Silviculture of Oak for High-Quality Wood Production

Effects of thinning on crown size, volume growth and stem quality in even-aged stands of pedunculate oak (*Quercus robur* L.) in Northern Europe

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Abstract

Oak is one of the most valuable noble hardwood species in Europe. The production of high-quality wood is associated with long rotations and high labour costs. The aim of this thesis was to quantify and model the effects of some silvicultural practices, mainly thinning, on crown size, volume growth and stem quality on pedunculate oak (*Quercus robur* L.), to provide a scientific basis to modify contemporary oak silviculture. The response pattern of specific silvicultural practices was tested in nine long-term thinning experiments and one operational stand located in Northern Europe.

Results showed that pruning led to an overall increase in the total production of new epicormic shoots, which decreased with increasing height along the stem and with decreasing stand density. This suggests that early, heavy thinning combined with high pruning at regular intervals may help shorten the rotation length. A set of models for predicting crown radius was presented, based on different levels of predictor variables that offer flexibility in terms of data availability. The models can be used, for example, to calculate the average area potentially available for final crop trees and therefore the potential number of trees at the end of the rotation. Models for individual tree volume were fitted separately for predicting total and stem volume, whilst accounting for thinning practice. Results showed an increase in prediction accuracy in comparison to similar models available in the literature. Stand volume growth was analysed and modelled in relation to age, thinning practice and site. The highest growth was for unthinned stands, decreasing with increasing thinning grade. Volume growth of 50 potential future crop trees ha^{-1} increased with increasing thinning grade at all ages, demonstrating a positive effect of thinning on the growth of selected crop trees. The results lend support to the concept of crop tree silviculture based on early initiated, heavy thinning for the 'best' trees at regular intervals.

Keywords: pedunculate oak, silviculture, thinning response, quadratic mean diameter, relative basal area, volume growth, crop trees, crown radius, epicormic branches

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To Denesio and Alvise

Homo sum, humani nihil a me alienum puto
Publius Terentius Afer (c. 190 – c. 159 BC)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Attocchi, G. (2013). Effects of pruning and stand density on the production of new epicormic shoots in young stands of pedunculate oak (*Quercus robur* L.). *Annals of Forest Science* 70, 663–673.

II Attocchi, G. & Skovsgaard, J.P. (2015). Crown radius of pedunculate oak (*Quercus robur* L.) depending on stem size, stand density and site productivity. *Scandinavian Journal of Forest Research*, doi:10.1080/02827581.2014.1001782.

III Attocchi, G. (2015).Volume function for pedunculate oak (*Quercus robur* L.) depending on tree size and stand characteristics. *Journal of Forest Science*. Accepted for publication.

IV Attocchi, G. & Skovsgaard, J.P. Effects of thinning on the stand volume growth of pedunculate oak (*Quercus robur* L.). (Manuscript)

V Attocchi, G. & Skovsgaard, J.P. Effects of thinning on the volume growth of crop trees in even-aged stands of pedunculate oak (*Quercus robur* L.). (Manuscript)

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The contribution of Giulia Attocchi (GA) to the papers included in this thesis was as follows:

I GA is the only author of the paper.

II GA conducted most of the fieldwork and data analysis. The manuscript was written together with the co-author. The overall contribution by GA was 90 %.

III GA is the only author of the paper.

IV GA conducted most of the analysis. The manuscript was written together with the co-author. The overall contribution by GA was 90 %.

V GA conducted most of the analysis. The manuscript was written together with the co-author. The overall contribution by GA was 90 %.

Abbreviations

CAI	Current annual increment
Dbh	Diameter at breast height
D_g	Quadratic mean diameter
D_{g50}	Quadratic mean diameter of the 50 thickest trees per hectare
G_{rel}	Relative basal area (basal area relative to that of the unthinned control plot)
H_{100}	Stand top height, defined as the mean height of the 100 thickest trees per hectare
H	Total tree height
N_{epi}	Number of epicormic shoots
V_{stem}	Stem volume at stand level
V_{tot}	Total (stem + branch) volume at stand level

1 Introduction

Wood quality is a primary management goal of noble hardwood silviculture in general and of oak in particular. To some extent wood quality can be controlled by genetic and silvicultural means (Fennessy & MacLennan, 2002; Turok *et al.*, 2001). This thesis investigates some of the silvicultural practices to produce high-quality oak timber.

But what is wood quality?

The concept of wood quality depends on the desired end product and should be assessed by different *ad hoc* standards. The potential uses of high-quality oak vary depending on the specific interests of furniture designers and industries, which are also influenced by fashion and market.

The primary use of oak timber is for wooden floors, furniture and joinery, but oak has also a reputation for barrels for wine and other alcoholic beverages. Premium quality logs are used for veneer, which is the best paid assortment, typically sold on auction. Other assortments are graded by different quality classes of sawn timber (*e.g.*, European standard EN 975-1, 2009). Poor quality timber is obviously less valuable, but it can still be processed to obtain planks or used for fencing posts, pallets or firewood (*e.g.*, Stern, 1973).

There are different specifications to define and grade the quality of a log, which vary among industrial, regional and national standards. Despite the variation, there are commonly accepted characteristics that identify the quality of a log (Attocchi, 2013), the most important being, diameter, clear bole length, straightness, (absence of) rot, shake and cracks, annual ring width and epicormic branches. Exceptions to this are crooked timber and knots which may be desirable for particular architectural or design features. Some defects may be regarded as decorative features (Moroşanu *et al.*, 2011), and in the future industry there could be specific demand for such products. However, defected timber will probably stay as a niche market and the production should generally aim for straight, knot-free timber.

Opinions about the effect of ring width on wood quality differ. Traditionally, a regular annual ring width less than 2 mm is considered crucial for veneer production, especially in France and Germany (*e.g.,* Evans, 1982a; Fleder, 1981; Polge, 1984). Past criteria for evaluating wood quality, especially the narrow width of growth rings were re-examined (Weaver & Spiecker, 1993). Nowadays an annual ring width of 3 mm is acceptable for veneer wood (Metzger, 1998), and in some cases, even 4-5 mm (Hochbichler & Krapfenbauer, 1988). As a result, annual ring width is no longer a limiting factor for veneer (Beinhofer, 2009), and this has important consequences for the silviculture of oak.

For centuries oak of high timber quality has been among the most demanded and highly valued products in the European timber market (Bary-Lenger & Nebout, 1993). The market for high-quality oak has always been rather stable and has steadily increased in recent years, consolidating its dominant position in the European flooring and joinery sectors (UNECE/FAO, 2012).

With climate change, broadleaved tree species seem to be a good strategic choice for adaptive forest management (Hemery, 2008; Lidner *et al.*, 2010) and for afforestation (Jensen & Skovsgaard, 2009; Petucco *et al.*, 2013). As a result new silvicultural prescriptions are needed. In addition, there is an urgent need for more knowledge on how to grow valuable broadleaved species for high-quality wood production (Hemery *et al.*, 2008; Wilhelm & Rieger, 2013). It is clear that oak possesses a substantial economic potential for the landowner when managed for high-quality wood production. However, the traditional way of growing oaks is associated with high labour costs and a long rotation length. This has led to the desire to modify contemporary oak silviculture to optimise the production of high-quality timber in a cost-efficient manner.

1.1 Objectives

The overall objective of this thesis was to provide a scientific basis to modify contemporary oak silviculture for optimising the production of high-quality timber. The investigations specifically focused on quantifying the effects of silvicultural practices and site on certain aspects of wood quality and on tree and stand growth, using established, long-term forest experiments of even-aged pedunculate oak (*Quercus robur* L.).

Epicormic shoots, also referred to as secondary branches or epicormic branches, originate from a previously dormant bud on the trunk or a limb of a tree. It is well known that oak species are particularly prone to develop epicormic branches which are often regarded as a timber defect, depreciating the value of a log.

- The objective of paper I was to analyse the effects of pruning and stand density on the emergence of new epicormic shoots.

In silviculture the crown size is often used as an indicator of stand structure and stand density and for outlining thinning guidelines or constructing forest growth models. This is because the crown status is a direct expression of the growth potential of trees. Models for predicting crown size that account for site, silviculture and actual stem size are useful tools in forest management. However, such comprehensive and numerical models are lacking in the literature.

- The objective of paper II was to quantify and model the dependence of crown radius on stem diameter, thinning practice/stand density and site productivity.

Functions for predicting individual tree volume and stand growth volume from easily obtainable forest measurements are useful and flexible tools for forestry practice as well as forest science. Additionally, detailed knowledge about site specific response patterns depending mainly on stand density and age, *e.g.* stand volume growth depending on residual stand basal area, may help optimize management practices in operational forestry, but also improve our understanding of how the tree and the forest respond to different treatments. In evaluating this relationship for pedunculate oak, the final objectives of the thesis were to develop:

- Models for individual tree volume function depending on stem diameter, total tree height, thinning practice (stand density) and site (paper III);
- Models for stand-level volume growth depending on thinning practice (stand density), age and site (paper IV);
- Models for stand-level volume growth of crop trees depending on thinning practice (stand density), age and site (paper V).

2 Oak Silviculture

2.1 Characteristics of oak in Europe

In Europe there are 27 native species belonging to the genus *Quercus* (Mabberley, 1990). Pedunculate oak and sessile oak (*Quercus petraea* (Matt.) Liebl.) are the two most common and valuable oak species in Europe, covering in EU34 approximately 49,000 and 38,000 km^2, respectively (Hemery, 2008). Another oak species with potential for timber production is downy oak (*Quercus pubescens* Willd.), which covers 25,000 km^2 (Hemery, 2008).

In the past there has been an identification issue for pedunculate, sessile oak and their hybrids, as discussed for example by Potter (1994). However the pedunculate and sessile oak can be separated botanically (Jones, 1959) and genetically (Kremer *et al.*, 2004; Muir *et al.*, 2000). This is a fundamental distinction, since the taxonomic status of oaks has implications for forest management (Bary-Lenger & Nebout, 1993; Evans, 1984; Muir *et al.*, 2000).

The natural range of pedunculate oak essentially defines the range of nemoral forests in Europe (Jahn, 1991). It is present in the lowlands of Europe from the Atlantic coast of France, Northern Spain, Portugal and Britain in the west, to the Ural Mountains in the east, reaching its northern limits in Northern Scotland and southern Scandinavia, while the southern limits extend to Italy, Greece, Northern Spain and Portugal. Sessile oak essentially overlaps pedunculate oak, but it is restricted to Central and Western Europe, without extending eastwards into Russia. To the north, it is present only where the climate is influenced by maritime conditions (Bary-Lenger & Nebout, 1993).

In general oaks are considered post-pioneer species and light demanding; pedunculate oak more so than sessile oak (Timbal & Aussenac, 1996). They are more susceptible than most broadleaved tree species to late frost, although pedunculate oak is less sensitive than sessile oak (Evans, 1984). Oaks flush late compared with many other broadleaved species. It is interesting to observe that the time of flushing is consistent in individual trees (Satchell, 1962), and this can be important in relation to wood quality and silviculture (Savill & Mather, 1990).

In terms of site requirements, both species occur on a wide range of soils and often grow together. However 'optimal' growth is associated with different site conditions and environmental factors (Bary-Lenger & Nebout, 1993; Evans, 1984). This indicates that optimal ecological conditions and site specific treatments are critical if the management goal is high-quality timber production (Bary-Lenger & Nebout, 1993), emphasizing that it is important to differentiate between the two species in silviculture.

Pedunculate oak prefers moist heavy soils or nutrient-poor very sandy sites, and it can withstand a considerable degree of waterlogging and even flooding, but badly drained and compacted soils should be avoided. It cannot tolerate summer droughts. Generally, the species occurs mainly on fertile, basic soils and limestone.

Sessile oak prefers well-drained, shallow soils, and it is limited by flooding intolerance. It has the tendency to grow on drier sites (sand and/or gravel) although moderate site fertility is required for reasonable growth rates. It can tolerate summer droughts. Generally, it occurs on acidic soils and sandstone, and is considered to be climatically more robust than pedunculate oak.

Major challenges connected with these species and the production of high-quality timber are addressed in detail below. In summary, these are slow growth, epicormic branches, numerous tending operations and long rotation length. Additionally, production risks are often associated with damages caused by abiotic (*e.g.,* interior stem cracks and shake, summer drought), biotic factors (*e.g.,* defoliating insects, parasitic fungi) and the combination of the two (*e.g.,* oak decline), which must be taken into consideration with oak management.

In terms of production, there are generally different ambitions for the two species. Sessile oak is preferred for premium quality logs, and it is managed according to a long tradition in Central Europe. Its reputation is well established, for example in Spessart (Germany) and Bercé (France).

Investigations conducted in this thesis are entirely focused on even-aged high forests of pedunculate oak, although results and conclusions hold, to some extent, for sessile oak and possibly other timber producing oak species such as downy oak.

2.2 Management goals

In the context of this thesis, the management goal of oak silviculture is the production of high-quality timber. Following the introduction of planned forestry and silviculture, the sustained yield of wood supply became a key concern in designing sustainable management practices (von Carlowitz, 1713; Duhamel du Monceau, 1764; Evelyn, 1670; Hemery & Simblet, 2014). Modern ideas of sustainability are broader in scope, embracing all the goods and services of the forest. During the last decades the integration of environmental, social and economic aspects has been advocated in management planning, resulting in a more holistic view of forest ecosystems, diversifying forest management objectives and thus raising new questions to silviculture (Jensen & Skovsgaard, 2009; Skovsgaard, 2004a; Wilhelm & Rieger, 2013).

Although this thesis deals with the production of high-quality oak wood, other objectives such as forest recreation, biodiversity and groundwater protection are becoming increasingly important and even a main concern in many forests. The implementation of different management objectives seems possible in oak stands, because the focus is on certain individual trees, giving the opportunity to manage parts of the remaining stand for other purposes.

2.3 Central European oak silviculture

Central European oak silviculture is practiced in many places in France (Bary-Lenger & Nebout, 1993; Jarret, 2004; Oswald, 1982; Sardin, 2008) and Germany (Kenk, 1993; Krahl-Urban, 1959; Mosandl & Paulus, 2000). The main goal is to produce high-quality timber. Ring width is often used as an indicator of wood quality. Traditionally it should not exceed 2 mm, at least for sessile oak, but this criterion is currently being relaxed (Jarret, 2004; Sardin, 2008). A general description of Central European silvicultural practices follows, based on the literature mentioned above and on field excursions in the Le Mans region of France (2011) and the Spessart region of Germany (2012 and 2014).

In France oak stands are regenerated naturally, using uniform shelterwood systems. In Germany methods of regeneration vary, natural regeneration is common where acorn production is sufficient and competition of beech (*Fagus sylvatica* L.) or hornbeam (*Carpinus betulus* L.) is not a threat, otherwise direct seeding or planting is used. The shelterwood is gradually removed over approximately ten years. When the oak regeneration has completely established, the number of seedlings per hectare is very high, and a series of intensive tending operations starts, including cleaning, pre-commercial thinning and thinning. Although these interventions are theoretically well-defined, in practice there is a gradual transition between them. This reflects the change in focus, moving from stand-based management in pre-commercial thinning, to individual tree promotion in commercial thinning. In some countries, France for example, more detailed terminology exists for these operations.

Cleaning interventions are often conducted to remove unwanted species and wolf trees typically when the stand height ranges between 4 and 8 m. Subsequently pre-commercial thinnings are conducted, where good candidates (potential future crop trees) are passively promoted, removing unwanted species, wolf trees and forked trees (negative selection). At this stage stand density is kept high to favour natural pruning, and the presence of beech, hornbeam or other tree species is desired to prepare a future understorey for the oaks, although the understorey should be carefully controlled such that it does not overgrow the crop trees.

The positive selection starts with the selection of future crop trees (see section 2.5.1), which traditionally takes place when the trees have reached a 8–10 m clear bole length, at a stand age between 50 and 60 years and a dominant height of approximately 18–20 m. At the same time an understorey of beech or hornbeam is managed under the oak canopy, to keep the stems of crop trees shaded and to promote self-pruning. Thinnings are light and frequent, where only one or two strong competitors are removed for each crop tree. The selection principle is crown thinning, targeted to promote crown development of crop trees while maintaining a high stand density to obtain narrow annual rings and prevent the emergence of epicormic branches. Thinning intervals increase with decreasing stand density, until the final stem number per hectare is reached. This is typically 50–60 tree ha^{-1} for pedunculate oak and 60–80 trees ha^{-1} for sessile oak. With a target diameter of 70 cm at breast height, the resulting rotation period is approximately 175 years in addition to the age to reach breast height.

According to more recent ideas, crop trees are selected earlier and thinning grades are slightly heavier (Jarret, 2004; Kenk, 1993; Sardin, 2008; Weaver & Spiecker, 1993), although the definition of heavy thinning remains different than the contemporary management model for young oak in Northern Europe, as described in the next section.

Central European oak silviculture, or variants thereof, are practised to some extent for example also in Switzerland (Schütz, 1987), Austria (Hochbichler, 1993), Poland (Andrzejczyk, 2009) and Romania (Nicolescu, 2010), although management prescriptions may differ depending on local circumstances and management objectives.

2.4 North European oak silviculture

The North European oak silviculture for high-quality timber production is characterized by a relatively short rotation based mainly on frequent heavy thinnings that are often combined with regular high-pruning of epicormic branches.

Central European oak silviculture, as described in section 2.3, is unsuitable for the climate and site conditions in Northern Europe. Soil and water table conditions are generally less stable in Northern Europe resulting in a higher risk for stem decay if rotations are long. Moreover, summer temperatures are less stable and this may lead to larger variation in annual ring width.

Seminal scientific studies investigating the effects of thinning on individual tree and stand growth of oak were initiated by C.D.F. Reventlow in Denmark and Northern Germany already in 1793. Criteria for maximizing the economic return or profit over a whole rotation indicated that a high-forest system with regular, heavy thinning for a low number of potential final crop trees would be economically beneficial (Reventlow, 1960, 1879, 1811). The management model for young stands is based mainly on results from a pre-commercial thinning experiment in the early 1900s (Hauch, 1915, 1908). Results indicated that in young stands, thinning of dominant trees combined with heavy thinning of socially intermediate trees and no thinning in the inferior understorey is beneficial for the growth as well as the wood quality of potential crop trees.

Based on these principles many stands of pedunculate oak in Northern Europe are now being managed accordingly, primarily for commercial timber production and often in essentially pure and even-aged stands with or without an understorey of other tree species, suppressed oaks and bushes, as in Great Britain (Evans, 1984; Hemery & Simblet, 2014; Savill, 2013), Denmark (Henriksen, 1988; Skovsgaard, 2004a, 2004b), Sweden (Almgren *et al.*, 1984, 2003; Ståål, 1986).

A general description of the North European silvicultural practices follows, based on the literature mentioned above, notes from and field excursions and personal observations during fieldwork conducted in Denmark, Sweden and Great Britain (Appendix).

Oak is often regenerated by planting or direct seeding, with or without a shelter of oak or other tree species. Typically three to four heavy pre-commercial thinnings are conducted before future crop trees are selected. Potential final crop trees are usually identified and marked at an age of approximately 40 years, when diameter at breast height reaches approximately 15–20 cm. At this stage, an undergrowth of shade tolerant species is introduced in some stands, depending on various conditions, although there are several examples of stands that are free from undergrowth. The selection principle is heavy crown thinning, aimed to promote good crown development of selected crop trees. Stand density is considerably lower throughout the rotation as compared to Central European oak silviculture (Figure 1), favouring growth of individual (crop) trees over total stand growth. It is often recommended to prune primary and dead branches once or twice, since early and heavy pre-commercial thinnings do not sufficiently promote self-pruning. The control of epicormic branches is an issue, and annual inspection and pruning of epicormic branches on future crop trees is generally recommended. However, the control of epicormic branches is often disregarded.

The final stem number is 50–55 trees ha^{-1} at the age of approximately 120 years, though there is substantial variation depending on site, management practices and other conditions.

A more radical idea of shortening the rotation was inspired by observations of several hundred hedgerows and parkland oak which demonstrated that free grown trees had greater radial increment than trees in forest stands (Hummel, 1951). This resulted in the concept of 'free growth of oak' (Jobling & Pearce, 1977; Kerr, 1996), where the goal is to produce a high proportion of veneer quality timber on a rotation of less than 100 years. Although “free growth of oak” is not widely used, it is definitely used as an inspiration for forest managers (*e.g.,* Lemaire, 2008; Wilhelm & Rieger, 2013) and in experiments (Jensen & Skovsgaard, 2009; Rune & Skovsgaard, 2007; Skovsgaard, 2004a).

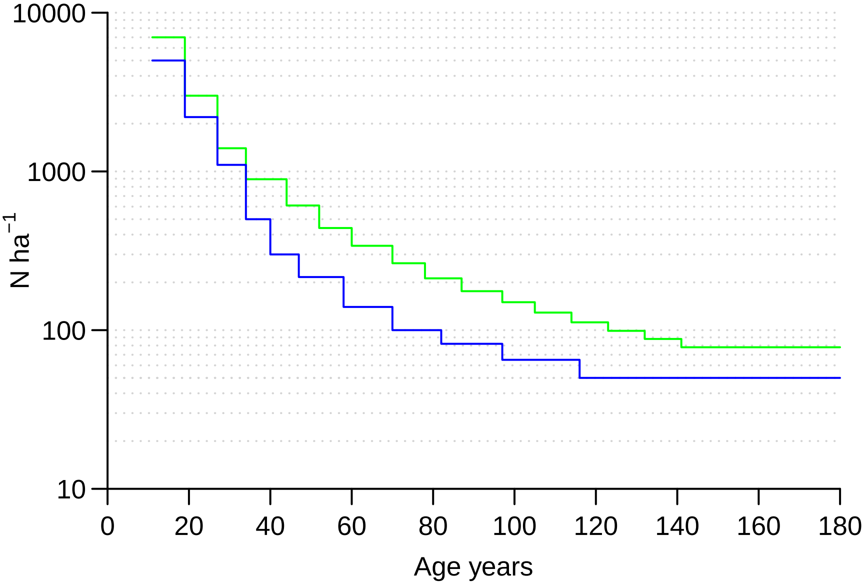

Figure 1. Stem number reduction for the Central European oak silviculture (green) and North European silviculture (blue). The first one is based on the model of Sardin (2008) for the classical sessile oak silviculture, whereas the second represents the typical stem number reduction at Bregentved in Denmark (Appendix).

2.5 Critical parts during the rotation

2.5.1 Crop tree selection

The early selection and visible marking of a small number of potential final crop trees is an efficient strategy to concentrate silviculture on the most valuable trees in the stand (Jagd, 1948; Jensen, 1992; Larsen, 1934; Lemaire, 2010; Nicolescu, 2001; Skovsgaard, 2004a; Ståål, 1986; Venet, 1968; Wilhelm & Rieger, 2013). Thereby the investment is targeted better towards the production of high-quality timber products such as veneer and saw logs, and it helps justify expensive tending operations such as early high-pruning (Beinhofer, 2009; Evans, 1982b; Jensen, 1989, 1993; Kerr, 1996; Skovsgaard, 2004a,b). It is a further asset of permanently marked crop trees that thinning decisions at subsequent interventions usually can be done much faster and with greater consistency.

Crop tree selection is usually done among those candidates with promising stem quality characteristics for becoming, in the long term, high-quality timber logs. A future crop tree should be vigorous (thick stem, indicating good growth potential) and have a large symmetric crown, a straight stem, no forking below the required final log length, an adequate branch-free bole (depending on pruning practice) and few or no epicormic branches. Moreover, future crop trees should be evenly distributed in the stand.

As a rule of thumb, the distance between future crop trees of oak should be of approximately 14 m for a target *dbh* of 70 cm, corresponding to a crown diameter of 14 m (the crown is approximately 20 times the *dbh*). In practice the distribution of future crop trees is not completely regular and often a compromise between an acceptable minimum distance and the location of the best future crop trees has to be made. Additionally, the current trend is towards a larger number of crop trees and possibly up 80 ha^{-1} (Jørgensen, 2013; Skovsgaard, 2004a), resulting in a shorter distance between crop trees. However, the smallest acceptable distance should be at least 50 % of the expected crown diameter distance at final harvest, since shorter distances may hamper a symmetric and homogeneous crown development. There is a general agreement on the criteria used for future crop tree selection, but there are contrasting opinions about the number of future crop trees per hectare, the time of selection, how thinnings should be conducted and whether reserve crop trees should be selected and marked (Lagarde, 1973; Lemaire, 2010; Martinot-Roy, 1975; Nicolescu, 2001; Skovsgaard, 2004a; Spellmann & von Diest, 1990; Spiecker, 1991; Ståål, 1986; Staun, 1989; Venet, 1968; Wilhelm & Rieger, 2013).

In Central Europe the desired number of oak crop trees at final harvest is generally larger than in Northern Europe, where the target stem number for pedunculate oak at final harvest may be as low as 50-55 ha^{-1} (Henriksen, 1988; Holten, 1986; Jagd, 1948, 1954; Jensen & Jensen, 1988; Schaeffe, 1952; Ståål, 1986), but currently the trend is towards a larger number of crop trees and possibly up 80 ha^{-1} (Jørgensen, 2013; Skovsgaard, 2004a). This is based mainly on documented reductions in stand volume growth with heavy thinning (Henriksen, 1988; Kramer, 1988), but for some site types also on the apparently increasing production risk associated with frequently recurrent periods of drought and defoliation.

The selection of future crop trees at an early stage of stand development, and that all tending operations are target to those trees, relies on long-term social stability among these and in young stands also among other trees. There are different and somewhat contrasting results for the social stability in oak stands. Some indicate that dominant trees tend to remain dominant and that heavy thinning possibly leads to a marginal reduction in social stability (Holten, 1995; Holten & von Diest, 1996), whereas others conclude that the social structure of oak stands is too unstable to justify early crop tree selection (Chroust, 2007; Nagel, 2007; Spellmann & von Diest, 1990).

2.5.2 Thinning practice

Thinning practice varies substantially between the two geographical areas described earlier, not only in terms of thinning grade, but also in terms of selection principles. There are also differences between pedunculate and sessile oak, depending on local prescriptions, forest type and site.

For pedunculate oak, investigations on thinnings have been conducted based on long-term thinning experiments in Denmark (Bryndum, 1957, 1965, 1966; Hauch, 1908, 1915; Henriksen, 1988; Kramer, 1988; Spiecker, 1991), Sweden (Agestam *et al.*, 1993; Carbonnier, 1975; Hagberg & Matérn, 1975), Great Britain (Hummel, 1951; Jobling & Pearce, 1977; Kerr, 1996) and Germany (Nagel, 2006, 2007). The studies in Great Britain attract special interest because of their individual-tree based approach to very heavy thinning. The studies and experiments in Denmark are of special interest because of the very heavy thinnings and because of the long unbroken periods of observations in consistently conducted experiments with multiple statistical replications in time and space.

For sessile oak, there are several classical studies which focus on traditional silvicultural prescriptions including less extreme thinning practices. Most of these originate from Germany (Assmann, 1961, 1970; Dittmar, 1990; Dong *et al.*, 1997, 2007; Erteld, 1962; Erteld & Hengst, 1966; Krahl-Urban, 1959 (including a summary of historical references); Kramer, 1988; Lockow, 2006, 2003; Noack, 2013; Pretzsch & Utschig, 1995; Utschig *et al.*, 1993; Utschig & Pretzsch, 2001) and France (Bary-Lenger & Nebout, 1993; Dhôte, 1997; Direction Forêt, 2007; Gibaud, 2007; Lorne, 1959; Ningre, 1990; Oswald, 1981; Pardé, 1979).

For downy oak and other important oak species in Europe (*e.g.*, Timbal & Aussenac, 1996) there are no experiments available to help quantify the species-specific thinning response.

The time and weight of thinning depends on management objectives (*e.g.*, ring width, potential economic return, cash flow) and on the point in time (stage of stand development) at which it is being conducted.

In Central Europe thinning interventions are often late and light, removing between one to a maximum of three competitors at each intervention, with careful management of the understorey such that it does not enter the canopy of the crop trees. In contrast to that, thinning interventions in Northern Europe are often conducted earlier and are heavier. As a result, the thinning frequency is higher in Central Europe than in Northern Europe.

During early stages of stand development, the differences in thinning practice between pedunculate and sessile oak are negligible, provided that the species are growing on suitable sites.

2.5.3 Pruning

Pruning is generally recommended when early and heavy thinnings are conducted (Beinhofer, 2009; Evans, 1982b; Jensen, 1989, 1993; Kerr, 1996; Kerr & Harmer, 2001; Skovsgaard, 2004a,b). Pruning is conducted for two main reasons: to remove green and dead branches (primary branches) and to remove epicormic shoots (secondary branches).

Pruning of primary branches on the lower bole aims to produce knot-free timber and is a straightforward operation on broadleaves. Pruning of primary branches is generally profitable. It is usually done once or twice on potential future crop trees at the time of crop tree selection.

Epicormic branches can be a serious problem that requires regular inspection and pruning on a sustained basis, as recommended by Kerr & Harmer (2001). In contrast, Spiecker (1991) discouraged pruning of epicormic branches based on results indicating an increase of epicormic shoots due to pruning. These results are partially explained by the fact that pruning weakens the tree due to reduction in foliage mass (Meier *et al.*, 2012) and it exposes more meristematic tissue to increased light levels (Fink, 1984). As a result pruning of epicormic branches represents a challenge in high-quality oak timber production. It is also recognised that pedunculate oak generally produces more epicormic shoots than sessile oak (Evans, 1982b; Jensen, 2000).

The implications of silvicultural practices for the occurrence of epicormic branches are unclear. It is known that there is a genetic component and a high degree of heritability in forming epicormic buds (Savill & Kanowski, 1993), but the physiological processes and environmental factors that contribute to the formation and emergence of epicormic branches are not well understood (Bary-Lenger & Nebout, 1993; Colin *et al.*, 2010; Harmer, 1990). Light, which has been at the centre of the discussion in many investigations (*e.g.*, Evans, 1982b; Roussel, 1978; Spiecker, 1991; Wignall & Browning, 1988), cannot alone explain the emergence of epicormic shoots, but the regulation of light intensity plays a fundamental role in their survival and growth (Evans, 1982b). Ideally the selection of crop trees should be done among trees that are free from epicormic shoots, but in operational forestry several criteria must be fulfilled and this condition is not always met. Additionally, pruning is a costly operation that is financially and economically justified if applied on selected trees and if a minimum volume of high-quality timber is achieved (Beinhofer, 2009).

2.5.4 Other issues

There are other critical issues in the context of oak silviculture for high-quality timber production that have not being studied as part of this thesis. Nevertheless they are important and issues such as regeneration, presence and maintenance of an understorey, timber defects, pests and diseases should be considered, since they might imply additional costs during the rotation or cause a reduction in the final yield.

Natural regeneration is often the preferred option for oak stand establishment in many regions of Central Europe (Dobrowolska, 2008; Jarret, 2004; von Lüpke, 2008; Sardin, 2008), whereas artificial regeneration by sowing or planting is more common in Northern Europe (Henriksen, 1998; Savill, 2013) and for afforestation (Madsen & Löf, 2005). Site preparation is recommended for sites where weed competition is a problem. Fencing is recommended where the browsing pressure is high. An alternative method to establishing oak over the whole are is cluster or group-wise planting, where groups of oak are being sown or planted in a matrix of other species (Andrzejczyk, 2007; Dong *et al.*, 2007b; Saha *et al.*, 2013; Schaffalitzky de Muckadell, 1959, 1983; Wilhelm & Rieger, 2013). Regeneration success is critical for the subsequent production of high-quality timber as the development of good stem quality relies strongly on stand density and completeness. The challenge generally is to strike the balance between stand density and tending costs in young stands. Very dense and complete stands may result in overly expensive tending costs. Very open stands may result in inferior wood quality and an associated reduction in economic revenue.

An understorey of shade tolerant species is desirable in oak silviculture as nursing trees. This practice is used in Central Europe (Bary-Lenger & Nebout, 1993; Jarret, 2004; Kenk, 1993; Krahl-Urban, 1959; Mosandl & Paulus, 2002; Sardin, 2008) as well as in Northern Europe (Almgren *et al.*, 1984, 2003; Henriksen, 1988; Ståål, 1986). The understorey is also useful in creating and maintaining an improved microclimate in the stand, potentially preventing frost cracks, the release of shake and reducing the risk of sapwood discoloration (so-called moon rings), while protecting and improving the soil (Evans, 1982a; Matthews, 1989). The understorey represents a potential for early return to the forest owner (Madsen, 1991) and may enhance the aesthetic appearance of the stand and, in turn, its recreational value (Jørgensen *et al.*, 2004). The experiments used in this thesis are essentially free from an understorey, and this might influence the interpretation of the results.

A shake is a longitudinal fracture in the wood of living trees. It is regarded as a timber defect, which reduces the rate of recovery at the sawmill and, in turn, depreciates the trade value. The occurrence of shake seems to be primarily related to the soil type (Evans, 1984; Henman, 1991; Mather, 1991), and is most frequent on sites where the water table is variable, particularly on drought prone sites and on soils with high proportions of sand or gravel (Mather, 1991). Shake and interior stem cracks are common problems in ring porous tree species, like oak, ash (*Fraxinus excelsior* L.) and chestnut (*Castanea sativa* Mill.). In oak, the susceptibility to shake increases with increasing earlywood vessel size (Savill, 1986). Trees that flush latest in the spring possess the largest early wood vessels and are consequently more predisposed to developing shake (Savill & Mather, 1990). Therefore shake-prone trees can be recognised earlier in the rotation by their time of flushing and may be removed during tending operations. Vessel size has been found to be a highly heritable trait of oak trees that is under strong genetic control (Kanowski *et al.*, 1991), indicating that a proper choice of provenances and individual trees should be effective in reducing the frequency of shake in oaks (Mather *et al.*, 1993).

A similar defect is represented by frost cracks, described as superficial vertical cracks produced near the base of trees during extremely cold weather. How frost cracks relate to silvicultural practices has not been scientifically investigated, but based on observations of few trees during spring 1989 in experiment QX, it appears that the frequency and size of frost cracks increases with increasing thinning grade (based on unpublished archival data). Similarly the presence of an understorey seems to reduce the occurrence of frost cracks (based on supervisor's observations in underplanting experiments and discussions with local forest managers at a field excursion during 2011 in France). Additionally, an understorey of coniferous species seems to result in less frost cracks than an understorey of broadleaved species. Eventually, what is perceived as frost cracks may simply be a shake in standing trees that was released by frost.

Over centuries oak species have periodically been suffering from episodes of various pest and pathogen attacks and periodic declines (Day, 1927; Denman *et al.*, 2010; Gibbs & Greig, 1997; Osmaston, 1927; Robinson, 1927). In the study areas described in this thesis, defoliation, attacks by *Armillaria* species and acute oak decline have been observed, and will briefly be described.

A recent report about the forest conditions in Europe (Fischer *et al.*, 2012) showed that pedunculate and sessile oak were the most frequently damaged species by defoliating insects such as the oak leaf roller moth (*Tortrix viridana* L.; Evans, 1984; Satchell, 1962) and the winter moth (*Operophtera brumata* L.; Tenow *et al.*, 2013).

Defoliation alone usually does not lead to extensive tree mortality, but attacks during two or more consecutive years may reduce tree vigour and predispose trees to infection by pathogenic fungi such as *Armillaria* species (Kwaśna, 2001). Pedunculate oak flushes earlier and this seems to be a cause of heavier infestation than in sessile oak. There may also be substantial variation among individuals, depending on flushing time, and this relates to maturation of the foliage after flushing (Wesołowski & Rowiński, 2006).

There are different *Armillaria* species on oak, some considered harmless secondary colonizers of weakened tissue, others may be pathogenic and inducing stem bleeds, which are different from the symptoms of acute oak decline (Denman *et al.*, 2014). Some *Armillaria* species are associated with the decline of pedunculate oak, mainly on hydromorphic sites. It seems that the fungus does not attack healthy trees, but is a secondary pathogen that attacks roots with an intermediate diameter (5–20 mm) at some distance from the trunk (Thomas *et al.*, 2002).

Since the 1990s, *Phytophtora* species have been suggested as a contributing factor to the oak decline in Europe (*e.g.*, Brasier, 1999; Jung *et al.*, 2000, 2013). This pathogen seems to occur on weakened trees, and in most cases lesions are correlated with root or tree collar infections (Denman, 2010). In particular *Phytophtora quercina* (T. Jung & T.I. Burgess) has proved to be very aggressive towards root systems of pedunculate oak (Jönsson, 2004). There may also be stem bleeding caused by *Phytophthora* species (*e.g., P. cinnamomi* Rands and *P. cambivora* (Petri) Buisman) that might be confused with the early stages of acute oak decline (Denman *et al.*, 2014).

Acute oak decline is a complex disease, which has the potential to pose a very serious threat to pedunculate, sessile and other oak species (Denman & Webber, 2009). The causes of acute oak decline are still under investigation, but it may appear to be driven by pathogenic bacteria. Symptoms include bleeding of dark sticky fluid, called "tarry-spots", on the stem, that is being followed by partial defoliation and dieback of branches when trees approach death (Denman *et al.*, 2014). The bacteria seem to interact with the buprestid oak splendour beetle (*Agrilus biguttatus* Fabricius), although it is presently not considered to be the primary cause of acute oak decline (Denman *et al.*, 2010). Pedunculate oak seems to be more attacked than sessile oak (Denman *et al.*, 2010). This could be due to differences in site conditions.

Although these factors have been described separately, they are connected. For example, successive defoliation years may weaken the trees, predisposing them to be infected by other pathogens. Additionally to biotic factors, the health status of oaks can be furtherly strained by abiotic factors (*e.g.*, droughts, air pollution described by Thomas *et al.*, 2002) that concur in weakening and eventually killing the trees.

3 Materials and methods

This section is an overview of the materials and methods used to investigate the effect of site and silviculture on crown size, volume growth and aspects of wood quality. A thorough description of the experiments used in this thesis is reported in the Appendix and details on methodology can be found in the individual papers I-V.

3.1 The study area

Data were collected from 53 plots in nine statistically designed thinning experiments and one operational stand of even-aged pedunculate oak, located across Denmark, Sweden and Great Britain (Figure 2). Selected plots were chosen for investigating specific objectives of each individual study.

Figure 2 Location of the experiments (circle) and of the operational stand (triangle).

Five experimental treatments (thinning grades) were investigated and implemented at plot level. Each plot was classified according to nominal thinning grade (Danish nomenclature), labelled A (strictly unthinned, *i.e.* no dead or dying trees removed from the plot at any time), B (light thinning), C (heavy thinning), D (very heavy thinning) or E (extremely heavy thinning). Labelling was based on documented treatment specifications and the development of relative basal area over time. The operational stand was consistently thinned similar to the C-grade.

There are no previous long-term studies with such comprehensive and strict experimental design, representing such a wide range of thinning grades, including extreme treatments of very heavy thinning, sites and ages, collected since the 19th century.

3.2 Data acquisition and analysis

Paper I was based on three thinning treatments (A-, D- and E-grade) replicated in experiment 1516 and 1517.

To test the effect of pruning on the production of new epicormic shoots, only plots thinned according to the D-grade were used. To test the effect of stand density on the production of new epicormic shoots, all three thinning grades were used.

Epicormic shoots were counted on selected sample trees and the location along the stem was also recorded to test if there is a trend with increasing height along the stem.

The research hypotheses were tested based on linear mixed-models.

Paper II was based on five thinning treatments (A-, B-, C-, D- and E-grade) using data from all nine experiments and one operational stand with three plots, shown in Figure 2.

In total, the crown projection of 620 trees was measured to analyse the dependence of crown radius on site, silviculture and actual stem size.

The research hypotheses and all models presented were tested based on linear mixed-models.

Paper III, IV and V were based on four thinning treatments (A-, B-, C- and D-grade) in experiment RA, QX, QY, QD and CT.

For paper III data on 1,522 trees sampled for the measurement of individual stem and branch volume were retrieved from the archive of University of Copenhagen and partly from DVMBASE (Johannsen, 2002). DVMBASE comprises repeated measurements from the permanent forest field experiments in Denmark. Individual tree functions for total and stem volume were developed using individual tree characteristics and stand level variables. The models presented were developed based on linear mixed-models.

For papers IV and V data were accessed through the database DVMBASE (Johannsen, 2002). Stand growth models for total and stem volume depending on thinning practice were developed based on the Chapman-Richards function and used a random coefficient modelling approach by means of nonlinear mixed-models.

All data for paper III, IV and V were collected during 1903-2014 by the forest research unit now located at University of Copenhagen and cover stand ages from 14 to 182 years.

4 Main results and specific discussion

The main results and discussion presented in this section refer to the specific objectives of each paper. A more general contextualization of the findings in relation to oak silviculture and the critical parts during the rotation is presented in Chapter 5.

4.1 Epicormic shoots, pruning and stand density

The influence of pruning on the emergence of new epicormic shoots was assessed in four plots treated with D-grade thinning in the young experiments of pedunculate oak (1516 and 1517), by comparing 42 pruned and 51 un-pruned trees. Results showed that on average the number of new epicormic shoots increased with the number of epicormic shoots and primary branches removed. Including the location along the stem of new epicormic shoots in the analysis, a significant interaction between pruning and height along the stem was found. This indicated that in the first three meters the number of new epicormic shoots was higher for not pruned trees than in the section above (Figure 3). Although there was part of the stem where pruning had a positive effect resulting in fewer new epicormic shoots, the hypothesis that pruning reduces the number of new epicormic shoots was rejected.

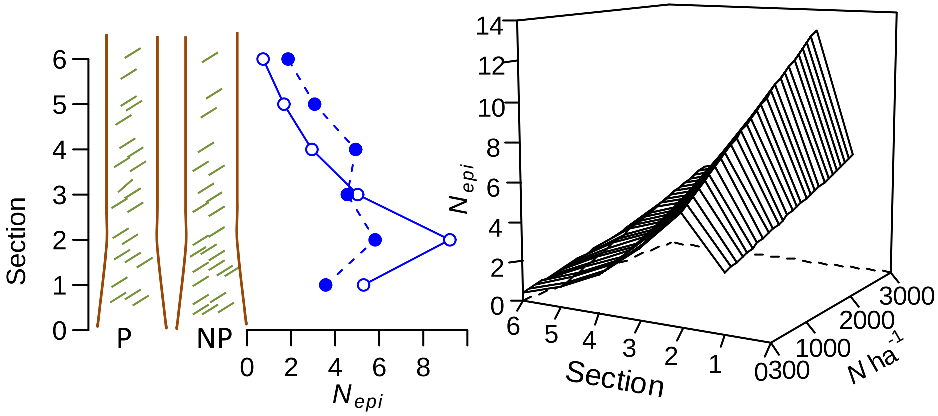

Figure 3. Number of new epicormic shoots (N_{epi}) depending on (left) pruning and height along the stem (section 1 = 0-1 m, section 2 = 1-2 m, *etc.*) and (right) on stand density (N ha^{-1}) and height along the stem (section). On the left, the dashed line indicates average number of new epicormic shoots on pruned trees (P) and the full line on un-pruned trees (not pruned, NP).

There are contrasting results and recommendations in relation to pruning, especially depending on the type of pruning (green branches and/or epicormic shoots). A higher number of epicormic shoots has been observed as a response to pruning of primary branches (Spiecker, 1991), whereas pruning of epicormic shoots has been found to lead to a decrease in the number of new epicormic shoots in heavily thinned stands (Morisset *et al.*, 2011). The fact that pruning provokes stress in the tree, because of the reduced photosynthetic capacity (Meier *et al.*, 2012) and through modifications of internal physiological processes relating to bud burst (Colin *et al.*, 2010), may explain the higher number of epicormic shoots when primary branches are removed.

The number of new epicormic shoots increased with increasing stand density. This was tested in thinning grades A, D and E, each replicated four times on two sites (1516 and 1517). The hypothesis that the number of new epicormic shoots decreases with increasing stand density was therefore rejected.

A high number of new epicormic shoots in denser stands was also reported in a former study by Fontaine *et al.* (2001). This is somehow in contrast to the classical light thinning regime and the resulting high stand density applied in Central Europe, which are conducted primarily for the narrow annual ring width, but also to prevent the emergence and the growth of epicormic branches.

There are different results about the emergence of epicormic branches as a response to heavy thinning indicating in some cases more (Jobling & Pearce, 1977; Kerr, 1996; Ward, 1966) and in other cases less epicormic shoots (Morisset *et al.*, 2011).

The number of new epicormic shoots generally decreased with increasing height along the stem, across all treatments considered. One of the explanations could be that there is a shading effect of the crown on the upper part of the stem that reduces the emergence of new epicormic shoots. In contrast, other studies on much older trees reported an opposite trend, namely an increasing number of epicormic shoots with increasing height along the stem for pedunculate oak (Henriksen & Sanojca, 1983; Spiecker, 1991) and for some American oaks (Smith, 1965; Ward, 1966). The different result may be attributed to older ages or species of oak investigated in the previous investigations.

In both analyses of pruning and stand densities, diameter at breast height (*dbh*) and total tree height (*h*) were not significant. It is important to note that stands used for this investigation were even-aged plantations at approximately the same age and the variation in tree size was probably too low to detect any difference. Another possible explanation could be that the occurrence of epicormic branches is unrelated to tree size, as suggested in other studies (Colin *et al.*, 2008; Harmer, 1990, 1992; Morisset *et al.*, 2012).

There are other aspects that were not included in this study in relation to the occurrence of epicormic shoots, but they are important in the general interpretation of the results. First the occurrence of epicormic branches is strongly under genetic control (Savill & Kanowski, 1993) and second it is influenced by the social position of the tree in the stand, where suppressed trees have in general more epicormic branches than dominant trees (Krajicek, 1959; Nicolini *et al.*, 2001; Spiecker, 1991).

4.2 Crown size

The dependence of crown radius on site, silviculture and actual stem size was analysed using the full set of 53 experimental and operational plots located across three countries in Northern Europe.

Models were specifically designed to predict crown radius (and therefore area occupied or needed by each individual tree) based on different levels of information on stem diameter, thinning practice/stand density and site productivity. As a result a set of hierarchical models was developed, starting with individual tree data only (*dbh*), adding first partial information at stand level (quadratic mean diameter, D_g) and second additional information at stand level (relative basal area, G_{rel} and stand top height, H_{100}).

The overall response pattern indicated an increasing crown radius with increasing *dbh*, increasing D_g (indicator of age and thinning grade) or decreasing G_{rel} (indicator of thinning grade) and decreasing H_{100} (indicator of site productivity for a given age) (Figure 4). H_{100} is an age-specific indicator of site productivity (Skovsgaard, 2004c; Skovsgaard & Vanclay, 2013, 2008), but age was not included in the final model, owing the confounding effect of age on stem size. However for oak, heavy thinning may lead to reductions in height growth (Johannsen, 1999). Moreover, for most of the experiments used in this study, there is little variation in site productivity (Nord-Larsen *et al.*, 2009). Consequently, the negative effect of H_{100} on crown radius could be an effect of heavy thinning rather than lower site productivity.

All models, except for the basic model, included a significant interaction term between tree and stand variables, indicating a modification depending on site productivity, stand treatment or age. Interactions between *dbh* and H_{100} and between *dbh* and D_g adjusted predictions negatively, suggesting a compensation for competition.

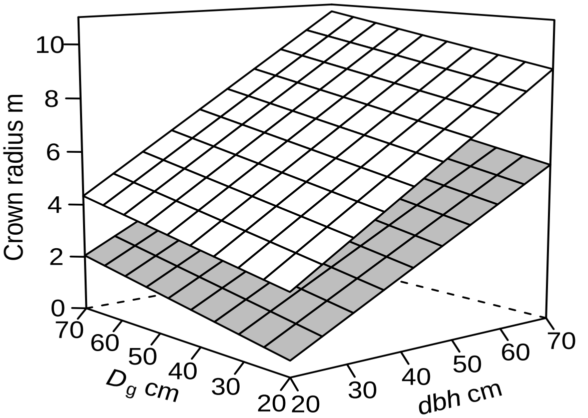

*Figure 4.*Wireframe for the model predicting crown radius as a function of *dbh* and D_g. The two wireframes indicate the fourth dimension, H_{100}, where the grey layer is for a larger stand top height (30 m) and the white one is for a lower (12 m).

It is interesting to notice that this analysis confirms the straight-line relationship between crown radius and *dbh* within the range of data used for model calibration (*dbh* ranging from 6 to 107 cm). However, as pointed out by Hemery *et al.* (2005), the true relationship between crown diameter and stem diameter may actually be sigmoid due to the distortion of the line at the lower end because stem diameter is usually measured at breast height, and the possible slower increase at the upper end due to senility.

The prediction accuracy increased with increasing level of information, and the model with all variables included and thinning grade expressed by G_{rel} was the best. The basic model, constructed to predict the crown radius as a function of only *dbh*, turned out to be less accurate for particular stands, because it did not use stand level information and hence variables reflecting thinning grade and site productivity.

The models have some limitations, namely, some combinations of small *dbh* and D_g resulted in negative predictions of crown diameter. This is thoroughly described in paper II. The recommendation was to use the models only above a certain tree size and to carefully evaluate predictions for small trees.

4.3 Volume

This part of thesis focussed on quantifying and modelling the effects of site and thinning practice on tree volume and stand volume growth. First, functions for predicting individual tree volume components (total and stem) from easily obtainable forest measurements were developed. Second, stand volume growth and crop tree volume growth at stand level were analysed and modelled based on age, indicators of site productivity and thinning practice (stand density).

4.3.1 Individual tree volume

Separate volume functions for total and stem volume of pedunculate oak were derived and calibrated based on measurements of individual stem and branch volume. The total volume was defined as the aboveground woody components of the tree, and calculated by adding stem and branch volume.

The individual tree volume functions were built on ideas developed by Madsen (1985, 1987) and Tarp-Johansen *et al.* (1997) to adjust for local site conditions and treatment practices. The variable that was included in the final models in addition to *dbh* and *h* was D_g.

For all tree components individual tree volume obviously increased with *dbh*, *h* and D_g. All models were constructed specifically to account for the effect of thinning practice on the total and stem volume of pedunculate oak. The inclusion of D_g resulted in a significant improvement of the prediction accuracy. The improvement may be attributed to the direct implementation of stand density or treatment effect in the model, as already suggested by

Skovsgaard & Nord-Larsen (2012), to the wider set of experimental data and to the statistical techniques used.

D_g was considered a suitable indicator of thinning grade, because it is a direct, combined expression of residual basal area and stem density that can be obtained easily and quickly. This is consistent with the objective of developing a model that could be used in research as well as in forestry practice. For economic or scientific reasons, the volume of interest may comprise only a specific component of the tree (branch volume can be obtained by subtraction) and it is the user's decision which model to choose. The limitation and criticism in using D_g is that it is not only a result of thinning practice, but also of age, growth rate, climate, soil type and these variables are not accounted for directly in the model. The expected gain in precision of the estimates of total and stem volume using D_g is discussed by an example in paper III.

The models were subjected to some limitations, which do not compromise their applicability and are partly justified by the need for functions easy to use in practice. One such limitation is that the models are not compatible or linked. Tree components are predicted independently. This was done to minimize the variance for each tree component, but it could potentially lead to a contradiction such as having a larger stem volume than total volume for the same tree. However, this did not occur in the prediction range used in model validation.

4.3.2 Stand level growth

Stand volume growth of even-aged pedunculate oak was analysed and modelled depending on thinning grade, age and, to some extent, inherent site productivity or soil texture. Models were calibrated using an unusually wide range of thinning treatments conducted consistently throughout observation periods of up to 110 years, and measurements were taken at regular intervals to consistent standards. Collectively, these characteristics are rather unique and no previous studies on the effects of thinning practice on the growth of pedunculate oak have included results from such comprehensive and rigorous experiments.

Separate models were developed for total and stem volume using an iterative parameter prediction or random coefficients approach for calibrating a Chapman-Richards function. Branch volume growth was obtained by subtraction between predicted values of total and stem volume growth. Throughout, continuous variables were used rather than categorical.

Volume growth, represented by volume periodic annual increment at stand level, was modelled as a function of age, site and G_{rel} or D_g, both of which are indicators of thinning grade and/or thinning weight. Pre-treatment mean annual volume growth or, alternatively, the texture of soil fractions, were used as potential indicator of site productivity for those experiments where the information was available. However, their inclusion led to a less accurate model for all components, and they were therefore excluded from the final models.

According to the calibrated models, total and stem volume increased with increasing stand density or decreasing thinning grade for both thinning practice indicators (D_g or G_{rel}). This trend is in agreement with previous analyses of pedunculate oak experiments in Denmark (Bryndum, 1957, 1965, 1966; Henriksen, 1988; Kramer, 1988; Spiecker, 1991;) and previous results for very heavy thinning of pedunculate oak in Great Britain (Hummel, 1951; Jobling & Pearce, 1977; Kerr, 1996), suggesting that stand cumulative volume production is substantially lower with increasing thinning grade due to a rapid reduction of stocking in the early life of the stand.

The age-dependent development of periodic annual increment followed the expected pattern of an initial increase, an early peak and a gradual decline with increasing stand age. The culmination occurred earlier in denser stands.

Similarly, the growth pattern observed is in line with the general response pattern for sessile oak except that in some cases the highest volume growth was observed for some light thinning regimes during certain age periods (*e.g.*, Direction Forêt, 2007; Gibaud, 2007; Ningre, 1990; Pardé, 1979). In contrast, the annual stand volume growth peaked earlier in heavily thinned stands of sessile oak in Germany (summarized by Kramer, 1988).

Branch stand volume increment decreased with increasing stand density. This makes biological sense since trees of identical age and stem diameter, but at different stand densities, have different crown diameters, *i.e.* larger for trees subjected to heavy thinning and gradually smaller with increasing stand density (Attocchi & Skovsgaard, 2015). By comparing the predicted growth of thinned to unthinned stands, it appeared that differences in growth tended to level out with increasing age. It was noted during model evaluation that in the initial stages of stand development, when trees are small, the models tended to slightly over-predict total and stem stand growth for very heavy thinning, but subsequently predictions remained unbiased. The different interval length between measurement occasions probably had an impact on the estimates of periodic annual increment and, in turn, model parameters, partially explaining this pattern.

Experiment CT was used for completing model evaluation. With an age range between 62 and 182 years it represents an interesting opportunity for evaluating the plausibility of model predictions far beyond the range of calibration data (14-119 years). Growth rates were consistently high for this very old oak stand (Figure 5), indicating that the age decline in the calibrated model possibly should be more shallow. A similar pattern was observed for sessile oak (Dhôte *et al.*, 2000) showing that current annual volume growth may remain high, without declining, throughout stand maturity. It is important to emphasize that the age-dependent growth decline predicted by the model most probably was penalised by recurrent, severe defoliations in some plots of experiment QX and QY since the mid-1990s.

Due to the rapid increase of growth in very young stands and the possible under-prediction of growth in very old stands, a general recommendation is to not use the models for extrapolation beyond the calibration range, *i.e.*, below ages of approximately 15 years or above 120 years.

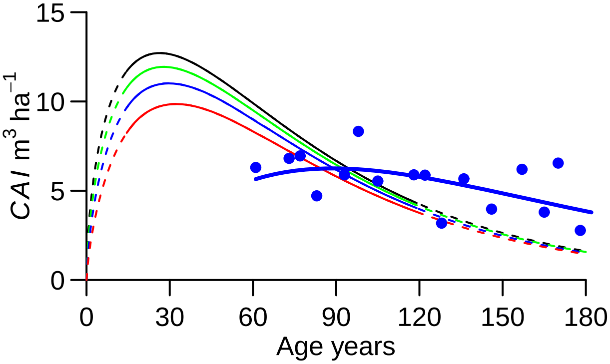

Figure 5. Simulated current annual increment (CAI) curve using values of relative basal area of 100, 80, 60, 40 % corresponding to the theoretical level of G_{rel} for thinning grades A (black), B (green), C (blue) and D (red), respectively. The points and thick blue line represent the development of periodic annual increment of the single-plot experiment CT. Dashed lines are outside the calibration range.

4.3.3 Crop trees growth

The development of 50 crop tree ha^{-1} (hereafter crop trees) was described in paper V. The volume growth of crop trees at stand level, represented by volume period annual increment, was modelled including indicators of thinning grade (G_{rel}) and site productivity (pre-treatment mean annual increment or soil texture). Models were fitted separately for total and stem volume growth of crop trees, with the same procedure used for modelling stand volume growth (section 4.3.2). In plots with more than 50 trees ha^{-1} at last measurement occasion, the 50 thickest trees were chosen.

The description of the development of crop trees indicated that generally plots treated with very heavy thinning had the largest values for basal area, D_g and total, stem and branch cumulative volume, which gradually decreased with decreasing thinning grade.

The final model for predicting periodic annual increment of crop trees included an indicator of thinning grade (G_{rel}). The inclusion of pre-treatment mean annual increment as an indicator of inherent site productivity did not improve model accuracy. According to the calibrated models, crop tree stand volume growth increased with decreasing stand density or increasing thinning grade. The predicted growth of the 50 thickest trees relative to that of the entire stand (based on paper III) increased exponentially (Figure 6). In the unthinned control (G_{rel} = 100 %) the models predicted that the 50 thickest trees were the only trees left in the stand by the age of 129 years. Stands thinned to a residual basal area of 50 % (G_{rel} = 100 %) included only 50 trees per hectare by the age of 106 years.

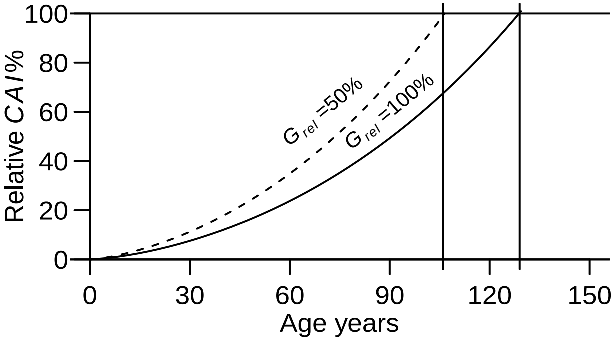

Figure 6. Predicted volume growth (current annual increment *CAI*) of the 50 thickest trees relative to the entire stand, calculated for G_{rel} = 50 % (dashed line) and for G_{rel} = 100 % (solid line).

Previous studies on future crop trees of oak have focused on specific parts of the production process or management cycle, such as the time of selection and the spacing of future crop trees (Chroust, 2007; Ningre, 1990; Pardé, 1979; Roy, 1975; Venet, 1968), the growth of a larger number (> 50 ha^{-1}) of selected trees (Nagel, 2007; Spellmann & von Diest, 1990), the 'free' unimpeded growth of released pre-selected trees (Hummel, 1951; Jobling & Pearce, 1977; Kerr, 1996) and the effects of pruning of epicormic shoots (Attocchi, 2013; Kerr & Harmer, 2001). The models presented in this part of thesis represent a comprehensive analysis of the long-term impact of thinning practice on the volume growth of crop trees, which could be valuable tools in forest management.

Similarly to the approach used in the individual volume models (paper III), the models for total and stem volume growth in paper IV and V are not linked. This model approach was chosen in line with the principle used by Skovsgaard & Nord-Larsen (2012) to minimize the variance for each volume component rather than the variance of the overall model.

5 General discussion and management implications

The experiments used in the different investigations of this thesis were established with the common general objective of quantifying and modelling short- and long-term effects of site and thinning practice on the growth, wood quality and value production of pedunculate oak. In Northern Europe, there is a long tradition for relatively fast production of high-quality oak timber based mainly on frequent heavy thinning that is sometimes combined with regular high-pruning (section 2.4).

Managing the balance between individual tree growth and development of epicormic branches and timber quality through thinning practice is a crucial issue in oak silviculture. Pruning of primary and secondary branches and stand density have an impact on the composition of epicormic branches, as demonstrated in paper I. However, which range of stand densities is optimal considering density-dependent production risks (section 2.5.4) and the possible interaction between pruning and stand density, remain to be clarified. The modification of light conditions is another key factor. An increased level of light favours the growth and persistence of epicormic shoots (Evans, 1982), but a decreased level of light with increasing canopy closure, suppresses the growth of epicormic branches, and a proportion of the new epicormic shoots will probably die (Spiecker, 1991). Additionally the social rank of the trees in the stand plays an important role. Certain individual trees consistently develop more epicormic shoots over time independent of the thinning practice (Henriksen & Sanojca, 1983; Morisset *et al.*, 2011; Spiecker, 1991; Ward, 1966).

The implication of the results presented in paper I is that early, heavy thinning combined with high pruning, initiated early and repeated at regular intervals, may help to shorten the rotation length for pedunculate oak without a further reduction in wood quality than that caused by wider annual growth rings. The lower number of epicormic shoots with decreasing stem density indicates that heavy thinning is economically beneficial in terms of pruning costs.

Despite of numerous investigations there is still a knowledge gap regarding the relationships between epicormic shoots, tree size and tree social rank in the stand and to how these are influenced by site and silviculture.

One common aspect across all investigations is the importance of crown development, specifically for potential future crop trees. Reliable models for predicting crown radius based on a wide set of predictor variables were formulated in paper II. Compared to former crown development equations for oak (Dubravac *et al.*, 2009; Hasenauer & Monserud, 1996; Hemery *et al.*, 2005; Kerr, 1996; Nutto, 1998; Shimano, 1997; Spiecker, 1991), the set of models presented in this study was specifically designed to predict crown radius based on different levels of information on stem diameter, thinning practice and site productivity. This offers flexibility depending on data availability. For example the basic model, predicting crown radius only from *dbh*, is mainly relevant for forestry practice. The partial model is tailored for forest planning and forest management based on inventory data that include an estimate of D_g. Since this is rather easily obtained, for example from a sample of some few trees, the partial model is also well-suited for forestry practice. The full model, requiring more data input, is probably more suitable for scientific purposes.

Based on the assumption of circular model crowns, the models assume regularly shaped crowns and regular spacing throughout the stand for which they are being used. Due to their completely empirical origin, the models do not assume any specific spacing pattern other than that of a “regular” and somewhat homogenous distribution of trees within the stand reached after a number of thinning interventions.

The variation in crown diameter for two contrasting thinning regimes can be calculated with the partial and extended models as shown and discussed in details in paper IV. This is only one possible application of the models, which can also be used in forest management to estimate, for example, how many trees can be accommodated at a given time during the rotation, given a specified thinning regime. In turn, this is useful for outlining or scheduling "optimal" stem number reductions and thinning regimes. This is relevant for forest management planning as well as for specific scientific purposes.

Models for estimating total and stem volume of individual trees adjusting for local site conditions and treatment practices were presented in paper III. Branch volume estimates were obtained by subtraction and compared to the measurements. The variable included in the final models in addition to *dbh* and height was D_g.

The difference in individual tree volume prediction for two trees with the same *dbh* and *h*, but in two contrasting thinning grade (unthinned and heavy thinning), is approximately 4.5 %. This difference indicates that, for the highly realistic range of stand conditions and tree sizes, this percentage is the expected gain in precision of the estimates of total and stem volume, using D_g. For oak this may lead to substantial changes in the specification of optimal stand treatment simply because the monetary value of individual stems may increase more with increasing growth rate of individual trees than the decreased value due to decreasing stand volume growth.

In the context of this thesis, the development of individual tree volume functions was a necessary step to ensure the best possible and most accurate analysis of volume growth at stand level and of volume growth of crop trees. A contributing reason was that previous models (Madsen, 1987; Tarp-Johansen *et al.*, 1997) included only very limited data from thinning experiments with the range of stand treatments represented in this investigation and could therefore potentially lead to treatment-specific bias in the analyses.

Detailed knowledge of the site-specific response pattern depending mainly on stand density and age may help optimize management practices in operational forestry and improve our understanding of how the forest responds to treatment. In paper IV this relationship has been investigated for stand volume growth depending on G_{rel} or D_g and age. The formalization of this relationship in models for total and stem volume (paper IV) can be used for exploring alternative silvicultural strategies. The models were developed based on sound statistical reasoning and are biologically justified and dynamic, in the sense that they adjust volume growth predictions according to site conditions and the actual stand density.

The experiments used for model calibration all included one or more strictly unthinned control plots against which the effects of thinning could be gauged objectively. Moreover, they included an unusually wide range of thinning treatments conducted consistently throughout observation periods of up to 110 years, and measurements were taken at regular intervals and to consistent standards. Collectively, these characteristics are rather unique and no previous studies on the effects of thinning practice on the growth of pedunculate oak has included so comprehensive, strictly conducted experiments.

The evaluation of the quantitative model, thoroughly described in paper IV, considered technical and biological aspects, as suggested by Vanclay & Skovsgaard (2007). The main recommendation was that due to the rapid increase of growth in very young stands and the possible under-prediction of growth in very old stands the models should not be used for extrapolation beyond the calibration range, *i.e.*, below ages of approximately 15 years or above 120 years. Moreover, predictions may deteriorate for extremely heavily thinned stands with a relative basal area below 30 %.

Particular attention is given to future crop trees from an early stage and throughout the rotation length (section 2.5.1 and paper II). The development of 50 crop trees ha^{-1} was described and the volume growth at stand level was modelled in paper V, following the same procedure as for stand volume growth (paper IV).

For 50 crop trees ha^{-1}, the growth rate increased with increasing thinning grade at all ages. Other studies on crop tree silviculture reported similar results (Jobling & Pearce, 1977; Kerr, 1996), emphasizing that although stand growth declines with increasing thinning grade this may be compensated for in terms of monetary revenue by the increased diameter growth and increased value of final crop trees. The models reported in paper V demonstrate and quantify the positive effect of thinning on the growth of the crop trees, and lends support to the concept of individual tree silviculture based on early initiated, heavy thinning for the 'best' trees at regular intervals.

6 Conclusions

The findings of the thesis contribute to the scientific basis to quantify how pedunculate oak trees and stands respond to specific silvicultural practices and to possibly modify contemporary oak silviculture. In line with the objectives of the thesis, the main conclusions follow.

Pruning of primary and secondary (epicormic) branches leads to an increased number of new epicormic shoots, which decreases with decreasing stand density. The lower number of epicormic shoots with decreasing stem density indicates that heavy thinning is economically beneficial in terms of pruning costs. In silvicultural practices these findings indicate that early, heavy thinning combined with high pruning, initiated early and repeated at regular intervals, may help shorten the rotation length.

A set of models for predicting crown radius based on different levels of information and a larger range of predictor variables indicating stem diameter, thinning practice/stand density and site productivity was presented. The basic model indicated that for the range of data used (*dbh* ranging from 6 to 107 cm) the dependence of crown radius on stem diameter can be described by a straight line relationship. Crown radius can be simply predicted by multiplying *dbh* with a factor of 11.7. The inclusion of stand variables showed that crown size responds to thinning even at later stages and probably at a higher rate that it was previously thought. This suggests that oak can adjust to changing stand conditions. The interaction between *dbh* and stand variables (D_g and H_{100}) adjusted predictions of crown size negatively, suggesting a compensation for competition. These findings can be used to optimise the design of thinning regimes and spatial distribution of individual trees within a stand.

Models for individual tree volume prediction including an indication of stand characteristics, represented by D_g, in addition to individual tree characteristics (*dbh* and *h*) resulted in higher prediction accuracy. The relative difference in total and stem volume for trees with the same *dbh* and height but in two extreme thinning grades (unthinned and heavy thinning), was approximately 4.5 %.The difference indicates that, for the highly realistic range of stand conditions and tree sizes, this percentage is the expected gain in precision of the estimates of total and stem volume, using the quadratic mean diameter.

Models for predicting stand volume growth depending on thinning grade and age were presented in paper IV. Models indicate that the largest stand growth (periodic annual increment) of total and stem volume occurs in unthinned control plots and the lowest in heavy thinning, irrespective of age. The growth peak is reached later with increasing thinning grade. This knowledge on site-specific response pattern depending mainly on stand density and age may help optimize management practices in operational forestry and improve our understanding of how the forest responds to treatment.

Similarly, paper V investigated the volume growth of crop trees (50 trees ha^{-1}), showing that the largest growth occurs for very heavy thinning and smallest for unthinned control plots. This is in line with the concept, in Northern European oak silviculture, of shortening the rotation length, where although stand growth declines with increasing thinning grade, there is a compensation in terms increased value of final crop trees.

7 Further research

Overall it would be interesting to monitor in the long-term the consequences of extreme thinning grades on tree growth as well as on wood quality, including stands with irregular silvicultural practices, *e.g.* no-thinning in young or old stands, since this is a current trend in many managed oak forests.

In relation to epicormic branches, it would be interesting to study the long-term consequences of different silvicultural practices, such as pruning and thinning. This is due partially to the fact that the recoding and monitoring of epicormic branches are very expensive operations, often difficult to consistently record in the long term.

In relation to crown size, it would be interesting to investigate the dynamics of crown development in relation to silvicultural practices and to model the dynamics of crown expansion.

In relation to individual tree volume and stand volume growth, future studies could aim at linking different components (total, stem and branches) in one model. Additionally it would be interesting to include below ground volume (roots and below-ground stump). Besides volume, biomass could be investigated, to provide models for the assessment of carbon stocks and carbon stock changes.

The impact of site could be further investigated, including soil analyses for the experiments for which such information are not yet available and possibly include other experiments.

The study on volume growth of crop trees is only one aspect of the development of crop trees. Further research could aim at analysing the continuity of crop tree selection in the long-term, starting from early stages of stand development and considering different characteristics of crop trees as well as wood quality.

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Appendix

Description of the stands and the experiments

The nine long-term forest experiments and the operational stand used in this thesis are located in essentially even-aged stands of pedunculate oak. The following description is organised by country (see also Figure 2). Additional references, where the experiments and the operational stand have been described, are listed in Table 1 of Paper II and IV.

Denmark

Seven experiments and one operational stand are located in Denmark, on glacial till deposits from the most recent glaciation, on essentially flat, but sometimes moderately sloping terrain at an elevation of 12 - 68 m above sea level. The average annual precipitation is 600 - 700 mm throughout the region (Frich *et al.*, 1997).

CT Wedellsborg Kongeskov

The stand was established by sowing in autumn 1831 with acorns possibly of nearby Sparretorn origin on former agricultural land. The area was unfenced and numerous trees were damaged from browsing by fallow deer (*Dama dama* L.). The experiment was installed in 1852 and consists of only one plot of approximately 0.56 ha (Figure A1). Two pre-commercial thinnings had been conducted before the installation, the first one in 1846. The experimental plot has been thinned heavily on a consistent and regular basis, following recommendations founded by C.D.F. Reventlow in the early 1800s (Reventlow, 1811, 1879, 1960). The first complete measurement available is from 1893. Notes from the 1920s and 1930s describe the stand as unusually beautiful, with straight stems and homogeneous crowns, and reported that good quality trees were pruned. The plot included a thick undergrowth of sycamore (*Acer pseudoplatanus* L.) which has been coppiced at various intervals. Experiment CT is considered a living monument documenting the most commonly applied thinning practice for oak in Denmark and is the inspirational base of the C-grade thinning.

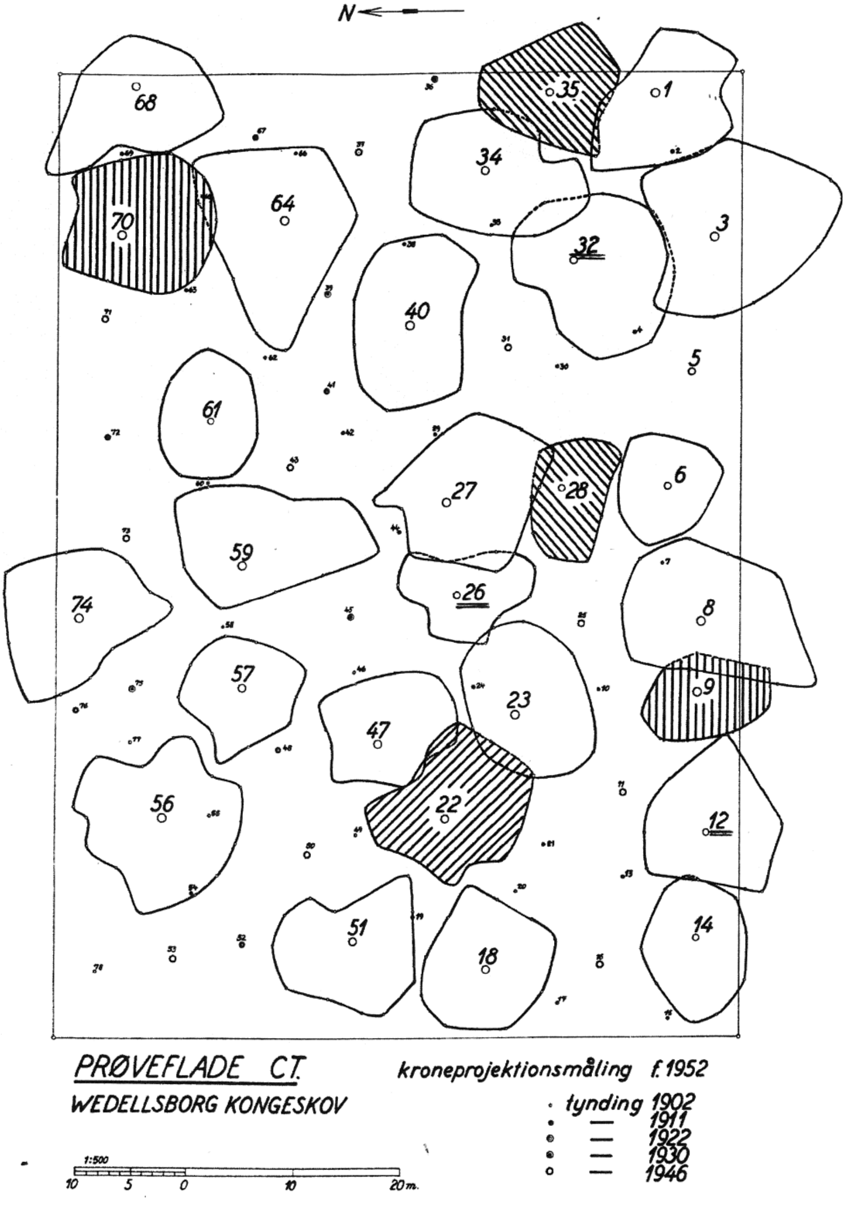

Figure A1. Stem and crown projection map of experiment CT in Wedellsborg Kongeskov. Trees cut during 1902-46 are marked by dots, while those remaining in spring 1952 were measured for crown projection.

Bjerge Meadows

The stand was established in three sowings, beginning in in the mid-1880s and finishing in 1891. The first thinning in this operational plot was conducted in 1906 and it has been thinned heavily ever since, somewhat similar to C-grade thinning.

Stand treatment and stand growth until the age of circa 60 years have been reconstructed based on historical records, old inventory data and detailed measurements in 1948. During that period the post-thinning basal area has been estimated to range between 7 and 11 m^2 ha^{-1}. The stem number at the age of 60 years was approximately 100 trees ha^{-1}. 2013-estimates from the inventory database for national forests indicate a stand basal area of approximately 15 m^2 ha^{-1}, a stem number of 30-35 trees ha^{-1} and an average *dbh* of 77 cm. Total stand volume is believed to range around 260 m^3 ha^{-1}.The stand include an undergrowth of various broadleaved tree species which has been coppiced several times.

QD Ganneskov

The stand was established by sowing in spring 1893 with acorns of local Danish origin. The area had previously been stocked with beech, which was used as shelterwood. The experiment was installed in 1902 and consists of one unthinned control plot (A-grade) and two plots treated with heavy thinning (C-grade), with an average plot size of 0.06 ha (Figure A2). The first complete measurement available is the one of 1920.

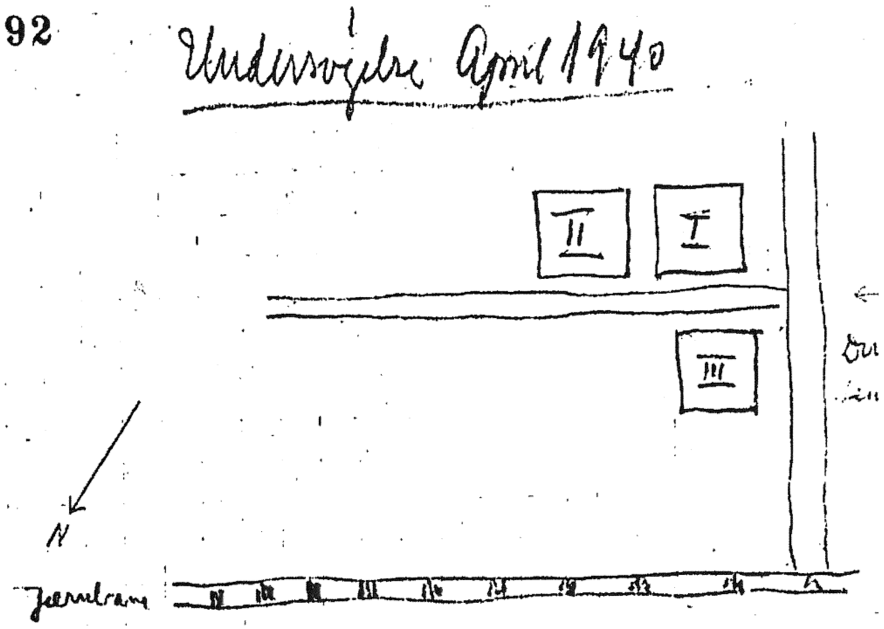

Figure A2. Sketch of plot layout of experiment QD in Ganneskov.

QX Grevindeskoven

The stand was established by sowing in spring 1924 with acorns of Dutch origin. The area had previously been stocked with beech, which was used as shelterwood. The last shelter trees were removed 13 years after establishment of the oak stand. The experiment was installed in 1945 and consists of ten plots representing replicates of four thinning treatments (A-, B-, C- and D-grade), with an average plot size of 0.50 ha. Two pre-commercial thinnings had been conducted before installation of the experiment, the first one in 1940-41. Thinning grades were specified mainly by stand residual basal area relative to that of the two strictly unthinned control plots (A-grade).

Epicormic branches have been pruned at regular intervals. Some plots have been severely defoliated several times since the mid-1990s.

QY Grevindeskoven

The stand was established by planting of one-year old transplants from experiment QX in spring 1925. The experiment was installed in 1945 and consists of eight plots representing replicates of four thinning treatments (A-, B-, C- and D-grade), with an average plot size of 0.51 ha (Figure A3). Two pre-commercial thinnings had been conducted before installation of the experiment, the first one in 1940-41. Thinning grades were specified mainly by stand residual basal area relative to that of the strictly unthinned control plot (A-grade).

Epicormic branches have not been pruned, unlike experiment QX. Some plots have been severely defoliated several times since the mid-1990s.

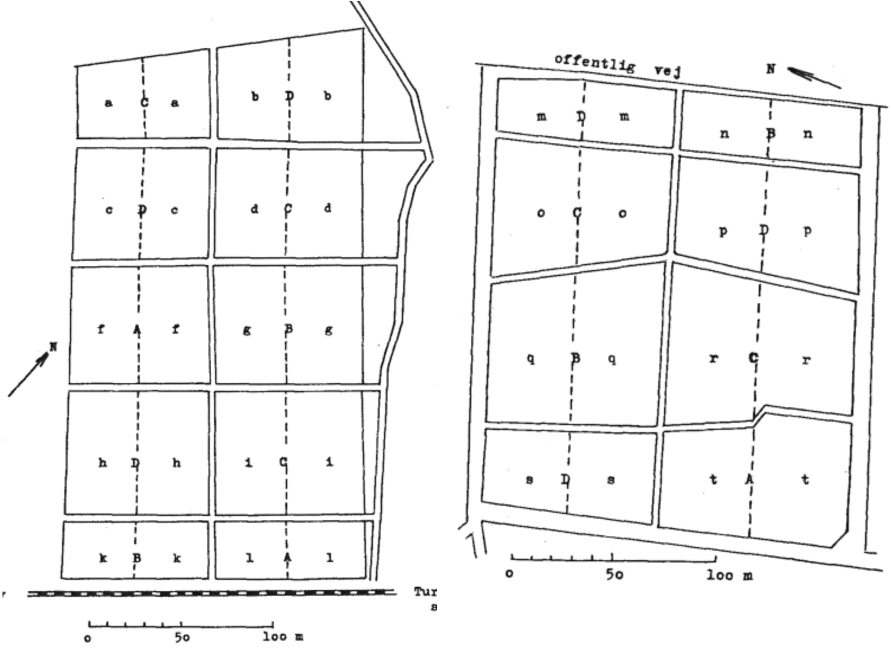

Figure A3. Ploy layout of experiment QX (left) and QY (right) in Grevindeskoven. Capital letters indicate thinning grade and lower case letters indicate plot id.

RA Grib Skov

The stand was established by sowing in spring 1944 with acorns of Petersgaard origin. The area was previously stocked with beech and oak. No shelter trees were retained, but a nurse crop of grey alder was introduced at stand establishment. The area was fenced for some years. The experiment was installed in 1958 and consists of twelve plots representing replicates of four thinning treatments (A-, B-, C- and D-grade), with an average plot size of 0.43 ha (Figure A4). Thinning grades were specified mainly by stand residual basal area relative to that of the strictly unthinned control plots (A-grade), leaving a slightly higher relative basal area compared to QX and QY experiments. No pre-commercial thinnings had been conducted before establishment of the experiment. Epicormic branches have not been pruned.

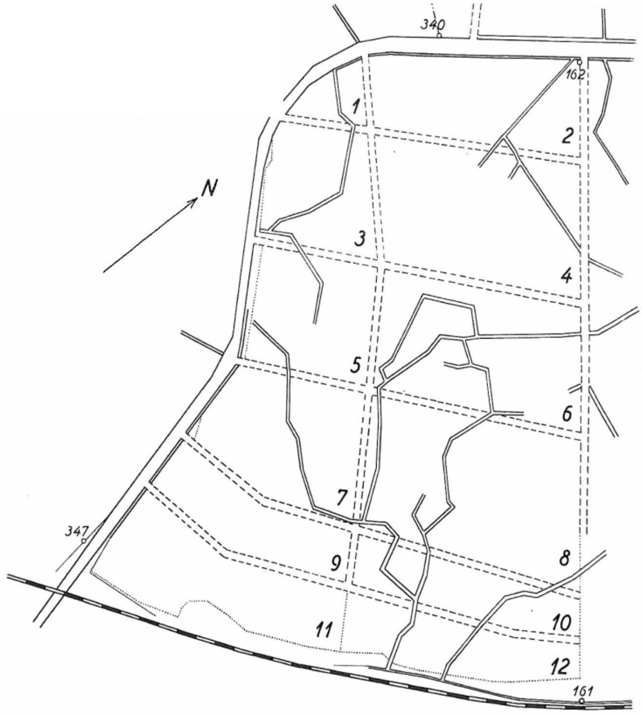

Figure A4. Map of experiment RA located in Grib Skov. Numbers indicate plot.

1516 Haslev Orned

The stand was established by sowing in spring 1989 with acorns of Dutch origin on a former meadow. The area was fenced for approximately 10 years. The experiment was installed in 2002 and consists of two blocks with eight plots each (Figure A5). At this stage of the experiment, the treatments comprise five types of pre-commercial thinning replicated once in each block. Remaining treatments will be finally decided and installed later. The treatments include the strictly unthinned control (A-grade), the most common thinning practice for oak on good sites in Denmark (C-grade) and three heavier treatments initially defined mainly by their residual stem number after the first pre-commercial thinning, namely 1000, 300 and 100 ha^{-1}. Using a notation similar to that of the older experiments treatment 1000 is similar to a D-grade thinning at this stage of stand development and 300 to an E-grade. Treatment 100 holds an extremely small residual basal area and lies outside the usual range for this style of notation The average plot size is 0.17 ha.

According to the original experimental design, 100 evenly distributed crop trees ha^{-1} should be pruned in all treatments, except for unthinned and extremely heavily thinned plots. So far, D and E-grade plots have been pruned.

1517 Brendstrup Skov

The stand was established by planting two-year old seedlings in autumn 1990 (Block East) and in spring 1991 (Block East) on former agricultural land. The genetic origin of Block East is Petersgaard F.181, whereas the genetic origin of Block West is believed to be Pederstrup F.369, but possibly with an admixture of Petersgaard F.181, Stensballegaard F.484 or Haderslev F.286. The area was unfenced and numerous trees were badly damaged from browsing by European hare (*Lepus europaeus* Pallas). The experiment was installed in 2003 and consists of two blocks with eight plots in Block East and twelve plots in Block West. At this stage experiment 1517 replicates the design and treatments in 1516. The additional plots in Block West have not been installed with treatments and are reserved for later use. The average plot size is 0.17 ha (Figure A6).

According to the experimental design, 100 evenly distributed crop trees ha^{-1} should be pruned in all treatments, except for unthinned and extremely heavily thinned plots. So far, D and E-grade plots have been pruned.

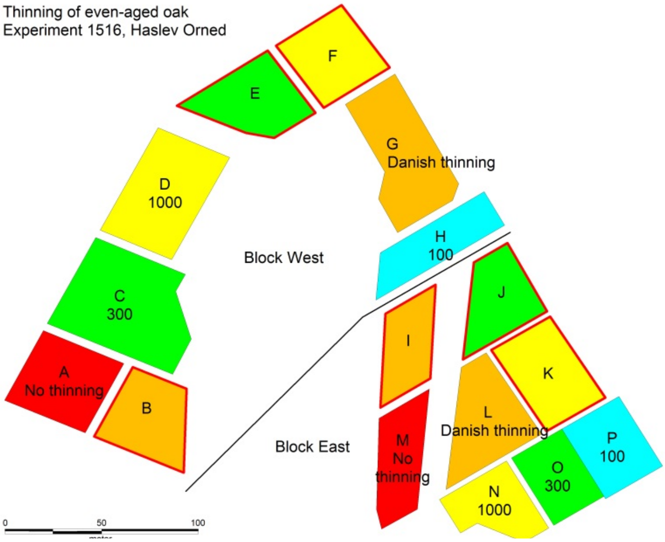

Figure A5. Plot layout of experiment 1516 in Haslev Orned. Capital letters indicate plot id, numbers indicate the residual stem number per hectare after first pre-commercial thinning. Colours indicate a specific thinning treatment, whereas perimeter colours indicate the time of the first thinning (grey=early thinning, red= late thinning).

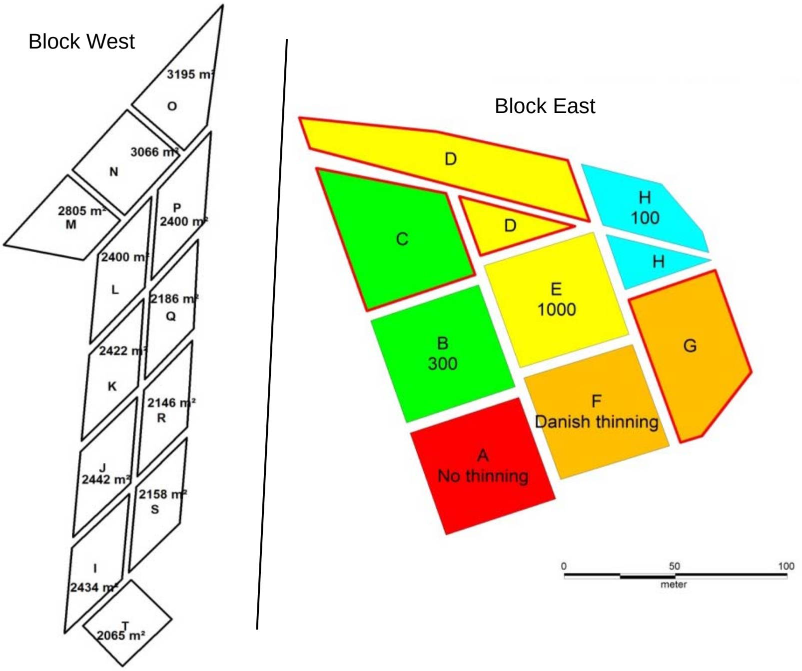

Figure A6. Plot layout of experiment 1517 in Brendstrup Skov. Capital letters indicate plot id. In Block East (right) colours indicate a specific thinning treatment, perimeter colour indicates the time of the first thinning (grey=early thinning, red= late thinning) and numbers indicate the residual stem number per hectare. In Block West (left) the scale is different than Block East.

Sweden

One experiment is located in Southern Sweden on flat terrain at an elevation of 100 m above sea level. The soil is brown earth developed from glacial till overlying a parental, sedimentary rock of Cambro-Silurian origin. The site is moist and subject to occasional drought. The annual precipitation averages 675 mm, ranging from around 500 to 900 mm per year (SMHI, 2013).

8800 Skarhult

The stand was established by planting in 1952 on former agricultural land using one- and two-year old seedlings probably of Dutch origin, but no documentation is available. At the same time 3,000 seedlings of grey alder (*Alnus incana* (L.) Moench) were planted as a nurse. In 1953 larch (*Larix* sp.) was planted as replacement for dead oaks and in 1959 hornbeam (*Carpinus* *betulus* L.) was planted to create an understorey. The stand was thinned in 1986 and the experiment was installed in 1991 at the second thinning. The experiment consisted of six plots representing replicates of three thinning treatments (A-, C- and D-grade), with an average plot size of 0.45 ha (Figure A7). Before installation of the experiment one or more pre-commercial thinnings had been conducted. Thinning treatments were specified as no thinning (strictly unthinned control), heavy thinning (as specified in the Swedish 'standard' regime (Carbonnier, 1975)) and very heavy thinning, where the crowns of crop trees are kept free to develop at all times throughout the rotation.

Each plot was divided into two subplots and in one subplot in each plot potential crop trees were pruned.

Figure A7. Plot layout of experiment 8800 in Skarhult Experimental Forest. Block B is to the left and Block A to the right. Numbers indicate thinning grade, and “K” is the part of the plot where future crop trees were pruned (Source: Agestam *et al.*, 1993).

Great Britain

One experiment is located in Great Britain on gently to moderately sloping terrain, mainly towards south and east and at an elevation of 225-246 m above sea level. The soil is well-drained loamy brown earth overlying Old Red Sandstone. The annual precipitation averages 960 mm (Met Office, 2013).

Crumbland 7 Tintern Forest

The stand was established by planting in 1931 using seedlings on unknown genetic origin. The area was previously stocked with a conifer plantation. The experiment consists of two separate areas each of which contains a series of so-called intensive and extensive plots. The following description is based on Kerr (1996; 2008). Intensive plots were installed in 1951, where the average plot size was 0.04 ha. Extensive plots were installed in 1953, where the average plot size was 0.40 ha (Figure A8). Originally there were four thinning treatments, specified as unthinned control (A), light crown thinning (C), free growth conditions (E) and free growth but with no thinning after a mean *dbh* of 39 cm (E1). Treatment E1 was applied only in extensive plots. The original experimental design was changed in 1964. The intensive plots treated with no thinning (unthinned control) or crown thinning, were then converted to free growth. The extensive plots treated with no thinning were divided into two. One part was converted into free growth in 1964; the other was converted in 1974.

A fire occurred in one of the two blocks in 1976 and destroyed one extensive plot of E-grade treatment and severely damaged one extensive plot of E1 treatment.

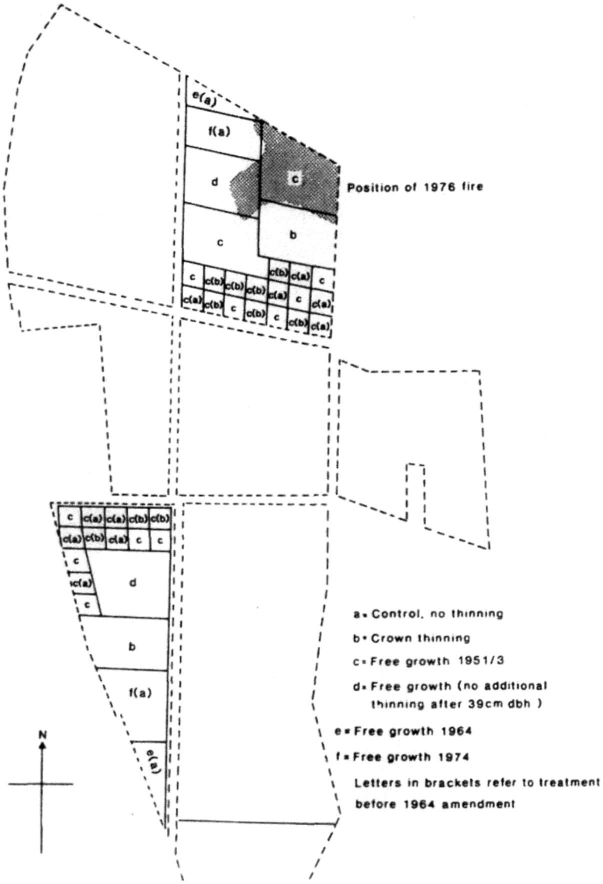

Figure A8. Plot layout of experiment Crumbland 7 in Tintern Forest (source: Kerr, 1996).

Description of thinning treatments and their implementation

All experiments have been managed consistently and measured at each thinning intervention. Plots that achieved the final stem number have been maintained and measured at regular intervals.

The plots used in this thesis represent five experimental treatments (thinning grades) ranging from the strictly unthinned control plot to extremely heavy thinning. Each plot was classified with a nominal thinning grade based on documented treatment specifications, labelled A (strictly unthinned, no thinning of dead or live trees at any time), B (light thinning), C (heavy thinning), D (very heavy thinning) or E (extremely heavy thinning). The treatment specification for each thinning grade is reported below.

A-grade thinning

This treatment is the unthinned control treatment, where no dead or dying trees were removed from the plot at any time. In experiment QX, QY and RA dead trees were removed on one occasion during the mid-1990s.

B-grade thinning

B-grade thinning corresponds to light thinning. The selection principle for this treatment is crown thinning, characterized by frequent interventions aiming to remove one or two competitors for each potential future crop tree at each intervention. This type of management is somewhat similar to the oak silviculture for high-quality timber production applied in Central Europe (described in section 2.3).

In experiment QX and QY the B-grade was defined in terms of relative basal area, so that a residual basal area of 73 % relative to that of the unthinned control plot should have been left at each thinning. In experiment RA the relative basal area of the B-grade was aimed at 81 %. These were the realized values, but the target values were 75 % and 83 %, respectively.

C-grade thinning

C-grade thinning corresponds to heavy thinning. The selection principle for this treatment is crown thinning aiming to favour potential future crop trees.

In experiment QX and QY the C-grade was defined in terms of relative basal area, so a residual basal area of 49 % relative to that of the unthinned control plot should have been left at each thinning. In experiment RA the relative basal area of the C-grade was aimed at 63 %. These were the realized values, but the target values were 50 % and 67 %, respectively.

The C-grade thinning of the experiments in Denmark have become associated with what is often called the Bregentved regime, named after one of the leading oak estates. The design of this treatment was inspired and based mainly on the stem number reduction applied in experiment CT in Wedellsborg Kongeskov.

The following description of the Bregentved regime is based on field tour notes on thinning practices for oak in Denmark by Jens Peter Skovsgaard:

Seminal experiments on thinning of oak in Denmark were initiated in 1793 by C.D.F. Reventlow (1811, 1879). Based on these and other studies, management practices by the end of the 1800s developed into earlier, heavier and more frequent thinning operations.

The management model for young stands is based mainly on results from a pre-commercial thinning experiment (now continued as experiment QD and included in this thesis) in the early 1900s (Hauch, 1908, 1915). Results indicated that in young stands, thinning among dominant trees to remove undesirable individuals combined with heavy thinning among socially intermediate trees, while retaining an understorey of suppressed oak trees, is beneficial for the growth as well as the wood quality of potential crop trees.

During the 1900s the combination of these principles developed into the so-called Bregentved regime for thinning of oak. This regime is widely practiced for the production of commercial, high-quality oak timber on good glacial till sites and is used as an inspiration also for oak growing under less optimal site conditions.

The Bregentved regime results in an average annual ring width of 3-3½ mm and a rotation age of 120 years. A recent review of the management practices for oak at Bregentved since the late 1800s widely substantiates this result and further analyses details of crop tree selection (including a possible increase of the final number of crop trees from 50 to possibly 80 ha^{-1}), pruning practices, production risks and the overall economic return (Jørgensen *et al.*, 2013).

D-grade thinning

D-grade thinning corresponds to very heavy thinning. The overall selection principle is crown thinningaiming at potential future crop trees. Initially, a reserve of 50-100 % more than the expected final number of trees was selected.

In experiment QX and QY, the D-grade was defined in terms of relative basal area, so that a residual basal area of only 35 % relative to that of the unthinned control plot should have been left at each thinning. In experiment RA the relative basal area was aimed at 45 %. These values correspond approximately to the target values.

E -grade thinning

E-grade thinning corresponds to extremely heavy thinning. The selection principle for this treatment was heavy crown thinning (in Great Britain) combined with substantial removals from below (in Denmark), both aiming to let future crop trees free from competition throughout the rotation, in order to maximize the growth potential of individual remaining crop trees.

In Great Britain this treatment is similar to the “free growth” concept developed for oak by Jobling & Pearce (1977). In this regime potential final crop trees are selected very early in the rotation and marked permanently. It was decided that all trees, whose crowns come in contact or within a predefined distance from selected crop trees, should be removed.

In experiment 1516 and 1517 this treatment was specified by a stem number reduction to 300 trees ha^{-1} at the first pre-commercial thinning, subsequently followed by other thinnings aiming to gradually reduce the stem number to approximately 100 ha^{-1} at an age of 75 years.

Implementation of thinning treatments

There were slight variations in residual basal area within each nominal thinning grade. The stand age when the first thinning was conducted ranged between 9 and 34 years across the experiments and the application of pre-commercial thinnings was not consistent across experiments. The definition of pre-commercial thinnings in the 1800s might have been different than how they are currently applied and the distinction between pre-commercial thinning and thinning is not always clear. In addition to natural variation, this could partly explain the variation within nominal thinning grades. There were also other factors that influenced the implementation of a specific thinning treatment. Labour and economic constrains, for example, that possibly prevented from conducting a thinning operation in a predefined year. Moreover, most of the experiments have been managed by different generations of foresters, all with different ideas and philosophies of silviculture and most likely influenced to some extent by what was in fashion at the time. This may have influenced, for example, how selection principles were interpreted.

The progress of stand development has been summarized for each experiment in terms of stem number (N, ha^{-1}), basal area (G, m^2 ha^{-1}), quadratic mean diameter (D_g, cm), stand top height, defined as the mean height of the 100 thickest trees per hectare (H_{100}, m), total stand volume (V_{tot}, m^3 ha^{-1}), stem stand volume (V_{stem}, m^3 ha^{-1}) and quadratic mean diameter of the 50 thickest trees ha^{-1} (D_{g50}, cm) (Figures A9-A17).

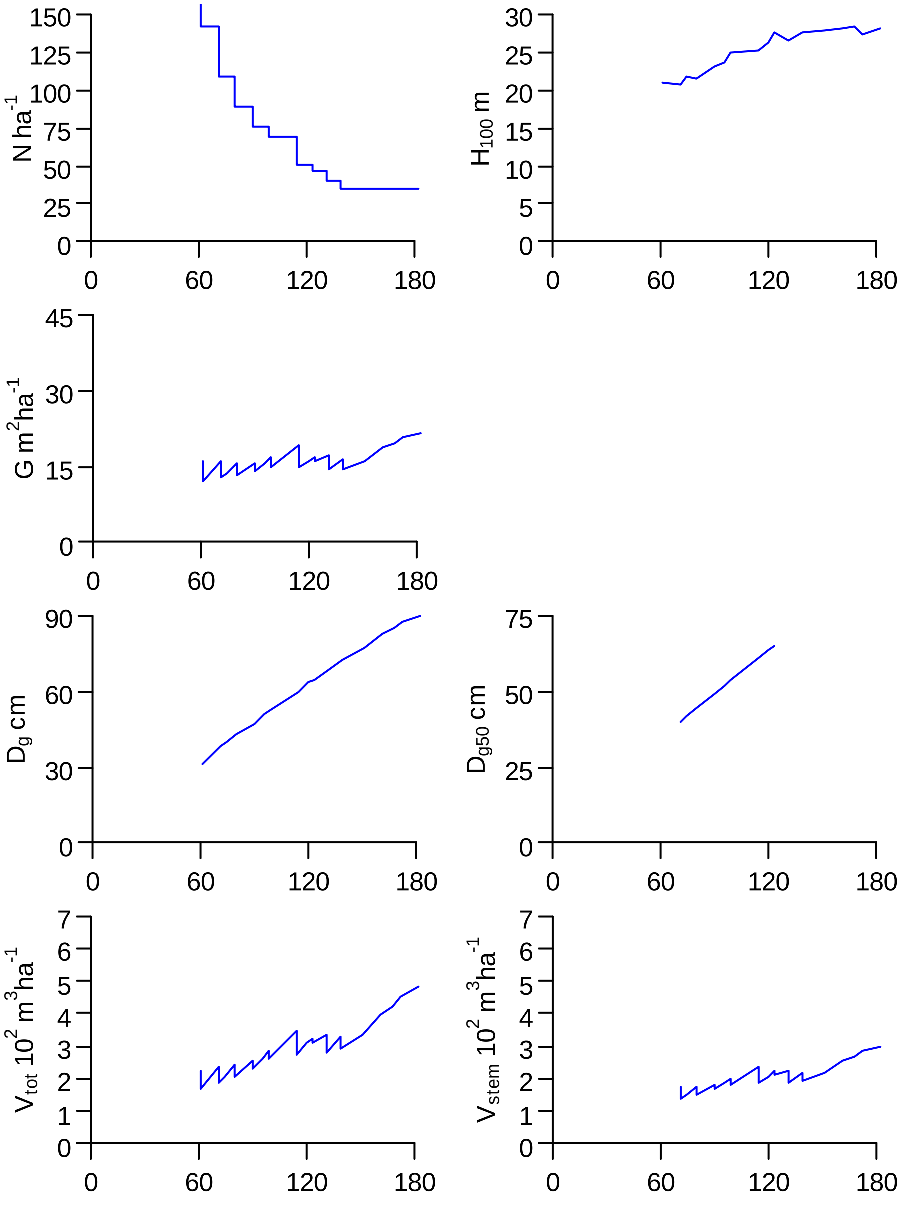

Figure A9. CT Wedellsborg Kongeskov.

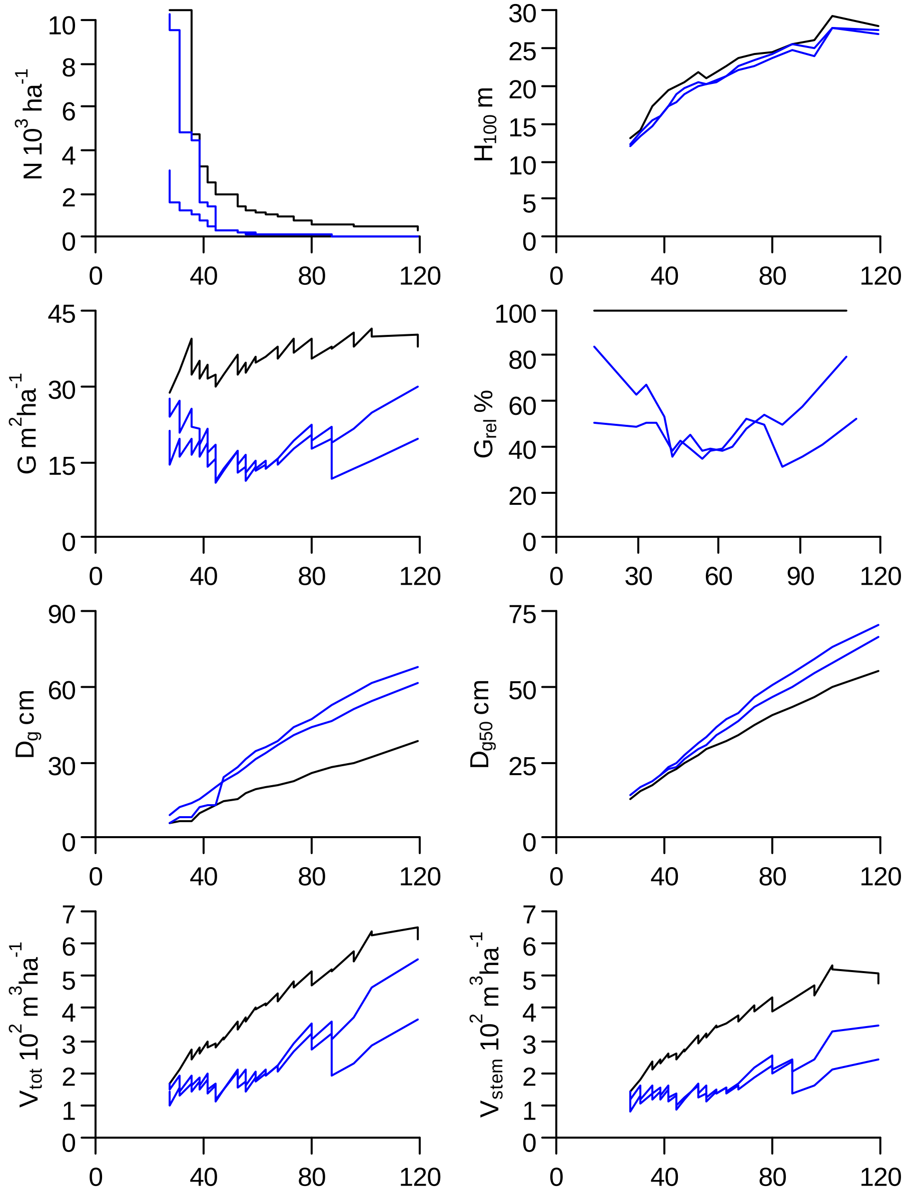

Figure A10. QD Ganneskov.

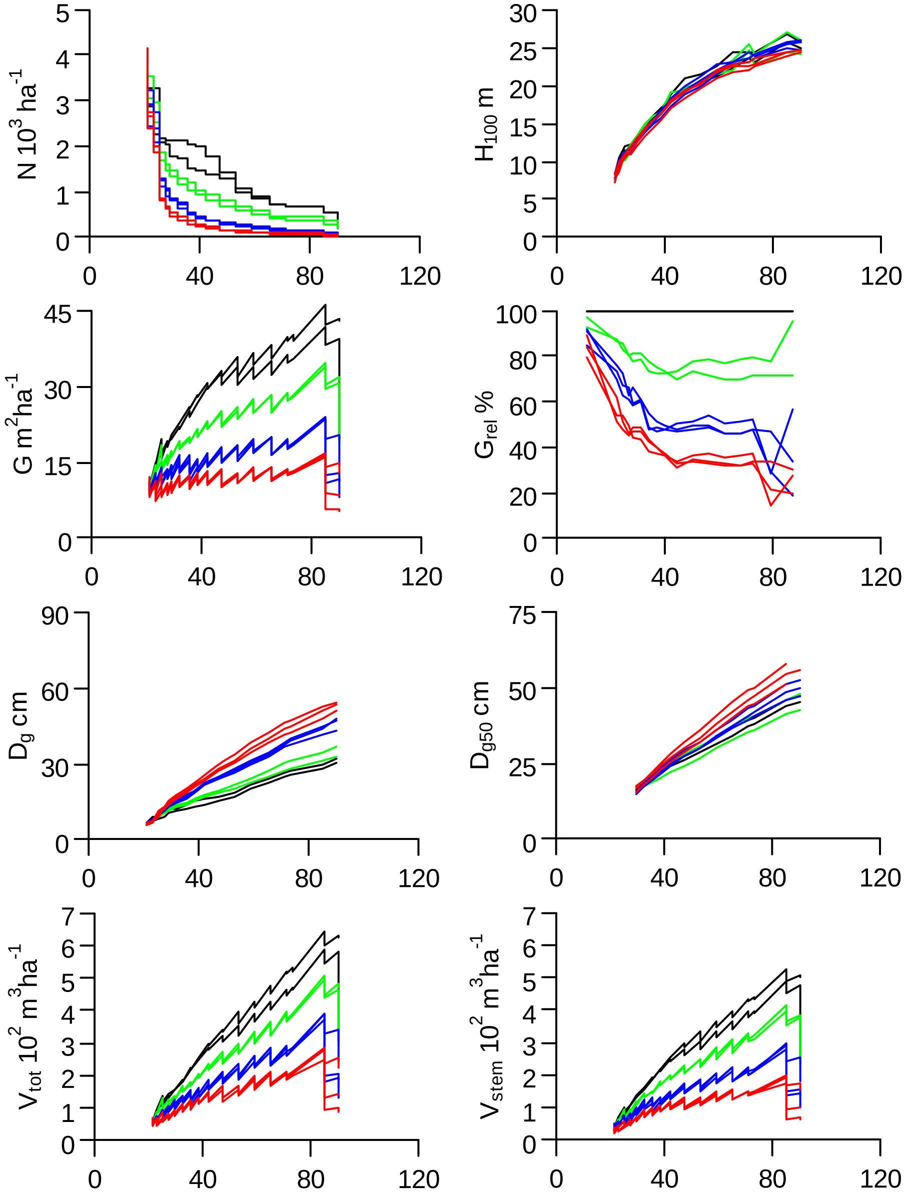

Figure A11. QX Grevindeskoven.

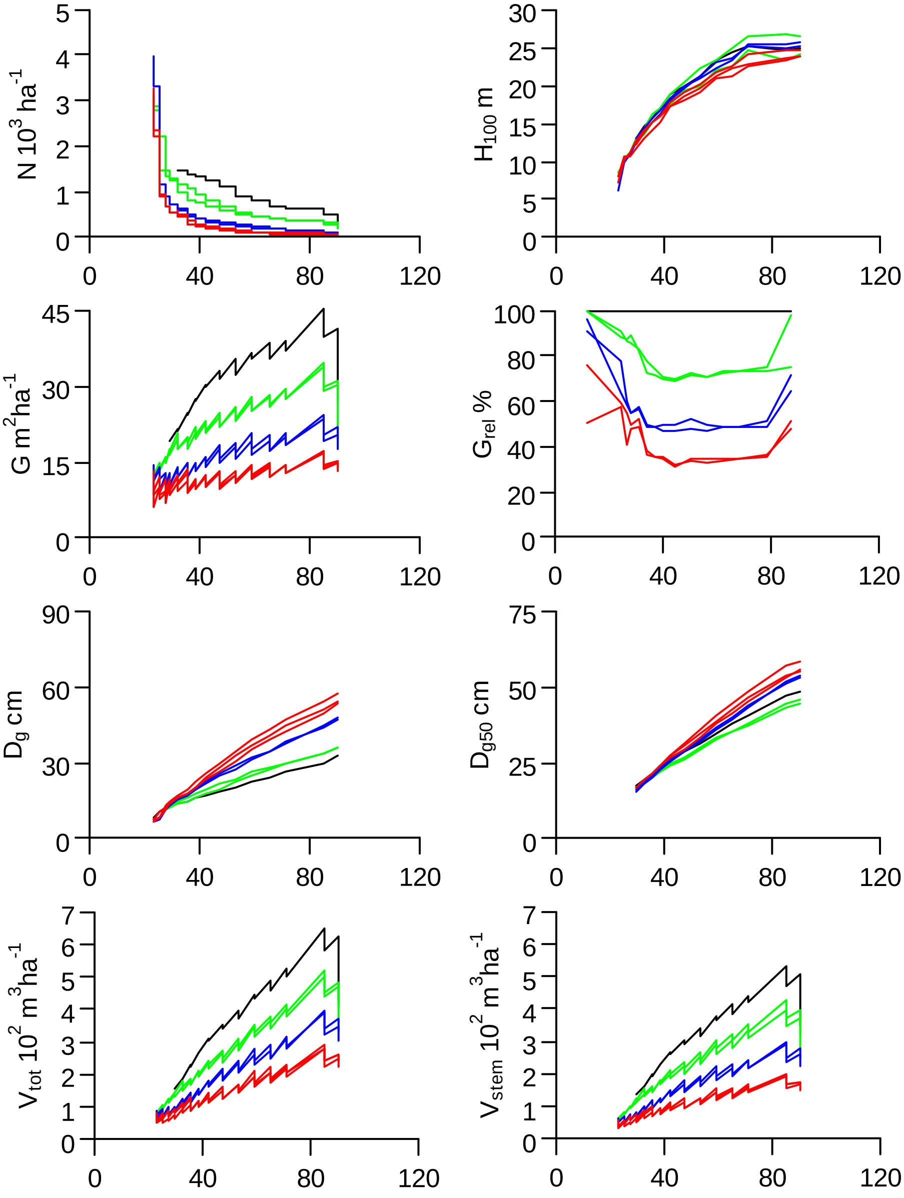

Figure A12. QY Grevindeskoven.

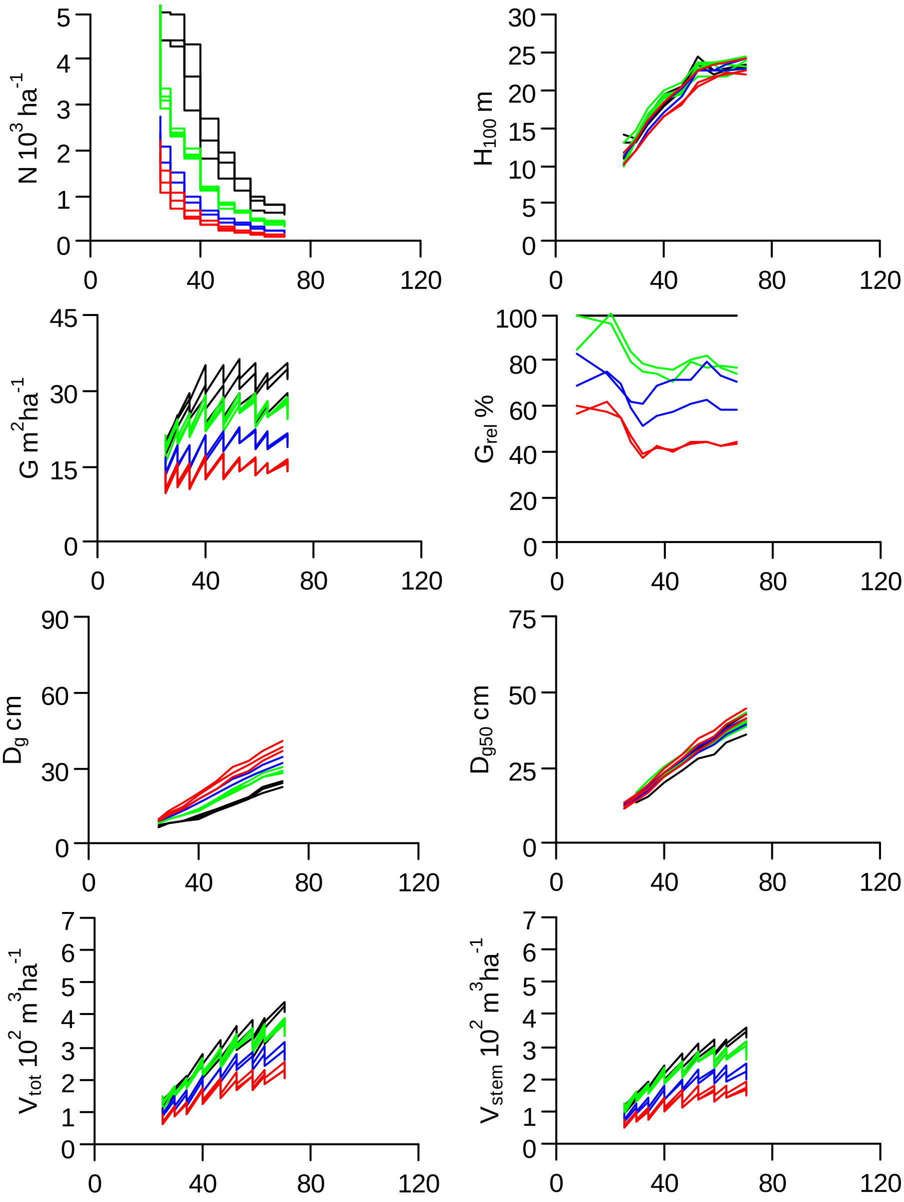

Figure A13. RA Grib Skov.

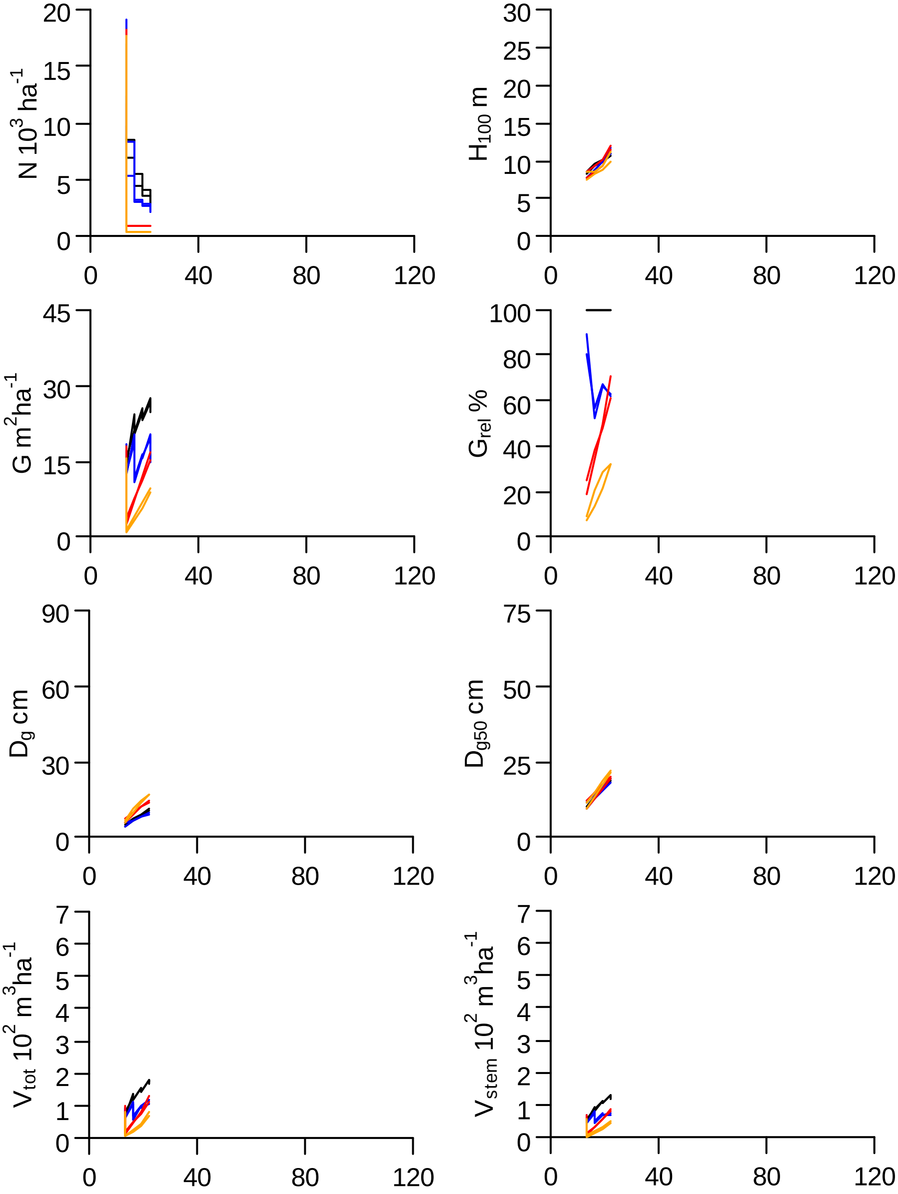

Figure A14. 1516 Haslev Orned.

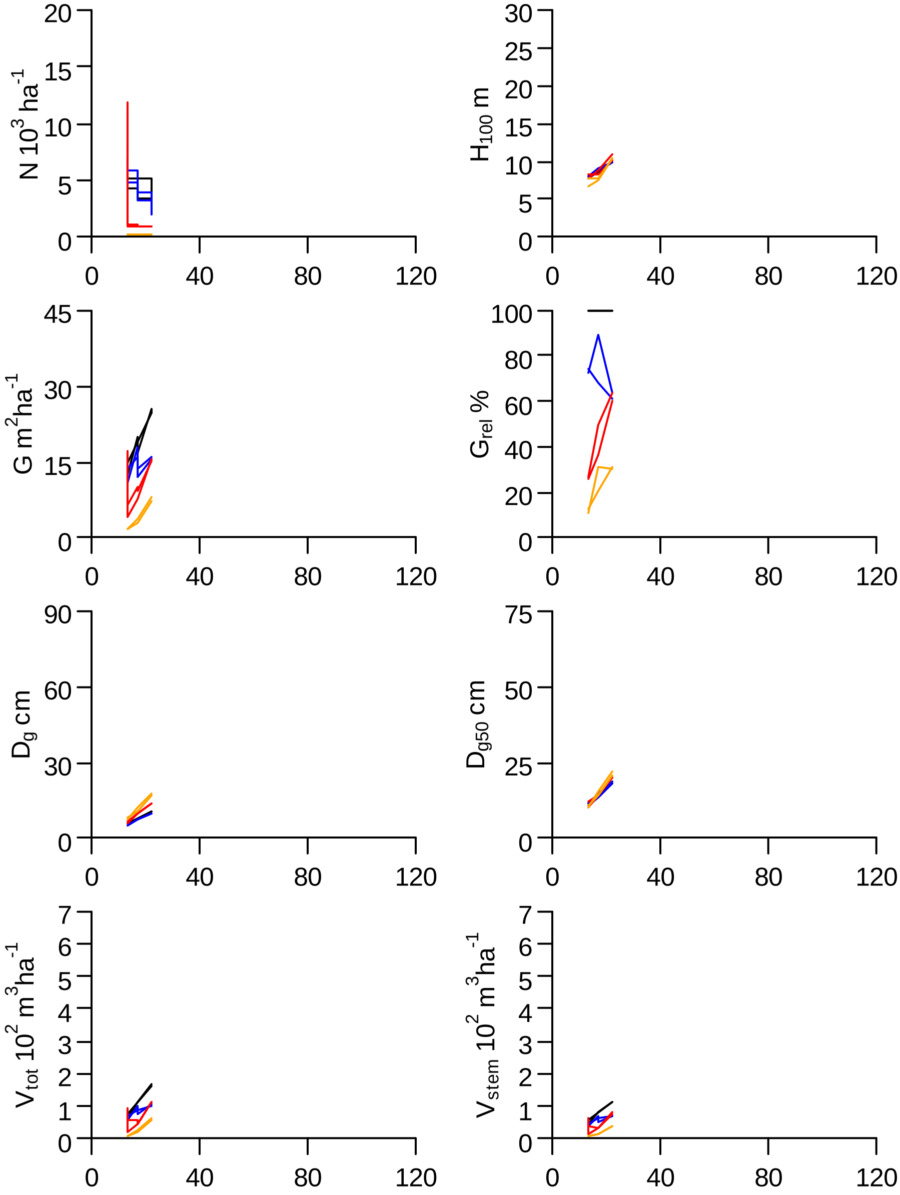

Figure A15. 1517 Brendstrup Skov.

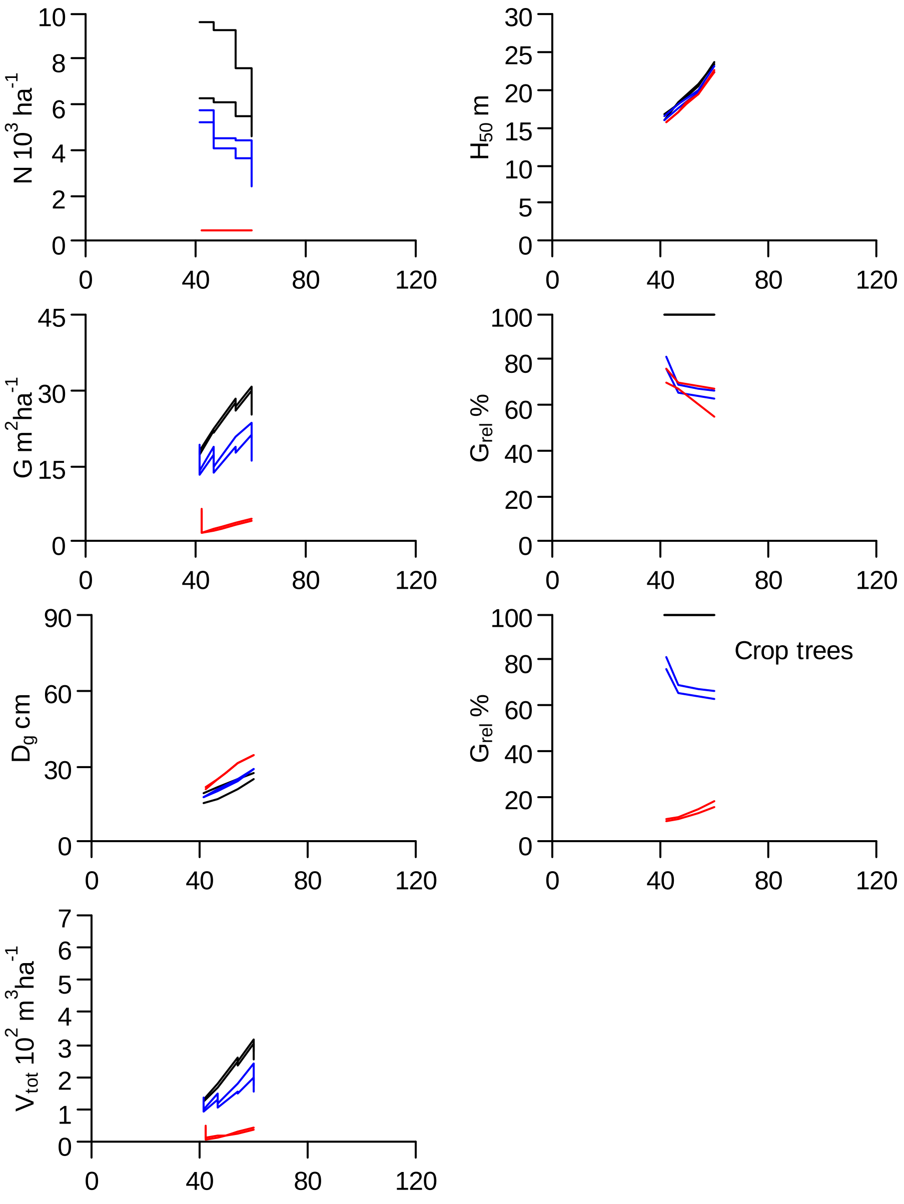

Figure A16. 8800 Skarhult.

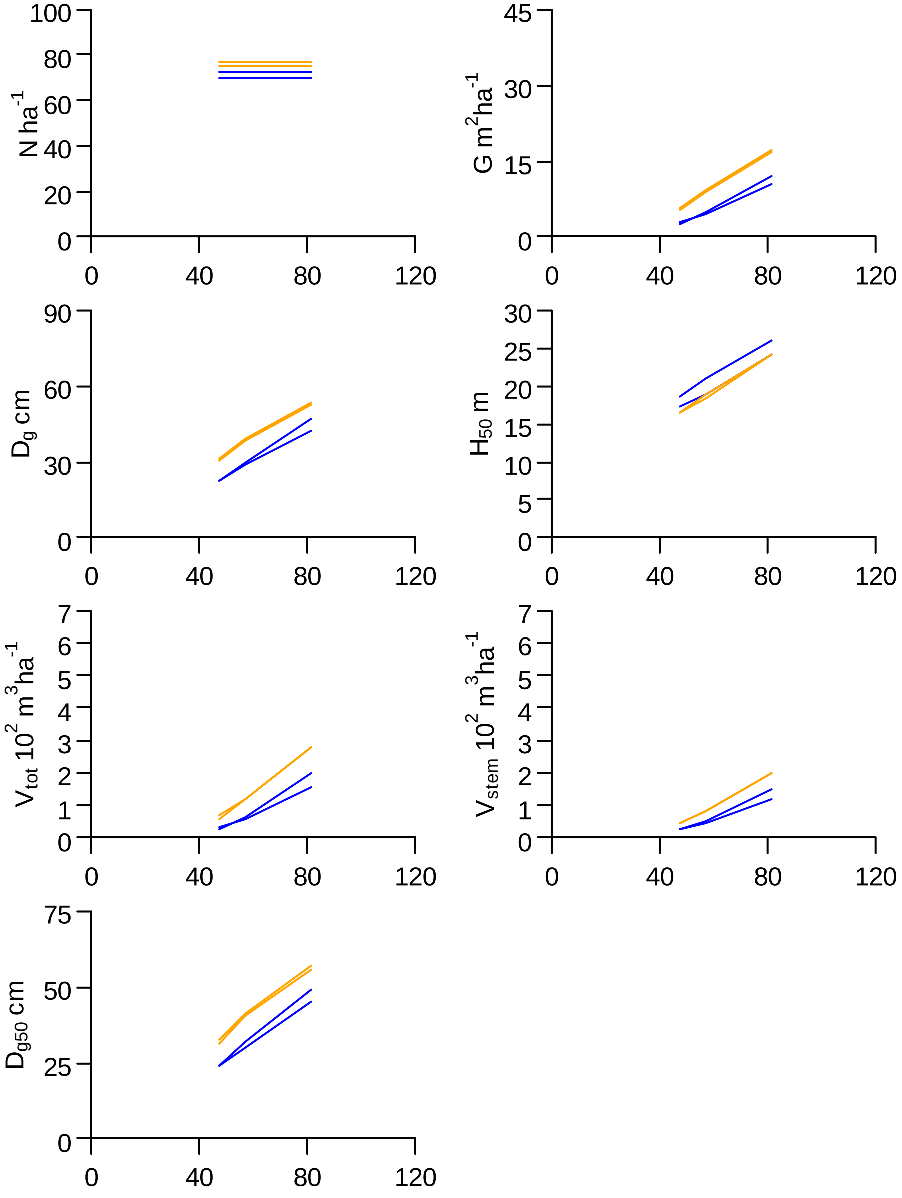

Figure A17. Crumbland 7 Tintern Forest.

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