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Crown condition dynamics of oak in southern Sweden 1988–1999

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Abstract Crown defoliation of oak (*Quercus robur* and *Q. petraea*) was analysed in 808 trees during three forest condition surveys (1988, 1993, and 1999) in the southern Sweden. From 1988 to 1999 crown defoliation increased by more than 20%. Changes in crown defoliation were related to the pH in the upper 20–30 cm of the mineral soils, which was closely connected to other measures of soil fertility (cation exchange capacity, CEC and C/N ratio). Trees growing on soils with a high pH (≥4.00, in $BaCl_2$ filtrate), high CEC and low C/N ratio had significantly lower crown defoliation than trees growing on more acid soils (pH <4.00), indicating that less favourable soil conditions may further enhance oak decline. Age did not differentiate trees with respect to crown defoliation, indicating that decline in crown condition was not due to an age-related increase in crown transparency. Considering only trees younger than 100 years, a significant interaction was observed between changes in crown defoliation and soil pH. Trees younger than 100 years old growing on more acidic soils had a greater increase in crown transparency than trees on more basic soils between 1988 and 1999. Trees ≥100 years old had significantly higher defoliation on more acidic than on more basic soils, however defoliation dynamics of these trees over 1988–99 was not related to soil acidity. Two biotic agents (insect and fungal leaf infections) evaluated in this study did not prove to be important drivers of defoliation dynamics.

Keywords Age structure · Biotic factors · Climate variation · Crown defoliation · Environmental monitoring · European hardwoods · Forest condition · Oak decline · Soil pH · Acidification

Introduction

Deterioration of forest condition in European oak-dominated forests has been reported regularly (Greig 1992; Landmann et al. 1993; Selochnik 1989; Thomas et al. 2002). In southern Sweden extensive monitoring of the forest condition has also suggested a considerable decline in the health of oak and beech stands (Sonesson 1999). The decline symptoms include different levels of crown defoliation, increased number

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of dead branches, and under-development of young shoots in the crown (Sonesson and Anderson 2001). The nature of this decline is most likely a complex reaction to the physiological stress imposed on the trees. According to the literature, dry periods during summer (Pilcher and Gray 1982; Siwecki and Ufnalski 1998), hard frosts (Barklund and Wahlström 1998), nutrient imbalances (Thomas and Buttner 1998), soil acidification (Persson and Majdi 1995; Raben et al. 2000), and possibly fungal root infections (Blaschke 1994; Jung et al. 2000, but see Hansen and Delatour 1999) are the most common stress-inducing factors.

Oak decline on a regional scale and lack of clear geographical patterns in the phenomenon reported in previous studies (Osipov and Selochnik 1989; Sonesson and Anderson 2001), implies that the decline is a product of interactions between regional forcing factors and site/tree properties. The available survey data from southern Sweden supports this idea. A study by Sonesson and Anderson (2001) showed a negative relationship between crown defoliation and soil base saturation in oak stands, with more intense defoliation on podsolic than on cambisolic soils. A study in Germany has shown that sites with dense topsoils can cause insufficient soil aeration and higher CO_2 concentrations in soils, which results in suppressed root activity leading to general tree decline (Gaertig et al. 2002). Comparative analyses of healthy and declining oak stands in northwestern Germany and eastern Austria, however, have failed to pinpoint a probable soil- or mycobiotic-related factor that reduces tree vitality (Halmschlager and Kowalski 2004; Thomas and Buttner 1998).

Accumulation of large regional datasets on forest condition should provide insight into spatial and temporal patterns of forest decline phenomena (De Vries et al. 2003; Parr et al. 2002; Seidling and Mues 2005). In Sweden this effort is coordinated by the Swedish Forest Agency (before 2006 – the National Board of Forestry), which has been collecting data on the forest condition of 287 oak and beech stands in southern Sweden since 1988 (Sonesson and Anderson 2001). To present, three inventories have been undertaken – in 1988, 1993, and in 1999. The data from these inventories were used in this study to (a) quantify the temporal trend in the oak crown defoliation assessed at the scale of single trees, and (b) evaluate if this trend is related to tree age and site soil conditions. Although the inventories were not specifically designed to assess biotic-causing damages to oak trees (primarily by insects and/or fungi), occurrence of these damages were nevertheless recorded. Henceforth, we used this information to evaluate the role of biotic agents in oak decline.

Materials and methods

Study area

The field data was collected in the counties of Scania, Blekinge, and Halland, in southernmost Sweden (Fig. 1). The mean annual temperature in southern Sweden is between 5 and 8°C. The mean temperature in January varies between −4 and 0°C; and between 15 and 16°C in July. A large variation in precipitation exists between the western (up to 1,200 mm/year) and the eastern (500 mm/year) parts of the region, the typical range being within 600–1,000 mm/year. Prevailing winds are typically westerly or southwesterly (Raab and Vedin 1995). The growing season, defined as the period with daily mean air temperature above 5°C, lasts for 180–240 days (Nilsson 1996). The soil bares a history of glacial dynamics and was formed on sandy and stony moraines (Fredén 2002).

The region lies within the nemoral and boreo-nemoral, also called hemi-boreal, vegetation zones (Ahti et al. 2004). A major part of the study region is a transition zone between the boreal and temperate biomes and species from both biomes are common in the vegetation cover. Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) are the main coniferous species while oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica* L.), together with small-leaved species (downy birch, *Betula pubescens* Ehrh. and aspen, *Populus tremula* L.), form a deciduous element in the vegetation.

The studied stands were mostly mixed oak-beech stands (80% of all stands) with common coniferous element in the canopy (Norway spruce or Scots pine). Of all the stands, 91% had an oak relative volume-based abundance between 3 and 10 (measured on a 10 unit scale). Most of the stands were located on brown forest soils (47%) and transitional brown soil – podzol soils (33%) with a minor proportion of the stands on podzol soils (16%) and former agricultural fields

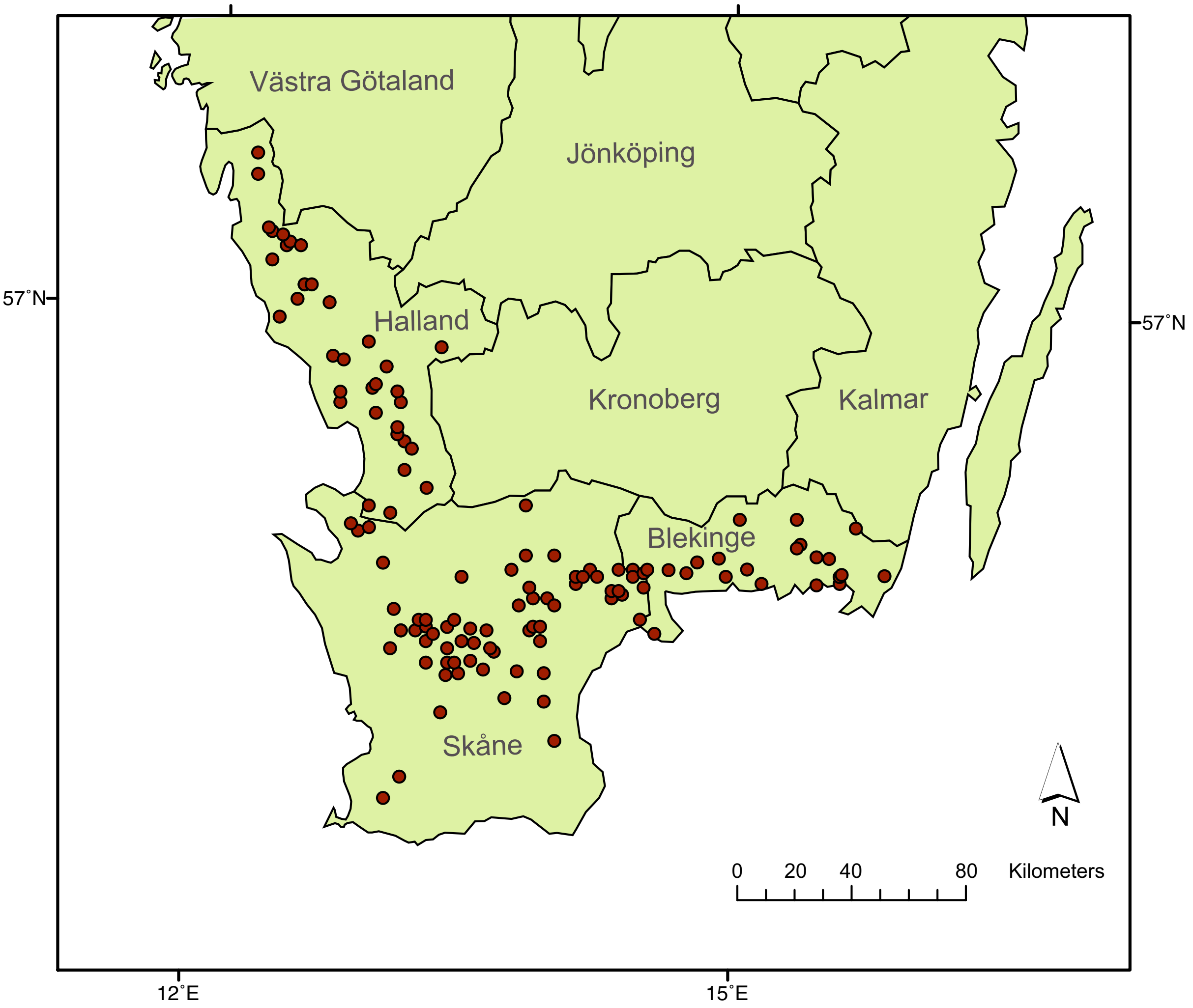

Fig. 1 Location of the oak stands (n=123) surveyed during the 1988, 1993 and 1999 inventories

(4%). The majority of the stands (98%) were self-regenerated forests.

Field surveys

The National Board of Forestry Södra Götaland carried out the surveys of crown condition, used in this study, in 1988, 1993, and 1999. The surveys mostly included two species – *Quercus robur* and *Fagus sylvatica* (not considered here), with a minor portion of *Q. petrea* trees. The sampling design aimed at obtaining a similar number of observation points among counties with randomly distributed points within each county. Sample plots were placed 25 m north, east, south and west of each observation point and the six predominant, dominant and co-dominant trees closest to the sample plot were inventoried. The crown condition was assessed on the trees with an estimated age above 60 years. In total, the 808 oak trees inventoried were from 123 sites in all three surveys. A detailed description of field inventory methods is given elsewhere (Sonesson 1999; Wjik 1989).

A range of crown properties recorded included the degree of leaf and branch loss, current shoot growth, degree of crown defoliation and the amount and size distribution of dying or dead branches. In the current study, only the degree of crown defoliation, the most integral characteristic, was used as proxy of crown condition. In the field, the crowns were compared with the best tree with full foliage that could grow at that particular site and the difference was assessed in percent. The assessments were done visually by a group of trained surveyors, equipped with field glasses. Since the surveys were based on visual assessments of crown condition, potential differences in the *relative scale* used by a field worker between years may be a source of possible error (Ghosh et al. 1995; Strand 1996). While the impact of such an error was not possible to evaluate in the current database, it was assumed that this error was relatively small since field staff were required to undergo training just prior to field work, in order to unify their judgments against selected "standard trees" (Sonesson and Anderson 2001). Furthermore, the inaccuracy associated with visual assessment of crown condition had no bearing on the significance of the results, since the variation in assessment acted toward increasing Type 2 error (accepting false 0-hypothesis), and decreasing Type 1 error (rejecting true 0-hypothesis). Stand stocking density, the number of stems per hectare (ha) was also recorded.

In this study we considered the correlation of oak crown defoliation to two biotic damage-causing agents (insects and fungi), stand-level variables (stand stocking density, average pH of the upper 20–30 cm of the mineral soil), and one tree-level variable (tree age). Insect-related damages were recorded in the field by observing the crown of the trees with field glasses and recording browsed, mined, wrapped leaves or galls. Fungi-related damages included mildew, rust fungi, blight, stem and branch cankers, poliporos fungi, root rot, and slime fungi. Both insect and fungi-related damages were recorded as being present or absent. Based on the visual assessment, a distinction was made between major and minor damaging factors. For example, if a tree exhibited both insect- and fungi-related damages but most of the damaged was caused by insects, it was assigned as the major damaging factor, and fungi-related damage was assigned to the minor damaging factor. During analyses we considered both the major and the minor damaging factors. To characterise soil condition at the sites, soil samples were taken with a soil-borer (Haglöf, Sweden) at 8–9 random points within each plot. The borer was inserted down to a depth of 30 cm and samples from 20–30 cm soil layer were collected for chemical analyses. The samples were combined in the field to give one sample per plot. In the laboratory soil samples were sieved through a 2-mm sieve and dried at an ambient temperature of 40°C for 2 days. Twenty grams of dry soil was extracted in 100 ml 0.1 M $BaCl_2$ at room temperature for 2 h and the pH of the $BaCl_2$ filtrate was measured. To estimate base saturation (BS), concentrations of Al, Ca, Mg, K, Na, Mn, and Fe were obtained using an inductively coupled plasma analyser (VarioMax CN, Elementar Analysensysteme GmbH, Hanau, Germany). Total nitrogen was determined by the Kjeldahl-method and a CR 12 method. An LECO instrument was used for the determination of total soil carbon and the concentration of C was normalized to the dry matter content at 40°C (Balsberg 1990).

Statistical methods

Three site-level factors considered were age of the tree, and the pH value of the soil, and stocking density. The age of the trees was visually assessed in the field and was coded in the following way: 1 – trees between 60 and 100 years old; 2 – trees older or equal to 100 years old. The threshold of 100 years was selected to allow for a balanced design of subsequent ANOVA analyses. For the coding of tree age we used data from 1988 and kept the same codes for all trees in 1993 and 1999, despite the fact that some trees moved from the younger to the older age class in the1993 and 1999 inventories. The absolute difference in years between two age classes, however, remained the same. The pH values refer to the subsurface mineral layer at a depth of 20–30 cm and were obtained in a $BaCl_2$ filtrate. This variable was coded as 1 – pH <4.00, 2 – pH ≥4.00. The value 4.00 was selected as the median of the pH distribution in the whole dataset.

Repeated-measures of MANOVA was used to assess the correlation between tree age and soil pH (two independent factors) and the change in crown defoliation between 1988 and 1999 (dependent repeated-measure variable). A Chi-square test was used to check for the sphericity (independence) of independent variables and a *F*-test was run to evaluate deviation of the empirical from the theoretical normal distribution. A Fisher LSD test was used to find significant differences among cells representing different combinations of independent variables.

The role of insects and fungi was studied by selecting trees with a particular type of damage (fungi and/or insect damage) and running one-factor ANOVA analyses with degree of defoliation as the dependent variable and an independent dichotomous (presence/absence) variable representing the factor in question. Correlation between biotic factors was assessed by a Chi-square test. To construct a 2×2 table we used data on both primary and secondary damage factors, assuming their independence from each other. Non-parametric Mann–Whitney *U* Test (Sokal and Rohlf 1995) was used to check for differences in age, pH, and stand stocking density between damaged and non-damaged sites.

Results

Defoliation related to tree age and soil pH

A significant increase in oak crown defoliation was observed between each pair of inventories (Fig. 2, Table 1). Taking into account all trees inventoried, crown defoliation increased on average by more than 20% between 1988 and 1999, the effect being replicated on all datasets generated from the original data. Age did not have an effect on the degree of defoliation at the level of the whole dataset (F=1.56; p=0.211). pH of the upper 20–30 cm of the mineral soil showed a significant correlation with crown defoliation: trees in stands with pH below 4.00 had higher defoliation in 1993 (22%) than trees in stands with pH above 4.00 (19%), and the similar pattern was observed in 1999 (35 vs. 30%, F=9.3; p=0.002).

Although soil conditions were only represented in the analyses by pH classes, this also indicates general soil fertility. pH classes were well correlated with cation exchange capacity and the C/N ratio within the subsurface mineral layer at a depth of 20–30 cm. Soils with pH below 4.00 had a significantly lower cation exchange capacity as compared to soils with higher pH: 39.6±0.52 vs. 24.2±0.47 for pH classes 1 and 2, respectively. C/N ratio was significantly higher in pH class 1 (21.1±0.22 SE), as compared to pH class 2 (20.2±0.20 SE).

Both Age and pH factors interacted significantly with change in the degree of defoliation over the period studied. In the case of tree age (Fig. 2b), no significant difference in defoliation was found in 1988 (p of Fisher LSD test=0.549). Trees ≥100 years old had higher defoliation in 1993 (p=0.012) whereas the opposite was observed in 1999 (p=0.022). Older trees showed a greater increase in crown defoliation over

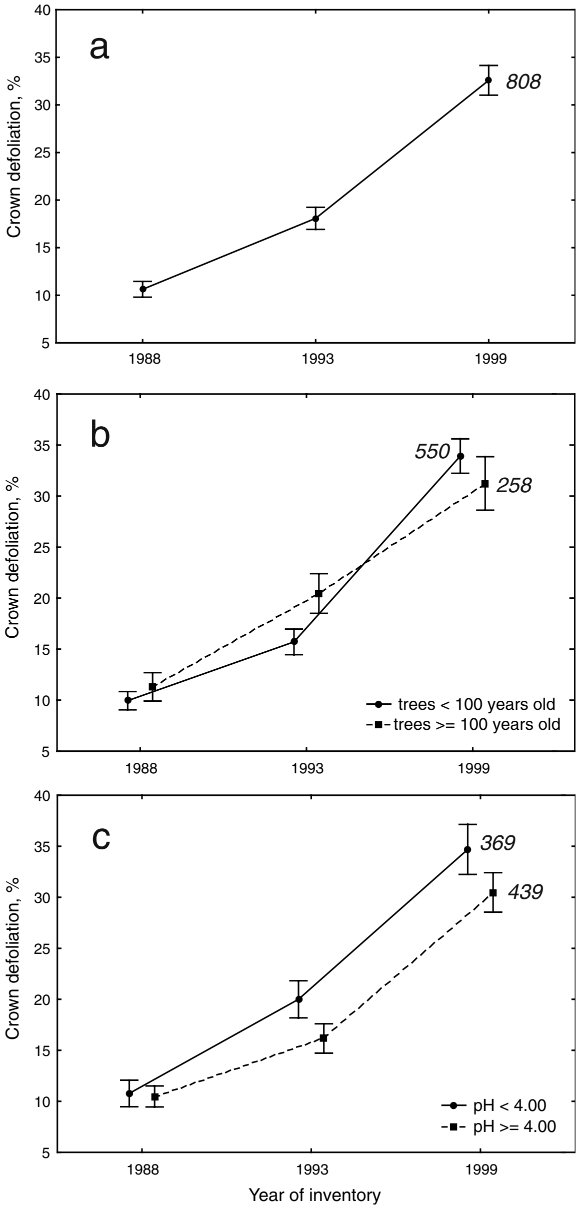

Fig. 2 Dynamics of crown defoliation in 808 oak trees on 123 sites inventoried in southern Sweden over the period 1988–1999. Results of repeated measures MANOVA. **a** Dynamics of crown defoliation for all trees included in the analyses. **b** Interaction effect between repeated measures factor (dynamics of defoliation) and tree age. **c** Interaction effect between repeated measures factor and soil pH at the subsurface mineral layer at a depth of 20–30 cm. *Error bars* are 95% distribution limits of population represented by a point. *Labels* refer to the number of trees represented by the *curve*. Numerical details of analyses are given in Table 1

Table 1 Defoliation dynamics of oak crowns as recorded by three inventories in 1988, 1993, and 1999

Effects	SS	df	MS	*F*	*p*-level
Effects of non-repeated factors					
Intercept	$8.07 \cdot 10^5$	1	$8.07 \cdot 10^5$	2013.40	<0.000
Age	627.1	1	627.1	1.56	0.211
pH	3,736.7	1	3,736.7	9.32	0.002
Age *x* pH	838.2	1	838.2	2.09	0.149
Error	$3.22 \cdot 10^5$	804	400.9		
Effects of repeated factor and interactions					
Change	160,681.4	2	80,340.7	465.40	<0.000
Change *x* Age	4,444.8	2	2,222.4	12.87	<0.000
Change *x* pH	1,505.4	2	752.7	4.36	0.013
Change *x* Age *x* pH	565.8	2	282.9	1.639	0.195
Error	277,586.1	1,608	172.6		

Results of repeated-measures MANOVA. *Change* refers to the repeated measures factor composed of crown defoliation data from three inventories. Graphic presentation of the results is given in Fig. 2.

the studied period as compared to younger trees. In the case of pH (Fig. 2c), there were more significant differences between factor levels: no significant differences were found in 1988 ($p=0.527$) or in 1993 ($p=0.075$), whereas in 1999 trees growing on more acidic soils had significantly higher defoliation than those on more basic soils ($p<0.001$).

The Chi-square test revealed a lack of sphericity between age and pH factors. While the younger age class (class 1) had a relatively equal number of trees growing on acidic and basic soils (284 and 266 trees, respectively), the older trees (age class 2) tended to grow on more basic than on acidic soils (173 and 85 trees, respectively). This imbalance resulted in significant Chi-square test (Chi-square=24.00, df=1, $p<0.001$) might affect the results of the MANOVA. To test this possibility, we ran two additional MANOVA analyses, for the sub-set of younger and older trees (Fig. 3).

For younger trees (< 100 years old) pH was not related to the degree of defoliation, given the average value for all 3 years considered (Table 2). The difference in the degree of defoliation between higher and lower pH sites did, however, change from 1988 to 1999 (Table 2, Fig. 3a). In 1988 and 1993 defoliation of trees on soils with lower pH did not differ from trees on soils with higher pH (p in Fisher LSD test being 0.17 and 0.15, respectively), however, in 1999 trees on soils with a lower pH had a significantly higher degree of defoliation than on more basic soils (p in Fisher LSD test<0.001). For older trees (≥100 years old), there was a significant correlation between pH and the degree of defoliation when considering all years (Table 2, Fig. 3b). The interaction between dynamics of defoliation and pH was, however, insignificant: none of the pair of contrasts (lower vs. higher pH) showed any significant differences (p in Fisher LSD test staying between 0.06 and 0.14).

Stand stocking density decreased with increasing tree age (from 505 stems/ha±9.3 SE for stands with trees <100 years to 384 stems/ha±11.9 SE for stands with trees ≥100 years).

Defoliation related to insect and fungi damages

Insect-related damages to oak crowns were minimal in 1988 and 1993, with 1.1 and 2.1% of trees affected, respectively. In 1999, insect-related damages increased to 13.5% with leaf-eaters being responsible for 64.8% of all damaged trees (8.8% of all inventoried trees). With respect to stand stocking density, no difference was found between stands with insect-damages and non-damaged trees ($z=-0.65$, $p=0.516$), nor soil pH ($z=-1.75$; $p=0.079$). However, trees damaged by insects were significantly older than undamaged trees (average age 90 and 86 years, respectively; $z=-2.27$; $p=0.023$).

Similar to the temporal pattern of insect damages, fungi did not appear to be an important damaging agent during 1988 or 1993, with 3.3% of all trees exhibiting this type of damage in both years. In 1999 fungal damages increased to 10.9%, with mildew fungi (*Uredinales*) contributing 42% to the pool of

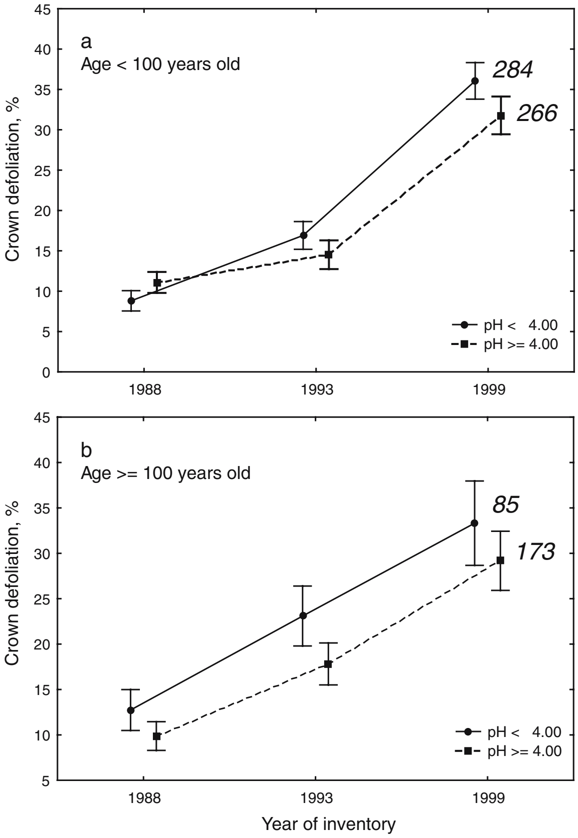

Fig. 3 Interaction between change in oak crown defoliation and stand pH, separately for younger (<100 years old) and older (≥100 years old) trees. *Labels* refer to the number of trees represented by the curve. Numerical details of analyses are given in the Table 2

fungi-damaged trees (4.7% of all trees). The age of fungi-damaged trees and trees not damaged by fungi did not differ significantly ($z=-1.95$; $p=0.051$), nor did the soil pH of the stands ($z=0.29$; $p=0.768$) or stand stocking density differ ($z=0.54$; $p=0.592$).

ANOVA was carried out on the 1999 data to compare damaged trees to undamaged trees. Trees damaged by insects or fungi had a higher degree of defoliation than trees unaffected by the factor in question. In the case of insect damages, average defoliation was 32% for trees unaffected by insects compared to 36% for the insect affected trees ($F=8.33$; $p=0.004$). In the case of fungi damages, respective values were 32 and 37% for unaffected and affected trees ($F=5.58$; $p=0.018$).

Insect and fungi damages were negatively correlated to each other. Insect damages were mostly observed on trees with no fungi damages (70% of all insect-damaged trees). Similarly, 68% of trees with fungi damages had no insect-related damages (Chi-square=38.57; $p<0.001$).

Since there was a relatively low proportion of trees affected by insects and fungi (13.5 and 10.9% of total amount of trees for insect and fungi damages in 1999, respectively) these factors were not included in the ANOVA analyses. An analysis of the whole dataset and a sub-set of undamaged trees produced identical results.

Discussion

General trend in oak crown condition

Between 1988 and 1999 the oaks in southern Sweden had a significant increase in crown defoliation. This result confirms the conclusions of a previous study (Sonesson 1999) where temporal dynamics of oak defoliation was analysed for the same region and the decline trend was evident across all sites of different age class and soil types. It remains unclear whether or not there is a long-term trend towards higher oak defoliation on the pan-European scale (Eichhorn et al. 2005). Decline phenomena reported in Europe in the 1980s resulted in the initiation of European Assessment and Monitoring programs, which apparently did not develop further in most of the European countries (Anon 1997). Recent data has shown a clear increase in defoliation between 2002 and 2004, with the trend in defoliation varying considerably across Europe (Anon 2005). A consistent negative trend in oak crown conditions observed in Sweden (this study; Sonesson 1999; Sonesson and Anderson 2001) suggests the presence of region-specific decline-predisposing factors. Unfortunately, no large-scale inventories have been done in southern Sweden since 1999 and current dynamics of crown defoliation in this region remains unknown.

It is likely that a 5-year temporal resolution of crown inventory is too rough to detect the timing of stress-inducing events, e.g. summer droughts (Pilcher and Gray 1982) and periods of low winter-spring temperatures (Barklund and Wahlström 1998). A dendrochonological study of penduculate oaks in southern Sweden indicated that growth reduction in heavily declining trees was associated with the timing of a strong drought in 1992 (Drobyshev et al. 2007).

Table 2 Interaction between change in oak crown defoliation and stand pH: results of two separate MANOVA analyses for (a) younger (age <100 years) and (b) older (≥100 years) subset of trees

Effects	SS	df	MS	*F*	*p*-level
Effects of non-repeated factors (age <100 years)					
Intercept	$6.50 \cdot 10^5$	1	$6.50 \cdot 10^5$	1701.56	<0.000
pH	882.5	1	882.5	2.31	0.129
Error	$2.09 \cdot 10^5$	548	382.2		
Effects of repeated factor and interactions (age <100 years)					
Change	$1.72 \cdot 10^5$	2	$8.60 \cdot 10^4$	524.08	<0.000
Change *x* pH	3131.7	2	1,565.8	9.54	<0.000
Error	$1.80 \cdot 10^5$	1,096	164.2		
Effects of non-repeated factors (≥100 years)					
Intercept	$3.02 \cdot 10^5$	1	$3.02 \cdot 10^5$	684.02	<0.000
pH	2,870.4	1	2,870.4	6.51	0.011
Error	$1.13 \cdot 10^5$	256	441.1		
Effects of repeated factor and interactions (≥100 years)					
Change	$4.54 \cdot 10^4$	2	$2.27 \cdot 10^4$	119.06	<0.000
Change *x* pH	165.8	2	82.9	0.435	0.648
Error	$9.77 \cdot 10^4$	512	190.7		

Data is from 1988, 1993, and 1999.

It follows that the frequency of climatically extreme years resulting in immediate (Dobbertin 2005) or lagging (Drobyshev et al. 2007) decline in crown conditions may be an important factor, which is difficult to assess during infrequent surveys. Although Level I and Level II monitoring sites do exist in Sweden and are inventoried every second year, number of sites is too small to sufficiently provide insight on oak crown condition on a National level.

A decade-long increase in defoliation (Fig. 2a) excludes the possibility that the observed change in crown condition was a result of tree reactions at the annual scale, and suggests the presence of more long-term effects. Although the main driving factors behind this decline still remain unclear, a number of regional studies point to various stress factors predisposing oak to crown condition decline (see review in Thomas et al. 2002). A combination of biotic (e.g. insect attacks, nutrient imbalances, infection by pathogenic fungi, poor development of mycorrhiza) and abiotic factors (climatic extremes) has been linked to decline symptoms in numerous studies, however there is little consistency of a particular combination of factors over time and for the wide oak distribution range in Europe. For example, the relationship between pollutant load, mycorrhiza development, and oak decline has been found in north-eastern Hungary (Holes and Berki 1988), in the Czech Republic (Fellner and Peskova 1995), and in Poland (Przybyl and Pukacka 1995). However, direct analysis of pollutant deposition in Austria has not supported the view that this has been a likely cause of a sudden and severe appearance of decline symptoms in the second half of the 1980s (Berger and Glatzel 1994). A growing body of research provides circumstantial evidence that decline phenomenon is a product of not one, but several predisposing factors (Balci and Halmschlager 2003; Osipov 1989; Thomas et al. 2002; Vannini et al. 1996).

Insect and fungi damages

Insect and fungal leaf infections in this study did not appear to be important drivers of defoliation dynamics, although the frequency of insect and fungi damages increased almost onefold between 1988–1994 and 1999. Interestingly enough, incidences of studied biotic agents were negatively correlated with each other, suggesting that the importance of decline-related biotic factors varied among sites. Biotic factors have previously been shown to affect the condition of oak crowns in Europe (Dobbertin 2005; Eichhorn et al. 2005; Hartmann 1996; Thomas et al. 2002). Our results, however, concur with the view that these two factors are generally not related to the health status of oak stands in southern Sweden (e.g.

Stååł 1996). Fungal root infections by *Phytophthora* spp. may present another biotic risk factor to oak (Jung et al. 2000) but while their possible contribution to oak decline in southern Sweden has been extensively studied (Jönsson 2004), the results remain inconclusive (Jönsson et al. 2005).

The strong increase in crown defoliation reported in this study did not, however, imply higher mortality rates, which remained at a relatively low level during the period studied (0.2–0.6% annually for the same dataset, Drobyshev et al. unpublished MS). A time lag between impact of stress factors and the appearance of decline symptoms may complicate the interpretation of the phenomenon. Insights from the studies of oak mortality suggest that the onset of stress conditions for oak may well precede the development of visually observed symptoms. In a study on oak mortality in southern Sweden (Drobyshev et al. 2007) tree-ring increment in recently dead oaks showed a decreasing trend as early as 15 years prior to death. Similar long-term growth declines, lagging several decades behind the periods of stressful weather conditions, have been found in American oaks (Pedersen 1998; Tainter et al. 1990). Thus, a decades-long time lag may exist between actual timing of decline factors and its expression as a change in crown defoliation.

Soil pH and tree age

More acid soils further enhance decline of oak crowns (Fig. 2c), the effect being more pronounced in trees older than 100 years (Fig. 3b). A lowering pH of the mineral soil is associated with reduction in fine-root growth and mycorrhizal development, higher nitrogen/cation ratios, and aluminium (Al) toxicity, and as a result, increased sensitivity of the root systems to environmental stress (Demchik and Sharpe 2000; Göttlein et al. 1999). Low soil pH has been shown to benefit oak root pathogens (Camy et al. 2003) and can, therefore, provide an indirect link between crown condition and secondary stress factors. However, the opposite may also hold true. A recent study of association between the oak root pathogen *Phytophthora* spp. showed that the pathogen frequency in the soil was higher on clay and loamy soils with higher pH, as compared with more acidic sand-rich and silty soils (Jönsson et al. 2005).

In southern Sweden soil acidification presents an increasing problem for sustainable forest management (Odén 1968; Sverdrup et al. 1994; Sverdrup and Stjernquist 2002) despite the decreasing trend in the deposition of acidifying compounds in this region (Eriksson et al. 1992; see Europe-wide data – Anon 2005). Increasing soil pH is beneficial for tree nutrient status. Liming of oak stands on acidic and nutrient poor soils has been shown to improve leaf nutrient status, increase specific root length and number of apices with mycorrhizae per cm of fine root length (Bakker 1998). A study in northeastern Austria revealed differences in mycorrhizae communities between healthy and declining oaks (Kovacs et al. 2000), further indicating a role of soil-related factors in causing decline symptoms. A previous study in southern Sweden revealed higher crown defoliation in oaks on podsolic than on cambisolic soils (Sonesson and Anderson 2001).

The significant interaction between defoliation dynamics and soil pH was owing to young oak trees (<100 years old, Table 1, Fig. 2c). Differences in crown condition of trees growing on more acidic compared to more basic soils increased towards the end of the studied period for young trees. Under conditions of increasing crown defoliation, more basic soil conditions may be buffering the effects of decline-related factors. Irrespective of its cause, this result indicates the importance of site selection for future oak stands: trees on less favorable acidic soils may have higher risk of decline symptoms than those on sites with more basic soils.

Considering all years, older trees (≥100 years) did not show higher crown defoliation (Table 1; Fig. 2b), indicating that decline in crown condition was not an age-related factor resulting from an increase in crown transparency (Mitscherlich 1978; Rust and Roloff 2002). However, in a previous study, which used data from 1988 and 1993 (Sonesson 1999), crown defoliation tended to increase with age. The different result between the current and the previous study may arise from a different grouping of age classes. In Sonesson (1999), the whole dataset was divided into four 20-year classes with the pronounced differences observed between 60 and 80 years age class and the rest of the dataset (Fig. 7 in Sonesson 1999). In contrast, only two age classes (<100 and ≥100 years) were used in the current study, in which changes in crown defoliation over time were pronounced much more than variation in defoliation between age classes (Table 1).

Separate analyses of two age classes revealed that older trees showed consistently higher defoliation on more acid soils then on more basic soils (Table 2; Fig. 3b). We speculate that a more developed root system in older oaks with higher maintenance costs, as compared to younger trees, might render these trees more sensitive to changes in soil conditions. Despite the fact that oak can develop deep root systems (Rothe and Binkley 2001) with detectable uptake of nutrients at depths below 30 cm (Göransson et al. 2006), it is the upper layers of the mineral soil which provide most of the nutrients for the trees (Wallander et al. 2004). Acidification of this part of the soil profile can therefore have detrimental effects on the uptake of soil nutrients, which in turn, may affect the trees capacity to resist environmental stresses (e.g. Katzensteiner et al. 1992; Thelin et al. 2002).

Conclusions

The clear negative trend in oak crown condition observed in Southern Sweden over period 1988–1999 may be partly related to the low soil acidity. Age of the trees appears to be a factor not directly related to this general trend. The increase in crown defoliation may not necessarily lead to oak dieback and decrease in its abundance in forest canopies. Although higher crown transparency may be indicative of higher mortality rates in the future (Dobbertin 2005; Dobbertin and Brang 2001), higher degree of crown defoliation and its partial dieback can be a temporal adaptation to minimise water use by the crown during periods with limited water availability (Klugmann and Roloff 1999; Thomas and Hartmann 1996) and may not lead to higher mortality rates (an example of Northern red oak – Demchik and Sharpe 2000). When such periods are over, the crown condition of oak trees appears to recover (Klugmann and Roloff 1999; Osipov and Selochnik 1989). Our study suggests that the pattern of crown defoliation is likely a product of both regional and stand-level factors. Therefore, management of oak-dominated stands, affecting age structure of oak population and soil properties of the stands, will likely influence the pattern of future crown defoliation in oak trees.

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