

QUERCUS FORESTS IN THE NORDIC COUNTRIES, A PRELIMINARY OVERVIEW

JONAS E. LAWESSON

*National Environmental Research institute, Department of landscape Ecology, Grenåvej 12,
8410 Rønne - Denmark, phone +45 89 20 15 01, fax +45 89 20 15 15*

ABSTRACT - *Quercus* is remarkable for its wide ecological amplitude, occurring from mild, humid and oceanic settings on dunes and ledges to drier, cooler continental conditions on gravel, sand, clays and moraines. It most probably constituted a prominent component of all forests in Denmark previously, but are now mainly found on oligotrophic soils, much resembling the oak forests in the rest of the Nordic area. Only relatively few eutrophic oak forests remain intact, as *Fagus sylvatica* artificially has replaced oaks in many places in Denmark. A review of the principal Danish oak forest types is given, with notes on related types in Norway, Sweden and Finland.

KEY WORDS - distribution, ecology, *Fagetalia*, phytosociology, *Quercetum*, *Quercetalia pubescenti-petraea*, *Ulmo-Tilietum*.

INTRODUCTION

The northern oaks (*Quercus robur* and *Quercus petraea*) are in much of Europe considered king of the trees, as they combine strength and beauty. Moreover, the oaks are among the oldest trees of Europe, easily reaching 800 years or more. The famous oak of the departement Charente Inférieure in France, is said to have had a build-in room with window, and being between 1800 and 2000 years old (Vaupell, 1863). The other important tree of northern, nemoral Europe, the beech, rarely obtains higher age than 300 years. Oaks are among the most important tree species in natural nemoral vegetation, and in Denmark the oaks together with lime, probably covered most of the landscape, until the 18th century, when drainage was started, and animal holds in the forests ceased. Yet, the oaks still play a significant role, especially on poorer and marginal soils where agriculture or forestry plantations of beech have not replaced the original vegetation.

The oaks, their ecology and the associated plant communities have since long been of major interest in Europe (Jones, 1959a, b) Scandinavia (Sjörs, 1965) and Denmark (Olsen, 1938; Gram, Jørgensen & Køie, 1944). As part of the Nordic vegetation survey initiative (Lawesson, Diekmann, Eilertsen, Fosaa & Heikkilä, 1997),

its seems highly relevant to compare the oak dominated forest types in the Nordic countries. As a part of the initiation of such a comparative and classificatory project, it is necessary to compile the available knowledge on the Nordic oak forest types. That is the main objective of this paper, in which we review the present knowledge on oak forests and their general ecology. A more detailed systematic and ecological analysis of the oaks in the Nordic countries will follow when the necessary data have been collected for a modern and comprehensive treatment.

DISTRIBUTION OF *QUERCUS ROBUR* AND *QUERCUS PETRAEA*

The two native oak species of the Nordic countries i.e. *Quercus robur* and *Quercus petraea* are widespread in the mild, oceanic settings of Denmark, southern Sweden and southern and western lowlands of Norway to Nordfjord, through sub-boreal to hemi-boreal and continental settings in the interior and eastern parts of Sweden, and further to Ural (*Quercus robur*), in addition to smaller populations in the southern most part of Finland. The northern *Quercus* species also extend to most of western Europe. *Quercus* is for phytogeographical reasons not native to Iceland and the Faroe Islands.

Some authors claim that the limit of *Quercus petraea* is due to low frost-tolerance (Rubner, 1960; Jones, 1974), while locally, as in southern Sweden, Weimarck (1947) indicates edaphic conditions (well-drained, acidic soils) as the main factor. This is also in accordance with the present distribution in Denmark. *Quercus robur*, however, occurs in a multitude of ecological situations, from nutrient poor, acidic soils to rich, moraine soils, and from dry sandy soils and dunes to wet sedimentary soils with temporary flooding. It also occurs abundantly on granite rocks on Bornholm island. Its only pre-requisite to rejuvenate seem to be open and light conditions. In the case that other tree taxa, such as *Fagus*, *Ulmus* and *Acer* invade the stand, the oak trees may slowly loose vitality and disappear. This is what has happened on well-drained moraine soils in Denmark.

THE GENERAL ECOLOGY OF *QUERCUS*

The oaks reach their largest size and highest age in Denmark and western Norway, where the relatively mild winters and humid summers allow for the optimal development. *Quercus robur* and *Quercus petraea* are in the Nordic region tall, but slow-growing deciduous trees, with ring porous wood and a late-emerging canopy. The Danish oaks commonly grow to heights of 30 m, and may easily obtain ages far more than 500 years. Some of the oldest oaks in Denmark are found on the isle of sjælland, in wet *Alnus glutinosa* vegetation, and are approximately 1000 years of age.

In Denmark, the oaks belong to the most important tree species in natural broad-leaved vegetation (Petersen, 1906; Warming, 1919; Bornebusch, 1923-26; Grøntved, 1936; Sissingh, 1941; Böcher, 1946), and they still play a significant role, usually present in most forests, and the dominant species on poorer and acid soils in western Denmark, on aeolian and glaciofluvial sands, or on wet and clayey soils of Lolland-Falster. In these areas, they compete well with *Fagus sylvatica*. Only under such conditions have true

Quercus forests persisted until now in Denmark. Otherwise, smaller compartments with *Quercus* are allowed in otherwise beech planted forests and plantations in most of Denmark. Oaks have also survived in many places in Denmark as low thicket-like vegetation (Worsøe, 1979; 1980). The presently narrow occurrence of oak should however not be interpreted as little competitive ability or ecological adaptation. On the contrary, the oaks have a very wide ecological amplitude, as shown by their wide geographical range. It is also a prominent invader in former heath-lands (Nielsen, 1982).

The oligotrophic oak forests have for centuries been strongly explored by man, for fuel and construction purposes, and the forests have generally been used for grazing by sheep and cattle, which has strongly influenced the floristic composition and physiognomy. Such rather open, and low oak forests are commonly called «egekrat» in Danish, and are seen as a cultural heritage, and are accordingly protected by the Danish Nature Protection Act. Consequently, forest management is carried out by state and private owners, in a way so to preserve the grazed, and rather low and poor types of oligotrophic forests in western Denmark.

While the soil nutrient status seems to be a major determinant of *Quercus* forest types in the southern parts of the Nordic countries, the exposure and local climatic conditions to a large extent determine the occurrence of oak forests in Norway and the boreo-nemoral zone of Sweden. On too cool and wet locations, conifer or birch forests usually compete better. South-exposed warmer and drier slopes thus constitute the only habitats for oak forest to the far north.

In Sweden, both species of *Quercus* occur in the nemoral and boreo-nemoral parts (Andersson, 1970; Brunet, 1992; Diekmann, 1994), but *Quercus robur* seems the predominant. *Quercus petraea* is confined to thermophilous acidic soils on hilly escarpments and slopes mainly in Bohuslän and Blekinge. Oak forests in Sweden are found both on aeolian and glaciofluvial sands, and on moraines and rocky soils. Both *Quercus* species have their optima in the poorest edaphic conditions as compared to other deciduous species, yet they are the most light-demanding species (Diekmann, 1996). The syntaxonomical literature on Swedish oak forests is scattered, without a total data analysis and synthesis. An overview was published by Klötzli (1975), and a regional comparison of oak forests in Skåne and eastern Småland by Rühling & Tyler (1986). Diekmann (1994) reviewed the deciduous boreo-nemoral forest types.

In Norway, the oaks occur in the coastal parts of southern and western Norway in a number of forest types (Bjørnstad, 1971; Øvstedal, 1985; Kielland-Lund, 1981, 1984; Fremstad, 1997).

In Finland, well-developed oak forests are found only in the southwestern part of the country, particularly on the Åland archipelago and the Turku area. A diverse literature on Finnish forest types is available (Cajander, 1909; 1921; 1926; Ilvessalo, 1937; Kujala, 1961; 1979; Hinneri, 1972).

MAJOR NORDIC OAK FOREST TYPES

The *Quercus* forests in Denmark, Sweden, Norway and Finland are usually with a rather dense canopy and often contain a rich ground flora on mesotrophic and eutrophic sites. On acidic sites, the canopy usually is more open, and the vascular

ground flora may be poor, but is often compensated for by a diversity of bryophytes and lichens.

The floristic and structural features of the Nordic oak forests are quite comparable between the countries, yet in Denmark and southern Sweden, certain southern species occur in the oak forests, e.g. *Carpinus betulus*, *Acer pseudoplatanus*, *A. campestre*, *Ilex aquifolium*, *Lamium galeobdolon*, and others, while certain boreal species occur exclusively in the northern parts, notably *Picea abies* and *Pinus sylvestris*.

Below, a preliminary overview is attempted, based on the types reported in the literature from Denmark, or from own analyses, with additional notes from the other Nordic countries. Dierssen (1996) treated some of the Nordic oak forest types, yet a complete overview, however, still awaits a systematic revision of the diversity of oak forests in the Nordic countries.

QUERCUS FORESTS ON OLIGOTROPHIC SOILS

These are the forests of poor, often acidic soils, dominated by broad-leaved deciduous trees (some conifers except in Denmark), and with a ground vegetation dominated by *Calluna vulgaris* or grasses, such as *Deschampsia flexuosa* (see table 1 for a Danish species list). A number of seral stages are found particularly in Denmark and Norway, where former antropogenic heathlands now through succession develop into forest types (Worsøe, 1981; 1988). Species that in particular indicate such former human influence are e.g. *Agrostis capillaris*, *Anthoxanthum odoratum* and *Holcus mollis*.

1. *Cladonia-Quercus* community

A particular and rare type of oak forest on acidic coastal dunes along the western coast of Jylland (fig. 1). This coastal dune forest consists of *Quercus robur*, up to 6-8



Fig. 1 - *Quercus-Cladonia* community, Store Løvklit, Jylland, July 1998.

m tall, and commonly with *Juniperus communis*, *Lonicera periclymenum*, *Populus tremula*, *Salix aurita* and *S. repens* in the woody layer. The herbs are e. g. *Campanula rotundifolia*, *Carex arenaria*, *C. pilulifera*, *Deschampsia flexuosa*, *Galium hercynicum*, *Hieracium umbellatum*, *Holcus mollis*, *Luzula pilosa*, *Maianthemum bifolium*, *Melampyrum pratense*, *Polygonatum odoratum*, *Polypodium vulgare*, *Solidago virgaurea*, *Trientalis europaea* and *Veronica officinalis*. A characteristic feature differentiating it from all other oak forests is the high abundance of lichens, in particular *Cladonia* spp. on the ground, but also epiphytic species (*Usnea*).

The type has been referred to as coastal oak forest (Gram *et al.*, 1944) and overblown oak forest (Jensen, 1993) and appears to be related to syntaxa (*Convallario-Quercetum*, *Populo-Quercetum*) reported from the German and Dutch isles (Olson & van der Maarel, 1989), western Sweden and Norway (Tüxen, 1951; Ellenberg, 1988).

The *Cladonia-Quercus* forest is protected by law as so-called natural forest of no intervention, i.e. forest reserve.

2. *Deschampsia flexuosa-Quercus* community

This vegetation is found on the poorest soils, with *Quercus*, *Sorbus* and *Betula* in the tree-layer (fig. 2). *Tilia cordata* also occurs locally (pers. obs.). The ground layer is dominated by *Deschampsia flexuosa*, co-occurring with e.g. *Galium saxatile*, *Carex*



Fig. 2 - *Deschampsia flexuosa-Quercus* community, Store Løvklit, Jylland, July 1998.

arenaria, *Dryopteris dillata*, *Athyrium filix-femina*, *Pteridium aquilinum*, *Anemone nemorosa*, *Oxalis acetosella*, *Trientalis europaea*, and *Melampyrum pratense*.

In Denmark and Norway, this vegetation often develops from former heathland. It is the initial stage of a long succession, usually of several decades or centuries, with very few species, dominated by *Deschampsia flexuosa*, *Empetrum nigrum*,

Vaccinium spp, and *Calluna communis*, the common heath plants, and then by slow establishment of *Quercus robur*, *Sorbus aucuparia*, *Fagus sylvatica* (in Denmark only) and *Betula* spp. It occurs scattered in Finland (Påhlsson, 1995) and in southern Sweden (Diekmann, 1994). It appears to be related to the *Deschampsio-Quercetum*. In Denmark this is one of the most exploited types of oak forest.

3. *Vaccinium myrtillus-Quercus* community

This is the predominant natural vegetation on acidic soils on light sandy soils, and shallow rocky locations (fig. 3). The tree-layer is usually rather open, and low-growing, rarely more than 20 m tall. It is dominated by *Quercus*, often with some



Fig. 3 - *Vaccinium myrtillus-Quercus* community, Flyndersø, Jylland, January 1998.

Sorbus aucuparia and *Betula pendula*, on drier grounds often with some *Populus tremula*, *Juniperus communis* and *Pinus sylvestris* (except Denmark). The shrub-layer is limited, with some *Frangula alnus*, and often many *Lonicera periclymenum* (only southern part). The ground layer is usually with much grass and bryophytes (e.g. *Mnium hornum*, *Dicranum scoparium* and *Pleurozium schreberi*). Common herbs are *Trientalis europea*, *Melampyrum pratense*, *Anemone nemorosa*, *Carex pilulifera*, *Deschampsia flexuosa*, *Gymnocarpium dryopteris*, *Luzula pilosa*, *Maianthemum bifolium*, *Melampyrum pratense*, *Oxalis acetosella*, *Vaccinium myrtillus*, *Blechnum spicant*, *Convallaria majalis*, *Lathyrus linifolius* and *Molinia caerulea*. *Pteridium aquilinum* may locally be very dominant.

It has been described from Denmark, Norway (*Populo-Quercetum*, Fremstad, 1997), Sweden (*Quercus-Betula* community, Diekmann, 1994) and Finland (Påhlsson, 1995) often divided into several sub-communities. This type was previously grazed, and the state forests are now managed in order to maintain the influence of grazing.

OAK FORESTS ON RICHER SOILS

On the meso- and eutrophic soils, *Quercus robur* occurs in various proportions together with *Fraxinus excelsior*, *Ulmus glabra* (*U. minor* to the east), *Fagus sylvatica*, *Tilia cordata*, *Acer platanoides* (*A. pseudoplatanoides* in Denmark), *Malus sylvestris* and several others (see table 2 for a Danish species list). Meso- and eutrophic oak forests are widespread on richer soils but cover far less than the oligotrophic types, partly because it has been replaced by *Fagus sylvatica* in many places to the south. On mesic soils, however, to wet to beech, the oaks still persist e.g. in Denmark, together with *Fraxinus* and *Alnus glutinosa*. The syntaxonomical affinities of the Nordic mesotrophic oak forests are unclear (Diekmann, 1994), awaiting a more detailed analysis and comparison. They have here with some hesitation been assigned to the most probable syntaxa.

4. *Melica-Quercus* community

This is a rather species-rich community, with many typical nemoral forest species.



Fig. 4 - *Melica-Quercus* community, with some *Tilia cordata*, Holt Krat, Jylland, May, 1999

It is found on well-drained, mesotrophic brown and clayey soils (fig. 4), often on warmer southward slopes to the north, usually in stony or rocky areas. This means it is widespread in eastern parts of Denmark, along the western parts of Norway, southern Sweden and Finland. Commonly found are *Quercus robur*, *Fagus sylvatica*, *Corylus avellana*, *Oxalis acetosella*, *Milium effusum*, *Campanula rotundifolia*, *Fragaria vesca*, *Carex digitata*, *C. pallescens*, *Hepatica nobilis*, *Hypericum pulchrum*, *Mycelis muralis*, *Melica uniflora* (*M. nutans* to the north), *Teucrium scorodonia*, *Poa nemoralis*, *Stellaria holostea*, *Anthoxanthum odoratum*, *Lathyrus montanus*, *Luzula pilosa*, *Melampyrum pratense*, *Brachythecium rutabulum*, *B. velutinum*, *Athyrium filix-femina*, *Dryopteris filix-mas*, *Eurhynchium praelongum*, *Mnium undulatum* and others.

It is usually assigned to the *Melico-Quercetum*, but sub-communities with dominance of e.g. *Corylus avellana* have been

mentioned by some authors.

5. *Quercus robur-Ulmus glabra-Tilia cordata* community

A closed and species rich forest type found on locations in all 4 countries, with rich soils and humid, but well-drained conditions. *Ulmus glabra*, *Fraxinus excelsior*, *Tilia cordata* and *Acer platanoides* (*A. pseudoplatanus* in Denmark) form the canopy together with the oaks, in various proportions. *Anemone nemorosa* is dominant, and among the several species present may be mentioned *Actaea spicata*, *Adoxa moschataellina*, *Bromus benekeni*, *Carex digitata*, *C. sylvatica*, *Mercurialis perennis*, *Paris quadrifolia*, *Primula veris*, *Roegneria canina*, *Dentaria bulbifera*, *Festuca gigantea*, *Hepatica nobilis*, *Silene dioica*, *Thuidium deliculatum*, *Urtica dioica*, *Stachys sylvatica*, *Circaea lutetiana* and *Geranium robertianum*.

In southern parts also containing *Fagus sylvatica*, *Lonicera periclymenum*, *L. xylosteum*, *Prunus avium*, *Ribes spp.*, *Taxus baccata* (except Denmark), *Allium ursinum*, *Cardamine bulbifera*, *Galium odoratum*, *Lysimachia nemorum*, and *Polystichum aculeatum*.

This type belongs to the *Ulmo-Tilietum* as described by Kielland-Lund (1994) from Norway. Diekmann (1994) divided it into two races. It may also be almost exclusively dominated by *Quercus* and *Tilia cordata*, in which case it has been called a *Quercus robur -Tilia cordata* community (Diekmann, 1994). This is probably one of the most original and virgin types of oak forest in Denmark on rich soils, unfortunately only protected in a few places.

6. *Quercus robur-Fraxinus excelsior* community

On the mesic eutrophic soils in the southern parts, this very rich and diverse forest is found, often in a mixture of *Fraxinus excelsior*, *Quercus robur* and *Ulmus glabra* in the very tall canopy layer, with many lower tree species such as *Prunus avium*, *P. padus*, *Acer pseudoplatanus*, *Crateagus spp.* and *Sambucus racemosa* while the rich and quite tall herb layer contains e.g. *Geum urbanum*, *Dactylis glomerata* and *Primula elatior* as the most characteristic species, but with many others as well, such as *Vicia sepium*, *Viola riviniana*, *Stachys sylvatica*, *Paris quadrifolia*, *Anemone nemorosa*, *A. Ranunculoides*, *Poa nemoralis*, *Hepatica nobilis*, *Lactuca muralis*, *Lapsana communis* and *Hieracium spp.*

The syntaxonomical location of this community is unclear at the alliance level, while it clearly belongs to the *Fagetalia sylvaticae* order according to Diekmann (1994).

7. Xerophile *Vincetoxicum-Quercus* community

A thermophilous xerophilous oak forest (*Peucedano-Quercetea*, Olsson, 1974) has been reported from Sweden exclusively (Småland to Vestergötland), as based on the occurrence of *Vincetoxicum hirundinaria*. Other typical species are *Cotoneaster integerrimus*, *Berberis vulgaris*, *Vicia pisiformis*, and *V. cassubica* in Sweden (Dierssen, 1996). Rühling and Tyler (1986) reported it from 31 sites in Småland. It also occurs in rocky terrain on Bornholm island, Denmark (Warming, 1914) as one of the most diverse Danish plant communities, with a number of southern and eastern species such as *Sorbus torminalis*, *Carpinus betulus*, *Anemone apennina* and *Helianthemum nummularium*.

It remains to be determined, whether the Swedish and Danish community with these species indeed belong to the *Quercetalia pubescenti-petraea* Klika 1933, as stated by Olsson (1974).

DISCUSSION

The main division of the Nordic *Quercus* forest types appears to be related to edaphic conditions, indeed as seen for so many plant communities. This is evident, when averaged unweighted Ellenberg indicator values (see Ellenberg, Weber, Düll, Wirth, Werner & Paulißen, 1992) are compared for the oligotrophic and meso-/eutrophic forest types in Denmark (table 3). While the indicator values for light (L), temperature (T) and continentality (K) are fairly similar, in particular the reaction values or Ph (R) and nitrogen contents (N) are clearly different. It will be interesting to make a similar comparison for all the Nordic countries.

Evidently, there is a rich diversity of oak forests in the Nordic countries, probably even more diversified than has been possible to show in this preliminary account. It is therefore worthy considering undertaking a complete analysis of all the old and new data on Nordic oak forests.

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TABLE 1 - LIST OF MOST CONSTANT SPECIES IN OLIGOTROPHIC FORESTS IN DENMARK

Trees and shrubs

Acer pseudoplatanus
Betula pendula
Fagus sylvatica
Frangula alnus
Ilex aquifolium
Juniperus communis
Populus tremula
Quercus petraea
Quercus robur
Sorbus intermedia

Herbs and others

Agrostis capillaris
Agrostis stolonifera
Ajuga reptans
Anemone nemorosa
Anthoxanthum odoratum
Athyrium filix-femina
Betula pubescens
Calluna vulgaris
Carex arenaria
Carex montana
Carex pilulifera
Convallaria majalis
Dactylis glomerata
Deschampsia flexuosa
Dryopteris dilatata
Dryopteris filix-mas
Empetrum nigrum
Festuca ovina
Festuca rubra
Fragaria vesca
Galium saxatile
Holcus mollis
Hypericum maculatum
Lathyrus linifolius
Lonicera periclymenum
Luzula pilosa
Luzula sylvatica
Maianthemum bifolium
Melampyrum pratense
Milium effusum
Oxalis acetosella

Poa pratensis
Potentilla erecta
Pteridium aquilinum
Rubus idaeus
Rubus plicatus
Rumex acetosa
Senecio sylvaticus
Solidago virgaurea
Sorbus aucuparia
Stellaria holostea
Trientalis europaea
Vaccinium myrtillus
Vaccinium vitis-idaea
Veronica chamaedrys
Vicia sepium
Viola reichenbachiana

TABLE 2 - LIST OF MOST CONSTANT SPECIES IN MESO-/EUTROPHIC FORESTS IN DENMARK

Trees and shrubs

Fagus sylvatica
Quercus robur
Fraxinus excelsior
Acer pseudoplatanus
Acer campestre
Tilia cordata
Ulmus glabra
Sambucus nigra
Corylus avellana
Sambucus racemosa
Acer platanoides

Herbs and others

Anemone nemorosa
Deschampsia cespitosa
Melica uniflora
Milium effusum
Oxalis acetosella
Rubus idaeus
Stellaria holostea
Dactylis glomerata
Galium odoratum
Carex sylvatica
Urtica dioica
Viola canina
Mercurialis perennis
Ranunculus ficaria
Galium aparine
Primula elatior
Rubus plicatus
Dryopteris filix-mas
Fragaria vesca
Geum urbanum
Anthriscus sylvestris
Athyrium filix-femina
Ajuga reptans
Stachys sylvatica
Brachypodium sylvaticus
Hordelymus europaeus

TABLE 3 - AVERAGED UNWEIGHTED ELLENBERG VALUES FOR THE TWO MAJOR GROUPS OF OAK FORESTS IN DENMARK. INDICATORS ARE LIGHT (L), TEMPERATURE (T), CONTINENTALITY (K), SOIL HUMIDITY (F), REACTION (R) AND NITROGEN (N)

Danish oak forests*Indicator values*

		L	T	K	F	R	N
Oligotrophic	(n=291)	4.9	5.2	3.7	5.0	3.7	3.5
Meso-eutrophic	(n=173)	4.4	5.3	3.4	5.5	5.6	5.8