Mortality dynamics in an old-growth stand of beech (*Fagus sylvatica*) in Southern Sweden

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ABSTRACT

Mortality patterns were assessed in an old growth beech stand in southern Sweden. A previous inventory of 1200 trees in 1996 was used as a base for an inventory in 2006. Mann-Whitney U test was used to compare statistical distribution between living and dead trees of those inventoried in 2006. Dendrochronological reconstruction was applied for assessment of the temporal patterns of mortality. The mortality rate was 18% in ten years, affecting mainly larger diameter classes >40cm dbh. During the study period, 6.9 % of the total amounts of living trees became high stumps, from which 45% subsequently died. In understory trees, growth reactions and scars related to tree falls and canopy damage increased by over 80 % between the 1970’s and the 1990’s, suggesting an increasing disturbance rate over this period. The causes of death could not be attributed to disturbances by themselves, but rather to a combination of fungal infection (mainly *Fomes fomentarius*) and wind in most cases. The mortality level found in this beech population is rather high compared to other studies in European deciduous forest. Since the age of the stand is near the reported maximum of the species, mortality is likely to be high in the future. Damaged beech trees that survive a long time (over ten years) provide unique substrate for species assemblages, constituting a desirable feature for conservation.

INDEX

No Title Page

FIGURES

TABLES

1. INTRODUCTION

Tree mortality in temperate deciduous forests can be provoked by aboitic factors such as drought (Peterken and Mountford 1996), storms (Peterken 1996, Pontailler et al. 1997, Mountford 2003, Wolf et al. 2004), or landslides (Stefanini 2004). Also biotic factors may damage or kill a single tree or groups of trees, for instance, insect outbreaks (Houston 1994) or fungal attacks (Baum et al. 2003). Researchers have reported different mortality rates for beech forest, ranging from 0.5 up to 3.3 % yr^{-1} (Runkle 1985, Peterken and Mountford 1996, Wolf et al. 2004) in respect to different disturbance agents. Mortality may affect cohorts composing the stand in different ways, due to, for example, difference in age and the distance to the closest competitor (Rozas and Fernández 2000). Therefore, seedlings growing in a cluster might experience higher risk of weakening and dying because of intraspecific competition (Peet and Christensen 1987; Collet and Le Moguedec 2007) or predation (Rozenbergar et al. 2007). Larger trees may run a higher risk of damage or death due to their greater area of exposure to wind (Rozas and Fernández 2000).

In temperate forests, the death of one or several trees often creates a gap in the canopy (Watt 1947, Runkle 1985). Big gaps are usually filled up by understory trees and seedlings, while very small gaps will be filled only with lateral branch expansion and undergrowth already established (Runkle 1982, Forrester and Runkle 2000). Branches suddenly exposed to sun light react with a vigorous growth, “release”, recorded in the radial growth as a sudden increase in the ring width (Gutiérrez et al. 2008). When the canopy opening becomes smaller, the under-growing trees start competing for light and soil nutrients. Due to this competition some of these trees may suffer a decrease in the radial growth (suppression) or even die. Through examination of growth releases and suppressions on samples obtained from branches or from the main stem of the tree it is possible to assess and reconstruct the events affecting the upper canopy (Gutiérrez 2002, Gutiérrez et al. 2004, 2008) and thereby assess the temporal aspects of disturbance dynamics (Fritts 1976, Runkle 1985). In this study I explore the dynamics of one of the best preserved beech stands in Sweden. The stand has retained characteristics of an old growth forest, such as high tree age and large amount of dead wood. The aims of this work are: (1) to test the hypothesis (*H0*) whether events causing mortality affect all diameters evenly; versus (*H1*) mortality affects a determined diameter class or group of trees in the stand; (2) to assess the mortality rate of the whole stand; (3) to assess the temporal patterns of the disturbance that induce mortality, in order to clarify whether there exists a temporal trend and (4) to suggest the possible causes of death.

2.-METHODS

2.1. Site description

The study was done in Biskopstorp (lat 56°, 48’ N, long 12°,52’ E), a nature reserve located 2 km NE of the village Kvibille, (lat 56° 47’ N, long 12° 53’E), about 15 km inland from the coastal shore in SW Sweden (Martinsson 2004) (Figure 1-a,b).

Figure 1 *a) Location of Biskopstorp in Sweden, b) Biskopstorp in Halland (www.eniro.se).*

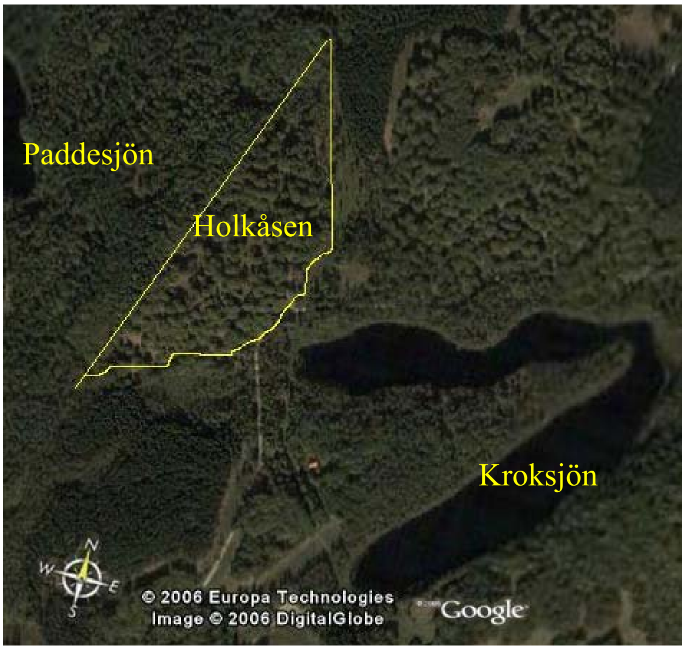

Figure 2. Satellite image of Biskopstorp kronopark. Within yellow borders the stand Holkåsen by the lake Kroksjön (Googleearth)

2.1.1. Topography

With an average elevation of 65 m.a.s.l., the topography varies from flat meadows with deep soils to a low mountain landscape with shallow soils. Several streams flow within the reserve (an average of four permanent streams per km^2). Seven lakes provide attractive scenery and habitat for fish and water living organisms, while mires occur at different places, creating a vegetation mosaic. The stream Gisslabolsbäcken is the main drainage of the reserve.

2.1.2. Climate

The climate is characterized by a rather strong oceanic influence with, by Swedish standards, mild winters and cool summers. Rainfall occurs throughout the year with an annual average of 1000 mm and the mean annual temperature reaches 7^{o}C (Bengtsson 1999, Martinsson 2004). Mean July temperature is 15,5^{o}C and mean January temperature -1.6 ^{o}C. (SGU 1988) …

2.1.3. Biological values

One noteworthy feature is the long-time forest continuity of many deciduous stands providing habitat and resources for endangered plant and animal species. The studied stand (Holkåsen) is remarkable as it hosts a great number of indicator and red-listed species including saproxylic insects, (Jansson 2004, cited by Heilmann-Clausen 2005) and epiphytic lichens and bryophytes (Fritz 2004, 2006). The broadleaved forests as a whole host 130 red-listed species and 33 key-habitats have been identified (Fritz 2004).

2.1.4. Vegetation

The forest cover in the reserve is a mosaic dominated mainly by spruce plantations of *Picea abies* (72 % before restoration back to deciduous forest), 17 % is beech (*Fagus sylvatica*), about 11 % oak (*Quercus robur* and/or *Q. petraea*), birch (*Betula pendula*) and pine, (*Pinus sylvestris*),(Bengtsson 1999). Other species such as alder (*Alnus glutinosa.*), hazel (*Corylus avellana.*), maple (*Acer platanoides.*), rowan (*Sorbus aucuparia),* and lime (*Tilia cordata*) can also be found, *Tilia* as well as *Ulmus sp*. are restricted to a few steep slopes, rich in boulders. Most deciduous forest types are frequently invaded by spruce seedlings.

2.1.5. The stand Holkåsen

The studied stand (3.96 ha), lies on a ridge approximately in the centre of the reserve, between the lakes Kroksjön and Paddesjön. On the east flank a road delimits the stand, while the western border, demarked by a stone wall, borders a spruce plantation (40 to 70 years old). At both the northern and southern ends the stand ends in wetlands (Fig 3.2). The stand is dominated by beech, ca 90% of the basal area, followed by spruce, birch and pine, and in a very low percentage, glossy blackthorn (*Frangula alnus*) oak (*Q. robur/petraea*), juniper and rowan (S*orbus aucuparia*).

The stand contains two different generations (cohorts), an older one ranging from 240 to 286 years, and a younger from 36 to 66 years of age based on counted year rings (Niklasson et al. 2005). The younger cohort is composed by younger trees densely grouped in some patches in the stand, while the older trees are sparsely distributed throughout the area. The stand has the highest conservational value (in terms of number and status of threatened and red listed species) of all stands in the whole reserve, and is one of the most valuable stands in southern Sweden (Fritz 2004, Heilmann-Clausen 2005).

2.2. The Inventory

2.2.1. Inventory 1996

During 1996, an individual based tree inventory was performed in Holkåsen (Karlsson 1996) used in this report as base data. In 1996, an optic theodolite was used in order to calculate and record coordinates (x,y). The “y” axis was referred to a stone wall deviated 10 to 17 degrees E from the true North. Every living tree within the stand with a dbh > 2 cm or taller than 1 meter was measured. The amounts of fungal bodies were counted; the bark loss and damages were visually estimated. Locations and diameters of logs and stumps were also measured.

2.2.2. Inventory 2006

According to the system used in Karlsson (1996), I surveyed every living and dead tree inventoried before. The trees that were not found and had a previously recorded dbh lower than 10 cm I assumed dead. The trees found in field 2006, but clearly not recorded in 1996, I measured and set apart from further analysis. New recruitment was not added (seedlings reaching 2 cm dbh and 1 m height) due to time constraints. TCC (tree condition class) was used as in Karlsson 1996. In order to collect information to analyze the data and possible causes of death, the presence of branches in the crown, presence of brown leaves, tree social status in respect to its neighbors and forest cover surrounding the trees were added to the set of variables measured in 1996 (Table 1).

2.2.2.1. Variables

For each tree a number of variables were measured or estimated (Table 1).

Table 1. Recorded variables in 1996 and 2006

Variable	*Symbol example*	*Comment*	*1996*	*2006*
Number of tree	001	Used as in 1996	Yes	Yes
Coordinate	(0, 15000)	South axe, 15 m to east	Yes	Yes
Status	1 /0	Alive/dead	Yes	Yes
TCC*	Lt, Ds, Hst, Stump.	Living tree, Dead standing tree, high stump and stump	Yes	Yes
Diameter	Dbh	Diameter at the breast height, at 130 cm height	Yes	Yes
Height	10 m	Estimated	n=427	n=264
Social status	E, D, I and S	Emerging; dominant; intermedial and suppressed	No	Yes
Number of trees with Fungal fruit bodies. (FFB)	1,2,3…	Trees that have Fungal fructiferous bodies on the stem	Yes	Yes

* TCC: (tree condition class) LTH, healthy living trees; LT_{DA} , damaged living tree; a tree with up to 50% of branches lost in the upper crown; DS, dead standing tree; HST_{L}, living high stump; HST_{DE} , dead high stump; LST_{L} , living low stump; LST_{DE} , dead low stump; LOG, a lying trunk or fragments of the tree bole. *Traces* are woody detritus remaining after decomposition of a stump or log. *Uprooted* are fallen trees with root plate exposed. *Not found* are trees recorded in 1996 but not found during 2006 census.

2.3. Data analysis

The software program Statistica 6.0. was used for statistical analyses. Man whitney U test was used to test distribution of living and dead trees (Dytham 2001).

2.3.1. Dendrochronological reconstruction of disturbances

2.3.1.1. Sample collection

I collected wedges, cross sections and cores from living and dead trees; spruce (n =191) and beech (n =30). The collection of samples was aimed towards trees that could give information of deaths or damages of trees in the stand during the last ten years. In addition, I analyzed wedges and cores collected in previous inventories performed in 1998 and 2004 respectively (n=69) (Fahlvik 1999, Niklasson et al. 2005).

2.3.2. Laboratory analysis

All the samples were labeled, cut and sanded using standard methods (Stokes and Smiley 1968). A stereoscopic magnifying glass (40 X) was used to visually cross-date the samples. Beech samples with white rot were wet and dyed with blue-methilene and analyzed under a blue filter and/or a polarity-inverter filter when needed. A simple cross-dating method was used to date samples of dead wood (Yamaguchi 1991). This method consists of examining the tree rings and identifying pointer years to achieve cross-dating among the samples. Different trees may react in similar ways to environmental variation and a pointer year is a year-ring for which different samples show similar characteristics, therefore it is possible to date a sample of a tree by using sequences of pointer years (Stokes and Smiley 1968, Fritts 1976).

2.3.2.1. Dating canopy disturbances: Releases and suppressions

Canopy disturbances were assessed by analyzing the following evidences: a) sudden changes in annual growth, so called “releases or suppressions” observed in samples of spruce undergrowth; b) scars, damages and irregularities (such as changes in color or colored spots in the cell walls of the early or summer wood) in the yearly growth of spruce undergrowth; and c) year of death of mature beech trees (when possible) and undergrowth of spruce samples (Gutiérrez 2002). The annual growth of a tree responds to the availability of resources. Sudden changes in the environmental conditions may provoke variations in the amounts of resources that trees can utilize. Growth releases for instance, can occur after a tree fall, as a reaction to the increased amounts of light, or the death of a competitor tree. This reaction will show as a sudden and sustained increase in the annual ring width. Growth suppressions instead show as narrowing of the annual ring width. A progressive narrowing in the ring width may indicate lessening of resources, perhaps due to competition, while a sharp decrease in annual ring-width may be a signal of sudden exposure to weather agents or to mechanical damages, for example damages caused directly by a falling branch. Reaction years were identified and recorded following the criteria used in Lorimer (1985), Lorimer and Frelich (1989) and Gutiérrez (2004). All the releases and the suppressions of the samples were weighed against the total number of samples to generate a relative frequency of reactions.

2.3.2.2. Dating canopy disturbances: Cross-dating scars

Agents such as fire, herbivores, mechanical damages, wind, frost, and insects among others, can provoke scars in the cambium of the growing stem. All scars recorded by different samples, weighed against the amount of samples will generate a relative frequency of the scars. This data is useful for comparing the time when scars have been registered, therefore the extent of disturbance events.

3. RESULTS

3.1 Mortality

3.1.1. Living and dead trees in the stand

3.1.1.1. Mortality.

From the total of 1189 living beech trees found in 1996, 217 (18.5 %) were found dead in 2006 (Table 2). When looking at living trees but damaged in 1996 (n=63), mortality was considerably higher, reaching up to 25.4 % in 10 yr (n=16). Trees classified as living high stumps in 1996 (n=148) had even greater level of mortality over the ten years, 70.3% (n=104, table 2). The great majority of the trees found dead in 2006 (alive in 1996) were recorded as high stumps (n=88, table 2), representing 40% of the pool of dead trees, followed by stumps (n=66, 30% of the pool of dead trees). The majority of the dead stumps inventoried in 2006 (n=47) have been recorded as high stumps or damaged trees in 1996's census.

3.1.1.2. Dead standing

Dead standing trees (DS) were more common in the smallest diameter class (13 with dbh <21cm versus 1 with dbh >40 cm), reaching up to 6% of the pool of dead trees recorded in 2006.

3.1.1.3. High stumps

High stumps created from the pool of living healthy trees reached up to 6.9% during the study period, conformed mainly by greater diameter classes (>40 cm).

3.1.1.4. Living trees damaged

From the total amount of living trees recorded as healthy in 1996, 198 were recorded as living trees damaged in 2006, within this group 67.1% were trees with dbh greater than 40 cm.

Table 2. Summary of the census data for the trees recorded as living during 1996 census. For each category absolute number of trees and number of trees per ha (in brackets) are given. TCC are: LTH, healthy living trees; LT_{DA} , damaged living tree; a tree with up to 50% of branches lost in the upper crown; DS, dead standing tree; HST_{L}, living high stump; HST_{DE} , dead high stump; LST_{L} , living low stump; LST_{DE} , dead low stump; LOG, a lying trunk or fragments of the tree bole. *Traces* are woody detritus remaining after decomposition of a stump or log. *Uprooted* are fallen trees with root plate exposed. *Not found* are trees recorded in 1996 but not found during 2006 census.

Diameter class, cm	TCC	Total count and density 1996	LTH	LT_{DA}	DS	HST_{L}	HST_{DE}	LST_{L}	LST_{DE}	LOG	Traces	Uprooted	Not found
< 21	LTH	528 (133.3)	364 (91.9)	97 (24.5)	13 (3.3)	4 (1.0)	3 (0.8)	-	12 (3.0)	4 (1.0)	13 (3.3)	-	18 (4.5)
< 21	LT_{DA}	12 (3.0)	3 (0.8)	7 (1.8)	-	-	-		2 (0.5)	-	-	-	-
< 21	HST_{L}	6 (1.5)	1 (0.3)	-	-	3 (0.8)	1 (0.3)	-	1 (0.3)	-	-	-	-
< 21	LST_{L}	6 (1.5)	-	-	-	-	-	2 (0.5)	4 (1.0)	-	-	-	-
21 - 40	LTH	213 (53.8)	164 (41.4)	36 (9.1)	-	6 (1.5)	3 (0.8)	-	2 (0.5)	1 (0.3)	-	1 (0.3)	-
21 - 40	LT_{DA}	10 (2.5)	3 (0.8)	2 (0.5)	-	1 (0.3)	3 (0.8)	-	1 (0.3)	-	-	-	-
21 - 40	HST_{L}	26 (6.6)	-	-	-	3 (0.8)	5 (1.3)	1 (0.3)	12 (3.0)	2 (0.5)	1 (0.3)	-	2 (0.5)
41 - 60	LTH	189 (47.7)	103 (26.0)	48 (12.1)	1 (0.3)	20 (5.1)	15 (3.8)	-	1 (0.3)	-	-	1 (0.3)	-
41 - 60	LT_{DA}	31 (7.8)	-	18 (4.5)	-	8 (2.0)	4 (1.0)	-	1 (0.3)	-	-	-	-
41 - 60	HST_{L}	93 (23.5)	-	1 (0.3)	-	20 (5.1)	35 (8.8)	1 (0.3)	29 (7.3)	4 (1.0)	2 (0.5)	-	1 (0.3)
> 60	LTH	44 (11.1)	15 (3.8)	17 (4.3)	-	4 (1.0)	8 (2.0)	-	-	-	-	-	-
> 60	LT_{DA}	9 (2.3)	2 (0.5)	1 (0.3)	-	2 (0.5)	4 (1.0)	-	-	-	-	-	-
> 60	HST_{L}	22 (5.6)	-	-	-	14 (3.5)	7 (1.8)	-	1 (0.3)	-	-	-	-
Total		1189 (300.3)	655 (165.4)	227 (57.3)	14 (3.5)	85 (21.5)	88 (22.2)	4 (1.0)	66 (16.7)	11 (2.8)	16 (4.0)	2 (0.5)	21 (5.3)

3.2. Statistical comparison between living and dead trees.

According to the results obtained using Mann-Whitney U test, trees recorded alive in 1996 and found dead in 2006 had significantly greater diameter than the group of trees found alive in 2006 ($p > 0.05$, Table 3). This result suggests that mortality affected mainly trees in larger sizes during the period of study.

Table 3. Summary table of Mann-Whitney U Test using individual diameters of living and dead trees. Marked tests are significant at $p > 0.05$.

Rank sum group 1	Rank sum group 2	U	Z	p-level	Z adjusted	P-level	Valid N group 1	Valid N group 2	2*1 sided exact p
38.000	287.000	2.0000	-3.8448	0.000121	-3.92570	0.000086	8	17	0.000007

(Figures of the statistical distribution of both groups are shown in the appendix).

3.3. Structure

3.3.1. Diameter distribution of living and dead trees in 1996 and 2006

The stand is composed by two cohorts; this feature is reflected in the dbh distribution of the living trees showing a bimodal curve. The youngest cohort ranged from 1 to 25 cm dbh (ca.153 trees ha^{-1}), and the older one ranged above 41 cm dbh (94 trees ha^{-1}) (Figure 3a and 3c, figure 8 in the appendix). The dbh distribution of dead trees was similar with the dbh distribution of older living cohort present in the stand (Figure 3and figure 9 in appendix). The contribution of the older cohort to the pool of dead wood was larger in number of trees and basal area if compared to the contribution of the younger cohort. The last experienced a decrease in its contribution to the pool of dead wood from 1996 to 2006 (Figures 3b, 3d and figure 9 in the appendix).

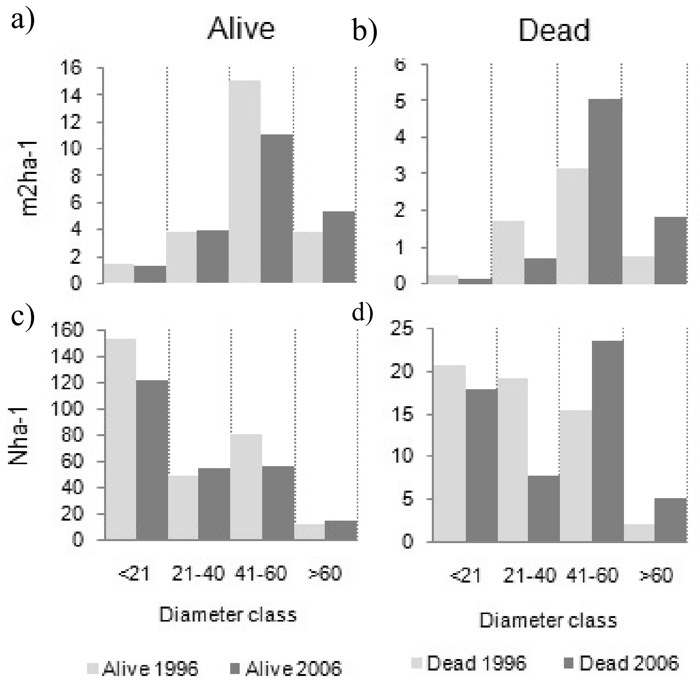

Figure 3 Diameter distribution of living and dead trees in Holkåsen: a) Living trees basal area, light bars living trees in 1996, darker bars living trees 2006. b) Dead trees basal area, light bars dead trees in 1996, darker bars dead trees 2006. c) Living trees density in N ha^{-1}, light bars l light bars living trees in 1996, darker bars living trees 2006 d) Dead trees density in N ha^{-1} light bars dead trees in 1996, darker bars dead trees 2006.

3.4. Temporal patterns and reconstruction of disturbances

3.4.1. Frequency of growth reactions in spruce and beech samples

The relative frequency of releases in spruce samples (Figure 4a) decreased between 1972 and 1982. From 1982 to 2000 releases increased. Since then, a decrease in releases continues until the year of study.

The frequency of suppressions in spruce samples increased between the years 1973 and 1985, diminishing until 1990. The years 1991, 1993 and 2001 were peaks in frequency of suppressions when reached same levels as the period between the years 1970 to 1980.

The frequency of releases in beech samples (Figure 4 b) was generally low until the year 1979, from this year shows a trend to increased until 2006, peaking in 1985 and 1999.

The frequency of suppressions in beech samples oscilated in low numbers but increased slightly in the years 1982 and 1994.

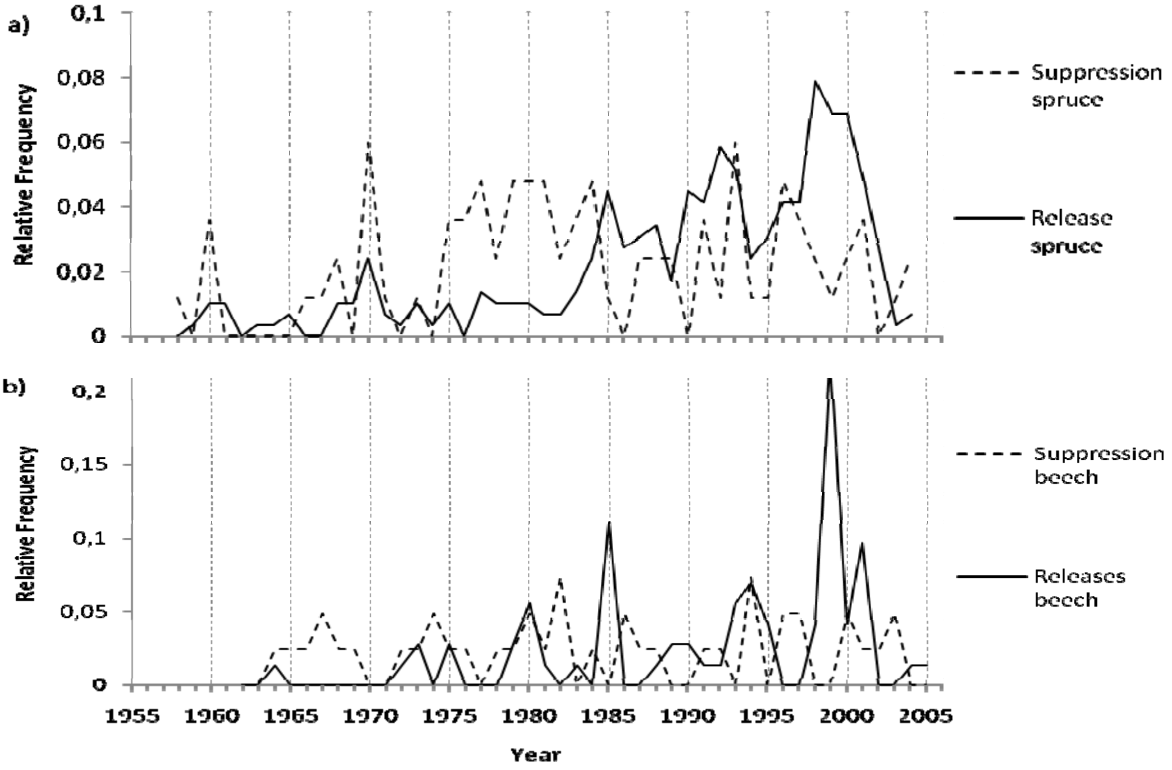

Figure 4 a) Relative frequencies of growth reactions in spruce samples, doted lines represent suppressions, and continue line represents releases. b) Relative frequency of reactions in beech samples, doted lines represent suppressions, and continues line represents releases.

3.4.2. Frequency of scars in beech and spruce trees

During the time span comprised by the samples, three periods of higher frequencies (many scars per year) can be identified: from 1958 to 1960; 1968 to 1974 and 1999 to 2004 (Figure 5), and two periods with consecutive years when scars have been dated: 1961-1969 and 1991-1996. The frequencies of scars in spruce samples nearly doubled the frequencies of scars on beech samples while the greatest amount of scars was showed by beech in the year 2000. The lowest scarring frequency is showed between 1973 and 1999.

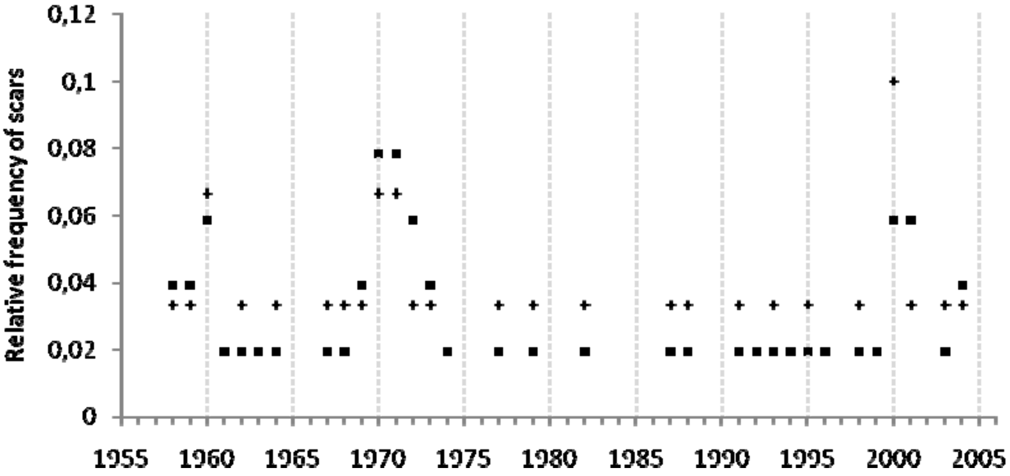

Figure 5. Frequencies of scars in beech (squares) and spruce (crosses) samples

3.4.3. Synchrony

The synchrony between the scarring frequencies for both species seems evident. Comparing the scarring frequecnies with reaction frequencies in *beech* samples, synchrony is unclear untill the period between 1998-2002 (Figure 4b). Nevertheless, when comparing scarring frequencies with reaction frequencies in *spruce* samples the figures seem to coincide in the periods 1968 - 1974 and 1998-2002. Also between 1991 and 1996 there are scars nearly every year, coinciding with a greater frequency of releases in spruce samples.

3.5. Fungi in beech trees

Fungal fructiferous bodies (FFB) were found in a total of 159 trees in 2006 (Table 4), 13.4% of the total amount of living trees counted in 1996. The majority of the infected trees belonged to diameter classes of 41-60 and > 60 cm with 61.1 and 20 % respectively. From 85 living high stumps counted in 2006, FFB were present in a total of 50 trees. From the total amount of dead trees, 40.1 % had FFB.

Table 4. Summary of the census data for the trees recorded as living and with no fungal fruit bodies recorded during 1996 census. For each category the absolute number of trees and number of trees·ha^{-1} (in brackets) are given. TCC follows the abbreviations used as in table 2: TCC_{FB} are the number of TCC with fungal fructiferous bodies on the stem.

DBH class (cm)		TCC_{FB} in 2006								
	TCC	Infected	LT_{DA}	HST_L	HST_{DE}	LST_L	LST_{DE}	Log	Traces	Uprooted
<21	LT	2 (0.5)	-	-	1 (0.3)	-	-	-	1 (0.3)	-
<21	HST_L	5 (1.3)	1 (0.3)	2 (0.5)	1 (0.3)	-	1 (0.3)	-	-	-
<21	LST_L	1 (0.3)	-	-	-	1 (0.3)	-	-	-	-
21-40	LT	13 (3.3)	3 (0.8)	3 (0.8)	5 (1.3)	-	1 (0.3)	-	-	1 (0.3)
21-40	HST_L	8 (2.0)	-	-	4 (1.0)	1 (0.3)	3 (0.8)	-	-	-
41-60	LT	46 (11.6)	6 (1.5)	22 (5.6)	16 (4.0)	-	2 (0.5)	-	-	-
41-60	HST_L	50 (12.6)	-	9 (2.3)	31 (7.8)	1 (0.3)	6 (1.5)	3 (0.8)	-	-
>60	LT	17 (4.3)	4 (1.0)	4 (1.0)	9 (2.3)	-	-	-	-	-
>60	HST_L	15 (3.8)	-	10 (2.5)	5 (1.3)	-	-	-	-	-
Total		157 (39.6)	14 (3.5)	50 (12.6)	72 (18.2)	3 (0.8)	13 (3.3)	3 (0.8)	1 (0.3)	1 (0.3)

4. DISCUSSION

4.1. Structure

The stand's mortality is distributed towards the greater diameter classes (Figure 3and figures 6 and 7 in appendix, table 2 in the text and table 5 in appendix) consistent with results reported by Forrester and Runkle (2000), Peterson (2000) and Wolf et al. (2004). The levels of mortality in the stand are slightly higher than reported from other beech forests in the literature (Runkle 1985, Parker et al. 1985, Parker 1989, Peterken and Mountford 1996, Peterken 1996, Pontailler et al.1997, Mountford et al. 1999, Forrester and Runkle 2000, Wolf et al. 2004). The group of dead trees evidences a change in the structure of the stand, as a tendency to thin off trees belonging to the 41 to 60 cm dbh class, and trees >60 cm dbh to a lesser extent. The stand is composed by only two different cohorts that share the area dating back to 1740 and 1850 respectively; showing different stages in the auto ecology for this species, between these two cohorts there was nearly no regeneration (Niklasson et al. 2005).The older cohort may be experiencing the loss of more individuals in proportion to the younger cohorts. Past management may have included pig farming and sheep husbandry, therefore, to harvest trees with bigger sizes was probably not a priority in the case of Holkåsen (Niklasson et al. 2005) preventing also beech regeneration by browsing (Watt 1947, Mountford and Peterken 2003, Kenderes et al. 2008).

4.2. High stumps

High stumps were more common in greater diameter classes; a possible reason for this could be that greater trees have longer time of exposure to environmental disturbances. Greater crowns have also more area of exposure to wind, hale, acid rain and pollutants (Franklin et al. 1987), and stressed or weakened trees have a greater susceptibility to suffer damages by wind and subsequently die (Nagel and Diaci 2006). From the living high stumps registered in 1996, 43% were found alive in 2006. Similar results were reported by Peterson (2000); after a storm event in 1985, 25% of snapped trees sprouted, four years later 68% of those trees were still alive the same author reports that after a second storm in 1994, 15.5% of trees damaged sprouted. These results reflect the high degree of resilience among the beech trees, enabling them to survive in harsh conditions evidencing evolutionary adaptation to a disturbance regime driven by windstorms for instance. The practical consequences of these characteristics can be many: Different degrees of crown damage allow canopy openings to be formed gradually, enabling the undergrowth to adapt progressively to open conditions. Sprouting capacity allows the forest to recover after disturbance, enhancing the capabilities of damaged canopy trees to reestablish. However, sprouting can also be varied between events. According to the degree of damages, sprouting was found to be greater after an event with less severe damage on the canopy trees (Peterson 2000). Another implication is that damaged and surviving trees provide substrate to a variety of species for long time periods, growing and rotting at the same time; a fact that may keep fungi or insects foraging on beech trees during long time within the stand.

4.3. Temporal patterns of mortality and dendrochronological reconstruction: Growth reactions and scarring rates

The frequency of both growth reactions and the scars registered in the undergrowth between 1967 and 1973 suggest that one or more events had affected the upper canopy in this period (Figure 4a, 4b and 5), coinciding with two major storms that affected southern Sweden in 1967 and 1969 (17-18 October storm and Orkanernas storm, SMHI) both recording wind speeds greater than 30 m/s. Between 1975 and 1997, low synchrony of the frequency of growth reactions with frequencies of scarring rate suggest that changes in the canopy are rather local, down to microsite level rather than stand level, therefore excluding causes related to a single disturbance event affecting the whole stand. In 1999 another storm hit Sweden, (Århundradets storm, SMHI) reaching wind speeds around 33m/s, coinciding with frequencies of scars which peak in the year 2000. Between 1997 and 1999 reaction frequencies are high but erratic; suggesting that other factors may also affect the growth rates during this period and to a degree perhaps, problems in dating some of the samples.

4.4. Fungal infections

Fungal infections seem to be very important in the stand considering the high amounts of living trees, living high stumps and dead trees with fungal bodies on the stem. It is reported in the literature that beech trees can host fungi in the branches or the stem decomposing the wood (Chapela and Bobbi 1988, Baum et al. 2003). Webb (1989) reported that tree mortality was related to the incidence of fungal pathogens. The absolute number of trees died due to fungal infection cannot be determined by the methodology used in this study, since trees may not necessary die as a cause of the infection. However, only the 26% of the trees recorded as infected in 1996 were found alive in 2006, suggesting that chances to die are high for infected trees. The fungi, while foraging on the stem's wood will provoke weakening and eventually breakage of the stem; by this contribute to the damaging and mortality rates reported here. Nevertheless, it is unclear whether some of the trees have been infected before or after suffering damages or die.

5. CONCLUSIONS

The stand Holkåsen is experiencing a process of mortality in which trees with dbh >41cm, probably the oldest generation, represent the major contribution to the pool of dead trees. The mortality levels reached in ten years period are slightly higher than rates reported for European beech forests. The results reported here suggest that wind disturbances such as the windstorms occurred in 1967, 1969 and 1999 may have affected the stand although, fungal pathogens such as *Fomes fomentarius* seems to have a permanent influence on the dynamics of mortality as well. The techniques used in this study helped to clarify the nature of the disturbance regime to a date earlier than the first census, although a comprehensive dendrochronological analysis may provide valuable information about the disturbance dynamics affecting the stand more than a hundred years back. Beech trees were observed to endure large damages for long periods of time, although damaged trees represent non timber values these trees help to conserve valuable species assemblages by providing substrate; this is a desirable feature in broadleaved forest in terms of conservation.

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7. LITERATURE

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8. APPENDIX

Statistical comparison between diameter distribution of living and dead trees

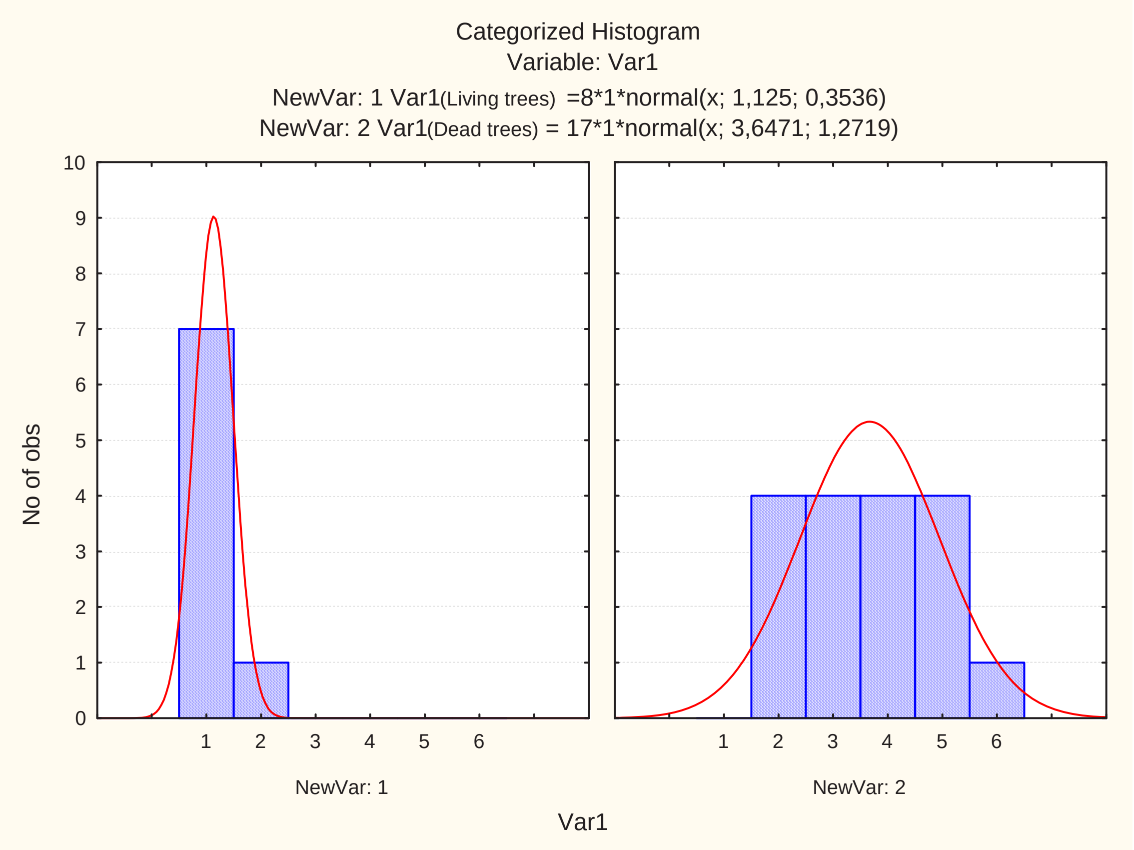

Figure 6. The categorized histogram, New var:1 represents living trees and New var:2 dead ones. Both groups are different from each other and from normal.

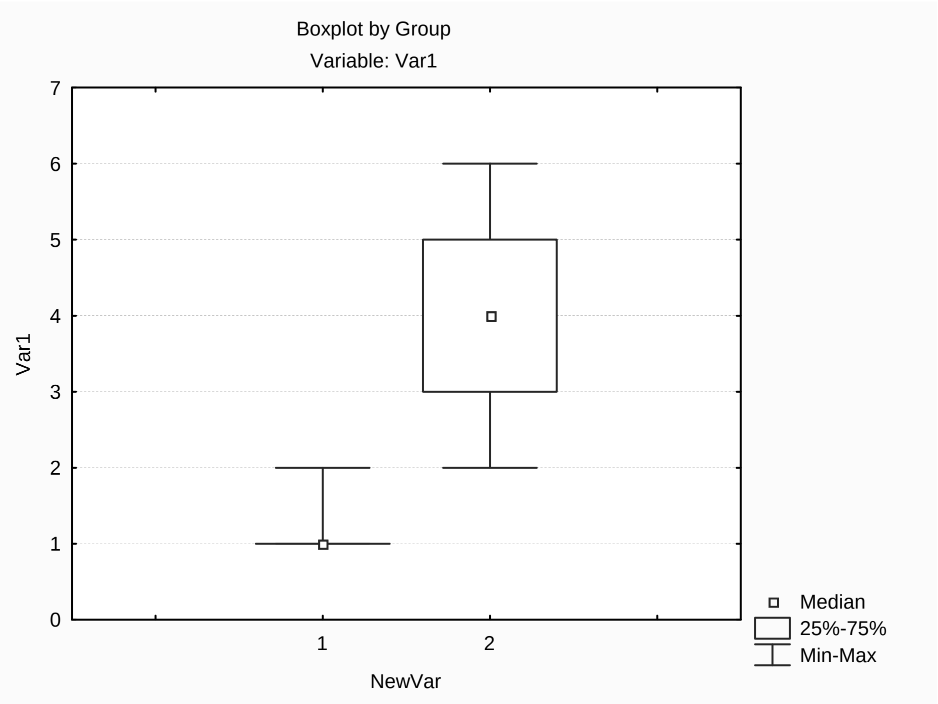

Figure 7. Box plot shows region used by variables 1 and 2 Dead and living trees respectively.

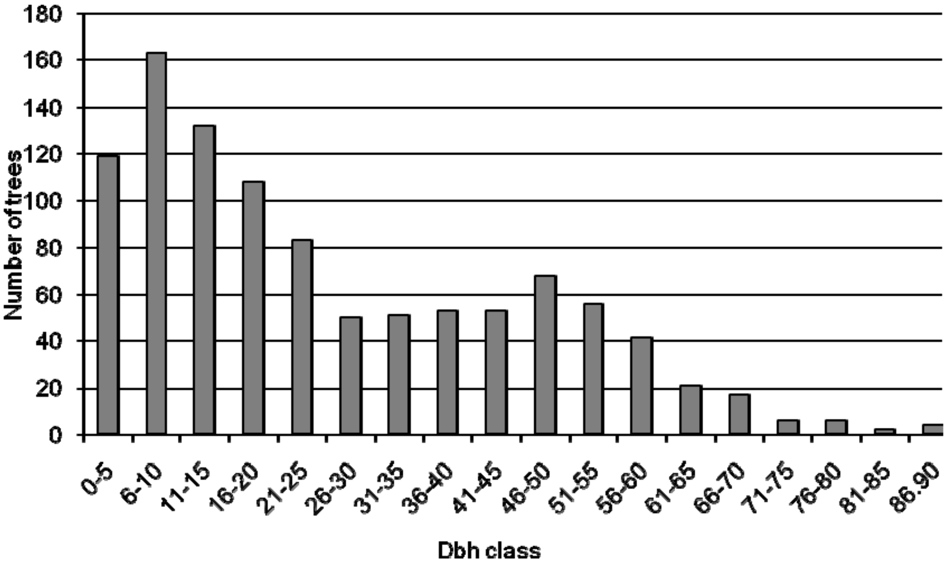

Figure 8 Diameter distribution of the living trees (2006) in the stand

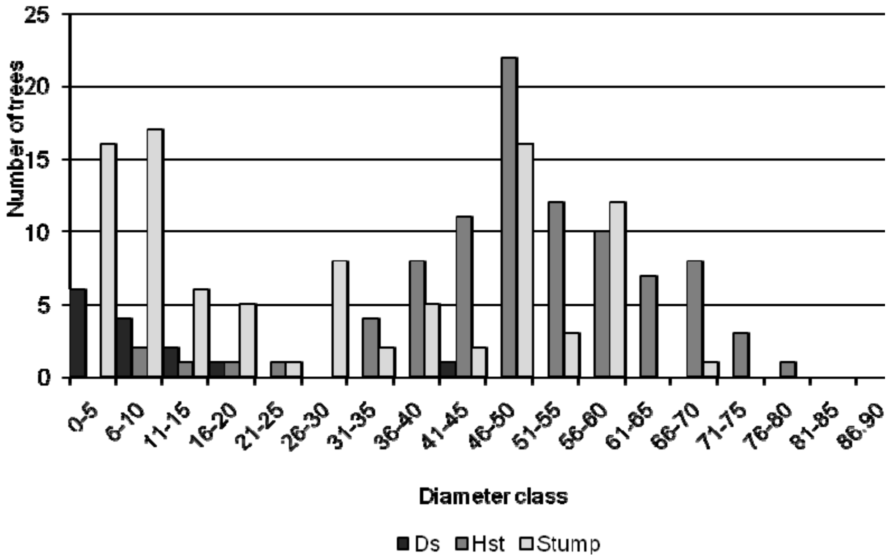

Figure 9. Diameter distribution of dead wood. Dead standing = dead trees with dead crown relatively complete; Hst= high stump= trees with dead crown lost higher than 1.3m; Stump = the remaining vegetative parts of the stem reach at the most 1.3 m height.

Table 5 Summary of the census data for the number of trees recorded as dead during 1996 census. For each category absolute number of trees and number of trees per ha (in brackets) are given. TCC are DS, dead standing tree; HST$_{DE}$, dead high stump; LST$_{DE}$, dead low stump. See Table 2 for explanation of other abbreviations.

DBH class, cm	TCC	Count & density	DS	HST$_{DE}$	LST$_{DE}$	LOG	Traces	Uprooted	Not found
< 21	DS	21 (5.3)	1 (0.3)		16 (4.0)	1 (0.3)	2 (0.5)		1 (0.3)
< 21	LST$_{DE}$	25 (6.3)		1 (0.3)	22 (5.6)				2 (0.5)
< 21	Uprooted	3 (0.8)				2 (0.5)		1 (0.3)	
< 21	LOG	36 (9.1)				36 (9.1)			
21 - 40	HST$_{DE}$	12 (3.0)		1 (0.5)	9 (2.3)	1 (0.3)			
21 - 40	LST$_{DE}$	14 (3.5)			13 (3.3)				1 (0.3)
21 - 40	LOG	50 (12.6)				50 (12.6)			
41 - 60	HST$_{DE}$	32 (8.1)		9 (2.3)	22 (5.6)	1 (0.3)			
41 - 60	LST$_{DE}$	14 (3.5)			13 (3.3)	1 (0.3)			

41 - 60	LOG	15(3.8)				15 (3.8)			
> 60	DS	1 (0.3)		1 (0.3)					
> 60	$\mathrm{HST}_{\mathrm{DE}}$	4 (1.0)		2 (0.5)	2 (0.5)				
> 60	$\mathrm{LST}_{\mathrm{DE}}$	2 (0.5)			1 (0.3)				1 (0.3)
> 60	LOG	1 (0.3)				1 (0.3)			
Total		230 (58.1)	1 (0.3)	15 (3.8)	98 (24.7)	108 (27.3)	2 (0.5)	1 (0.3)	5 (1.3)