, Anemonastrum fasciculatum*) with *Trifolium bordzilowsky*, partly tall-forb communities (*Milium effusum, Gagea orientalis*) alternating with dry grasslands (*Festuca ovina, Carex humilis*) with true steppes (*Festuca valesiaca, Stipa tirsa, S. pulcherrima*), partly with thorn-cushion mountain vegetation (*Astragalus aureus*)

D32 West Caucasian fir, spruce-fir and beech-fir forests (*Abies nordmanniana, Picea orientalis, Fagus orientalis*) with evergreen understorey *Rhododendron ponticum, Prunus laurocerasus, Ilex colchica*), often alternating with Oriental beech forests (*Fagus orientalis*)

D33 Caucasian fir, spruce-fir and beech-fir forests (*Abies nordmanniana, Picea orientalis, Fagus orientalis*) without evergreen understorey, partly alternating with Oriental beech forests (*Fagus orientalis*)

D64 Caucasian pine forests (*Pinus kochiana*), partly alternating with birch forests (*Betula litwinowii*, *B. raddeana*) and spruce forests (*Picea orientalis*)

F163 East Euxinian-Caucasian Oriental beech forests (*Fagus orientalis*) partly with *Picea orientalis*, mostly with evergreen understorey (*Prunus laurocerasus*, *Rhododendron ponticum*, *Daphne pontica*) with *Hedera colchica*, *Ilex colchica*, *Ruscus colchicus*

F164 Caucasian Oriental beech forests (*Fagus orientalis*) with *Carpinus C. caucasica* partly with *Picea orientalis*, without evergreen understorey partly alternating with oak-hornbeam forests (*Carpinus betulus*, *Quercus iberica*)

F165 East Caucasian submontane to montane hornbeam-maple-Oriental beech forests (*Fagus sylvatica subsp. orientalis*, *Acer velutinum*, *Carpinus caucasica*) with *Hedera pastuchowii* in combination with hornbeam-chestnut-oak forests (*Quercus iberica*, *Castanea sativa*, *Carpinus caucasica*)

F169 East Euxinian oak and hornbeam-oak forests (*Quercus iberica*, *Carpinus orientalis*, *C. caucasica*), alternating with hornbeam-chestnut-Oriental beech forests (*Carpinus caucasica*, *Fagus orientalis*, *Castanea sativa*) with evergreen understorey

F170 Transcaucasian oak forests (*Quercus iberica*), hornbeam-oak forests (*Quercus iberica*, *Carpinus caucasica*) and Oriental hornbeam-oak forests (*Quercus iberica*, *Carpinus orientalis*), with *Sorbus torminalis*, partly in combination with shibliak communities (scrub)

H1 Colchic lowland to submontane mixed oak forests (*Quercus imeretina*, *Q. hartwissiana*, *Zelkova carpinifolia*, *Carpinus caucasica*, *Castanea sativa*, *Fagus orientalis*) with evergreen understorey species (*Rhododendron ponticum*, *Prunus laurocerasus*), alternating with oak and hornbeam-oak forests (*Quercus iberica*, *Carpinus betulus*) in the submontane belt

K24 West Caucasian *Pinus pityusa*-forests with *Carpinus orientalis*, *Cistus crecitus*, *Ruscus aculeatus*

K33 Transcaucasian colline-montane juniper open woodlands (*Juniperus polycarpos*, *J. foetidissima*), partly in combination with *Pistacia mutica* – open woodlands

M4 Transcaucasian altimontane herb-grass- and meadow steppes (*Stipa tirsa*, *S. pulcherrima*, *Festuca ovina*, *Carex humilis*, *Poa densa*, *Bromopsis variegata*, *Onobrychis altissima*, *O. transcaucasica*, *Aster ibericus*, *Scutellaria orientalis*)

M11 Pre- and Transcaucasian Stipa-steppes (*Stipa tirsa*, *S. pulcherrima*, *S. pontica*) with Onobrychis transcaucasica, Botriochloa ischaemum – steppes with *Onobrychis kachetica*, *Medicago coerulea*, *Polygala transcaucasica*, alternating with tomillares (*Thymus tiflisiensis*, *Scutellaria orientalis*) and thorn-cushion communities (*Astragalus denudatus*, *A. microcephalus*)

N6 East Transcaucasian thorn-cushion vegetation (*Astragalus caucasicus*, *A. microcephalus*, *Acantholimon lepturoides*. *A. fominii*) and tomillares (*Salvia garedji*, *Thymus tiflisiensis*)

O7 East Transcaucasian wormwood deserts (*Artemisia lerchiana*) with ephemeroids (*Poa bulbosa*, *Catabrosella humilis*)

08 East Transcaucasian *Salsola nodulosa* and *Salsola ericoides* – deserts with ephemeroids (*Poa bulbosa*, *Catabrosella humilis*), with *Artemisia lerchiana*

S26 Colchic herb-rich tall sedge fens with *Carex acuta*, *Cladium mariscus*, *Ludwigia palustris* in combination with Sphagnum-mires (*Sphagnum austinii*, *S. papillosum*) with *Rhododendron luteum*, *Osmunda regalis*, *Rhynchospora caucasica*

T3 Colchic alder carrs (*Alnus barbata*) in combination with alluvial forests (*Alnus barbata*, *Fraxinus excelsior*, *Pterocarya pterocarpa*), tall reed vegetation (*Phragmites australis*, *Typha latifolia*) and sedge swamps (*Carex* spp.)

U22 Transcaucasicum hardwood alluvial forests (*Quercus pedunculiflora*, *Ulmus minor*) in combination with poplar and willow alluvial forests (*Populus x canescens*, *P. nigra*, *Salix excelsa*) as well as *Tamarix ramosissima*-scrub

Source: The map is given according to Bohn et al. (2003), where the Caucasus part was prepared by D Bedoshvili, A Dolukhanov, M Ivanishvili, G Nakhutsrishvili, N Zazanashvili.

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Contents

Environmental Conditions

1

Georgia occupies an interesting geobotanical position as a part of Caucasia – the region which links Europe with Asia. The country is characterized by rather contrasting natural conditions which account for the extremely high degree of divergence of plant communities within this comparatively small area. The landscape of the country includes different types of desert and semi-desert vegetation mainly in the eastern parts of Georgia, luxuriant Colchic forests of moist, almost subtropical climate in the west, and high-mountain plant communities in the north and in the south (See "Map of the Natural Vegetation of Georgia" 2003).

The complex orographic structure of Georgia and its geographical position account for the geographical and ecological isolation of certain plant communities, which has resulted in a high ratio of local endemism (particularly endemics of the Greater Caucasus Range and of the Colchis) as well as a variety of species of different phytochorological groups, like Iberian and Anterior-Asian group, etc.

1.1 Orography

Geologically, the territory of Georgia belongs to the Alpine System of Eurasia. Its geological and geomorphological structure reveals a great genetic diversity, as a result of tectonic, volcanic, petrological, gravitational, erosional and other processes.

Structurally, the area can be divided into the following major landforms:

1. The range of the Greater Caucasus (Kavkasioni);
2. The Georgian Intermontane Area (between the Greater and the Lesser Caucasus);
3. The Mountain System of the Lesser Caucasus (Meskheti-Trialetian Range), including the South Georgian Volcanic Upland.

Georgia comprises the southern side of the middle part of the Kavkasioni as well as the north-western parts of the Transcaucasian Depression, the Lesser Caucasus, i.e. the South Caucasian Upland.

Altitudes in Georgia vary considerably from the sea level (at the Black Sea) to some of the highest peaks of the Greater Caucasus, reaching 4,695 m (mt. Ushba),

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5,068 m (in the Shkhara massif), and 5,047 m a.s.l. (mt. Kazbegi, Kazbek). From the geological point of view, this area consists, mainly, of Meso- to Cenozoic deposits. Ancient Precambrian and Paleozoic formations are poorly represented and of secondary importance (Gerasimov 1966).

1.2 Climate

The climate is one of extremes. It is possible to distinguish several climatic zones from the humid, almost subtropical climate to the climate of permanent snows and glaciers. Such a considerable range of climatic conditions is caused both by the orographic structure and the presence of the Black Sea and the Caspian Sea. The Black Sea and high mountain ranges of the Greater Caucasus are the most important orographic factors determining the climate of Georgia by preventing the invasion of cold air masses from the north. The climate of the country has been formed by the air masses blowing from sea, as well as by the latitudinal position between southern Russia and the Inner-Anatolian mountains system.

The highest mean annual temperature amounts to 15 °C (Sukhumi in Abkhazeti, on the Black Sea coast). The warmest winter (5–7 °C, in January) is in Colchis (West Georgia, on the Black Sea coast).

Annual precipitations in Georgia range from over 4,500 to 400 mm or less. Increase of altitude e.g. in Svaneti (north-western Georgia) and Javakheti (south-western Georgia) is paralleled by reduction of precipitation, while in other districts (Kazbegi region, Kakheti, etc.) the amount of rainfall increases with elevation. The highest amounts of precipitation occur at the following altitudes: from 300–500 m to 3,500 m a.s.l. in Western Georgia, and from 1,200 to 3,500 m in the eastern part of the country.

The climatic conditions of several districts of Georgia are demonstrated diagrammatically (Fig. 1.1). Notwithstanding the short distance between these districts (60 km between Batumi and Bakhmaro, 380 km between Batumi and Shiraki, 155 km between Shiraki and Kazbegi), their climatic conditions are noticeably different.

1.3 Soils

There is a great diversity of soil types in Georgia. The following soil provinces can be distinguished:

1. The soil province of Western Georgia;
2. The soil province of Eastern Georgia;
3. The soil province of Southern Georgia.

The main types of soil are allocated in accordance with the altitudinal zones. In the Western Georgia soil province (between the Black Sea and Likhi mts.) it is possible to distinguish the bog and podzolic soil zone in the lowlands, the krasnozem and zheltozem zone in the hilly piedmonts, the zone of mountain-forest and the mountain-meadow soils.

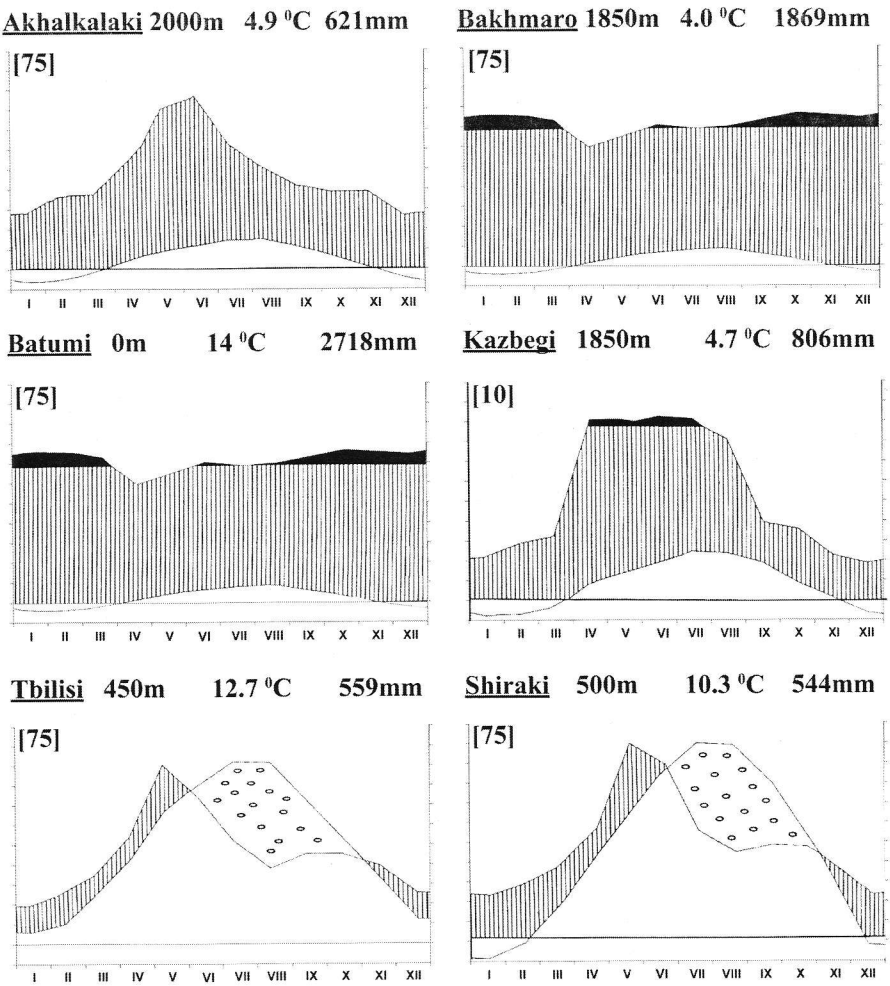

Fig. 1.1 Climadiagrams of several regions of Georgia

The soil province of Eastern Georgia comprises the plains, piedmonts and mountain massifs, situated eastwards from Likhi mountain range. Chestnut soils, chernozems, brown humic-sulphates, saline soils of steppes and semi-deserts, as well as intermediate forest-steppe and mountain-meadow soils occur in this province.

The Southern Georgia soil province includes Javakheti, Tsalka-Dmanisi and Erusheti uplands, the hollow of Akhaltsikhe, etc. A considerable part of this area is covered both with the mountain chernozems (which are formed at altitudes from 1,200 to 2,200 m) and meadow chernozem-like soils. In highlands they are replaced by mountain-meadow soils. Besides, the alluvial soils, redzinas, brown as well as the meadow-brown soils occur here, with the predominance of brown forest type of soil in the mountain forest belt (Urushadze 1987).

History of the Flora and the Vegetation 2

The history of the flora and, especially, the vegetation of Georgia is very complicated and, despite the intensive paleobotanical investigations of the recent past, still needs to be studied.

The earliest records of fossil flora stem from the Paleozoic. Species of *Lepidodendron* (large trees reaching a height of nearly 40 m), *Sigillaria* (high plants with erect stems and characteristic rhizophore system: stigmarias), *Asterocalamites* were determined from the Lower and Middle Carboniferous deposition of the Khrami crystalline massif (South Georgia). Cordaitales – a group with anatomical structures (tracheids, well-developed pith) very similar to that of conifers (Shatilova et al. 2011) – are known from the same period.

In the Early Jurassic, almost the entire territory of Georgia was covered by sea, except for Khrami, Loki and Dzirula ancient massifs.

The climate of this period was warm-temperate. Water temperature in the sea reached 23–24 °C, but in Late Toarcian it decreased considerably (7–15 °C). Calamitales are of special interest with the only species *Neocalamites hoerensis* present in the early Jurassic depositions. The above mentioned period was characterized by the wide-spread occurrence of equisetoids, which were restricted to marshes as it is nowadays (Svanidze 1972).

Pteridophytes were represented by 25 taxa. Microfossils found belong mainly to the genus *Cladophlebis* (Osmundaceae). At the same time *Ginkgo* was represented by two species: *G. mziae* (specific to Georgia) and *G. huttonii*. The species *Sphlenobaiera spectabilis* and *Phoenicopsis angustifolia* also belong to Ginkgoaceae. In the early Jurassic, a considerable group was formed by Bennettitales – the ancestors of the flowering plants (according to the viewpoint of several botanists). *Eucommiidites troedssonii* (gymnosperms pollen) and many other plants were present in the same period too.

In the Bajocian (Middle Jurassic) the entire territory of Georgia was under the sea; by the end of it, first the eastern part and afterwards (in Bithonian) the whole territory has emerged. The appearance of freshwater basins was characteristic to that period, as well as the process of peat accumulation (Kakhadze 1947). The Early Jurassic flora is much richer than that of the Early Jurassic. Today nearly 175 plant

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species are known from the Middle Jurassic. 55 of them are ferns (*Coniopteris*, Cyatheaceae, Osmundaceae, Gleicheniaceae) and representatives of *Paracycas* (Cycadaceae), *Ptilophyllum* (Benettitaceae), etc. The climate of the Middle Jurassic was probably tropical; representatives of Cycadales and Ginkgoales dominated the woodlands (Svanidze 1972).

In the Late Jurassic the territory of Georgia was covered by sea, except the Svaneti Elevation, as well as the southern parts.

The occurrence of remnants of the new species *Angiopteris iberica* (Marattiaceae) in the Late Jurassic fossiliferous deposits is of great importance. It underlies the opinion that these archaic living ferns disappeared from the floras of the Northern Hemisphere after the Middle Jurassic.

According to Vakhrameev (cited by Shatilova et al. 2011), the Late Jurassic paleofloristic province of the Caucasus was a part of the Euro-Sinian region.

The flora of the above-mentioned province could be characterized by the presence of occasional equisetoids, a few ferns, Ginkgoales, the absence of *Czekanowskia* and the predominance of Cycadales, Bennettitales as well as *Pachypteris, Sagenopteris, Pagiophyllum.*

2.1 The Tertiary

In the **Paleocene** and **Eocene** a long island was formed on the territory of the Caucasus as a basis for further development of mountain range. In the Eocene, the dominant position was occupied by the Angiosperms, representatives of evergreen Fagaceae and *Myrica*.

At the same time the process of migration of the Boreal cold-resistant plants, which had begun previously in the Cretaceous, resumed at the end of the Eocene.

At the Eocene/Oligocene boundary, the folded structure of the Alpine system started to form in the Mediterranean orogenetic band. It comprised the (geosynclinal) regions of the Southern Slope of the Greater Caucasus range and Ajara-Trialeti, the main part of today's Georgia. Uplift caused a change in the climatic conditions; the latter determined the character of the vegetation: the number of conifers increased and warm-temperate plants became more numerous (Tumajanov 1955; Shatilova et al. 2011).

During the **Oligocene**, the Caucasus was a small island surrounded by a vast basin with scattered islands, where the tropical flora of the Poltava type (palms, laurels, etc.) was well developed. In West Georgia (near the town Chiatura), in the Oligocene deposits remnants of conifers (species of *Pinus*) were found, indicating the penetration of northern taxa into the Caucasus.

The Oligocene plant world was greatly influenced by the Arcto-Tertiary or Turgay flora, formed in the eastern and northern parts of modern Asia. Representatives of this flora, especially pines, penetrated into the Caucasus. Many botanists consider that migration of the Turgay elements became more intensive after the Turgay Strait had become dry by the end of the Oligocene.

According to Grossheim (1948), Turgay migrants began to change and gave rise to the ancient mesophytic forest flora, called Mediterranean-Turgay flora by this author.

During the **Miocene** the Caucasian island started to expand. Fossil assemblages from different parts of Georgia, especially from Western Georgia (Guria), confirm the subtropical nature of the Miocene flora with the predominance of evergreen woody plants, accompanied by the deciduous *Castanea sativa*, as well as by conifers of northern origin *(Pinus neptuni)*.

The following plants have been known since the Early Miocene deposites of Kartli (East Georgia): *Myrica neriifolia* (=*M. lignitum*), *Laurophyllum primigenium*, species of *Apocynophyllum*. Of the 46 taxa two are pteridophytes and five gymnosperms. The dominant position is occupied by Angiosperms, namely *Comptonia acutiloba*, *Myrica neriifolia* (=*M. lignitum*), etc. The greatest part of the Early Miocene flora, studied by macrofossils, is represented by Angiosperms. Among them the predominance of Myricaceae, Juglandaceae and Lauraceae should be noted, whose role has somewhat increased since the Paleogene. Evergreen Fagaceae, Lauraceae and other thermophilous plants, contributing to the formation of moist-subtropical forests in the Paleogene, adapted to the reduced humidity of the Early Miocene.

In the Middle Miocene plants of warm and dry climate participated in sclerophyllous formations. *Myrica* species covered river banks. Sclerophyllous plants were represented by the species of *Myrtus, Callistemophyllum, Acacia, Quercus (Q. drymeja)*. Several species of Lauraceae, *Sapindus, Smilax* and *Magnolia* formed moist-subtropical forests.

It is possible to suggest that an altitudinal differentiation of vegetation already existed in the Middle Miocene. Coastal and low mountainous areas were covered by subtropical forests with high numbers of Sterculiaceae, Araliaceae, Lauraceae, evergreen Fagaceae, arborescent ferns, *Hymenophyllum*, etc. The next altitudinal belt was occupied by mesophilous deciduous forests of *Platanus, Comptonia, Juglans, Pterocarya*, etc. Cold-resistant plants occurred even higher; mention should be made of species of *Betula, Fagus, Acer, Tilia, Ulmus*, accompanied by *Cathaya, Keteleeria*, etc. (Shatilova et al. 2011).

During the Sarmatian (Upper Miocene), the Caucasian island, known in the literature as Jephethis, was situated close to Iranian and Central Asian land. This encouraged the immigration of xerophilous elements into the Caucasus. It is suggested that the forestless formations of xerophytic plant communities were widely distributed during the Early Miocene. According to Grossheim (1946), *Pelargonium endlicherianum*, the fern *Ceterach*, etc., are relicts of the ancient xerophytic flora of this period.

The close position of Jephethis to the Iranian mainland, separated as a cape, caused a division of the mesophytic Mediterranean-Turgay flora into western and eastern parts. In the west, the Colchic flora began to form, while the Hyrcanian elements evolved in the eastern part. Both were of mesophytic nature. The analysis of the contemporary vegetation makes many botanists suggest the existence of a third xerophytic flora.

Based on the fossils, it is possible to build up a picture of the Sarmatian flora: evergreen *Magnolia dianae,* species of Lauraceae (*Cinnamomum, Laurophyllum primigenium, Laurophyllum pseudoprinceps,* etc.), as well as the representatives of the Mediteranean-Turgay and Turgay deciduous flora, such as *Salix, Pyrus, Carpinus, Juglans, Ulmus,* etc. Conifers (*Pinus saturi, Sequoia langsdorfii*) and xerophytic species of *Myrica* have been known from the same age.

Kolakovsky and Shakril (1976) pointed out that the richest Sarmatian floras occurred in Abkhazeti (Colchis). They were closely related to the southern subtropical and tropical floras (*Melastomites* sp., *Mastixia microphylla, Ventilago* etc.). The Sarmatian floras of Abkhazeti are very similar to Oligocene-Miocene European floras. These floras indicate the wide distribution of subtropical evergreen plants, mainly Lauraceae, such as *Ocotea, Persea, Aniba,* and many others, and the deciduous arborescent plants of warm climate which have survived until now only in Central and South America, partly in the Mediterranean area and in South-Eastern Asia. These forests show a great similarity to the vegetation, confined to mountainous Japan during the Miocene-Pliocene. It is suggested that this vegetation is similar to that now found in the mountain systems of South-Eastern Asia, Himalaya and China, where relic forests of *Ulmus, Fagus, Quercus, Abies* and *Cryptomeria* were well represented.

The Tertiary-relic species of Colchic type, such as species of *Buxus, Pterocarya,* etc. and the hemixerophytic Mediterranean plants *Arbutus, Celtis, Smilax, Thelycrania (Cornus), Quercus*, have been found in the Sarmatian deposites of Abkhazeti.

The territory of East Georgia, where steppes and semi-deserts are distributed now, is considered to have been covered with both sclerophyllous and moist-subtropical forests.

In South Georgia the shrubs of subtropical and temperate climate dominated by Lauraceae, were represented by narrow-leaved xerophytic elements.

In the Meotian, after the regression of the Mediterranean Sea, the strait separating the Jepethis from the southern mainland disappeared and the Caucasus became a peninsula. The formation of the main folded systems reached the final point, and the vegetational belts were formed. The Meotian macrofossils included *Cryptomeria japonica*, species of Lauraceae, *Salix coriacea, Myrica neriifolia* (=*M. lignitum*). Ferns, especially *Dicksonia*, were represented by a large number of species. Palynological data attest to the fact that the following genera of conifers were present: *Abies, Picea, Tsuga* (five species), *Cedrus,* as well as *Carya, "Castanopsis furcinervis"* (leaf remnants of *Quercus),* representatives of Hamamelidaceae or Altingiaceae *(Liquidambar*, etc.).

According to the composition of the fossiliferous deposits, in this period, coniferous and broad-leaved forests *(Taxodium, Cryptomeria, Magnolia,* species of Hamamelidaceae, etc.) with the species of *Quercus, Carya, Fagus, Castanea* and *Platanus* began to prevail.

Relatively dry habitats were occupied by the following hemixerophytes: *Quercus drymeja, Celtis punica, Pistacia miocenica, Sophora europaea, Pyracantha coccinea.* At the same time the following plants began to crop up (present-day

members of the Georgian flora): *Rhododendron caucasicum, Fagus orientalis, Zelkova crenata (=Z. carpinifolia).* During the period of Pontian Sea expansion, the Caucasus and Transcaucasia became consolidated.

The fossil flora of Goderdzi pass (South-Western Georgia) was distinguished by the features characteristic of Sarmatian flora; in Pontic it had already been a relic flora.

Taking into account fossil deposits of this region, mesophytic flora obviously prevailed here. Representatives of Annonaceae, Hamamelidaceae and Lauraceae are known from this period which was characterized by a warm maritime climate. Ferns, distributed in Georgia during the Pontian, can now be found only in the tropics.

During the Pontian, gymnosperms were widespread. Nowadays, they occur in montane forests of tropical and subtropical countries. In the beginning of the Pliocene, *Pinus pithyusa* was widely distributed.

Investigations carried out by Kolakovsky (1964) in Kodori (Abkhazeti) point to the existence of lowland and low-mountain forests with *Myrica lignitum, Salix varians, Alnus subcordata.* Coastal lowlands were covered with forests of *Quercus kodorica* and *Carya denticulata*, while the riversides were occupied by species of *Liquidambar, Taxodium, Nyssa, Tectocarya, Ocotea,* evergreen Fagaceae like *Pasania, Castanopsis*, etc., which were characteristic of the subtropical forests of the Pontian. In the lower montane zone, considerable areas were populated by Laurisilva with tree ferns *(Cyathea, Alsophila, Dicksonia).*

In the lower montane zone sclerophyllous formations were distributed with the elements of maquis. Pines occupied rocky habitats.

Kolakovsky (1974) pointed out that an important change in the flora of the warm-temperate climate took place during the Pontian. The mid-mountain belt was populated by *Fagus, Castanea, Acer, Tilia* species. The presence of conifers – *Ginkgo, Keteleeria* – , ferns like *Polypodium*, etc., lianas like *Vitis betulifolia, Parthenocissus quinquefolia* becomes fairly possible.

Dark coniferous forests (with species of *Abies, Tsuga, Picea, Cedrus,* etc.) occupied relatively higher altitudes.

On the territory of West Georgia a great number of angiosperms has vanished since the Pontian.

In Cimmeridian (Middle Pliocene), the shrinking of the Tethys led to the exposure of new land, fit for colonization by xerophytic vegetation, such as semi-desert vegetation, shibliak, light forests, maquis, etc., so characteristic of the Mediterranean. Meanwhile, taxa of Araliaceae, as well as ferns were well represented. The dominant position was occupied by species of *Pteris* and *Polypodium.* According to Kolakovsky and Shakril (1978), forests of warm-temperate climate began to prevail in Cimmeridian; they were composed by the species of moist monsoon climate, now peculiar of the mountains of Eastern Asia and xerophytes, ecologically similar to the plants of xerophytic forests of the Mediterranean. Above the warm-temperate forest zone hardwood and coniferous forests grew.

During the Kuyalnitskian-Akchagylian (Upper Pliocene), a large part of East Georgia lay under the sea. The Greater and Lesser Caucasus were connected by a land bridge to the Near East (Asia Anterior–South-West Asia) in the south. The

most striking feature of the fossil floras of this period is the absence of Poltava floral elements and evergreen plants. The following plants are known from this period: species of *Populus, Ostrya, Fagus, Zelkova, Tilia, Pyrus, Ligustrum, Salix, Prunus, Acer, Quercus, Pterocarya*, together with representatives of *Carex* and *Phragmites*. All these plants are members of the present-day flora of Georgia, though they have changed their habitats. For example, remains of *Fagus orientalis* and *Ostrya carpinifolia* have been found in Akchagyl deposits of the Shiraki steppe. Due to increasing aridity, these trees are no longer there.

According to Grossheim (1948) the Akchagylian flora by its nature is closely connected with that of the Quaternary. To quote his words: "The period between Sarmatian and Akchagylian was the turning-point in the floristic history of the Caucasus; the tropical flora had been replaced by that of temperate climate" (Grossheim 1948: 171). Broad-leaved forests were replaced by conifers, namely species of *Picea, Abies,* and *Tsuga*. In general, during the late Pliocene, the role of polydominant forest vegetation was reduced and, instead, the formation of communities with one or two dominant species was stimulated. These changes in the vegetational cover were probably provoked by the intensification of cold at the end of the Miocene and in the Pliocene.

The existence of a dry and hot climate between the cold periods encouraged the enrichment of the Caucasian flora with xerophytes. In Akchagylian times, many recent Mediterranean plants penetrated into the present area from the west.

Therefore, in the **Pliocene**, the piedmonts and the lower montane zone were clothed by subtropical forest vegetation. Forests of warm-temperate climate were situated higher up. Many species known from this period are still members of the modern forest flora. In the beginning of the Pliocene, within the territory of West Georgia and adjacent areas (e.g., Turkey), a Colchic refuge was formed for many relics of mesophytic forest flora. This was a direct result of the warm and humid climate of this territory. The Colchic refuge was of great importance as one of the most stable "shelters" for relic species during the Late Pliocene and especially in the Pleistocene, including the Ice Ages. Many species, which continue to exist in the Colchis died out many millions of years ago on the territory of West Eurasia. Members of the Colchic flora are such relics and/or neoendemics as *Betula medwedewii, Quercus pontica, Rhamnus imeretina, Hedera colchica, Pterocarya pterocarpa, Laurocerasus officinalis, Arctostaphylos caucasica, Rhododendron ponticum, Rh. ungernii* and *Rh. smirnowii*. At present, their relatives with a similar autecology have mainly survived in the mountains exposed to the summer monsoon in eastern and south-eastern Asia, in the Appalachians of North America, etc.; for instance, the genus *Epigaea* is represented now by just three species, one of which is distributed in Japan, the second in North America and the last in Ajara (Georgia) and Lazistan (N. Turkey).

2.2 The Quaternary

Thus, having surveyed the Tertiary history of the Georgian flora, we now come to the **Pleistocene**. During the Pleistocene, most of the thermophilic elements vanished from the flora of Georgia. The role of cold-resistant plants considerably increased, at the same time vertical shifts of the vegetational belts appeared, especially during the glacial periods.

Another event, which might have occurred during the Pleistocene is the development of boreal elements. Though the flora of Georgia was strongly influenced by the neighbouring floristic centres of Eastern Mediterranean and SW. Asia (Near East, Anterior Asia), the process of autochthonous development provided a large number of endemic species, including present-day local endemics.

In the Early Chaudian (the **Early Pleistocene**) deposits the highest taxonomical diversity and an abundance of Taxodiaceae and Cupressaceae could be observed; these families were manifested by the following genera: "*Athrotaxis*" (=extinct Taxodiacea), *Cryptomeria, Metasequoia, Sequoia, Sequoiadendron, Taxodium; Cupressus, Chamaecyparis, Libocedrus, Juniperus.*

The dominant position was occupied by *Abies nordmanniana, Tsuga diversifolia*, whereas *Abies alba, Cedrus* aff. *libani* and some others had vanished.

In the Chaudian flora, Juglandaceae were represented by several genera: *Pterocarya, Carya, Juglans*, etc. Pollen of *Zelkova* was found in the Chaudian of Georgia.

In the Chaudian, beech forests were as widely spread as the representatives of the genus *Tilia*. Chaudian pollen assemblages contained pollen of plants very closely allied to evergreen shrub *Fatsia japonica*, which is now confined to the forests of Japan, as well as that of *Symplocos* which is largely distributed in tropical areas. Obviously, the prevailing types of vegetation in the Early Chaudian were monodominant forests of *Tsuga, Abies*, representatives of Taxodiaceae and *Fagus*. Lower montane and piedmont belts were covered by the forests of *Juglans, Carpinus, Quercus, Zelkova*, and also by subtropical species of *Magnolia, Fatsia, Symplocos*, etc.

At the same time, many ferns and spore-bearing plants vanished together with the most thermophilic elements. In the Late Chaudian, almost all the plants of subtropical and temperate climate died out. The representatives of *Tsuga* and Taxodiaceae lost their leading position in forests.

The second half of the Chaudian was characterized by the predominance of *Picea-Abies* communities in almost all the mountain belts, whereas the lower parts were covered with broad-leaved forests (Tchotchieva 1965).

Middle Pleistocene. Many ferns, which can be found in the contemporary flora of Georgia, have been known since the old Euxine period. During that period, taxonomic diversity of *Abies*, *Cedrus*, *Picea* and *Tsuga* was reduced. Members of the Taxodiaceae family prevailed in forest communities. Within the territory of Georgia, only 6 out of 66 taxa, known from the Old Euxine became extinct.

In West Georgia, the old Euxinian depositions are covered by that of Uzunlar (Shatilova et al. 2011). The Uzunlarian ferns were represented by those species which continue to exist in present-day Georgia. A dominant position in forests was

occupied by widely spread *Abies nordmanniana, Picea orientalis* with an admixture of *Cedrus deodara, Tsuga diversifolia* and *T. shatilova. The* Taxodiaceae family was represented by *Taxodium, Cryptomeria, Sequoia,* and *Glyptostrobus.* Hardwood forests consisted of the following species which have become members of the modern Georgian flora: *Fagus orientalis, Castanea sativa, Carpinus caucasica,* etc. It should be mentioned here that mesophytic species were substituted in East Georgia by those of *Pinus, Carpinus, Quercus,* etc.

In the **Late Pleistocene**, there were still a number of species which have since disappeared from the territory of Georgia. Mention should be made of the representatives of Taxodiaceae, of *Cedrus deodara* and *Carya aquatica.* Except for *Carya*, angiosperms were represented by species which are characteristic of modern Georgian flora.

Man introduced considerable changes into the vegetational cover of Georgia. Forest destruction, development of secondary meadows, cultivated lands are the results of human activities. At the same time, the Georgian flora was enriched both by cultivars and adventive weeds.

On the Altitudinal Differentiation of the Vegetation of Georgia

3

Considerable difference between the climates of East and West Georgia determined the diversity of their vegetal landscapes, as well as the structure of altitudinal zonation (See "Map of the Natural Vegetation of Georgia" 2003).

The absence of arid and semi-arid vegetation belts is characteristic of West Georgia. It accounts for a more simple profile of altitudinal zonation here, which is represented by five main belts: forests (0–1,900 m a.s.l.), subalpine (1,900–2,500 m), alpine (2,500–3,100 m), subnival (3,100–3,600 m), nival (above 3,600 m).

In East Georgia, the altitudinal zonation is more complicated. One can observe here six main belts: deserts, dry steppes and arid light forests (150–600 m), forests (600–1,900 m), subalpine (1,900–2,500 m), alpine (2,500–3,000 m), subnival (3,000–3,500 m), and nival (above 3,500 m). The borderline between the semi–arid belt and that of forests varies considerably due to the climatic conditions and the exposure of slopes. Within the forest and subalpine belts of South-Georgian Upland there are small areas occupied by semi-arid ecosystems with the prevalence of mountain-steppe vegetation.

Thus, almost all the altitudinal belts, characteristic of the Nemoral Zone of Northern Hemisphere, are represented in Georgia.

We would like to illustrate the differentiation of vegetation by vertical gradients in two strongly different parts of Georgia: the East and the West (the profiles are shown in Figs. 3.1 and 3.2a). In East Georgia, the vegetation of deserts, semi-deserts and hemi-xerophytic light forests is replaced by *Quercus iberica* forests with the admixture of *Carpinus orientalis* on southern slopes. At an altitude of 1,300 m, there is a narrow zone of *Carpinus-Fagus* forest, which is substituted higher by that of *Quercus macranthera*. Comparatively dry meadows can be observed at an altitude of 2,250–2,300 m.

On the northern slopes, the situation is different. Above the hemi-xerophytic vegetation belt, there is a subzone of *Carpinus-Quercus* forest, higher up substituted by beech forest which occupies large areas from 600 to 1,800 m. *Acer trautvetteri* is a common associate of the dominant *Fagus orientalis*. Still higher up, these communities are replaced by a birch forest with tall herbaceous vegetation confined to glades. Above the timberline, all slopes are covered with *Rhododendron*

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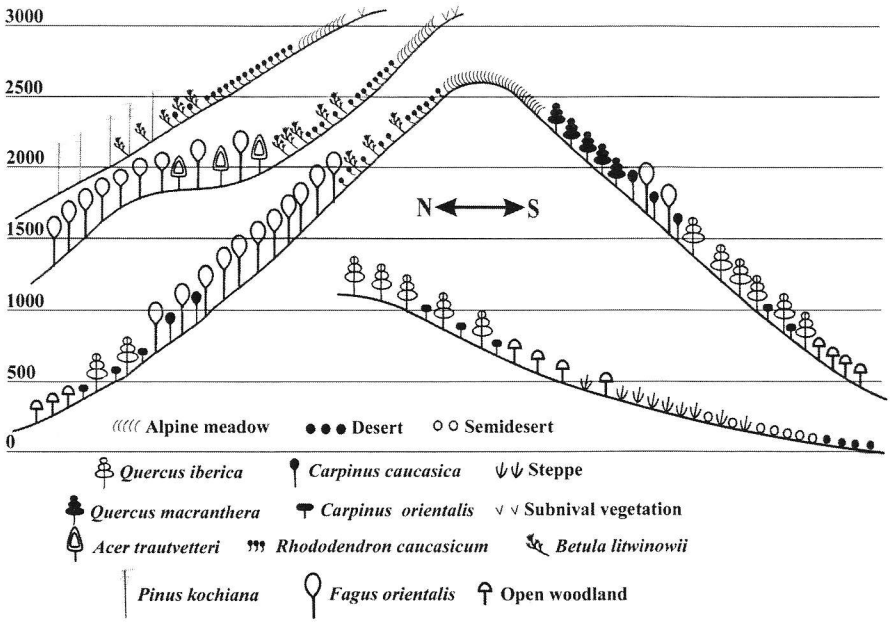

Fig. 3.1 The regularities of vertical distribution of vegetation in the East Georgia

scrub ("dekiani" is a native name of these communities, suggested for scientific use by Ketskhoveli) and carpet-like alpine meadows.

Beech forest is substituted by that of *Pinus kochiana* under more continental conditions (e.g. in Tusheti).

Unlike East Georgia, in the western part of the country, namely in South Colchis, forests begin to dominate from the sea level. The most characteristic species of these lowland forests are *Pterocarya pterocarpa, Alnus barbata, Pinus pityusa* (in north-western Colchis), etc. Southern slopes are populated by the forests of *Quercus iberica, Q. hartwissiana* and *Carpinus caucasica.* At 600–700 m, beech forests appear with admixture of *Abies nordmanniana;* spruce-fir forests (*Picea orientalis* and *Abies nordmanniana*) occur at 1,200–1,300 m. Near the timberline, *Picea orientalis* forests and that of *Betula medwediewii* are distributed. The alpine meadows occur higher up.

The oak forests are substituted by that of *Carpinus caucasica* and *Castanea sativa* on the northern slopes. Beech forests, situated higher up, form crook-stem woods at the extreme altitudinal range of their distribution.

The second variant of altitudinal zonation in West Georgia (Svaneti) is also of particular interest. *Alnus barbata* forests populate the lowland area (Fig. 3.2b). The leading species of these communities is often accompanied by *Carpinus caucasica* and *Matteuccia struthiopteris.* At 600 m, beech forests begin to dominate; their undergrowth is represented by *Rhododendron ponticum.* At about 1,300 m a.s.l., beech is usually accompanied by fir (*Abies nordmanniana*). The subalpine belt is

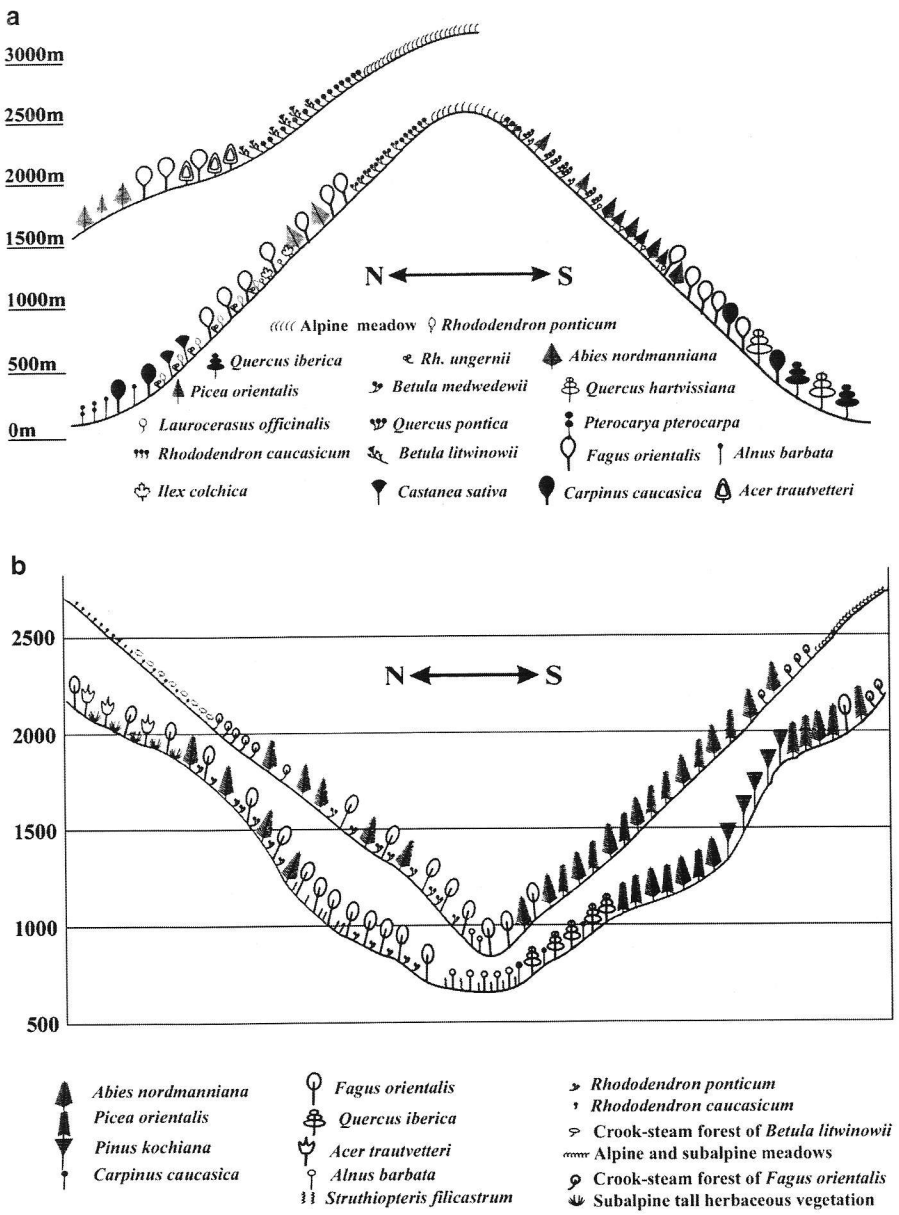

Fig. 3.2 The regularities of vertical distribution of vegetation in Colchis (*a* – Ajara, *b* – Svaneti)

characterized by the dominating position of *Acer trautvetteri* growing together with *Fagus orientalis*. The herbaceous vegetation is also characteristic of this belt. It should be noted that in several gorges the lower part of the subalpine belt is

occupied by crook-stem beech forests, while the upper part is dominated by decumbent beech forests and *Rhododendron* scrub. On the southern slopes, lowland forests are substituted by those of oak, which are replaced by fir-spruce forests at about 1,000 m; rocky habitats are covered by pine forests. Near the upper limit of forests, crook-stem beech forests occur. At 1,850–2,400 m, subalpine and alpine meadows appear (Gulisashvili 1964).

On the Classification and Nomenclature of Plant Communities

4

I find it necessary to make the reader acquainted with the principles and methods of plant community classification, used to recognize syntaxa given in this book.

In the former USSR, the main approach to the classification of vegetation units was based on the dominant species. The "Formation" (higher syntaxon) was defined by the dominant species in the layer. According to the former Soviet authors, an association includes plant communities with the same set of dominants in each layer. Communities with the same dominant species in the main layer and ecological-biomorphologically similar co-dominants or dominants of secondary layers belong to groups of associations.

The above-mentioned principle of classification is known also as an ecological and physiognomical approach. The names of the syntaxa used in this book are constructed according to the below instructions.

The names of associations may be constructed in two ways. The simplest way is the following: the association is named after the names of the dominant and the subdominant species of different layers connected by a hyphen (−) (e.g., "Festuca varia-Carex meinshauseniana"). While regarding the association which consists of two dominant species in one layer, the names of such species are connected by the sign "+" (e.g., "Bromopsis variegata + Agrostis planifolia-Trifolium ambiguum").

As mentioned above, there is also a second way of construction of association names. Concerning the association where the dominant species is accompanied by the subdominant one, the name of the association should be constructed in the following way: the genus name of the dominant taxon is used with the suffix "-etum", followed by the genus name of the subdominant with the suffix "-osum" or "-etosum" (e.g. "Festucetum caricosum"). When the association consists of two dominants in the main layer, its name is constructed as follows: "Brometo-Agrostietum trifoliosum".

Names of groups of associations are constructed as follows: the genus name of the dominant taxa of the main layer has the suffix "-eta" followed by the genus name of the co-dominant or the dominant taxa of the secondary layer with the suffix "-osa" ("Fageta rhododendrosa"). In the case of formation the genus name of the dominant is used with the suffix "eta". An example is "Fageta". If we are dealing

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with the formation dominated by two or more taxa, a compound noun is constructed using the same suffix "eta" ("Pineto-Piceeta", "Festuceta-Bothriochloeta").

Syntaxa with names constructed by the suffixes "-etum" or "-eta" mentioned in the present book, in many cases bear no syntaxonomic meaning.

The Vegetation of Semi-Deserts, Steppes and Arid Open Woodlands

5

Semi-desert and steppe vegetation, as well as arid light forests, are confined mainly to the intermountain part of East Georgia, namely to the Inner Kartli and the Lower Kartli Lowlands and the Iori plateau.

These parts of Georgia enjoy a dry subtropical climate marked by cold winter and dry hot summer. The climate of Iori plateau is more continental. The mean annual temperature varies in intermountain area of East Georgia between 9 °C and 13 °C, the mean monthly temperature in January between 1 °C and 4 °C, in August between 20 °C and 25 °C. Extreme minimum temperature falls to −20 °C to 25 °C, and extreme maximum temperature amounts to 35–40 °C. Annual precipitations range from 350 to 600 mm (Fig. 1.1).

In the area under review, the common soil types are chestnut soils, chernozems and grey–brown soils.

5.1 Vegetation of Semi-Deserts

Though typical desert vegetation is not represented in Georgia, it is remarkable that some fragments of it, namely solontchaks, can be found in the eastern part of the country (from 100 (90) to 820 m in places to 1,200–1,400 m a.s.l. in Lower Kartli Lowland, Tbilisi environs, Inner Kartli, Meskheti) (Lachashvili and Khachidze 2010). Grossheim (1948) points out that these fragments are predecessors of the semi-desert vegetation. The following species belonging to these communities should be mentioned:

Salsola ericoides	*Petrosimonia brachiata*
S. dendroides	*Nitraria schoberi*
S. nodulosa	*Atriplex cana*
Gamanthus pilosus	*Artemisia lerchiana*
Suaeda microphylla	

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Dominants of this desert vegetation are florogenetically connected with the Turan-Anterior Asian and Eastern Mediterranean floristical centres (Sakhokia 1958).

According to Lachashvili and Khachidze (2010) the following desert plant communities are present there: *Artemisia lerchiana – Salsola ericoides, Artemisia lerchiana – Salsola nodulosa, Artemisia lerchiana – Botriochloa ischaemum, Artemisia lerchiana – Reaumuria altrnifolia, Salsola nodulosa – Gamanthus pilosus – Petrosimonia brachiata, Salsola dendroides – Anabasis aphylla, Salsola dendroides – Tamarix ramosissima, Salsola dendroides – Kalidium caspicum, Gamanthus pilosus – Eremopyrum orientale – E. distans, Salsola dendroides – Artemisia lerchiana – Alhagi pseudalhagi* (Fig. 5.1a). The following ephemeral species are well represented in the above listed plant communities:

Anthemis candidissima	*Torularia torulosa*
Bombycilaena erecta	*Herniaria hirsuta*
Calendula gracilis	*Astragalus asterias*
Garhadiolus angulosus	*Vicia cinerea*
Koelpinia linearis	*Adonis aestivalis*
Arnebia decumbens	*Veronica amoena*
Alyssum desertorum	*Valerianella rimosa*
Lepidium vesicarium	*Bromus japonicus*
Leptaleum filifolium	*Rostraria glabriflora*
Sterigmostemum incanum	*Rochelia disperma*

From the ephemeroids the following are noteworthy:

Poa bulbosa var. *vivipara*
Allium rubellum
Catabrosella humilis

The following ephemeral plants grow on strongly saline soils:

Aizoon hispanicum	*Parapholis incurva*
Eremopyrum ssp.	*Spergularia diandra*
Psylliostachys spicata	

The presence of ephemers and ephemeroids are characteristic for desert vegetation, including: *Poa bulbosa* var. *vivipara, Catabrosella humilis, Bromus japonicus, Eremopyrum orientale, Alyssum desertorum, Helianthemum salicifolium,* etc. The above mentioned plants should not be regarded as xerophytes because their short duration is connected with the vernal and autumnal vegetation period. In general, these plants are mostly of mesic nature.

The above communities are characterized by the presence of species of bryophytes (*Tortulla sp., Barbula sp.*), lichens (*Toninia caeruleonigricans, Collema tenax, etc.*) and algae (species of *Nostoc*, etc.).

Fragments of desert communities dominated by *Nitraria schoberi* occur in Inner Kartli, Kiziki and Meskheti. Some variants of erosional-desert vegetation are to be

Fig. 5.1 (continued)

found in the Iori plateau (Kiziki, East Georgia) (Khintibidze 1990; Lachashvili and Khachidze 2010). Vegetation is very poor on eroded slopes with washed soil cover and is manifested by individual species of *Stipa szovitsiana, Artemisia lerchiana,* etc. The following species with flowering period in spring can be mentioned: *Tulipa eichleri, Allium rubellum,* etc.

Stipa szovitsiana, Astragalus xiphidium, Salsola nodulosa grow on the loess-like loams near the ravines and river beds, where the soil cover is absolutely denuded.

From the viewpoint of many botanists wormwood *(Artemisia lerchiana)* communities belong to desert vegetation, while others regard them as semi-desert communities. They play a considerable part in landscape formation in East Georgia, namely on the Iori plateau (Eldari) and in Lower Kartli.

Fig. 5.1 (**a**) Artemisietum lerchianae, Chachuna, East Georgia (Photo O. Abdaladze), (**b**) Stipeta (*S. pennata*) in Tbilisi vicinity, East Georgia (Photo Sh. Sikharulidze), (**c**) *Iris iberica*, East Georgia (Photo M. Akhalkatsi)

The climate of Iori plateau is dry subtropical, the dominating soil types here are grey–brown soils and chernozems.

Artemisia lerchiana is the dominant of wormwood communities. Besides the monodominant wormwood communities, Artemisieto-Salsoletum dendroides can also be found in this area.

Wormwood/salt-wort communities are restricted to the clay-brown soils and chernozems. Floristically, these communities are very poor (they include just 26 species, according to Sokhadze and Sokhadze 1991). The dominating position is occupied by annuals and ephemers (*Eremopyrum orientale, Lepidium vesicarium,* etc.); in communities with the preponderance of *Artemisia lerchiana, Stizolophus coronopifolius* is a common species.

Artemisia – Caragana grandiflora communities occur in poorly populated alluvial and grey–brown soils. According to Sokhadze and Sokhadze (1991), only 24–26 species participate in the formation of these communities. The following

species, peculiar for this type of vegetation should be mentioned: *Salsola ericoides, S. dendroides,* etc. The commonest ephemers are *Lepidium vesicarium.* Examples of rare species are *Spergularia diandra, Calendula persica, Tetradiclis tenella, Aizoon hispanicum.*

Wormwood communities are widely distributed in Eldari, occupying both flat and hilly locations on salty greyish–brown soils. Floristically, these communities are also poor (about 30 species). Wormwood *(Artemisia lerchiana)* is characterized by wide ecological amplitude. The coenotypes of these communities are mainly ephemers, especially *Poa bulbosa* var. *vivipara, Bromus japonicus, Rostraria glabriflora, Medicago minima, Torularia contortuplicata.*

Bothriochloa-wormwood communities require special attention. They are the commonest vegetation type in Eldari lowland, they occur on grey–brown, skeleton and stony soils. The coverage is about 30–50 %. Wormwood communities in this area are replaced by *Bothriochloa*, due to the reduction of salt in washed out soils and increasing degression of pastures. The flora of these communities comprises over 30 species with predominance of ephemers and ephemeroids. Examples are *Poa bulbosa* var. *vivipara, Trachynia distachya, Lappula echinata, Medicago minima, Velezia rigida,* etc. (Sokhadze and Sokhadze 1991; Lachashvili and Khachidze 2010).

Pure variants of wormwood communities are widely distributed in the Caucasus, namely Georgia, but there also occur intermediate types, mixed diffusely or completely with the variants of saltwort deserts.

Wormwood communities with ephemers are found in Gardabani district (Lower Kartli). They are dominated by the following ephemers: *Adonis aestivalis, Astragalus brachyceras, Koelpinia linearis, Medicago minima, Queria hispanica,* etc.

Communities with less desert-like nature are developed under more humid conditions and on rich soils (Iaghluja, Lower Kartli). The leading species of wormwood in these communities is accompanied by the following perennials: *Salsola dendroides, Bothriochloa ischaemum, Limonium meyeri,* etc. The geophytes are represented by the species of *Iris, Gagea, Tulipa.*

Wormwood is not used for fodder, but its ephemeral synusium is important as natural grassland.

5.2 Steppe Vegetation

Steppe vegetation largely contributes to the formation of foothill landscapes (300–700 m a.s.l.) of East Georgia. It belongs to the second altitudinal belt above the desert vegetation zone.

Present-day expansion of steppes is due to the anthropogenic influence on forests, arid light forests and even on secondary shrubwoods (Sakhokia 1958).

The dominant species of steppe vegetation – *Bothriochloa ischaemum* – is a representative of the subtropical-tropical genus *Bothriochloa* widely distributed in both hemispheres. Many Georgian botanists are inclined to attribute *Bothriochloa* to semi-steppes. Typologically, they are very diverse.

The following plant communities of Bothriochloeta are distinguished by Lachashvili and Khachidze (2009):

Botriochloa ischaemum-Glycyrrhiza glabra
Botriochloa ischaemum-Festuca valesiaca
Botriochloa ischaemum-Stipa lessingiana
Botriochloa ischaemum-Paliurus spina-christi
Botriochloa ischaemum-Artemisia lerchiana
Botriochloa ischaemum-Onobrychis kachetica
Botriochloa ischaemum-with ephemerals

Some of them are described below.

Bothriochloa communities mainly occur on chestnut soils and are rare on chernozems.

Glycyrrhizieto-Bothriochloeta. These communities are mostly distributed in areas of 500–600 m a.s.l. The above communities are rather rich floristically, e.g. in an area of 100 m^2 the average number of species is 65 (Sokhadze and Sokhadze 1991). Besides the edificator and sub-edificator, the following species should be mentioned: *Koeleria cristata, Phleum phleoides, Medicago caerulea, Bromus japonicus, Trifolium campestre, Vicia angustifolia, Crucianella angustifolia, Arabidopsis thaliana, Androsace elongata.*

Bothriochloa communities with xerophytes are restricted to slopes of eastern and western exposures; they occur mainly on thin chestnut soils (600–700 m a.s.l.). The following herbs play an essential part in these communities: *Teucrium nuchense, Galium verum, Picris strigosa, Scorzonera biebersteinii, Inula britannica, Aster ibericus, Stachys atherocalyx*. Among *Fabaceae* species a mention should be made of *Onobrychis kachetica, O. cyri, Astragalus brachycarpus*. An example of the commonest species is *Festuca sulcata*.

The early vernal vegetation is dominated by the following ephemers and ephemeroids: *Arabidopsis thaliana, Anthemis candidissima, Crocus adamii, Merendera trigyna, Muscari caucasicum, Gagea commutata*. These communities include endemics of Georgia and Caucasus, such as: *Polygala transcaucasica, Aster ibericus, Cephalaria media, Thymus tiflisiensis*, etc. The following species are to be found in Glycyrrhizieto-Bothriochloetum varioherbosum:

Bothriochloa ischaemum	*Bromus japonicus*
Dactylis glomerata	*Festuca sulcata*
Koeleria gracilis	*Melica transsilvanica*
Phleum phleoides	*Stipa capillata*
Trisetum pratense	*Carex bordzilowskii*
Glycyrrhiza glabra	*Medicago caerulea*
Trifolium arvense	*Achillea nobilis*
T. campestre	*Allium pseudoflavum*
Vicia angustifollia	*Crepis marschallii*
V. hirsuta	*Bellevalia wilhelmsii*

(continued)

V. tetrasperma	*Crucianella angustifolia*
Daucus carota	*Dianthus inamoenus*
Echinops sphaerocephalus	*Eryngium campestre*
Falcaria vulgaris	*Galium verum*
Gladiolus italicus	*Hieracium pilosella*
Linum corymbulosum	*Muscari caucasicum*
Ornithogalum ponticum	*Picris strigosa*
Polygala transcaucasica	*Potentilla recta*
Tragopogon graminifolium	*Rumex tuberosa*
T. tuberosus	*Turritis (Arabis) glabra*
Phlomis pungens	*Xeranthemum squarrosum*
Ph. tuberosa	*Ranunculus illyricus*

Bothriochloeta ephemerosa. These communities are confined to stony southern slopes of chestnut soils. The following ephemers can be mentioned: *Alyssum campestre, Callipeltis cucullaria, Sideritis montana, Meniocus linifolius, Ziziphora capitata, Trigonella spicata*. Examples of geophytes are *Juno caucasica, Allium atroviolaceum*, etc.

The less xeric variants of *Bothriochloa* communities are Bothriochloeta pratoherbosa, which populate depressions and dells with chernozem-like soils. Besides the leading species of *Bothriochloa*, the following plants can be found: *Agropyron cristatum, A. pectinatum, Elytrigia (Agropyron) repens* var. *glaucescens*.

Festuceta-Bothriochloeta. These communities are restricted to the slopes of hills. Associate of *Bothriochloa* is *Festuca sulcata*. Fragments of these communities have remained only in Lower Kartli (Iaghluja).

Stipa-Bothriochloa coenoses are also found in the above-mentioned area; they are restricted to the northern mountain slopes, ridges, stony habitats. Most of the soils in these areas are grey–brown, thin, skeleton and saltless.

The leading species of these communities are accompanied by shrubs like *Paliurus spina-christi, Rhamnus pallasii*, etc. Herbs are represented by steppe elements. Examples are *Stipa* spp., *Onobrychis* spp., *Phleum phleoides*. The number of ephemers is relatively small.

Alyssum campestre
A. desertorum
Androsace elongata
Arabidopsis thaliana
Callipeltis cucularia
Echinaria capitata
Helianthemum lasiocarpum
H. salicifolium
Kohlrauschia prolifera
Linum corymbulosum
L. nodiflorum

(continued)

Pterotheca sancta
Salvia viridis
Scabiosa micrantha
Trigonella spicata
Vicia angustifolia
Ziziphora capitata

The following list of species mentions members of Bothriochloeta varioherbosum:

Stipa lessingiana	*Tragopogon pusillus*	*Thalictrum minus*
S. capillata	*Campanula hohenackeri*	*Filipendula vulgaris*
S. pulcherrima	*Crucianella angustifolia*	*Potentilla recta*
Phleum phleoides	*Trigonella spicata*	*Veronica multifida*
Medicago coerulea	*Bromus japonicus*	*Bilacunaria caspia*
Inula germanica	*Bothriochloa ischaemum*	*Seseli grandivittatum*
Galium verum	*Festuca sulcata*	*Cephalaria media*
Leontodon asperrimum	*Koeleria macrantha*	*Xeranthemum squarrosum*
Thymus tiflisiensis	*Cleistogenes bulgarica*	*Linum corymbulosum*
Picris strigosa	*Astragalus brachycarpus*	*L. nodiflorum*
Pimpinella aromatica	*Stachys iberica*	

According to Sakhokia (1958), *Bothriochloa* communities and their edificators are closely related to savannas florogenetically, rhythmologically and by the character of soding; though it is not the case, when the above communities get compared with the typical *Stipa* steppes. This opinion is confirmed by the fact that *Bothriochloa* communities are combined with arid light forests, which, in the past, had zonal significance in the Caucasus. The same author has proposed the term "savannoid vegetation" for the complex of *Bothriochloa* communities and arid light forests.

Typical steppe vegetation is illustrated by the comunities of *Stipa* (*S. tirsa, S. pennata, S. lessingiana, S. pulcherrima, S. capillata*) (Fig. 5.1b). Participation of the above communities in landscape formation is insignificant. *Stipa* communities are of secondary origin. They favour the areas which have previously been occupied by mesic mountain forests, shrubwoods and herbaceous vegetation. Very often in the ridges of mountain ranges, *Bothriochloa* steppe becomes replaced by the communities of *Stipa*, including more xeric species, such as *S. pulcherrima, S. lessingiana, S. pontica,* and *S. capillata*. These communities are characterized by the presence of the following xeric species: *Seseli grandivittatum, Teucrium nuchense, T. polium, Thymus tiflisiensis, Scorzonera eriosperma, Psephellus carthalinicus, Carex bordzilowskii, Tulipa biebersteinii, Tulipa eichleri, Iris iberica* (Fig. 5.1c).

Stipa tirsa and its communities are confined to thick chernozems with a higher amount of moisture in soil. *S. tirsa* is known as a soding plant. Communities of *S. tirsa* are to be found in Gareji steppe. The associates of the dominant *Stipa* are *Glycyrrhiza glabra, Medicago coerulea, Koeleria cristata,* etc.

Drier habitats are occupied by *Stipa joannis* and *S. lessingiana*. The plant communities, which the above-mentioned species enter as the leading ones, do not include *Stipa tirsa*. Chernozems and grey–brown soils, mostly calcareous, are typical for this area. Slightly destroyed communities, restricted to the northern slopes, are characterized by the presence of *Dianthus subulosus*, and *Pyrethrum corymbosum*; among other associates is *Bothriochloa ischaemum*. Under the influence of intense animal grazing *Bothriochloa* becomes a co-edificator of the species of *Stipa*, whereas the community gets floristically poorer.

In rocky areas, such as the vicinity of David Garedja Monastery, the communities are dominated by the species of *Bothriochloa, Festuca*, etc., while *Stipa lessingiana* is not found here (Sokhadze and Sokhadze 1991).

Festuceto valesiaca-Botriochloeta is one of the widespread plant communities with the following set of perennials:

Teucrium polium
Thymus coriifolius
Achillea biebersteinii
Eryngium campestre
Euphorbia seguieriana
Falcaria vulgaris
Onobrychis cyri
Koeleria cristata
Medicago coerulea
Poterium polygamum
Scorzonera biebersteinii
Stachys atherocalyx
Of the annuals the following are noteworthy:
Alyssum alyssoides
Helianthemum lasiocarpum
H. salicifolium
Kohlrauschia prolifera
Scabiosa micrantha
Trifolium campestre

Forb steppes (with *Stipa tirsa*) are rather rich in species; besides the representatives of *Stipa*, various forbs participate in the composition of this community.

It should be pointed out, that mountain steppes are peculiar only for South Georgia. Their altitudinal distribution ranges from 1,800 to 2,500 m a.s.l. They occur on leached chernozems. Mountain steppes are represented by that of *Festuca-Stipa* and meadow steppes.

Festuceto (*F. sulcata*)-Stipeta (*S. capillata*). These are developed on flat grounds and southern slopes. They are characterized by high presence of *Dactylis glomerata, Stipa tirsa, Phleum phleoides, Trifolium alpestre, Medicago dzhavakhetica*, etc. Geophytes are exemplified by species of *Gagea, Muscari*, etc.

Meadow steppes are situated on the northern slopes. *Stipa tirsa* is an edificator of these communities. Tall dense herbage with a large amount of species is typical for this variant of steppes; a mention should be made of the high-presence of dicots (*Betonica macrantha, Aster ibericus*, etc.). Besides, geophytes are well developed here.

Difference of opinion has arisen upon the issue of a possible connexion between the northern plain steppes (South Russia) and those of the Transcaucasian mountains.

Grossheim (1948) indicates that South Russian and Transcaucasian mountain steppes, being separated from each other nowadays, have formed an integral steppe

massif in the past. The formation of the above massif was connected to the process of peneplainization of the Caucasus during more or less xerothermic periods. The uplifting of the Greater Caucasus caused separation of the steppe massif from its northern part; it has been preserved under more or less favourable conditions in mountainous areas. Probably, the above mentioned events account for the great floristic and phytocoenotic similarity between the steppes of South Russia and those of the Transcaucasian highlands.

5.3 Arid Open Woodlands

Xeric (arid) open woodlands favour foothills and plains under the dry climatic conditions of East Georgia among steppe and desert vegetation. These communities are provided by the xerophytic woody plants on the background of drought-resistant grass cover (Fig. 5.2a–c).

The arboreal components of open woodlands or "light forests" (a term used by some Caucasian botanists) never make dense stands. In Georgia, these forests are well developed on the territory between the Alazani and the Iori river valleys, near the place Vashlovani, which holds an area of 5,000 ha.

The following types of communities of open woodland can be distinguished: pistache-woodlands, juniper open woodlands, communities dominated by species of *Pyrus* and *Celtis*.

***Pistacia mutica* communities** occur on cinnamon-coloured and chernozem-like soils. These plant communities belong to West-Iranian type. The undergrowth of these open woodlands is represented by the following shrubs: *Paliurus spina-christi, Rhamnus pallasii, Cotinus coggygria, Cerasus incana, Lonicera iberica, Pyrus salicifolia Colutea orientalis, Caragana grandiflora, Ephedra procera, Punica granatum, Rhus coriaria*. The ground layer is made of xerophytic species; it is rather rich in species (*Bothriochloa ischaemum, Festuca sulcata*, species of *Stipa*, etc.). One can distinguish within the pistache-woodland the communities with: *Bothriochloa, Stipa*.

It is also possible to find pure *Pistacia*-woodlands and the pistache-woodlands with the admixture of single trees and shrubs (*Ulmus minor, Celtis caucasica, Pyrus salicifolia*, etc.).

Open woodland-communities of *Pyrus salicifolia, P. georgica*, etc. are formed by the xeric species of pear, which join the sections *Xeropyrenia* and *Argyromalon*.

From the coenotic point of view, the commonest types of the above-mentioned woodlands are the communities with shrubs and steppe elements (Ketskhoveli 1960).

Juniperus open woodlands occur on, steep northern slopes of low ranges of southeast part of Iori plateau and the environs of Mtskheta. In both places, the dominants of forests are *Juniperus foetidissima* (East-Mediterranean species) and *J. polycarpos* (species of Asia Anterior–South-West Asia). In southeast part of Iori plateau they are accompanied by *Pistacia mutica*.

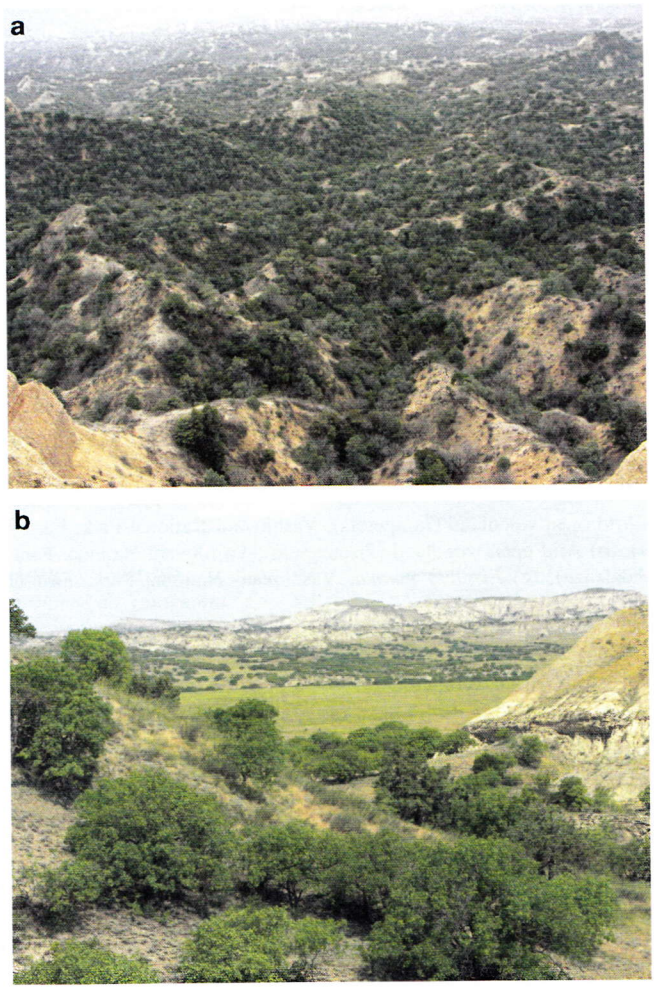

Fig. 5.2 (continued)

Besides the above mentioned species, the East-Mediterranean *J. rufescens* and the Caucasian *J. oblonga* occur in *Juniperus* open woodlands as undergrowth.

Open woodlands occur on grey–cinnamon soils. The climate in the area of their distribution varies between dry subtropical and warm temperate with not very hot summer season. The amount of annual precipitation is 400 mm in Vashlovani. In the environs of Mtskheta, the climate is warmer temperate with hot summer and the amount of precipitation equals to 600–700 mm p. a. (Sakhokia 1958; Lachashvili et al. 2004).

Open woodlands of *Celtis caucasica* hold rather small areas. Usually, solitary plants or groups of plants of *Celtis caucasica* can be found.

Natural vegetation in the east is preserved in the Vashlovani Reserve in Kiziki, at the far southeastern end of Georgia, near the Azerbaijani border (Lachashvili et al. 2004).

Fig. 5.2 (**a**) Arid open woodland (Junipereta), Vashlovani National Park, East Georgia (Photo O. Abdaladze), (**b**) Arid open woodland (Pistacietum), Vashlovani National Park, East Georgia (Photo O. Abdaladze), (**c**) *Pistacia mutica*, Vashlovani National Park, East Georgia (Photo O. Abdaladze)

The most interesting steppe type is meadow-steppe, the relatively tall (to 1 m), forb-rich grassland type of the Ukraine (Walter 1974; Walter and Breckle 1986) equivalent to the true (i.e. tall-grass) prairie of North America. A sample from a small but representative patch of meadow-steppe in the Vashlovani Reserve is shown by the relevé in Table 5.1. *Botriochloa* (=*Andropogon*) *ischaemum* is the dominant in this stand, as in most of the Georgian steppes. The relevé also, however, includes *Stipa pulcherrima*, one of several "feather grass" species characteristic of Ukrainian to Middle Asian steppes, as well as some *Paliurus spina-christi* shrubs, as characteristic of "savannoid" steppe areas extending westward at least as far as Tbilisi. Meadow-steppe undergoes a continuing metamorphosis during the growing season, mainly from April to June, as early forbs are replaced by taller forbs and grasses, which finally yield to the dominants of the early-summer aspect (Walter 1968; Walter and Breckle 1986). As with other meadow-steppe areas, grasses make up most of the biomass. Only 12 of the 63 species in the relevé, however, are grasses.

The other important landscape type from the east is the *Pistacia-Juniperus* "arid woodland" (Fig. 5.2a–c), an open woodland on foothills and plains in the driest parts of eastern Georgia. Areas of arid woodland are also well represented in the Vashlovani Reserve, a sample of which is shown in Table 5.2. The main structural elements are three *Juniperus* species plus deciduous *Pistacia mutica*, all of which grow in the form of small trees. Spiny *Paliurus spina-christi* is a major understorey shrub, as are *Jasminum fruticans*, *Berberis iberica*, *Rhamnus pallasii*, *Cerasus* spp., and younger individuals of the juniper species. On flatter terrain these woodlands generally constitute parklands of wooded patches (20–50 % of the area) embedded within a grassy Stipetum matrix. This grassy matrix is not completely represented

Table 5.1 Meadow-Steppe in Easternmost Georgia (relevé G-16) (Box et al. 2000) (Location: Vashlovani Nature Reserve, border with Pantishara Gorge (31 May 1999))

S	2.0 m	5 %	550 m, aspect: 5–10° to N	
H	0.8 m	85 %	10 × 30 m	
S	1.1	*Paliurus spina-christi*	1.1	*Cotinus coggygria*
	+.2	*Asparagus officinalis*	+	*Convolvulus cantabrica*
	+	*Lonicera iberica*		
H	4.4	*Botriochloa ischaemum*	2.2	*Koeleria cristata*
	2.2	*Stipa pulcherrima*	1.1	*Stipa capillata*
	1.1	*Cleistogenes bulgarica*	1.1	*Festuca valesiaca*
	1.1	*Bromus japonicus*	1.1	*Phleum phleoides*
	+	*Hordeum crinitum*	+	*Aegilops triuncialis*
	+	*Trachynia distachya*	(+.2)	*Dactylis glomerata*
Legumes				
	2.2	*Medicago coerulea*	2.2	*Onobrychis kachetica*
	1.1	*Medicago minima*	+	*Astragalus brachycarpus*
	+	*Onobrychis cyri*		
Forbs				
	2.2	*Thymus tiflisiensis*	2.2	*Galium verum*
	1.2	*Filipendula hexapetala*	1.1	*Poterium* (=*Sanguisorba*) *polygamum*
	1.1	*Achillea nobilis*	1.1	*Potentilla recta*
	1.1	*Scorzonera biebersteinii*	1.1	*Tragopogon tuberosus*
	1.1	*Jurinea blanda*	1.1	*Plantago lanceolata*
	1.1	*Helianthemum salicifolium*	1.1	*Hypericum perforatum*
	1.1	*Teucrium nuchense*	1.1	*Euphorbia seguieriana*
	1.1	*Teucrium polium*	1.1	*Inula germanica*
	1.1	*Scutellaria orientalis*	1.1	*Polygala transcaucasica*
	1.1	*Onosma armeniaca*	+	*Crepis marschalii*
	+	*Hippomarathrum crispum*	+	*Veronica multifida*
	+	*Orobanche* cf. *speciosa*	+	*Seseli grandivittatum*
	+	*Picris strigosa*	+	*Dianthus inamoenus*
	+	*Bellevalia wilhelmsii*	+	*Malabaila dasyantha*
	+	*Sisymbrium loeselii*	+	*Linum austriacum*
	+	*Echinops sphaerocephalus*	+	*Muscari caucasicum*
	+	*Crinitaria villosa*	+	*Ziziphora serpyllacea*
	+	*Thalictrum minus*	+	*Reseda lutea*
	+	*Cuscuta speciosa*	+	*Phlomis pungens*
	+	*Eryngium campesetre*	+	*Falcaria vulgaris*

Total number of species: 63

in the relevé (Table 5.2) but was similar to the meadow-steppe site of Table 5.1, dominated, as elsewhere in the region, by *Botriochloa ischaemum*, along with *Stipa* species such as *S. pulcherrima*. Although arid woodland may be considered a west Iranian community, dry woodlands and related shrublands are important throughout much of especially eastern Georgia, extending westward to Tbilisi and on through

Table 5.2 Arid open Woodland Mosaic in easternmost Georgia (relevé G-17) (Box et al. 2000) (Location: Vashlovani Nature Reserve, down road from field station (31 May 1999))

T	8 m	20 %	550 m, slope: 5–20°, rollintg	
S	3 m	30 %		
H	0.5 m	50 %	50 × 50 m	
T	2.4	*Pistacia mutica*	2.4	*Juniperus foetidissima*
	1.1	*Juniperus polycarpos*	1.1	*Juniperus rufescens*
S	3.4	*Paliurus spina-christi*	3.4	*Jasminum fruticans*
	2.4	*Juniperus foetidissima*	1.1	*Juniperus polycarpos*
	1.1	*Juniperus rufescens*	1.1	*Rhamnus pallasii*
	1.1	*Berberis iberica*	1.1	*Cerasus incana*
	1.1	*Cerasus microcarpa*	1.1	*Lonicera iberica*
H	3.4	*Achnatherum bromoides*	1.1	*Achillea nobilis*
	1.1	*Polygala transcaucasica*	1.1	*Dactylis glomerata*
	1.1	*Potentilla recta*	1.1	*Cleistogenes bulgarica*
	1.1	*Falcaria vulgaris*	1.1	*Dictamnus caucasicus*
	1.1	*Campanula hohenackeri*	1.1	*Rumex tuberosus*
	1.1	*Koeleria cristata*	+	*Helianthemum salicifolium*
	+		+	*Silene boissieri*

Total number of species: 25

central Georgia along the Mtkvari river valley to the Meskheti region near the Turkish border.

5.4 Hemixerophytic Shrubwoods

Interzonal drought-resistant shrubwoods occur almost in every mountain belt, except in the highlands. In the geobotanical literature, different terms are applied to this type of vegetation, for example, "thorny shrubwoods", "shibliak", etc.

Many authors consider the above communities to be analogues of the Mediterranean shibliak. This affinity confirmed by Rikli (1943) – an eminent specialist of the Mediterranean vegetation.

About 25–30 species contribute to the formation of shibliak. Mediterranean shibliak consists of the following species: *Paliurus spina-christi, Berberis vulgaris, Cotinus coggygria, Punica granatum, Carpinus orientalis.*

Communities dominated by the Christ's thorn are the commonest ones in the area under review; a mention should be made of Paliureto Bothriochloeta, Spiraeeto (*Spiraea hypericifolia* (Fig. 5.3))-Paliureta, as well as hemixerophytic mixed-shrub shibliak with *Paliurus spina-christi, Crataegus orientalis, Lonicera iberica,* etc. (Figs. 5.4 and 5.5a).

On dry slopes endemic *Amygdalus georgica* can rarely be found (Fig. 5.5b).

The most xeric variant of shibliak is confined to mother rocks and stony slopes *(Rhamnus pallasii, Caragana grandiflora, Atraphaxis spinosa, Ephedra procera).*

Fig. 5.3 *Spiraea hypericifolia*, East Georgia (Photo N. Lachashvili)

Fig. 5.4 Bothriochloeto-Paliuretum, Tbilisi surroundings (Photo O. Abdaladze)

Within this certain area, the following types of shibliak are distinguished: (1) primary shibliak, restricted to slopes and steppe dell belts, as well as to beams, ancient detrital cones and naked rock outcrops; (2) the remnants of open woodland dominated by *Pyrus* and *Pistacia*; (3) secondary shibliak, the origin of which is connected with the destruction of forests (Sakhokia 1958).

In East Georgia, phrygana, the second type of hemixerophytic Mediterranean vegetation, is distributed. In order to outline the difference between the Caucasian phrygana and the true Mediterranean one, many botanists define it by the term

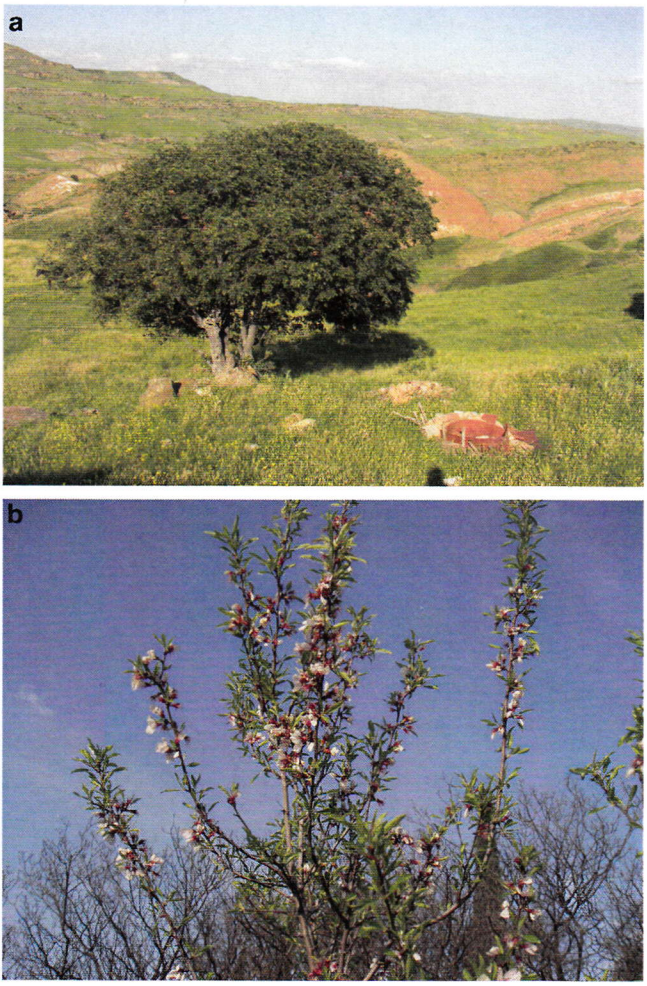

Fig. 5.5 (**a**) *Celtis caucasica* (Photo O. Abdaladze), (**b**) *Amygdalus georgica*, Tbilisi surroundings (Photo O. Abdaladze)

"phryganoid vegetation". In the classical sense, phrygana is regarded as a community dominated by dwarf xeromorphic shrubs and subshrubs with an admixture of therophytes and geophytes. In the Caucasus and particularly in Georgia, it is often found among the xeric mountain vegetation.

Among its coenological formations, the following should be noted:

1. Tragacanthic communities, dominated by thorny *Astragalus* species *(A. denudatus, A. microcephalus,* etc.*)* and species of *Acantholimon (A. lepturoides,* etc.);
2. Tomillares, low shrub and semi-shrub formations with the dominance of *Thymus tiflisiensis* (and other species of *Thymus*), *Teucrium spp., Salvia garedji,* etc.

Forest Vegetation of Georgia

6

Forest is the prevailing type of vegetation in Georgia. The forest area makes up 36.7 % of the country's total land area.

During the Holocene, when the climatic conditions were similar to those of nowadays, the entire territory of Georgia was occupied by forests. Very surprisingly, today beech *(Fagus orientalis)* occupies a dominating position, namely 51 % of the total forest area. The following species are further dominants of Georgian forests: *Abies nordmanniana* (8.5 % of the forest-coverage). *Quercus iberica* and other representatives of *Quercus* (10.5 %), *Picea orientalis* (6.3 %), *Pinus kochiana* (3.6 %), *Alnus barbata* (3 %), *Castanea sativa* (2.1 %), *Betula litwinowi* and other *Betula* species (*c.* 2 %). Negligible areas are covered by *Carpinus caucasica, Tilia begoniifolia, Acer platanoides, A. trautvetteri, Fraxinus excelsior,* etc. (Dolukhanov 2010).

As it was pointed out, the plains and mountain slopes in West Georgia are covered by forests from the very sea level, while lowland woods in the eastern part of the country are peculiar for riversides. At the same time, the plateau of Javakheti Upland (South Georgia) is absolutely devoid of forests.

Located in the eastern (E, SE, NE) portion of the Black Sea catchment basin the climate of the Colchis region is characterized as having moderately warm (24–25 °C summers and cool 4–6 °C winters) with abundant annual precipitation (1,800–2,200 mm up to 4,500 mm).

Colchic forests like Hyrcan forests (Azerbaijan, Iran) are the most important relicts of the Arcto-Tertiary forests in western Eurasia with many relict and endemic plants and rare fauna. Many plants have ancient boreal affinities from the Tertiary period, and, therefore, the Caucasus is considered a global "hot spot" – an area where numerous species are highly concentrated – as recognized by Conservation International (also see www.nationalgeographic.com/wildworld/profiles/terrestrial/pa/pa0422.html) and a globally unique ecoregion as recognized by the World Wildlife Fund.

Although the region has temperature levels that exceed thresholds used in the global temperate rainforest model, and some authors consider the Colchic rainforest subtropical (Rikli 1943) but with temperate tree composition (Lavrenko 1958;

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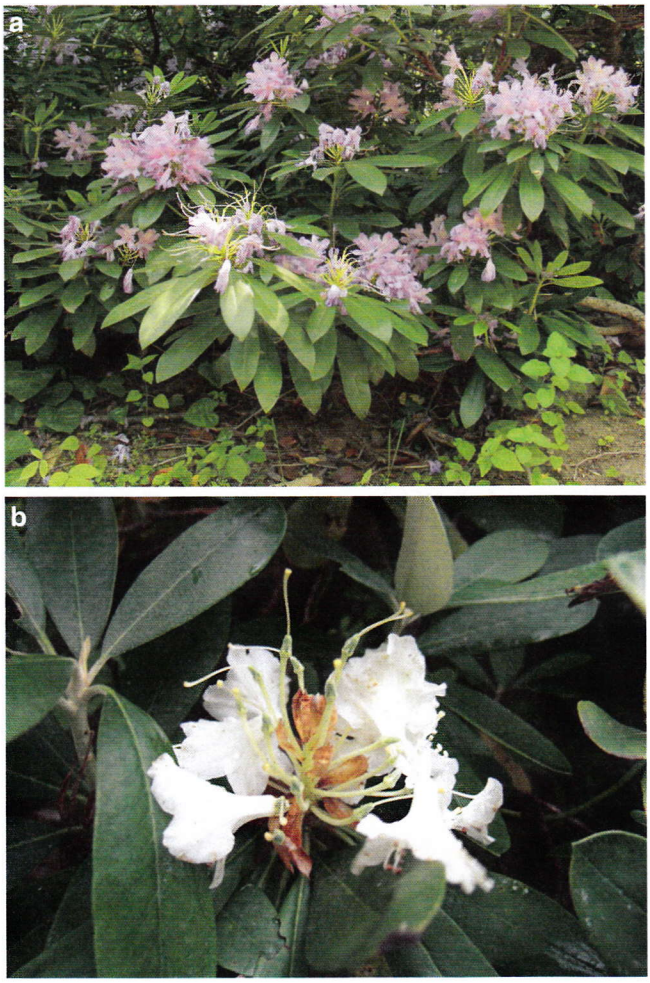

Fig. 6.1 (continued)

Dolukhanov 1980), this region should qualify as temperate rainforest. For instance, Colchis cannot be considered subtropical climatically or structurally in terms of plant communities: air temperatures are lower, seasonal distribution of rainfall is largely continuous, and there is no broad-leaved evergreen forest as in subtropical regions. Further, in the explanatory text to the Map of Natural Vegetation of Europe (Bohn et al. 2003), the Colchic forests are considered humid- and warm-requiring (hygro-thermophilous) broad-leaved forests (Dolukhanov 1980; Nakhutsrishvili 1999; Doluchanov and Nakhutsrishvili 2003).

Evidence for temperate rainforest in the Caucasus is generally related to the mountainous chains located along coastlines trap a large portion of the moisture arising from oceanic air masses on their windward side. In the Caucasus, these barriers are formed by a topographical triangle created by the intersection of the

Fig. 6.1 (**a**) *Rhododendron ponticum*, (**b**) *Rhododendron ungernii*, (**c**) (1–2) *Rhododendron smirnowii*, South Colchis (Photos Z. Manvelidze)

western part of the Greater Caucasus Mountain Range (Georgia, Russia), western part of the Lesser Caucasus Mountains (Turkey, Georgia) and Likhi Ridge (bridge ridge between Greater and Lesser Caucasus, Georgia) at the Black Sea. The warm and humid climate of this region has been present since the late Tertiary, the primary reason the Caucasus has acted as a shelter for hygrothermophilous relicts during the previous ice age. Consequently, Colchic forests along with the Hyrcanian forests are the oldest forests in Western Eurasia in terms of their origin and evolutionary history, most diverse in terms of relict and endemic woody species and tree diversity, and most natural in terms of transformation of historic structure. Both Colchis and Hyrcan, whose formation is attributed to the Upper Pliocene (Kolakovsky 1961), have a number of common features.

The total area of all forests of the Colchis region, estimated by the GIS unit of WWF Caucasus using Google images, is ~ three million hectares. There are a number of forest types belonging to this region: lowland hardwood forests; foggy gorges and mixed broadleaf forests; sweet chestnut forest (*Castanea sativa*); beach (*Fagus orientalis*) forest; dark coniferous forest; and oak woodland. But the main distinguishing feature of these forests is the half-prostrate shrubs characterized by vegetative reproduction, forming dense and high understory (up to 4 m). Forests are marked by broad-leaved evergreens, including several rhododendrons (*Rhododendron ponticum* (Fig. 6.1a), *R. ungernii* (Fig. 6.1b), *R. smirnowii* (Fig. 6.1c), the last two are local endemics of Southern Colchis), Cherry-laurel (*Laurocerasus officinalis*), Black sea holly (*Ilex colchica*), as well as deciduous mountain cranberry (*Vaccinium arctostaphylos*), and oriental viburnum (*Viburnum orientale*) (Zazanashvili 2009; Nakhutsrishvili et al. 2011).

6.1 Lowland Hardwood Forests

In the Caucasus, including Georgia, the lowland forests are spread on swamps, flood plains and in the lowlands, where local irrigation conditions or groundwaters stimulate the development of forest vegetation (Grossheim 1948).

Swamp forests occupy the Colchic Lowland with its mainly damp and poorly drained soils. The leading species of this community is *Alnus barbata*. The above forests are floristically rather rich – about 160 species can be found. The number of exclusive species is negligible; among them *Matteuccia struthiopteris*. *Alnus* forests with *Buxus colchica* are rather rare; near the upper range of distribution, *Alnus* forest with tall herbs (*Telekia speciosa, Heracleum ponticum*) is developed. Due to the extreme swampy conditions, alder becomes dwarfed and provides large hillocks, on which the following plants are developed: *Smilax excelsa* (climbing on alder), *Iris pseudacorus, Leucojum aestivum, Oenanthe abchasica*, etc. (Kolakovsky 1961).

Riparian or flood forests are to be met on river banks in both woody and woodless regions. In riparian forests of East Georgia, as well as in Colchis, *Pterocarya pterocarpa* is a typical species. Besides, these communities are characterized by presence of *Quercus pedunculiflora* (= *Q. longipes*), *Populus alba, Elaeagnus angustifolia, Tamarix ramosissima, T. hohenackeri, Hippophae rhamnoides*, etc.

Among the lianas climbing on these trees are the following: *Vitis sylvestris, Periploca graeca, Cynanchum acutum, Solanum persicum*, etc.

Lowland forests are characteristic of Kakheti, the East Georgia district, where the annual precipitation amounts to 900 mm p. a. These forests are dominated by *Quercus pedunculiflora* with the admixture of *Acer velutinum, Tilia caucasica, Fraxinus excelsior, Pyrus caucasica*. Frequently occurring as underwood in these communities are: *Crataegus pentagyna, Mespilus germanica*, etc. The following lianas are also present here: *Hedera pastuchowii, H. helix, Vitis sylvestris, Clematis vitalba, Smilax excelsa*. According to Grossheim (1936, 1948), these forests reflect the vegetation of the Hyrcanian territory which is the refuge area of Tertiary flora in the Caucasus.

6.2 Lowland Coniferous Forests

These communities are demonstrated by *Pinus pityusa* forests.

The area of distribution of *Pinus pityusa* occupies almost the whole eastern coast of the Black Sea from Mussera (southwards from Bichvinta/Pitsunda cape) to Anapa (Ukraine). This relic species is closely related to the Mediterranean *P. halepensis*, to the Crimean *P. stankevichi* and to the east-Transcaucasian *P. eldarica*. In Bichvinta it forms high-trunk pine forests, where almost all the trees are of the same age; this community holds an area of 200 hectares and is considered to be of secondary origin, due to the elevation of the sea coast and the exposure of sandy-pebble deposites of Bichvinta cape. Undergrowth of this forest is illustrated by *Cistus creticus, Ruscus ponticus, Rhododendron luteum* and *Mespilus germanica*. The following types of these communities are to be distinguished: *Pinus pityusa* forest with *Carpinus orientalis*, mixed pine-broad-leaved forest, Pitsunda pine forests of coastal area, etc. (Tumajaniv 1980).

A mention should be made of *Pinus eldarica*, which is confined to the Eilar-Ougi mountain range near the Georgian/Azerbaijan frontier.

The distribution range of Eldari pine includes the Mtkvari-Araxian desert and mountain-steppe province of the Afro-Asian desert region. The floristic complex of Eldari pine communities is greatly influenced by paleogeographical peculiarities of the present-day distribution area of *Pinus eldarica*. The associates of Eldari pine are the plants of arid open woodlands.

6.3 Mountain Forests

In the mountains of Georgia, within the forest belt, three sub-zones can be outlined: low mountain, mid-mountain and high-mountain (from 500 to 1,900 m a.s.l.). Polydominance is one of the most striking features of mountain forests (except beech woods). Timberline today varies in altitude between 2,200 and 2,750 m, but almost everywhere it has been lowered by man. In the western part of the Greater Caucasus the upper limit of woody vegetation is decreased to 350–400 m, whereas in central and eastern parts – to 500–600 m (Fig. 6.2). The same situation is in the Lesser Caucasus. Due to the impact of anthropogenic factors, the forest vegetation of the Kazbegi region (eastern part of the Central Caucasus) has almost completely been destroyed.

Below, we try to characterize the main formations of forest vegetation of Georgia.

6.3.1 Beech Woods

Beech woods of the Caucasus and particularly Georgia, are dominated by the ancient east Mediterranean species of the Oriental beech *Fagus orientalis* (Fig. 6.3a, b). Its distribution range comprises Mountainous Crimea, the Greater and Lesser Caucasus, Pontian Mountains and the Caspian sector of Iran.

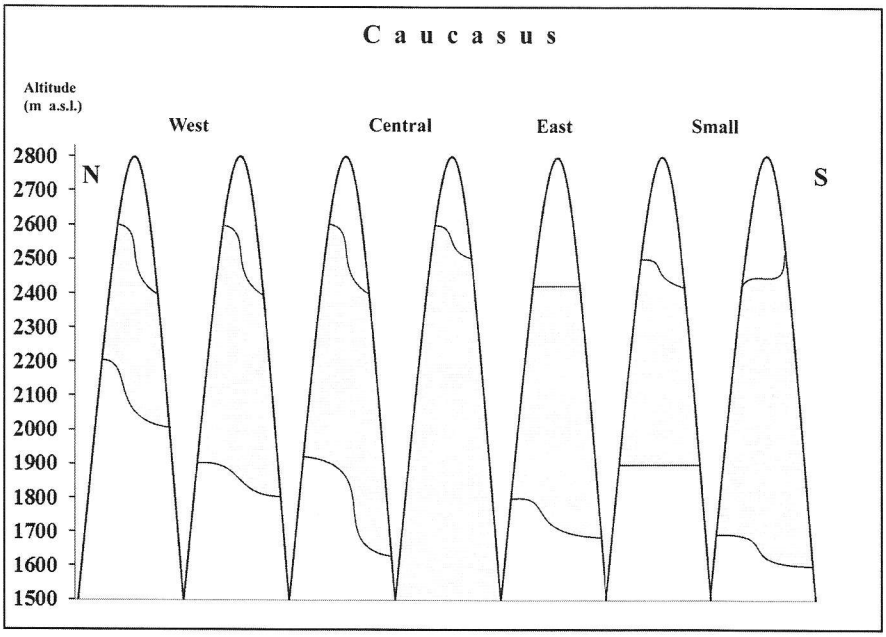

Fig. 6.2 The upper limits of forests

The lower limit of beech forests ranges from sea level (Colchis) to 1,000 m a.s.l., sometimes rising to 1,200–1,300 m (under the most arid conditions). The upper limit varies in altitude between 1,400 and 2,000–2,200 m, and this is the most constant boundary of their altitudinal distribution, which usually depends on the humidity of climate. This accounts for the fluctuations of the upper limit of beech woods in different districts of Georgia. For instance, in moist Colchis, the scope of distribution varies from sea level to 2,200–2,380 m, whereas in the eastern part of the country (Alazani basin) the lower limit of beech forests comes to approximately 350–400 m. In Trialeti mountains (southern Georgia) beech woods appear at an altitude of 800–900 m above sea level.

In Colchis very little of the original forest remains, and only in relatively inaccessible mountainous places. Samples from Colchic *Fagus* forest with evergreen understorey, from about 1,000 m on Mt. Mtirala near Batumi, are shown in Table 6.1. This very stately forest reaches 35 m in height. The forest, as represented by an area of 40 × 30m on a 30 ° mid-slope, is nevertheless an extremely simple forest, completely dominated by *Fagus orientalis* and containing a total of only nine species. The understorey is composed entirely of evergreen Colchic elements, mainly *Rhododendron ponticum* and *Ilex colchica* plus *Laurocerasus officinalis* and *Ruscus ponticus*. On a lower slope below the access road the forest was even taller, over 40 m, but contained *Rubus nigra* (sensu lato) and *Castanea sativa* in place of *Vaccinium arctostaphylos* and *Viburnum orientale*. One 40 × 40 m plot below the

Fig. 6.3 (continued)

road contained a total on only six species, with only *Rhododendron ponticum* as a significant understorey. All plots showed some seedlings of *Fagus* or Colchic evergreens (mainly *Rhododendron*) in the herb layer, suggesting that the forest is regenerating and will remain if not destroyed by man (Box et al. 2000).

An example of a montane *Fagus-Picea* forest from about 1,700 m on a steep north-facing slope in this area is shown in Table 6.2. *Fagus orientalis* is the dominant species in all but the herb layer. *Picea orientalis* also occurs in the canopy but did not seem to be regenerating significantly in the *Fagus* forest (Fig. 6.4). The herb layer is diverse, but the total cover (20 %) was low despite the relatively open canopy (60 %).

According to Dolukhanov (2010), the upper limit of the vertical distribution of beech depends on temperature regime and the amount of winter precipitation, protecting young beech trees from frosts, while the lower boundary depends on

Fig. 6.3 (**a**) Fagus orientalis, Dmanisi region, Lower Kartli. (Photo O. Abdaladze), (**b**) *Fagus orientalis*, Bakuriani (Photo Sh. Sikharulidze)

air humidity. Beech is the most shade- enduring plant among the deciduous woody species of Georgia.

One of the most characteristic species of the beech woods is *Carpinus caucasica* (=*C. betulus*). Under the continental climatic conditions, beech forests are replaced by hornbeam forest communities. In Colchis, *Castanea sativa* is a common associate of beech woods. Among the other species accompanying *Fagus orientalis* are: *Quercus iberica, Q. macranthera, Fraxinus excelsior, Ulmus elliptica, Acer platanoides, A. laetum, Tilia caucasica, T. cordata, Sorbus caucasigena,* etc. Examples of species present exclusively in Colchic beech forests are *Vaccinium arctostaphylos, Viburnum orientale, Trachystemon orientale*. All these species are the local endemics of Colchis. Although in the majority of cases the dominant position in forests is occupied by beech, it frequently is a constituent of the formation of beech-fir, beech-chestnut and beech-spruce forest communities.

Table 6.1 Colchic *Fagus* forest samples on Mt. Mtirala, near Batumi (relevés G-3, G-4, G-5) (Box et al. 2000)

	Relevé G-3 (1,120 m, 30° SSE)				Relevé G-4 (990 m, 20° SSE)				Relevé G-5 (990 m, 20° SSE)			
	T1	T2	S	H	T1	T2	S	H	T1	T2	S	H
	35 m	12 m	3 m	2 m	50 m	20 m	5 m	8 m	50 m	20 m	4 m	8 m
	85 %	10 %	75 %	15 %	80 %	20 %	40 %	30 %	80 %	10 %	80 %	5 %
Fagus orientalis	5.4	2.2			5.4	2.2	3.3	1.1	5.4	2.2	+.2	+
Castanea sativa							1.1					
Rhododendron ponticum			3.4	1.2			2.3	+			5.4	1.2
Laurocerasus officinalis			2.3				2.3				+	
Ilex colchica			3.3	1.1			1.2	+				
Vaccinium arctostaphylos			+.2									
Viburnum orientale			+									
Euonymus latifolia			+				+					
Ruscus ponticus			1.2	+			1.2	1.2				
Rubus hirtus							3.4	3.3			+.2	+.2
Hedera colchica		+	+	2.2				1.2				+.2

In the mountains populated by coniferous forests (1,200–2,000 m), beech woods have partially been extinct. Pure beech forests are not replaced by coniferous woods.

Beech woods occur on brown forest acid soils (dry and fresh forest types) and brown forest pseudopodzols (moist types of forest). Dolukhanov (2010) differentiates two classes of associations in the beech woods of Georgia: beech woods without developed woody undergrowth (underwood) and beech woods with Colchic woody undergrowth.

According to the above-mentioned author, the following groups of associations belong to the first class, i.e. that lacking shrubby undergrowth (some groups are not included):

1. Fageta festucosa (*Festuca drymeja*)
2. Fageta nuda
3. Fageta dentariosa (*Dentaria iberica*)
4. Fageta asperulosa (*Asperula odorata*)
5. Fageta pachyphragmosa (*Pachyphragma macrophyllum*)
6. Fageta rubosa (*Rubus hirtus*)

Table 6.2 Montane *Fagus-Picea* forest above Bakuriani (relevé G-8) (Box et al. 2000) (Location: Above Bakuriani, roadside slope below treeline (25 May 1999))

T1	25 m	60 %	1,700 m, Slope: 30° to NW	
T2	18 m	20 %		
S	3 m	10 %		
H	0.5 m	20 %		
M		1 %		
			30 × 30 m	AM, GN, KF, *EB*, RJL
T1	4.4	*Fagus orientalis*	2.2	*Picea orientalis*
T2	2.2	*Fagus orientalis*		
S	2.2	*Fagus orientalis*	+.2	*Picea orientalis*
	+	*Carpinus caucasica*		
H	2.2	*Dryopteris filix-mas*	2.3	*Arum albispathum*
	1.2	*Myosotis sylvatica*	1.2	*Asperula odorata*
	1.2	*Polygonatum verticillatum*	1.2	*Arabidopsis thaliana*
	1.2	*Paris quadrifolia*	+.2	*Petasites albus*
	+.2	*Urtica dioica*	+	*Rubus saxatilis*
	+	*Veronica peduncularis*	+	*Calamagrostis arundinacea*
	+	*Anthriscus nemorosa*	+	*Geum rivale*
	+	*Carex sylvatica*	+	*Campanula rapunculoides*
	+	*Asplenium nigrum*	+	*Ribes biebersteinii*
	+	*Senecio rhombifolius*	+	*Ligusticum alatum*
	+	*Senecio caucasica*	+	*Erodium cicutarium*
	+	*Taraxacum officinalis*	+	*Geranium sylvaticum*
	+	*Orobanche* sp.		
M	+	*Polytrichum commune*		

7. Fageta trachystemosa (*Trachystemon orientale*)
8. Fageta filicosa (*Dryopteris filix-mas, D. pseudomas,* etc.)
9. Fageta luzulosa (*Luzula sylvatica*)

Among beech woods with Colchic woody undergrowth the following may be mentioned:

1. Fageta rhododendrosa (*Rhododendron ponticum, Rh. ungernii*)
2. Fageta laurocerasosa (*Laurocerasus officinalis*)
3. Fageta ilicitosa (*Ilex colchica*)
4. Fageta ruscosa (*Ruscus colchicus* (Fig. 6.5))
5. Fageta magnovacciniosa (*Vaccinium arctostaphylos*)
6. Fageta azaleoza (*Rhododendron luteum*)
7. Fageta viburnosa (*Viburnum orientale*)

Below, we have attempted to give a brief description of some association groups of beech woods which is based on the results of investigations carried out by Dolukhanov (2010).

Fageta festucosa (Fig. 6.6a). These communities are widely distributed in East Georgia at 1,100–1,750 m above sea level. In the western part of the country they are replaced by fir and spruce forests and are a rare phenomenon here. *Carpinus*

Fig. 6.4 *Fagus orientalis*, *Picea orientalis* with *Paeonia steveniana* (Photo Sh. Sikharulidze)

caucasica is frequently presented in the first stratum along with the leading species of beech. These communities prefer relatively dry climatic conditions and good lighting. At comparatively higher altitudes, the above-mentioned forests are restricted to the slopes of southern exposure.

Fageta nuda. Bare-floor beech woods are confined chiefly to the mountains of the Greater Caucasus. They are poorly represented in Colchis. Bare-floor beech woods lack shrubby undergrowth, but at the same time not a single herb is present in the undergrowth. These forests are distributed at an altitude varying from 500–600 to 1,200 m, only rarely at 1,400 m a.s.l. The fact that Transcaucasian bare-floor beech forests are distributed mostly in Georgia is of particular interest. They are restricted to the slopes of northern exposure. Bare-floor beech forest in Georgia occurs on the soils characterized by poorly developed horizon of humus and belongs to the subtype of brown forest pseudopodzolic soils with a strongly

Fig. 6.5 *Ruscus colchicus*, South Caucasus (Photo D. Kharazishvili)

pronounced process of pseudopodzoliation. (Dolukhanov and Urushadze 1968). The Colchic variant of *Fageta nuda* reminds that of East Georgia. The main difference is in the presence of *Vaccinium arctostaphylos, Rhododendron luteum, Ilex colchica,* and *Laurocerasus officinalis* in the clearings of beech forests (although these species can rarely be found).

The origin of bare-floor beech forests is still under question.

Fageta asperulosa is a corresponding association to the west European beech woods with the same species (*Asperula odorata* = *Galium odoratum*) in the herbaceous undergrowth. But these Caucasian and European beech forest communities vary by their floristic composition and their process of succession; based on this difference, Dolukhanov (2010) is inclined to regard the Caucasian communities as a separate group – Fageta asperulosa caucasica. The woody undergrowth is missing here except for a small amount of *Ilex colchica*.

Beech forests with *Galium (Asperula) odoratum* are to be found in comparatively moist habitats, on well-drained brown forest soils. They are situated on the slopes of medium steepness of the northern exposure; their altitudinal distribution ranges from 1,100 to 1,550 m.

Fageta pachyphragmosa (Fig. 6.6b). These communities require moist temperate conditions. The regeneration is rather high in these beech woods. The subdominant *Pachyphragma macrophyllum* belongs to an ancient, local endemic monotypic genus of Colchic stock. These beech woods are characterized by the admixture of such arboreal species as *Acer velutinum, A. pseudoplatanus, Tilia begoniifolia, Fraxinus excelsior,* sometimes *Abies nordmanniana. Ulmus glabra* (*U. elliptica*) was an associate of beech until the second half of twentieth century. The woody undergrowth consists of *Sambucus nigra* and *Corylus avellana*, although the latter is often absent. The herbaceous field layer is well developed.

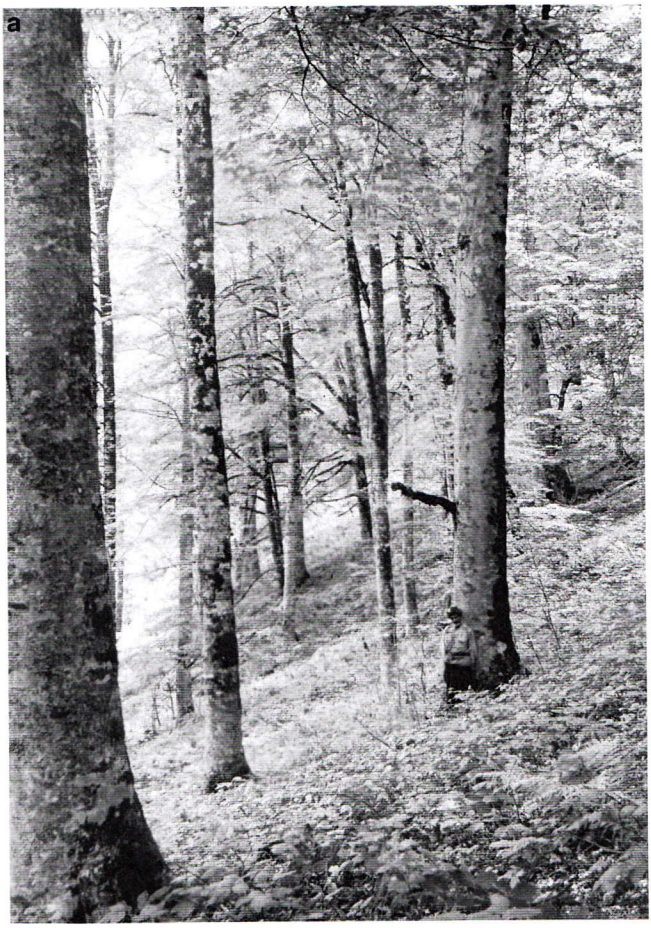

Fig. 6.6 (continued)

Typical forests of this group are met at the altitudes from 500 to 1,000–1,100 m.

Fageta pachyphragmosa are well represented in Lagodekhi Reservation (East Georgia), where it is protected from destruction. The upper limit of such communities reaches 1,820 m in the mountains of Upper Svaneti (Dolukhanov 2010).

Fageta rubosa. These forests are confined to the middle parts of the forest belt; they are commonest among the moist beech woods of Georgia. These forests are characterized by a relatively high regeneration and dominance of *Rubus hirtus (sect. Glandulosi)* in the undergrowth. In Georgia, the area of distribution of Fageta rubosa comprises the southern slopes of the Greater Caucasus mountain system. The above communities are less characteristic of the Lesser Caucasus.

Typical Fageta rubosa are met on northern slopes at 1,100–1,600 m.

Fageta trachystemosa are characteristic for West Georgia. *Trachystemon orientale* is a relic species of Colchic stock. Under the moist climatic conditions

Fig. 6.6 (**a**) Fageta festucosa (Photo A. G. Dolukhanov), (**b**) Fagetum with *Pachiphragma macropyllum*, Lagodekhi National Park (Photo O. Abdaladze)

it reveals a high synecological amplitude from the sea level up to the alpine zone (700–1,200 m). In these forests, *Corylus* and *Sambucus nigra* are solitary, and the semi-prostrate *Viburnum orientale*, as well as other Colchic plants are to be found.

Fageta filicosa. These communities develop under moist conditions. One can find a stratum of large ferns, manifested by *Dryopteris filix-max, Athyrium filix-femina, Matteuccia struthiopteris,* etc., in this type of forest. It must be stated that natural regeneration is suppressed in the above-mentioned communities. Beech woods with ferns are widely distributed in West Georgia, whereas in the east of the country under relatively dry conditions, these forests are restricted to the upper parts of the forest belt. The floristic diversity is the most striking feature of beech forests with ferns.

Fageta luzulosa are typical only for upper parts of the forest belt of Svaneti (western part of the Greater Caucasus). Woody undergrowth consists of *Vaccinium arctostaphylos* with rather abundant *Laurocerasus officinalis, Rhododendron luteum, Viburnum orientale*. Herbaceous vegetation is sufficiently developed. Beech forests with Colchic undergrowth are of considerable interest because of to the absence of their analogues within the territory of West Eurasia. The Colchic undergrowth is rather dense and is constituted of semi-prostrate evergreen and partially deciduous shrubs. Floristic composition of the above undergrowth is related florogenetically to the relic complex of semi-prostrate plants, which represent subalpine crook-stem forests of Colchis. These plants require wet climatic conditions and equal distribution of precipitation during the year.

Fageta rhododendrosa unites two different associations of beech woods with *Rhododendron ponticum* (Fig. 6.7) and those with *R. ungernii*.

Fig. 6.7 Colchic forest with *Rhododendron ponticum* (Photo. G. Nakhutsrishvili)

The first association is one of the commonests in Colchis. It can be found almost everywhere in West Georgia, while in the eastern part of the country it is quite rare. Under the moist climatic conditions (in districts with the annual precipitation over 1,400–2,000 mm) it is distributed from the sea level to 1950 and even to 2,100–2,200 m. The most favourable conditions are provided at the altitude of 1,000 to 1,300–1,500 m above sea level.

Beech forests with *Rhododendron ungernii (Rh. ungernii* is a relic local endemic of Colchis) are typical for districts with a very high amount of precipitation (3,000 mm p.a.). They are to be found at an altitude of 1,200–2,000 m. Under very moist climatic conditions they descend to 800, sometimes to 600 m a.s.l.

Fageta laurocerasosa. These communities extend from the sea level up to 2,250 m. Typical beech woods with *Laurocerasus* are distributed from 700 to 2,000 m. Their vertical distribution depends on the humidity of climate. *Laurocerasus officinalis, Rhododendron ungernii*, require winter precipitation to protect them from frost. Unlike Fageta rhododendrosa, beech forests with *Laurocerasus* are well developed on limestones, and under the moist climatic conditions they are situated on the southern slopes with abundant sunlight. These communities occupy also some gorges of East Georgia.

Fageta ilicitosa. These communities extend from 500 up to approximately 2,000 m, but they are most common from 1,000 up to 1,800 m. They occupy a larger distribution range than beech woods with *Rhododendron* and they almost coincide with that of Fageta laurocerasosa. Beech woods with *Ilex* are typical for Colchis, though in some localities they penetrate into East Georgia. It must be noted, that *Ilex colchica* is more shade-enduring, than *Ilex aquifolium*.

Fageta magnovacciniosa comprises the most common associations of West Georgia. In East Georgia these communities are rare. In the west, they are very common from 900 up to 2,150 m above sea level. They never grow below 500 m.

Vaccinium arctostaphylos is a relict endemic species of Colchis closely allied to the plants distributed nowadays in Japan and Maccaronesia (Madeira Island). That species is rather shade-enduring and is connected with beech woods.

Typical beech-woods with *Vaccinium arctostaphylos* can be found in the areas where precipitation amount does not exceed 1,400–1,500 mm p.a.

Fageta azaleosa associations prefer both moist and relatively dry climate. On the mountains of West Georgia they extend from 800 up to 1,500 m above sea level, in the areas with precipitation amount of 1,200–2,000 mm p.a. Beech-woods with *Rhododendron luteum* of the upper part of forest belts extend to 1,900 m. These beech-woods in East Georgia are situated on prominent mountain slopes from 1,000 to 1,700 m above sea level (Aragvi river basin, Upper Alazani and Iori rivers).

Fageta viburnosa associations are characterized by a narrow synecological distribution range. *Viburnum orientale* is a local endemic of Colchis; mainly, it forms undergrowth in beech-woods, but it can also be found in fir forests. Beech-woods with *Viburnum orientale* occupy moist ecotopes of Colchis, though they can also be met in East Georgia (Aragvi river basin and Upper Alazani). The above mentioned communities extend on the northern slopes of 900–1,900 m above sea level. Typical beech-woods with *Viburnum orientale* are developed in a middle forest belt of West Georgia (1,100–1,600 m). These communities are peculiar for the presence of blackberry (*Rubus hirtus* group), as well as of *Hedera colchica, Trachystemon orientale* and *Dentaria bulbifera*. In the upper forest belt (above 1,700 m) beech-woods with *Viburnum orientale* are spread only in West Georgia.

6.3.2 Dark Coniferous Forests

In Georgia, 5–6 % of the entire forest area is occupied by coniferous forests (forests dominated by spruce) (5, 6 %) and fir (10 %). Excluding beech-woods, dark coniferous forests are most abundantly developed in Georgia.

Fir forests are dominated by the Caucasian fir, *Abies nordmanniana*, whereas the Caucasian spruce, *Picea orientalis,* is a leading species in spruce forests. Caucasian fir (belonging to *sect. Abies*) is closely allied to *Abies bornmuelleriana*, which inhabits northern Anatolia. *Picea orientalis* belongs to *sect. Omorika*; as a typical species of this section, *P. omorika* occurs on rocky limestones of South-West Serbia.

In these forests, the dominant species of fir and spruce are associated with oriental beech. *Pinus kochiana* is more frequent in spruce forests than in fir communities (Fig. 6.8a, b, c).

Dark coniferous forests are widely distributed in Western Georgia and in the western part of East Georgia. These forests never form a continuous belt, though their development is connected with the definite altitudinal-climatic zone, which extends from 1,000 up to 2,000 m a.s.l. Dark coniferous forests represent the commonest type of vegetation between 1,400 and 1,900 m.

Dark coniferous forests of Georgia and of the Caucasus, in general, are quite different from those of the taiga. Some typical representatives of taiga vegetation,

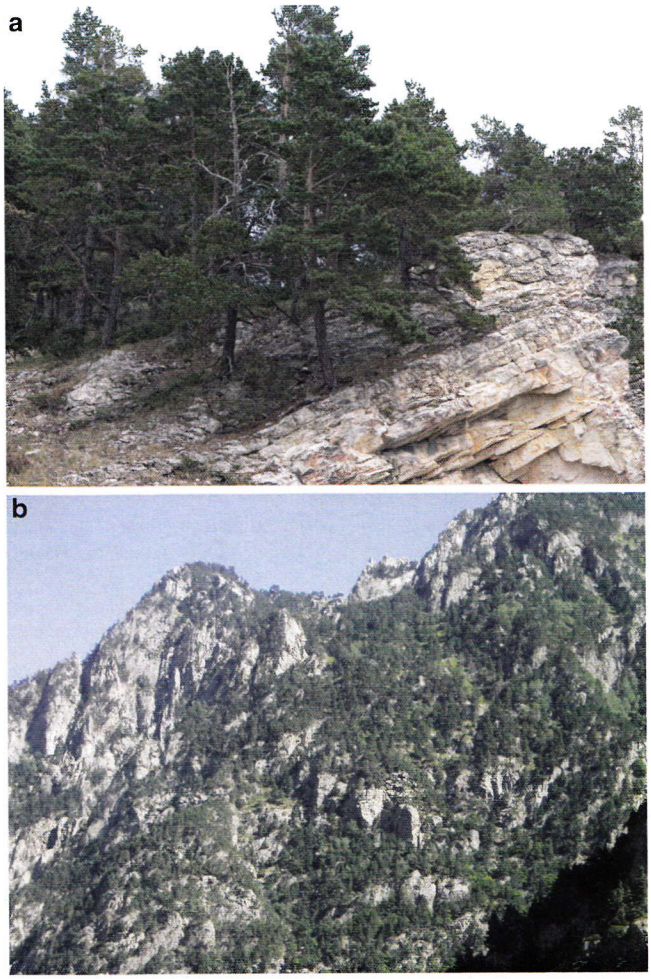

Fig. 6.8 (continued)

such as larch, boreal species of spruce and fir, though unavailable in the Caucasus, can be found in West Europe (Dolukhanov 2010).

The distribution area of oriental beech covers that of *Picea orientalis* (Fig. 6.9) and *Abies nordmanniana* (Fig. 6.10), while the distribution area of Caucasian fir coincides with that of the Caucasian spruce. However, due to the factor of moisture necessary for *Abies nordmanniana*, fir is missing in the most continental parts of its area. In East Georgia spruce penetrates into the area of upper parts of the river Didi Liakhvi and of the Aragvi gorge (in the Greater Caucasus). *Picea orientalis* occupies northern slopes of the Lesser Caucasus up to Tedzami basin; it is also scattered around the districts of Tbilisi (upper reaches of r. Vera). In dark coniferous forests of East Georgia the role of spruce is reduced.

Fig. 6.8 (**a**) *Pinus kochiana*, Tetrobi Reserve, Javakheti plateau, Lesser Caucasus, (**b**) Pine forest on the rocks, Kazbegi, Central Caucasus, (**c**) *Pinus kochiana*, Bakuriani, Trialeti range (Photo O. Abdaladze)

Fig. 6.9 Piceetum, Bakuriani, Trialeti range (Photo O. Abdaladze)

Abies/*Picea* forests occur on crystalline schists and rocky soils.

In fir dominated forests, *Fagus orientalis* is a common species.

Although dark coniferous forests are very rich in endemic and relic species, no exclusive species is to be found here.

Spruce and fir possibly penetrated into the Caucasus earlier than the Quaternary, in the Paleogene and mostly in the Pliocene. In the postglacial period spruce forests

Fig. 6.10 *Abies nordmanniana*, the Lesser Caucasus (Borjomi-Bakuriani area) (Photo O. Abdaladze)

withdrew far westwards to their present limits because of climatic changes; there were replaced by broad-leaved and pine forests. Later the pine forests were displaced by broad-leaved forests and their small fragments remained on steep rocky and stony slopes in some ravines and moraines (Gulisashvili 1949).

Reduction of temperature during some of the Pleistocene periods promoted maximal development and wide distribution of dark coniferous forests. According to Dolukhanov (2010), their further decline is due to fir and dark beetles. From the view point of Kolakovsky (1961), this phenomenon is due to the natural process of

substitution of dark coniferous forests in Colchis by broad-leaved ones, namely beech woods, caused by the changes of climate during the Quaternary.

Floristic composition of fir and beech forests seems identical; boreal elements are more abundant in spruce forests.

Dolukhanov (2010) specifies two classes of associations of these forests on the basis of their undergrowth. The first class of dark coniferous forests is devoid of any developed woody undergrowth and includes the following groups of associations:

1. Piceeta orientalis maculato-muscosa
2. Abieteta festucosa, Fageto-Abieteta festucosa, Piceeta-Abieteta festucosa, Piceeta festucosa
3. Piceeta sicca
4. Abieteta luzulosa
5. Piceeta nanoherbosa, Piceeta-Abieteta nanoherbosa, Abieteta nanoherbosa, Fageto-Abieteta trachystemosa
6. Fageto-Abieteta filicosa
7. Abieteta subalpina calamagrostidosa
8. Abieteta subalpina heteroherbosa
9. Abieteta rariherbosa

Dark coniferous forests with Colchic undergrowth belong to the second class and include the following groups of associations:

1. Piceeta rhododendrosa, Piceeta-Abieteta rhododendrosa, Abieteta rhododendrosa, Fageto-Abieteta rhododendrosa
2. Piceeta laurocerasosa, Piceeta-Abieteta laurocerasosa, Abieteta laurocerasosa, Fageto-Abieteta laurocerasosa
3. Piceeta ilicitosa, Piceeta-Abieteta ilicitosa, Abieteta ilicitosa, Fageto-Abieteta ilicitosa
4. Piceeta-Abieteta magnovacciniosa, Abieteta magnovacciniosa, Fageto-Abieteta magnovacciniosa
5. Abieteta viburnosa, Fageto-Abieteta viburnosa

Piceeta orientalis maculato-muscosa. Associations of this group are characteristic for spruce and pine forests. They extend from 1,100 to 2,100 m a.s.l. The characteristic and constant species is *Goodyera repens*. Within well developed bryophytes in these forests the following may be mentioned: *Hylocomium splendens, Pleurozium schreberi,* etc. The appearance of these forests as well as the floristic composition of bryophytes is very similar to those of Eurasia boreal zone. Mossy spruce forests are well represented in the western part of East Georgia and in Colchis (Nakhutsrishvili, Hübl et al. in press).

Dark coniferous forests with *Festuca*. The predominance of *Festuca drymeja* in the herbaceous undergrowth is characteristic for fir, fir-spruce and beech-fir forests. The altitudinal distribution of these forests ranges from 900 to 2,100 m. The above-mentioned communities are characterized by the presence of following species: *Dryopteris filix-mas, Oxalis acetosella, Sanicula europaea, Viola reichenbachiana.*

Piceeta sicca. These communities are spread only in East Georgia at 1,000–1,500–1,700 m. They occur on poor skeletal soils of steep and sunny slopes. *Picea orientalis* is associated here with pine and Georgian oak (*Quercus iberica*). The ground layer is rather poor in species (*Poa nemoralis, Brachypodium sylvaticum, Oxalis acetosella,* etc.).

Abieteta luzulosa (*Luzula sylvatica*). These forests are restricted to the mountains of Svaneti (West Georgia). They extend from 1,600 to 2,150 m. These communities populate almost all the slopes, though northern slopes are still more favourable for them. There is no woody undergrowth in these forests, although the ground layer is well developed.

Dark coniferous forests with dwarf herbs. These associations prefer moist climatic conditions; they extend from 1,300 up to 2,000 m nearly in all massifs of dark coniferous forests. The main components of these communities are dwarf herbs; grasses are rather poor in species. In East Georgia these communities are exemplified by spruce forests, in the west of the country, however, by fir, fir-spruce and beech-fir forests. Among the species characteristic for fir and spruce communities the following may be mentioned: *Oxalis acetosella, Sanicula europaea,* and *Galium rotundifolium*. Frequently occurring as underwood in spruce forests of West Georgia are *Vaccinium arctostaphylos* and *Daphne pontica*.

Piceeta trachystemosa. These communities occur chiefly in the mountains of northern Colchis (900–1,900 m a.s.l.) under slightly moist conditions. *Fagus orientalis* is a common associate of spruce in these forests; sometimes spruce is even replaced by beech. Underwood consists of scattered *Vaccinium arctostaphylos, Viburnum orientale, Ilex colchica,* and *Rhododendron ponticum*. The ground layer is characterized by the prevalence of *Trachystemon orientale*.

Fageto-Abieteta filicicosa. These communities occupy almost all massifs of fir forests of West Georgia. They belong to the middle and upper parts of dark coniferous forest zone and are characterized by the presence of large ferns: *Athyrium filix-femina, Dryopteris filix-mas, D. oreades, Oreopteris limbosperma, Matteuccia struthiopteris,* etc. Natural regeneration is not satisfactory.

Dark coniferous forests with Colchic undergrowth are not as widely distributed as those of beech. As it was pointed out above, they occupy the mountains of West Georgia.

A special attention should be paid to the series of dark coniferous forests with *Rhododendron ponticum*; spruce, fir and beech are arboreal components of these communities. *Rhododendron ponticum* is more abundant in beech-spruce forests. Such forests can be rarely met in East Georgia. Dark coniferous forests above 1,900 m can be found only in the mountains with moist climate (Dolukhanov 2010).

Natural regeneration is suppressed here. Dark coniferous forests with *Laurocerasus* are peculiar for the upper part of the dark coniferous forest belt. They are developed under moist climatic conditions, but, contrary to those with *Rhododendron ponticum*, they are restricted to the slopes of southern exposure; they also occur on limestones. Fir forests with *Laurocerasus* represent a very rare type of vegetation in East Georgia.

Table 6.3 Chirukhistkali gorge, Mt. Chirukhi (Kharazishvili 2005)

T1 22–25 m	70%	1,990 m, 20 ° N
T2 10–12 m	20%	
S 2.5 m	60%	
H 2 m	80%	
T1	*Abies nordmanniana*	4
	Picea orientalis	3
	Acer trautvetteri	+
T2	*Abies nordmanniana*	2
	Picea orientalis	+
	Acer trautvetteri	+
S	*Vacciniumm arctostaphylos*	3
	Lonicera caucasica	2
	Rubus buschii	2
	Viburnum opulus	+
	Daphne pontica	+
H	*Senecio propinquus*	3
	Athyrium filix femina	3
	Pyrola minor	3
	Valeriana alliariifolia	3
	Festuca montana	2
	Lilium kesselringianum	1
	L. szowitsianum	1
	Taraxacum litwinowii	1
	Dactylorhiza flavescens	1
	Gadellia lactiflora	1
	Silene wallichiana	+
	Geranium psilostemon	+
	Veratrum lobelianum	+
	Polygonatum verticillatum	+
	Trifolium pratense	+
	Alchemilla retinervis	+
	Plantago lanceolata	+
	Prunella vulgaris	+
	Pyrethrum roseum	+
	Ranunculus repens	+
	Luzula forsterii	+
	Fragaria vesca	+
	Tussilago farfara	+
	Petasites albus	+
	Hesperis matronalis	+
	Grossheimia polyphylla	+
	Knautia involucrata	+
	Galium album	+
	Centaurea nigrofimbria	+

(continued)

Table 6.3 (continued)

Scrophularia chlorantha	+
Potentilla recta	+
Heracleum cyclocarpum	+
Pyrethrum marcophyllum	+
Aruncus vulgare	+
Sanicula europaea	+
Gentiana shistocalyx	+
Rumex acetosella	+
Carex capitellata	+
Cirsium kosmelii	+
Sedum tenellum	+
Symphytum asperum	+
Paris incompleta	+
Inula orientalis	+
Oxalis acetosella	+

Laurocerasus officinalis is less shade-resistant than *Rhododendron ponticum*. That is why it is not typical for dense fir forests. In the underwood of dark coniferous forests, *Ilex colchica* can be frequently observed with *Laurocerasus*; in many cases the above-mentioned species occupies a dominant position and forms series of associations. Among these associations, restricted to the middle part of the forest zone (1,200–1,700 m), special attention is paid to *Picea* forests with *Ilex* and with *Fagus-Ilex*. *Vaccinium arctostaphylos* and *Ruscus colchicus* are rather rare in Georgia. *V. arctostaphylos* is very common in the second stratum of beech-fir forests from 1,200 to 1,900 m. The ground vegetation is composed of *Festuca drymeja, Asperula (Galium) odorata, Oxalis acetosella, Dentaria bulbifera*, etc.

Associations of spruce-fir forests with *Vaccinium arctostaphylos* occur only in Svaneti. The less common group of associations is Piceeta viburnosa. These communities are confined to several parts of Svaneti and extreme western parts of Trialeti Mts.

One of the examples of the association **Abieteta subalpina heteroherbosa** is represented in the river of Chirukhistskali gorge, Adjara (Colchis) (Kharazishvili 2005). The community is distinguished by diversity of shrubs as well as herbs (Table 6.3). Undergrowth is constituted by such Colchic elements as *Daphne pontica* (Fig. 6.11), *Vaccinium arctostaphylos*. The following species of the subalpine meadows are worth mentioning: *Pyrethrum roseum, Alchemilla retinervis, Ranunculus ampelophyllus, Lilium spp., Geranium psilostemon, Dactylorhiza flavescens*, etc. Representatives of the tall herbaceous vegetation occurring in coenoses of the association are *Senecio propinquus, Athyrium filix femina, Grossheimia polyphylla, Heracleum cyclocarpum, Gentiana schistocalyx*. The following endemics can be found in this community: *Senecio propinquus, Gadellia lactiflora, Symphytum asperum* (Caucasian), *Grossheimia polyphylla, Lilium kesselringianum* (Colchic).

Fig. 6.11 *Daphne pontica*, Colchis (Photo Z. Manvelidze)

The forest owing to the mountain resort Bakuriani on the Lesser Caucasus is grazed by cattle (Nakhutsrishvili, Hübl et al. in press, s. Table 6.4). The tree layer is made up of *Picea orientalis*, *Pinus kochiana* (*Pinus sylvestris* subsp. *kochiana*) and *Fagus orientalis*. Grazing creates a mosaic structure consisting of forest with typical undergrowth and thinnings with plants typical of pastures. The study was conducted to find out vegetation units of the grazed forest. Twenty one relevés were compiled according Braun-Blanquet scheme. It was impossible to separate forest and pastures by micro-relevés. Therefore most of the descriptions contain portions of both forest and pasture.

The common knowledge about the relation between the dominant trees *Picea orientalis*, *Pinus kochiana* and *Fagus orientalis* seems to be similar as in case of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica* in Central Europe. *Pinus kochiana* has the lowest demand for depth and moisture of the soil, but the highest on light. *Fagus orientalis* has the highest demand for soil and the lowest on light. *Picea orientalis* is in between.

Fagus orientalis dominates alone only in one relevé (1), and here the tree layer has the highest coverage (95 %). There are no lower trees and shrubs in the relevé. The herb layer is very poor (5 %). Plants typical of pastures are not present. The moss cover is also very poor (2 %). In the relevé 2 *Fagus orientalis* and *Picea orientalis* are co-dominants. The tree layer is the highest with 90 % coverage. The second layer (5 %) has a very low coverage and consists only of young *Fagus* and *Corylus avellana* trees. The herb layer is a little more developed, but also without plants of pastures. The moss cover is absent.

Picea orientalis is the most frequent tree and also the most frequently dominating, and reaches 80 % in the tree cover. *P. orientalis* is also the most frequent species in the layer of lower trees and shrubs, in 16 of the 21 relevés. *Fagus*

Table 6.4 Table of relevés within the Bakuriani Alpine Botanical Garden

Number of relevé	1	2	15	14	13	18	12	19	16	17	4	9	5	6	10	11	3	7	8	20	21
Fall	5	10	7	5	5	10	20	5	20	15	20	15	5	5	10	10	10	15	20	25	30
Exposure	S	SSE	SW	S	SW	SE	SW	S	SSW	SW	WSW	SW	W	E	SW	W	SW	SW	W	S	SSW
Plot size (m^2)	200	200	400	400	200	200	200	100	200	200	200	300	100	200	200	200	400	100	80	200	200
Height tree	25	30	30	30	30	30	30	30	30	35	30	30	30	30	30	30	30	30	30		30
Tree cover (%)	95	90	30	10	60	50	40	80	80	80	70	60	60	50	50	50	20	25	10		5
Height shrub		4	10	20	20	15	15	10	5	10	10	4	4	10	10	20	15	3	10	20	20
Shrub cover (%)		5	15	30	10	15	40	10	20	10	5	5	1	10	10	10	5	1	10	40	20
Hight herb	10	40	100	100	50	50	100	50	50	30	95	30	60	30	80	120	40	30	30	100	100
Herb cover (%)	30	10	70	50	60	60	50	15	2	10	40	35	10	60	50	70	10	5	60	50	60
Trees																					
Fagus orientalis	5	3	1	+																	
Picea orientalis		3	2	2	4	3	2	5	5	5	4	4	4	3	3	3	3	2	2		
Pinus kochiana			2	+	+	2	2														1
Pyrus caucasica	+			+																	
Shrubs																					
Fagus orientalis		+			+			1	+	+	1	+		1	1	1	+	+	+		
Picea orientalis			+	+	2	2	3	2	2	2	2	+	+	2	2	2			2		+
Pyrus caucasica			2	2	+	+															
Pinus kochiana						+													+	3	2
Lonicera caucasica			+		+	+		+						+			+			+	
Corylus avellana		+	+																		
Salix caprea			+											+	+						
Malus orientalis				+		+	+													+	
Prunus divaricata			+	+																	
Rosa canina agg.						1						+								+	+
Quercus macranthera						+														+	+

(continued)

Table 6.4 (continued)

Prunus avium						+																+
Ribes biebersteinii								+			+											
Herbs																						
Festuca drymeia	+	1	1		2		1	+	+	1	1	2	+	2	3	3	+	+	3		+	
Fragaria vesca	+	+	1	1	2	+	+	+	+		1	+		1	+	+	2	+	2		1	
Fagus orientalis	+		+			r	+			+	+	+	1	+	+			+				
Galium odoratum	+	+	+	+							1	1		1	+	2						
Orobus cyaneus		+	+	+	+	+	+	+	+	2	+	2		2	1	+	1		+		+	
Sanicula europaea		1	+	+	1	+	+	+		+	1	+		1	+				+			
Primula macrocalyx		+	1	+	+	1	+	1			1	+		+	+	+	1		+	+	1	
Primula woronowii		+	2	2	2	2	1	1			2	1		2	1	2	2		1		+	
Picea orientalis		+	+				+	+	+			+	1	+							+	
Prunella vulgaris			2	2	2	+	+				+	1		1	+	1	1		2	+		
Brachypodium sylvaticum			2	+	2	2	2	1														
Clinopodium vulgare			+	+	+	+	1			+	1	+		1	+	+	+		+		1	
Trifolium ambiguum			1	1	+	+	2	+			+				+		+		+	+		
Valeriana tiliifolia			+	+	+	+	+	+			+	1	+	1	+		+	+	+		+	
Digitalis ferruginea			+	+	+		+						+	+	+		+		+		+	
Sedum stoloniferum			2	1			+	1			+	+	+	+	+	+	1					
Centaurea salicifolia			1	+	+	+											+		+			
Geranium gracile	+		1	1	+							+										
Luzula sylvatica			+		+		+	1			1			1	+	+	1	+	+			
Trifolium medium			+		+						+	+		+			+					
Poa nemoralis			+	+		+	1	1			1	1	+	1		1	+		+		1	
Veronica peduncularis			1				+				+	+			+		+			+	+	
Salvia glutinosa			+		+			+			+	+		+		+						
Ranunculus caucasicus			+	+	+	+	+															

Carex muricata agg.	+	1	+		+													+	
Pyrus caucasica	+	+		r									+		r			r	
Gentiana septemfida	+	+	+	+															
Hieracium hoppeanum	+			2	+							+	+						
Trifolium canescens	1				+							+				+			
Myosotis arvensis	+			+	+													+	+
Viola reichenbachiana	+				+					+			+	+	+				
Festuca pratensis		1		+					1	2				3					
Leontodon danubialis		2	+	1	+														
Leontodon hispidus		1	1	1	2													+	
Cruciata glabra		1		+	+										+			+	
Carex sylvatica		2	+	1			+		+										
Cardamine impatiens		+	+		+			+	+	+	+	+	+	1	+				
Lapsana grandiflora		+	+	+	+				+		+	1	+	+	1				+
Trifolium fontanum		+		+	+	+									+		1	+	
Achillea millefolium agg.		+		+					+						+			1	+
Gentiana schistocalyx		+	1			+								+			+		
Pyrethrum demetrii		+		1	+				+	+								+	
Mycelis muralis		+				+		+	+	+	+	+	+			+	+		
Moehringia trinervia		+				+			+			+	+	+					+
Sorbus caucasigena		+				+	+	+						+					
Alliaria petiolata		+							1					+	+				
Trifolium repens		+				+								+	1				
Urtica dioica		+				r								+	+				
Hieracium murorum			+		+	+	+	+	+	+	+	+	1		+	+	+		
Veronica officinalis			+		+	+		+	+	+		+	+			+	+		
Campanula rapunculoides			+		+	+			+	+	+	+	+				+	+	+

(continued)

Table 6.4 (continued)

Oxalis acetosella					+			+		1		1		1	2	+				
Potentilla crantzii					+	+	+												1	1
Dryopteris filix-mas					+						+		+	+	+					
Coronilla varia					+								+			+			+	+
Trifolium trichocephalum						+								+		+			1	1
Silene ruprechtii				r		+	+	1												1
Myosotis sylvatica							+					+	+		+	+			+	
Calamintha grandiflora							+	+		+		+		+	1					
Plantago lanceolata							+									+		+	+	+
Galium aparine								+	r		+	+	+	+		+				
Galega orientalis								+			+	1	+	+						
Orthilia secunda								+	+	1							+			
Solidago virgaurea								+		+	+	+		+						
Geranium robertianum				+							+	+			+	+				
Lonicera caucasica					r			+				+			r					
Lamium album											+		+			+				+
Cruciata laevipes											+		+			+				+
Cytisus caucasicus													+	+				+	1	1
Dentaria bulbifera	+				r								+							
Prunus avium	+															+				+
Polygonatum multiflorum	+	+													+					
Lathyrus pratensis			+			+								r						
Ajuga genevensis				+		+												+		
Hieracium vulgatum				+			+							+			+			
Trisetum flavescens				1												+			+	
Viola tricolor agg.				+												+			+	
Quercus macranthera						r	+	+												

Sedum gracile						+	+														+
Astrantia trifida						1									r		+				
Corylus avellana						+				+			+								
Chaerophyllum aureum						+					+						+				
Dactylorhiza urvilleana						+					+							+			
Cirsium cosmelii							+								r						+
Cerastium holosteoides							+									+					+
Rubus caucasicus										+				+	r						
Anemone caucasica	+	+																			
Vicia			+											+							
Prunus divaricata			+																	+	
Silene italica			+																	+	
Lilium szovitsianum				r	r																
Alchemilla rigida				+		+															
Cynosurus cristatus				2		+															
Poa trivialis				+												1					
Rumex obtusifolius				+												+					
Sedum tenellum				+																1	
Geranium pallens					+							+									
Taraxacum officinale agg.						+						r									
Neottia nidus-avis							+	+													
Astragalus glycyphyllos							2				+										
Sambucus ebulus								+			+										
Goodyera repens										+					+						
Cicerbita racemosa											1				+						
Galium valantioides											+						+				
Cephalanthera rubra													+	1							

(continued)

Table 6.4 (continued)

Sedum pallidum																+					+
Veronica chamaedrys																		+			+
Coronilla balansae							1													1	1
Arenaria serpyllifolia																				1	+
Alyssum murale																				1	1
Cephalaria procera																				+	1
Carex humilis																				1	+
Helianthemum grandiflorum																				1	2
Melampyrum arvense																				+	+
Phleum phleoides																				1	+
Origanum vulgare																				+	1
Scabiosa bipinnata																				1	+
Teucrium nuchense																				+	+
Verbascum pyramidatum																				+	+
Number of taxa	13	18	44	62	46	55	60	43	12	21	50	41	17	47	45	44	50	15	30	54	61
Moss cover (%)	2	0	10	5	80	20	10	70	20	40	80	80	80	70	60	40	25	90	70	5	0
Hylocomium splendens								3			4	3	4		3			5			
Pleurozium schreberi								3				3	3		1			1			
Mnium sp.															+						

orientalis occurs in this layer in 13 relevés. In the herb layer *Fagus* is a little more frequent (in 11 relevés) than *Picea* (in nine relevés). This is remarkable because *Fagus* was found only in five relevés in the highest tree layer. Therefore fruiting trees are not common. It seems that animals spread the fruits of *Fagus*. The low demand for light of the seedlings ensure there survival. Probably the young beech trees are eaten by cattle. This may explain the minor frequency and the minor coverage of *Fagus* in the second layer. Sometimes the reproduction of *P. orientalis* on mouldering trunks is observed, which is characteristic also to *P. abies*.

Pinus kochiana is the co-dominant with *Picea orientalis* in three relevés. In these cases the whole tree layer has a relatively low coverage (30 %, 40 %, 50 % in the relevés 12, 15, 18). The herb layer is well developed (50 %, 70 %, 60 %) and do not differ significantly from the relevés without *Pinus*.

The relevés 20 and 21 were made on a steep south facing slope with a loose tree layer of *Pinus kochiana* together with a few *Quercus macranthera*. The herb layer is well developed (50 % and 60 %) and differs markedly from the other relevés. In the both relevés species of open habitats prevail. *P. kochiana* do not occur in any relevé in the herb layer. The following Vasilevich and Bohn (2003) are islands of the forests of *P. kochiana* on steep slopes. Pine does not form a separate altitudinal zone.

The undergrowth is very diverse. In the relevés the species typical of forests prevail. The most common are *Festuca drymeja* and *Fragaria vesca* in 18 of 21 relevés. The second position has *Orobus* (*Lathyrus*) *cyaneus* (in 12 relevés) typical of pastures and meadows. A second relatively common species typical of meadows is *Trifolium ambiguum* (in 11 relevés). Several species occur in forests as well as on meadows, for instance *Prunella vulgaris* and *Poa nemoralis*.

Species which prefer substrate reach in bases like *Sanicula europaea* and *Galium odoratum* can be found as well as species growing on acid soil like *Luzula sylvatica* and *Veronica officinalis*. In spite of the fact, that *Picea orientalis* is the dominant tree, species of coniferous forests are rare. *Orthilia secunda* occurs in four relevés, *Goodyera repens*, which is typical of spruce forests in the Caucasus – only in 2. More frequent are mosses typical of coniferous forests: *Hylocomium splendens* (in six relevés), *Pleurozium schreberi* (in five relevés). It seems that the predominance of *Picea orientalis* is encouraged by human impact.

Many species of the herb layer occur also in Central Europe. Frequent species which are absent in Central Europe are *Orobus cyaneus*, *Primula macrocalyx*, *Primula woronowii*, *Valeriana tiliifolia*, *Trifolium ambiguum*.

Festuca drymeja which is most frequent and often dominating in the herb layer reaches the eastern border of the Alps in the Southeast in Slovenia and in the Northeast in Austria (Aeschimann et al. 2004). In the Vienna Wood *Festuca drymeja* is a characteristic species of the beech forests (Nakhutsrishvili, Hübl et al. Table 6.4).

6.4 Mixed Broad-Leaved Forests of Colchis

These forest communities belong to the Euxinian broad-leaved forests; they are restricted to Colchis. Stands of these forests can be observed on the eastern slopes of the Ajara-Imeretian mountain range, in the north-western part of the Greater

Caucasus, etc. Mixed forests of Colchis are extended from approximately 200 m up to 1,000–2,000 m, though in South Colchis they almost approach the sea level. These forests occur on podzolized zheltozems, as well as on mountain forest brown soils and krasnozems.

These forest communities are developed under moist climatic conditions with precipitation amount of 2,500 mm p. a.

Mixed broad-leaved forests are very rich floristically; a considerable number of relic mesophytic species of the Caucasus occur here. These forests mostly cover moist gorges with uniform air humidity all year long. High air humidity of these gorges is caused by the peculiarities of atmospheric precipitation and moderate temperature regime, which keep the surface of the slopes cool. Owing to these favourable conditions, many representatives of the Tertiary flora continue to exist in Colchis. A vivid example of Tertiary relics is the poikilohydric fern, *Hymenophyllum tunbridgense*, restricted to one of the moist gorges of South Colchis. Mixed broad-leaved forests are characterized by the occurrence of 50 arboreal and 80 herbaceous species (Kolakovsky 1961; Sakhokia 1980). Major forest-building species include: Old-Mediterranean *Castanea sativa*, Old-East-Mediterranean *Fagus orientalis*, Colchic-Hyrcanian *Zelkova carpinifolia*, Colchic *Quercus imeretina*, Euxinian *Q. hartwissiana*, south-Caucasian *Q. iberica* and Minor Asia-Caucasian *Carpinus caucasica*. The arboreal associates of the above-mentioned species are Colchic-Hyrcanian *Acer laetum* and *Pterocarya pterocarpa*, Colchic *Ficus colchica* and *Salix alba* subsp. *micans*, Caucasian *Pyrus caucasica, Malus orientalis* and *Salix pantosericea*, as well as European *Acer platanoides, Fraxinus excelsior, Taxus baccata*, etc. Additionally, a mention should be made of *Tilia caucasica, Ulmus glabra, U. elliptica;* Mediterranean-East-Asian *Diospyros lotus*, etc. Mediterranean *Rhododendron ponticum, Ruscus ponticus, R. colchicus, Daphne pontica;* Colchic *Ilex colchica, Rhododendron ungernii, Epigaea gaultherioides* and *Buxus colchica* frequently occur as undergrowth in these communities. Among the deciduous plants of the Colchic undergrowth, relics occupy the dominant position; examples are Colchic *Vaccinium arctostaphylos, Staphylea colchica, Viburnum orientale, Euonymus leiophloea, Hypericum xylosteifolium;* Colchic-Caucasian *Rubus caucasicus;* Colchic-Hyrcanian *Crataegus microphylla*, etc.

The ground vegetation (field layer) is characterized by the presence of such ferns as *Matteuccia struthiopteris, Athyrium filix-femina*, etc. Epiphytic ferns are exemplified by *Polypodium serratum*. Moist rock crevices and stony sites are inhabited by *Phyllitis scolopendrium, Pteris cretica*, etc.

Lianes (vines), though typical for Colchis forests, never form thickets even in forest margins. The commonest lianas are: *Hedera colchica* and *Dioscorea caucasica* (both are Colchic endemics); *Tamus communis* and *Periploca graeca* (Mediterranean species); *Smilax excelsa* and *Clematis vitalba*, etc. As indicated before, Colchic forests include epiphytes. Epiphytic plants are manifested by lichens (*Usnea barbata*), mosses (Neckeraceae representatives) and ferns.

Of the main plant communities *Fagus-Castanea, Carpinus-Castanea, Carpinus-Fagus-Castanea* and *Alnus-Carpinus-Fagus-Castanea* forests should be mentioned. Among these communities, forests dominated by five and more species

can be observed. An example is the community where the dominant position is occupied by *Castanea sativa, Fagus orientalis, Tilia caucasica, Carpinus caucasica, Alnus barbata* and *Taxus baccata*. In the ground vegetation (where developed) *Brachypodium sylvaticum* and the adventive grass *Oplismenus undulatifolius* are dominants. They are associated with *Cardamine impatiens* and *Oxalis corniculata*.

Quercus imeretina forests with *Carpinus caucasica* are spread on river terraces.

It should be stated, that Colchic river gorges are characterized by a considerable amount of heterogeneity of natural conditions. Forest communities with *Buxus colchica* as undergrowth are typical for limestone regions, while in non-limestone areas forest undergrowth is composed of *Rhododendron ponticum, Rh. ungernii*, etc.

According to Kolakovsky, these moist gorges covered by protective heavy snow in winter, have prevented Tertiary flora remnants from destruction, which overwhelmed the similar vegetation of exposed slopes.

The term "Shkeriani" is usually applied to define thickets of evergreen shrubs and even creeping trees. Golitsin (1939) attributes this term to a whole complex of evergreen shrubs, including *Epigaea gaultherioides, Ilex colchica* and also to deciduous *Betula medwedewii, Quercus pontica, Vaccinium arctostaphylos, Viburnum orientale*. According to Kolakovsky, "Shkeriani" should be referred to the formation of shrubs, developed below the forest canopy and which now build up the second stratum. Mainly, the components of "Shkeriani" are the derivatives of forest vegetation, and such plants as *Epigaea gaultherioides, Ilex colchica, Betula medwedewii* should be excluded from its composition.

Destruction of Colchic forests in the lower part of the forest belt is the effect of man's agricultural activities; these areas, made subject to intensive farming, are manifested by the following cultivated plants: *Citrus* species, tea, tung tree, tobacco, maize, etc.

These areas are populated by many adventive plants like *Baccharis halimifolia* (North American), *Paspalum paspaloides* (pantropical), *Andropogon virginicus*, etc.

6.5 Pine Forests

Mountain pine forests of Georgia are dominated by *Pinus kochiana* which belongs to *P. sylvestris* group. The distribution area of *P. kochiana* comprises the Caucasus, Crimea and the northern Asia Minor up to the western part of the Pontic Mts. In the west, this species occurs in the Balkan Peninsula Tumajanov (1980) indicates that *P. kochiana* forests are to be found in all forest regions of moist temperate climate throughout the Euxinian phytogeographical province.

Main massifs hold by the above-mentioned forests, are situated on the mountains of the Greater Caucasus. In Georgia, pine forests cover negligible areas. In the eastern part of the country, these forests are distributed over the Mtkvari (= Kura) river basin, eastwards from Tbilisi and in Tusheti. In West Georgia they usually occur on stony and rocky slopes, where they cannot be replaced either by dark coniferous woods or by broad-leaved forest communities (Dolukhanov 2010).

Dolukhanov (2010) noticed an interesting exception, specific for the pine forests of Georgia. In some parts of East Georgia, namely in the depth of Tushetis and Pirikitis Alazani river gorges, pine forests typical for stony and rocky slopes, also occur in habitats with a developed soil cover. These biotopes are favourable not only for pine but also for such forest-building trees as spruce and beech. Nevertheless, in the gorges, mentioned earlier, spruce and beech are absent and the climax communities of pine forests are formed instead. Dolukhanov explains this phenomenon by the orographic and geographic isolation of these gorges. Due to historical circumstances, only pine has been preserved in these sites; it escaped being replaced by beech and spruce only because their seeds never got to this area.

Mountain pine forests extend from 700 up to about 2,400 m a.s.l. The most favourable conditions for pine forests are provided at an altitude of 1,000–2,200 m. In several parts, pines have been recorded at 2,500–2,600 m (Tumajaniv 1980).

P. kochiana grows on both limestone and acid magmatic rocks.

It is accepted that distribution of the pine forests of the Caucasus is closely connected with the regions of maximum glaciation in the Quaternary (Gulisashvili 1949). Formation of the present montane pine forests of the Caucasus took place under the influence of the Pleistocene glaciers (Tumajaniv 1980).

The main part of the pine forests in confined to the mountains of the Greater Caucasus and mostly, to its northern slope.

In the North Caucasus the pine forests form a wide line from 900–1,000 to 2,500–2,600 m a.s.l. On northern slopes in conditions of the deep snow cover they are usually replaced by birch forests (Betuletum) (Tumajaniv 1980).

Pinetum siccum astragalosum microcephalus is characteristic to the Lesser Caucasus.

Pine forests of the western South Caucasus are, in contrast, characterized by their connections with dark coniferous forests, especially spruce forests and formation of a spruce-pine association of the order Hylocomiosa.

Following Dolukhanov (2010), the distribution of *P. kochiana* is controlled by phytogeographical conditions, while the influence of climate is less important. Occurrence of climax communities of pine forests on stony and rocky slopes accounts for their floristic composition, which is rich in endemic species.

Within the pine forests of Georgia, the following groups can be outlined: climax communities of the above forests and temporal-derivative pine forests.

Pine is well known as a pioneer tree to occupy the naked stony substrata, morain and fluvioglacial drifts. In Transcaucasia and particularly in Georgia, development of pine forests is subject to the impact of climatic fluctuations and activities of man (Dolukhanov 2010).

The climax pine forests of Tusheti are very diverse, despite the fact that they occupy a limited area. They occur on substrata different by the character of weathering, as well as by the peculiarities of the lithological composition of the rocks (Tumajanov 1938; Dolukhanov 2010).

Dolukhanov (2010) differentiates the following categories of mountain pine forests:

1. Caucasian mountain pine forests of relatively dry ecotopes;
2. Caucasian mountain pine forests of moderate-moist ecotopes;

3. Caucasian mountain pine forests of swampy habitats;
4. Caucasian mountain pine forests occurring on stony screes and rock streams.

6.5.1 Caucasian Mountain Pine Forests Restricted to Rocky Slopes

Mountain pine forests of relatively dry ecotopes can be found almost everywhere within the distribution area of *Pinus kochiana*. They occur on skeletal and poorly-developed soils of prominent southward slopes. These pine forests are characterized by rich and diverse ground vegetation.

From the viewpoint of Dolukhanov (2010), several groups of associations can be distinguished within this forest type. Our aim is to give a short description of some of them.

Pine forests with sparse herbaceous undergrowth are confined to prominent southern exposure. Availability of scattered herbs in the undergrowth is due to the washout of soils and destruction of ground vegetation. Pine forests of dry habitats with xerophytic herbs in the undergrowth are usually the climax communities which occupy northern slopes of Trialeti Mts, Meskheti, etc. The second stratum of these forests consists of *Quercus iberica* (below 1,500 m), *Q. macranthera* (above 1,500 m) and species of *Acer*. Species dominant in the herbaceous undergrowth include *Carex buschiorum, Poa nemoralis, Brachypodium sylvaticum, Sesleria anatolica,* etc. Particular interest arise pine forests with tragacanthic species of *Astragalus* and those with *Juniperus (J. oblonga, J. hemisphaerica)* as undergrowth, frequent at 1,900–2,000 m a.s.l. Northern slopes of Trialeti Mts. are inhabited by pine forests with *Chamaecytisus caucasicus*, whereas those with *Ch. hirsutissimus* are restricted to mountainous Abkhazeti. In Ajara, the undergrowth of pine forests is dominated by *Cistus salviifolius*.

It is pertinent to note that Caucasian mountain-steppe pine forests and mountain meadow-steppe *P. kochiana* communities belong to the above-mentioned ecological type; they participate in generating park-like landscapes on the background of mountain meadow-steppe vegetation (usually in distant parts of the Javakheti Upland plateau). The communities mentioned earlier are characterized by rather dense ground vegetation, extremely rich floristically. These forests occur at the altitude between 1,700 and 2,400 m. These communities are also observed in Turkey.

Caucasian mountain pine forests of moderately moist ecotopes are characterized by the admixture of spruce, as well as *Betula litwinowii, Abies nordmanniana, Sorbus caucasigena, Fagus orientalis, Fraxinus excelsior,* etc.

According to Tumajanov (1938), the above-mentioned pine forests can be divided into the following series: (1) *Hylocomiosa*, including Pineta myrtillosa, Pineta oxalidosa, Pineta vacciniosa, and (2) *Composita* with Pineta rhododendrosa (*Rhododendeon caucasicum*), Pineta mixtofruticosa, Pinetum azaleosum, and Pinetum tiliosum communities.

As indicated above, these pine forests are examples of climax communities. The series Hylocomiosa deserves special interest. These communities are dominated by

representatives of the typical Taiga florogenetical complex. They populate steep slopes of northern exposure. The above forests can only be found in Tusheti.

Aside from these types of pine forests, the following communities may be mentioned: Pinetum siccum, Pinetum cytisosum, Pinetum calamagrostidosum, Pinetum prasinosum, etc. Oak-pine forests are attributed to a special group of forests; they are confined to lower parts of the pine forest belt (in East Georgia they occur at 800–1,100 m.a.s.l., whereas in Ajara they descend to 300 m).

6.6 Oak Forests

From the coenotical and floristical points of view, the oak forests are among the richest forests of Georgia. According to Dolukhanov (2010), in prehistoric times, the area covered by oak trees was twice as large as it is today. These forests have also suffered from agricultural activities of man.

Oak forests which escaped destruction, are characterized by unsatisfactory regeneration and usually developed on poor soils.

In Georgia, the most abundant oak forests are those dominated by *Quercus iberica*, which is closely related to the widespread European *Q. petraea*. The distribution area of *Q. macranthera* is more limited. Broad-leaved forests of Colchis are characterized by the admixture of *Q. hartwissiana*. Alluvial plains of the valley of river Mtkvari (=Kura) are covered by *Q. pedunculiflora* forests; this species is very close to *Q. robur*, in the lowlands of West Georgia this species becomes replaced by *Q. imeretina*. Remnants of *Q. dschorochensis* communities, which were widely distributed in the past, have survived in Ajara. The characteristic species of crook-stem forest is *Q. pontica* – an ancient relic of the Colchic flora. This species can be found only within the creeping crook-stem forests.

6.6.1 Forests of Georgian Oak (*Q. iberica*)

The distribution area of these forests involves almost the entire territory of Transcaucasia, Daghestan and partly Chechnya-Ingushetia.

As it was pointed out, the south-Transcaucasian species *Q. iberica* displays close taxonomical connections with *Q. petraea*, though they are separated ecologically and phytosociologically.

Q. iberica is typical for eastern and south-eastern semi-arid parts of Transcaucasia; although, it can be encountered also in the Black Sea coastal area of Georgia. Even extreme conditions provided in the areas where the above oak forests come into contact with steppe and mountain-xerophytic vegetation, do not hinder their development. *Q. iberica* forests extend from sea level up to 1,500 and even 1,800 m (in Svaneti).

Being very sensitive to excessive soil moisture and bad drainage, Georgian oak avoids alluvial plains.

Due to the fact that Georgian oak requires much light, in the areas favourable for the development of beech-woods, populations of oak are replaced by more shade-enduring ones of beech.

Unlike in Europe, in Georgia *Fagus orientalis* and *Q. iberica* are never found to grow together.

Of the arboreal components of *Q. iberica* forests the following should be mentioned: *Carpinus caucasica, C. orientalis, Acer laetum, Sorbus torminalis, Zelkova carpinifolia.*

Depending on the degree of anthropogenic succession, derivatives of oak forests are illustrated by *Carpinus caucasica* forests and shibliak vegetation consisting of *Carpinus orientalis, Cornus mas, Cotinus coggygria, Swida (Cornus) australis, Crataegus pentagyna, Spiraea hypericifolia* and *Paliurus spina-christi.* At the last stages, shibliak is substituted by *Bothriochloa ischaemum.* Very often, meadows occupy the areas once covered with oak forests.

Taking into account that *Q. iberica* forests were replaced in many areas by beech-woods, dark coniferous forests, etc., and that a considerable part of the above *Quercus* forests was destroyed by man, many associations of these forests have disappeared by now. Therefore, we assume that oak forests were well developed on the foothills and in the low mountain zone where competition between oak and beech, spruce, chestnut trees, etc. was impossible (Dolukhanov 2010).

Oak forests are very rich floristically, owing to the illumination under the canopy and the heterogeneity of the physico-geographical conditions within the distribution area of Georgian oak. *Q. iberica* forests are confined to rocky sites which promote enrichment of their floristical composition. In limestone regions many local endemics penetrate into the undergrowth of these forests (Dolukhanov 2010).

Dolukhanov specifies the following variants (sub-formations) of *Q. iberica* forest communities:

1. Monodominant forests,
2. *Carpinus orientalis-Quercus iberica* forests,
3. *Carpinus caucasica-Quercus iberica* forests.

Today *Carpinus orientalis-Quercus iberica* forests are confined to the lower parts of the forest belt and occupy the largest area.

Carpinus caucasica-Quercus iberica communities occur on fertile and moist soils at relatively high altitudes. Monodominant forest communities are represented by forests with well-developed undergrowth as well as by those with no undergrowth. The same author specifies by convention the following ecologically different series within monodominant oak forests:

1. Hemi-xerophytic,
2. Xero-mesophytic.

Hemi-xerophytic oak forests develop under the driest conditions, regarding forest vegetation. In prehistoric times, these forests were widely distributed in semi-arid districts of East Georgia. Due to the impact of anthropogenic factors, these forests have always been subject to destruction.

As to the forest maintenance and timbering, regeneration in the above-mentioned forests is unsatisfactory.

Different associations of oak forests include Quercetum iberici multifruticosum siccum and the communities of oak forests with *Cotinus coggygria*.

It is suggested that in the past, oak forests included the following species as undergrowth: *Spiraea hypericifolia, Pyracantha coccinea, Juniperus oblonga*. Georgian oak forests with *Sesleria anatolica* and with *Psoralea bituminosa* are widespread in Abkhazeti.

It should be pointed out, that Iberica-Quercetum genistosum can be observed in east Transcaucasia (with *Genista transcaucasica*) as well as in Northern Colchis (*G. kolakowski, G. abchasica*).

Xerophytic *Q. iberica* forests without woody undergrowth are characterized by presence of rich herbaceous ground vegetation. Associations of these forests have been united by Dolukhanov (2010) into the Iberica-Querceta multiherbosa transcaucasica group. This group involves typical oak forests with forbs, *Q. iberica* communities with various herbs and grasses, and *Q. iberica* forests with various herbs and sedges.

Q. iberica forests with various herbs are confined to river gorges of Pshavis Aragvi, Mtiuletis Aragvi, Gujaretis Tskhali and Nedzviskhevi; these forests extend from 830 up to 1,460 m a.s.l.

Of the arboreal components of these forests the following should be mentioned: *Carpinus orientalis, C. caucasica, Sorbus torminalis, Acer laetum, Picea orientalis, Abies nordmanniana, Chamaecytisus caucasica, Lonicera caucasica*, and *Mespilus germanica*. Composition of the herbaceous undergrowth includes: *Clinopodium vulgare, Veronica peduncularis, Polygonatum glaberrimum, Campanula rapunculoides, Dactylis glomerata*, etc.

The commonest association of *Q. iberica* forests with grasses is the one with various herbs and *Brachypodium sylvaticum*.

Q. iberica forest with various herbs and *Carex buschiorum* is the typical representative of Georgian oak forests with sedges.

The group of associations of oak forests with *Epimedium* chiefly occurs on seaside mountains of Abkhazeti. The presence of *Epimedium colchicum* and *Hypericum xylosteifolium* as constant species is typical for these communities. *Dioscorea caucasica* is a constant species of oak forests restricted to limestone regions of West Georgia. The common species include *Sesleria anatolica, Trachystemon orientale, Ruscus ponticus, Carex transsilvanica, Dorycnium graecum*. Less common species are manifested by *Iris colchica, Dianthus imereticus, Hypochaeris radiata, Psoralea bituminosa, Aristolochia steupii, A. iberica, Primula sibthorpi, Veronica peduncularis, Helleborus abchasicus*, etc. These forests are inhibited by such Colchic shrubs as *Rhododendron luteum, Rh. ponticum, Vaccinium arctostaphylos*. Undergrowth of the forests confined to the cape of Bichvinta (Pitsunda) involves *Erica arborea*. Examples of common lianas are *Lonicera caprifolium* and *Smilax excelsa*. Right at the seashores, *Arbutus andrachne* occurs as an arboreal component of oak forests. The following associations may be regarded as typical for the given group:

Quercetum hypericoso-epimediosum
Quercetum ericosum
Quercetum dioscoreoso-epimediosum
Quercetum multiherbosum-ibericum.

Q. iberica forests with developed woody undergrowth are characterized by the presence of dense thickets of shrubs and sparse undergrowth. The following associations belong to the above-mentioned first type of oak forests: *Querceta azaleosa (Rhododendron luteum), Querceta rhododendrosa (Rh. ponticum), Querceta staphyleosa (Staphylea colchica* is characteristic of West Georgia, whereas *S. pinnata* is of East Georgia). According to Dolukhanov (2010), the second type of these forests involve too many variants to make them subject for any classification.

6.6.2 *Q. iberica* Forests with *Carpinus orientalis*

These communities are widespread in East Georgia. Under the driest conditions they extend from 600 to 1,000 m a.s.l., while in humid districts of West Georgia from 350 up to 700–800 m. At lower altitudes the above communities are restricted to northern slopes, whereas at higher altitudes to southern ones. They can also be found in limestone regions of Abkhazeti and Samegrelo. In East Georgia they occur on different rocks. Dolukhanov (2010) distinguishes three main associations detectable in the oak forests with *C. orientalis*:

1. Carpinuleto-Quercetum xerocaricosum (*Carex buschiorum*),
2. Carpinuleto-Quercetum poosum (*Poa nemoralis*),
3. Carpinuleto-Quercetum brachypodiosum (*Brachypodium sylvaticum*).

The associations of oak forests with *Epimedium* are typical for West Georgia. In addition the following associations should be mentioned:

Carpinuleto-Querceta ruscosa (*Ruscus colchicus*),
Carpinuleto-Querceta azaleosa (*Rhododendron luteum*),
Carpinuleto-Querceta cotinosa (*Cotinus coggygria*).
Carpinuleto-Querceta sesleriosum (*Sesleria anatolica*) and Carpinuleto-Querceta xerobrachypodiosum (*Brachypodium sylvaticum*) favour the driest climatic conditions.

6.6.3 *Carpinus caucasica-Quercus iberica* Forests

These forests occupy transition zones between oak forests and those of beech. The second stratum is composed of *Carpinus caucasica*, which is a shade-enduring tree. Very little information is available on the typology of the above-mentioned forests because of the poor state of remnants of the climax communities. Dolukhanov (2010) indicates that *Carpinus-Quercus* forests with *Festuca drymeja* are abundant

Table 6.5 Semi-natural *Carpinus-Quercus* deciduous forest near Tbilisi (relevé G-1) (Box et al. 2000) (Location: Just past Kojori along Kojori Road, beyond Botanical Institute (22 May 1999))

T1	10 m	70 %	1,600 m, Slope: 2–15 ° to SW	
T2	6 m	10 %		
S	3 m	20 %		
H	0.4 m	70 %		
			20 × 20 m	
T1	4.4	*Carpinus caucasica*	2.2	*Quercus iberica*
	1.1	*Fagus orientalis*		
T2	2.2	*Carpinus caucasica*		
S	2.2	*Carpinus caucasica*	1.2	*Crataegus monogyna*
	1.2	*Corylus avellana*	1.1	*Acer campestre*
	1.2	*Lonicera caucasica*	+	*Cornus mas*
	+	*Viburnum lantana*	+	*Rosa canina*
	+	*Pyrus caucasica*	+	*Prunus divaricata*
	+	*Malus orientalis*		
H	3.3	*Anthriscus nemorosa*	2.2	*Primula woronowii*
	1.1	*Galanthus caucasicum*	1.2	*Poa nemoralis*
	1.2	*Carex sylvatica*	1.1	*Galium verum*
	+.2	*Polygonatum verticillatum*	+.2	*Lathyrus* sp.
	+.2	*Taraxacum officinale*	+.2	*Cyclamen vernum*
	+.2	*Cruciata laevipes*	+.2	*Lonicera caucasica*
	+	*Quercus iberica*	+.2	*Viola odorata*
	+	*Carpinus caucasica*	+	*Fragaria viridis*
	+	*Acer laetum*	+	*Campanula rapunculoides*
	+	*Acer campestre*	+	*Calamagrostis arundinacea*
	+	*Geum urbanum*	+	*Primula macrocalyx*
	+	*Paris quadrifolia*	+	*Arum albispathum*
			+	*Potentilla* sp.

in East Georgia. Examples of typical species of these forests are *Cornus mas, Corylus avellana, Thelycrania (Cornus) australis.*

Carpinus caucasica-Quercus iberica forests with *Rhododendron luteum* are common in West Georgia.

Most of the natural vegetation has been greatly disturbed if not completely destroyed. An idea of the potential composition of natural *Quercus-Carpinus* forest on slopes around Tbilisi is given by the relevé in Table 6.5, from a secondary forest at about 1,600 m in the hills southwest of Tbilisi. The forest is short (10 m) and young but contained 39 species in the 20 × 20 m plot, including *Fagus orientalis, Acer campestre*, and various forbs characteristic of more mature mesic *Quercus iberica-Carpinus* forests of the region (Box et al. 2000)

The pote ntial composition of subhumid woodland is suggested by the relevé in Table 6.6, from the second terrace above the Mtkvari river about 15 km northwest of Tbilisi. The sample (15 × 15 m) is from a concavity on a lower slope, ranging

Table 6.6 Degraded *Fraxinus-Juniperus* stand in concavity on riverine terrace near Tbilisi (relevé G-12) (Box et al. 2000) (Location: Northwest of Tbilisi, 2nd terrace above river (27 May 1999))

T	7 m	85 %	540 m, Slope: 3–20 ° to SSE	
S	3 m	20 %		
H	0.4 m	60 %		
			15 × 15 m (patch) KF, GN, *EB*, RJL	
T	4.4	*Fraxinus excelsior*	2.2	*Juniperus oblonga*
	1.1	*Quercus iberica*	+.2	*Prunus divaricata*
	+	*Cornus mas*	+.2	*Cotoneaster racemiflorus*
			+	*Prunus spinosa*
S	1.2	*Cotinus coggygria*		
	1.2	*Juniperus rufescens*	1.1	*Prunus divaricata*
	+.2	*Cornus mas*	+.2	*Juniperus oblonga*
	+	*Spiraea hypericifolia*	+.2	*Cotoneaster racemiflorus*
			+	*Prunus spinosa*
H	3.3	*Ruscus ponticus*	2.2	*Brachypodium sylvaticum*
	1.2	*Fraxinus excelsior*	1.3	*Juniperus rufescens*
	1.2	*Campanula rapunculoides*	1.2	*Dactylis glomerata*
	1.1	*Tanacetum vulgare*	1.1	*Fragaria viridis*
	1.2	*Viola odorata*	1.2	*Convolvulus lineatus*
	+.2	*Cruciata laevipes*	+.2	*Draba* sp.
	+	*Astragalus offinalis*	+.2	*Stellaria media*
	+	*Dictamnus caucasicus*	+	*Tragopogon graminifolius*
	+	*Polygonatum verticillatum*	+	*Euonymus caucasicus*
	+	*Thalictrum foetidum*	+	*Astrodaucus orientalis*
	+	*Poa bulbosa* var. *vivipara*	+	*Chelidonium majus*
	+	*Trifolium arvense*	+	*Taraxacum officinale*
	+.2	*Viburnum lantana*	+	*Geranium pallens*
	+.2	*Carex* sp.	+	*Euphorbia glareosa*
	+	*Ajuga genevensis*	+	*Vicia iberica*
			+	*Avena barbata*

from 20 ° above to about 3 ° at the base and sloping toward the south-southeast. The canopy is low (7 m), and the dense cover by *Fraxinus excelsior* is probably not representative of most of the slopes. Otherwise the sample shows a composition which may be fairly typical, including *Juniperus, Prunus, Cotinus* and other shrub genera which were also seen in more natural stands of this vegetation type in eastern Georgia. At 48, the number of species in this plot suggests the diversity of these open woodland landscapes (Box et al. 2000).

Much of the Lagodekhi reserve is covered by deciduous *Quercus iberica* forest, always with *Carpinus caucasica* and usually with *C. orientalis* as well. A relatively rich example of this forest, including also *Fraxinus*, *Acer*, and *Tilia*, is shown in

Table 6.7 *Quercus iberica* forest in Kakhetia, Eastern Georgia (relevé G-13) (Box et al. 2000) (Location: Lagodekhi State Nature Reserve, *Quercus* area (30 May 1999))

T1	25 m	85 %	520 m, Slope: 30 ° to SSE	
T2	8 m	20 %		
S	4 m	20 %		
H	0.4 m	35 %		
			40 × 40 m	
T1	3.3	*Quercus iberica*	3.3	*Carpinus caucasica*
	2.2	*Fraxinus excelsior*	2.2	*Tilia begoniifolia*
	2.2	*Acer laetum*		
T2	2.2	*Carpinus orientalis*	1.1	*Crataegus caucasica*
	1.1	*Cornus mas*	+	*Quercus iberica*
	+	*Fraxinus excelsior*	+	*Cerasus sylvestris*
Vine: +.2		*Hedera pastuchowii*		
Epiphyte: +.2		*Viscum album*		
S	2.3	*Rubus caucasicus*	2.2	*Cornus mas*
	1.2	*Acer laetum*	1.1	*Carpinus orientalis*
	1.1	*Crataegus caucasica*	+	*Mespilus germanica*
	+	*Lonicera caprifolium*		
Vine: 1.1		*Hedera pastuchowii*		
Epiphyte: +		*Viscum album*		
	3.3	*Festuca drymeja*	2.2	*Hedera pastuchowii*
	1.3	*Rubus caucasicus*	1.2	*Laser trilobum*
	1.2	*Aristolochia iberica*	1.2	*Geranium robertianum*
	1.1	*Galium aparine*	1.1	*Carex sylvatica*
	1.1	*Primula woronowii*	1.1	*Asplenium*
	1.1	*Viola odorata*	+.2	*Platanthera chlorantha*
	+	*Carpinus caucasica*	+	*Acer laetum*
	+	*Vicia crocea*	+	*Polygonatum verticillatum*
	+	*Alliaria officinalis*	+	*Dentaria quinquefolia*
			+	*Ajuga genevensis*
	+	*Poa nemoralis*	+	*Lamium album*
	+	*Salvia glutinosa*	+	*Asplenium trichomanes*
	+	*Concolvulus* sp.		
	+	*Scrophularia nodosa*		
	+	*Vicia iberica*	+.2	*Vicia iberica*
	(+)	*Silene wallichiana*		
	(+)	*Dactylis glomerata*	(+.2)	

Table 6.7, from a steep SSE-facing slope at 520 m elevation. In this forest, *Cornus mas* grew to small-tree size, and there was a fairly rich understorey of *Rubus caucasicus, Festuca drymeja, Hedera pastuchowii* vines, and a good variety of herbs. A richer floodplain forest from the same area, with less *Quercus*, is shown in Table 6.8 (Box et al. 2000).

Table 6.8 Floodplain *Carpinus-Acer-Fraxinus-Tilia* forest in Eastern Georgia (relevé G-14) (Box et al. 2000) (Location: Lagodekhi State Nature Reserve, plot "Matsimis Ubani" (30 May 1999))

T1	30 m	50 %	430 m Level (floodplain)	
T2	12 m	50 %		
S	4 m	20 %		
H	0.5 m	60 %		
M		15 %		
			40 × 20 m *EB*	
T1	3.3	*Carpinus caucasica*	3.3	*Acer campestre*
	2.2	*Fraxinus excelsior*	2.2	*Tilia begoniifolia*
	1.1	*Pterocarya pterocarpa*		
Vines: 1.1		*Hedera pastuchowii*	1.1	*Smilax excelsa*
T2	3.3	*Carpinus orientalis*	2.2	*Acer campestre*
	+	*Alnus barbata*		
Vines: 1.2		*Hedera pastuchowii*	+.2	*Smilax excelsa*
Epiphyte: 1.2		*Viscul album*		
S	2.2	*Carpinus orientalis*	1.1	*Carpinus caucasica*
	+	*Fagus orientalis*	+	*Pterocarya pterocarpa*
	+	*Ulmus elliptica*	+	*Sorbus graeca*
	+	*Mespilus germanica*	+	*Sambucus nigra*
	+	*Corylus avellana*	+	*Pyrus caucasica*
	+	*Cornus mas*	+	*Smilax excelsa*
	+	*Calystegia sepium*		
H	2.2	*Asperula odorata*	2.2	*Pachyphragma macrophyllum*
	2.2	*Sanicula europaea*	2.2	*Hedera pastuchowii*
	2.2	*Carex sylvatica*	1.3	*Oplismenus undulatifolius*
	1.2	*Geranium robertianum*	1.2	*Dryopteris filix-mas*
	1.1	*Primula woronowii*	1.1	*Deschampsia cespitosa*
	1.1	*Geum urbanum*	1.1	*Alliaria officinalis*
	1.1	*Galium aparine*	1.2	*Viola odorata*
	+.2	*Asplenium trichomanes*	+.2	*Geranium sylvaticum*
	+.2	*Asplenium pseudolanceolatum*	+.2	*Phyllitis scolopendrium*
	+.2	*Sedum stoloniferum*	+.2	*Convolvulus*
	+	*Acer campestre*	+	*Fraxinus excelsior*
	+	*Carpinus orientalis*	+	*Cormus mas*
	+	*Ajuga orientalis*	+	*Laser trilobum*
	+	*Stellaria media*	+	*Impatiens noli-tangere*
	+	*Euphorbia macroceras*	+	*Lamium album*
	+	*Fragaria vesca*	+	*Orobanche* sp.
	+	*Vicia* sp.		
M	2.2	*Mnium* spp. (3 spp.)		

Table 6.9 Primary deciduous forest with Hyrcanian elements, in Eastern Georgia (relevé G-15) (Box et al. 2000) (Location: Lagodekhi State Nature Reserve, "Rachis Ubani" section (30 May 1999))

T1	28 m	75 %	480 m, Slope: 2–3 ° to WSW	
T2	12 m	10 %		
S	5 m	20 %		
H	0.4 m	90 %		
			30 × 30 m	
T1	3.3	*Carpinus caucasica*	3.3	*Fraxinus excelsior*
	2.2	*Acer laetum*	2.2	*Acer platanoides*
	2.2	*Juglans regia*	1.1	*Acer campestre*
	1.1	*Fagus orientalis*	1.1	*Acer velutinum*
	1.1	*Cerasus sylvestris*		
T2	2.2	*Carpinus caucasica*	1.1	*Carpinus orientalis*
Vine: +.2		*Hedera pastuchowii*		
S	2.2	*Corylus avellana*	1.1	*Fraxinus excelsior*
	1.1	*Fagus orientalis*	1.1	*Acer campestre*
	1.3	*Rubus caucasicus*	1.1	*Euonymus latifolia*
	+.2	*Mespilus germanica*	+	*Ulmus elliptica*
	+	*Cornus mas*	+	*Prunus divaricata*
	+	*Hedera pastuchowii*		
H	2.3	*Asperula odorata*	2.3	*Stachys sylvatica*
	2.2	*Alliaria officinalis*	2.2	*Aristolochia iberica*
	2.2	*Hedera helix*	1.2	*Oplismenus undulatifolius*
	1.2	*Stellaria media*	1.2	*Viola odorata*
	1.2	*Lamium album*	1.2	*Salvia glutinosa*
	1.2	*Geranium robertianum*	1.1	*Euonymus latifolia*
	1.1	*Carex sylvatica*	1.1	*Galium aureum*
	1.1	*Dentaria quinquefolia*	1.1	*Pachyphragma macrophyllum*
	1.1	*Sanicula europaea*	1.1	*Poa nemoralis*
	1.1	*Dryopteris filix mas*	1.1	*Geum urbanum*
	1.1	*Athyrium distentifolium*	+.2	*Phyllitis scolopendrium*
	+	*Fraxinus excelsior*	+	*Acer campestre*
	+	*Primula woronowii*	+	*Euphorbia macroceras*
	+	*Polystichum*	+	*Moehringia trinervia*
	+.2	*Orobanche* sp.	+	*Chaerophyllum maculatum*

Although not significantly richer in species per relevé, a more impressive forest is the primary mesophytic forest in the Rachis Ubani area of the Lagodekhi reserve. A sample from this forest is shown in Table 6.9, from a very slight WSW-facing lower slope with rocky brown forest soil. This forest, which has apparently never been cut, has a canopy composed of *Fraxinus excelsior*, *Carpinus caucasica*, four *Acer* species, *Fagus orientalis*, *Jyglans regia*, and scattered canopy-size individuals

of *Cerasus sylvestris*. These are mostly typical European (or eastern European) species, but some elements of the Hyrcanian (east Caucasian-Caspian Tertiary) flora also appear in this forest, such as *Acer velutinum*, *Pterocarya pterocarpa*, and *Hedera pastuchowii*. The canopy on this plot had only 75 % cover, and the herb layer was correspondingly dense (90 %). On a nearby area the canopy reached 30 m and 90 % cover, with more *Fagus* and one individual of *Tilia begoniifolia* with 0.6 m-high plank buttresses. On this area, the T2 and S layers remained sparse and the herb-layer cover dropped to 50 % (Box et al. 2000).

6.6.4 *Q. macranthera* Forests

These forests are dominated by *Q. macranthera* (*sect. Macranthera*), which is known as "highland oak". The distribution area of these species comprises the eastern parts of the Greater Caucasus (including both northern and southern macroslopes), the Lesser Caucasus and mountains of Talysh. It is also found in West Caucasus (Svaneti). *Q. macranthera* forests are developed in north-eastern Turkey and in northern Iran (Elburs mts.).

These forests are confined to mid-mountain, high-mountain and subalpine zones; they are developed under relatively dry conditions at an altitude between 1,450 and 2,400 m a.s.l. (in some places at 2,600–2,700 m). The most favourable conditions for *Q. macranthera* are provided at an altitude of 1,450–1600 m near the upper limit of its distribution. Due to the aggravation of the process of regeneration, caused by overgrazing and other factors, highland oak started to form open woodlands and even crook-stem forests (Sakhokia 1980; Dolukhanov 2010).

Q. macranthera forests grow on mountain forest brown soils; close to timberline they occur on mountain forest-meadow brown soils and those of meadow-steppe.

Q. macranthera forms both mixed and monodominant forests. Birch-oak open woodlands (*Q. macranthera* is accompanied by *Betula litwinowii*) and those of *Sorbus-Betula-Quercus (Sorbus caucasigena) and Acer-Quercus (Acer trautvetteri)* are developed in subalpine and high-mountain belts. Constant species of these forests are manifested by *Carpinus caucasica* and *Fraxinus excelsior*; less characteristic species are *Fagus orientalis*, species of *Tilia*. *Spiraea hypericifolia, Lonicera caucasica, Berberis iberica, Cotoneaster racemiflora*, etc. frequently occur as underwood in these communities.

Common oak forests are those with:

1. Forbs (*Polygonatum verticillatum, Silene wallichiana, Chaerophyllum aureum*, etc.);
2. Forbs and ferns (*Dryopteris filix-mas*);
3. Subalpine tall herbaceous vegetation (*Senecio platyphylloides, Cephalaria gigantea, Grossheimia macrocephala, Telekia speciosa*);
4. *Calamagrostis arundinacea, Phleum phleoides, Dactylis glomerata.*

Q. macranthera forests with tall herbaceous vegetation are in contact with the vegetation of timberless volcanic uplands of South Georgia. Contact zones are of dry and cold climate; oak forests developed here bear the following names: "oak

forests with sheep's fescue [*Festuca ovina* group]", "steppe oak forests with forbs and grasses", "oak forests with sedges" (Dolukhanov 2010). The herbaceous ground vegetation is exhibited by the following species: *Carex buschiorum, Festuca valesiaca, Achillea biserrata,* etc.

Monodominant forests of *Q. macranthera* occur exclusively on steep southward slopes with poor skeletal soil. On the more fertile and moist soils *Q. macranthera* communities are replaced by hornbeam-oak forests (Dolukhanov 2010).

6.6.5 *Q. pedunculiflora* Forests

These forests occupy river valleys. *Q. pedunculiflora (Q. longipes)*, closely allied to the European species *Q. robur*, is an endemic species of Transcaucasia. It frequently occurs as arboreal component of oligo- and polydominant forests. *Q. pedunculiflora* is often accompanied by *Carpinus caucasica*, and also by *Ulmus minor, Acer campestre, A. platanoides, A. velutinum, Tilia begoniifolia,* and sometimes by *Fagus orientalis*. Under moist conditions, *Pterocarya pterocarpa* appears as admixture to these forests (Fig. 6.12).

In past times the above forests covered vast areas in East Georgia, whereas today only few remnants of these, once luxuriant forests, can be found (Dolukhanov 2010). Main massifs of these forests are situated in the valley of the river Alazani (Kakheti).

The following lianas are typical for *Q. pedunculiflora* forests: *Smilax excelsa, Periploca graeca, Clematis vitalba, Vitis vinifera* and *Hedera helix*.

6.6.6 *Q. imeretina* Forests

Quercus imeretina, endemic species of West Georgia, is related to *Q. pedunculiflora*. Distribution area of *Q. imeretina*, which once was well developed in West Georgia and occupied relatively dry areas on the right bank of river Rioni, has reduced under the impact of anthropogenic factors (cutting for timber, destruction of forests for arable land, etc.).

Q. imeretina forms both monodominant and mixed forests with *Carpinus caucasica, Zelkova carpinifolia, Fraxinus excelsior, Pterocarya pterocarpa, Alnus barbata*. Dolukhanov (2010) outlines the following groups of *Q. imeretina* forest types of Georgia:

1. Moist oak forests with *Smilax excelsa,*
2. Fresh oak forests with *Rhododendron luteum,*
3. Dry oak forests with *Carpinus orientalis,*
4. Dry oak forests with *Ruscus colchicus,*
5. Dry oak forests with *Hypericum xylosteifolium,*
6. Dry oak forests with *Zelkova carpinifolia.*

Fig. 6.12 Colchic lowland forest at Paliastomi lake, West Georgia (Photo O. Abdaladze)

6.6.7 *Q. dschorochensis* Forests

Q. dschorochensis forests are restricted to the south-western part of Ajara. Outside Georgia they occur in Chorokhi (Coruh) valley (Turkey). The remnants of these forests have survived only on sunny and dry rocky slopes (Dolukhanov 2010).

6.6.8 *Q. hartwissiana* Forests

Contrary to other Caucasian oaks, *Q. hartwissiana* has never formed monodominant forests. Today it participates in the formation of oligo- and polydominant forests of West Transcaucasia; it frequently occurs as a characteristic component of mixed forests of Colchis. *Q. hartwissiana* grows on rich moist soils. It populates foothills and low-mountain zone within the altitude of 1,200 m. The above-mentioned oak is often accompanied by *Zelkova carpinifolia*.

6.7 Hornbeam Forests

Carpinus caucasica is widely distributed throughout the Caucasus; it prefers fertile soils with good drainage.

These thermophilous species appear as dominants of the second stratum, forming hornbeam-beech and hornbeam-oak forests. *C. caucasica* and *Cerasus sylvestris* (Fig. 6.13a) is a usual component of polydominant forests. It should be underlined, that Caucasian hornbeam is adaptive to various conditions of environment (Shelyag-Sosonko 1980; Box et al. 2000; Dolukhanov 2010).

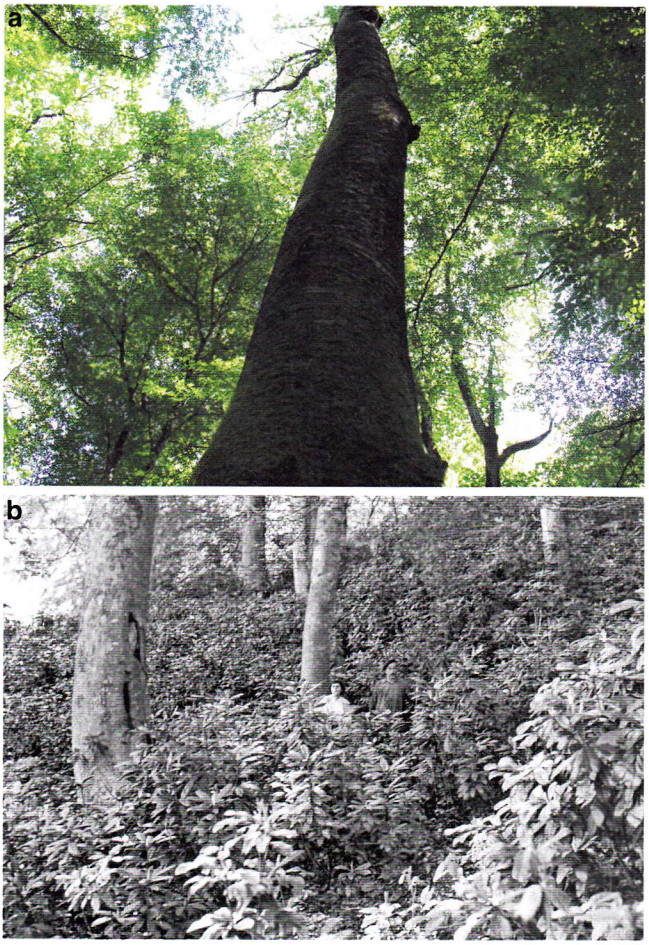

Fig. 6.13 (**a**) *Cerasus sylvestris*, Lagodekhi National Park, East Georgia (Photo O. Abdaladze), (**b**) *Castanea sativa* with *Rhododendron ponticum* (Photo A. G. Dolukhanov)

Hornbeam forests are very diverse phytosociologically. Dolukhanov (2010) distinguishes the following two classes in hornbeam forests: *C. caucasica* forests with Colchic undergrowth and those without Colchic undergrowth. The first class involves the following communities:

1. *C. caucasica* forests with *Poa angustifolia,*
2. *C. caucasica* forests with *Festuca drymeia,*
3. *C. caucasica* forests with forbs,
4. *C. caucasica* forests with *Trachystemon orientalis.*

Hornbeam forests with Colchic undergrowth are abundant in lower parts of the forest zone, where they are not replaced by beech-woods and dark coniferous forests. The above-mentioned forests include the following associations:

1. *C. caucasica* forests with *Rhododendron luteum*,
2. *C. caucasica* forests with *Vaccinium arctostaphylos*,
3. *C. caucasica* forests with *Rhododendron ponticum*,
4. *C. caucasica* forests with *Laurocerasus officinalis*.

Hornbeam communities with *Rh. luteum* are characteristic of West Georgia, though they can also be met in East Georgia (Kakheti and Aragvi river basin).

C. caucasica forests with *Vaccinium arctostaphylos* occur in West Georgia (Abkhazeti, Upper Svaneti, Guria) between 900 and 1,750 m, whereas those with *Rh. ponticum* are restricted to northern slopes of the lower part of the forest zone of non-limestone regions of West Georgia; they extend from 100 up to 800 m.

Hornbeam forests with *Laurocerasus officinalis* occupy steep stony northern slopes of West Georgia at 300–800 m. They occur on both calcareous and non-calcareous soils.

6.8 Sweet-Chestnut Forests

Castanea sativa forests are developed in both West and East Georgia, but to the west of the country they occupy larger areas. In some localities pure stands of *C. sativa* can be found, but mainly sweet-chestnut occurs as a component of oligodominant beech-sweet-chestnut and hornbeam-beech-sweet-chestnut forests. In prehistoric times, the distribution area of *C. sativa* noticeably exceeded the present one.

Sweet-chestnut forests are chiefly restricted to shady slops. In West Georgia they extend from 100 up to 900–1,000 m a.s.l.; approximately the absolute upper limit of *C. sativa* is situated at 1,400–1,450 m. In East Georgia (Kakhetis Kavkasioni) the lower limit of sweet-chestnut forests is about 400–500 m, and the upper 1,350–1,380 m (Dolukhanov 2010). *C. sativa* forests occur on yellow-brown soils (Urushadze 1987). Though sweet-chestnut generally avoids calcareous soils, it can be found on limestone substratum in several localities in Georgia as well.

The forests of *C. sativa* are made subject to cutting in many regions. Besides, the bad state of *C. sativa* populations can be accounted by the impact of parasitic fungi. Dolukhanov (2010) considers that sweet-chestnut forests of Georgia still need to be adequately studied. He outlines the main association groups of *C. sativa* forests:

1. Sweet-chestnut forests with *Trachystemon orientalis*; these communities found in West Georgia, are represented mostly by beech-sweet-chestnut and hornbeam-beech-sweet-chestnut forests.
2. *C. sativa* forests with ferns (*Dryopteris filix-mas*). These communities occupy stony localities. Here sweet-chestnut is accompanied by *Alnus barbata, Ulmus minor, Acer laetum, Fagus orientalis, Carpinus caucasica*.
3. *C. sativa* forests with forbs (*Sanicula europaea, Galium (Asperula) odoratum, Festuca montana, Paris incompleta, Polygonatum polyanthemum*). These communities are typical for West Georgia. *Hedera helix* is a common liana here.
4. *C. sativa* forests with *Rhododendron luteum*. These communities are widespread in West Georgia. They occupy several localities in mountainous Kakheti.

5. *C. sativa* forests with *Vaccinium arctostaphylos*. These forests are abundant in Abkhazeti. Their arboreal components are represented by *Fagus orientalis* and rarely by *Carpinus caucasica*.
6. *C. sativa* forests with *Rhododendron ponticum*. They are confined to the mountains of West Georgia. Sweet-chestnut is accompanied by beech and especially by hornbeam (*Carpinus caucasica*). *Rh. ponticum* extends up to 3–4 m here (Fig. 6.13b).
7. *C. sativa* forests with *Laurocerasus officinalis*. Contrary to the communities with *Rh. ponticum*, these forests are rarely found. They are characterized by the admixture of *Rh. ponticum* to the dense thickets of *Laurocerasus officinalis*. These communities are confined to West Georgia.

6.9 Forests with *Zelkova carpinifolia*

Zelkova carpinifolia (Fig. 6.14) is a relict of the Tertiary flora. The present-day distribution area of this species involves the refuges of Lenkoran (Azerbaijan) and Colchis; *Z. carpinifolia* sometimes occurs in Kakheti (East Georgia) and Karabakh (Armenia).

Monodominant forests of *Zelkova* are rarely found; usually it forms mixed communities with oak species (*Q. imeretina, Q. iberica, Q. hartwissiana, Carpinus caucasica* and *C. orientalis*).

In many areas in Transcaucasia the upper limit of *Z. carpinifolia* varies in altitudes between 1,200 and 1,700 m a.s.l., whereas in Georgia it lies at 750 m. In West Georgia, *Zelkova* is chiefly confined to plains; very often it is met in forest margins and exposed locations. In Kakheti *Z. carpinifolia* occupies all slopes, excluding northern ones. This species occurs on both thin and rich soils, but avoids saline soils. In West Georgia *Zelkova* forests grow on alluvial-skeleton, sandy and clayey-sandy soils, whereas in Kakheti they are found on both deep brown and thin skeletal soils.

In West Georgia (Colchis) *Zelkova*-hornbeam-oak forests are well preserved. To the east of the country, *Zelkova* forests are represented by *Z. carpinifolia-Carpinus orientalis* communities (Sharashidze 1967)

According to Sharashidze, in West Georgia, *Z. carpinifolia* participates in generating the following associations:
Zelkoveto-Querceta (*Q. imeretina*) hypericosa (*H. inodorum*),
Zelkoveto-Querceta ruscosa (*R. colchicus*),
Zelkoveto-Querceta brachypodiosa (*Brachypodium sylvaticum*),
Zelkoveto-Querceta rhododendrosa (*Rh. luteum*),
Zelkoveto-Querceta juncosa (*J. effusus*),
Zelkoveto-Querceto carpinosa (*C. orientalis*).

The following associations are typical for East Georgia:
Paliureto (*Paliurus spina-christii*)-Zelkoveta astragalosa (*A.brachycarpus*),
Zelkoveto-Carpineta (*C. caucasica*),
Zelkoveto-Crataegeta (*C. pentagyna*) geraniosa (*G. palustre*),
Juglandeto-Zelkoveta clinopodiosa (*Calamintha clinopodium*).

Fig. 6.14 *Zelkova carpinifolia*, Babaneuri Reserve, East Georgia (Photo O. Abdaladze)

6.10 Forests with Yew *(Taxus baccata)*

Taxus baccata was once widely spread in Georgia. Forests with considerable admixture of the yew are preserved in Batsara Reserve (East Georgia). It occupies fresh moist soils, developed on carboniferous rocks. Within the territory of the reservation the yew extends from 900 up to 1,350 m; in some locations it is registered to have reached 1,500 m. In Colchis, the lower limit of *T. baccata* descends to the sea level, whereas in East Georgia the yew never comes down to 700 m. Below the dense canopy, *T. baccata* grows slowly and under the abundant sunlight it is characterized by stag headedness (Dolukhanov 2010) (Fig. 6.15a).

Fig. 6.15 (**a**) *Taxus baccata*, Batsara Reserve, East Georgia (Photo P. Shanshiashvili), (**b**) *Buxus colchica*, Colchis, West Georgia (Photo O. Abdaladze)

6.11 Forests with *Buxus colchica*

Buxus colchica is closely related to *B. sempervirens*, which is widely distributed throughout the southern sector of West Europe and Mediterranean. *Buxus colchica* is confined to West Georgia, especially to the limestone regions of Abkhazeti, Samegrelo, Racha-Lechkhumi. In East Georgia it has been cultivated since pagan times (Fig. 6.15b).

B. colchica extends from sea level up to 1,300 m. It is an arboreal component of scattered forests of hornbeam and other broad-leaved trees. Cochic box, highly valued for timber, undergoes intensive cutting.

The flora of the forests with *B. colchica* which occupy limestone slopes is very rich in local endemics and Mediterranean species. These forests involve such constant species, as *Ruscus ponticus, Hedera helix, Asplenium adiantum-nigrum, Carex divulsa, C. transsilvanica, Cyclamen abchasicum, Veronica peduncularis* and *V. persica* (Dolukhanov 2010).

6.12 Forests with Maples (*Acer velutinum* and *A. laetum*)

Acer velutinum is a typical representative of Hyrcanian (Azerbaijan) forests. In Georgia it occurs only in the valley of river Alazani. The upper limit of *A. velutinum* amounts to 1,000 m. *A. laetum* is confined to West Georgia and extends from sea level up to 1,400–1,600 m (higher 2,400 m it is *replaced by A. trautvetteri*). In East Georgia, *A. laetum* is restricted to moist mountain forests. Both maples occur in beech-woods and mixed forests.

Near-Timberline Vegetation

7

In the Caucasus and, particularly, in Georgia, the upper limit of forests is lowered. Straight-trunk forests of dense stands have definite climatic limits in their vertical distribution. Climate above this upper boundary noticeably varies: summer temperature falls with the increase of precipitation, slopes receive abundant solar radiation with the prevalence of ultraviolet refraction, etc.

Low forests composed of the species of *Abies, Pinus, Picea, Fagus* occur on relatively dry and sunny slopes above the forest belt, whereas subalpine crook-stem forests (*Betula litwinowii, Sorbus caucasigena*) are developed under moist conditions. Low forests have become very thin, due to the fatal effect of even slight anthropogenic influence. Continuous low forests, which have probably existed before, are unavailable in present-day Georgia.

Treeline in this area occurs at about 2,300 m, where the treeline krummholz is composed mainly of *Salix kazbekensis* and *Betula litwinowii*, within a matrix of dense *Rhododendron caucasicum* patches and grassy areas, as suggested by the relevé in Table 7.1. There is also a significant moss cover.

Main forest communities of Georgia which reached the subalpine belt, involve the forests of spruce, pine, beech, fir and oak (*Q. macranthera*).

As it was pointed out, dark coniferous forests extend to the altitude of 2,100–2,200 m on prominent slopes. According to Dolukhanov (2010), the upper limit of pine forests does not surpass the level of the 11 °C – isotherms of the warmest month, and that of low forests: 10.5°C. Under moist climatic conditions, the above-mentioned forests are rarely found at altitudes higher than 2,150 m, whereas in continental areas (Tusheti) they reach 2,400 m a.s.l.

Crook-stem forests of *Fagus orientalis* (Fig. 7.1a) extend to 2,300 m in some areas; at the same time vertical limits of these communities are located at 2,350–2,570 m in the moist mountains of South Colchis. It should be noted that beech does not occur under more continental conditions above 2,200 m, and it never surpasses the level of 11 °C isotherms of the warmest month. Vertical distribution of *Quercus macranthera* attract particular interest. Under dry climatic conditions *Q. macranthera* occupies higher altitudes, than in areas with moist climate. The upper limit of its vertical distribution varies between 2,100 and 2,350 m.

G. Nakhutsrishvili, *The Vegetation of Georgia (South Caucasus)*, Geobotany Studies,
DOI 10.1007/978-3-642-29915-5_7,

Table 7.1 *Rhododendron-Salix* treeline krummholz, above Bakuriani (relevé G-6) (Box et al. 2000) (Location: Treeline above Bakuriani, embankment along road (25 May 1999))

S1	2.0 m	40 %	2,300 m, Slope: 30 ° to NW	
S2	1.0 m	90 %		
H	0.1 m	30 %		
M		40 %		
			5 × 10 m	KF, GN, *EB*, RJL
S1:	3.3	*Salix kazbekensis*	2.3	*Betula litwinowii*
	+	*Salix apoda*		
S2:	5.4	*Rhododendron caucasicum*	1.2	*Vaccinium myrtillus*
H:	2.3	*Deschampsia cespitosa*	2.3	*Calamagrostis arundinacea*
	1.2	*Poa longifolia*	1.2	*Agrostis planifolia*
	1.2	*Alchemilla retinervis*	1.1	*Betonica macrantha*
	1.1	*Polygonum carneum*	1.1	*Athyrium filix-femina*
	+	*Daphne glomerata*	+	*Vaccinium vitis-idaea*
	+	*Oxalis acetosella*	+	*Primula ruprechtii*
M:	3.3	*Hylocomium splendens*	1.2	*Pleurozium schreberi*
	+.2	*Dicranum elongatum*		
lichen	+.2	*Cetraria islandica*		

Betula litwinowii, closely related to *B. pubescens*, is one of the most characteristic and common species of subalpine crook-stem forests of the Caucasus. Its upper distribution limit does not exceed the level of the 11 °C isotherms of August, while in the areas where it is unprotected by snow coat, the 9.5 °C isotherms. The common associate of the above-mentioned species is *Sorbus caucasigena*.

In Bakuriani (the Lesser Caucasus) and Kazbegi (the Greater Caucasus) birch forest vegetation was studied in the subalpine zone (2,200–2,400 m) (Nakhutsrishvili et al. 2009, an unpublished list 12). The following phytocoenoses were distinguished:

Bakuriani 2,200–2,350 m:

Betula litwinowii-Salix kazbekensis
B. litwinowii-Rhododendron caucasicum
B. litwinowii-Sorbus caucasigena
B litwinowii-Acer trautvetteri
B. litwinowii-Salix caprea
B. litwinowii-Tall herbaceous (*Geranium sylvaticum, Anthriscus nemorosa, Astrantia maxima, Valeriana tiliifolia, Heracleum sosnowskyi*, etc.)

Kazbegi 2,200–2,400 m:

B. litwinowii-Salix kazbekensis
B. litwinowii-Salix caprea
B. litwinowii-Sorbus caucasigena
B. litwinowii-Rhododendron caucasicum
B. litwinowii-Vaccinium myrtillus

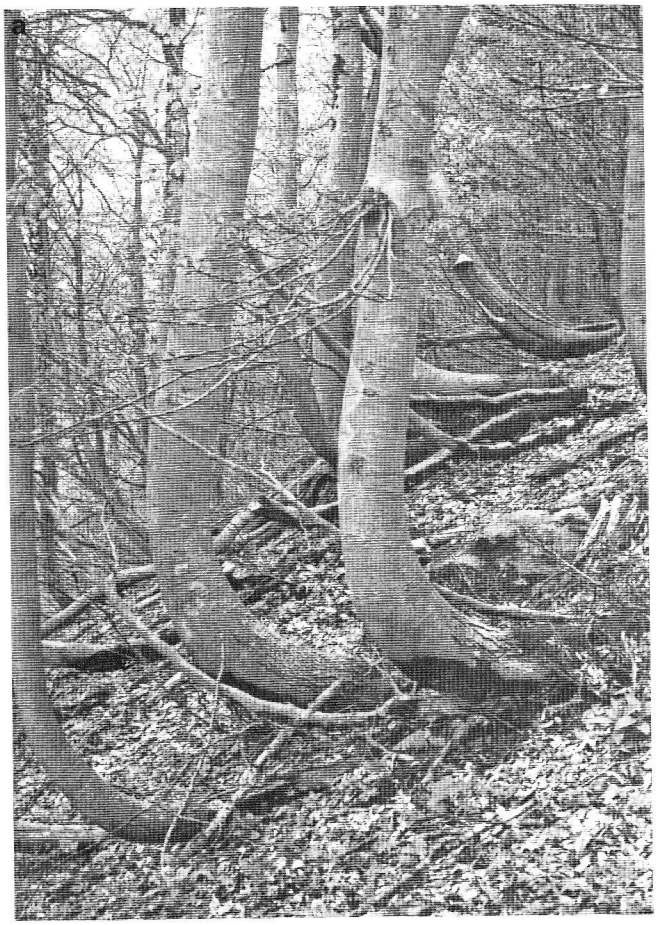

Fig. 7.1 (continued)

B. litwinowii-Tall herbaceous (*Swertia iberica, Cephalaria gigantea, Aconitum nasutum, Senecio caucasigenus, Valeriana tiliifolia*, etc.)

B. litwinowii with meadow elements: *Calamagrostis arundinacea, Deschampsia flexuosa, Alchemilla laeta, Betonica macrantha*, etc.

The Colchic endemics *Betula medwedewii, B. megrelica* and *Quercus pontica* are less frost-resistant, but they are well adapted to cold and moist subalpine summer. As components of crook-stem forests they reach 2,300–2,700 m, whereas under more continental conditions their upper limit is lower. Dolukhanov ascribes this dependence of upper limits on continentality of climate to the specific features of each species (Figs. 7.1b, c and 7.2a–c).

Open woodlands, low forests and crook-stem forests are very diverse and floristically rich. In the subalpine belt these communities are restricted to prominent

Fig. 7.1 (**a**) Crook-stemmed Fagetum (Photo A. G. Dolukhanov), (**b**) *Quercus pontica*, Colchis, West Georgia (Photo D. Kharazishvili), (**c**) Timberline, Kazbegi, the Central Caucasus (Photo U. Bohn)

slopes; they are rarely found at altitudes higher than 2,150 m. Fir and spruce forests lose their productivity with the increase of altitude. Under the impact of anthropogenic factors, pine forests and those of *Quercus macranthera* have almost everywhere and quite irregularly retreated from their natural upper boundaries.

The upper limit of straight-trunk beech forests is situated at about 2,050–2,100 m (rarely at higher altitudes). At altitudes higher than approximately 2,200–2,300 m, beech forests are represented by dwarf semi-creeping formations; trees are pressed to the ground under the snow mass and lower parts of their trunks are rooted. The fact, that due to the increase of altitude, trunks of beech become dwarfed, is worth special interest. Crook-stem forests of *Fagus orientalis* are characteristic of Colchis. Several creeping, vegetative-migratory representatives of undergrowth (*Vaccinium arctostaphylos, Ilex colchica, Laurocerasus officinalis, Ruscus colchica,* and rare *Rhododendron ponticum*) grow under the canopy of these above-mentioned forests.

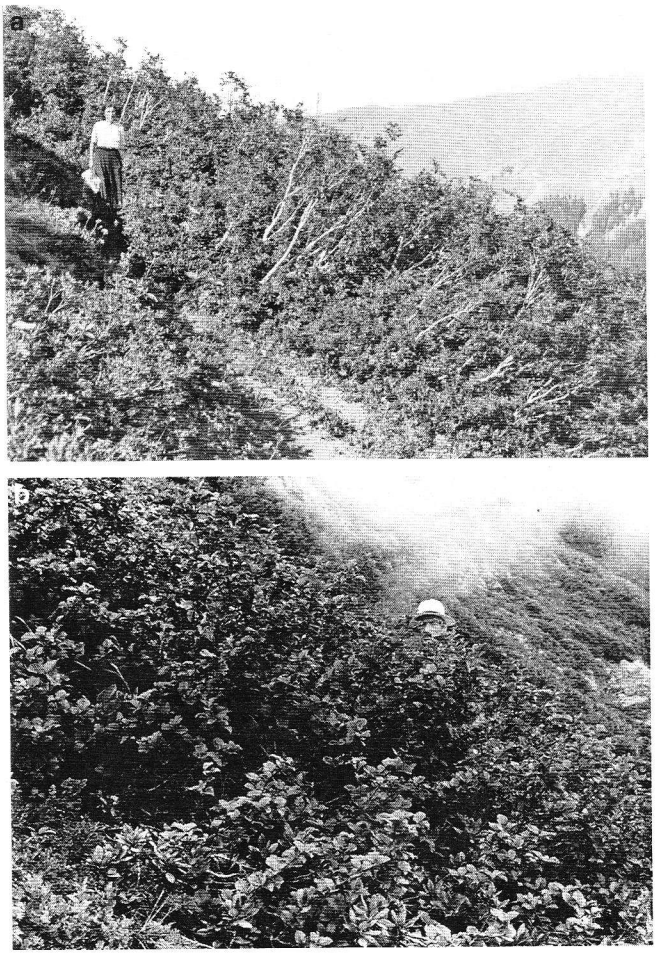

Fig. 7.2 (continued)

In the areas with less contrasting conditions, crook-stem forests of beech are in contact with *Sorbus-Betula* forests as well as with thickets of such Colchic endemics as *Rhamnus imeretina, Corylus colchica, Sorbus subfusca*, and the species of *Salix* distributed in highlands. Low forests of *F. orientalis*, unavailable today, might have existed before.

Crook-stem forests of *Betula litwinowii* are the most typical communities of subalpine belt. This endemic species of the Caucasus is closely related to *B. pubescens*.

Under relatively continental climatic conditions, the lower limit of *B. litwinowii* comes to approximately 2,000 m a.s.l., and the upper boundary varies between 2,400 and 2,600 m. At the same time, *B. litwinowii* occurs also at lower altitudes; it

Fig. 7.2 (**a, b, c**) Crook-stemmed *Betula medwedewii*, Bakhmaro, West Georgia (Photo A. G. Dolukhanov)

comes down by moraines, scree, rocky slopes, etc. Although *B. litwinowii* is a light consumer, it occupies the slopes of northern exposure to secure protection by snow cover in winter.

The specific feature of *B. litwinowii* low forests is that they occur exclusively on dry mountains of East Georgia. Today these communities are almost completely destroyed.

Crook-stem forests of *B. litwinowii* contrary to beech communities are rarely monodominant: the constant species of these communities is *Sorbus caucasigena*. This species is represented in the Caucasus by the following two races (microspecies): *S. caucasigena* and *S. boissieri*. The distribution area of another Caucasian birch, *B. raddeana*, includes Tusheti mountains and the upper parts of the rivers Didi Liakhvi, Aragvi and Tergi river basin. In Georgia, *B. raddeana* extends up to 225 m. In the lower sector of the subalpine belt *B. litwinowii* is found along with *Acer trautvetteri, Salix caprea, Padus avium*, etc. In Colchis *B. litwinowii* is accompanied by *Sorbus subfusca, Rhamnus imeretina, Ribes biebersteinii*, and *Rubus buschii*.

Rhododendron caucasicum, an endemic of the Caucasus, is a characteristic species of crook-stem forests of birch (Figs. 7.1c and 7.3a, b).

It is specific that birch forests with *Rhododendron* are characterized by presence of representatives of the flora of taiga. Examples are *Huperzia selago, Lycopodium annotinum, L. clavatum, Diphasiastrum (Lycopodium) alpinum, Gymnocarpium dryopteris, Cystopteris montana, Listera cordata, Deschampsia flexuosa, Orthilia secunda, Pyrola minor, Vaccinium vitis-idaea*.

Vaccinium myrtillus, V. uliginosum and *Oxalis acetosella* are the exclusive species of these communities.

Fig. 7.3 (**a**) *Rhododendron caucasicum*, Kazbegi, Central Caucasus (Photo O. Abdaladze), (**b**) *Rhododendron caucasicum*, Colchis, West Georgia (Photo A. G. Dolukhanov)

Bryophytes growing in the above-mentioned forests are very diverse and peculiar for coenotic variability. These communities are rather rich in species (over 600) (Dolukhanov 2010).

Kvachakhidze (1979) outlines 15 associations of birch forests situated on the southern slope of the Greater Caucasus. These associations may be united into the following 5 groups, such as:

1. Birch forests with evergreen undergrowth,
2. Birch forests with summergreen undergrowth,
3. Birch forests with tall herbs,
4. Birch forests with forbs,
5. Birch forests with grasses.

Fig. 7.4 *Rhamnus imeretina*, Colchis, West Georgia (Photo Z. Manvelidze)

Fig. 7.5 Crook-stemmed *Quercus pontica*, Colchis, West Georgia (Photo A. G. Dolukhanov)

West Georgia (especially South Colchis) is characterized by subalpine vegetation, which is unavailable in any other areas of West Eurasia (Kolakovsky 1980; Dolukhanov 2010). Only creeping and semi-creeping woody plants grow in this subalpine belt, and among them, there are light-demanding and shade-bearing trees. Light-demanders are exemplified by *Betula medwedewii, B. megrelica, Quercus pontica, Rhamnus imeretina* (Fig. 7.4), *Sorbus subfusca* and *Corylus colchica.*

Crook-stem forests of *Quercus pontica* (Fig. 7.5) and *Betula medwedewii* emerge from under the snow cover only in June. Vegetative reproduction is typical for these species (Dolukhanov 1956; 2010).

The following shade-enduring plants frequently occur as underwood in the creeping crook-stem forests: *Rhododendron ponticum, Laurocerasus officinalis, Ruscus colchicus, Ilex colchica.*

At present, relatives of the species forming crook-stem forests and Colchic undergrowth have mainly survived in the mountains exposed to the summer monsoon in eastern and south-eastern Asia, in the Appalachians of North America and on Maccaronesia. Thus, the Colchic refuge is isolated from the other centres of these floristic elements. This leads to the suggestion that the corresponding endemic species of the subalpine belt of Colchis belong to the relics of a rather remote past (Dolukhanov 1956; 1966a, b; 1980).

Below are given Betuleta relevés from Bakuriani and Kazbegi compiled in 2009–2011 (Tables 7.2 and 7.3).

Interesting example of Betuleta (*Betula medwedewii*) represented in the river Chirukhistskali gorge, Adjara (Colchis) was described by D. Kharazishvili (2005). *B. medwedewii* and forests dominated by this species are quite widespread in the subalpine belt of the seaside part of southern Colchis (Guria, Adjara, Lazistan of Turkey). As reported by Dolukhanov, *B. medwedewii* is a conservative relict of the ancient flora. It is referred to a section *Costatae*, other representatives of which are in the main distributed in southern and south-eastern Asia. A number of its species occur in the Himalayas and mountains of the North America. According to this author, Colchis is the only place throughout the vast areas of the west Eurasia, where two representatives of this section, namely, *B. medwedewii* and *B. megrelica* have remained. The frequency of the latter species is lower and it occurs in northern Colchis. *B. medwedewii* represents the isolated, vegetatively motile, semi-prostrate life form, which is well adapted to highly humid (perhumid) climate.

Fago-Betuleta are elfin forests. The coenoses of such composition, characterized by the elfin form, such distribution pattern and, first of all, not subjected to human intrusions are rare (Table 7.4). These coenoses are formed on very steep slopes, at quite high altitudes. They are primary owing to the high inclination degree of slopes. Woody plants are diverse. The maximum tallness of the trees is 3 m, some trees have the elfin form (beech), others do not exceed shrubs (birch, willow, poplar). *Gypsophila tenuifolia* is a noteworthy endemic (Caucasian).

7.1 Treeline Biotopes

On the Central Greater Caucasus the natural treeline ecotone consists of open and elfin crooked-stemmed (Krummholz) birch forests, tall herbaceous vegetation, scrub and meadows. The treeline vegetation in this part of the Caucasus is strongly degraded and lowered (at the average by 200–400 m) because of long-term overgrazing, tree cutting, etc. (Dolukhanov 1966a, b; 1978; 2010; Nakhutsrishvili 1999). The treeline in the Central Caucasus is characterized by high level of plant diversity and endemism (Kharadze 1948; Sakhokia and Khutsishvili 1975; Gagnidze 2000). In the Kazbegi region, the ecological state of the treeline ecotone can be assessed as normal only on certain massifs. These forests have been

Table 7.2 Betuleta, Bakuriani (Leser Caucasus, Trialeti)

Nr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fall	50			40	40	45	35	45	40				20	70	80	30
Exposure	N	N	N	N	NNE	N	NE	NE	N	N	N	N	NW	N	N	NNE
Plot size (m^2)	50		200	100	50	50	50	100	100		100	100	200	100	100	200
Height tree		8					8		10	15	10	10	10	7	7	7
Tree cover (%)		20					20		70	60	40	70	80	70	80	80
Shrub height	4	4	4	4	4	5	4	3		4						
Shrub cover (%)	80	60	20	80	60	70	30	30		10						
lHerb height	1	1	120	60	60	60	1	1	1	150	150	120	1	120	120	120
Herb cover (%)	70	90	70	70	90	90	90	90	90	90	90	80	85	70	80	80
T + S																
Betula litwinowii	5	2/2	1		2	3	1	1	4	3/1	3	4	5	4	5	4
Salix kazbekensis	2	3														
Salix caprea		†	2				2/1	2	†	2	2	†	†	†	†	2
Sorbus caucasigena			1	5	3	1	2	2	†				1		†	2
Salix kusnetzowii														†		
Ribes biebersteinii			†	†		†	†							†	†	†
Acer trautvetteri							†		0/1		2					
Quercus macranthera													†			
Fagus orientalis														†		
H																
Rubus saxatilis	†															
Ranunculus caucasicus	†	1	1				†	†		†		†	†			
Polygonum carneum	†	†					†			†			†		†	†
Calamagrostis arundinacea							2	1	1			1			1	
Swertia iberica	1	2														
Deschampsia flexuosa									†							

Chaerophyllum roseum	†															
Sorbus caucasigena												†			+	
Sedum stoloniferum	†	2														
Alchemilla oxysepala	1	1					†	1			2		†	1	2	
Hieracium pannoniciforme								†					†			
Veratrum album				†		†	2		1	2	†	†	†	†	†	1
Myosotis arvensis		1	+				+						+		+	
Cruciata glabra	2												+			
Cephalaria gigantea	2	2					+			+	+	1	2	+	1	+
Vicia grossheimii	+															
Fritillaria lutea											+					
Vaccinium myrtillus			+								1					
Trollius ranunculinus			+			+	1	+	1	2						
Betonica macrantha	3	3						+	+	+			+			+
Veronica gentianoides	+	+														
Macrotomia echioides	+	+														
Primula amoena			1								+					
Pimpinella rhodantha											+		+			
Cirsium frickii						+										
Valeriana alpestris		1														
Primula macrocalyx			1													
Scabiosa caucasica																+
Festuca varia subsp. *woronowii*	2	2										1			1	
Dolichorrhiza caucasica	+															
Rhododendron caucasicum			3	2	5	2	2	5								
Geranium sylvaticum						+	2	1	1			2		+	+	+
Poa iberica				+								+			+	

(continued)

Table 7.2 (continued)

Nr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Lathyrus cyaneus	+															
Bromopsis variegata											+					
Alchemilla sp.			+	+		1										
Polygonatum verticillatum									1							+
Lapsana grandiflora			+			1	1	+	1	+	+	+	+	1	1	1
Aconitum nasutum				+		1	+		1		+		+	+		+
Vicia balansae										+		2	1	1	1	1
Festuca sylvatica		2							1		2		2		2	3
Senecio caucasigenus							+			1						
Anthriscus nemorosa							+		+				3			
Chaerophyllum maculatum						+							2	1	1	1
Cirsium obvallatum	+	+					+			+	+		+	+		
Silene vulgaris			+				+		+	+	+		+	+	1	
Vicia sepium									2	1			+	+		
Urtica dioica				1							+					
Pedicularis condensata								1	+	+		+	+	+		
Salix caprea											1					
Trifolium ambiguum								+			+					
Inula orientalis	+															
Poa nemoralis	+										2		1		+	+
Dryopteris filix-mas				2					+					1		
Pyrethrum roseum	+											+				
Ranunculus oreophilus															+	
Trifolim trichocephalum												1		+		
Angelica tatianae			+								+			+	1	+
Geranium ibericum													1			

Lotus caucasicus								+			+					
Campanula collina								+								
Ligusticum alatum											1					
Leontodon hispidus											+					
Valeriana tiliifolia	2			1	3		2		2			2		3	3	1
Heracleum asperum			+						+	1	+	2	1	1		2
Cirsium vulgare	+	+							+							
Cerastium hemschinicum	+															
Vicia crocea		+														
Epilobium angustifolium			2								+					
Milium effusum			2	3		2	2		2	2		2		1		
Rubus idaeus			1				1									
Rumex alpinus			1	+		+	+				1			+	1	
Doronicum macrophyllum			+					+		1						
Senecio othonnae			+			2										
Cardamine uliginosa			+	+		+										
Oxalis acetosella				2		+										
Rhynchocorys elephas				+												
Epilobium alpestre				1		+										
Geum Cf. *montanum*				+												
Symphytum asperum				+						1	1					+
Heracleum wilhelmsii						2					+				+	
Cruciata laevipes						+					+					
Cicerbita macrophylla						+										1
Doronicum macrophyllum						1						+				
Inula grandiflora							2	1								
Saxifraga cymbalaria							+	+	+					1	1	
Aquilegia caucasica							+									
Erigeron alpinus								+								

(continued)

Table 7.2 (continued)

Nr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Gentiana schistocalyx								+								
Doronicum orientale								+		+						
Traunsteinera globosa								+								
Astrantia maxima								1		1			2	+		
Petasites albus									2			1				
Galium odoratum									+				+	+		
Primula amoena									+							
Athyrium filix-femina									1							
Veronica gentianoides.									+							
Dactylorhiza maculata									+							
Veronica chamaedrys									+							
Galega orientalis										2	2					
Rhynchocorys elephas										+						
Cerastium sp.										1	+	+			+	+
Dactylis glomerata										+			+		+	+
Heracleum sosnowskyi													+	2		1
Grossheimia macrocephala										+						
Knautia montana											1					
Lamium album											+					
Bunias orientalis											2					
Cicerbita macroyphylla											+					
Achillea millefolium											+					
Trifolium medium											+		+			
Trifolium pratense											1					
Betula litwinowii											+			+		
Inula helenium											+					
Campanula latifolia											+	+		2	1	+

Tripleurospermum caucasicum			+				
Phleum pratense			+				
Tragopogon graminifolius			+				
Linum hypericifolium	+		+	+			
Trisetum flavescens				+			
Bupleurum nordmanianum				+			
Acer trautvetteri				+		+	+
Seseli transcaucasicum				+			
Senecio rhombifolius					+		
Aconitum orientale					+		
Ptarmica ptarmicifolia					+		
Barbarea minor					+		
Heracleum wilhelmsii					+		
Veronica crista-galli					+		
Veronica longifolia					+		
Trifolium repens						+	
Galium aparine						+	
Poa alpina						+	
Rumex arifolius						+	
Poa longifolia						+	
Rosa sp.							1
Hesperis matronalis							+
Lilium szovitsianum							+
Euphorbia macroceras							+
Aconitum orientale							+
Hypericum hirsutum							+
Lathyrus aureus							2

Table 7.3 Betuleta, Kazbegi (Central Greater Caucasus)

Nr	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	14	15	16	17	18	19	20	21
Fall	15	20	25	30	25	25	20	25	25	30	35	40	35	45	25	40	60	40	55	20	30
Exposure	N	N	NW	NW	N	NW	N	N	N	NE	N	N	N	NE	NE	NE	NE	N	N	N	N
Plot size (m^2)	100	100	25	50	50	100	100	100	100	100	100	100	100	100	50	50	50	100	100	100	100
Height tree					15	15	12	12	15	15		6						10	10	10	
Tree cover (%)					20	75	70	60	75	70		40						70	50	50	
Height shrub	4	4	3	2	4	3	2	2	2	2	5	2	5	150	150	150	150	150		3	5
Shrub cover (%)	80	80	90	60	80	20	20	15	30	10	25	10	40	60	60	70	90	5		20	80
Height herb	40	40	50	40	1	1	50	1	50	50	1	1	1	120	70	70	70	120	120	120	120
Herb cover (%)	60	50	70	100	80	80	80	90	80	80	90	80	90	100	100	100	100	90	80	70	70
T + S																					
Betula litwinowii	5	5	5	3	3	5/1	4	4/2	4/3	4/2	2	3	3	1	1	1	+	3	3	2	3
Salix kazbekensis	2	1	2	2			+								+		1				
Salix caprea					3				+		1	+						2			1
Sorbus caucasigena					+	2	1	1	+	+		1	+							1	
Rosa mollis					+	+	2		+		1										
Salix kusnetzowii					2									2	1						
Lonicera caucasica						+															
Populus tremula									1												
Rhododendron caucasicum															2	2	3			2	2
Ribes biebersteinii																				+	
Rosa oxyodon																		1		+	
Rubus idaeus																1					
Vaccinium myrtillus														1		2	2				
H																					
Rubus saxatilis	2	2	2	+	1	2	3	3	2		2		+	1				+	+	+	+
Ranunculus caucasicus	+		+	1	+		+	+	+	1	1	1	1	+	+						

Polygonum carneum	1	1		1	1	1	1	+	1	1	1	+		+		+		1	+	+			
Calamagrostis arundinacea	1	1	2				1	3	3	1	2	2	3			1							
Swertia iberica	+		+		+	+																	
Deschampsia flexuosa	+	+		+			+							2	1								
Chaerophyllum roseum	+	+									2	2	1										
Sorbus caucasigena	+	+												+									
Daphne glomerata	1	1	+											1	+	1							2
Sedum stoloniferum	+					+	+										+	+	+				
Alchemilla laeta	1	1	+	1			3	2	2	3			2					1					
Hieracium pannoniciforme	1	+		+		1	1	1	1	2	1	1	1	+		1							
Veratrum album	+	+			3	+	1	+						+				1	+	1			
Salix kazbekensis	2																						
Anemonastrum fasciculatum	1													1		1			1				
Myosotis arvensis	+	+		+	+		+			+	+							+	+	+			
Cruciata glabra	+	+	+				+	+	1	2	+	1	+										
Cephalaria gigantea	+			1			+							+									
Cerastium hemschinicum	+																						
Vicia grossheimii	+	+	1	+			1	1	1			1											
Fritillaria lutea	+	+																					
Vaccinium myrtillus	+	1	1	3			+	+															
Viola odorata	+		+																				
Trollius ranunculinus	1						1			+													
Betonica macrantha	+	1	+			+	2	2	2	+		+	+	1		1		+	1	+	+		
Veronica gentianoides	r			+		+	+				+												
Macrotomia echioides	+		+																				
Dactylorhiza amblyoloba	+									+													
Primula amoena		1		+																			

(continued)

Table 7.3 (continued)

Nr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Cerastium holosteum		+																			
Pimpinella rhodantha		+	+		+			+	+	1											+
Carex leporina		+																			
Vaccinium vitis-idaea		+													2	+	1				2
Valeriana alpestris		+		+												+	+		1	1	
Primula macrocalyx		+					+			+											
Scabiosa caucasica			+												+						
Festuca varia subsp. *woronowii*			2	2										2		1					
Dolichorrhiza caucasica			+	2	+	1		+													
Rhododendron caucasicum				3																	
Cirsium horridum				1																	
Salix kusnetzowii				1																	
Centaurea cheiranthifolia				+										+							
Geranium sylvaticum				+	+	2	1	1			+			1				1	1	1	
Poa iberica				+																	
Viola somchetica				+																	
Lathyrus(Orobus) cyaneus				+							+			1		+					
Bromopsis variegata				+											2	1					+
Anthoxanthum alpinum				+							1										
Carex meinshauseniana				+												1	1				
Alchemilla oxysepala					+						+	2								+	1
Polygonatum verticillatum					+	+	+	+	+		+	+	2							1	
Lapsana grandiflora					+	+	+		+	+				+							
Rumex acetosa					+							+	+								
Aconitum nasutum						+	+	1										+			
Vicia balansae						3													2	1	

Pyrola media					+		+	+											
Festuca sylvatica					2								+				1	2	2
Lathyrus pratensis					+		+			1	1	1							
Senecio caucasigenus					+							r							
Anthriscus nemorosa						+	+	2	+										
Chaerophyllum maculatum						+		+	+										
Cirsium obvallatum	+				+	+	+	+					1						
Silene vulgaris						+			+	+		+							
Vicia sepium						+	+												
Solidago virgaurea						+	1							+		+			
Urtica dioica						+											1		
Luzula pilosa						+													
Helictotrichon pubescens						+							1		1	+			
Pedicularis condensata						r				+									
Geranium depilatum							+												
Daphne mezereum							+												
Salix caprea							+												
Trifolium ambiguum							+	+	2		2	+	+	+					
Platanthera chlorantha							+	+	+	+									
Inula orinetalis							+		+		+								
Carex pallescens							+												
Dactylorhiza euxina							+	+											
Cicerbita racemosa								+											
Lotus corniculatus								+											
Carum meifolium								+											
Rosa mollis								+											
Poa nemoralis									1		3	2							

(continued)

Table 7.3 (continued)

Nr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Dryopteris filix-mas										+											
Pedicularis chroorrhyncha										+											
Trifolium alpestre										1	2	1									
Poa pratensis										2											
Festuca ovina											1				1	+	2				
Koeleria luerssenii											+										
Phleum montanum											1		+								
Pyrethrum roseum											1	2	+								
Ranunculus oreophilus											1	+	+								
Trifolim trichocephalum											+	+	+	+							
Angelica tatianae											+	+						1			
Taraxacum officinale											+										
Geranium ibericum											2	1									
Lotus caucasicus											+										
Pastinaca armena											1			+							
Campanula collina											+	1	+	1		1					+
Ligusticum alatum											+	1	1								
Cerastium arvense											+	+									
Leontodon hispidus											1			+	+	+					
Valeriana tiliifolia												2						1			
Heracleum asperum												+	3					+			
Leontodon danubialis												+									
Heracleum roseum												+									
Vicia alpestris													+								
Agrostis planifolia														2	+	1	+				
Alchemilla retinervis																+					

Alchemilla rigida			1	1				
Alchemilla sericata	1	1						
Allium victorialis							3	
Anemone speciosa		+		+				
Antennaria caucasica		+						
Anthemis sosnovskyana		+						+
Anthoxantun alpinum			2	1				
Anthyllis variegata		1						
Arenaria lychnidea	+			+				
Aster alpinus		+	+					
Bromopsis variegata					1			
Campanula biebersteiniana				+				
Carex tristis		2	1					1
Carum caucasicum		1	1	+				
Chaerophyllum aureum					+			
Cirsium pugnax					+	+	1	
Dolichorrhiza renifolia						1		
Dryas caucasica								1
Empetrum caucasicum		1	1	2				
Galega orientalis					2			
Galium rotundifolium					1			
Gentiana pyrenaica			+	+				+
Gymnadenia conopsea	+	+	1					
Helictotrichon asiaticum	1	2						
Hesperis matronalis					+			
Iris sibirica							+	
Kobresia capilliformis								+

(continued)

Table 7.3 (continued)

Nr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Lilium georgicum																			1		
Luzula pseudosudetica																	+				
Minuartia caucasica															+						1
Minuartia oreina																+	+				
Oxalis acetosella														+							
Oxytropis cyanea														1		+					
Pedicularis wilhelmsiana																	+				
Poa alpina														1			1				
Poa longifolia																1					
Polygala alpicola																1					
Polygonatum orientale																			2		
Polygonum viviparum															+						
Primula amoena																			+		
Rhinanthus minor															1	+					
Podospermum alpigenum															+						
Senecio rhombifolius																		1			
Sibbaldia parviflora																	1				
Sibbaldia semiglabra														+							
Silene linearifolia														+							
Traunsteinera sphaerica															+						
Trifolium canescens																					1
Trifolium repens																1					

Table 7.4 Chirukhistkali Canyon, Mt. Tbethi (Kharazishvili 2005)

T 3 m	85 %		2,380 m, 60 ° NE	N 41 °32′640″
S 1.5 m	60 %			
H 0.8 m	90 %			E 42 °11′512″
T	*Betula medwediewii*	4		
	Fagus orientalis	4		
	Picea orientalis	+		
	Salix caucasica	+		
	Populus tremula	+		
m	*Rhododendron luteum*	3		
	Vaccinium arctostaphylos	2		
	V. uliginosum	2		
	Juniperus pigmaea	2		
	Sorbus boissieri	2		
	Rubus hirtus	+		
H	*Polystichum lobatum*	3		
	Gypsophila tenuifolia	2		
	Pyrola minor	2		
	Achillea millefolium	2		
	Alchemilla retinervis	+		
	Dentaria quinquefolia	+		
	Valeriana alliariifolia	+		
	Draba hispida	+		
	Phleum pratense	+		
	Gentiana schistocalyx	+		
	Senecio platyphylloides	+		
	Aruncus vulgare	+		
	Veratrum lobelianum	+		
	Geranium psilostemon	+		

protected because of their religious significance and they are called "Holy Forests". According to the degree of naturalness of these fragments, they should be attributed to the first level of hemeroby: natural and close to natural (Nakhutsrishvili et al. 2004a, b).

A study was conducted to reveal and characterize the main treeline biotopes of the Kazbegi region (the eastern part of the Central Greater Caucasus).The studies were carried out in the Kazbegi region which is situated on the north-facing major slope of the Main Watershed Range of the Greater Caucasus (N 42°39′; E 44°37′), on the valley of the river Tergi. This region is located on the highest and geomorphologically the most complex central part of the Greater Caucasus. The topography is formed by Jurassic rocks, Palaeozoic and even older granites, young lava and moraines. The mountain massives of the Kazbegi volcanic area are overlayed by Quaternary and Contemporary glacial or river deposits and stone falls as well as strong accumulation of calcareous tuffs and travertine. Glacial and other continental Wьrm deposits occur in many places. The elevation range in the

region varies from 1,210 m up to 5,033 m a.s.l. (the highest peak is Mkinvartsveri); the average elevation is 2,850 m a.s.l.. Brown and light brown skeletal soils of medium and shallow depth and degraded forest and secondary meadow soils are predominant in the treeline ecotone.

In the Kazbegi region the natural treeline ecotone is located between 2,450 and 2,550 m a.s.l. The climate between 1,900 and 2,600 m a.s.l. is moderately humid. Winter is relatively dry and cold, and summer is short. The mean temperature of the warmest months (July, August) ranges from 10 °C to 14 °C (the absolute maximum is 33 °C). The mean temperature of the coldest month (January) is −11 °C (the absolute minimum is −32.5 °C). The number of days with freezing temperature is 124 per year. Stable snow cover persists for 5–7 months and reaches its maximum depth (115–120 cm) in March. The average annual precipitation is 1,000–1,200 mm, and the summed precipitation during May-August is about 100 mm. The mean air humidity in summer is 75 %. Mist is frequent in the area (135 misty days per year), especially in summer. Winds of mountain-gorge type prevail. Duration of growing season is 6 months (Nakhutsrishvili 1999, 2003).

Phytosociological surveys have been carried out according to the method of Braun-Blanquet (Braun-Blanquet 1964) during 1961–2004. For biotope classification we were guided by the works of Holzner (Holzner (Hrsg.) 1989), Pott (1996) and Pedrotti (1998). We followed the work of Pott (1996) to individualise the hemeroby levels. Priority habitat types were distinguished according to 92/43 EEC from September 1993. Mean and standard deviation were determined for every data set (Nagy and Grabherr 2009).

The total area of the subalpine zone in the Kazbegi region amounts to 245.75 km^2. About 1,100 species of vascular plants are recorded in the whole region. The species number in the subalpine zone (from 1,800–1,900 up to 2,400–2,500 m a.s.l.) is 595, of which 33.2 % are endemics. The total area covered by forest is 8,707 ha.

Below are given some characteristic features of the main treeline biotopes of the Kazbegi region (the Central Greater Caucasus).

7.2 Biotope Complex: Biotopes of Woody Plants

Birch forest (*Betula litwinowii*). The range of the birch, which belongs to the periglacial plants, was remarkably diminished in the xerothermic period of the postglacial epoch and the species has remained only in the subalpine zone (Dolukhanov 1966a, b; 2010). At present the birch is dispersed at the treeline of the whole Caucasus, although the areas occupied by the species are not large. Individual trees grow at an elevation of 2,550 m in some places and single specimens broken down by avalanches may be found even in the middle-mountain forest belt. ***Habitat:*** Humid north-facing slopes (10–25° of inclination) with stable snow cover. Deep and slightly skeletal brown soils covering volcanic rocks, light, loamy; humus content in the upper 10–20 cm layer is about 7 %. ***Distribution:*** fragmentary (between 1,850 and 2,200 m): the Liphu forest (above the village

Gergeti), the Sno gorge, the surroundings of the village Sioni and village Djuta; the forest is best developed in the Devdoraki and Khde gorges; a fragment is found on northwest-facing slopes in the Gudauri region (2,000–2,300 m). ***Characteristic species:*** *Betula raddeana, Salix caprea, Heracleum roseum, Aconitum nasutum, A. orientale, Swertia iberica, Geranium sylvaticum, Campanula latifolia, Dolichorrhiza caucasica, Senecio propinquus, Aquilegia caucasica, Vicia balansae, Lathyrus roseus, Cephalanthera longifolia, Platanthera chlorantha.* ***Ecological importance:*** Water-regulatory, protection against avalanches and erosion. ***Threats:*** Tree felling, intensive grazing, construction of roads, climate global change (warming) (Akhalkatsi et al. 2006).

Elfin crooked-stemmed birch forest (*Betula litwinowii*). These forests occur at the treeline, particularly, in areas with abundant snow in winter. The elfin form is due to the weight of the snow covering trees in winter. Such a life form helps woody plants to adjust to severe winter conditions. In the period following the Ice-age the range of the birch forests diminished drastically; they have remained only in the subalpine belt. Its upper distribution limit does not exceed the level of the 11 °C isotherms of August, while in the areas where it is unprotected by snow coat, the 9.5 °C isotherms (Nakhutsrishvili 1999). ***Habitat:*** North-facing slopes with deep snow cover as well as various inclinations (15–70°). Peat brown soils of medium depth, which are situated mainly on volcanic rocks. ***Distribution:*** The upper line of the subalpine belt between 2,350 and 2,500 m; in the Sno gorge, on the Qvena Mt., in the Devdoraki gorge. ***Characteristic species:*** *Sorbus caucasigena, Salix kazbekensis, Rhododendron caucasicum, Vaccinium myrtillus, Anemonastrum fasciculatum, Swertia iberica, Aconitum nasutum, Calamagrostis arundinacea, Dolichorrhiza renifolia, D. caucasica, Cicerbita racemosa, Cephalanthera longifolia.* ***Ecological importance:*** Water-regulatory function, protection of slopes from avalanches, mud-streams, debris-flows, landslides and erosion. ***Threats:*** Tree felling, intensive grazing, construction of roads, climate global change (warming) (Akhalkatsi et al. 2006).

Scrub with dominant *Rhododendron caucasicum*. *Rhododendron caucasicum* – a semi-prostrate evergreen shrub, vegetatively spreading by subterranean creeping stems – is a dominant species in an ecosystem dependent on snow cover. It occurs almost over the whole Caucasus forming dense thickets, in which the cover of this species is usually not less than 90–100 %. *R. caucasicum* forms an endotrophic mycorrhiza, which enables this shrub to successfully colonize poor, acidic soils. ***Habitat:*** Slightly inclined (10–15°) as well as steep (40–70°) north- facing hillsides with deep snow cover in winter. Peat soils of shallow depth (30–40 cm); peat layer located at the depth of 10–15 cm; humus content in the upper soil layer is 23 %. ***Distribution:*** Almost in all the gorges of the region (2,300–2,900 m a.s.l.); individual specimens of *Rhododendron caucasicum* are brought down to 1,800–1,900 m a.s.l. by avalanches (e.g. on the right bank of the river Bidara). ***Characteristic species:*** *Vaccinium myrtillus, V. vitis-idaea, Empetrum caucasicum, Daphne glomerata, Pyrola minor, P. rotundifolia, Anemonastrum fasciculatum, Calamagrostis arundinacea.* Besides the characteristic species noted, the following plants can also be found in the *R. caucasicum* scrub: *Juniperus sabina, Salix*

kazbekensis. ***Ecological importance:*** Protection of slopes from erosion, avalanches, landslides and mud- and debris-streams; water-regulatory function. ***Threats:*** Intensive grazing, climate global change (warming), uncontrolled collection of leaves and shoots for medicinal purposes (Akhalkatsi et al. 2006).

Low scrub community with dominant *Dryas caucasica*. The areas occupied by these communities are not large. ***Habitat:*** Skeletal and stony, calcareous soils; slaty humid steep (20–50°) slopes with North and North-West aspects. ***Distribution:*** Relatively wide in the Truso gorge and on the Mt. Kuro slopes; between 2,000–2,600 m a.s.l. ***Characteristic species:*** *Deschampsia flexuosa, Daphne glomerata, Vaccinium vitis-idaea, Selaginella helvetica, Primula amoena, Polygonum viviparum, Leontodon danubialis, Parnassia palustris*. ***Ecological importance:*** Protection of humid slopes from erosion. ***Threats:*** Overgrazing, climate warming.

7.3 Biotope Complex: Biotopes of Herbaceous Plants

Subalpine tall herbaceous vegetation (Megaphorbia). The subalpine tall herbaceous vegetation constituted by tall herbs (2.0–2.5 m, rarely 3.0 m tall) is mainly distributed on the western and central parts of the Greater Caucasus, although fragments of this vegetation are scattered all over the Caucasus. Species richness of an individual community is not high. One of the principal characteristics of these plants is their rather rapid development during the growing season. In May and June the vegetation comprises only one layer of low herbs, whilst in the middle of the growing season (the end of July and the beginning of August) it already consists of tall herbs. Tall herbaceous vegetation is typically three-layered; these three layers are constituted not only by one and the same species, but also by one and the same individual plants. Thus, the first layer consists almost completely of generative stems; leaves of the same plants form the second layer, which actually "controls" species content of the community and suppresses the development of other species and individual plants. Strong shading prevents the growth of other autotrophic plants in the third layer except some early spring plants; only stems and elongated leaf stalks are developed in this layer. The main constituents of the tall herbaceous vegetation are forbs; the ecosystem is stenotopic. It is principally distributed in the subalpine belt; however, avalanches often take plants of the community down to lower belts (Dolukhanov 1966a, b; Gagnidze 1974). The main factors in the development of the tall herbaceous vegetation are high air humidity and soil moisture as well as gradual (and not rapid) thawing, slight fluctuations of daily temperatures, frequent fog. ***Habitat:*** Humid north- and west-facing slopes of low inclination (until 10–15°); near subalpine open birch woodlands or in strongly rarefied birch forests; the communities are especially dense on river banks. ***Distribution:*** Between 1,900 and 2,300 m a.s.l. Best developed in the Devdoraki gorge; fragments occur in the Liphu forest, the Sno gorge, near the village Sioni, in the Khde gorge. ***Characteristic species:*** *Heracleum sosnowskyi, Aconitum nasutum, A. orientale, Cephalaria gigantea, Angelica tatianae, Cicerbita macrophylla, Senecio*

rhombifolius, Agasyllis latifolia, Doronicum macrophyllum. ***Ecological importance:*** Water-balance regulatory function. ***Threats:*** Grazing, tree felling and carry out of firewood, uncontrolled collection of medicinal herbs (especially *Senecio rhombifolius*).

Meadows with dominant *Bromopsis variegata*. These grasslands are widespread. They belong to rare-turf meadows. The dominant species – *Bromopsis variegata* – flowers in the first half of June. The degree of coverage amounts to 95–100 %. ***Habitat:*** Plateaus and south-facing hillsides of low and medium degree of sloping (5–15°) as well as alluvial cones. Moderately dry skeletal soil. ***Distribution:*** Between 1,850 and 2,700 m a.s.l. in the whole Caucasus. ***Characteristic species:*** *Agrostis tenuis, Anthoxanthum alpinum, Festuca ovina, Koeleria luerssenii, Trifolium ambiguum, T. trichocephalum, Ranunculus oreophilus, Alchemilla sericata, Leontodon hispidus, Lotus caucasicus, Platanthera chlorantha.* ***Ecological importance:*** Protection from erosion. ***Practical use:*** Hay-meadows. ***Threats:*** Overgrazing, construction of roads.

Dry meadows with dominant *Agrostis tenuis*. These meadows are widespread in the subalpine belt, but occur in the alpine belt too. Very often *Agrostis tenuis* is a co-dominant of *Bromopsis variegata.* ***Habitat:*** Plateau or south-facing hillsides of medium slope (10–12°). Humid northwest-facing slopes in the alpine belt. Rare-turf meadows. ***Distribution:*** Between 1,800 and 2,600 m a.s.l. in all the gorges and on all the ranges. ***Characteristic species in the subalpine zone:*** *Bromopsis variegata, Festuca ovina, Phleum phleoides, Koeleria luerssenii, Helictotrichon asiaticus, Pedicularis chroorrhincha, Ranunculus oreophilus, R. caucasicus, Trifolium ambiguum, Alchemilla sericata, Gymnadenia conopsea, Coeloglossum viride.* ***Characteristic species in the alpine zone:*** *Poa alpina, Phleum alpinum, Carum caucasicum, Leontodon caucasicus, Taraxacum confusum, Sibbaldia semiglabra.* ***Ecological importance:*** Protection from erosion. ***Practical use:*** Hay-meadows (in the subalpine zone), pastures (in the alpine zone). ***Threats:*** Overgrazing, construction of roads.

Dense-turf xerophilous meadows with dominant *Festuca varia*. These meadows are widespread in the high mountains of the Caucasus. The meadows develop mainly on very steep slopes of any aspect (more often on south-facing slopes). *Festuca varia* is a densely tufted, summer-wintergreen plant (Kimeridze 1965). ***Habitat:*** Very steep (30–50°) stony south-facing slopes. If grazed, they also occur on north-facing slopes. Unlike in the subalpine belt, *Festuca varia* develops in cold and dry environment in the alpine belt, where fluctuations of daily temperatures are sharp. Mountain meadow soil, soddy turf, skeletal. ***Distribution:*** In all the gorges and on all mountain ranges of the region, both in the subalpine and alpine belts. Fragments occur in the subnival belt too. ***Characteristic species in subalpine zone:*** *Helictotrichon asiaticus, H. pubescens, Calamagrostis arundinacea, Oxytropis cyanea, Betonica macrantha, Inula orientalis, Polygonum carneum, Pyrethrum roseum*; ***Characteristic species in alpine zone:*** *Kobresia schoenoides, Carex tristis, Alopecurus dasyanthus, Anthoxanthum alpinum, Alchemilla caucasica, Festuca ruprchechtii, Bromopsis riparia, Polygonum carneum, Primula amoena, Chaerophyllum roseum, Helictotrichon asiaticus, H. pubescens, Podospermum*

alpigenum, Cerastium purpurascens, Betonica macrantha. ***Ecological importance:*** Protection of slopes from erosion. ***Practical use:*** Grazed well by cattle and satisfactorily by sheep until flowering (while leaves are tender). Hard for grazing after leaves have toughened (Sakhokia 1983). ***Threats:*** None.

Humid broad-leaved meadows with dominant *Trollius ranunculinus*. These meadows are distributed in humid places; they are found in forest openings as well as on slightly sloping hillsides (until 10°) and small depressions of both subalpine and alpine belts. The areas occupied by these meadows are not large. They occur as patches scattered over the other vegetation belts. *Trollius ranunculinus* blooms in May and June. ***Habitat:*** Slopes and small depressions of high as well as medium humidity. ***Distribution:*** Patchy distribution in almost all the gorges of the region; between 1,800 and 2,800 m a.s.l.; these meadows cover relatively large areas on the Kolteshi range, in the Gudauri region. ***Characteristic species:*** *Veratrum lobelianum, Dactylorhiza euxina, D. urvilleana, Poa alpina, Swertia iberica, Deschampsia flexuosa, Pedicularis crassirostris.* ***Threats:*** Extensive grazing, climate global change (warming).

Broad-leaved mesophilous meadows with dominant *Anemonastrum fasciculatum*. These meadows are distributed almost throughout the Caucasus. ***Habitat:*** Moderately humid North and North-West slopes. ***Distribution:*** They occupy quite small areas in the region and develop mainly in the subalpine belt (on the Kolteshi range, in the Oevdoraki gorge) between 2,000 and 2,300 m a.s.l. *Anemonastrum fasciculatum* occurs at forest edges, in *Rhododendron caucasicum* scrub, meadows dominated by *Calamagrostis arundinacea* and *Festuca varia* growing on humid slopes. ***Characteristic species:*** *Trollius ranunculinus, Geranium ibericum, Scabiosa caucasica, Betonica macrantha, Veratrum lobelianum, Polygonum carneum.* ***Threats:*** Extensive grazing, tree felling, climate global change (warming).

Dense-turf meadows with dominant *Nardus stricta*. These meadows are widely spread in the subalpine and alpine belts of the Caucasus. The subalpine meadows made up of *Nardus stricta* are generally secondary, developed as a result of overgrazing (Kimeridze 1965). ***Habitat:*** In level places as well as on hillsides of medium (10–15°) and high degree (20–30°) of slope, on slopes of any aspect (except very steep, south-facing). ***Distribution:*** In the subalpine and alpine belts between 2,000 and 2,800 m a.s.l.; in the subalpine belt the *Nardus stricta* meadows replace the forb-grass meadows, on all the mountain ranges of the region (Sakhokia 1983). ***Characteristic species:*** *Agrostis tenuis, A. planifolia, Luzula pseudosudetica, Anthoxanthum alpinum, Trifolium trichocephalum, T. ambiguum, Leontodon danubialis, Phleum alpinum, Poa alpina, Sibbaldia semiglabra, Hieracium pilosella, Carum caucasicum, Dactylorhiza euxina, D. urvilleana.* ***Ecological importance:*** Protection of slopes from erosion. ***Threats:*** Over-grazing.

Meadows with dominant *Carex tristis*. These meadows are widespread in the alpine belt of the Caucasus. Some fragments of these meadows are also present in the subnival belt. ***Habitat:*** The meadows occupy moderately humid slopes with low (3–5°) and medium (10–15°) degree of inclination (of different aspects) and plane areas. ***Distribution:*** In all the gorges and on all mountain ranges of the region;

between 2,300 and 2,900 m a.s.l. ***Characteristic species:*** *Kobresia capilliformis, Thalictrum alpinum, Poa alpina, Gnaphalium supinum, Nardus stricta, Luzula spicata, L. multiflora, Festuca supina, Anthennaria caucasica, Polygonum viviparum, Alchemilla caucasica.* ***Ecological importance:*** Protection of slopes from erosion. ***Threats:*** Over-grazing.

Meadows with the *Kobresia capilliformis*. These meadows are especially widely distributed in the Central and East Caucasus. The meadows occupy quite small areas in the West Caucasus on limestone. Their invasion of the Caucasus coincides with the xerothermic period after the glacial epoch. ***Habitat:*** Glacial relief, ridges, windy places with thin snow cover; mainly on carbonate soil.

Distribution: Widely distributed between Mt. Kvena Mta and Betlemi Pass, in the Truso gorge and Kolteshi mountain range; between 1,900 and 2,800 m a.s.l. ***Characteristic species:*** *Kobresia persica, Alchemilla elisabethae, Thalictrum alpinum, Polygonum viviparum, Carum caucasicum, Campanula biebersteiniana.* ***Ecological importance:*** Protection of slopes from erosion. ***Threats:*** Extensive grazing.

Mesophilous rare-turf meadows with dominant *Calamaerostis arundinacea*. ***Habitat:*** Level places, slightly inclined (2–5°) as well as steep (20–25°) slopes; mostly within the range of the birch. ***Distribution:*** limited – the Liphu forest, the Sno birch forest, the Devdoraki gorge. ***Characteristic species:*** *Agrostis planifolia, Helictotrichon asiaticus, Deschampsia flexuosa, Geranium ibericum, Anemonastrum fasciculatum.* ***Threats:*** Tree felling, global climate change (warming).

7.4 Biotope Complex: Biotopes of Rocks and Scree

Distinct fluvio-glacial topography, intense present-day denudation process, granitoids bared in consequence of Tergi erosion, black shale and quartzite of Lower Lias age remained uncovered with soil on steep slopes, volcanic lava of the Quaternary with glacial, alluvial and colluvial layers – all these create the environmental conditions necessary for the development of the rock and scree biotopes.

The biotopes of rocks and scree of the Kazbegi region are distinguished by quite high species richness. According to the data reported by Ivanishvili (Ivanishvili 1998), 25 % of the Kazbegi flora is represented by the species of the biotopes mentioned and half of them are stenotopic endemics. It is worth mentioning that there are several mono- and oligotype endemic genera in the flora of the rocks and scree biotopes of the Kazbegi region.

Biotope of moist rocks. ***Habitat:*** Shaded rocks moistened with horizontal precipitation or water flowing down from hillsides. ***Distribution:*** The Devdoraki, Dariali, Kazbegi, Sno, Truso gorges, etc. ***Characteristic species:*** *Parietaria micrantha, P. judaica, Campanula sosnowskyi, C. hypopolia, Diphasium alpinum, Cryptogamma crispa, Polypodium vulgare, Woodsia fragillis, Dryopteris pumila, Primula darialica.* ***Threats:*** Climate warming.

Table 7.5 Species number in the various treeline biotopes of the Central Greater Caucasus (n = 14)

Biotopes	Minimum species number per 25 m^2	Maximum species number	Average species number
Elfin crooked-stemmed forest dominated by *Betula litwinowii*	24	29	27.0 ± 1.6
Shrabbery dominated by *Rhododendron caucasicum*	16	38	25.7 ± 9.3
Low scrub community dominated by *Dryas caucasica*	23	35	30.3 ± 6.4
Tall herb vegetation dominated by *Heracleum sosnowskyi*	6	9	7.5 ± 1.3
Meadow dominated by *Calamagrostis arundinacea*	27	38	31.6 ± 3.9
Meadow dominated by *Festuca varia*	17	43	31.2 ± 7.8
Meadow dominated by *Nardus stricta*	20	47	32.3 ± 7.9
Meadow dominated by *Carex tristis*	25	28	26.5 ± 2.1
Meadow dominated by *Kobresia capilliformis*	22	34	27.7 ± 4.1

Biotope of marly and slaty scree. ***Habitat:*** Dry slaty scree, north-facing slopes. ***Distribution:*** In the subalpine belt, in the whole region. ***Characteristic species:*** *Silene lacera, Erysimum ibericum, E. substrigosum, Linaria vulgaris, L. meyeri, Thalictrum foetidum, Salvia verticillata, Scutellaria leptostegia, Thymus collinus, Bromopsis riparia, B. biebersteinii, Trigonocaryum involucratum.* ***Threats:*** Avalanches and landslides.

Biotope of stones. Rather different plants settle on stones of various origin (glacial, volcanic, etc.); the abundance of the plants growing on stones is often quite high. Many of the species settling on stones are the constituents of the meadow vegetation and communities of rocks and scree. ***Habitat:*** South-facing stones. ***Characteristic species:*** *Sempervivum pumilum, Campanula bellidifolia, Silene ruprechtii, Thymus collinus, Pulsatilla violacea, Festuca ovina, Koeleria caucasica, K. luerssenii, Carex buschiorum, Sedum oppositifolium.* ***Threats:*** Out of danger.

The lowest index of species number is found in the biotope of tall herbaceous vegetation, which is caused by the specific feature of its canopy structure and microclimate (Table 7.5). Other biotopes are characterized by rather high value of species richness.