

OAKS AND OAK FORESTS IN CAUCASIA

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Introduction to the Caucasus Region

When regarding the "Caucasus," some authors refer only to the high mountains of the Great Caucasus. Here the term "Caucasia" will be used to refer to the entire area located between the Black Sea and the Caspian Sea of the Caucasus Region. Besides the Great Caucasus, the North Caucasian Plain belonging to the Russian Federation, as well as the depressions and lowlands, mountain ranges and the highland south of the Great Caucasus up to the southern border of the states Armenia, Azerbaijan, Georgia (South Caucasia, often called "Transcaucasia"), are also included.

The Great Caucasus extends between the Black Sea and Caspian Sea over a distance of 1500 km and a breadth of 30-180 km. It consists of several parallel mountain ranges. The main ridge is preceded towards the north by a second ridge (here the Elbrus, the highest peak 5633 m, and the Kasbek, the highest peak 5044 m), as well as the rocky ridge (chain of limestone massifs). These high mountains form an important climate and water divide between East Europe and Southwest Asia, and thus between two continents. Geological development, as well as the unique orographic and climatic situation, gives rise to a unique natural setting and biological diversity of Caucasia. The cultural diversity characteristic of mountainous regions is not less unique. Likewise, the cultural history and land use dating back for millennia have influenced the landscapes and habitats.

Characteristic orbiomes rich in relics and endemics (from near-shore montane forests up to the alpine grasslands) meet within a small geographic area with submediterranean and warm-humid biomes, as well as continental semiarid biomes (cf. BFN 2000, Zazanashvili et al. 2000, Krever et al. 2001, Schmidt 2002). In the north Caucasian Plain steppe and woodland steppe areas, and in the east, Caspian semideserts closely approach the Caucasus. The steep southern sloping of the Great Caucasus contains very different ecotopes and different phytogeographic provinces of southern Caucasia:

- In the west with its humid climate, it transforms into the coastal area of the Black Sea and the Lowland of Colkhети,
- East of the Suram Mountains, it forms a bridge to Minor Caucasus towards the Kura Lowland, extending in the east to the arid Kura-Arax Lowland at the Caspian Sea.

To the south ascend the mountainous system of Minor Caucasus characterised by its diverse, but human-influenced, montane vegetation. The Minor Caucasus forms the margin of the Armenian Highland. It is poor in forests, being covered over large tracts with xerophytic vegetation, including open woodland up to montane steppes and Oriental thorn-cushion formations. Two landscapes stand out here, distinguished by summer-warm and winter-mild climate, abundant rainfall, and high air humidity. They represent refuges of Tertiary deciduous broad-leaved trees, which otherwise in Western Eurasia are

extinct, as well as habitats of endemic oak species (relicts): Colchetic at the Black Sea and Lenkoran at the Caspian Sea. The Colchic and Hyrcanian deciduous broad-leaved forests are rich in evergreen woody species in the undergrowth, with plenty of lianas and epiphytes, and are characteristic of a warm-humid climate of submeridional latitudes (not subtropical vegetation, as often referred to in Caucasian and Russian literature).

Species concepts – seventeen versus eight oak species

Depending on the taxonomic conception of the authors, the data about the number of *Quercus* species occurring in the Caucasus Region vary considerably (8 to more than 17 species). The "splitter" concept of species according to the KOMAROV school (e.g. Czerepanov 1995), and accepted by most of the authors of the Caucasus states (e.g. *Flora Kavkazal* Grossheim 1945, *Flora Azerbajdžanal* Bandin 1952, *Dendroflora Kavkazal* Matika'vili 1961, *Flora Gruzii* 1975, Artjunjan & Artjunjan 1985, and other floras and dendrological handbooks, or Krever et al. 2001), contrasts with the "lumper" concept (e.g. Govaerts & Frodin 1998) which is also referred to by the monograph of the East European, Caucasian and Asian oaks, by Menitsky (1968-2002). If, however, his subspecies are taken into consideration, the number of the taxa regarded as essential deviate from each other to a lesser extent (see **Table 1**).

Up to now most of the Caucasian authors differentiate between 17 oak species, with deviations of single authors being possible, partly due to recognizing additional species (e.g. *Q. hypochrysa*) or lesser species (e.g. of the species complex *Q. infectoria*). Semagina (1999), for instance, refers to 7 species alone from the limited area in the western Great Caucasus (Caucasus State Nature Reserve). Kolakovski (1982) considers Caucasia as one of the centres of speciation in the genus *Quercus* and of conservation of relics in Eurasia.

The species concept followed here largely corresponds to that of Menitsky (1968-2002). Similar are also the species interpretation in the *Flora of Turkey* (Hedge & Yaltirik 1982) and in the *World Checklist* by Govaerts & Frodin (1998), even though the number of subspecies accepted by these authors is lower and the delimitations of which (and thus data of distribution) may differ. Hence, in Caucasia with regard to broader interpretation of *Q. robur*, *Q. petraea* and *Q. infectoria*, 8 species and 11-14 taxa, respectively, occur, being accepted as species, or at least in the rank of subspecies.

In southwest Asia hybridisation seems to essentially contribute to the formation of taxa and to the blurring of species limits, respectively (cf. Menitsky 1968-1984, Kasapliligil 1981). According to Kolakovski (1982) e.g. in the overlapping area of the respective closely related taxa of *Q. robur* sensu lato and *Q. petraea* sensu lato, a great number of hybrid forms occur in Caucasia, but he accepts the Caucasian taxa each as independent endemic species (*Q. imeretina*, *Q. iberica*). Concerning the European species, hybridisation has been verified based on crossing experiments and genetic analyses. Numerous combinations identified as hybrids, or those assumed as such, were given binary names, which also applies to the three occurring between the three far-spread European-West Asian species likewise stocking in Caucasia: *Q. petraea* x *Q. pubescens* (*Q. x streimii* Heuff. or *Q. x calvescens* Vuk.), *Q. petraea* x *Q. robur* (*Q. x rosacea* Bechst.), *Q. pubescens* x *Q. robur* (*Q. x kernerii* Simonk.). If the three species are seen in a narrow taxonomic context and several species designated each, the

Table 1. Survey of the oaks of Caucasia according to various authors

CZEREKANOV (1995), floras of the Caucasus Region	MENITSKY (1984, 2002)	GOVAERTS & FRODIN (1998)
<i>Q. castaneifolia</i>	<i>Q. castaneifolia</i>	<i>Q. castaneifolia</i>
<i>Q. hartwissiana</i>	<i>Q. hartwissiana</i>	<i>Q. hartwissiana</i>
<i>Q. macranthera</i>	<i>Q. macra0nthera</i>	<i>Q. macranthera</i>
<i>Q. pontica</i>	<i>Q. pontica</i>	<i>Q. pontica</i>
<i>Q. pubescens</i>	<i>Q. pubescens</i>	<i>Q. pubescens</i> , but not mentioned for Caucasia
	<i>Q. infectoria sensu lato</i>	
<i>Q. araxina</i>	<i>Q. infectoria</i> ssp. <i>boissieri</i>	<i>Q. infectoria</i> ssp. <i>veneris</i>
<i>Q. boissieri</i>	<i>Q. infectoria</i> ssp. <i>boissieri</i>	<i>Q. infectoria</i> ssp. <i>veneris</i>
<i>Q. infectoria</i>	<i>Q. infectoria</i> ssp. <i>infectoria</i> not in Caucasia	<i>Q. infectoria</i> ssp. <i>infectoria</i> not in Caucasia
	<i>Q. petraea sensu lato</i>	
<i>Q. dalechampii</i>	<i>Q. petraea</i> ssp. <i>medwediewii</i>	ssp. <i>medwediewii</i> = ssp. <i>iberica</i> <i>Q. dalechampii</i> not in Caucasia
<i>Q. dshorochensis</i>	<i>Q. petraea</i> ssp. <i>dshorochensis</i>	<i>Q. petraea</i> ssp. <i>iberica</i>
<i>Q. gagriana</i>	<i>Q. petraea</i> ssp. <i>iberica</i>	<i>Q. iberica</i>
<i>Q. petraea</i> ssp. <i>iberica</i>	<i>Q. petraea</i> ssp. <i>iberica</i>	<i>Q. petraea</i>
<i>Q. petraea</i> ssp. <i>petraea</i>	<i>Q. petraea</i> ssp. <i>petraea</i>	
<i>Q. pinnatiloba</i>	<i>Q. petraea</i> ssp. <i>pinnatiloba</i>	<i>Q. petraea</i> ssp. <i>pinnatiloba</i> (not mentioned for Caucasia)
	<i>Q. robur sensu lato</i>	
<i>Q. imeretina</i>	<i>Q. robur</i> ssp. <i>imeretina</i> , 2002: = ssp. <i>robur</i>	<i>Q. robur</i> ssp. <i>imeretina</i>
<i>Q. pedunculiflora</i>	<i>Q. robur</i> ssp. <i>pedunculiflora</i>	<i>Q. robur</i> ssp. <i>pedunculiflora</i>
<i>Q. robur</i>	<i>Q. robur</i> ssp. <i>robur</i>	<i>Q. robur</i> ssp. <i>robur</i>
17 species	8 species, one with 2, another with 5 subspecies (13 taxa)	8 species, one of them not mentioned for Caucasia, less subspecies (10 taxa)

number of the respective hybrids increases (cf. 10 nothospecies alone for the Czech flora, Hejny & Slavík 1990) and thus, the probability of wrong interpretations. Certainly Menitsky (e.g. 1984) points to the hybrids known from Europe and indicates such ones having Caucasian species (e.g. *Q. hartwissiana* x *Q. petraea*, *Q. hartwissiana* x *Q. robur*), but he renounces binary names. He attaches high significance to the introgressive hybridisation and indicates, given joint

occurrences of the species, the presence of respective populations regarding almost all Caucasian species (exceptions *Q. castaneifolia* and *Q. pontica* being also morphologically quite stable). He interprets several taxa as products of introgressive hybridisation, so e.g. *Q. petraea* ssp. *medwediewii* (*Q. petraea*/*Q. pubescens*) and *Q. pubescens* ssp. *anatolica* (*Q. pubescens*/*Q. infectoria*). Between *Q. petraea* ssp. *iberica* and *Q. infectoria* ssp. *veneris* in the Armenian Highland, all transitional forms occur. Govaerts & Frodin (1998) refer to a hybrid between both taxa (*Q. x mannifera* Lindl.) for eastern Turkey to northern Iran, allocating to it numerous species described by authors of older publications (e.g. *Q. longifolia* K. Koch, *Q. komarowii* A. Camus).

In dendrological literature reference has been made repeatedly to cultivated plants, which were identified as hybrids between species occurring in Caucasia, e.g. *Q. pontica* x *Q. robur* (Rehder 1940), *Q. castaneifolia* x *Q. macranthera* and *Q. macranthera* x *Q. robur* (Hillier 1998).

Classification of the Caucasian oaks into the system of the genus *Quercus*

The Caucasian oaks belong to the subgenus *Quercus* (Syn. *Lepidobalanus*). The majority of species is allocated to the section *Quercus* (Syn. *Robur*), one species (*Q. castaneifolia*) to the section *Cerris*, and another one (*Q. infectoria*) to the group of the *Galliferae* that is sometimes regarded as an independent section and sometimes as part of the section *Quercus*. In particular, concerning *Q. pubescens*, the conceptions differ. Menitsky (1968, 1984, 2002), by whom the following taxonomic survey is oriented, allocates the species at the beginning to subsection *Robur* (1968). Later on, however, he doubted the usual allocations into the groups of relationship of *Q. robur*/*Q. petraea* or of *Q. macranthera*, and interpreted it as another representative of the *Galliferae* (1984, 2002).

Quercus

Subgenus *Quercus* (Subgen. *Lepidobalanus* [Endl.] Oerst.)

I. Sect. *Quercus* (Sect. *Robur* Loud., Sect. *Eulepidobalanus* Oerst.)

1. Subsect. *Ponticae* (Stef.) A. Camus

Q. pontica

2. Subsect. *Quercus* (Subsect. *Robur* [Endl.] Guerke)

Q. hartwissiana, *Q. petraea* sensu lato (incl. *Q. dshorochensis*, *Q. iberica*, *Q. petraea*, *Q. pinnatiloba*, *Q. polycarpa*), *Qu. robur* sensu lato (incl. *Q. haas*, *Q. imeretina*, *Q. longipes*, *Q. pedunculiflora*, *Q. robur*)

3. Subsect. *Macrantherae* (Stef.) A. Camus

Q. macranthera

4. Subsect. *Galliferae* (Spach) Guerke

Q. infectoria sensu lato (incl. *Q. araxina*, *Q. boissieri*), *Q. pubescens* sensu lato (incl. *Q. anatolica*, *Q. crispata*)

II. Sect. *Cerris* Dumort.

1. Subsect. *Cerris* (Dumort.) Guerke

Q. castaneifolia

Distribution types of Caucasian oaks

According to Kreyer et al. (2001), 14 out of 17 species occurring in Caucasia are said to be "endemic to the Caucasus Region," with 11 being

included as "Rare and endangered species listed in the Red Books of the Caucasian countries" (Tab. 2). Even if all taxa – whether as species or as subspecies – were accepted, most of them would go beyond the boundaries drawn by the authors of the reference Caucasus Region (southern boundary regarded as coinciding with the southern borders of the countries Armenia, Azerbaijan, and Georgia). Hence, the number of Caucasian endemics that has been assumed is clearly too great. Partly endemic taxa of the Submediterranean or Oriental Region are referred to here (via Anatolia up to the Balkan Peninsula or into Iran) or such ones of the Euxinian or Hyrcanian Province (also in north Anatolia or in northwest Iran). Nakhutsrishvili (1999) designated *Q. pedunculiflora* as an endemic species of "Transcaucasia;" however this taxon (*Q. robur* ssp. *pedunculiflora*) is not only distributed in South Caucasia, but extends via the Isle of Krim and Turkey up to the Balkan Peninsula. Contrary to this, *Q. imeretina* is an "endemic species" of west Georgia, certainly only known from western Caucasus region. The designation as species, however, has been significantly overestimated, even as subspecies (*Q. robur* ssp. *imeretina*), and today is no longer accepted by the monographer of oaks of Caucasia (Menitsky 2002).

It is true that the number of Caucasian endemics among the oaks is considerable, in terms of the biogeographical entity Caucasia, but even then it is not as great as mentioned in Kreyer et al. (2001), as is obvious from an analysis of distribution types:

Submediterranean/montane-Middle European: *Q. robur* with 3 subspecies (geographical races)

- Submediterranean/montane-Atlantic-Sarmatic: **ssp. *robur*** (in Caucasia mainly north of the Great Caucasus)
- East Submediterranean: **ssp. *pedunculiflora*** (in Caucasia chiefly south of the Great Caucasus)
- Colchic: **ssp. *imeretina*** (only lowland and adjacent uplands of Colchheti)

Submediterranean/montane-Middle European: *Q. petraea* including several subspecies disputed as to their delimitation (geographical and/ or ecological races):

- Submediterranean/montane-Atlantic-Central European: **ssp. *petraea*** (in Caucasia primarily north of the Great Caucasus)
- East Mediterranean/montane-Oriental: **ssp. *pinnatiloba*** (by the Armenian-Northwest Iranian part of distribution area extending as far as the southern fringe of Caucasia)
- South Caucasian (incl. Colchic and Hyrcanian Provinces): **ssp. *iberica*** (in Caucasia mainly south of Great Caucasus; however according to Govaerts & Frodin 1998 with the inclusion of the following subspecies not limited to Caucasia, but East Submediterranean)
- East Submediterranean: **ssp. *medwediewii*** (in Caucasia mainly north of the Great Caucasus)
- Northeast Anatolian (subeuxinian): **ssp. *dshorochensis*** (only in the utmost southwest of Caucasia)

Mediterranean/montane-Submediterranean-Pannonic-South Subatlantic: *Q. pubescens* (in Caucasia chiefly north of the Great Caucasus)

Eastern Mediterranean-Oriental: *Q. infectoria*, with the eastern (to Armenian-Iranian) subspecies *ssp. veneris* extending as far as to the southern fringe of Caucasia

North Anatolian-Caucasian-Hyrcanian: *Q. macranthera*

Euxinian: *Q. hartwissiana*

Colchic: *Q. pontica*

Hyrcanian: *Q. castaneifolia*.

Three polymorphic and polytypic species (*Q. robur* sensu lato, *Q. petraea* sensu lato, *Q. pubescens*) occur in nemoral deciduous broad-leaved forest areas of Europe and southwest Asia (Asia Minor and Middle East), and also in Caucasia. Among the taxa designated as subspecies (referred to as a species by most of the Caucasian authors), two occur exclusively or almost exclusively in Caucasia, and two just touching upon Caucasia. One species being likewise very variable, which is distributed in the Eastern Mediterranean Region, Asia Minor and the Middle East, has but few occurrences in the southernmost south Caucasia (*Q. infectoria*). Four well-characterized and less variable species have their main distribution in the Caucasian countries, but are not confined to them. They are very characteristic elements of the Caucasian flora and vegetation. Two species are found in the Black Sea region (Euxinian or Colchic), one species in the uplands near the southern Caspian Sea (Hyrcanian), and one in the Great and the Minor Caucasus. Among these two species are typical elements of the hygrophilic, deciduous, broad-leaved mixed forests (*Q. hartwissiana* and *Q. castaneifolia*); two species thrive in the upper montane and subalpine belts (montane forests up to the timberline: *Q. macranthera*, krummholz: *Q. pontica*).

Oak forests

The Caucasian oak forests are extraordinarily diverse and belong to the most structured and species-abundant forests of Caucasia. This biodiversity (numerous ecosystem types and species) is enhanced by the great variety of landscapes and by the special evolutionary history (refuges of Arcto-Tertiary deciduous broad-leaved forest vegetation, oaks as relics and endemic taxa). However, the distribution area of oak forests has been much reduced by logging and land use. The fertile soils of the lowlands up to the lower uplands have been used for agriculture for centuries (arable farming, viticulture, fruit growing). Oak forests were mostly pushed back to poor sites not suitable for agriculture, to steep slopes or to remote gorges. Also the oak forests that were preserved were subject to changes as well. Wood utilization, lopping systems (twigs and foliage for animal feeding), woodland pasture, and overgrazing led to the degradation of sites. Poor natural regeneration of oaks, changes in the spectrum of species and stand structure resulting from thinnings and stump sprouting (coppice-managed woodland), caused the formation of secondary dry woodlands up to anthropozoogenic open land formations devoid of forest (steppe formation of former oak forest tracts). The currently complicated economic situation in the Caucasian States has led to an extension and intensification of utilization of natural resources. This does not even stop at protected areas, which, among others, had been established to protect close-to-nature oak forests and populations of rare or endangered oak species. (See **Table 2**) This also raises landscape ecological problems, because the oak forests fulfil an important function against soil erosion.

Table 2. Rare and endangered species listed in the Red Books of the Caucasian countries according to Krever et al. (2001)

	Armenia	Azerbaijan	Georgia
<i>Q. castaneifolia</i>		x	
<i>Q. hartwissiana</i>			x
<i>Q. infectoria sensu lato:</i>			
- <i>Q. araxina</i>	x		
- <i>Q. boissieri</i>	x	x	
- <i>Q. infectoria</i>	x		
<i>Q. macranthera</i>			x
<i>Q. petraea sensu lato:</i>			
- <i>Q. dshorochensis</i>			x
<i>Q. pontica</i>			x
<i>Q. robur sensu lato:</i>			
- <i>Q. imeretina</i>			x
- <i>Q. pedunculiflora</i>	x		x
- <i>Q. robur</i>	x		
	5	2	6

IUCN Red List 2000, The World List of Threatened Trees (Oldfield et al. 1998):
Q. robur ssp. imeretina (Colkhети) - category **Vulnerable**

Numerous publications are available, taking the Caucasian types of vegetation of the oak forests into consideration (e.g. Bandin 1954, Mahatadze 1957, Gulisa_vili et al. 1975, Alentev 1976, Nakhutsrishvili 1999, BFN 2000, Zazanashvili et al. 2000, Kvachakidze 2001) or data of the single oak species are given, and which forest associations they occur in (e.g. Sokolov et al. 1977, Menitsky 1984). Since the major number of oak taxa is also distributed in Anatolia, a comparison with the forest vegetation of the Euxinian region and the woodland steppe vegetation of Turkey (e.g. Mayer & Aksoy 1986) is of interest. The description of the vegetation of the oak forests follows various geobotanical schools, which results in completely different classifications. In general, the methods of the Russian forest typology are applied, only very seldom the west-European Braun-Blanquet school (few syntaxa with *Quercus* species as characteristic and differential species in Korotkov et al. 1991), partly also mixed forms. Since different methods are applied and homonymous terms (e.g. formations, associations) are defined differently, a comparison of the oak forest vegetation types of the single authors is more difficult. In Georgia alone, of the 23 "formations" and 280 "associations" of the forests designated by Kvachakidze (2001), 5 "formations" and 45 "associations" belong to the "Quercetea":

- 27 to *Q. petraea sensu lato* (25 ssp. *iberica*-, 2 ssp. *dshorochensis*-) forest associations;
- 10 to *Q. robur sensu lato* (6 ssp. *pedunculiflora*-, 4 ssp. *imeretina*-) forest associations;
- 8 to *Q. macranthera* forest associations.

Corresponding to their ecological norm of reaction, oaks are characterized by a wide variety of sites. They occur as stand-forming entities or as mixtures of tree species from the lowland (alluvial and lowland forests, e. g. *Q. robur* subsp. *imeretina* et subsp. *pedunculiflora*) up to the timberline and the subalpine belt (*Q. macranthera*, *Q. pontica*). The main distribution is found in forest belts of lower and medium elevations (e.g. *Q. petraea* along with its subspecies being widely distributed as main and mixtures of tree species ranging from sea level up to 1200 m or the Hyrcanian *Q. castaneifolia* in Lenkoran up to 1800 m). As light-demanding tree species, the oaks are absent from forests where shade-bearing trees are predominant (beech forests, spruce-fir forests). (See **Table 3**) The west Caucasian *Q. hartwissiana* is slightly more shade-tolerant and requires higher humidity. In contrast to this, species like *Q. infectoria* and *Q. pubescens* still thrive in xerophytic open woodlands with low rainfall, frequently with shrubby habit encouraged by coppicing.

Table 3. *Quercus* species and subspecies in common with other trees in Georgian forests. The figures give the number of common occurrences according to the diagnostic tree-species groups of forest associations of Kvachakidze (2001)

	<i>Quercus petraea</i> ssp.		<i>Quercus robur</i> ssp.		<i>Quercus macranthera</i>
	<i>iberica</i>	<i>dshorochensis</i>	<i>pedunculiflora</i>	<i>imeretina</i>	
<i>Carpinus betulus</i> (<i>C. caucasicus</i>)	35	1	5	2	11
<i>Fraxinus excelsior</i>	26	-	7	1	3
<i>Fagus orientalis</i>	9	-	-	-	10
<i>Acer cappadocicum</i> (<i>A. laetum</i>)	11	-	-	-	1
<i>Pinus sylvestris</i> ssp. <i>hamata</i> (<i>P. sosnowskyi</i> , <i>P. kochiana</i>)	8	1	-	-	3
<i>Sorbus torminalis</i>	15	-	-	-	-
<i>Tilia begoniifolia</i> (<i>T. caucasica</i>)	18	-	5	-	1
<i>Acer campestre</i>	5	-	3	-	-
<i>Pyrus caucasica</i>	2	1	2	-	-
<i>Zelkova carpinifolia</i>	4	-	-	1	-
<i>Carpinus orientalis</i>	5	-	-	-	-
<i>Castanea sativa</i>	4	-	-	-	-
<i>Ulmus glabra</i> (<i>U. elliptica</i>)	3	-	-	-	-
<i>Corylus colurna</i> (<i>C. iberica</i>)	2	-	-	-	-
<i>Ostrya carpinifolia</i>	-	1	-	-	-
<i>Pinus brutia</i> ssp. <i>pityusa</i>	1	-	-	-	-
<i>Juniperus foetidissima</i>	1	-	-	-	-
<i>Juniperus excelsa</i> ssp. <i>polycarpus</i>	1	-	-	-	-
<i>Ulmus minor</i> (<i>U. foliacea</i>)	-	-	7	-	-
<i>Prunus cerasifera</i> ssp. <i>divaricata</i>	-	-	2	-	-
<i>Salix alba</i> sensu lato. (<i>S. excelsa</i>)	-	-	1	-	-
<i>Quercus hartwissiana</i>	-	-	-	2	-
<i>Alnus glutinosa</i> ssp. <i>barbata</i>	-	-	-	1	-
<i>Betula litwinowii</i>	-	-	-	-	7
<i>Acer trautvetteri</i>	-	-	-	-	5
<i>Picea orientalis</i>	3	-	-	-	1
<i>Populus tremula</i>	1	-	-	-	2
<i>Sorbus aucuparia</i> (<i>S. caucasigena</i>)	-	-	-	-	2
<i>Salix caprea</i>	1	-	-	-	1
<i>Acer platanoides</i>	1	-	-	-	1
<i>Acer hyrcanum</i>	-	-	-	-	1
<i>Quercus petraea</i> ssp. <i>iberica</i>	-	-	-	-	1

The following listing gives orientation as to the vegetation types in which Caucasian oaks can be found. The most important forest types of the oak forests and the oak mixed forests formed by the individual oak species are given in the *Survey of oaks of Caucasia* (see chap. 6), each under the respective taxa.

Forest formations and main forest vegetation types including oaks as dominant or characteristic tree species

Alluvial and wet lowland forests of large river valleys

- Alder and hardwood alluvial forests and wet lowland forests: *Q. robur* ssp. *imeretina*
- Poplar-willow and hardwood alluvial forests: *Q. robur* ssp. *pedunculiflora*, ssp. *robur*

Hygro-thermophilous mixed deciduous broad-leaved forests

- Lowland to submontane, partly to montane oak and mixed broad-leaved forests: *Q. castaneifolia*, *Q. hartwissiana*, *Q. robur* ssp. *imeretina*

Thermophilous mixed deciduous broad-leaved forests

- Colline Oak and Oriental hornbeam (*Carpinus orientalis*-) oak forests: *Q. pubescens*

Xerophytic open woodland and forests

- Submediterranean pine (*Pinus brutia* ssp. *pityusa*-) forests: *Q. petraea* ssp. *iberica*
- Open juniper (*Juniperus excelsa* ssp. *polycarpus*-, *J. foetidissima*-) woodland: *Q. petraea* ssp. *iberica*
- Submontane-montane oak forests and open woodland: *Q. infectoria* ssp. *veneris*

Mesophytic mixed deciduous broad-leaved forests

- Colline-submontane to montane oak and mixed hornbeam-oak forests
 - oak forests and hornbeam (*Carpinus betulus*-) oak forests: *Q. petraea* ssp. *petraea* and ssp. *iberica*, *Q. robur* ssp. *robur* and ssp. *pedunculiflora*
 - hygrophilous types of oak, hornbeam-oak and hornbeam-chestnut-beech forests with evergreen understory: *Q. petraea* ssp. *iberica*
 - Oriental hornbeam (*Carpinus orientalis*-) oak forests: *Q. petraea* ssp. *iberica*
- Submontane to montane hornbeam (*Carpinus betulus*-) beech forests: *Q. petraea* ssp. *iberica*
- Montane beech (*Fagus orientalis*-) forests, partly with evergreen understory: *Q. castaneifolia*, *Q. petraea* ssp. *iberica*
- Altimontane oak forests: *Q. macranthera*

Montane to subalpine coniferous forests

- Montane pine (*Pinus sylvestris* ssp. *hamata*-) forests: *Q. petraea* ssp. *iberica*
- Montane to subalpine pine forests: *Q. macranthera*

Subalpine open woodlands, krummholz, scrub: *Q. macranthera*, *Q. pontica*

Survey of oak species and their subspecies

The species and their subspecies are given below in alphabetical order and their synonyms and distribution are explained. Taxonomically difficult species complexes are also discussed. The forest vegetation types coined by them are outlined.

Quercus castaneifolia C. A. Mey. – Chestnut-leaved oak

The species is unmistakable by virtue of its leaves, the small triangular mucronate teeth (7-14 pairs), the cup with subulate, spreading or reflexed scales, and the persistent stipules of the buds. It is a typical Hyrcanian species, occurring exclusively in the east of South Caucasia (Azerbaijan; Red book species of the country) and in the Elburs Mountains (northern Iran). In Lenkoran it is one of the most important forest-forming trees, 40-45 (occasionally up to over 50) m in height, 100-150 cm stem diameter and growing for 300 years or more. *Quercus castaneifolia* forests occur in the lowland as coastal vegetation of the Caspian Sea up to the mountain regions (up to 1800 m, Talysh Mts.). As lowland and mountainous oak forests they represent the Hyrcanian type of the hygro-thermophilous deciduous broad-leaved forests, and thus residual stock of the Arcto-Tertiary deciduous broad-leaved forests in Caucasia abounding in relics and endemics. Among others, *Parrotia persica*, *Zelkova carpinifolia*, *Acer velutium*, and *Gleditsia caspica* occur as mixtures of tree species in the Hyrcanian colline to montane oak forests. Mixed deciduous broad-leaved forests with *Q. castaneifolia* are also found in the Talysh Mountains, and in the beech forest belt, where *Fagus orientalis* forests with evergreen lianas and shrubs (e.g. *Hedera pastuchowii*, *Ilex hyrcana*, *Danae racemosa*) are predominant.

Quercus hartwissiana Steven – Hartwiss' oak

Syn.: *Q. armeniaca* Kotschy - *Q. stranjensis* Turill

This species is similar to *Q. petraea* (leaves very similar to the ssp. *iberica*), its fruits however are long pedunculate (3-4.5 cm). This Euxinian species is distributed in western Caucasia (mainly south of the Great Caucasus) and extends via north Anatolia along the Black Sea up to eastern Bulgaria. According to Kolakovski (1982), this is a Tertiary relic that used to be widely distributed. This shade-tolerant tree (among the Caucasian oaks it is the most shade-tolerant species) grows to 34-36 m in height, does not form stands, but merely occurs as with other species. For instance in the Colchic deciduous broad-leaved mixed forests (in particular the hygro-thermophilous broad-leaved forests of warm-humid climate), it occurs on eutrophic, fresh-to-wet soils from the lowland up to the mountain region (up to 1200-1500 m). The German name Armenian oak for the species in Bärtels (2001) is misleading, as it does not occur in Armenia. Moreover in the English literature (Hillier 1998) – not appropriate either - *Q. pontica* is referred to as Armenian Oak. According to Krüssmann (1978), *Q. hartwissiana* as a cultivated plant is often confused with *Q. pubescens*.

Quercus infectoria Oliv. – Aleppo oak

This species is variable, with sclerophyllous, partly semi-evergreen leaves, pubescent beneath at the first, the shape of which undergoes conspicuous change along the annual shoots (basal ones mostly entire, and the subsequent ones with acute teeth). The large distribution range extends from the southern Balkan Peninsula via Asia Minor up to the Middle East. The small (up to 8 m in height), small-leaved and small-fruited (leaves with 5-7 paired teeth, cup up to 1 cm in diameter) type taxon ssp. *infectoria* is missing in the Caucasus countries; its easternmost north-Anatolian occurrences are at Artvin, not extending as far as Georgia. However, this species is represented in Caucasia, even though very

limited, since the following East Mediterranean-Oriental subspecies has isolated occurrences in the southern South Caucasia (Karabakh, Megri):

- ssp. *veneris* (A.Kern.) Meikle – Boissier's oak, Araxes oak
Syn.: *Q. boissieri* Reut. - *Q. infectoria* ssp. *boissieri* (Reut.) O. Schwarz - *Q. araxina* (Trautv.) Grossh.

The subspecies (in Caucasia treated as separate species) can grow as tall as 8-16 (-20) m, and general has a shrubby habit due to coppicing. The leaves have 8-12 pairs of leaf-teeth, and the cupules are up to 2 cm in width. In the south Caucasian area, all morphological transitions between *Q. infectoria* and *Q. petraea* ssp. *iberica* can be found (Gulisa_vili et al. 1975, Menitsky 1984). This oak tolerates drought (annual mean precipitation is only 300-350 mm) and hot summers (average July temperature 26-27° C). It is a characteristic element of the xerophytic open woodland of dry mountainous areas (up to 1000-1300 m) in southernmost Armenia and Azerbaijan. The rare *Quercus infectoria* ssp. *veneris* forests (i.e. with *Fraxinus oxycarpa*, *Celtis glabrata*, *Acer monspessulanum* ssp. *ibericum*) generally occur on the slopes of the Arax valley (see *Q. araxina* for this taxon). In lower tracts they transition into the arid *Pistacia mutica* open woodland (adjacent to semi-deserts), at elevations from 900-1000 m, to *Q. petraea* ssp. *iberica* forests. Intact stands are rare. There are no longer high forests and regeneration takes place via stump sprouting. The stands have been greatly reduced and are endangered (likewise those of *Pistacia mutica*, cf. Schmidt 2003), because of fuel wood extraction, missing natural regeneration (feeding on acorns by grazing animals, woodland pasture), utilization of the foliage for winter-feeding, and high incidences of mistletoe infestations. For its rarity and endangerment this oak was included in the Red Books of the two south Caucasian countries (in Krever et al. 2001 under several species names: *Q. infectoria*, *Q. boissieri* and *Q. araxina*). In Armenia, a total ban of felling was imposed (Red Data Book 1988).

Quercus macranthera Fisch. et C. A. Mey. ex Hohen. – Persian oak,
Highland oak

This is a readily identifiable species with tomentose shoots, persistent stipules at the buds, and rather large (7-15cm in length) leaves, grey to yellowish tomentose beneath. In Caucasia the Caucasian-Hyrcanian type-taxon ssp. *macranthera* occurs. No occurrences are known for the northern Anatolic subspecies ssp. *syspirensis* (K. Koch) Menitsky, from the Caucasus countries. This oak can grow as old as 300 years, achieving 20-(35) m in height, as well as 80 cm in stem diameter. It is highly light-demanding, but can tolerate both drought and frost. In Great Caucasus (here in the East also extending as far as north Caucasia) as in Minor Caucasus, its significance as a stand-forming forest tree increases towards the east. Forests consisting of, or including, *Q. macranthera* are, above all, rather spread out in South Caucasia. They occur from middle montane belts up to the timberline in the subalpine belt (1450-2400, occasionally up to 2700 m), with the most favourable conditions between 1450-1600 m. But even here the stands have almost totally become opened up due to overgrazing and timber utilization, or they are characterized by crookedness of boles and insufficient natural regeneration. In the dry, only sparsely forest-covered highland of South Caucasia (S Armenia, S Azerbaijan), *Q. macranthera* is the only forest-

forming oak in the uppermost forest belt. It occurs as monospecies stands, mainly on south-facing slopes, on skeletal soils. In the subalpine krummholz and open woodland of Caucasia, *Acer trautvetteri*, *Betula litwinowii* and *Sorbus aucuparia* s.l. (*S. caucasigena*) are often concomitant, while in open woodlands in southeast South Caucasia, *Acer hyrcanum* and *Pyrus zangezura* are accompanying species.

Quercus petraea L. ex Liebl. sensu lato - Sessile oak

Incl. *Q. calcarea* Troitsky non Gand. - *Q. dshorochensis* K. Koch - *Q. gagriana* Rossinsky - *Q. iberica* Steven - *Q. pinnatiloba* K. Koch - *Q. polycarpa* Schur

Of the *Q. petraea* group, numerous species have been described from Caucasia, and even today, up to 7 species are designated (in addition to those given in Tab. 1, others such as *Q. hypochrysa*, e.g. Artjunjan & Artjunjan 1985). Likewise in Europe, *Q. petraea* was, and partly still is, seen in the narrower sense (separation of *Q. polycarpa*, *Q. dalechampii*), also in dendrological handbooks (e.g. Rehder 1940 after Krüssmann 1978) *Q. iberica* and *Q. polycarpa* are named as separate species. On the other hand, *Q. petraea* has recently been classified merely as a subspecies of *Q. robur* by some authors (Roloff & Bärtels 1996). The classification of *Q. petraea* sensu lato in Menitsky (1968-2002) for Caucasia and southwest Asia deviates from that in the *Flora of Turkey* (Hedge & Yaltirik 1982) and the *World Checklist* (Govaerts & Frodin 1998). The latter regard *Q. dalechampii*, which Menitsky allocates to its ssp. *medwediewii*, as another species not occurring in Caucasia, and differentiate between 3 subspecies of *Q. petraea*. In this context ssp. *iberica* is understood in the broader sense with the inclusion of the subspecies ssp. *dshorochensis* and ssp. *medwediewii* designated by Menitsky. The named authors agree as to the classification of *Q. polycarpa* in *Q. petraea*, although in European floras it is often accepted as a separate species (e.g. Hejny & Slavik 1999). However, it is allocated to different subspecies, so to ssp. *iberica* by Govaerts & Frodin (1998), to ssp. *medwediewii* by Menitsky initially (1968), and later on to ssp. *petraea*. The latter (Menitsky 1984) emphasised that a designation of *Q. polycarpa*, irrespective of whether as species or subspecies, would presuppose the description of a whole series likewise of such "small" taxa, being virtually indistinguishable (ecotypes).

Q. petraea sensu lato, like *Q. robur* sensu lato, belongs to the Submediterranean/montane-Middle European species, but contrary to the latter, it is absent in the East-European deciduous broad-leaved and mixed forest region (*Fagus sylvatica* type of distribution areas according to Meusel & Jäger 1992). Being widely distributed in Europe, the range of which extends from the eastern Mediterranean region via Asia Minor to Middle East, it is an important forest tree of Caucasia (20-40 m in height and >1 m in stem diameter). It occurs in various forest ecosystems on dry and fresh sites from the lowland up to 1200 m, predominantly in the lower forest belt, but at higher elevations (1100-1800 m), in semiarid areas. *Quercus petraea* forests (incl. hornbeam-oak mixed forests) are the most widespread oak forests of Caucasia, mainly represented by ssp. *iberica* south of, and by ssp. *petraea* north of, the Great Caucasus. Korotkov et al. (1991) refer to *Q. petraea* as characteristic species or as differential species of various forest communities of Caucasian beech and hornbeam-beech forests, as well as hornbeam-oak forests, without differentiating between the subspecies:

- suballiance Orobo-Fagenion (ordo Rhododendro pontici-Fagetalia orientalis; Central Caucasus, southern slope),

- alliances Crataego-Carpinon (Central Georgia) and Carpino-Quercion *petraeae* (i.a. along with association *Rhododendro lutei-Quercetum*; northwest part of Great Caucasus range) of the ordo Lathyro-Carpinetalia caucasicae.

- **ssp. *dshorochensis*** (K. Koch) Menitsky – Chorokhi oak

Syn.: *Q. dshorochensis* K. Koch

This taxon was classified by Russian (e.g. Czerepanov 1995) and Georgian (e.g. Dmitrieva 1990) authors as a separate species, but other authors do not accept it as an independent taxon, and is therefore controversial. It occurs on sunny, rocky dry slopes of river valleys of the uplands in the southeast of the Black Sea (southeast subeuxinian). This small area extends from southwest Ajara into the east of the North Anatolian Province. Nowadays, *Q. petraea* ssp. *dshorochensis* forests are reduced to residual occurrences on the slopes of the Ajarsckali and Chorokhi River valleys in southwest Ajara (therefore belonging to the rare and endangered species of Georgia; Papunidze et al. 1978, Krever et al. 2001) and adjoining Turkey. However, in the *Flora of Turkey* such a taxon is not designated; rather is it incorporated – like in Govaerts & Frodin (1998) – into ssp. *iberica*. It is true that Menitsky (1968, 1984) accepted the similarity with this subspecies (xeromorphic descendant of the ssp. *iberica* with transitional forms to this one), but he believed that the small and oblong leaves (5-8[10] cm in length, 3-4 cm in breadth) justified a designation of a separate race. However, the leaves of the stands occurring in Ajara are described by Dmitrieva (1990) as oblong-elliptical, 8-12 cm in length, and 3-6 cm in width. According to my own observations, the plants differ greatly from the ssp. *iberica* in where they grow, being distributed in Georgia, but a xerophytic population on very dry slopes of shallow soil might have to be referred to. However, other factors may play a role. Unfortunately, few normally developed trees exist, because the stands are used for fuel wood extraction (coppicing) and animal feed (pollarding), thus being more liable to a shrubby habit. According to Menitsky (1984), in western Turkey tree forms appear, pointing to an introgressive hybridisation of ssp. *dshorochensis* with *Q. infectoria*. The occurrence of such transitional forms supposedly explains why the species described by authors of older publications such as *Q. woronowii* Maleev or *Q. komarowii* A. Camus are regarded as synonyms on the one hand of ssp. *dshorochensis* (Menitsky 1984, Czerepanov 1995), or on the other hand of *Q. infectoria* or their hybrid with *Q. petraea* (*Q. x mannifera*, Govaerts & Frodin 1998).

- **ssp. *iberica*** (Steven) Krassiln. – Georgian oak

Syn: *Q. gagriana* Rossinsky - *Q. grossheimii* Sachok. - *Q. hypochrysa* Steven - *Q. iberica* Steven - *Q. kozlowskyi* Woronow ex Grossh. - *Q. szowitzii* Wenz.

The subspecies, in general designated as separate species by Caucasian authors, differs from ssp. *petraea* by larger, thicker (more leathery), and slightly more pubescent undersides of leaves, the lobes (at least 1-2 additional pairs) of which are shorter (not exceeding 1/3 of the width of half the lamina). According to Menitsky (1984), it represents the most primordial taxon of the relationship of *Q. petraea* sensu lato. This oak is a characteristic forest tree of the lower and middle mountainous belts of South Caucasia (0-1800 m), which towards the north, hardly extends past the Great Caucasus (only Daghestan, Chechnya, Ingushetia); in the south, it extends up to Karadag Mountains; in the east up to the

Elburs Mountains (Iran); and in the west up to the Black Sea coast (here in the Gagra populations with tendency to winter-green foliage it is described as *Q. gagriana*). In the *Flora of Turkey* and Govaerts & Frodin (1998) this subspecies is referred to in greatly broader terms, and the distribution range thus extending with the inclusion of ssp. *dshorochensis* and ssp. *medwediewii*, as well as *Q. polycarpa* via Anatolia and the Krim up to the Balkan Peninsula and into the Pannonian Region (up to Slovakia). *Q. petraea* ssp. *iberica* forests among the oak and hornbeam-oak forests in South-Caucasia are distinguished by the widest geographical distribution, from the coastal region of the Black Sea extending as far as the uplands (occasionally up to 1800 m) and into semiarid regions. Nowadays, they are often found bordering on xerophytic woody vegetation and steppes, which partly occupy their former sites. Frequent associated tree species are *Carpinus betulus* (*C. caucasica*), *C. orientalis*, *Acer laetum*, *Sorbus torminalis*, and *Zelkova carpinifolia*. Overexploitation of oak, site degradation, erosion etc. lead to the establishment of monospecies of *Carpinus betulus* forests, of *C. orientalis* shibliak or *Bothriochloa* grassland.

Dolukhanov 1992 (according to Nakhutsrishvili 1999) differentiates between the following types (sub-formations) of the *Q. petraea* ssp. *iberica* forests:

- monodominant forests (hemi-xerophytic and xero-mesophytic series),
- *Carpinus orientalis*-*Q. iberica* forests (in arid regions at elevations of 600-1000 m, in humid locations 350-800 m; in lower belts on north slopes and on south slopes in higher belts),
- *Carpinus betulus*-*Q. iberica* forests (in the transition zone to beech forests). Kvachakidze (2001) indicates 25 Querceteal/*Q. iberica* forest associations for Georgia, among which those being rich in shrubs (e.g. *Quercetum azaleosum*, *cornosum*, *cotinosum*), those rich in dwarf shrubs (*Quercetum ericosum*, *ruscosum*), and those rich in herbs (e.g. *Quercetum epimediumum*, *trachystemosum*), as well as those rich in grasses (e.g. *Quercetum festucosum*, *poosum*).
- ssp. *medwediewii* (A. Camus) Menitsky – Medvedevs oak
Syn.: *Q. lanuginosa* Lam. ssp. *medwediewii* A. Camus - *Q. calcarea* Troitsky non Gand.

As compared to the other subspecies, this one is distinguished by a stronger pubescence and (with the exception of ssp. *pinnatiloba*) by deeper divided leaves (lobes extend as far as 1/3-3/4 of the width of half the lamina). Initially young shoots, petioles and the lower sides of leaves are very pubescent (discernible also with the naked eye); they become glabrescent, however, in the course of the vegetation period. The pubescence is maintained at the base of the lamina and the lateral veins. According to Menitsky (1968-1984), introgressive hybridisation with *Q. pubescens*, linked with an ecological differentiation, is decisive for the formation of this taxon. This "ecological race" that grows mainly on limestone in the northern Great Caucasus, as well as in its northern and western piedmont (at the Black Sea coast to the south up to Soczi; 0-1600m), takes a transitional position in view of the sites it occupies (less xerophytic than *Q. pubescens*, more thermophytic and calciphytic than *Q. petraea*).

According to Menitsky (1968-84), ssp. *medwediewii* does not only occur in the Caucasus region, but is likewise distributed in the Mediterranean/montane

and Submediterranean Europe (from East France up to the Krim), as well as in Anatolia. In this regard, he incorporates *Q. dalechampii* Ten. (as synonym). This is the reason why this taxon known as a south to southeast European species of the relationship of *Q. petraea* by authors who do not follow the "subspecies concept" of Menitsky is designated as a species also for Caucasia (e.g. Czerepanov 1995, Semagina 1999). Govaerts & Frodin (1998) accept *Q. dalechampii* as a separate species, however, not occurring in Caucasia, while they designate ssp. *medwediewii* as a synonym of ssp. *iberica*. This situation is confusing due to the contrary conceptions, and the structure of the taxon and nomenclature need to be clarified. Obviously, the transitional forms or hybridogenous populations between *Q. petraea* and *Q. pubescens*, as they often occur in the joint geographic range of both species, occupy a greater area in northern Caucasia, in which *Q. pubescens* no longer occurs. Hence, it seems conceivable that an independent taxon has formed. Although the morphological characteristics mediate between both species, and respective plants could be allocated to this (cf. *Q. lanuginosa* [= *pubescens*] ssp. *medwediewii*) or that (*Q. petraea* ssp. *medwediewii*) species, the failure of *Q. pubescens* and the continued existence of the contact with *Q. petraea* gives good reason for Menitsky's procedure (1968-2002). Finally, it would also be conceivable to designate nothosubspecies of a hybrid *Q. petraea* x *Q. pubescens*, because the wide distribution area of the subspecies in Menitsky, which apparently includes hybrids from the overlapping geographic ranges of both species.

- **ssp. *petraea*** - Durmast oak

Syn.: *Q. petraea* L. ex Liebl. sensu stricto

This subspecies is distributed in the western, middle and south European deciduous broad-leaved forest areas, being more mesophytic as compared to the more southern ssp. *iberica*. It occurs exclusively in the North Caucasian Plain, as well as the adjoining Great Caucasus (60-1800 m). In South Caucasia it is replaced by the ssp. *iberica*.

- **ssp. *pinnatiloba*** (K. Koch) Menitsky

Syn.: *Q. pinnatiloba* K. Koch

This is easily distinguished by the more xerophytic leaves, finely pubescent beneath and deeply lobed (1/2 and more of the width of half of the lamina). Certainly this taxon occupies an extended area that is disjunct due to the restriction to mountains (1000-2700 m) in the eastern Mediterranean and western Oriental-Turanic Regions. One of the partial areas of distribution extends up to the farthest south of Caucasia (only very occasional occurrences in the Armenian highland: Zangezour, Megri).

Quercus pontica K. Koch - Armenian oak

This species is unmistakable by its undivided, sharply serrate leaves, 12-30 cm in length, the 20-30 paired teeth being mucronate. The English name Armenian Oak (Hillier 1998) is not so appropriate, since this species does not occur in Armenia (cf. also the German name Armenian oak in Bärtels 2001 as for *Q. hartwissiana*).

The distribution of *Q. pontica*, an ancient relict of the Colchic flora (next relatives in the Himalayas and East Asia), is restricted to the western part of

South Caucasia: Colchic Province from Bzyb river valley of the Great Caucasus (Abkhazeti) and the southwest Georgian part of Minor Caucasus up to Lazistan (northeast Turkey). Because of its limited geographical range in Georgia, it belongs to the rare and endangered plants of Georgia (Papunidze et al. 1978, Krever et al. 2001). According to Kolakovski (1982), the increased air humidity and soil moisture that continued to exist in Colchheti almost invariably facilitated the survival of this Tertiary relict. The species occurs in the uplands in locations with high amounts of rainfall and high air humidity (1200-1800 up to 2300 m, in near-shore gorges also at lower elevations), thriving exclusively on acid subsoil. In the subalpine vegetation *Q. pontica* occurs as a component of the shrub layer in open woodlands (*Betula litwinowii*, *Fagus orientalis*, *Acer trautvetteri*) with *Betula medwediewii* sensu lato (incl. *B. megrelica*), *Rhododendron caucasicum*, *Prunus laurocerasus* etc. Moreover, this oak grows either alone or together with other species (e.g. *Rhododendron ponticum*, *Prunus laurocerasus*, *Vaccinium arctostaphylos*) a dense, hardly pervious, krummholz. The procumbent-ascendant stems (30-40cm in diameter) grow as tall as 12 m, attaining however only 6-7 m in height. Under extreme conditions the plants can remain shrubby, growing only 1.5-2 m in height. At timberline the fruits rarely come to fruition—being compensated by vegetative propagation. The procumbent branches, being partly covered with soil, may initiate roots, thus giving rise to the formation of clonal scrub stands.

Quercus pubescens Willd. – Downy oak

Syn.: *Q. crispata* Steven - *Q. lanuginosa* Lam. ssp. *crispata* (Stev.) A. Camus - *Q. pubescens* ssp. *crispata* (Steven) Greuter et Burdet - *Q. pubescens* subsp. *anatolica* O. Schwarz - *Q. anatolica* (O. Schwarz) Sosn. ex Bandin

The Submediterranean area of distribution extends from the Balkan Peninsula via the Krim to Caucasia, whereas from Anatolia it extends as far as South Caucasia. In the Caucasus region this species appears to have two isolated partial ranges, one in the utmost northwest in the area of the Russian Black Sea coast, and one in the far east on the slope of Great Caucasus towards the Caspian Sea (Dagestan, northeast Azerbaijan). The trees are generally only 8-10 m in height (often shrubby) and, like *Q. macranthera*, tolerate drought, being however less frost-hardy. Therefore this species occurs in the influential zone of the inland seas (coastal slopes up to 500 m), above all in thermophilous, deciduous, broad-leaved forests or open woodlands. In the western part of its distribution, it forms together with Submediterranean species *Carpinus orientalis*-*Q. pubescens* forests (i.e. with *Pistacia mutica*, *Rhus coriaria*, *Juniperus oxycedrus*, *J. excelsa*), while in the eastern part the Dagestanian *Q. pubescens* forests (i.e. including *Pyrus salicifolia*, *Rhamnus pallasii*). Korotkov et al. (1991) assigns *Q. pubescens* to the groups of the characteristic and differential species of the alliance *Carpinion orientalis* (order *Quercetalia pubescentis*), for which they indicate, referring to West Caucasia, the associations *Pistacio muticae-Juniperetum excelsae* (Black Sea coast) and *Quercio pubescentis-Carpinetum orientalis* (slopes with cinnamomic soils or rendzina on limestone).

Regarding pubescence, leaf-size and leaf-form, *Q. pubescens* has a great amount of variability, encouraged by hybridisation and introgression (e.g. with *Q. petraea*, *Q. robur*, *Q. infectoria*), hence the delimitation to other species and the intraspecific classification becoming more complicated. Several taxa were

designated as separate species by authors of older publications, so also in Azerbaijan two other species were separated from *Q. pubescens* (Bandin 1952): *Q. crispata*, *Q. anatolica*. Until now, both names have been differently interpreted, thus causing confusion. Govaerts & Frodin (1998), who surprisingly do not name *Q. pubescens* sensu lato at all regarding the Caucasus countries, assign its occurrences in the eastern part of the distribution area (E Balkan Peninsula, Krym, Turkey) to ssp. *crispata*. Contrary to this, according to the outline map in Menitsky (1984), the Turkey area contains the ssp. *anatolica*, which he regards as a product of introgressive hybridisation of ssp. *pubescens* with *Q. infectoria*. All Caucasian occurrences, among them also *Q. crispata* (according verification of Steven's type material), are designated by him (Menitsky 1968-2002) to ssp. *pubescens*.

***Quercus robur* L. sensu lato – Pedunculate oak**

In Caucasia generally three species of *Q. robur* relatives have been distinguished until now: *Q. robur* (s.str.) in the north, *Q. pedunculiflora* (often as *Q. longipes*) in the east, and *Q. imeretina* in the western lowlands and river valleys of South Caucasia. According to Menitsky (1968-84) three subspecies are referred to here, although he eventually (2002) reduced this number to two (ssp. *robur*, ssp. *pedunculiflora*).

Like *Q. petraea*, this species belongs to the Submediterranean/montane-Middle European species of the nemoral European deciduous broad-leaved forests. However it occupies a greater range of distribution (*Tilia cordata* type according to Meusel & Jäger 1992). Hence, the most widely distributed oak species of Europe is referred to here, its range extending further from the Balkan Peninsula via Asia Minor up to the Middle East. Likewise, it is an important forest tree in Caucasia, where it often colonizes moister sites (also water-logged sites as compared to *Q. petraea*, not achieving the tree heights of the latter). Forests comprising and including taxa of *Q. robur* sensu lato mainly occur in the lowland, riverine, and flood-plain forests.

- ssp. *imeretina* (Woronow) Menitsky – Imeretian oak

Syn.: *Q. imeretina* Steven ex Woronow

This subspecies differs from ssp. *robur* by the extremely short petioles (1-4 mm, smaller than 10 mm), which are almost completely covered by the auricles of the leaf lamina base, and by the less deeply lobed leaves (only up to 1/3, not up to 1/2 of the width of half the lamina). In 1984 Menitsky emphasised the small morphological differences, considering a designation as subspecies (ssp. *imeretina* as pronounced Colchic race) as justified for phytogeographical reasons. Later on (Menitsky 2002) no longer attached any taxonomic rank to this population, i.e. in contrast to Govaerts & Frodin (1998), and allocated it to the type subspecies (synonym of ssp. *robur*). Contrary to this, Kolakovski (1982) regarded the geographical isolation as an essential argument for recognizing it as separate species (*Q. imeretina*).

This taxon, which only occurs in the western part of South Caucasia (west Georgia with small part extending into Russia along the Black Sea coast), particularly in the Rioni lowland, in flood-plain forests and on river terraces (0-400 m), is endemic to the Colchic Province.

Q. robur ssp. *imeretina* forests used to be largely distributed in west

Georgia from the lowland up to the lower mountain region, both on moist and dry sites, both in monodominant stands and in mixed forests, so in flood-plains and river valleys with *Carpinus betulus*, *Fraxinus excelsior*, *Alnus glutinosa* ssp. *barbata* and *Pterocarya pterocarpa* or in dry locations with *Zelkova carpinifolia* and *Carpinus orientalis*. In the hygro-thermophilous Colchic mixed oak forests with evergreen understory (e.g. *Rhododendron ponticum*, *Prunus laurocerasus*), the subspecies may occur together with other oaks (*Q. hartwissiana*, *Q. petraea* ssp. *iberica*), but also *Zelkova carpinifolia*, *Carpinus betulus* or *Castanea sativa*. Because of the very restricted area and the depletion of the stands due to clear-cutting and agriculture (e.g. only occurrence in Ajara extinct, nowadays a tea plantation; Dmitrieva 1990), it was not only classified as rare and endangered species of Georgia (Papunidze et al. 1978, Krever et al. 2001), but was put on the IUCN Red List (Hilton-Taylor 2000) and the World List of Threatened Trees (Oldfield et al. 1998; Category Vulnerable).

- **ssp. *pedunculiflora*** (K. Koch) Menitsky – Long-stalked oak

Syn.: *Q. erucifolia* Steven - *Q. haas* Kotschy - *Q. kurdica* Wenz. - *Q. longipes* Steven - *Q. pedunculiflora* K. Koch - *Q. pedunculiflora* var. *erucifolia* (Steven) Gagnidze

This subspecies adapted to dry-warm climatic conditions is extraordinary heterogeneous, but as such, fairly well characterised. It is distinguished by more leathery leaves, as compared with other taxa of *Q. robur* s.l., which are more deeply divided (lobes longer than $\frac{1}{2}$ of the width of half the lamina); the leaves are often pubescent beneath and the cup is thicker-walled. The distribution area of the east Submediterranean taxon extends from the Balkan Peninsula via the Isle of Krim and Asia Minor up to Caucasia (mainly in central and eastern South Caucasia, in East Caucasia also in the northern Caucasus piedmont) and in the adjacent northwest Iran. In the Caucasian countries the taxon has been regarded as a separate, even endemic, species, either as *Q. longipes* (e.g. Kvachakidze 2002) or as *Q. pedunculiflora* (e.g. Nakhutsrishvili 1999, Krever et al. 2001). Likewise, in the European Floras (e.g. Hejny & Slavik 1990) and in the standard dendrological works like Krüssmann (1978) or Hillier (1998), it is often designated as a separate species. *Q. robur* ssp. *pedunculiflora* occurs as a predominant or admixture tree in oak and hornbeam-oak forests (i.a. with *Carpinus betulus* and *Ulmus minor*) from the lowland up to the lower uplands (up to 1000-1100 m). In this context, it is also found in hornbeam-oak forests on drier sites, according to Papunidze et al. (1978), even together with *Pistacia mutica* on slightly saline dry soils. This oak is a characteristic element of the hardwood alluvial forests, which occur in combination with poplar (*Populus alba*, *P. canescens*, *P. nigra*) and willow (*Salix alba* sensu lato: *S. excelsa*) alluvial forests in the river valleys of South Caucasia, especially upon the Kura and its tributaries (noticeable residual stands e.g. in Iori- and Alazan valleys, E Georgia). In Armenia the area has markedly shrunk due to overexploitation of timber, so that only single individuals survive, thus having been included in the Red Data Book of Armenia (1988).

- **subsp. *robur*** – Common oak, English oak

Syn.: *Q. medwedewii* Sosn. - *Q. robur* L. sensu stricto

This thin-leaved, more mesophytic subspecies, as compared with ssp.

pedunculiflora, represents the species in the middle European area of deciduous broad-leaved forest, in the east up to the Urals and northern Caucasia. It occurs in the North Caucasian Plain and on the foothills (300-1400 m). From the northern slopes of the Great Caucasus (Teberda River Valley) a microphyllous alpine ecotype was described as a separate species under *Q. medwedewii* (not to be confused with *Q. petraea* ssp. *medwedewii*! likewise occurring in northern Caucasia). *Q. robur* ssp. *robur* is found in colline-submontane north Caucasian oak and hornbeam-oak forests (i.a. with *Carpinus betulus* and *Ulmus minor*), as well as in the hardwood alluvial forests of river valleys. Small open oak woodlands (i.e. with *Caragana frutex*, *Prunus tenella*) occur as residual trees of the steppe woodland, also on riparian slopes in the North Caucasian Plain.

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