Long-term Succession and Loss of Foundation Species in a Temperate Broadleaved Forest in Southern Sweden

Yulia Bukina
Supervisor: Jörg Brunet

Swedish University of Agricultural Sciences
Master Thesis no. 194
Southern Swedish Forest Research Centre
Alnarp 2012

Long-term Succession and Loss of Foundation Species in a Temperate Broadleaved Forest in Southern Sweden

Yulia Bukina
Supervisor: Jörg Brunet
Examiner: Matts Lindbladh

Swedish University of Agricultural Sciences
Master Thesis no. 194
Southern Swedish Forest Research Centre
Alnarp 2012

Msc Thesis in Biology, Euroforester Master Program,
30 ECTS Advanced level, SLU course code EX0279

SUMMARY

Dalby Söderskog is an old-growth temperate forest dominated by pedunculate oak *(Querus robur)*, wych elm *(Ulmus glabra)*, European ash (*Fraxinus excelsior)*, and beech (*Fagus sylvatica)*. After being released from a historical management regime of livestock grazing, autogenic succession began in the forest. This allowed for shade tolerant species to prevail. A steady state forest community dominated by elm was affected by Dutch elm disease (DED), while ash dieback negatively impacted on the ash population at the end of the 20th century. In this study, we report on 95 years of secondary succession in Dalby Söderskog with emphasis on the effects of DED and ash dieback on forest compositional dynamics. Additionally, future trends in forest succession were discussed in response to changing environmental conditions.

In 2012, an inventory of trees > 10 cm in diameter at breast height was carried out. This was done across 74 systematically distributed plots which were reconstructed from a survey of herb layer vegetation conducted in 2010. The results were compared with similar investigations completed in 1909, 1916, 1935 and 1970. The new inventory data representing species composition and forest structure were analyzed and discussed in relation to DED, ash dieback and oak decline. For each sample tree vitality was also recorded in order to explain compositional dynamics and succession trends.

The results show that oak has been retreating from the stand for a long time, while elm is declining in abundance only recently after a period of dominance. Ash has become a dominant species in 2012 due to its ability to regenerate vigorously in gaps created where elms have fallen because of DED. However, a large amount of infected ash were observed in 2012. For beech, increased recruitment was found in Dalby Söderskog during the last sampling period. Despite dramatical changes in compositional dynamics, overall structural dynamics look more stable than species level diameter structure indicates.

I conclude that oak will disappear in the long run if no actions are taken in the future, as historically its presence was a result of a wood pasture regime in Dalby Söderskog. DED had a significant impact on the tree species composition and will continue to affect young elm trees, resulting in an understory population with high turnover. Ash and beech will probably increase and maintain a dominant position in the canopy. Although, changes in composional dynamics occured, the forest still proved to be relatively resistant as an ecological system as seen in its consistency pertaining to structural dynamics.

1. INTRODUCTION

1.1 Background

For centuries, the management in much of the European temperate forest was either grazing by domestic livestock combined with irregular selective logging, or short-rotation coppice and coppice-with-standards systems. Natural processes were intermingled with human activities in complex and subtle ways (Peterken 1996). Traditional use as wood pasture kept the canopy relatively open with scattered trees among the grasslands (Rackham 1989). During the course of the 19th century, this management system was abandoned in most areas in favour of modern high forest silviculture. In some wood pastures however, traditional management continued, whereas other areas were left to natural succession. Many of the ancient, semi-natural deciduous forests have been given a protected status during past decades and were left for natural succession (Verheyen et al. 2012).

In unmanaged temperate forests with a low grazing pressure, post-disturbance succession is usually driven by internal processes, in particular competition for light. The process of spontaneous succession in abandoned wood pastures generally results in denser canopies and an increase in shade-tolerant tree species at the expense of shade-intolerant species (Malmer et al. 1978; Bernadzki et al. 1998; Mountford et al. 1999; Tybirk and Strandberg 1999; Emborg et al. 2000; Strandberg et al. 2005). The abandonment of traditional management has also led to significant accumulation of nitrogen in these ecosystems (Hofmeister et al. 2004).

Beside changes in historical land use, natural disturbances also have a great potential to impact temperate forest dynamics. Temporal and spatial patterns of natural disturbances are generally unpredictable. These disturbances include fire, drought, wind and pathogen outbreaks (Peterken 1996). Some disturbances influence the mortality of dominant and co-dominant trees, and it is these which are most important in terms of forest succession. Over the past century the population of such foundation tree species (e.g. oak, beech, elm) in forests has been declining in many areas throughout the world (Ellison et al. 2005). Species such as oak, beech and elm are important for the structure and function within forests. The abundance of foundation species in natural forests is in decline due to disturbances such as non-native herbivores, pests and pathogens (Ellison et al. 2005; Rackham 2008).

Forests are assumed to approach a steady successional state after several hundred years of undisturbed growth (Bormann and Likens 1979) and studies which have long time spans and repeated measurements are critical for identification of these trends and understanding forest dynamics (Bakker et al. 1996; Burrow 1990; Samonil and Vrska, 2008). These types of studies provide basic information on rates of successional change in forests, on the interaction of multiple disturbances and on forest resilience in response to changing environmental conditions (McLachlan et al. 2000).

Taking into consideration the well-documented human and natural disturbance history of the forest reserve Dalby Söderskog in southern Sweden, its long-term succession has been an issue for extensive discussion and research (e.g. Malmer et al. 1978). Therefore, Dalby Söderskog was chosen as case study for this master thesis. Dalby Söderskog was managed as a wood pasture from medieval times until grazing ceased at the end of the 19th century. The last significant tree cutting was carried out in 1914-16. In 1918, Dalby Söderskog was established as a forest reserve comprising an area of 36 ha, surrounded by arable fields and open pastures (Lindquist 1938). Prior to protection, the effects of moderate life stock grazing and irregular tree cutting had allowed the coexistence of the four most important tree species of eutrophic temperate forests in southern Scandinavia, i.e. the light demanding oak and ash, along with the shade tolerant beech and elm (Lindquist 1938; Diekmann 1994).

1.2 Study aim

The aim of this project was to study 95 years of secondary succession in the temperate broadleaved forest Dalby Söderskog, southern Sweden, and to analyse the effects of Dutch elm disease (DED) and ash decline which have affected the forest since the last tree survey in 1970. This knowledge is useful in order to accurately predict what will happen to forest stands of similar structure to those found in Dalby Söderskog. Understanding the development of the forest and the tree species resulting from widespread diseases is a useful tool in preventative forest management. Diameter distributions for all tree species were analyzed along with corresponding diseases for trends in species composition over time. Compositional forest dynamics were evaluated to determine how diseases and land use have influenced forest development. Specifically, we analyzed if the observed changes since last tree inventory in 1970 are consistent with the following hypotheses

1) Oak will continue to decline in the canopy layer due to natural mortality and lack of regeneration; however gaps caused by DED could cause pulses in oak regeneration since the last inventory.
2) Beech will remain fairly constant and will regenerate in the close proximity to previously existing beeches.
3) Ash will show a continuous increase at the understory level due to DED gap dynamics along with a loss of individuals at the canopy layer because of ash dieback.

4) Elm will show a decreasing trend because of DED, however its vigorous recruitment will allow to keep a dominant position in the understory.

2. MATERIAL AND METHODS

2.1 Study site description

Dalby Söderskog is situated in the County of Skåne, which is located in southern Sweden, 10 km east of Lund (55°41´N, 13°20´E, 65m a.s.l.). The mineral soil is derived from Baltic moraine (Weichsel glacial period) and is a calcareous, nutrient-rich clay. The soil type is eutric cambisol and the humus type is mull. The climate is temperate suboceanic, with a mean annual temperature of 7.5 °C and a mean annual precipitation of about 650 mm (Oheimb and Brunet 2007).

2.2. Major tree species in the study area

Oak

Pedunculate oak is a common tree species in European lowlands (Larsen et al. 2005) and is represented in Dalby Söderskog by mainly old individuals (Malmer et al. 1978). Until the 19th century the forest was managed as grazed land in which oaks could regenerate under relatively open tree canopies. Oak seedlings have high requirements for adequate light and the mortality of seedlings germinating in gaps is high due to insufficient gap size (Hofmeister et al. 2004). Recently an oak decline has been reported from northern Europe, it is considered a complex phenomenon where possible factors could be cold winters, drought in the vegetation season and infection by pathogenic fungi, nitrogen eutrophication and nutrient imbalances (Sonesson and Drobyshev 2010).

Beech

Dalby Söderskog has eutric cambisol soil and at these sites beech has a high growth potential. In terms of light, beech is a shade tolerant species and it is a typical climax component attached to late successional stages of forests (Larsen et al. 2005). Beech is considered to be non-problematic with regard to its susceptibility to pathogens (Butin 1996). Dispersal of beech in Dalby Söderskog is limited due to high soil moisture that results in its patchy distribution and dominance in only a small part of the forest.

Ash

The presence of ash in Dalby Söderskog is related to the successional stage in the forest at the beginning of the 19th century which was a result of high light availability facilitating oak and ash regeneration simultaneously. Canopy gaps in Dalby Söderskog currently offer favorable conditions for recruitment of ash (Oheimb and Brunet 2007). Pertaining to pathogens, ash is known to be relatively resistant; however, recently it has come under a great threat in most of Europe due to a pathogenic fungus causing ash dieback (McKinney et al. 2011).

Elm

Elm regeneration is vigorous in the shade of growing trees in Dalby Söderskog (Oheimb and Brunet 2007). Elm prefers moist, fertile, neutral soil (Peterken and Mountford 1998). Its ecological requirements are similar to ash which provides a base for their co-existence (Martin et al. 2010). The elm population became dominant in Dalby Söderskog since the ceasing of grazing when the forest was protected. However, Dutch elm disease (DED), which already had killed millions of elms during the 20th century (Martin et al. 2010), has affected Dalby Söderskog since ca 1990, and seems to be an important factor in changing forest succession trends.

2.3 Previous inventories

Tree inventories from Dalby Söderskog were available from the years 1916, 1935, and 1970 (Lindquist 1938; Malmer et al. 1978). Lindquist (1938) used a straight path through the forest as a base line and arranged 74 sample plots along lines perpendicular to the path. The distance between the lines was 50 m. The distance between plots along the lines was in most cases 100 m (50 or 75 m in a few cases due to stand margins). The development of the tree layer was investigated using standard forestry methods, including recording tree species, and measuring their diameters at breast height (dbh). Accompanying three complete trees inventories from 1916, 1935 and 1970, supplementary information was available from 1909. During inventories in 1916 and 1935, only trees > 20 cm at breast height had their diameters measured. During the inventory carried out in 1970 all trees > 10 cm at breast height were included in diameter measurements (Lindquist 1938; Malmer et al. 1978).

2.4 This inventory

In early spring 2010, the plot system was reconstructed for a survey of the herb layer vegetation, using an aerial photograph of the forest with Lindquist´s map as an overlay in ArcPad and the corresponding GPS coordinates (Brunet, unpublished data). Together with a plastic stick, a short iron tube was placed in the ground in 2010 which should enable future relocation of the plot with a metal detector in case the stick is lost.

The field work was carried out in February 2012. All tree specimens having a dbh >10 cm were measured and identified in 100 m^2 (5,7 meter radius) plots using the centre points from the 74 plots created for the previous studies. In 314 m^2 plots (10 meter radius) all trees > 20 cm at dbh were inventoried. Graphics displaying diameter classes are depicted beginning at an initial class range of 0 to 10 cm. Trees with stem diameters less than 10 cm at breast height were not measured and thus the frequency in this data range is always zero.

Oak trees were mapped (100 m^2 grid) if they had a dbh >1 cm and a height of at least 1,3 m in order to define the recruitment rate and determine trends in regeneration over the past century. The diameter of trees up to 50 cm dbh in the sample plots were measured with a hand calliper along two axes. These two values were averaged and rounded to the nearest whole cm. Larger trees were measured with a diameter measuring tape.

2.5 Vitality classes

For each sample tree within plots, vitality class, diameter and species were recorded. Elm sample trees were split into three classes which differ according to bark condition, being either vital, sick or dead. Vital trees had a vigorous crown and healthy bark. Elms were judged as infected elms by epicormic sprouting, dying bark and dieback at the top of the tree. Elms with completely dead bark without regeneration by sprouting were classified as dead.

A similar classification was applied to ash for vitality estimation. The main indicator here was crown condition which differentiated trees among different vitality ratings. Vitality ratings for ash include vital, partly dead crown and dead.

2.6 Data analysis

The main analyses focused on tree diameter distributions between the inventories. Comparisons between years 1916 and 1970 were performed on the basis of all trees in Dalby Söderskog, as all trees were surveyed at those times (Malmer et al. 1978). In the case of comparing to the inventories taken in 1935 (20% line taxation, Lindquist 1938) and 2012 the extrapolation method was applied and the numbers of total trees were estimated in 2012. The extrapolation method entails that all trees across the 74 sampling plots were multiplied by a coefficient according to each plots area, resulting in absolute number of trees in the 36 ha which comprises the whole park.

In order to interpret and more directly compare the results of the tree analyses for the inventory in 2012, the number of trees for different diameter classes was presented per hectare. In addition, the change in overall tree numbers of each species between the inventories was determined, and an analysis of the overall distribution for each tree species by diameter classes between all inventories was done.

In order to explain compositional and structural dynamics an analysis of vitality classes was done for the inventory conducted in 2012. In order to see general tendencies of vitality, species-wise vitality values were calculated. The amount of trees was done in relative numbers to allow comparison of vitality classes within species.

A linear regression model was made in order to better predict the presence of oak in the forest into the future.

3. RESULTS

3.1 Oak

Between the years of 1916 and 1935 the numbers of oak stems increased slightly by 9%, and middle range diameter classes (50 cm to 70 cm) dominated in 1935 (Fig. 1). The general diameter distribution remained the same from 1916 to 1935. From 1935 to 1970 the number oak stems was reduced by 25% and the diameter distribution shifted. There was a reduction in the frequency of trees falling into mid-range diameter classes, and regeneration has also dropped since 1935 (Fig. 1). From 1970 through 2012 the larger diameter classes are dominant, especially those ranging from 70 cm to 90 cm (Fig. 2). From 1970 through 2012 the number of oaks was reduced by 35%, from 1010 to 651. During the field inventory in February of 2012 five oaks/ha between 1 cm and 30 cm at breast height (dbh) were found. This shows that younger generations of oaks are not strongly prevalent throughout the forest stand. Outside of the study plots some young oaks less than 20 cm dbh were noticed. At the beginning of the study period (1916) oaks were normally distributed regarding their diameter distribution and regeneration was strong, as seen in the presence of smaller diameter trees (Fig. 1). Over the past 95 years regeneration has continuously declined, creating a negatively skewed diameter distribution.

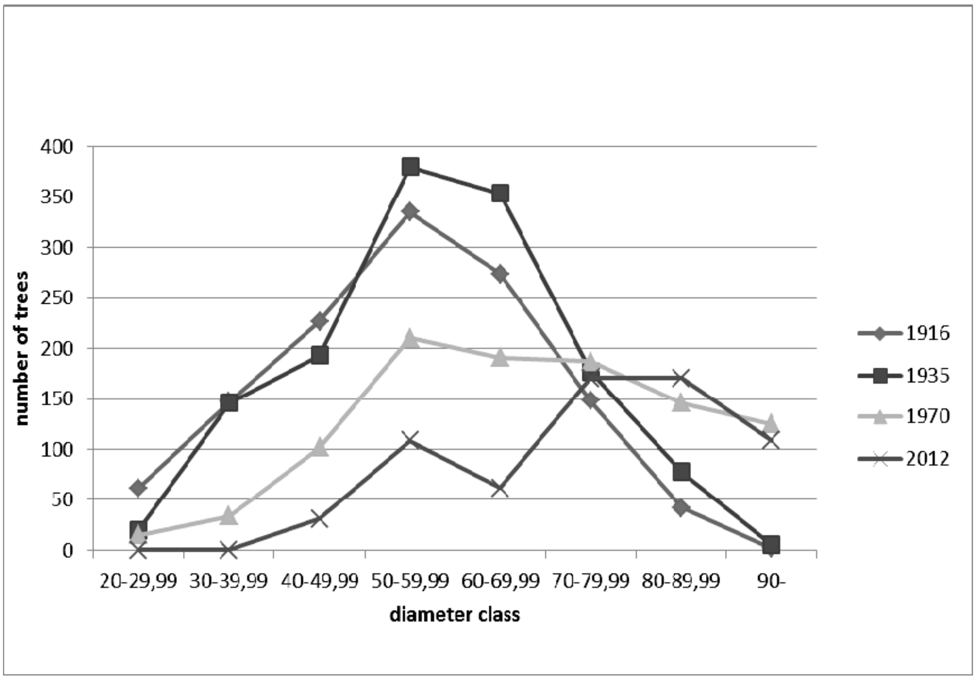

Figure 1. The diameter distribution for oak in absolute numbers in Dalby Söderskog according to measurements from 1916 to 2012. Only trees with stem diameter > 20 cm at breast height are included.

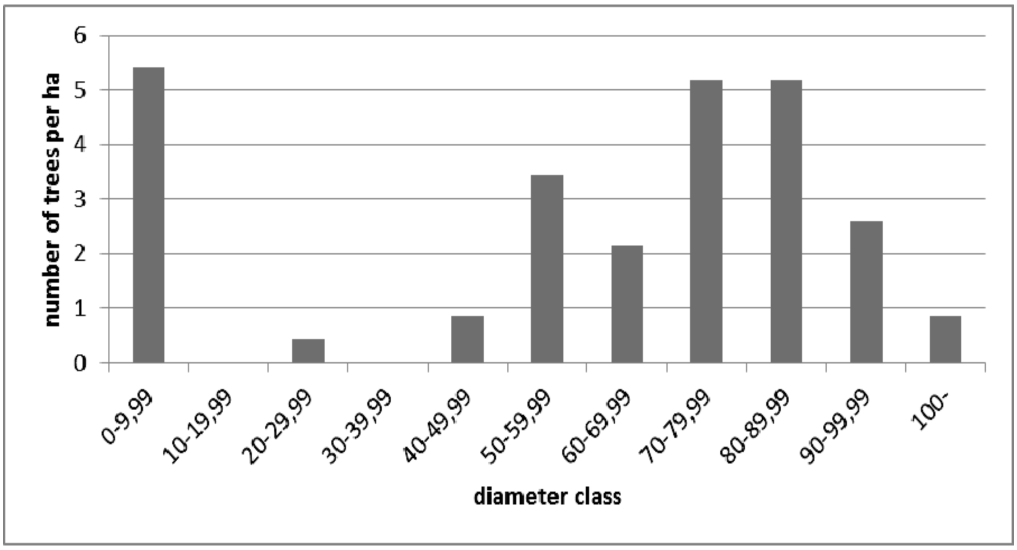

Figure 2. The diameter distribution for oak per hectare in Dalby Söderskog according to measurements in 2012. Only trees with stem diameter > 1 cm at breast height are included.

3.2 Beech

The present distribution of beech is strongly represented by trees which fall into the diameter class range of 10 to 40 cm (Fig. 3). Beech is regenerating vigorously in Dalby Söderskog as shown by the abundance of young, small diameter vital trees. Following Lindquist (1938) many of the existing large beeches may be more than 250 years old today, as they were regenerating during a period which coincided with less intensive grazing.

From all previous inventories until 2012 there has been an increase in the number of stems in diameter classes ranging from 20 - 40 cm, although a drop was seen between 1935 and 1970 (Fig. 4). After 1935 the distribution of beech shifted towards a decrease in beech with diameters between 30 cm and 50 cm at breast height along with a constant amount of small trees ranging from 20 to 30 cm (Fig. 4). The total number of beech dropped by 5 % between 1935 and 1970, mainly among the diameter class ranging from 30 to 40 cm. The number of stems has increased by 33% in 2012 compared to the inventory in 1970. The diameter class of 20 cm to 30 cm at breast height has doubled since the last inventory and trees ranging 30 cm to 40 cm increased more than 30%. Also, the number of beech stems greater than 80 cm at breast height has slightly increased.

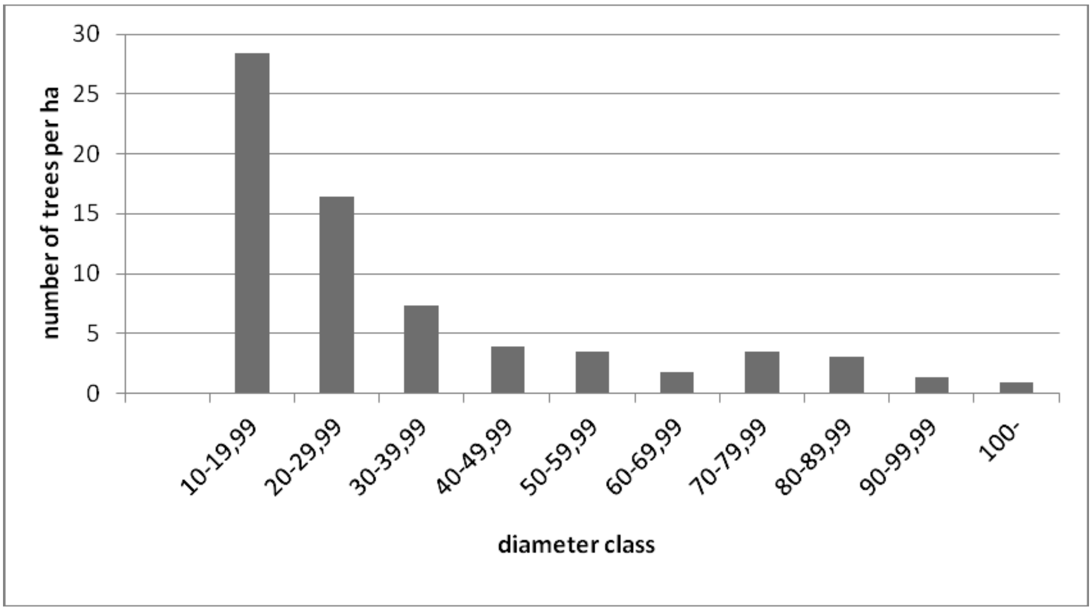

Figure 3. The diameter distribution for beech per hectare in Dalby Söderskog according to measurements in 2012. Only trees with stem diameter > 10 cm at breast height are included.

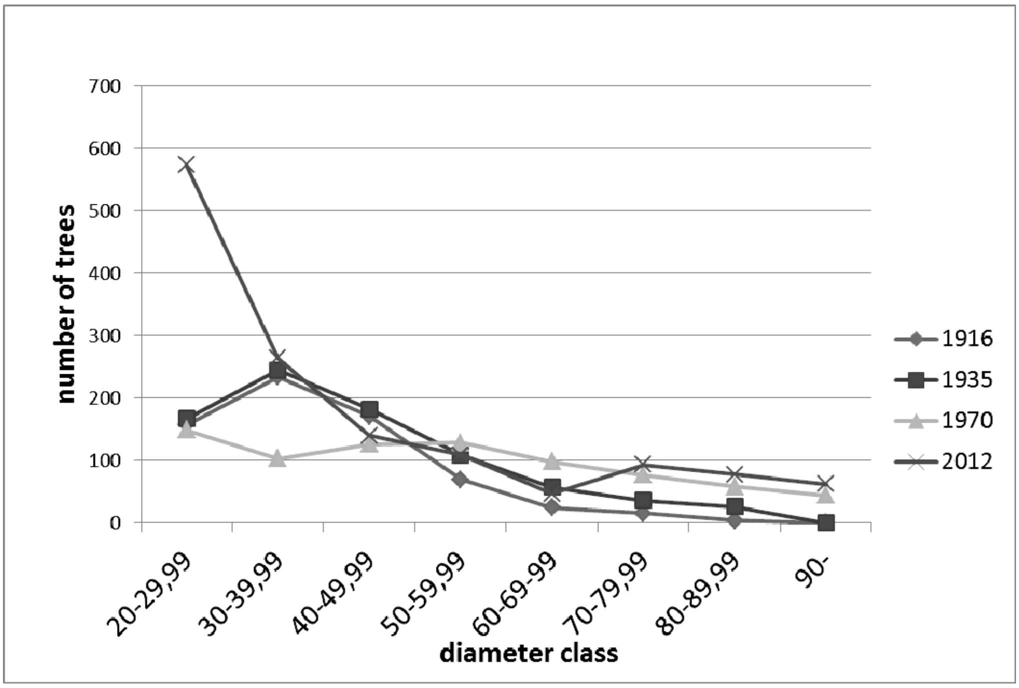

Figure 4. The diameter distribution for beech in absolute numbers in Dalby Söderskog according to measurements from 1916 to 2012. Only trees with stem diameter > 20 cm at breast height are included.

3.3 Ash

In 2012 diameter classes are strongly represented within the range of 20 cm to 50 cm. The frequency of ash occurring in diameter classes greater than 50 cm at breast height is relatively constant except for the diameter class ranging from 90 cm to 100 cm (Fig. 5).

According to the inventory in 1916 there were not many ash trees, especially among smaller diameters (Fig. 6). In 1916 diameter classes ranging from 30 cm to 50 cm were prevailing in Dalby Söderskog, and the number of old ash trees present was low. The number of ash trees falling into the diameter class of 20 cm to 30 cm increased by 78% between 1916 and 1935. Since 1935 the number of ash trees has increased by nearly 15% as seen among small diameters classes. In 1970 the dynamic structure of ash seemed to be typical for natural forests and could be described by an inverse J-shaped diameter distribution curve. The total number of ash trees between 1970 and 2012 further increased by 22%. However, the current diameter distribution curve illustrates an irregular pattern among the ash population, and the total number of ash trees, ranging from 20 cm to 30 cm, decreased by 50% between 1970 and 2012. Trees falling into the diameter class of 50 cm to 60 cm demonstrate a 23% reduction in the total number of trees between 1970 to 2012 (Fig. 6).

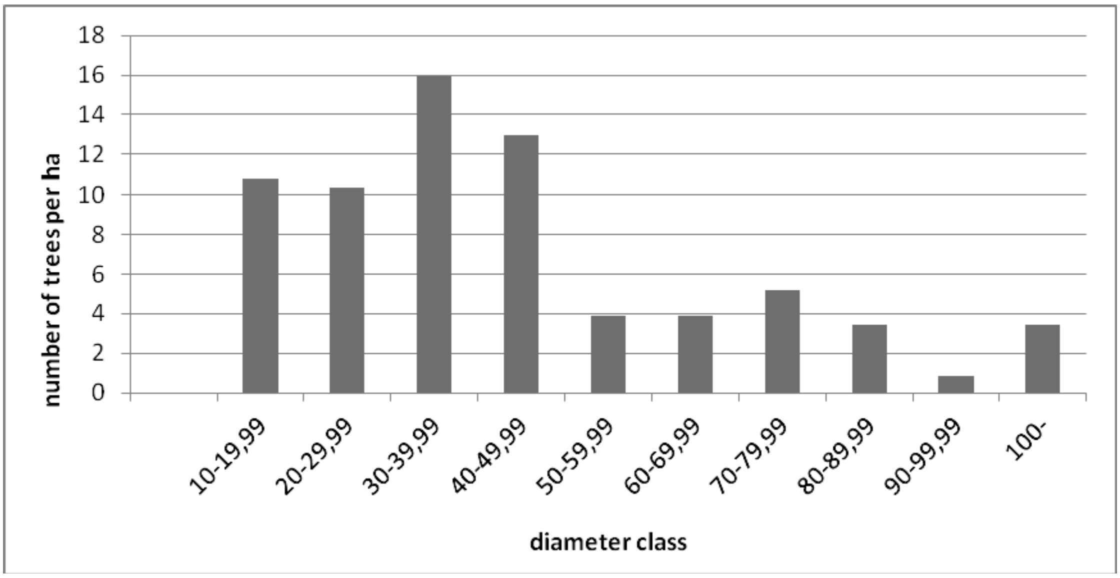

Figure 5. The diameter distribution for ash per hectare in Dalby Söderskog according to measurements in 2012. Only trees with stem diameter > 10 cm at breast height are included.

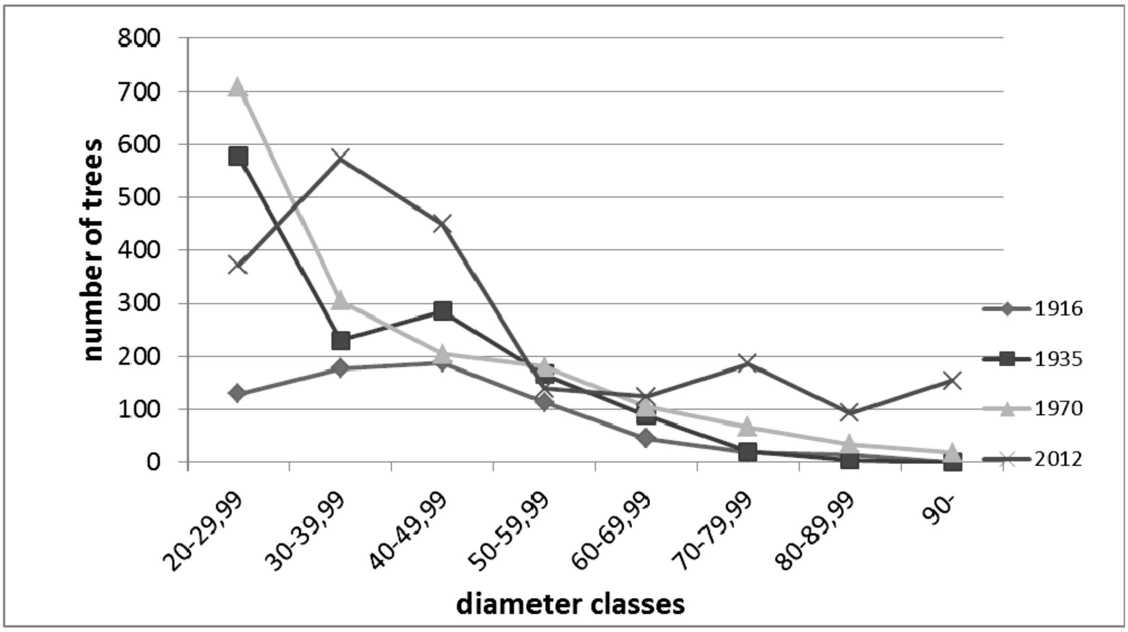

Figure 6. The diameter distribution for ash in absolute numbers in Dalby Söderskog according to measurements from 1916 to 2012. Only trees with stem diameter > 20 cm at breast height are included.

3.4 Elm

Between the years of 1916 and 1935 the number of elm stems increased by 30% mainly because of an increase of trees falling into the diameter class ranging from 20 cm to 30 cm. The overall diameter distribution shows an increase in the numbers of small stems while maintaining almost the same number of total stems in the other diameter classes from 1916 to 1935 (Fig. 8). From 1935 to 1970 the number of elm stems increased by nearly 25% and the diameter distribution shifted. This shift occurred among young trees falling into the diameter class of 20 cm to 30 cm, showing an increase in stem number by 42%, representing a high level of regeneration. However, the overall amount of trees in other diameter classes found in 1970 did not differ significantly from the previous inventory in 1935. Data from 2012 show a high proportion of trees falling into the diameter class of 10 cm to 20 cm, resulting in the appearance of an inversely J-shaped diameter structure curve (Fig. 7). The overall number of elms decreased from 2975 to 1070 between 2012 and the inventory in 1970. The amount of trees ranging from 20 cm to 40 cm decreased by almost factor two between 1970 and 2012 (Fig. 8). The distributions of other diameter classes show the same tendency of a reduction in the frequency of elms. This reduction in the elm population is seen in the low amount of middle diameter class elms throughout the last 42 years and a resulting near absence of older trees.

At the beginning of the study in 1916 up through 1970, elm was strongly dominant in smaller diameter classes (Fig. 8). DED caused significant mortality in mature stems after its introduction around 1990, but a high recruitment rate was maintained. Although, there is high rate of mortality among young elm, the diameter structure is still represented by an inversely J-shaped curve that shows a large turnover in the elm population in the recent few decades (Fig. 8).

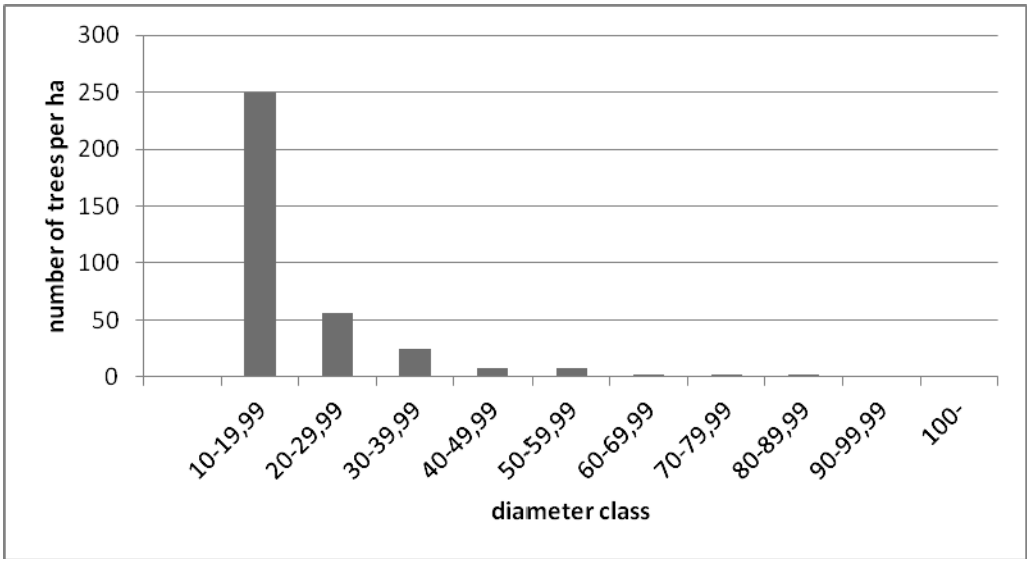

Figure 7. The diameter distribution for elm per hectare in Dalby Söderskog according to measurements in 2012. Only trees with stem diameter > 10 cm at breast height are included.

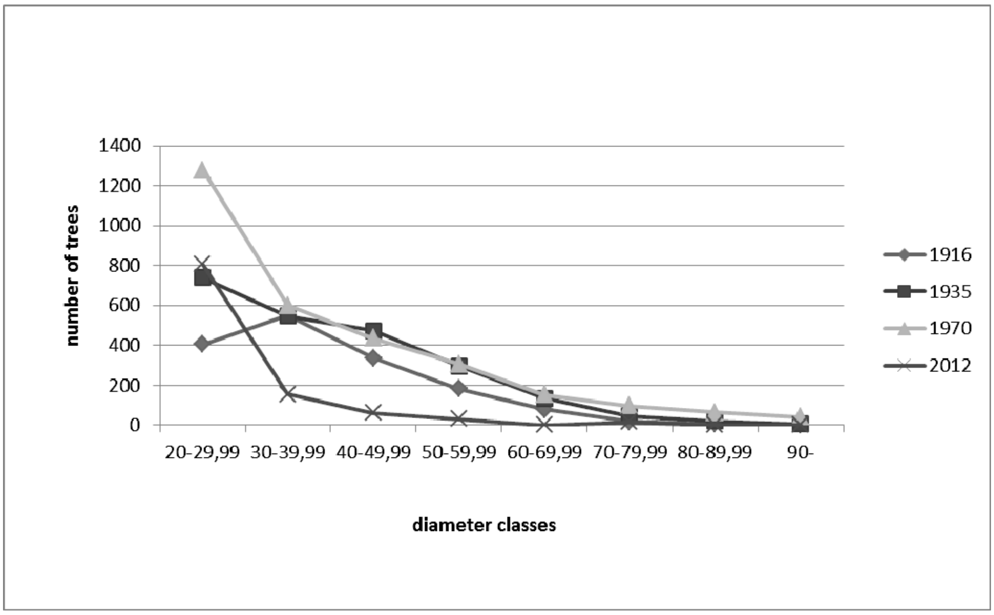

Figure 8. The diameter distribution for elm in absolute numbers in Dalby Söderskog according to measurements from 1916 to 2012. Only trees with stem diameter > 20 cm at breast height are included.

3.5 Species composition

The total populations and changes over time for all trees species in Dalby Söderskog are presented in Fig. 9. Over the entire period of 1909-2012, the four main tree species (oak, ash, beech and elm) remained the same. The total number of stems is 14 % lower today compared to 1909, reaching a maximum value in 1970 and a minimum value in 1916.

In 1909, oak was the most abundant species, constituting 37% of the total number of individuals (Fig. 9). By 2012, its density had decreased to 12% of its initial value. After a period of decrease due to cutting in 1916, elm increased again between 1916 and 1970, comprising 44% of the total tree population. However, after 1970 this species started to decline dramatically down to 20% of the total tree population in 2012.

Ash has been systematically increasing throughout all inventories. In 1909, it constituted only 14% of the total number of individuals and was one of the least abundant species (Fig. 9). Between 1916 and 1935 there was ample regeneration and thus recruitment continued until the most recent inventory, reaching a maximum density in 2012. By the inventory in 2012, ash had reached almost 40% of the total proportion among the tree species composition.

As a total proportion of trees in 2012, beech ranked second in Dalby Söderskog following ash. Initially beech was the least abundant species and represented only 13% of the forest trees, however, after 1970 its percentage increased to 26% of the total number of individuals within the forest.

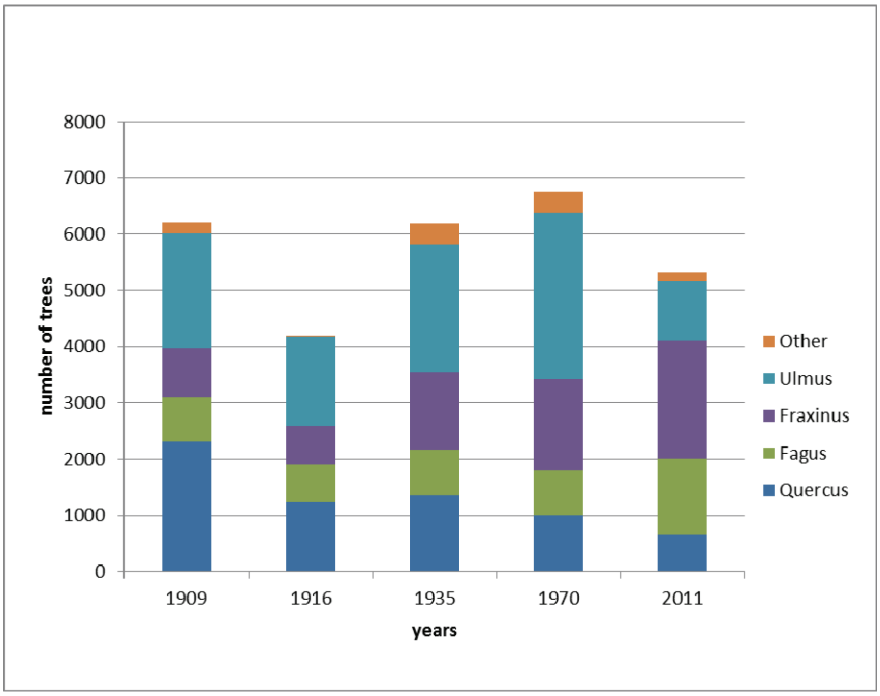

Figure 9. Distribution of trees in absolute numbers over the period 1909-2012. Only trees with stem diameter > 20 cm at breast height are included.

3.6 Changes in overall diameter structure

Through all inventories a diameter structure appears, which can be described as an inversely J-shaped distribution curve (Fig. 10). Small diameter trees ranging from 20 cm to 30 cm were constantly increasing until the last inventory period between 1970 and 2012. This increase, observed at the begining of study, is related to the early successional stage of forest. At the same time the number of trees in intermediate diameter classes, particularly ranging from 30 cm to 70 cm, had decreased since the inventory in 1935 (Fig. 10). There was a significant loss in the elm population after 1970 which also contributed to the decrease in population among middle diameter classes (Fig. 10). In contrast, the largest diameter classes ranging from 70 cm to 100 cm increased constantly over all inventories representing a continuity of long-term succession in the forest and accumulation of old trees. Absence of strong natural disturbances such as storms allowed Dalby Söderskog to form an inversely J-shaped diameter distribution curve until 1970. During the last sampling period, when the DED outbreak occurred, changes in the diameter structure in Dalby Söderskog appeared as seen in a reduction in presence among small and middle diameter classes. As a result, the inversely J-shaped distribution curve, observed during the 20th century, changed into a more irregular pattern with an unsmooth distribution (Fig. 10).

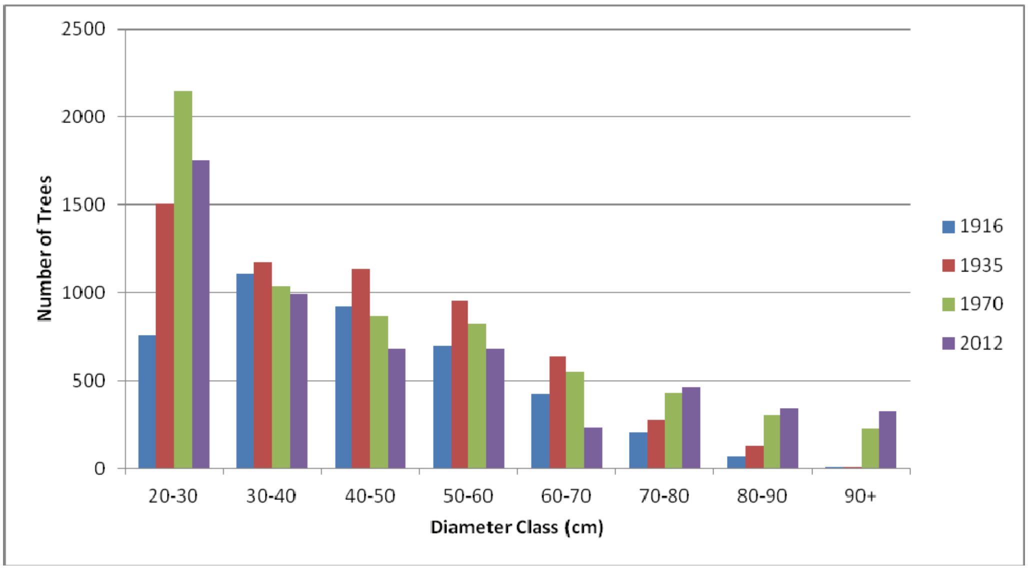

Figure 10. Changes in diameter structure during the period from 1916-2012 in absolute numbers (all trees).

Figure 11 shows losses and gains in the overall amount of trees in Dalby Söderskog in each diameter class over the study period. Between 1916 and 2012 the total number of large trees (with dbh >70 cm) increased, as did the number of trees in the smallest diameter class (with dbh 20-30 cm). At the same time the number of trees in intermediate diameter classes, particularly in the range of between 30 and 50 cm decreased. However, the overall shape of the distribution curve did not changed significantly, revealing relative structural stability of the stands (Fig. 10).

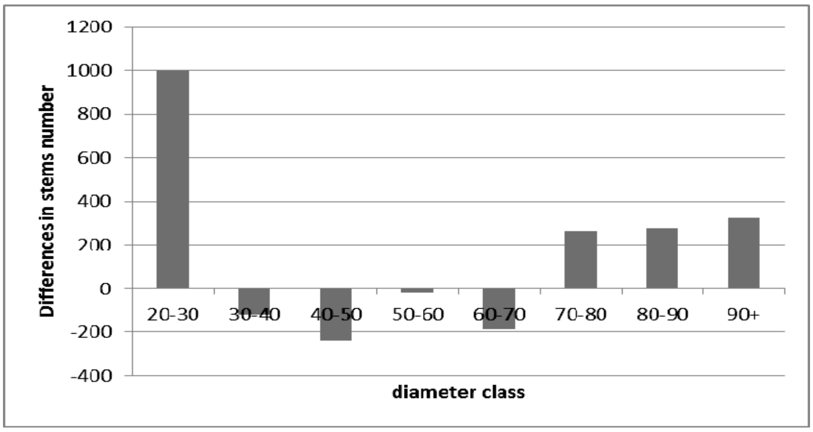

Figure 11. Difference in diameter structure during the period from 1916-2012 (all trees).

When looking at the most recent changes in diameter structure between 1970 and 2012, the situation is not similar to the overall picture throughout the past century (Fig. 12). There was a substantial reduction among small diameter trees ranging from 20 cm to 30 cm along with a decrease among middle diameter classes, particularly from 50 cm to 70 cm (Fig. 12).

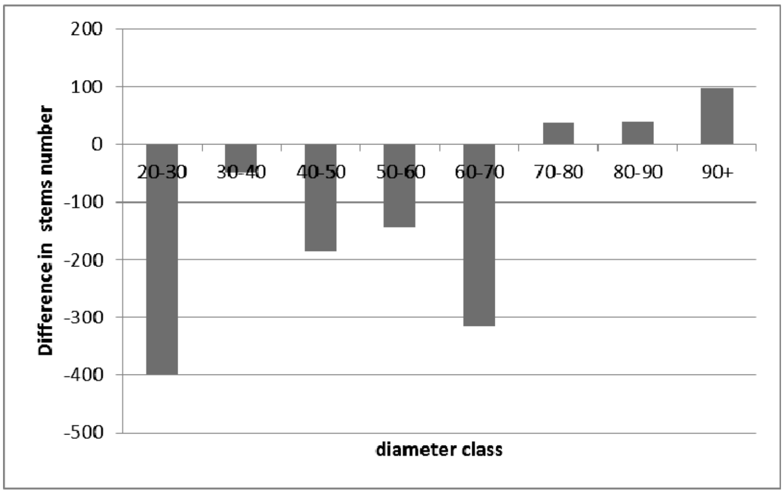

Figure 12. Difference in diameter structure during the period from 1970-2012 (all trees).

3.7 Vitality classes

With respect to tree vitality, beech displayed the highest percentage of individuals that were classified as healthy, constituting 91% of the total number of beech individuals (Table 1). Despite ash dominance in the tree canopy layer, it has the largest proportion of sick trees which constituted 55% of the ash individuals and exceeds the percentage of healthy trees (43%). Oak, which was abundant in old growth individuals, showed a relatively high percentage of healthy trees (75%) and smaller roughly equal percentages of sick and dead stems (12% and 13%, respectively). For all above mentioned species the percentages of dead trees are relatively low compared to elm. Elm had a share of 58% dead stems of the total population surveyed in 2012. At the same time, there is a high number of sick elms ranking second to ash at 23% (Table 1).

Table 1. The vitality classes in percentages for oak, beech, ash and elm in Dalby Söderskog according to measurements in 2012.

Species	**dead (%)**	**Sick (%)**	**healthy (%)**
Quercus	13	12	75
Fagus	7	2	91
Fraxinus	2	55	43
Ulmus	58	23	19

The number of elm trees, which were classified as dead, was highest in small diameter classes, particularly in the range from 10 cm to 20 cm (Fig. 13). However, their relative abundance increases into larger diameter classes. Healthy trees are absent in intermediate and large diameter classes which creates a short rotation time for elm, despite it is considered as a long living secondary succession species.

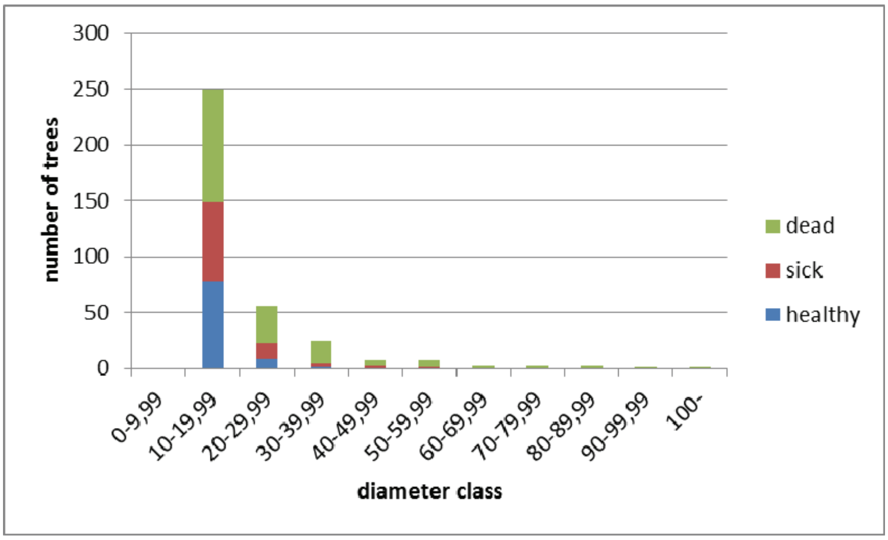

Figure 13. The distribution of vitality classes in stem diameter classes per hectare for elm in Dalby Söderskog according to measurements in 2012.

Although the distribution pattern is asymmetric, there is a tendency of vitality classes for ash. Most healthy ash trees were recorded in intermediate diameter classes, particularly ranging from 30 cm to 50 cm (Fig. 14), but the relative amount of healthy trees was higher at higher diameter classes.

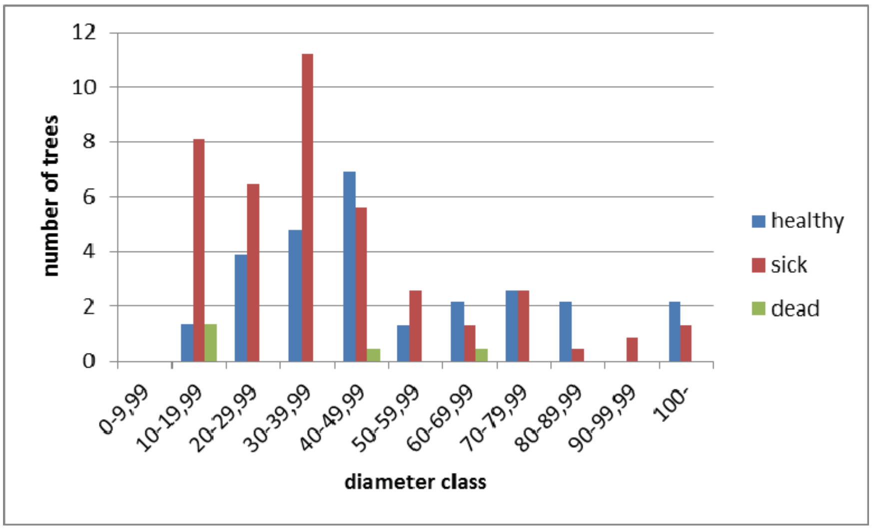

Figure 14. The distribution of vitality classes in stem diameter classes per hectare for ash in Dalby Söderskog according to measurements in 2012.

3.8 Linear regression model for oak

A linear regression analysis of the oak population indicates a continuous decline of oak in the forest if no action is taken in the future, and may cease to exist in Dalby Söderskog around the year 2080 (Fig. 15).

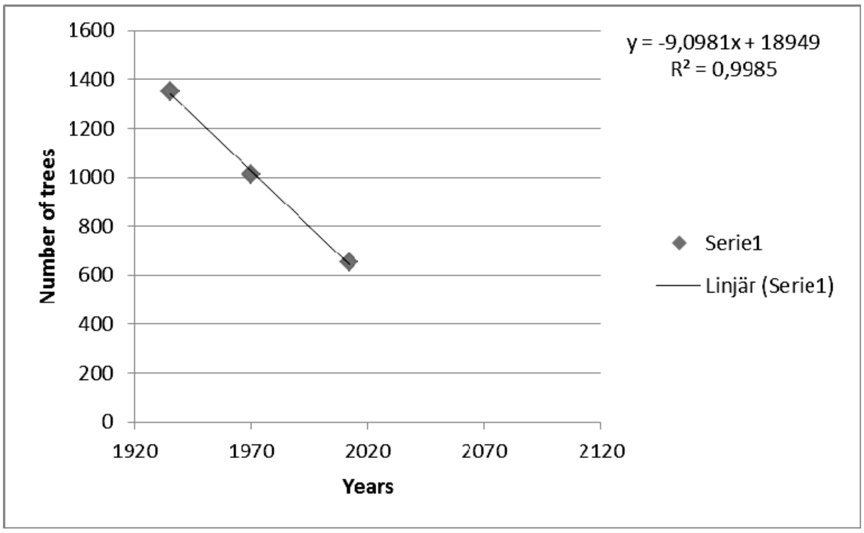

Figure 15. Linear regression for oak trees in Dalby Söderskog according to measurements between 1935 and 2012.

4. DISCUSSION

4.1 Tree species dynamics

Oak

Oak is evidently retreating from Dalby Söderskog, reflecting long-term successional trends from wood pastures to the present day forest which is characterized as having a relatively closed canopy (Emborg and Heilmann-Clausen 1992). A long-term decline in oak regeneration has been reported from a wide range of studies throughout Europe (Bernadzki et al. 1998; Mountford et al. 1999; Thomas et al. 2002; Sonesson and Drobyshev 2010). The absence of management at Dalby Söderskog since 1916 has led to the development of a closed canopy, preventing regeneration of light demanding species such as oak. During the inventory in 2012, some young oak saplings were noticed outside of the plots but their future depends heavily on light availability. The currently marginal regeneration of oak does not probably support its presence in the future. According to the suggestions of Lindquist (1938) and Malmer et al. (1978) oak may disappear from Dalby Söderskog.

Large oak trees from the period with grazing can naturally survive to the later phases of forest succession (Leemans 1992). The evidence supports that old oaks are surviving as seen in the diameter distributions. Present old growth individuals are characterized by a slow rate of degradation which allows more undergrowth to develop, resulting in already established regeneration of other trees after its decay (Emborg et al. 2000). Thus, old oaks at Dalby Söderskog allow for regeneration under their canopy.

Oaks are poorly adapted to regeneration in small canopy gaps with a strong competition for space and light. Furthermore, its competitive abilities are highest under stressful conditions, produced by low nutrient supply, high grazing level or marginal water supply (Diekmann 1996). Mountford (1999) described this process from a similar forest in terms of historical management at Denny Wood, where beech outcompeted oak due to low light availability.

The future role of oak is interesting because sudden oak death (SOD) has been reported as a common disease for oaks in southern Sweden (Drobyshev et al. 2007). Even though the rich soil in Dalby Söderskog creates favourable sites for SOD (Sonesson and Drobyshev 2010), it has not been observed among the oak population during the inventory in 2012. Insect- and fungi related crown damage did not appear to be a main reason for oak decline in southern Sweden (Sonesson and Drobyshev 2010). However, damage from SOD could impact on oak population in Dalby Söderskog in the future.

A potentially predisposing factor for oak decline could be high nitrogen input from the atmosphere and acidification processes in the soil which is currently observed across Europe, including Dalby Söderskog (Persson et al. 1987; Bobbink et al. 2010). The consequences of these processes reduce the stress tolerance and destabilize the flow of nutrients in oak ecosystems (Jonsson 2004). There was a reported correlation between nitrogen deposition and insect activities which means that oak will be more susceptible to damage by insects or pathogens (Fluckiger and Braun 1998). Oak powdery mildew could be a potential threat for oaks as well because it is common in Europe and could be present in stands without signs of excessive mortality (Camy et al. 2003). This means that future oak wellbeing may be at risk, especially for young oaks due to negative development of the regional soil conditions (Sonesson and Drobyshev 2010).

Beech

Beech was the first species to benefit from the retreat of oak at Dalby Söderskog. Until 1970 beech was represented by a small amount of trees at Dalby Söderskog (Lindquist 1938). However, after 1970 the frequency of beech in small diameter classes increased significantly and beech regeneration was most significant in close proximity to previously existing beeches. This regenerative pattern resulted in many plots lacking beech in Dalby Söderskog during the inventory in 2012. Light conditions were an unlikely reason for poor regeneration of beech until 1970 since beech is a shade-tolerant species. Seed dispersal is also not expected to be a limiting factor in regeneration on a long time scale. One possible explanation could be the high ground water level at Dalby Söderskog which inhibits the regeneration of beech since it prefers well-drained soils. It was observed recently that moisture-demanding species are declining throughout the park; this is a result of the decreasing ground water level (Oheimb and Brunet 2007). Continuation of this tendency will allow beech to spread further throughout the park and increase its relative importance in the tree species composition. Another possible explanation could be its competitive strategy known as "stop and go". The interpretation for "go" strategy is when a tree is slowly approaching a dominant position in the canopy. The "stop" phase is when a species stagnates in its development toward dominance, which occurs in the absence of favorable conditions (Emborg 2007). Such a growth pattern is a part of the forest cycle in which ash and beech compete with each other for dominance, creating a climax micro-succession from ash to beech.

Increased beech recruitment in Dalby Söderskog explains the forest dynamic with regard to a successional trend where a shade-tolerant climax species such as beech naturally substitutes a light-demanding species such as oak. In the long run, beech seems to be able to outcompete regeneration of ash and elm populations in Dalby Söderskog, especially in relatively dark places, such as gap edges and small gaps.

However, the recently reported beech decline due to Phytophthora diseases in European forests reveals a susceptibility to pathogens and may reduce its value as a competitive species (Jung 2008). Since Phytophthora symptoms have been reported from southern Sweden, we could expect their appearance in Dalby Söderskog and an increasing instability and vulnerability of the beech population.

Ash

With respect to stem frequency, it is clear that ash has become dominant in Dalby Söderskog as its population increased significantly over time, especially during the last 40 years. This is consistent with a tendency in ash populations of other European forests (Hofmeister et al. 2004; Emborg and Heilmann-Clausen 2000). Previous research in Dalby Söderskog during 1970 stressed that regeneration of ash was infrequent (Malmer et al. 1978). The inventory in 2012 showed increasing middle diameter classes and less ash recruitment into the 10 cm-30 cm classes. This tendency could be explained by ash ecology; ash has a high growth rate when it is exposed to increased light levels (Leemans 1992). Furthermore, ash is known as a light demanding gap specialist with a strong competitive strategy. The successional establishment and high growth rate of ash is thus related to canopy gaps (Emborg 2007). Therefore, the reduction of elms because of DED in Dalby Söderskog and the resulting gaps facilitated a rapid growth of ash after 1970. Interestingly, ash is the only species which had a recruitment rate constantly higher than its mortality in Dalby Söderskog between 1916 to 2012, despite of its specific preferences for soil and light conditions. These results are supported by research in Suserup Skov in Denmark (Emborg and Heilmann-Clausen 2007).

Besides gap regeneration, the increase of the ash population could be explained by increased nutrient availability at Dalby Söderskog since its conversion to a National park (Persson et al. 1987). Therefore, decomposing organic material which was previously removed due to grazing now provides an important source of nitrogen enrichment and helps facilitate ash recruitment (Hofmeister et al. 2004).

Ash is tolerant to pathogens such as Phytophthora (Jung, 2008). However, it is noteworthy that more than half of the ash population in Dalby Söderskog is now affected by ash dieback (caused by the fungus *Chalara fraxinea*), a fact that casts doubt on its continuing dominance in the future succession. The majority of infected ash trees are relatively young or middle age. This phenomenon could be due to better vigor of larger trees (McKinney et al. 2011). A large variability in ash susceptibility to the pathogen was, so far, observed at Dalby Söderskog. However, based on the above mentioned data we suggest that ash dieback could lead to a reduction in the ash population in the long run at Dalby Söderskog.

Another scenario could include a long-term coexistence of early successional species such as ash in a late successional forest as was reported in Suserup Skov (Emborg 2007). In Dalby Söderskog this scenario is plausible because of the differences in the regenerative niches of beech and ash in terms of soil requirements and decreasing competition from elm due to DED along with a still large fraction of healthy ash trees. In sum, ash could be an important species in long-term forest succession in Dalby Söderskog unless the recent ash dieback will not lead to further increased mortality.

Elm

Inventories from Lindquist (1938) and Malmer et al. *(*1978) predicted dominance of elm in the forest canopy at Dalby Söderskog. However, the last inventory indicates a significant reduction in the frequency of elm among all diameter classes. In fact, almost no old elm trees were recorded in Dalby Söderskog. This species experienced rapid growth in number of stems between 1935 and 1970, but since then more than two thirds of the elm population disappeared from Dalby Söderskog because of Dutch elm disease (DED). DED was recorded in Skane in 1979, in Dalby Söderskog it appeared after 1986 and rapidly started to spread (Oheimb and Brunet 2007). By 2012, dead elm trees could be seen all over the forest and many canopy gaps had been created, where infected elm had been killed. Therefore, a significant proportion of elm trees were reported as dead or sick. Elm lost its dominant position in the tree species composition at Dalby Söderskog, and currently it is ranked only third after ash and beech. However, a high level of elm mortality has been compensated by plentiful recruitment of smaller elms in Dalby Söderskog. Therefore, successful regeneration from seeds has been a main survival mechanism of elm at Dalby Söderskog over the DED outbreak period. In the unmanaged Suserup Skov forest, which has been subjected to DED since 1994, similar trends with large dead trees and resulting gaps were found (Emborg and Heilmann-Clausen 2007).

Different scenarios for forest succession in Dalby Söderskog were reported, including Leemans (1992) simulation model that forest equilibrium will be achieved by 2020. This model described forest succession at Dalby Söderskog as elm stands with scattered individuals of oak and ash, while beech will keep the patches that initially were regenerated by it within the same location. The assumption about elm dominance in a future at Dalby Söderskog was supported by Lindquist (1938) and Malmer et al. (1978) and based on elm ecology as a late successional shade-tolerant species with a competitive regeneration strategy. However, DED reversed this successional trend. DED attacks probably will continue and it is too early to evaluate the full consequences of these relatively slow developed disturbances (Emborg and Heilmann-Clausen 2007) in Dalby Söderskog. It is noteworthy that increased nitrogen accumulation in the topsoil of Dalby Söderskog (Persson et al. 1987) could extend the duration of susceptibility period and greatly increase the intensity of external symptoms of elm (Martin et al. 2010). Moreover, climatic extremes, that become more frequent throughout the world, are likely to increasingly constrain the ability of elms to resist against DED (de Dios et al. 2007). Therefore, the DED situation in Sweden and particularly in Dalby Söderskog probably will be the same in a short term along with DED impact being an important factor in forest succession.

Since infected elms are still able to produce seeds and establish in the gaps of fallen trees, we expect its continuous regeneration at Dalby Söderskog resulting in a short rotation of small fast-growing individuals. Therefore, elm might be able to maintain itself as an important component of the understory or at canopy level for many decades in Dalby Söderskog even in the presence of DED. Reviews from Michigan (Richardson and Cares, 1976) supports this assumption since DED impact in *Ulmus Americana* population did not change elm dominance in terms of density and total basal area, despite most of the trees being infected.

4.2 Disturbance and succession

The earlier use as wood pasture provided conducive light conditions for light demanding species, for example, hazel and hawthorn in the understorey, and oak in the canopy layer. The development from relatively open forest to the dense dark forest during last century appeared as a normal autogenic succession in Dalby Söderskog. However, continued existence of oak is dependent on human activity that maintained its predominance. The cease of grazing after the protection of the forest in 1918 resulted in a combination of inherited large old trees, a long period of natural infilling, and natural gap creation. Absence from silvicultural interventions generated an age structure which spans the natural range of the main species and a near-natural gap pattern (Mountford et al. 1999).

Steady state represents a dynamic equilibrium, in which variables such as species composition do not change significantly over time (Loucks 1970). However, in small areas such as Dalby Söderskog, the changes in successional trends could be more dramatic due to acceleration from random disturbances (Emborg et al. 2000). Random influences could not be avoided from the forest system and they periodically occur in the form of invasion of new species, pathogen outbreaks, climate change or small scale disturbances. Therefore, forests are always structurally and functionally changing over time (Davis 1981). During all observation periods species composition has varied in Dalby Söderskog, but nevertheless the general tendency before 1970 held closely to predictions. After the forest was released from livestock grazing and irregular cutting, successional stability reigned for a couple of decades and an elm dominated community was prevailing accompanied by a closed canopy stage. However, DED impact afterwards appeared as a random influence on the forest ecosystem causing significant changes in successional trends. DED has affected gap dynamics and forest composition respectively to a big extent at Dalby Söderskog. Considering ash dieback and potential beech Phytophtora disease, the amount and size of gaps will probably increase and a closed canopy stage will not dominate at Dalby Söderskog in the near future.

A similar compositional instability was reported in Bialowieza National Park, where a decline of both early- and late-successional species was reported (Bernadzki et al. 1998). However, both parks showed overall structural stability that could be explained by gradual accumulation of large diameter trees along with continuous recruitment process of other species.

The Suserup Skov model that considers succession as a directional process within the cycle dynamics could be applied also to Dalby Söderskog (Emborg et al. 2000). According to this concept, cyclic and directional processes are intermingled: Dalby Söderskog has achieved overall structural stability with some oscillation due to DED disturbance, while species composition is still changing. The directional process in this case is a long-term successional change regarding species composition (Emborg et al. 2000). Oak presence in this system is a result of human influence and therefore, it has been slowly vanishing from Dalby Söderskog.

5. CONCLUSION

To conclude, this example from Dalby Söderskog represents a complex relationship between succession and climax, between directional trends and cycles along with human and natural disturbance regimes. The long term effects of successional processes in Dalby Söderskog are not possible to predict in detail. However, it seems that large scale ecological disturbances cause pulses of rapid change in species composition followed by the steady periods with continuous development. At present, it seems that the ash dieback is about to stop the increasing trend for ash, while beech will spread further in the forest, and oak and elm will continue to decline.

As an ecological system, the forest has proved to be relatively resistant. Although some changes in structural and compositional dynamics have occurred, the forest ecosystem has not yet been generally pushed back to an early successional stage. That means that Dalby Söderskog may be able to maintain itself as a multi-aged, multi-layered forest under the current disturbance level unless additional large scale disturbances take place. However, it is noteworthy that consequences of DED and oak decline in Dalby Söderskog could lead to loss of habitats for organisms which are species specific, negatively affecting forest-related biodiversity within Dalby Söderskog.

6. LITERATURE

Anonymous (2008): The condition of forest in Europe. – Executive Report, World Forestry, Hamburg.

Baeten, L., Hermy, M., Van Daele, S., Verheyen, K. (2010): Unexpected understory community development after 30 years in ancient and post-agricultural forests. – Journal of Ecology, 98: 1447-1453.

Bakker, J.P., Olff, J.H., Willems, J.H., Zobel, M. (1996): Why do we need permanent plots in the study of long-term vegetation dynamics? – Journal of Vegetation Science, 7: 147-155.

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajaczkowski, J., Zybura, H. (1998): Compositional dynamics of natural forests in the Bialowieza National Park, northeastern Poland. – Journal of Vegetation Science, 9: 229-238.

Blaha, J., Kotecky, V. (2008): Over-abundant animals graze tree samplings in Czech forest. – Hnuti Duha, Brno.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., et al. (2010): Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. – Ecological Application, 20: 30-59.

Bormann, F.N., Likens, G.E. (1979): Catastrophic disturbance and the steady state in northern hardwood forests. – American Scientist, 67: 660-669.

Butin, H. (1996): Tree diseases and Disorders, Causes, Biology and Control in Forest and Amenity trees. Oxford University Press.

Camy, C., Delatour, Marcais, B. (2003): Relationships between soil factors, *Quercus robur* health, *Collybia fusipes* root infection and *Phytophtora* presence. – Annals of Forest Science , 60: 419–426.

Davis, M.B. (1981): Quaternary history and stability of forest communities, in D.C. West, Shugart, H., Botkin, D.B., Forest Succession: Concepts and Application. Springer-Verlag, New York, 132-177.

De Dios, V. R. et al. (2007): Climate change effects on Mediterranean forests and preventive measures. – New Forests, 33: 29-40.

Diekmann, M. (1996): Ecological behaviour of deciduous hardwood trees in boreo-nemorial Sweden in relation of light and soil conditions. – Forest Ecology and Management, 86: 1-14.

Drobyshev, I. , Linderson, H., Sonesson, K. (2007): Temporal mortality pattern of pedunculate oaks in southern Sweden. – Dendrochronologia, 24: 97-108.

Ellison, A., Bank, M., Clinton, B., Colburn, E., Elliott, K., Ford, C. et al. (2005): Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. –Frontiers in Ecology and the Environment, 3: 479-486

Emborg, J., Christensen, M., Heilmann-Clausen, J. (2000): The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. – Forest Ecology and Management, 126: 173-189.

Emborg, J. (2007): Suppression and release during canopy recruitment in *Fagus sylvatica* and *Fraxinus excelsior*, a dendro-ecological study of natural growth patterns and competition. – Ecological Bulletins, 52: 53-67.

Eriksson, O., Cousins, S., Bruun, H. (2002): Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. – Journal of Vegetation Science, 13: 743-748.

Etherington, J. R. (1975): Environment and plant ecology. – Wiley, London.

Flückiger, W., Braun, S. (1998): Nitrogen deposition in Swiss forests and its possible relevance for leaf nutrient status, parasite attacks and soil acidification. – Environmental Pollution, 102: 69–76.

Hofmeister, J., Mihaljevic, M., Hosek, J. (2004): The spread of ash (*Fraxinus excelsior*) in some European oak forests: an effect of nitrogen deposition or successional change? – Forest Ecology and Management, 203: 35-47.

Jonsson, U. (2004): *Phytophtora* and oak decline –impact on seedlings and mature trees in forest soil. – Ph.D. thesis, Lund University, Sweden.

Jung, T. (2008): Beech decline in Central Europe driven by the interaction between *Phytophthora* infection and climatic extremes. – Forest Pathology, 39: 73-94.

Larsen, J., Rasmussen, K., Callesen, I. (2005): Træartsvalet – de enkelte træarters økologi. – Dansk Skovbrugs Tidsskrift, 90: 139-169.

Leemans, R. (1992): Simulation and future projection of succession in Swedish broadleaved forest. –Forest Ecology and Management, 48: 305-319.

Lindquist, B. (1938): Dalby Söderskog, en skånsk lövskog i forntid och nutid. – Acta Phytogeographica Suecica, 10: 1-273.

Loucks, O. (1970): Evolution of diversity, efficiency and community stability. – American Zoologist, 10: 17-25.

Malmer, N., Lindgren, L., Persson, S. (1978): Vegetational succession in a south Swedish deciduous wood. – Vegetatio, 36: 17-29.

Martin, J., Fuentes-Utrilla, P., Gil, L., Witzell, J. (2010): Ecological factors in Dutch elm disease complex in Europe – a review Ecological Bulletins, 53: 209-224.

McLachlan, J., Foster, D., Menalled, F. (2000): Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. – Ecology, 81: 717-733.

McKinney, L., Thomsen, I., Kjar, E., Nielsen, L. (2011): Genetic resistance to *Hymenoscyphus pseudoalbidus* limits fungal growth and symptom occurrence in *Fraxinus excelsior*. – Forest Pathology, 42: 69-74

Mountford, E.P., Peterken, G.F., Edwards, P.J., Manners, J.G. (1999): Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). – Perspectives in Plant Ecology, Evolution and Systematics, 2: 223-272.

Oheimb, G.v., Brunet, J. (2007): Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. – Acta Oecologica, 31: 229-242.

Persson, S., Malmer, N., Wallen, B., (1987): Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest. – Vegetatio, 73: 31-45.

Peterken, G.F. (1996): Natural woodland. – Cambridge University Press, Cambridge.

Peterken, G.F., Mountford, E. (1998): Long-term change in an unmanaged population of wych elm subjected to Dutch elm disease. – Journal of Ecology, 86: 205-218.

Rackham, O. (1989): The last forest: the story of Hatfield Forest. – London, UK.

Rackham, O. (2008): Ancient woodlands: modern threats. – New Phytologist, 180: 571-586.

Richardson, C.J., Cares, C.W. (1976): An analysis of elm (*Ulmus Americana*) mortality in a second-growth hardwood in south-eastern Michigan. – Canadian Journal of Botany, 54: 1120-1225.

Samonil, P., Vrska, T. (2008): Long-term vegetation dynamics in the Sumava Mts. natural spruce-fir-beech forests. - Plant Ecology, 196: 197-214.

Sonesson, K., Drobyshev, I. (2010): Recent advances on oak decline in southern Sweden. – Ecological Bulletins, 53: 197-207.

Strandberg, B., Kristiansen, S.M., Tybirk, K. (2005): Dynamic oak-scrub to forest succession: Effects of management on understory vegetation, humus forms and soils. – Forest Ecology and Management, 211: 318-328.

Szabo, P. (2010): Driving forces of stability and change of woodland structure: the case study from the Czech lowlands. – Forest ecology and management, 259: 650-656.

Thomas, F. M., Blank R., Hartmann, G. (2002): Abiotic and biotic factors and their interactions as causes of oak decline in central Europe. – Forest Pathology, 32: 277-307.

Tybirk, K., Strandberg, B. (1999): Oak forest development as a result of historical land-use patterns and present nitrogen deposition. – Forest Ecology and Management, 114: 97-106.

Vera, F.W.M. (2000): Grazing ecology and forest history. – CAB International, Wallingford.

Verheyen, K., Baeten, L., Pieter-Frenne, Bernhardt- Romermann, M., Brunet, J. et al. (2012): Driving factors behind the eutrophication signal in understory plan communities of deciduous temperate forest. – Journal of Ecology, 100: 352-365.

Welander, J. (2000): Spatial and temporal dynamics of wild boar (Sus scrofa) rooting in a mosaic landscape. – Journal of Zoology, 252: 263-271.

Whitmore, T.C. (1989): Canopy gaps and the two major groups of the forest trees. – Ecology, 70: 536-538.

7. ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisor Jörg Brunet for the time he spent with me, explaining things and being able to provide consultation as many times as I needed, and especially for his comments on earlier versions of this thesis. Also I appreciate him sharing data with me and for his help during the field work.

I would also like to thank Matts Lindbladh for helpful comments on the preliminary version of this thesis and for taking over the work as examiner.

A special thank goes to Mark Brand for supporting me during the whole time while working on this thesis.