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Oak *(Quercus robur* L.*)* mortality in south-eastern Sweden: influence of weather and environmental variables

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Sammanfattning
Abstract:

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Nyckelord
Keyword:

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Contents

1 Abstract

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Keywords: dendrochronology, extreme weather, growth depression, growth pattern, insect defoliation, oak decline, oak mortality, pointer year, tree-ring.

2 Introduction

Changes in land use and management strategies during the last century have reduced the areas of old-growth temperate deciduous forests in Europe to a small fraction of its original distribution (Hannah et al., 1995). This have had a severe impact on species diversity because deciduous trees, and in particular old large-diameter trees, have been identified as the most important element contributing to species diversity in forested ecosystems (Berg et al., 1994). In order to develop appropriate management strategies aimed at preserving biodiversity connected to these areas, there is a great need of a better understanding of the fundamental dynamics structuring forest stands. In addition to regeneration and growth, tree mortality is one of the major processes causing structural and compositional change. Both internal mortality, originating from competition or senescence, and external mortality, caused by exogenous disturbance agents, attribute to what commonly is viewed as the mortality of a tree species. While the internal mortality is relatively easy to predict, using species specific information about stand age and density, the external mortality is more complex because it depends on factors difficult to predict (Drobyshev et al., 2007). Additionally, several direct and indirect factors tend to act together over long periods of time, making it even more difficult to identify the actual causes of tree mortality with certainty (Thomas et al., 2002).

Occurrences of oak *(Quercus* spp*.)* declines have been recorded in many parts of Europe during the past three decades (Thomas et al., 2002). Several attempts have been made in order to identify factors triggering the onset and outbreak of the declines, but no uniform results have been formulated. Reports of declines in European oak stands suggest that factors responsible for the tree mortality include summer droughts (Dreyer, 1994, cited by Thomas et al., 2002) and winter or spring frosts (Thomas and Hartman, 1996; Barklund, 2002). Other possible factors are site conditions (Thomas and Hartman, 1996; Thomas et al., 2002), root pathogens of the genus *Phytophthora* (Brasier et al. 1993; Jung et al., 2000; Jönsson et al., 2005) and direct and indirect effects of nutrient imbalances (Thomas and Blank, 1996; Kinney et al., 1997; Thomas and Schafellner, 1999, cited by Thomas et al., 2002).

In Sweden, oak *(Quercus robur* L.*)* declines have been reported from various locations within its distribution range since 1987 (Barklund, 2002). Oaks are of particular importance for nature conservation in Sweden, since they support species diversity by providing essential habitats for numerous species found on the national Red List (Drobyshev et al., 2008). A dendrochronological study of oak stands performed in southern Sweden showed a significant increase in the mortality in the middle and late 1990s, believed to have been caused mainly by a severe spring and summer drought in 1992 (Drobyshev et al., 2007). A time lag in the mortality induced event and the actual death of the tree is supported by several other studies (Pedersen, 1998; Marçais and Caël, 2001; Haavik et al., 2008), emphasizing the importance of using a wide time perspective when analysing factors causing tree declines.

This study was performed in an area holding one of the highest concentrations of old oaks in northern Europe (Ranius et al., 2009). The results presented will contribute to a better understanding of oak declines and their relation to different site properties. The main objective was to identify individual tree and environmental variables that increased the risk of oak mortality. Core samples were analysed in order to clarify the temporal process of the oak decline and to detect a possible growth depression prior to death.

3 Methods

3.1 Study area

Three sites within the county of Östergötland, south-eastern Sweden, were used for the field data collection; Tinnerö, Norrköping and Sturefors (Figure 1.). All sites were parts of grazed, oak dominated nature reserves, representing one of the few landscapes in northern Europe still holding high densities of old oaks (Ranius et al., 2009). Choosing sites within the boundaries of nature reserves minimized the influence of forest management, such as removal of dead trees. The region has an annual precipitation of 500-700 mm and a mean temperature of between -2 and -4° C in January and around 16° C in July (Vedin, 2004).

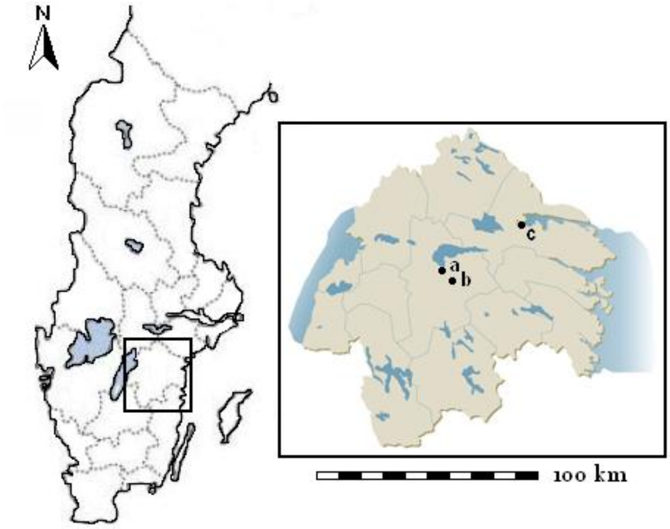

Figure 1. The study was performed in the county of Östergötland, Sweden. Three sites were used for the field data collection; (a) Tinnerö, (b) Sturefors and (c) Norrköping. Sites a and b were situated 13 km apart and site c was located about 45 km NE from the other sites.

3.2 Tree and environmental variables

All dead, standing oaks with a diameter of >25 cm were localized and sampled at the three sites. A grid system was used for selecting living trees to act as a control, and their position in field were located by GPS coordinates (GPSMAP 60CSx, Garmin). In total, 216 dead and 335 living oaks were sampled (Table 1). For each individual tree, the circumference, depth of bark crevices, crown silhouette and the presence/absence of holes and shelf fungus were recorded. The circumference of the trees was measured at breast height (130 cm above ground) and the depth of the bark crevices was calculated as the average of four samples taken perpendicularly to each other, each representing the maximum depth of the crevices facing each particular direction. Three categories were used for describing the crown silhouette; open, closed or intermediate (Glimskär, 1997). The shape of the crown silhouette gives a reflection of the long term growing conditions of the tree, for which an open crown silhouette indicates a single standing tree and a closed crown silhouette indicates a tree growing in a dense canopy. The presence/absence, size and location of holes were recorded, as well as the presence/absence of shelf fungus *(Polyporus* spp.*)*. Environmental variables investigated included soil moisture, soil type, cover of bare rock and sun exposure. Indicator plants were used to determine the soil moisture and a rolling test for establishing the soil type (Essen et al., 2007). The soil type was divided into two categories; clay (<3 mm) and not clay (>3 mm). The percentage ground covered by bare rock was estimated in an area equaling the size of the tree crown. Sun exposure was calculated as the percentage ground area not covered by other trees (with a height of >3 m) in an area reaching from the trunk and 5 m outside the crown edge.

Data of individual tree and environmental variables were analyzed in SPSS 16.0. In order to detect differences between dead and control trees, the continuous data was analyzed using the Kolmogorov-Smirnov two-sample test, and the Chi^2-test of independence was used for the categorical data. A 95 % confidence level was used for defining significant values.

3.3 Core samples

Core samples were taken from 72 dead and 72 living oaks, representing all sites, using a Swedish increment borer (Table 1). Each tree was cored twice at breast height, the cores taken perpendicularly to each other and in general 30 cm into the tree. The dead trees cored were randomly chosen out of all dead oaks within the sites. A pairwise design was used for selecting the control trees, wherein the living oak growing closest to the sampled dead one, having approximately the same circumference, was selected. Furthermore, the resemblance of the surroundings was taken into consideration when choosing the control tree, particularly when several oaks within the same size range were obtainable. Once sampled, the cores were brought back to lab and were left to air dry, before being mounted on wooden plates and polished with sandpaper no. 60/80, 120, 180, 240 and 320.

In order to clarify the temporal process of the oak decline, tree ring growth patterns were analyzed using dendrochronological methods. Due to obscurities in defining tree ring widths in the sapwood, the 15 outermost tree rings were initially examined using a magnifying glass, before being scanned (Nashuatec MP C3500, 400 dpi) and measured in Cybis CooRecorder 7.1. The data was compiled and analyzed in Cybis CDendro7.1. To minimize the risk of errors caused by missing or false rings, the original ring widths of two cores from each individual tree, having a correlation value of ≥ 0.5, were averaged into one single tree ring series. Due to difficulties in identifying the tree rings of the entire core, or obvious differences caused by branch formations, a few exceptions to the correlation threshold were made.

Cross dating was used to determine the specific year of death of the dead oaks (Wiles, 1996). To enable comparison of trees of varying age and growing conditions, all curves were detrended using a negative exponential curve. In order to enhance the high frequency signals, primarily used when cross dating, the curves were normalized using a moving average. A master chronology for each site was composed out of those control trees showing the highest inter-correlation values. To ensure correct dating, threshold values were generated by cross dating all dead trees against a non related curve[1], where all matches found represented a possible incorrect dating. Trees fulfilling two of the three threshold values generated, Correlation ≥ 0.5, BNDiff ≥ 0.01, TTest ≥ 4.5, were considered to be accurately dated. The correlation value describes the relationship between the curves, the BNDiff presents the difference between the best and the next best match of the curves and the TTest is based on the correlation, but also takes the length of the overlap into consideration. In total, 47 pairs of dated dead and living trees were used for the forthcoming analyzes.

Changes in growth over the years proceeding death were analyzed using multiple chronological clustering (Brodgar 2.5.7), in which breakpoints common for the majority of the individual ring width series were detected over the last 44 years. Raw ring width series of dead trees were used to examine the length of a possible growth depression and the yearly difference in growth between the dead and the control tree in each pair was used for detecting a common year representing the offset of the growth depression.

Table 1. Site properties and number of dead/control oaks selected for tree/environmental variables and core samples. All trees were not suitable to represent all types of variables. Cross dating was used for dating the dead trees.

	Location	**Area**	**Variables**		**Sampled cores**		**Dated cores**
	(WGS84)	*(ha)*	*Dead*	*Control*	*Dead*	*Control*	*Paired cores*
Tinnerö	*58°23’N, 15°37’E*	113	122	194	40	40	26
Norrköping	*58°37’N, 19°10’E*	20	35	64	12	12	7
Sturefors	*58°20’N, 15°45’E*	4	59	77	20	20	14
All sites	-	137	216	335	72	72	47

3.4 Influence of weather factors

Using continuous time series analysis for investigating the correlation of tree growth and weather variables normally result in a large amount of signal noise remaining unexplained, in general caused by the influences of tree ring widths shaped by factors other than the weather. One way of getting around this problem is to concentrate the analysis only on those years in which the majority of the trees have pronounced wide or narrow tree ring widths occurring simultaneously. By doing so, the relationship of the growth and weather is enhanced and the end result is less affected by signal noise (Heinrich et al., 2008). In this study, a hierarchical classification system, consisting of five intensity classes, was used to calculate pointer years and their intensity values (Neuwirth et al., 2004). All raw tree ring widths were initially normalized, using a moving average based on the four adjacent tree rings, in order to generate the difference in growth of a single tree ring relative to its neighbouring tree ring widths. Thereafter, the normalized values were expressed as intensity classes, with the maximum intensity class (5) reached for a difference greater than 80% and the minimum intensity class (1) reached for differences less than 20%. Based on the intensity classes, pointer year intensity values (I), were calculated using the formula:

$$I = \frac{100}{kn} \sum_{j=1}^{k} h_j i_j \qquad [\%]$$

k: number of intensity classes
n: total number of trees
h: number of trees with event
i: intensity class of event year

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[1] The international tree-ring data bank. Satellite and Information Service (NOAA). Available at: ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/chronologies/europe/pola006.crn Accessed on 7th October 2008.

Correlation analyses between pointer year intensity values and climatic factors were performed using Pearson’s correlation, SPSS 16.0. Average monthly air temperature and the sum of monthly precipitation were obtained from Malmslätt meteorological station, located 5-45 km from the sampling sites. The climatic factors were expressed as standard deviation units based on the long term monthly mean for the period 1961-2007. The 20 most extreme pointer years were used for the correlation analyses, and for each selected pointer year the weather was identified for the period previous year’s August to current year’s December.

4 Results

Data of individual trees and their surroundings were collected for 216 dead and 335 living oaks (Table 1). The diameter at breast height (DBH) ranged from 25-176 cm, with a mean value of 60 cm. Core samples were taken from 72 dead and 72 living oaks, resulting in 47 accurately dated pair of trees (Table 1). The total length of the master chronology, represented by a minimum of half the cores dated, covered the time period 1845-2008. The cores had an averaged ring width of 1.40 mm, with values ranging from 0.13 mm to 7.68 mm.

4.1 Tree and environmental variables

In order to detect possible differences between the dead and control trees, individual tree and environmental variables were analyzed. When pooling all sites or studying Tinnerö exclusively, the size distribution (DBH) differentiated between the dead and the control trees, with the dead trees being more concentrated to the central part of the size span (Table 2). In particular, the dead oaks exhibited fewer small sized trees, eg. trees with a DBH of 25-40 cm. Analyses of the depth of the bark crevices confirmed this general pattern (Table 2). The amount of bare rock enclosing the oak did not affect the vitality of the tree, and neither did the soil type when pooling all sites (Table 2). In Tinnerö, however, a somewhat higher frequency of dead oaks grew on non-clay soils (Table 2). The impact of soil moisture differentiated among the sites (Table 2). In Tinnerö, there was a higher frequency of dead oaks growing on moist soils, while most of the dead oaks in Sturefors grew on mesic soils. No significant trend was detected when pooling all sites. Dead oaks were more likely to have shelf fungus *(Polyporus* spp.*)* and holes when pooling all sites (Table 2). There was a higher occurrence of shelf fungus on dead oaks in Tinnerö and holes on dead oaks in Sturefors. Compared with the other sites, oaks in Sturefors generally grew under more closed conditions. Nevertheless, the dead oaks at this site were exposed to less sunshine and had more closed crown silhouettes than the control trees (Table 2).

Table 2. Differences in tree and environmental variables between dead and control oaks. The continuous data was analysed using the Kolmogorov-Smirnov two sample test, and the categorical data was analysed using the Chi^2-test of independence. Values significant at the 95 % confidence level are presented in bold.

	Data	**All sites**		**Tinnerö**		**Norrköping**		**Sturefors**	
	Con. / Cat.	χ^2 / *Z*	*P*	χ^2 / *Z*	*P*	χ^2 / *Z*	*P*	χ^2 / *Z*	*P*
Size (DBH)	Continuous	1.456	**0.029**	1.957	**0.001**	0.820	0.512	1.144	0.146
Bark crevices	Continuous	1.629	**0.010**	1.685	**0.007**	0.829	0.497	0.356	1.000
Bare rock	Continuous	0.771	0.592	0.824	0.505	0.809	0.529	0.506	0.960
Soil type	Categorical	2.603	0.110	5.391	**0.020**	0.010	0.918	0.000	1.000
Soil moisture	Categorical	4.186	0.123	8.843	**0.012**	1.885	0.390	5.800	**0.050**
Shelf fungus	Categorical	16.079	**0.000**	11.412	**0.001**	2.502	0.114	1.958	0.162
Holes	Categorical	10.912	**0.010**	0.396	0.529	0.453	0.501	8.458	**0.004**
Sun exposure	Continuous	0.682	0.741	1.266	0.081	0.932	0.350	1.425	**0.034**
Crown silhouette	Categorical	1.697	0.428	3.686	0.158	1.434	0.488	6.872	**0.032**

4.2 Core samples

Cross dating showed that most trees died during the last decade, with two pronounced peaks in 2004 and 2006 (Figure 2). Studying each site separately revealed that the peak in 2004 was represented mainly by data from Tinnerö, while the peak in 2006 could be devoted foremost to data from Sturefors. No distinct pattern in the frequency of dead oaks was observed for Norrköping. Averaged growth chronologies of dead and control trees reaching 150 years back in time illustrated an excellent match up until around 1992, after which the dead trees started to express reduced growth (Figure 2). Two main breakpoints in the growth trend were detected at 1989 and 1992 when applying multiple chronological clustering on data expressing the yearly difference between dead and control tree ring widths (α=0.01). Averaged chronologies of both dead and control trees showed a particularly strong growth reduction in 2003-2004, after which a recovery of the control trees was observed over the following years (Figure 2). When studying each site separately, Tinnerö and Sturefors showed trends applicable to the pattern described above. Norrköping, however, showed a distinct decrease in growth starting around 1991, but illustrated no particularly strong growth reduction during the time period 2003-2004.

Averaged raw chronologies of dead trees expressed on a time-prior-to-death scale, representing each site separately, revealed that the general growth trend differentiated among the sites, with trees from Tinnerö expressing an overall higher growth rate (Figure 3). Several more or less pronounced growth depressions were observed over time when studying data covering the final 100 years of the trees life histories. While Tinnerö and Norrköping showed a distinct period of reduced growth over the years preceding death, the trend for Sturefors was somewhat more obscure. The length of the growth depression varied among the sites, with Tinnerö and Sturefors having a relatively short time period of reduced growth compared to the decade long process illustrated by Norrköping. Multiple chronological clustering showed main breakpoints at 5 years prior to death for Tinnerö, 1 year prior to death for Sturefors and 25 years prior to death for Norrköping (α=0,005).

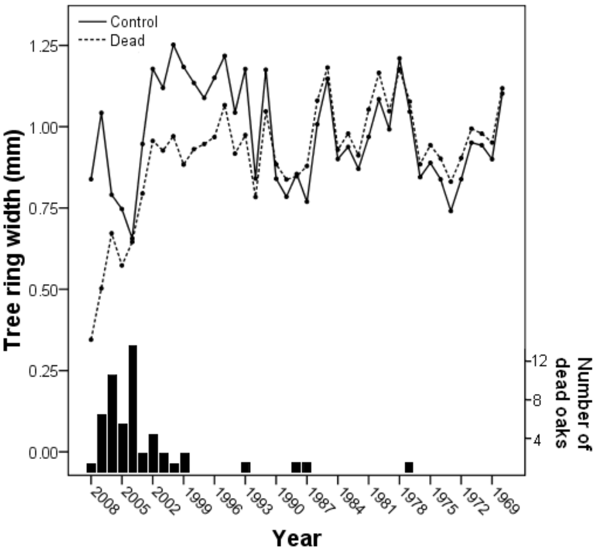

Figure 2. Mean chronologies of control and dead oaks. Trees contributing to the dead tree chronology decrease with time. Two main breakpoints were detected at 1992 and 1989, using multiple chronological clustering. Bars represent the frequency of dead oaks each year.

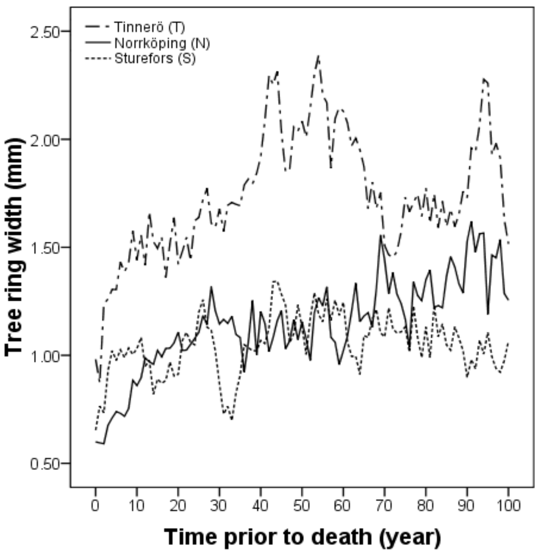

Figure 3. Mean chronologies of dead trees' ring widths on a time-prior-to-death scale at the three sites (n_T=26, n_N=7, n_S=14). The average growth trend differentiated among the sites, with trees from Tinnerö showing a notably higher growth rate.

4.3 Influence of climatic factors

Pointer years are defined as years in which the majority of the trees have pronounced wide or narrow tree ring widths occurring simultaneously, presumably caused by extreme weather conditions. Three positive (1963, -67, -85) and two negative (1965, 2004) extreme pointer years were detected for the time period 1961-2006 (Figure 4). These years had absolute intensity values of >25 and were represented by high intensity values at all three sites. To determine how climatic factors influence oak growth, correlation analyses were performed on pointer year intensity values and temperature/precipitation data the corresponding and previous year. Only those 20 years showing the greatest absolute intensity values were included in the analysis, in order to minimize signal noise caused by factors other than the weather (Table 3). Pearson correlation coefficients of pointer year intensity values and temperature/precipitation are shown for previous year's August to current year's December (Figure 5). Previous year's October temperature (*r=0.508, p=0.022*) and September precipitation (*r=0.463, p=0.040*) corresponded positively to oak growth. When pooling several months, precipitation during the period August-October the previous year (*r=0.527, p=0.017*) and March-June the current year (*r=0.480, p=0.032)* corresponded positively to tree growth.

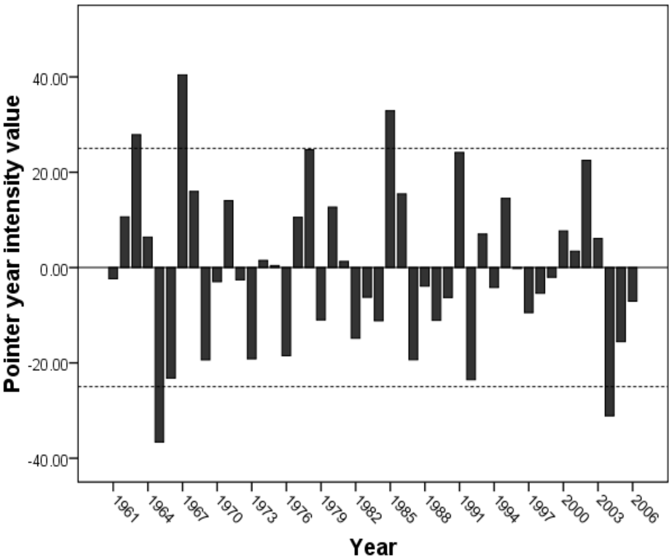

Figure 4. Pointer year intensity values for the time period 1961-2006, all sites pooled. Dashed lines at intensity values ± 25 represent the threshold for extreme pointer years.

Table 3. Maximum absolute intensity values. Years in bold are represented by high intensity values at all sites.

Positive			**Negative**		
Year	Intensity	(n)	Year	Intensity	(n)
1967	40.4	94	**1965**	-36.6	94
1985	32.9	93	**2004**	-31.1	63
1963	27.9	94	**1992**	-23.5	91
1978	24.7	93	1966	-23.2	94
1991	24.1	92	**1969**	-19.4	94
2002	22.5	91	1987	-19.3	92
1968	16.0	94	**1973**	-19.1	94
1986	15.4	92	1976	-18.5	93
1995	14.5	91	2005	-15.6	54
1971	14.0	94	1982	-14.8	93

5 Discussion

In areas where tree growth is limited mainly by climatic factors, ring widths of individual trees vary from year to year, making it possible to use core samples for dating certain events taking place in a tree's history. Variations in ring widths reflect the tree's vigour over time and give valuable information about the temporal process of the death event. During the last three decades, a large number of studies from various locations in Europe have reported severe oak declines (Thomas et al., 2002). Less information is available describing the vigor of Swedish oak stands, but several reports of rapid oak declines have been recorded since 1987 (Barklund, 2002). This study indicated that the mortality of oaks situated in the central parts of the county of Östergötland increased during the last decade, with two pronounced peaks in 2004 and 2006.

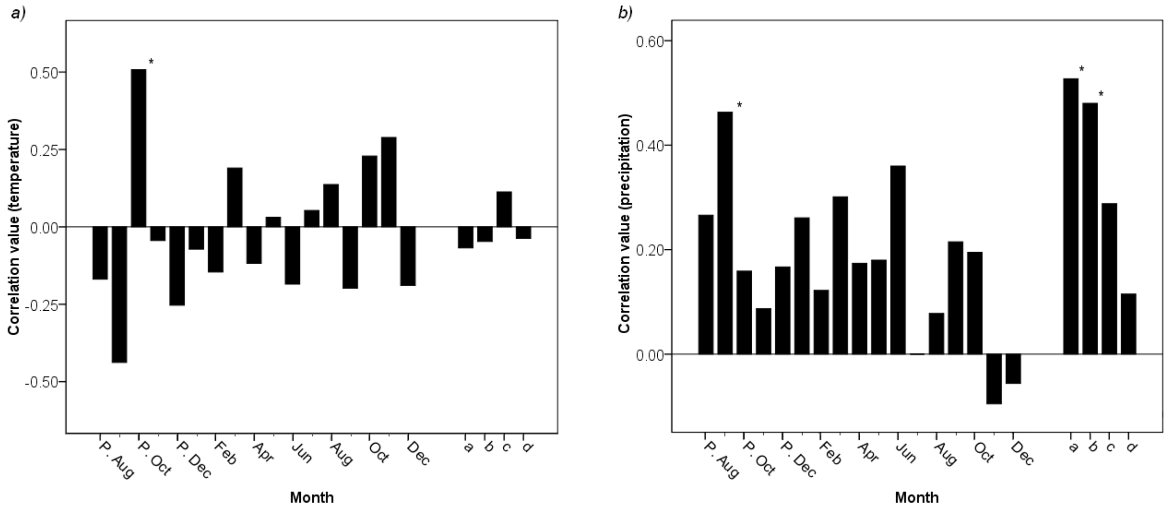

Figure 5. Coefficients of correlation for pointer year intensity values and temperature (a) / precipitation (b). The analyses were based on those 20 years showing the maximum absolute intensity vales. Previous year's months are marked P. Small letters at the right represent pooled months; a: previous year's August-October, b: current year's March-June, c: current year's July-October, d: current year's November-February. Significant values at a 95 % confidence level are marked with an asterisk (*).

5.1 Impact of climatic factors on tree growth

Pointer years are characterized by years in which the majority of the trees in an area have particularly wide or narrow ring widths occurring simultaneously. Three positive (1963, -67, -85) and two negative (1965, 2004) years reached absolut intensity values of more than 25 and were therefore identified as extreme pointer years in this study. Even though there is a notable inconsistency in the years identified as pointer years among European reports, the most extreme pointer years presented in this study corroborated with results from other studies. 1965 is reported as a negative pointer year for oak stands in southern Sweden (Drobyshev et al., 2008a) as well as for trees in a study compiling numerous sites across central Europe (Neuwirth et al., 2007). The latter one also identifies 1967 as a positive pointer year, in line with results from an investigation performed in the western parts of France (Lebourgeois et al., 2004). Intensity values of 1978, 1991 and 1992 were found just beneath the threshold defining extreme pointer years in this study, but are presented as strong pointer years in other reports; 1978 (Kelly et al., 2002; Lebourgeois et al., 2004), 1991 (Lebourgeois et al., 2004) and 1992 (Drobyshev et al., 2008a). However, the overall resemblance among pointer years presented in this and other European studies were rather low. This supports the suggestion that regional weather, rather than the Arctic or North-Atlantic oscillations, controls oak growth at sites located close to the northern oak distribution limit. (Drobyshev et al., 2008a).

Correlation analyses showed that oak growth was primarily controlled by previous year's September precipitation and October temperatures. Overall, precipitation seemed to have a greater influence on tree growth than temperature, and correlated positively for most part of the year. In addition to precipitation previous year's September, the time period August-September previous year, as well as the period March-June the current year, were of significant importance for oak growth. This is mainly in line with results from other studies, stressing the importance of precipitation during previous year's autumn (Fredrichs et al., 2008; Drobyshev et al., 2008a) as well as spring and early summer precipitation during the current year (Bednarz, 1990; Lebourgeois et al., 2004; Čufar et al., 2008). Somewhat surprisingly was the indication that the amount of precipitation during July had no effect on the oak growth, because several European studies assign June and July precipitation as essential controlling factors for oak growth (Pilcher and Gray, 1982; Rozas, 2002; Drobyshev et al, 2008a). The inconsistency in the results might however be explained by the fact that the sites in this study were located at the northern range of the oak distribution in Europe, where summer temperatures seldom reach levels high enough to cause harsh droughts. Furthermore, most oaks were growing on moist soils, presumably making them less influenced by low precipitation during the summer months.

Temperature correlated rather poorly to tree growth, with an exception of previous year's September and October values. A positive impact of high temperatures during previous year's late growing season can be explained by an extended period of physiological activity at the end of the growing season (Drobyshev et al., 2008a). It has been showed that the concentration of sucrose in leaves of red oak (*Quercus rubra* L.) drastically drops in late October as a translocation to the main steam takes place (Xu and Griffin, 2006). Warmer October temperatures might therefore enable more carbohydrates to be relocated, resulting in more available energy reserves during the following growing season.

Weather during the winter months exerted a weak influence on the growth, in line with results from another study performed on oak stands in southern Sweden (Drobyshev et al., 2008a). This indicates that even in areas situated close to the northern European distribution range of oaks, growth is not particularly affected by the cold part of the year. However, oak declines in southern Sweden have been attributed to frost damage of the roots, enhanced by a particularly thin snow cover (Barklund, 2002). Additionally, severe winter frost has been shown to cause damage to the living tissue of the bark on oak stands in Germany (Thomas and Blank, 1996).

5.2 Influence of water accessibility on oaks vigour

To determine whether the oak decline in this study could be attributed to a specific environmental factor, the cores were analyzed for a possible common year for which the majority of the trees destined to die started to express reduced growth. When studying averaged chronologies of dead and control trees, 1992 was identified as the offset year of a growth depression affecting the dead trees. Two main breakpoints were detected at 1989 and 1992 when using multiple chronological clustering, giving support to the proposition of 1992 as the onset year for which the dead trees started to express reduced growth. Climatic data showed that the precipitation for 1992 were well below normal for most part of the year, and in combination with an extremely high summer temperature, the oaks were most likely under a severe drought stress during most part of the growing season (Karlstöm, 1993; Bréda and Badeau, 2008).

Site specific factors influencing the water accessibility of oaks might affect the tree's ability to withstand drought events. However, no distinct pattern applicable for all sites was found when analyzing soil structure and moist conditions. Clay was the predominant soil type at all sites and the locations were overall characterized by moist soil conditions. Soil moisture might on the other hand not give a fair illustration of the true water availability for the tree, because water uptake principally is controlled by the development of the root system. Trees growing on moist soils tend to posses a lower root:shoot ratio, because light rather than water is the limiting factor (Kabrick et al, 2007). The larger root system typically developed by trees growing on less moist sites might therefore compensate for the lower water ability, making trees growing at differently moist sites equally capable to withstand drought events.

High clay contents in the subsoil promote prolonged periods of stagnant moisture, increasing the risk O_2 depletions. This, in combination with more sharply changes between stagnant moisture and droughts at sites with high clay contents, is considered a contributing factor to crown damage of oaks in north-western Germany (Thomas and Hartman, 1998). The rooting intensity among oaks growing on soils with high clay contents drastically decrease with increased soil depth (Thomas and Hartman, 1998) and a restriction of the fine roots into the more superficial soil layers is believed to increase the risk of drought stress under dry periods of the growing season (Thomas and Hartman, 1996). An impairment of the rooting into the subsoil is particularly high for old oaks (Becker and Lévy, 1986, cited by Thomas et al., 2002), which could explain the lower frequency of dead, small-sized trees found in this study. The small-sized young trees might have a greater ability to expand their root system into areas containing higher water supplies, making them more capable to withstand drought events.

5.3 Additional factors contributing to a reduced vigour of the oaks

Even though the drought in 1992 is believed to be the triggering factor of the oak decline examined in this study, it should not be considered the only factor responsible for the death of the trees. Drought stress as a single factor is not strong enough to cause the actual death of a tree, but rather acts as a weakening component, making the tree more susceptible to other stress factors (Thomas et al., 2002). The weakening of the tree is caused by an imposed durable stomatal closure, resulting in decreased photosynthesis and carbohydrate reserves (Dreyer, 1994, cited by Thomas et al., 2002). A particularly strong reduction in growth was detected for the averaged chronologies of both dead and living trees in 2003-2004. This is believed to be the result of a combination of a defoliation caused by the European oak leaf roller *(Tortrix viridana* L.*)*, taking place in Tinnerö 2002-2003, and a mildew infection of the replacement shoots during the following year (pers. comm. Anders Jörneskog, Linköpings kommun, Sweden). Several oak declines have been attributed to insect attacks (Rubtsov, 1996) in combination with mildew infections (Marcais and Bréda, 2006) or extreme drought events (Breda and Badeau, 2008). Defoliations cause extensive losses of photosynthates of trees, because the assimilating leaf area becomes heavily reduced. Trees do, however, generally have substantial carbon reserves, allowing them to regenerate the reduced foliage by developing new replacement shoots which over time can compensate for the lost energy. Trees already suffering from reduced carbohydrate reserves when becoming defoliated might, however, not have the energy needed for a formation of new regeneration shoots, wherefore the depletion of carbohydrates will continue (Thomas et al., 2002).

A recovery in growth following the insect outbreak and the mildew infection in this study was detected only for the control trees, indicating that trees weakened from the drought in 1992 were less resistant to the insect attack and did not have the energy reserves needed for a recovery. Even though the defoliation and mildew infection is confirmed only for oaks growing in Tinnerö, it is likely that also trees in Sturefors were affected, because the sites are closely located and the growth chronologies showed the same general pattern. Trees in Norrköping showed no obvious decline in the growth during the years 2003-2004. The distance to the location was presumably too long to enable a spread of the insect and mildew infection.

5.4 The mortality process

Several more or less pronounced growth depressions were detected over time when studying averaged dead tree ring series on a time-prior-to-death scale, representing each site separately. The length of a growth depression prior to death gives valuable information about the character of the death inducing event. Extensive growth depressions occurring over several decades before the death event are thought to be caused by long-term stresses, such as competition or changes in climate, while shorter growth depressions are more likely to be caused by short-duration stress factors, such as insect defoliations or extreme droughts (Pedersen, 1998). Even though long-term stresses rarely cause the actual death of a tree, they significantly increase the tree’s susceptibility to other stress factors and reduce the probability of the tree’s recovery following a short-durational stress event. Trees that do not recover from these relatively short durational stress events are extremely sensitive to all kinds of stresses, and are most often attacked by rather weak pathogens which further reduce the vigour of the tree until death occurs (Pedersen, 1998).

In this study, a growth depression prior to death was evident for at least 1- 5 years prior to death for Tinnerö and Sturefors, and at least 25 years prior to death for Norrköping. This gives support to the proposal of the insect outbreak and mildew infection as the ultimate mortality factor causing a relatively rapid death of the oaks in Tinnerö, and most likely also in Sturefors. The more extended mortality process illustrated by trees growing in Norrköping suggests a rather long-term stress, such as climate, as the triggering factor of the oak decline. A time lag in the mortality inducing event and the actual death of the oak is supported by several other studies (Pedersen, 1998; Marçais and Caël, 2001; Drobyshev et al., 2007; Haavik et al., 2008), indicating that oak-mortality should be seen as a several year long process most likely caused by a complex interplay among several stress factors acting together over time. The fact that only those trees remaining relatively unaffected by the drought in 1992 recovered from the defoliation and mildew infection emphasizes the importance of a tree’s history when examining mortality patterns.

The rather different growth chronologies expressed when studying raw values of each site separately implied that in addition to weather; local site specific variables had a considerable impact on tree growth. Oaks representing Tinnerö had an overall higher growth rate compared to oaks growing in Norrköping and Sturefors. While the overall greater circumference might contribute to the lower growth rate of oaks in Norrköping, the lower growth rate in Sturefors was more likely caused by less favourable growing conditions. The density of oaks in Sturefors was considerably higher compared to the other sites, forming a more closed canopy with higher competition for resources. Dead trees in Sturefors were characterized by being exposed to less sunshine and having more closed crown silhouettes, indicating that poor growing conditions could be seen as a long-term stress making the trees less efficient to withstand additional stress events. Oak mortality rates have been shown to correlate with stand density, emphasizing the effect of competitive interactions on oak mortality (Drobyshev et al., 2008b). Higher frequencies of shelf fungus and holes were observed among the dead trees when pooling all sites. However, this is presumably a consequence of the decreased vigour of the trees, rather than the actual cause of it.

Cross dating revealed that most oaks in this study died during the last decade, with two pronounced peaks in 2004 and 2006. Whether this expresses an actual increase in the mortality during the last decade, or rather is the result of an overrepresentation of recently dead trees with a superior suitability for sampling and dating, is difficult to conclude. Indications of increased mortality rates have been shown for oaks growing in southern Sweden (Sonesson, 1999), even though these values are found well below the mortality rates reported for oaks in other European studies (Drobyshev et al., 2007).

5.5 Conclusions

Results from this study support the concept of attributing oak mortality to a combination of long- and short-term stresses, wherefore an identification of one specific factor causing the actual death of a tree is impossible. In order to fully understand the causes of oak mortality there is an equal need of studying present as well as past factors influencing the oaks’ vigour, since the history of a tree is essential for its present chances of survival. The majority of the dead trees in this study showed a period of reduced growth prior to death, indicating that oak-mortality should be seen as a several year long process most likely caused by a complex interplay among several stress factors acting together over time. In order to develop successful management strategies aimed at preserving areas holding old large diameter oaks, there still is a need for a better understanding of the interplay between various long- and short-term factors. Although this study presented a rather modest influence of the impact of environmental variables on oak mortality, site specific properties should not be considered unessential when analysing the causes of oak mortality.

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