Regeneration dynamics of pedunculate oak in natural temperate forests: a case from southern Sweden

Olle Finnström
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Supervisor: Jörg Brunet, SLU Southern Swedish Forest Research Centre
Examiner: Matts Lindbladh, SLU Southern Swedish Forest Research Centre

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Abstract

Oaks are some of the most wide-spread and iconic trees in human culture, yet populations of oaks are declining due to land conversion, disease and because of lack of disturbance in temperate forests. Oaks are fairly light demanding trees, requiring large-scale disturbance to create suitable environments for regeneration. After germination, light availability is a key factor for the survival and growth of oaks. This is largely determined by competing vegetation. Responses to competition can be complex, as surrounding vegetation can hamper the development of oaks, but could also benefit young oaks by improving microclimate and reducing browsing pressure. This study aimed at investigating principal threats and opportunities of advanced oak regeneration (>1.3 m height) in the national park of Dalby Söderskog, southern Sweden, after recent outbreaks of Dutch elm disease and Ash dieback. Historic records along with recent inventories provide useful information in determining the status of the oak population. Measurements on plant- and crown size of oak regeneration were compared with data on the abundance of competing trees and shrubs and to the level of encroachment by competing stems. Browsing pressure and fraying damage from ungulates was also registered.

Results demonstrate that disease outbreaks can have similar effects as other large-scale disturbances such as storms, grazing or fire in terms of creating beneficial conditions for regeneration of pedunculate oak. The subsequent establishment of trees and shrubs will however influence the health and development of young oaks. The length of the green crown, crown diameter, diameter at breast height (Dbh) and total plant height of young oaks decreased with an increasing number of competing stems within a 2 meter radius. Crown encroachment also had a significant effect, as crown size and Dbh were severely affected for plants that were overtopped by competing stems. In the case of height development, plants that were completely encroached by competing stems without the disadvantage of being overtopped were taller than plants that were free growing, partially encroached, or overtopped. Both inter- and intraspecific competition had negative effects on the development of oak saplings. Beech, hawthorn and hazel had comparatively large effects, while effects of elm and oak were moderate and ash induced the least negative effects. Animal induced damages had only minor effects on the health and survival of oaks.

Keywords: Eutrophic temperate mixed broadleaf forest, competition, crown size, disturbance, oak regeneration, pedunculate oak, *Quercus robur*, stem diameter, tree height

Sammanfattning

Eken är ett av de mest spridda och ikoniska träden, trots detta minskar ekpopulationer globalt på grund av ändrad markanvändning, sjukdomar och till följd av minskad störningsgrad i tempererade skogar. Ekar är ljuskrävande och behöver storskaliga störningar för en lyckad spridning och etablering. Efter groning är mängden tillgängligt ljus en avgörande faktor för ekplantornas överlevnad och vitalitet och detta avgörs till stor del av konkurrens från andra träd och buskar i undervegetationen. Effekterna av konkurrens är komplexa då konkurrerande stammar kan påverka ekarnas utveckling och tillväxt negativt, men å andra sidan gynna dem genom att förbättra mikroklimatet och skydda mot bete. Denna studie ämnar undersöka hot och möjligheter för ekföryngring (>1.3 m höjd) i nationalparken Dalby Söderskog, Skåne, efter utbrott av almsjuka och askskottssjuka som skapat nya, öppna miljöer. Många årtionden av tidigare studier kan tillsammans med nya data ge en bild av tillståndet för denna ekpopulation. Värden för plant- och kronstorlek samlades in för all ekföryngring och jämfördes med data kring förekomst av konkurrerande av träd och buskar, samt med hur trängda ekarnas kronor var. Även information om betes- och fejningsskador analyserades.

Resultaten visar att störning orsakad av sjukdomar kan ha motsvarande effekt som andra storskaliga störningar, som exempelvis storm, bete eller brand när det gäller att skapa förutsättningar för lyckosam ekföryngring. Etablering av andra träd och buskar påverkade däremot ekarnas vitalitet och tillväxt negativt. Ekarnas kronlängd, krondiameter, diameter vid brösthöjd (Dbh) samt totala höjd minskade med ökande förekomst av konkurrerande stammar inom två meters radie. Graden av intrång i ekens krona från konkurrerande stammar hade också stor effekt då kronans storlek samt Dbh påverkades mycket hos plantor som var överväxta. Angående höjd visade det sig att plantor som var helt omringade men utan att vara överväxta, var högre än plantor som var friväxande, delvis trängda eller överväxta. Både konkurrens mellan arter, samt konkurrens mellan ekar hade en negativ effekt på ekplantornas utveckling. Bok, hagtorn och hassel hade jämförelsevis stor negativ effekt, medan effekterna av alm och ek var jämförelsevis måttliga och ask hade minst negativ effekt. Skador orsakade av bete och fejning hade tämligen liten påverkan på ekarnas hälsa och överlevnad.

Nyckelord: Näringsrik tempererad ädellövskog, brösthöjdsdiameter, ekföryngring, höjd, konkurrens, kronstorlek, *Quercus robur,* skogsek*,* störning

Contents

Introduction

Oak ecology

Oaks (*Quercus spp*.) are recognized as some of the most iconic trees in human culture (Savill, 2013), having a highly prized wood and a distinctive importance in history of providing means of subsistence for people throughout their natural range (Johnson *et al.*, 2002). The existence of large, mature oak trees is one of the most familiar attributes in many temperate forests (Smit *et al.*, 2012; Götmark *et al.*, 2011; Lorimer *et al.*, 1994). Oaks are also essential for biodiversity conservation in many areas, as they support a great variety of organisms and many animal populations depend on annual supply of acorns (Schmidt, 2003; Johnson *et al.*, 2002). Animals such as jays and mice also help with the dispersal of acorns, facilitating the establishment of new oaks (Smit *et al.*, 2012; Vera, 2000). Old or ancient oaks with coarse bark and stem cavities are especially important for sustaining populations of invertebrate animals, fungi, lichens and bryophytes (Bruun *et al.*, 2011; Ranius *et al.*, 2009). In Sweden alone, oaks may host as many as 1500 species (Leonardsson, 2015), many of which are red-listed (Sandström *et al.*, 2015).

The most prominent and widely spread of the European oaks are pedunculate oak (*Quercus robur L.*) and sessile oak (*Quercus petraea L.*) which are also the only species of oak that occur naturally in Sweden. In Sweden, oak is the most common of the noble broad-leaved tree species, constituting 1.2 % of the total volume and, of the two species, pedunculate oak is by far the most common. Oaks inhabit a wide spectrum of site conditions; from dry acid soils, regularly regenerating in pine stands (Löf *et al.*, 2009), to wet base-rich soils and riparian forests. Sessile oak is commonly found in a mild climate, often on slightly drier soils while pedunculate oak expands to a more northern and continental distribution. In addition, pedunculate oak will grow in wetter conditions than sessile oak, even withstanding occasional flooding (Ellenberg, 1988). In a silvicultural context, oaks are known as a tree species also suitable for heavy clay soils, sites otherwise known to be difficult in terms of timber production (Löf *et al.*, 2009). Even though oaks will grow in most conditions - and certainly on nutrient-rich, well-drained sites - their natural distribution is often limited to sites of more extreme character due to the occurrence of competing tree species. European beech (*Fagus sylvatica* L.) is a strong competitor, and east of its range in Europe the lime-hornbeam dominance (*Tilio-carpinetum*) is recognized as a limiting factor (Bobiec *et al.*, 2011a; Ellenberg, 1988).

Oaks are considered to be mid-successional and moderately shade-tolerant species (Annighoefer *et al.*, 2015; Götmark & Kiffer, 2014; Kuehne *et al.*, 2014) and successful regeneration of oak requires large-scale disturbances (Götmark & Kiffer, 2014; Bobiec *et al.*, 2011b; Götmark, 2007). Historically, oak-rich areas have been characterized by a semi-open structure and relatively high frequency of disturbance. Oaks distinguish themselves from other broadleaves by being fairly resistant to fire, and recurring fires has been a key factor in maintaining oak-rich habitats (Paltto *et al.*, 2008; Niklasson *et al.*, 2002). Similar patterns have been found in North America where active burning of woodlands was an effective tool of managing oak woodlands (Aldrich *et al.*, 2003; Johnson *et al.*, 2002). Grazing and browsing by wild animals such as aurochs, wild horses, European bison, and later by domestic cattle, has been pointed out as another important disturbance agents in such environments (Nilsson *et al.*, 2005; Vera, 2000).

Oak decline and regeneration issues

Many areas that were previously populated with oaks, such as wooded pastures, have been converted into agricultural land or coniferous forest, in particular during the past three centuries (Lindbladh & Foster, 2010; Ståål, 1986) and today, oak-rich forests with old and mature trees are scattered and partly confined to low-productive areas (Ranius *et al.*, 2009). The subsequent absence of disturbance in many oak woodlands has led to the establishment of late successional tree species and a shift into a denser canopy structure (Aldrich *et al.*, 2003; Niklasson *et al.*, 2002). Oak regeneration in broadleaved forest dominated by shade tolerant species is often very limited or completely absent. Hence, oaks are seldom viewed as climax species under natural conditions of forest succession (e.g Savill, 2013; Aldrich *et al.*, 2003; Vera, 2000; Ellenberg, 1988). In addition, the phenomena often referred to as "oak decline" is causing damage on oak populations across the European continent. The degeneration of such trees is believed to be an interaction between pathogens, pollution and climatic events such as drought (Barklund, 2002).

The rate of disturbance in closed canopy temperate broad-leaved forests is normally low, with a mortality rate of 0.5 – 3 % (Wolf *et al.*, 2004). In a study by Drobyshev *et al.* (2008) the annual tree mortality in oak forests in southern Sweden was on average 1.7 % and even lower (1.1 %) for forests older than 200 years. However, in forests with a tree density over 100 trees per hectare mortality was 3.2 %. Light levels in closed-canopy forests may be as low as 1 % of full daylight (Dey & Parker, 1996). Oak seedlings appear to require light levels of at least 20 % of full daylight in order to avoid severe growth depression (Ligot *et al.*, 2013; Johnson *et al.*, 2002; Dey & Parker, 1996; Ziegenhagen & Kausch, 1995). European Beech (*Fagus sylvatica* L.) only require half that amount of light to ensure successful growth (Ligot *et al.*, 2013). Disturbance regimes in such forests are density-dependent mortality (self-thinning), senescence of old trees, or stochastic events such as gap formation during storms or disease outbreaks (Drobyshev *et al.*, 2008; Wolf, 2005). Large-scale disturbances such as storms can however increase oak regeneration (Götmark & Kiffer, 2014; Aldrich *et al.*, 2003). In a wind-thrown stand in Southern Sweden, oaks managed to survive both browsing and competition from pioneer- and secondary tree species and became a co-dominant tree species, although at a relatively low density (Götmark & Kiffer, 2014). Tree disease outbreaks are becoming more frequent and can initiate successional changes in forest ecosystems (McCormick & Platt, 1980). Two relatively recent outbreaks in European broad-leaved forest that are currently affecting species composition and biodiversity are Dutch elm disease (Peterken & Mountford, 1998) and Ash dieback (Pautasso *et* *al.*, 2013). Active thinning and creation of canopy gaps may however be an alternative to increase survival and growth of oak seedlings and ensure continuity of oak-rich forests and survival of the many organisms that depend on them (Leonardsson, 2015; Ligot *et al.*, 2013).

The preservation of oak-rich habitats also faces other issues besides from the lack of light in closed-canopy broad-leaved forests. Seed predation, especially from birds, rodents and wild boar, can severely affect the potential for oak regeneration (van Ginkel *et al.*, 2013). Regeneration of oak is correlated with occurrence of large oaks in the surrounding area, demonstrating the importance of seed sources nearby (Annighoefer *et al.*, 2015; Götmark & Kiffer, 2014) and regeneration is often random due to animal dispersal. Also, oak is a preferred species among browsing ungulates. Intense browsing is a serious threat against young oaks, reducing growth and health of the plants (Bobiec *et al.*, 2011b; Götmark *et al.*, 2005a).

Oaks and competition: benefits and drawbacks

While canopy openings created by storms, disease outbreaks and selective thinning may lead to an increase in oak regeneration, they are also likely to increase growth of other plants, including herbaceous ground vegetation and woody trees and shrubs, especially in nutrient-rich sites (Annighoefer *et al.*, 2015; Götmark *et al.*, 2011; Löf & Welander, 2004). Oak seedling occurrence responds negatively to occurrence of other trees and shrubs (Götmark *et al.*, 2011) as well as to a dense herbaceous ground vegetation (Jensen *et al.*, 2011). An increase in the growth of understorey species can reduce or neutralize growth and survival of oaks and other tree species that are sensitive to competition (Beckage *et al.*, 2005). Surrounding trees and shrubs may increase competition for light as well as for water and nutrients (Jensen *et al.*, 2012c).

Crown size is an indicator of the growth potential of trees as it is correlated to the photosynthetic capacity. It therefore holds a key significance in determining the development status of oaks. Crown diameter is also closely connected to the stem diameter of oaks, and the two variables normally have a positive relationship (Attocchi & Skovsgaard, 2015). Diameter increment of oaks can however be heavily affected by competition (Saha *et al.*, 2012). Competition may also lead to decreasing height growth. Shade-bearing species can be particularly strong competitors and can decrease height growth of young oaks, especially oak seedlings that are overtopped by such species are likely to suffer from growth depression (Ligot *et al.*, 2013; von Lüpke, 1998). Overall, strong competition from woody and herbaceous vegetation is likely to decrease total biomass of young oaks (Jensen *et al.*, 2011).

Oaks can however respond positively to a moderate degree of competition, and there are signs that seedlings growing in close proximity to other woody vegetation will be taller than other plants (Jensen *et al.*, 2012c; Götmark *et al.*, 2011). Heavy thinning in oak stands can even result in reduced height growth (Attocchi & Skovsgaard, 2015). Occurrence of woody vegetation can promote oaks by decreasing herbaceous ground cover (Jensen *et al.*, 2011). Although the effect was found to be short-term, the planting of undergrowth species or trainer trees is a well-known method to decrease competition from ground vegetation and brambles and to improve microclimate in production stands of oak. Shade-bearing species with dense crowns such as lime (*Tilia cordata* Mill.), hornbeam (*Carpinus betulus* L.) and beech (*Fagus sylvatica* L.) are often used but do need monitoring if not to outcompete the oaks (Saha *et al.*, 2012). Also hazel (*Corylus avellana* L.) is used for similar purpose, for casting shade, preserving moisture and improving soil properties (Ståål, 1986). Trees and shrubs growing in association with oaks can decrease browsing intensity on oak plants (Götmark *et al.*, 2005a). This interaction, called "associational assistance", has been suggested to have played a substantial role in facilitating oak establishment in pre-historic grazed areas where now extinct animal species like aurochs and European wild horses were frequent, and later in pastures with domestic cattle (Vera, 2000).

Biological adaptations and shifting threats

Oaks have the ability of producing more than one flush of growth during a single growing season if conditions are favourable (Johnson *et al.*, 2002; Ståål, 1986). This behaviour of periodic growth means that oaks can have several alternating stages of shoot elongation followed by a resting period with formation of a new terminal bud. However, under natural conditions growth is usually restricted to only one or two flushes of growth (Collet *et al.*, 1997). This ability can enable young trees to acclimatize to changes in light availability, which is exhibited through morphological and physiological adaptations during the formation of new shoots and leaves. It can result in seasonal variations in terms of light gathering abilities and photosynthetic capacity (Jensen *et al.*, 2012a). For instance, oak seedlings can respond to competition by shoot elongation and increasing the individual leaf area, resulting in an overall increased stem to root ratio (Ziegenhagen & Kausch, 1995). The leaf area of oaks is however comparatively low under shaded conditions, partly due to lower nitrogen use efficiency (Niinemets, 1998) and relative to several other broad-leaved species in the European temperate zone, pedunculate oak photosynthesizes less efficiently under low and medium light conditions. This makes it sensitive to competition from more shade-tolerant species (Kuehne *et al.*, 2014).

Growth requirements of oaks change during the course of their development, as do the most important obstacles and threats to young oak trees. Light is not a requirement for germination (Ligot *et al.*, 2013) as seedlings largely rely on energy from the acorn during the first season. Therefore large amounts of seedlings can initially be found under unfavourable light conditions (Annighoefer *et al.*, 2015). Soil water content can however affect seedling survival (Götmark *et al.*, 2011) and the need for light rapidly increases. Where there is no disturbance, most seedlings quickly succumb due to light deficiency (Annighoefer *et al.*, 2015). Risk of browsing increases as the seedlings grow taller. Saplings above the height of 50 cm are more likely to be browsed than smaller specimens (Annighoefer *et al.*, 2015; Bobiec *et al.*, 2011b; Götmark *et al.*, 2005a).

Light requirements increase as oaks grow older and larger, becoming the single most important factor for saplings above breast height (>1.3 m). Accordingly, a dense overstorey will prevent establishment and growth of young oaks, especially when constituted by species other than oak (Annighoefer *et al.*, 2015).

Study aim

The scope of the study is on the effects of inter- and intraspecific competition on the physical development of oak regeneration. An inventory was conducted to collect measurements on the size of oak saplings along with data on the abundance of competing woody vegetation and its encroachment on the oaks. This will be the basis for the investigation. In addition, data on fraying damage and browsing were collected to examine the significance of animal induced damages.

Specifically, the following hypotheses were tested:

1) Competition from woody trees and shrubs will negatively affect the crown size of young oaks.
2) Severe competition will negatively affect the height- and diameter growth of young oaks.
3) Plant height of oaks will show a positive relationship to a moderate occurrence of competing trees and shrubs.
4) Shade-tolerant species are more severe competitors than light-demanding species.

This study can be viewed as a step towards understanding threats and opportunities of oak regeneration following severe disturbance and forest succession in a European temperate broad-leaved forest. The long history of research in the study area, Dalby Söderskog in southern Sweden, offers a convenient opportunity of relating new results to historic records of forest development in a time when the issue of insufficient oak regeneration is a major challenge for conservation in temperate ecosystems. Results could potentially also be of use in production forestry as crown development is a key factor for determining management operations in broad-leaved stands.

Material and methods

Study area

The study was carried out in Dalby Söderskog (55°41´N, 13°20´E), a forest reserve of 37 ha located close to Dalby village, about 10 km east of Lund in the county of Skåne, southern Sweden. The history of Dalby Söderskog is rather well recorded (Lindquist, 1938). The forest has most likely been at least partly covered by trees for many centuries. Records of a semi-open environment with large trees, mostly oak and beech, exist from the beginning of the 14th century. To the north, the forest is connected to an area of open semi-natural pastureland continuing into a wooded pasture dominated by oaks. Since medieval times, horse keeping in the nearby Dalby Monastery, which was later on converted into a royal estate, resulted in the area being subject to grazing. The intensity of grazing has varied, with short periods of extensive use and at other times being irregular or even absent. The grazing eventually stopped completely in the end of the 19th century. Partial cuttings have also occurred sporadically for centuries, and continued even after the grazing had stopped. A series of cuttings from 1914–1916 arose awareness among botanically interested groups, which ultimately led to the forest being established as a national park in 1918. Following the establishment of the national park, a debate was present about what type of management should be assigned to the forest. Early on it was pointed out that with no active management there was a severe risk of a shift from the relatively open oak-rich woodland that was so characteristic for the area, into a dense elm- (and beech-) dominated forest (Lindquist, 1938). However no such management was undertaken, and to this day the forest is largely subject to natural development. Dalby Söderskog has however been the subject of extensive ecological studies, especially with investigations of changes in understorey plant- and tree species composition (Brunet *et al.*, 2016; Brunet *et al.*, 2014).

The study area is characterized by a maritime climate with an annual mean temperature of 7.5 C° and annual an precipitation of 650 mm (Brunet *et al.*, 2014). The mineral soil is of glacial origin (Baltic moraine) and consists of calcareous clay, and the humus type is a mull (Malmer *et al.*, 1978). Apart from the grassland to the north, the forest is mostly surrounded by agricultural land and is considered to be situated in a particularly productive area. The soil is generally moist or wet, apart from the slightly more well-drained slopes that surround a small stream in the southwestern part of the forest. During winter and spring, surface water may be visible in depressions throughout the area (Malmer *et al.*, 1978; Lindquist, 1938). Several of the major European broad-leaved tree species are represented in Dalby Söderskog. Pedunculate oak *(Quercus robur* L.*)*, European ash *(Fraxinus excelsior* L.*)*, European beech *(Fagus sylvatica* L.*)* and wych elm *(Ulmus glabra* Huds.*)* are the most dominant species in the canopy, although several other species occur (Lindquist, 1938). The forest is also home to a number of threatened species of bryophytes, fungi and saproxylic beetles (Brunet *et al.*, 2014). Large mammals in the area include wild boar (*Sus scrofa* L.), roe deer (*Capreolus capreolus* L.) and fallow deer (*Dama*

dama L.). The shrub flora is rich and varied, but typically consists of hazel (*Corylus avellana* L.), and species of hawthorn (*Crataegus spp*.) together with the regeneration of multiple tree species. The rich ground vegetation is one of the most distinctive characteristics of the forest, especially the vernal flora with holewort (*Corydalis cava* Mill.) and species of *Anemone spp*. Later in the season, species such as dog's mercury (*Mercurialis perennis* L.), wood avens (*Geum urbanum* L.) and yellow archangel (*Lamium galeobdolon* L.) are common (von Oheimb & Brunet, 2007), although several herbaceous species are now being reduced in abundance due to increasing populations of wild boar and the invasive Spanish slug (*Arion vulgaris* Moquin Tandon) (Brunet, 2015).

Previous studies in Dalby Söderskog

Surveys of the forest have been carried out at several occasions since the establishment of the national park. Brunet *et al.* (2014) reconstructed the 74 permanent sample plots that had been used in previous inventories by Lindquist (1938) and compared the new data with previous studies in order to investigate successional changes over time. The results showed that the total basal area increased by 70 % from 1916 to 1970. Elm had increased the most and was the most common species measured in basal area for trees in small and medium size classes. Regeneration of the remaining tree species, including beech, declined or remained at a low level. Regeneration of oak was completely absent, and high mortality rates decreased the number of mature oaks. In contrast, the basal area of oak, beech and ash increased slightly during this period due to growth from existing trees in the canopy. However, the situation soon changed due to the outbreak of Dutch elm disease in 1988. The population of elms crashed and by 2011 it had the smallest share of basal area among the four major species. Instead, ash had become the most common species in both basal area and number of stems, frequently filling gaps created by fallen or standing dead elms. At this point however, ash dieback had begun to spread through the forest, damaging and killing trees. Ash dieback can affect trees of all sizes, and the mortality of young ash trees infected by the disease is high (Pautasso *et al.* (2013).

In addition, Brunet *et al.* (2014) concluded that elm had been confined to the shrub layer, where it survived as shrubs or small trees, a phenomena also found by Peterken and Mountford (1998). Meanwhile, the population of large oaks in Dalby Söderskog continued to decline and was at a density of 17 trees per hectare in 2011. In contrast, oaks were regenerating once more, and a total number of 455 young oaks with a height >1.3 m were recorded in 2012. Also, the number of small oak seedlings had increased. Some shrub species, mainly hazel and hawthorn, were also showing increased establishment and growth. The large-scale disturbances caused by Dutch elm disease and Ash dieback also seemed to benefit beech ingrowth, especially from increased growth of advanced regeneration. In conclusion, the development of Dalby Söderskog before the outbreak of Dutch elm disease showed a clear advantage to shade-tolerant species, and a shift into a denser canopy structure. Subsequently, the near extinction of large elms seem to have benefited several other tree species, and most notably light demanding species such as ash and oak.

Besides from presenting data on forest structure, Lindquist (1938) also summarize extensive historical information on the development of the forest since medieval times, and most importantly information concerning the population of large oaks. The origin of the mature oaks in Dalby Söderskog today can be traced back to a very limited number of regeneration pulses in history. There are records of three such occasions when oaks have, on a larger scale, successfully regenerated and contributed to formation of the dominant tree layer during the past five centuries. The first one was in the late 16th century after a heavy cleaning of hazel. The second one was during the Great Northern War in the beginning of the 18th century when the area was subjected to heavy grazing as well as cuttings, and the third was after a series of cuttings in the beginning of the 19th century. Most of the trees that now form the oak population in this forest originate from the latter two of these regeneration pulses.

Data collection

A complete inventory of oak regeneration in Dalby Söderskog was conducted in 2015. Two separate surveys were done. The first one spanned from February to April, before the vegetative season, and the second one in September, after the vegetative season.

All oaks with a total height of 1.3 m (breast height) or more and a diameter at breast height (Dbh) of less than 20 cm before the start of the vegetative season of 2015 was recorded and measured along with variables concerning competing vegetation, health and quality (Table 1). A handful of trees that had reached 1.3 meter or more in the second round of the inventory were excluded as they had only reached breast height with the help of the most recent terminal shoots. For all oak individuals, alive or dead, measurements for plant- and crown size were collected. In the case of dead oak plants, measurements for height of lowest living branch were redirected to whichever branch was located furthest down. Concerning the inventory of competing vegetation, two separate variables were collected (Table 1). The first one was notification of all living woody plants within a radius of two meters from each measured oak and reaching at least equal height as this focal oak. However the number of stems alone may not provide sufficient information on the effects of competition as the size of nearby plants and the degree of their intrusion may vary. Therefore, a second variable was collected, consisting of an estimation of crown encroachment. Collectively, this data can provide a better estimate of the effects from competing vegetation.

Table 1. *Variables that were collected from all oak plants taller than 1,3 m in Dalby Söderskog during the inventories in 2015.*

Variable	**Definition**	**Unit/Classification**
Position	Latitude/longitutde	RT 90
Diameter (Dbh)	Stem diameter at breast height (1,3 m)	cm
Height	Total plant height, rounded off to closest half meter	m
Crown diameter	Diameter of the crown at the widest point	dm
Height of lower branch	Height where the lowest living branch is positioned	dm
Competing stems	Number of living woody shrubs/trees within 2 m radius and of at least equal height as the oak, separate for each species and as sum of all species	numeric
Crown encroachment	Classification of encroachment from competing stems	1: free growing, 2: partial encroachment on at least one side, 3: encroachment on all sides except from above, 4: overtopped (encroached from above)
Fraying damage	Classification of the level of damage caused by fraying	1: no damage, 2: older wound (healed), 3: partial damage, 4: ring barked
Bonsais	Heavily browsed oak that has developed many side shoots, of which at least one has reached breast height (1,3 m) or more	yes/no
Dead oaks	Notification of dead oak plants	dead

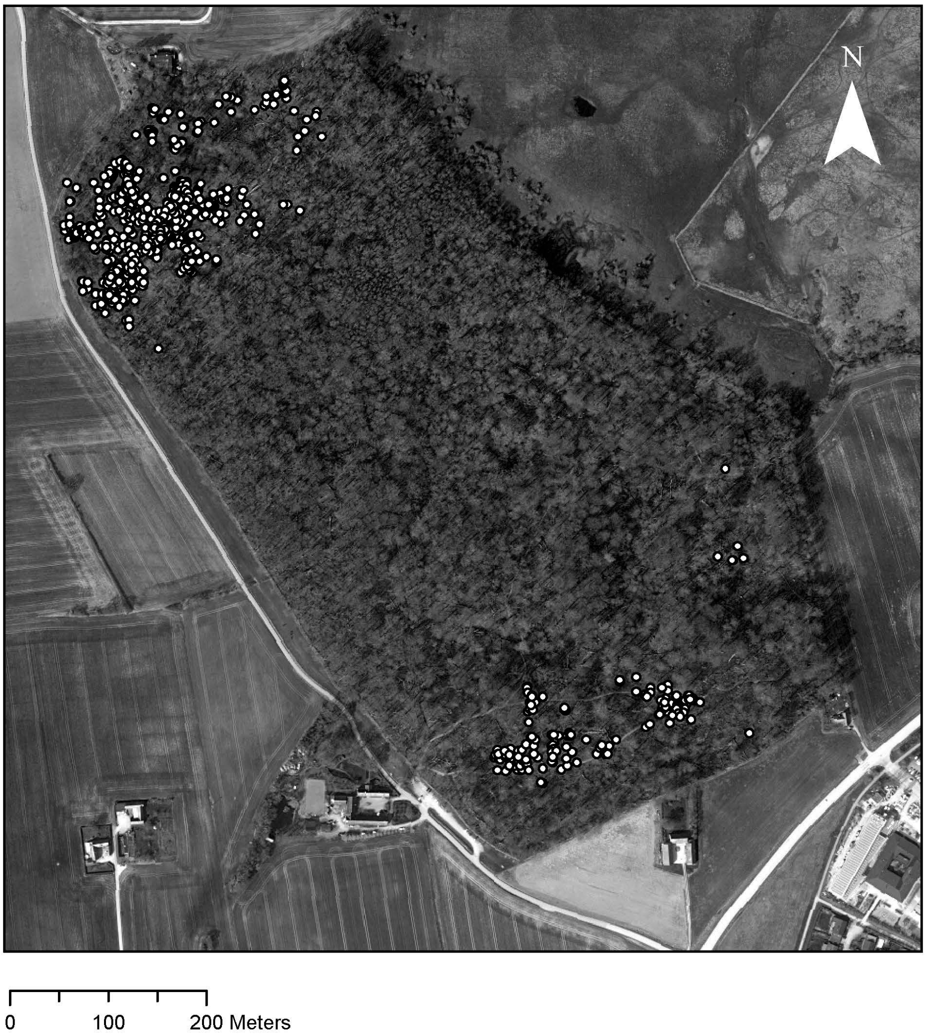

Figure 1. *Aerial photograph of Dalby Söderskog with markings of all oak saplings recorded during the inventory of 2015 (© Lantmäteriet i2014/764).*

Data analysis

Data for several of the measured variables were first analyzed through descriptive statistics. Oak regeneration was summarized into classes for height- and diameter distribution. For diameter, one-centimeter classes were used. For height, the half-meter classes used in the inventory were applied again to describe the height distribution. Frequency of competing stems of all species was summarized to enable further analysis of inter- and intraspecific competition in the forest. In order to investigate potential effects of competition on the vitality and development of the oak regeneration, measurements for plant height, encroachment of the crown and crown size were used in the statistical analysis. The crown length, or length of the green crown, was calculated for each tree by using data for total plant height and height of the lowest living branch. The variable produced can be used as a measurement for describing the effect of competition on plant size and vitality.

Statistical analysis was conducted to derive more detailed information about interactions and relationships between different variables. Although based on a total population sample, these analyses can provide valuable information concerning variation and extreme values within groups. P-values derived from standardized tests provide further information concerning the strength of relationships, and permutation tests are likely to produce similar results (A P-value example, 2008). Basic relationships between tree size variables were established with regression analysis. In the analysis on the effects of competing stems, data for the most common species was used. This was to ensure comparability of effects between different species. Measurements for height, length of crown and crown diameter were compared to the frequency of competing stems. Both the total number of stems as well as stems divided by species was used in order to investigate potential species-specific effects. For this, simple- and multiple regressions analysis was used. The relationship between crown encroachment and frequency of competing stems was examined via comparisons in the non-parametric Kruskal-Wallis test to detect differences, and then further examined with Mann-Whitney tests to look at specific differences between groups. Corresponding tests were conducted to test the effects of crown encroachment to total plant height, crown diameter and crown length. For two oak plants, both of them dead, no data on crown size or on competing vegetation were obtained. Analysis concerning the named variables did therefore not include these two oaks. Finally, a geographical overview, including the findings of all oak regeneration was as created (Figure 1). All statistical analyses were done in Minitab 16 and 17 (Minitab Inc.)

Results

The oak regeneration was distinctly confined to two large openings caused by Dutch elm disease and Ash dieback. One is situated in the southeastern end of the national park and the second one on the opposite side of the forest, in the northwestern side (Figure 1). Previous surveys on vegetation conducted by Brunet *et al.* (2014) concluded that advanced oak regeneration was only present in these two rather well defined areas. A number of large dead stems of elm and ash were present in the area, but several large dead or dying oak stems were also noted. A total amount of 784 oak saplings above the height of 1.3 meter were recorded and measured during the inventory. Of these, 281 plants were noted in (and east of) the smaller opening in the southeastern corner of the forest to a density of approximately 140 plants per hectare. The remaining 503 plants were found in the larger opening in the northwestern part, to a density of approximately 125 plants per hectare (Figure 1).

General regeneration patterns

Diameters ranged from < 1 cm to 13 cm and are summarized in centimeter classes in Figure 2. Heights ranged from 1.3 m to 8 m, these are summarized into half-meter classes in Figure 3. The largest share of plants can be found in the lower dbh- and height classes. Both diameter and height distribution exhibit a gradual decrease in abundance of plants in higher classes, forming a reversed J-shaped regeneration pattern. The relationship between dbh to plant height and crown diameter is seen in Figure 4, where both height and crown diameter exhibit a strong positive correlation to dbh.

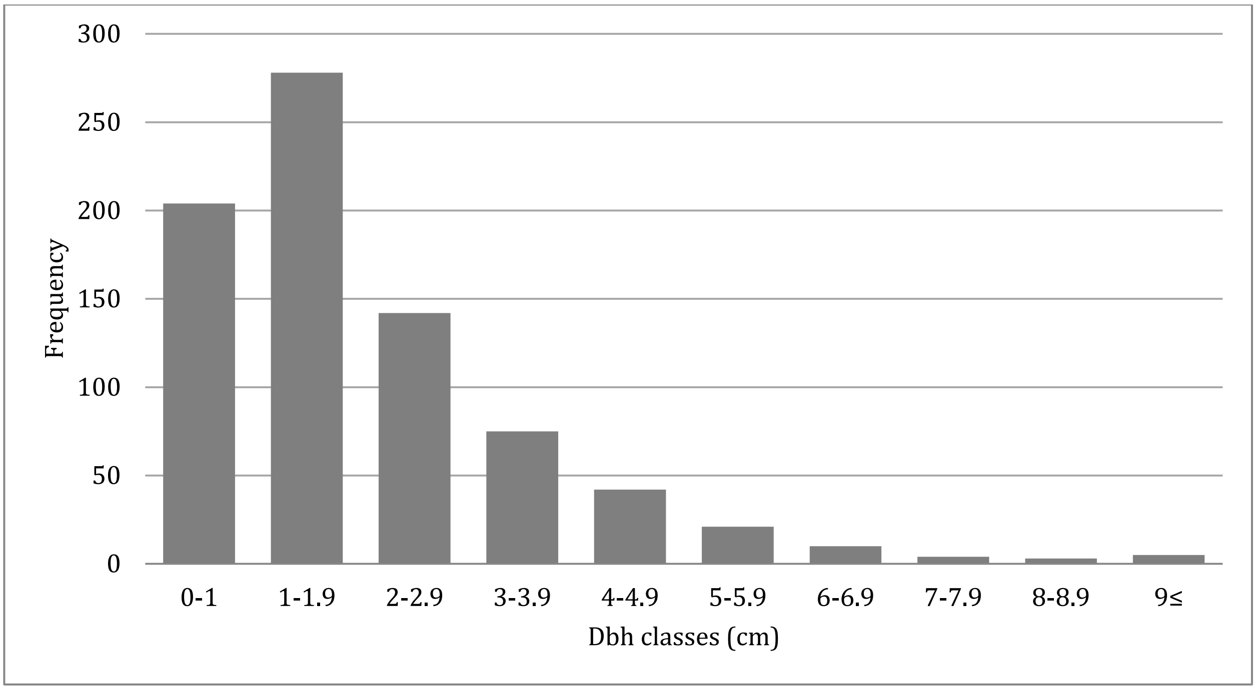

Figure 2. *Diameter distribution for all oak saplings above the height of 1.3 m, showing the frequency in each diameter class.*

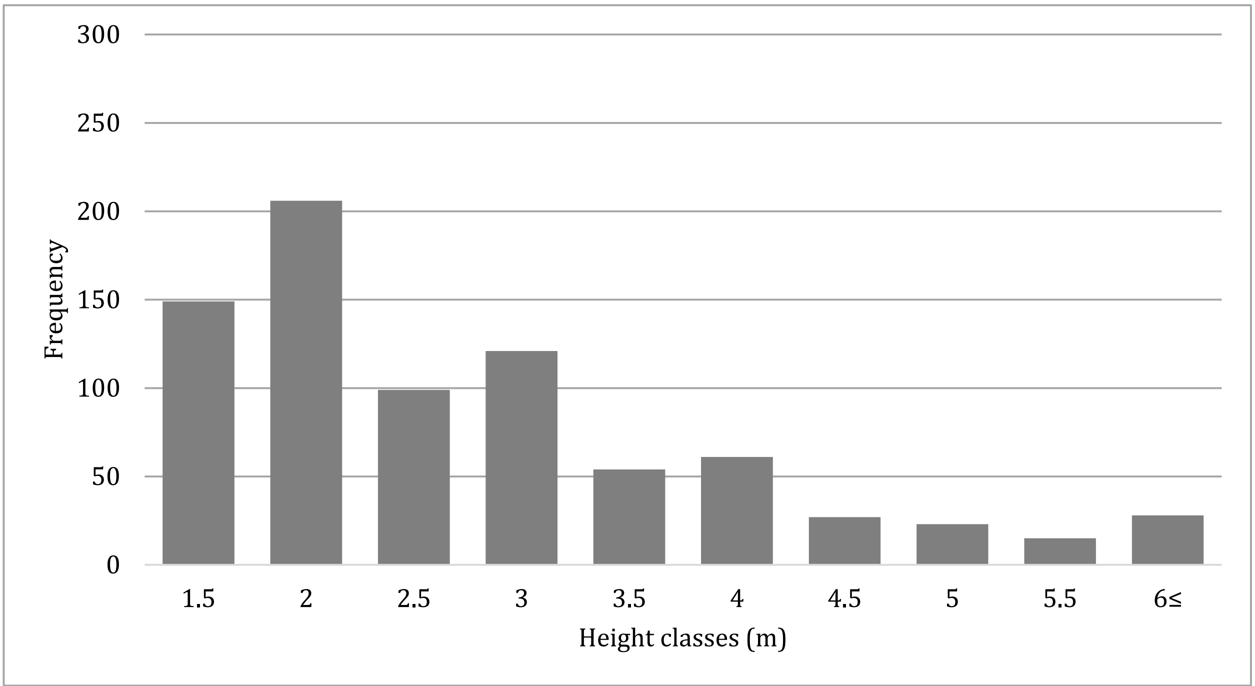

Figure 3. *Height distribution among all oak saplings above the height of 1.3 m showing frequency in each half-meter class.*

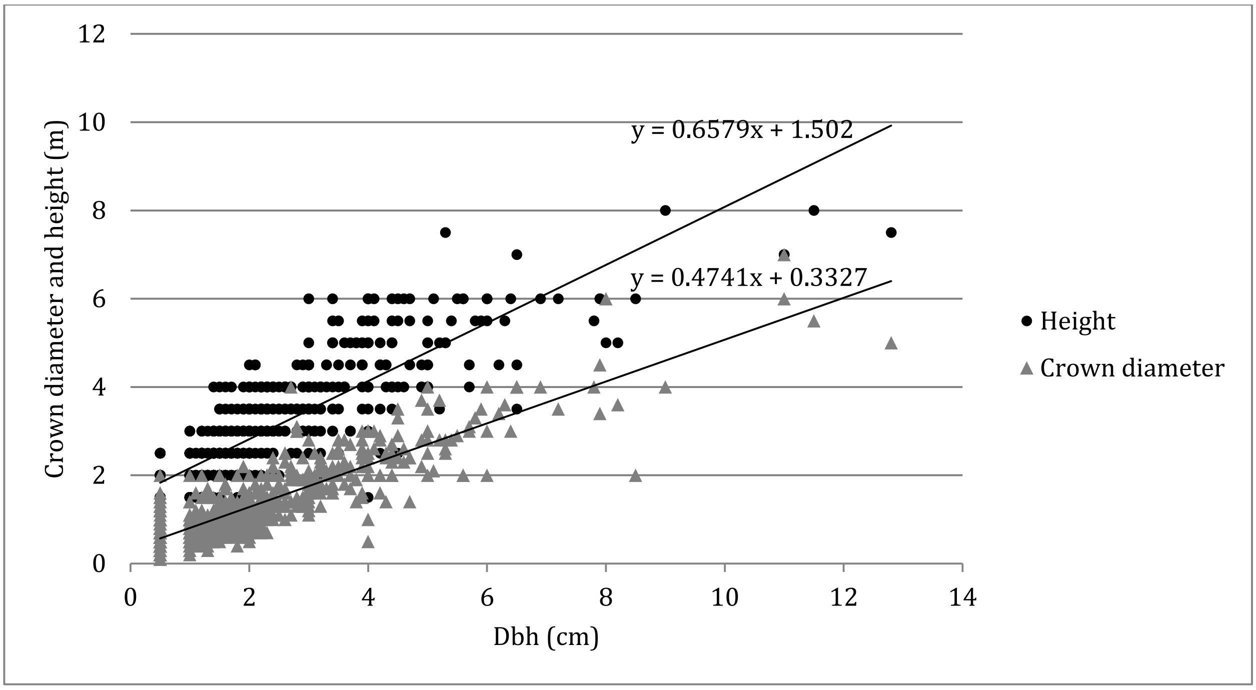

Figure 4. *Relationship between stem diameter at breast height (dbh) and crown diameter (N = 782, P < 0.0001, R² = 77.6 %) and height (N = 782, P < 0.0001, R² = 75.5 %) for the oak saplings.*

Competing woody vegetation

The vegetation surrounding young oaks was dominated by the regeneration of various tree species, but a limited number of shrub species also were common. Many oaks were surrounded by more than one species, and the mean number of competing stems was 4.4 stems per measured oak plant. The density of the shrubbery varied greatly. Ash was the most abundant woody species to surround oak saplings, both by occurrence as well as in total number of recorded stems (Figure 5). One ash or more was present within two meters proximity of 489 oaks, which translates to 63 % of all oaks recorded. Ash dieback was observed among the ash regeneration, including a fairly large amount of dead specimens. The second most common species to surround young oak plants was hazel which was recorded in close proximity to 52 % of all oaks recorded, although fewer stems were noted than for oak (Figure 5). Other oaks were indeed common as a competing species, and were present in close proximity to 49 % of all oaks recorded. Elm was the fourth most common species both in terms of occurrence to oak regeneration and in number of stems. One living elm or more was present within two meters of 38 % of all oaks that were recorded, often in the shape of stump shoots from larger dead elms. Another common shrub species was hawthorn (*Crataegus spp.*). This shrub was present in close proximity of 16 % of all oak plants that were recorded. Beech was present in close proximity to 6 % of all recorded oaks.

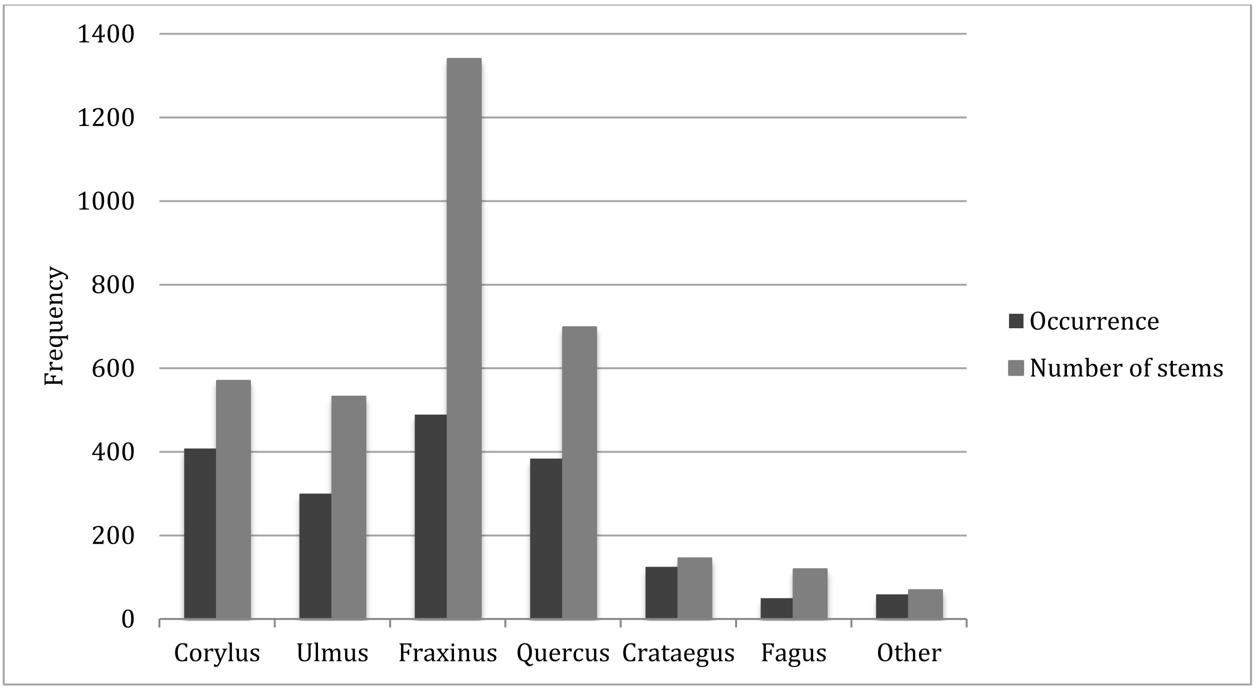

Figure 5. *Distribution of species recorded within 2 meters proximity to oak saplings. Occurrence of each species refers to the number of times that each species were recorded within 2 meter proximity to each of the measured oaks. The graph also shows the total number of stems recorded of each species.*

The remaining species were much fewer in number and have been treated collectively. Locally however, relatively significant occurrences of Norway maple and roses (*Rosa spp*.) were noted. Other species recorded during the inventory include wild cherry (*Prunus avium* L.), European spindle (*Euonymus europaeus* L.) and guelder rose (*Viburnum opulus* L.). A few species were found in very low numbers, these include European fly honeysuckle (*Lonicera xylosteum* L.), blackthorn (*Prunus spinosa* L.), horse chestnut (*Aesculus hippocastanum* L.), elder (*Sambucus nigra* L.) and willow (*Salix spp*.).

Increasing numbers of competing stems negatively correlated to all three size variables that were included in the analysis (Figures 6 – 8), with p-values close to minimum. The total number of stems is connected to the encroachment of the oak regeneration (Table 2). Plants classified as free growing (1) had the fewest surrounding stems. Partially encroached plants (2) had an intermediate number of competing stems while plants that were completely encroached (3) or overtopped (4) had the highest number of competing stems, without significant differences between the two groups. The majority of oak plants were partially encroached by competing vegetation (class 2), however plants under heavy competition were fairly common, judging by the number of plants in classes 3 and 4. Completely free growing plants were relatively few.

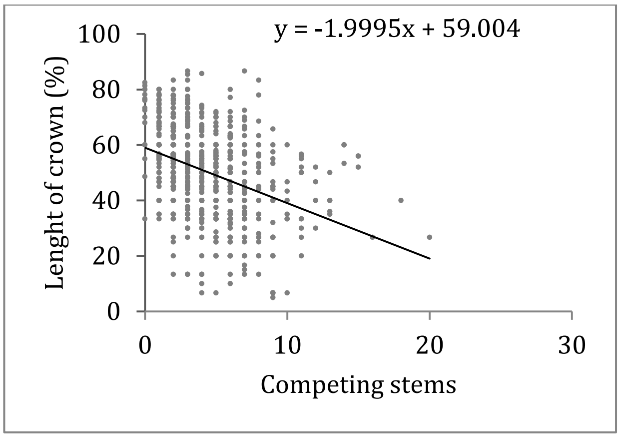

Figure 6. *Model of crown length (% of total plant height) as response to the total number of competing stems within 2 m radius of the oak saplings (N = 782, P < 0.0001, R² = 12.94 %).*

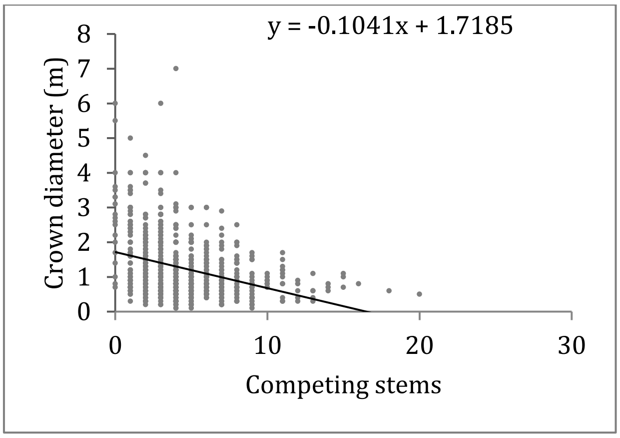

Figure 7. *Model of crown diameter as response to the total number of competing stems within 2 m radius of the oak saplings (N = 782, P < 0.0001, R² = 11.16 %).*

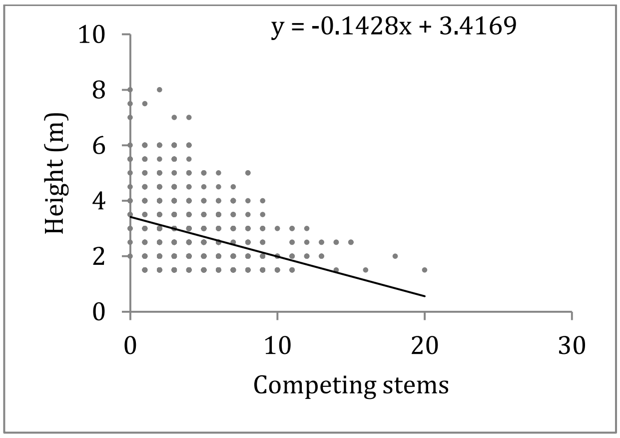

Figure 8. *Model of total plant height as response to the total number of competing stems within 2 m radius of the oak saplings (N = 782, P < 0.0001, R² = 10.63 %).*

Table 2. *Stem numbers in different encroachment classes. Medians that do not share a letter are significantly different (P < 0.05) according to Kruskal-Wallis and pairwise Mann-Whitney U-tests.*

Encroachment class	N	Median	Grouping		
1	54	2	A		
2	411	3		B	
3	144	5			C
4	173	5			C

Saplings that were overtopped by competing stems had significantly smaller crowns than saplings that were free growing, with lower values for both length of crown and crown diameter (Table 3). Free growing plants were in general shorter with a longer and wider crown than plants subjected to competition. Results indicate a gradual decrease in crown size with increasing degree of encroachment. The height pattern is somewhat different. Plants that were completely encroached by competing stems were significantly taller than trees in other groups, which were all fairly similar in height and with no significant differences. Plants that were overtopped were in general of similar height as free growing plants, but with significantly smaller crowns.

Table 3. *Comparisons of size variables of oak regeneration in different encroachment classes. Medians that do not share a letter are significantly different (P < 0.05) according to Kruskal-Wallis and pairwise Mann-Whitney U-tests.*

		Length of crown (%)				Crown diameter (m)			Height (m)		
Encroachment class	N	Median	Grouping			Median	Grouping		Median	Grouping	
1	54	55.5	A	B		1.05	A		2	A	
2	411	55	A			1.1	A		2.5	A	
3	144	50		B		1	A		3		B
4	173	40			C	0.7		B	2	A	

All common species growing in proximity of the oak regeneration had significantly negative influence on all three size variables used in the analysis (Table 4). Estimates indicate that beech and hawthorn consistently have the most negative influence on all three size variables. Hazel had a fairly high negative influence and had the third most negative effect in all three cases, while values for oak and elm were low to intermediate. Overall, ash had the least negative effect out of the species used in the analysis.

Table 4. *Summary of multiple regression models describing species specific effects on size variables of the oak saplings, based on recorded stems of the most common species.*

	Length of crown (%)			Crown diameter (m)			Height (m)		
Variable	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
(Constant)	60.019	1.033	< 0.0001	1.76	0.0584	< 0.0001	3.469	0.083	< 0.0001
Corylus	-3.2901	0.626	< 0.0001	-0.1521	0.0354	< 0.0002	-0.1794	0.05	0.0004
Ulmus	-2.313	0.4582	< 0.0001	-0.1113	0.0259	< 0.0003	-0.1544	0.037	< 0.0001
Fraxinus	-1.8795	0.2475	< 0.0001	-0.0823	0.014	< 0.0004	-0.1215	0.0198	< 0.0001
Quercus	-1.4603	0.4462	< 0.0001	-0.1161	0.0252	< 0.0005	-0.1545	0.0357	0.0002
Crataegus	-4.302	1.141	0.0011	-0.2154	0.0645	< 0.0006	-0.3899	0.0914	< 0.0001
Fagus	-4.0134	0.6989	0.0002	-0.228	0.0395	0.0009	-0.2113	0.0556	< 0.0001

R^2 (Length of crown) = 15.04 %, R^2 (Crown diameter) = 12.99 %, R^2 (Height) = 11.8 %

Mortality and animal induced damages

A total number of 20 dead oak saplings were found. A large proportion of these had been overtopped by competing stems (83 % compared to 22 % for the whole population). Fraying damage was also common on the dead saplings (30 % compared to 10 % for the whole population). Several of the dead plants were subject to both fraying damage and overtopping by competing stems. The number of competing stems per oak did however not differ from the rest of the population. In total, 25 living oak saplings (3.2 % of the entire population) had older, healed bark wounds. 48 saplings (6.1 % of the population) showed signs of recent, partial damage to the stem. Only 3 saplings (0.4 % of the population) were completely ring-barked.

A total number of 26 oak plants classified as bonsais were recorded. However many plants, if not the majority of the oak regeneration, had traces of some level of browsing on side shoots and/or terminal shoots (personal obs.). In general the vitality of these plants was good.

Discussion

Conditions for establishment and recruitment of oak regeneration

Dutch elm disease and Ash dieback have caused high tree mortality in the study area, creating open, high-light environments (Brunet *et al.*, 2014). Oaks have responded to the disturbance, and a total amount of 784 plants were found, which means a new generation is appearing for the first time in 200 years. This is in line with previous findings on pioneer species aggregating in large gaps after a major disturbance event (Götmark & Kiffer, 2014; Aldrich *et al.*, 2003). Diameter- and height distributions reveal a gradual increase of regeneration. Since tree size, and height especially, is mainly the result of tree age followed by site index (Carbonnier, 1975), this implies a fairly extended regeneration process. A likely explanation for this is a gradual opening of the canopy during the infection and senescence of old elms and ash trees. Apart from growth of trees and shrubs, a gradual increase of herbaceous vegetation after canopy disturbance is likely to have decreased the amount of oak regeneration with time (Löf & Welander, 2004). The dbh- and height distribution may therefore actually be normally distributed. This can however not be fully concluded as no plants below the height of 1.3 m were included in the inventory.

Previous occasions of oak regeneration in the study area have been few and far between, and were the result of periods of grazing and/or selective cuttings. These are occasions when the level of disturbance exceeded what can usually be expected in a mixed, natural broad-leaved forest (Wolf *et al.*, 2004). Bobiec (2007) showed that oak regeneration could be the result of canopy gaps created by the death of large canopy trees. That was the outcome of fallen spruce trees that had been weakened and diseased during a process of a forest changing into a state of mixed broad-leaved dominance, and oak regeneration was infrequent in areas where no spruce was present. Similar results were found by Götmark *et al.* (2005b). Other studies question the effect of canopy gaps as a basis for recruitment of oaks, as gaps are often too small to create the high-light levels that are needed (Aldrich *et al.*, 2003). No spruce is present in Dalby Söderskog, and the frequency of disturbance after the establishment of the national park has been low. In fact, the last century has been characterized by a distinct increase in late-successional species and a gradual decrease of oak (Brunet *et al.*, 2014). Recent establishment of a new oak generation indicates that large-scale disturbance was necessary to promote oak regeneration and that gaps created by disease outbreaks may induce similar effects as storm damage, grazing, cuttings or fire. Long-term importance of disease as a reliable catalyst for oak regeneration is however uncertain, as there are no previous records of disease playing a role in creating major disturbance in the area. It has been suggested that the relative success and persistence of oaks in natural forests is due to their longevity and ability to spread seeds effectively, combined with their ability to survive many different site conditions and disturbances, including a high resistance to fire and storms (Götmark & Kiffer, 2014; Savill, 2013). The same abilities appear to have played a vital role in the survival and regeneration of oaks also in Dalby Söderskog.

Forest areas that are under formal or voluntary protection are often subject to "non-intervention" management, with the purpose of developing or maintaining biodiversity values. Experiences concerning active management of biodiversity hotspots and forest reserves are rather scarce, although extensive trials and research on mimicking natural disturbances and historic forest conditions have been conducted in recent years (Leonardsson, 2015; Götmark, 2007). For light demanding species, and most noticeably for oaks, non-intervention can be especially problematic, as they do not exhibit the characteristic shade-bearing abilities of climax species under natural forest succession, and disturbance levels in most protected broad-leaved forests today are low (Löf *et al.*, 2016). The exclusion of any significant active management in the study area of Dalby Söderskog since the establishment of the national park exemplifies the issues concerning preservation of oak rich forests. Oak-rich forests on nutrient-rich soils are becoming less common (Ranius *et al.*, 2009). A species composition that includes several of the most prominent European noble broad-leaved species also adds to the usefulness of the forest as an area of research on the subject (Lindquist, 1938).

Plant response to competing stems and encroachment

The total number of competing stems was connected to encroachment classes (Table 2). Responses on plant development did however differ between encroachment classes, even when stem numbers were similar (Table 3). In general, plants that were overtopped were more severely affected, similar results have been found previously by von Lupke (1998) and Ligot *et al.* (2013). Although the variations in response to stem number were large (Figures 6 – 8), the number of competing stems had a highly significant effect on the development of oak saplings. This in spite that tree size is normally highly affected by tree age and site index (Carbonnier, 1975).

An increasing number of competing stems within a 2-meter radius of oak regeneration will decrease the length of the crown, or more specifically the length of the green crown. Effects were particularly large when plants were overtopped. Crown length is commonly used as a measurement for health status and for determining suitable points of thinning operations in production forestry. A goal of at least 50 % green crown is recommended to maintain high growth (Löf *et al.*, 2009). In line with this standard and with conditions like the ones in Dalby Söderskog, oaks overtopped by competing vegetation are at risk of being excluded from future oak stands (Table 3), along with plants that are surrounded by an average of more than about 5 competing stems within a 2-meter radius (Figure 6). Respectively, remaining plants could be classified as "vital" and the overall status for most the oak regeneration appears to be rather favorable at this stage.

Crown diameter was reduced with an increasing number of competing stems, and as both crown size variables are affected, there is strong support for hypothesis 1. As with crown length, plants that were overtopped were more seriously affected. Crown diameter is an important variable as it is linked to the photosynthetic capacity and thereby the growth potential of trees (Attocchi &

Skovsgaard, 2015). Crown diameter and dbh proved to be highly correlated, this means that we can expect negative effects of competition on dbh, which is in line with hypothesis 2. Reduction of stem diameter growth could possibly increasing the risk of bending and breakage of plants due to wind or snow (Saha *et al.*, 2012). Plants that are free growing or only partially encroached could on the other hand develop into trees with widely developed crowns and thick stems. These trees which are typical for free growing oaks in wooded pastures are considered to be especially important for biodiversity (Ranius *et al.*, 2009).

Total plant height decreased with increasing number of competing stems, which is according to hypothesis 2. The pattern seen with crown length and crown diameter was however broken in the sense that plants that were completely surrounded but not overtopped were taller than other plants, which gives strong support to hypothesis 3. This also supports previous findings on height response to varying degrees of competition (Saha *et al.*, 2013; Jensen *et al.*, 2012c; Götmark *et al.*, 2011).

Competing species and their effect on oak regeneration

Beech was confined to the more well-drained southeastern part of the forest. This is manifested in the relatively low abundance of young beech trees in the inventory. Where beech is present however, it induces comparatively large negative effects on the crown size and height of oaks. However, due to the small population number, conclusions should be made with caution. Beech is recognized as a formidable competitor in closed forests due to its shade-tolerance, but has been found to outcompete oaks also in high-light conditions (Ligot *et al.*, 2013). Beech dominance is strong on intermediate soils but not in the moist conditions that dominate Dalby Söderskog (Ellenberg, 1988). This may have added to the success of oaks in this forest, but could result in less successful recruitment of oak in areas of the forest where beech is present.

Elm regeneration is less abundant than for ash, oak and hazel. Some elms are the result of stump shoots from trees that have succumbed to Dutch elm disease. The species is now reduced to the shrub layer, which is likely to be a long-lasting condition as larger elm specimens usually become infected with the disease (Brunet *et al.*, 2014; Peterken & Mountford, 1998). The health of such plants should be questioned, and their effect on the oak regeneration is likely to be limited in a long-term perspective. This may help to explain the modest effect of elm on the development of oak regeneration in spite of previous elm dominance in the study area. Also, the lack of mature elms will naturally restrict the amount of new regeneration.

Ash was most common of the competing species. It is common for pioneer species to produce an abundance of regeneration and unlike beech, ash thrives very well on moist, nutrient rich sites such as Dalby Söderskog (Ellenberg, 1988). Negative effects induced by ash on the oak regeneration were however comparatively low. The crowns of ash are generally straight growing (Löf *et al.*, 2009), and as a pioneer species it has a crown structure which may allow relatively large amounts of light to permeate (Saha *et al.*, 2013). Ash may therefore not be heavily responsible for intruding on the crowns of oaks. In addition, the long-term health of ash trees is unclear due to the effects of ash dieback (Pautasso *et al.*, 2013). There is a reasonably high abundance of oak regeneration in the clearings and hence a significant effect of intraspecific competition, which can be described as moderate compared to that of the other species. Similar results were found by Saha *et al.* (2013) who also concluded that late-successional tree species induced more severe effects than pioneers. Pioneers are in this study is mainly represented by ash, and partly by oak, which is considered to be only moderately shade-tolerant.

Hazel and hawthorn dominated among shrubs in the study area. Shrubs often respond quickly to disturbance, growing fast with multiple stems and with vegetative reproduction (Leonardsson, 2015). Shrubs differ from trees by their limited final size, and their influence on the oak regeneration is therefore restricted to the first few meters of growth. The existence of a healthy undergrowth has proven to facilitate growth of trees and preventing establishment of a dense layer of ground vegetation (Jensen *et al.*, 2011) but sub-canopy trees may eventually damage the health of oaks (Saha *et al.*, 2012). Hence, shrubs such as hazel may in some ways be a "preferred" species as it unlike trees, rarely grows past six meters in height while still reducing herbaceous groundcover and improving microclimate (Ståål, 1986). A positive scenario is that an interaction between the two species could eventually lead to hazel decreasing levels of competition from other tree species under a canopy of oaks. The close relationship between oak and hazel in the study area has been suggested previously by Lindquist (1938) who also discussed the possibilities of hazel preventing the regeneration of trees. In a more general perspective, Vera (2000) argues that high levels of disturbance and light created a co-dominance of oak and hazel in semi-open forests in pre-historic times, which in many ways reflects the historic conditions in Dalby Söderskog. On the negative side, the relative shade-tolerance and dense crown structure of hazel (Leonardsson, 2015), means it could still have a strong negative influence oak saplings. Indeed, notes made during the inventory indicate that hazel often surpassed other species due to its crown size, with long horizontally angled stems and branches. There was often a tendency of hazel being responsible for the out-shading and overtopping of oak saplings (personal obs.).

Surprisingly severe effects from hawthorn on the oak regeneration do however not follow hypothesis 4, which predicted more severe effects of competition from shade-tolerant species than pioneers. In contrary, hawthorn is often pointed out as a potentially vital species for facilitating oak establishment in wooded pastures through associational resistance (Bobiec *et al.*, 2011b). An overall low number of hawthorn in the analysis may have contributed to uncertainties in the results, and any conclusions concerning the influence of hawthorn should be cautiously made.

Results are inconclusive in determining if late-successional species had more negative influence than pioneers, leaving hypothesis 4 in need of further study. The number of hawthorn and beech are small which allows for greater uncertainties. The situation for determining differences was not optimal due to the fact that two of the species are currently under threat of disease, leaving their health and vitality under questioning. The competitive abilities of elm has however been treated previously in the study area, and both beech and oak were indeed on the expected side of the spectrum, according to hypothesis 4.

Influence of ungulates and competition on oak mortality

Many oak plants, although not being characterized as bonsais, had been subject to browsing at some level. Subsequent growth on such plants after the point of damage rules out the possibility of making further conclusions concerning the frequency of bonsais. The overall image does however indicate that the browsing intensity is not severe enough to prevent successful oak regeneration. In habitats where food resources are abundant, the importance of "associational resistance" has been put under questioning, as oaks have proven to escape browsing even without significant associations with other vegetation (Bobiec *et al.*, 2011b). Synergy effects of browsing and competition may induce higher mortality (Jensen *et al.*, 2012b). In contrast, free growing trees may have higher possibility of overcoming physical damage caused by animals. Another issue was the damage caused by fraying, as it was common among dead oak plants to have signs of unhealed bark wounds. Although not visible in the case of browsing, it is possible that combined effects from competition and fraying may have contributed to the loss of young oaks in Dalby Söderskog. With quite few dead oak plants found, it can be assumed that mortality rates are low. A precise measurement of mortality was however not done in this study, and a fair assumption is that dead, small trees without leaves could have been overlooked, or dead trees were decomposed. The loss of oaks may therefore be higher than indicated by the results.

Conclusions

This study demonstrates that disease outbreaks can have similar effects as storms, grazing, fire or other types of large-scale disturbance in creating beneficial conditions for oak regeneration. However, inter- and intraspecific competition will negatively affect the development of oak regeneration that is established after a major disturbance event. Large quantities of competing stems can decrease development of crown size, stem diameter and height of oak regeneration that are established. The manner in which competing stems intrude on the oak regeneration is also a key factor in determining the degree of such effects. Crown length, crown diameter and stem diameter at breast height is severely affected when plants are overtopped by surrounding stems. The effect on height growth is more complex, as plants that are completely encroached by competing stems without being overtopped, are likely to be taller than other plants, including ones that are free growing. Both inter- and intraspecific competition had negative effects on the oak regeneration. There are slight tendencies that late-successional species, but more specifically densely leafed species, inducing more severe effects than pioneers. However the health of both ash and elm may be compromised due to ash dieback and Dutch elm disease respectively. The level of competition between oaks was moderate in comparison with other species.

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Olle Finnström

Umeå, February 2016

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Photo appendix

Photo 1. *The shrubbery of tree saplings along with species such as hazel and hawthorn was sometimes very dense.* Photo: Olle Finnström.


Photo 2. *The size variation among tree saplings and shrubs was typical for much of the area, as was the existence of dead elms and ash trees. A few oak saplings are visible in the foreground.* Photo: Olle Finnström

Photo 3. *In some parts of the large openings, the density of oak saplings is relatively high*. Photo: Jörg Brunet.

Photo 5. Young oak sapling close to fallen large oak. Photo: Jörg Brunet.