Recent advances on oak decline in southern Sweden

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During the last decades of the 20th century, the condition of oak species throughout Europe generally deteriorated. In southern Sweden, oak decline represents a recent phenomenon with complex temporal and spatial patterns. In this region, crown defoliation of the most common oak species, pedunculate oak *Quercus robur*, increased by >20% from 1988 to 1999. In 1999, 59% of the oaks were considered damaged, i.e. showing >25% crown defoliation. However, a trend of improving crown conditions was observed in southeastern Sweden during 2000–2008. Available research suggests unfavorable climatic variability as the main cause of negative dynamics in oak crown conditions. Studies have demonstrated the important role of climatic extremes (e.g. cold winters during the dormant season and drought events during vegetation season) in initiating decline phenomena, and a strong correlation between crown condition dynamics and tree-ring increments. *Phytophthora quercina* (class *Oomycetes*, kingdom *Chromalveolata*), a soil-born pathogen of oak, is present in declining oak stands with soil pH (BaCl$_2$) >3.5. The role of *Phytophthora* spp. in initiating the decline in southern Sweden remains unclear, since most oak stands in this region have more acidic soil conditions (pH <3.5). Similar to other European studies, our results point to the multi-factorial nature of oak decline and the importance of stand conditions in decline dynamics. This paper reviews recently published studies on the topic and presents a simple conceptual model of oak decline. We discuss future research themes that may advance our understanding of oak decline.

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Deterioration of oak (pedunculate oak *Quercus robur* and sessile oak *Q. petraea*) forest condition in Europe has been reported regularly during the past three decades (Oleksyn and Przybyl 1987, Greig 1992, Landmann et al. 1993, Oszako 2000, Barklund 2002, Thomas et al. 2002). Recently, these two species have, relative to other common trees, shown the highest share of damaged and dead trees in Europe-wide inventories (Anon. 2008). In the most recent survey of 2007, the proportion of damaged deciduous oaks (crown defoliation >25%) reached a level of 35.2% (Anon. 2008) with pedunculate oak more severely affected than sessile oak in a number of regions (Thomas et al. 2002). Similar to the situation in southern and central Europe, oaks in Sweden, and particularly *Q. robur*, have generally shown deterioration in crown conditions at the end of the 20th century. From 1988 to 1999, crown defoliation in mature oak stands increased by 20% (Sonesson 1999, Sonesson and Anderson 2001, Drobyshev et al.

2007a). In 1999, 59% of the observed oaks were considered as damaged, i.e. showing >25% crown defoliation, compared to 9% in the first survey in 1988. Overall, the mean value of defoliation rose from 11 to 33% between 1988 and 1999 (Sonesson and Anderson 2001).

Oak decline symptoms include crown thinning and defoliation, dieback of branches, formation of leaf clusters, underdevelopment of young shoots in the crown, discoloration or yellowing of the leaves, formation of epicormic shoots, and exudations from the bark and bark lesions (Sonesson 1999, Sonesson and Anderson 2001, Barklund 2002, Thomas et al. 2002). The most commonly used measure of oak decline is crown defoliation assessed on the uppermost 2/3 of the crown and is given as a percentage of a normal ample crown (=0–10% defoliation). The estimated defoliation includes leaf loss, crown transparency, branch losses and dying branches. Since defoliation and many accompanying symptoms are not specific to a par-

ticular set of physiological conditions, it is often difficult to identify principal factors behind decline symptoms. Today oak decline is considered to be a complex phenomenon in which predisposing, inciting, and contributing factors interact simultaneously in a particular oak forest ecosystem (Führer 1992, Gibbs and Greig 1997, Oszako 2000, Thomas et al. 2002, Jönsson 2004b). Reports on the decline of European oak stands suggest that the factors responsible for deterioration on crown conditions may include summer droughts (Pilcher and Gray 1982, Epron and Dreyer 1993, Bréda 2000, Bridge and Winchester 2000), changes in precipitation, excess precipitation and summer droughts (Pilcher and Gray 1982, Oosterbahn and Nabuurs 1991, Bridge et al. 1996, Gibbs and Greig 1997, Siewecki and Ufnalski 1998, Thomas and Hartmann 1998, Thomas et al. 2002), cold winters and winter/spring frosts (Hartmann et al. 1989, Hartmann and Blank 1992, Barklund and Wahlström 1998, Barklund 2002, Thomas et al. 2002). Other possible factors that predispose oak to decline may include: inappropriate forest management through high stand densities and suboptimal choice of proveniences and sites (Breda 2000, Yakovlev and Yakovlev 2000, Olano et al. 2009), nitrogen eutrophication and nutrient imbalances (Thomas and Blank 1996, Flückiger and Braun 1998, Thomas and Buttner 1998, Thomas and Hartmann 1998, Thomas and Ahlers 1999, Bréda 2000), infection by pathogenic fungi and microorganisms (Blaschke 1994, Hansen and Delatour 1999, Jung et al. 1999, 2000, Marcais et al. 1999, 2000, Marcais and Caël 2006, Hajji et al. 2009), and insect defoliation and borer attacks (Gieger and Thomas 2002, Thomas et al. 2002). Certain pathogenic organisms are considered to act as stress-inducing factors, whereas others, such as oak powdery mildew, *Armillaria* spp., bark beetles, and borers (e.g. the two-spotted oak borer *Agrillus angustulus*) are mostly regarded as secondary agents killing already weakened trees (Manion 1991, Wargo 1996, but see also Hartmann 1996).

Available studies suggest that the relative roles of decline-associated factors vary considerably across Europe. For example, although insects are mostly regarded as minor or secondary factors in oak decline, in some areas they are considered to be the primary threat to oak forests (Moraal and Hilszcanski 2000a, b). In Hungary, an increase in the population of the two-spotted oak borer *A. angustulus* led to intensive attacks of this beetle on oak trees (Somogyi 2000). Similarly, this insect was regarded as one of the most influential secondary agents of oak decline in the Flemish region (Roskams and Sioen 2000).

Oak powdery mildew caused by *Erysiphe alphitoides* (formerly *Microsphaera alphitoides*) is one of the most common diseases of pedunculate and sessile oaks in Europe (Hajji et al. 2009). However, the disease is generally considered as less damaging to mature trees than to younger ones, though it can reduce tree vigor, in conjunction with other factors such as defoliation by insects, and thus con-

tribute to oak decline (Thomas et al. 2002, Marcais and Breda 2006, Hajji et al. 2009).

Several studies have demonstrated the involvement of soil-borne species of the genus *Phytophthora* (class Oomycetes, kingdom Chromalveolata) in European oak decline, mostly on soils with pH ($BaCl_2$) >3.5 (Jung et al. 1996, 1999, 2000, Gallego et al. 1999, Thomas et al. 2002, Vettraino et al. 2002). The oak-specific species *P. quercina* has been proved to be aggressive towards root systems of oak seedlings in greenhouse studies (Jung et al. 1996, 1999, 2002, Jung 2003) and significant correlations have been found between the presence of *P. quercina* and the condition of the fine roots and crown in mature oak stands (Jung et al. 2000, Vettraino et al. 2002, Balci and Halmschlager 2003a, b). Presence of *Phytophthora* has therefore been suggested to be a predisposing factor in oak decline or even the principal factor (Brasier et al. 1995, Jung et al. 2000). However, further studies have shown that *P. quercina* may be present in non-declining oak stands without signs of excessive mortality (Hansen and Delatour 1999, Camy et al. 2003).

Air pollutants are generally not considered among the main factors contributing to oak decline (Thomas et al. 2002), although the importance of air-born agents may have been increasing over recent decades. The chemically active form of molecular oxygen, ozone, is a likely contributor to forest declines (King et al. 2005, Bussotti and Ferretti 2009): ozone levels commonly observed over central Europe have been shown to affect growth and physiological processes of forest trees (Braun et al. 2007). The relative sensitivity of both *Q. petraea* and *Q. robur* is, however, lower than of other European oak trees (Karlsson et al. 2007). Correlative studies in mature forests showed a statistically significant effect of ozone exposure, expressed as AOT 40 (accumulated ozone exposure over a threshold of 40 parts per billion), on crown conditions and growth. However, this effect was weaker than the impacts of site conditions (including soil conditions), of water regime, and of management alternatives (Stribley and Ashmore 2002, Zierl 2002, De Vries et al. 2003, Karlsson et al. 2006, Seidling 2007, Bussotti and Ferretti 2009). Thus, the biological significance of ozone exposure on crown conditions remains uncertain (Bussotti and Ferretti 2009).

The deposition of anthropogenically fixed nitrogen from the atmosphere has strong influence on terrestrial ecosystem processes. High input of N and acidifying compounds, currently observed across European subcontinent, was proposed as a factor destabilizing the flow of nutrients in oak ecosystems and reducing the stress tolerance of trees (Jönsson 2004b). However, direct correlation between nutrient status and oak health has not been conclusively shown (Berger and Glantzel 1994, Thomas and Kiehne 1995, Simon and Wild 1998, Thomas and Büttner 1998). Recent research expands our understanding of how N deposition can affect forest ecosystems, though the knowledge of indirect effects of N deposition is still inadequate. For example,

N deposition has been linked to changes in insect activity, insect population densities, and within-community interactions (Throop and Lerdau 2004), all of which could be potentially important for decline phenomena. Specifically, N deposition was suggested to increase the susceptibility of trees to damage by insects or pathogens (Skeffington and Wilson 1988, Flückinger and Braun 1998), and to decrease frost hardiness (Thomas and Blank 1996, Thomas and Ahlers 1999). N excess, in combination with drought, possibly lead to reduced concentration of allelochemicals in the leaves of *Q. robur* (Thomas and Schaffellner 1999, Thomas et al. 2002). In a recent experiment with *Quercus kelloggi*, a North American oak species, leaf nitrogen and nitrate were significantly higher at the high pollution site than at the low pollution site (Jones et al. 2008). Foliar nitrate concentrations were positively correlated with abundance of sucking insects, leaf rollers, and plutellids, suggesting higher degree of insect-related damage with higher level of N input.

In Sweden, earlier studies have proposed unusually cold winters at the end of the 1980s (Barklund and Wahlström 1998, Barklund 2002, see also Helama et al. 2009 on Finnish oaks) and a low availability of soil base cations (Sonesson and Anderson 2001) as factors associated with oak decline. To further advance our understanding of this phenomenon we review results of the recent Swedish studies on this topic. Over the recent decades, research on regional oak-decline has concentrated on three themes: a) crown condition dynamics and their relationship with diameter increment, b) mortality patterns of oak in Sweden, and c) involvement of the oak-specific pathogenic microorganism *Phytophthora quercina* in decline phenomena. Several potentially important factors such as elevated ozone concentration, nitrogen deposition, the role of single species (*Erysiphe alphitoides*, *Agrillus angustulus*) have not yet received proper attention in this context. These knowledge gaps make it difficult to confidently connect decline effects with underlying causes, and assess the relative importance of different factors. In an attempt to advance our understanding of oak decline phenomena we summarize the results of recent studies in southern Sweden and propose directions for future research.

Recent case studies

Crown condition dynamics and growth

Decline of oak forests in southern Sweden has been reported for more than two decades (Drobyshev et al. 2007c) and an extensive monitoring program has shown an increase in crown defoliation by >20% from 1988 to 1999 (Drobyshev et al. 2007a). The changes in crown defoliation have been related to the pH in the upper 20–30 cm of the mineral soils, which was closely connected to other measures of soil fertility, including cation exchange capacity and C/N ratio. Oaks growing on soils with high pH (>4.0 in $BaCl_2$-filtrate), high CEC and low C/N ratio had significantly lower crown defoliation than trees growing on more acid soils (pH <4.0), indicating that less favorable soil conditions further enhance oak decline. A significant interaction was observed between changes in crown defoliation from 1988 to 1999 and soil pH for trees younger than 100 yr. The trees on the more acid soils had a greater increase in crown transparency than trees on less acid soils. Surprisingly, 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 defoliation.

Generally, insect- and fungi-related crown damages did not appear to be an important factor in oak decline in southern Sweden, although minor damages due to these agents were increasingly common (1.1, 2.1, and 13.5% in 1988, 1993, and 1999 inventories respectively, Drobyshev et al. 2007a). A similar pattern was observed in relation to mildew occurrence on oak, with an increase from 3 to 11% between 1988 and 1999. Oaks damaged by insects or fungi had a higher degree of crown defoliation than oaks unaffected by these factors, (36 and 37% vs 32%, respectively), suggesting that both agents contributed to decline of oak crowns. Interestingly, insect and mildew damages were negatively correlated to each other, which implies that the presence of one damaging agent did not make trees more susceptible to others.

A follow-up study revealed strong correlation between crown conditions and tree-ring widths in both pure and mixed oak stands (Drobyshev et al. 2007b). The highest annual tree-ring increments have been observed in trees with healthy crowns (1.05–1.2 mm, <25% defoliation), intermediate in trees with moderately declined crowns (0.95–1.05 mm, 25–60%), and lowest in trees with heavily declining crowns (0.8–1.05 mm, >60%). The study also showed variation in the growth trends of trees as a function of crown condition class. Over the last decade of the 20th century, trees with healthy crowns showed increasing annual increments, whereas growth decline was observed in oaks with defoliation >60%. Similar to results obtained from inventory datasets, stand soil properties affected the relationship between growth and crown conditions: the growth trends among crown classes were more pronounced in oaks growing on nutrient-poor soils, compared to trees on more fertile soils.

Oak mortality pattern

The most recent peak in oak mortality apparently occurred in southern Sweden around the year 2000 (Drobyshev et al. 2007c). The temporal pattern and the presence of pre-death growth depressions were studied in detail by analyzing a dataset of dendrochronologically dated dead and living *Q. robur* at thirteen sites. Year- and site-spe-

cific growth data from living trees were used as a control to identify growth depressions in dead trees. Altogether, growth depressions were recorded in 80% of all dead oaks and were most prominent during the 1990s. While some oaks showed an obvious reduction in growth over several decades, 51% of the dead trees indicated heavy growth depression for at least 4 yr prior to death. About one fourth of all trees showed growth depression during 1–3 yr prior to death, while no growth depression was detected in one fifth of all dated dead trees. Pre-death growth depression in tree-ring chronologies implies that mortality of oak is a decade-long process and the actual death events might be lagged behind the timing of the mortality-inducing factors. Competition among trees could be a factor predisposing trees to decline as the dead oaks in the study had lower diameter at breast height (dbh) than living trees during the same growth period (Drobyshev et al. 2007c).

A compilation of empirical data from natural and seminatural forests, mostly in northern Europe, showed annual oak mortality rates varying between 0 and 6.3%, with a mean of 1.68% (Drobyshev et al. 2008a, 2009). The variation was higher in trees younger than 150 yr than in older oaks, although the differences in mortality rates between age groups were not significant. Oaks in high density stands (100 trees ha^{-1}) showed significantly higher mortality as compared to trees growing in stands with lower density (Drobyshev et al. 2008a).

Occurrence and involvement of *Phytophthora quercina* in oak decline

To evaluate geographical distribution of *Phytophthora*-infected soils, Jönsson et al. (2003a) sampled 27 declining oak stands located at 55.3–59.4°N latitude, on the border between the northern nemoral and the southern boreal vegetation zones. Soil-borne species of *Phytophthora* were geographically widespread in southern Sweden. The oak-specific fine root pathogen *P. quercina* was the most frequently recovered species, and it was isolated from rhizosphere of 10 out of 27 stands. The isolation frequency was on average 35% in the *Phytophthora* infested stands, and the pathogen was present in the rhizosphere of all sampled trees at two investigated sites. Two further species, *P. cactorum* and *P. cambivora*, were recovered from one declining stand each. The *Phytophthora* seemed to be more likely to occur in declining than in healthy stands, as no species of *Phytophthora* was isolated from five healthy oak stands investigated in Skåne, the southernmost province of Sweden (Jönsson et al. 2005). Although infested oak stands were in the stage of decline more often than non-infested stands, analysis showed no statistically significant relationship between the stand vitality and the occurrence of *Phytophthora* over 32 stands surveyed.

The soil conditions of the stands infested by *Phytophthora* species ranged from mesic sediments to moraines, with silty, loamy, and clayed textures and with soil pH (BaCl$_2$) between 3.5 and 5.0 (Jönsson et al. 2003a, 2005). The pathogen was associated more with clayed and loamy soil than with silty and sandy soils and no *Phytophthora* species were recovered from sites with sandy soil or from sites with soil pH (BaCl$_2$) <3.5. There were no differences in average summer precipitation or average annual precipitation between infested and non-infested stands.

Isolates of two *Phytophthora* species, *P. quercina* and *P. cactorum*, infected and caused substantial root damage to *Q. robur* seedlings in two greenhouse studies (Jönsson et al. 2003b, Jönsson 2004a). In the first soil infestation test, two isolates of *P. quercina* from two different oak stands and two different soils (nutrient-rich and nutrient poor) were used (Jönsson et al. 2003b). The seedlings (8–12 weeks old at the start of the experiment) were growing under a restricted mesic water regime without prolonged flooding during three months. Both isolates caused fine-root decay, dieback of nonsuberized and suberized fine roots, and necrosis of fine (diameter 0–2 mm) and coarse roots (2–5 mm). Necroses on suberized, coarse roots usually developed via infection of nonsuberized lateral roots, occasionally leading to the death of taproots. The study found significantly more dead fine roots in the two soils infested with the two isolates of *P. quercina* than in the control. The trend was similar for both soil types and isolates, but there was a higher percentage of fine-root dieback and more severe damage on coarse roots in the acid forest soil. However, aboveground growth and leaf nutrient concentration did not differ between trees on infested and controls soils.

In the second soil infestation test, the pathogenicity of seven southern Swedish isolates of *P. quercina* and one isolate of *P. cactorum* was tested (Jönsson 2004a). *Quercus robur* seedlings (14–18 weeks old at the start) were grown during 25 weeks in a natural, nonsterilized, and *Phytophtora*-free soil. The soil chemistry was acidic and representative of southern Swedish oak stands. The applied water and temperature regimes attempted to simulate regional summer conditions. The seedlings were flooded with deionized water for 15 min once a day, on three consecutive days every third week. Both *Phytophthora* species caused a significant dieback of nonsuberized as well as suberized fine roots of seedlings. Nerotic lesions were observed mainly on fine roots (0–2 mm), but also some necroses and dieback of coarser roots (2–5 mm) occurred. Total and live root lengths were significantly lower in seedlings infected by the isolates than in controls. Similarly, dead taproots and dieback of mother roots were more common among the infected seedlings. The necroses on the coarser roots usually developed via infections of nonsuberized lateral roots. These differences were not, however, paralleled by significant variation either in aboveground growth or in nutrient concentration between infested and control groups of seedlings.

A negative impact of *P. quercina* on fine-root systems of naturally growing mature oaks has been shown in the study of Jönsson and Rosengren (2005). The healthy oaks growing in infested stands had significantly higher live fine-root length than moderately and severely declining trees. In non-infested oak stands, no difference was found in live fine-root length among trees of differing vitality. The study found a substantial dieback of non-suberized fine roots of severely declining oaks in the *Phytophthora*-infested stands. The suberized coarse roots of declining trees often had discolored necrotic areas and one to several lesions in the lateral roots. The lesions varied in size, 10–15 mm in length and 2–5 mm in width. Necrotic areas and lesions appeared, but only to a smaller extent, on roots of the healthy trees. No significant effects on above-ground growth or leaf nutrient concentration were found. Soil chemistry showed few differences in comparisons of healthy and declining stands. However, in stands with *P. quercina*, the concentration of total N in the organic soil layer was higher under healthy trees than under declining ones, while the opposite pattern was observed in pathogen-free stands (Jönsson and Rosengren 2005). The concentration of P in the organic layer and the upper 30 cm of the mineral soil was significantly lower in stands with presence of *Phytophthora*.

Discussion

Insights from Swedish oak decline studies

Oak decline in southern Sweden represents a relatively recent phenomenon with complex temporal and spatial patterns. Although further studies are needed to reveal the driving factors behind the decline, available research points to unfavorable climatic variability as the most likely cause of negative dynamics in oak crown conditions. Support for this conclusion comes from strong climatic control of oak growth in southern Sweden (Drobyshev et al. 2008b) and similarly strong correlation between growth and tree crown conditions (Drobyshev et al. 2007b). Ongoing research (Drobyshev et al. unpubl.) indicates that negative growth anomalies in regional oak chronology are primarily driven by the pattern of growing season water availability, which may also drive crown condition dynamics. The same decline mechanism was proposed for Slovenian oak forests, where strong correlation was found between crown defoliation and precipitation (Cater and Levanic 2004).

Due to the more resilient nature of crown dynamics, it apparently lags behind changes in the ring-width increment, as suggested in Drobyshev et al. (2007b). Given the same set of factors guiding both growth and crown condition dynamics, we explain general deterioration of crown conditions as a reaction to a) prolonged water deficit during the growing season, and b) unusually strong and/or late cold spells during the dormant season or during the transition between dormant and growing seasons. In the first case, we interpret loss of the parts of oak crown as a tree's adaptation to decrease water expenditures through evapotranspiration. In the second case, frost-induced tissue damages including damages to meristems and the tree's water transport system are likely physiological factors behind the decline.

A wider temporal perspective on the decline phenomena may add to understanding its temporal scale. In Sweden, observations of decline in oak crown conditions consistently coincided with negative growth anomalies in the regional oak chronology (Fig. 1). First observations of crown declines in early 1940s (Barklund 2002) were associated with strong negative growth anomaly in that period. The increasingly deteriorating state of oak forests during 1988–1999 (Drobyshev et al. 2007a) was paralleled by decline in regional ring-width indexes (Fig. 1). The negative trend, however, might have changed around the turn of the 20th century. In line with dendrochronological data, the
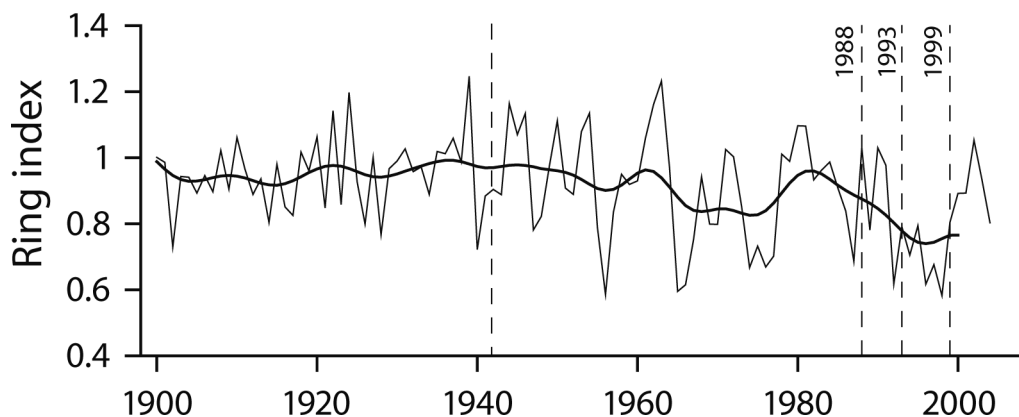

Figure 1. Regional southern Swedish oak chronology (Drobyshev et al. 2008b) and timing of three regional forest inventories (Sonesson and Anderson 2001) and decline in crown conditions reported in Barklund (2002) during early 1940s (dashed lines).

most recent, although limited, inventory data from southeastern Sweden suggest general improvement of oak crown conditions (Fig. 2). Considering regional oak chronology as a proxy of crown conditions, it should be possible to estimate the typical length of the decline-prone periods. In the 20th century, such periods probably extended over one to two decades.

Since regional tree-ring chronology was developed from live trees, periods of improved growth are likely indicative of periods with positive growth/crown dynamics, and cannot be attributed to loss of dead tree chronologies contributing with low increments before tree mortality. This suggests, therefore, that the negative trend in crown conditions may be reversible. Our studies indicate that growth recovery occurs in trees with crown transparency below 60% (Drobyshev et al. 2007b). In accordance with this observation, a review of oak mortality rates showed generally similar values (around 1–2% annually) across both different age cohorts and time periods, including the decline-prone period during the 1980s–1990s (Drobyshev et al. 2008a). Instead, a change in stand densities, often resulting from changes in land-use practices, may be an important factor affecting mortality rates. We argue, however, for cautious interpretation of mortality patterns since actual waves of mortality may lag considerably behind the onset of unfavorable environmental conditions (Pedersen 1998). In southern Swedish oaks, such lag may reach 8–10 yr (Drobyshev et al. 2007c).

Soilborne *Phytophthora* is present in declining oak stands in Sweden and is probably involved in the decline in tree crown conditions. In general, *Phytophthora* are considered to be more aggressive at higher pH values (Schmitthenner and Canaday 1983), and Jung et al. (2000) showed an increase in the production of sporangia in *P. quercina* with increasing soil pH. Local soil conditions may therefore have a strong impact on the pathogenicity of the microorganism. Indeed, in southern Sweden, the pathogen seems only to occur at sites with soil pH ($BaCl_2$) >3.5, and most oak forest sites in the region are more acidic (Sonesson and Anderson 2001). More acidic soil conditions may also explain lower diversity of *Phytophthora* species in the region (with only three species identified), compared to high species diversity within this genus in central and south Europe. The lower diversity of *Phytophthora* species, however, may be an artifact of the relatively recent immigration of *Phytophthora* in southern Sweden.

It remains unclear to what degree the results obtained on oak seedlings can provide explanations of declining dynamics of mature stands. The results of two different experiments confirm pathogenicity of *P. quercina* to *Q. robur* seedlings under restricted water availability (Jönsson et al. 2003b, Jönsson 2004a). Jönsson and Rosengren (2005) have demonstrated a negative impact of *P. quercina* on fine roots of mature oaks in infested oak stands in a field study. It has been suggested that continuous root infections may result in an increased susceptibility of the tree to further pathogen infections as well as to other stress factors (Jönsson 2004b). However, studies have repeatedly found a poor association between *Phytophthora* infection and trees' aboveground status (nutrient balance and growth) (Jönsson et al. 2003b, Jönsson 2004a). Further, the pathogen was only recovered from a moderate proportion of the declining oak stands surveyed. This may indicate the importance of other site-specific factors, as well as methodological difficulties in identifying soil infection even with multiple sampling occasions (Jönsson 2004b).

The contribution of other non-climatic factors in oak decline in southern Sweden remains unclear and requires further studies. For example, the mildew *E. alphitoides* impact on trees previously defoliated by insects has been documented in European studies (Thomas et al. 2002). Swedish inventory data, however, show no clear statistical relation between this parasite and crown defoliation (Drobyshev et al. 2007a). Likewise, the buprestid beetle *A. biguttatus* which attacks mostly stressed and declining oaks (Vansteenkiste et al. 2004) is rarely found in Sweden, and for that reason is probably of little significance (Barklund 2002). Recently, interactions between different pathogens were proposed as an important driver of oak decline (Marcais and Breda 2006), but there is almost no data to discuss these interactions in the southern Swedish context.

Even with favorable climatic conditions, oak wellbeing may be at risk due to negative development of regional soil conditions. Swedish oak forests are growing on soils ranging from haplid podsols to eutric cambisols. Over the second half of the 20th century, forests in southern Sweden have been affected by acid and nitrogen deposition through air pollution, which caused soil acidification, nutrient imbalance, and decreased tree vitality (Nihlgård 1997a, b, Jönsson et al. 2003c). The soil nutrient pool has decreased substantially even on highly productive cambisols (Stjernquist et al. 2002). A survey on soil chemistry
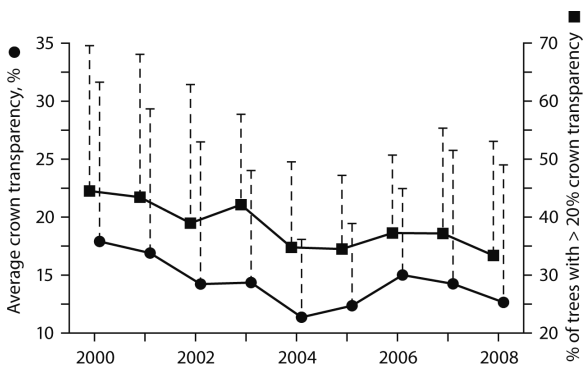

Figure 2. Dynamics of crown transparency in oak stand in southeast Sweden (Kalmar region, 5 plots, data from Swedish Forest Board, 2009, <www.svo.se>) for 2000–2008. Data – average crown transparency (circles) and average percentage of damaged trees (squares, >20% in crown transparency) with SD plotted for each year.

in >250 oak and beech stands in southern Sweden showed low pH-values (<4.2 in $BaCl_2$-filtrate) in 86% of the stands and low (10–20%) and very low (<10%) base saturation in more than one third of the stands surveyed (Sonesson and Anderson 2001).

Soil acidification is still proceeding in southern Sweden, which leads to soil depletion and may compromise nutrient sustainability on commercial oak stands (Sverdrup et al. 2006). A number of Swedish studies indicate low levels of foliar nutrients, macro as well as micro elements, in oak, as compared to the range suggested for Europe by ICP-forests (Sonesson 2000, Schlyter et al. 2002, Hagen-Thorn et al. 2004). The Swedish nutrient ratios to N reflect low, but in general balanced, nutrient conditions. The only exceptions are Ca/N and Mg/N ratios that show a more narrow span, and lower ratios, than what is present in the continental European data. In certain areas, oak forests would need addition of Ca (Sverdrup et al. 2006). Nihlgård (1997b) has proposed acid and nitrogen deposition due to air pollution as predisposing factors of the stresses leading to forest decline.

Conceptual model of forest decline

We summarize the current understanding of oak decline phenomena in a simple model linking climatic variation, site-level condition, and the risk or proportion of trees affected by the decline (Drobyshev unpubl., Fig. 3). Climate defines an "envelope" for species' geographical distribution, and climatic variation exercises the main
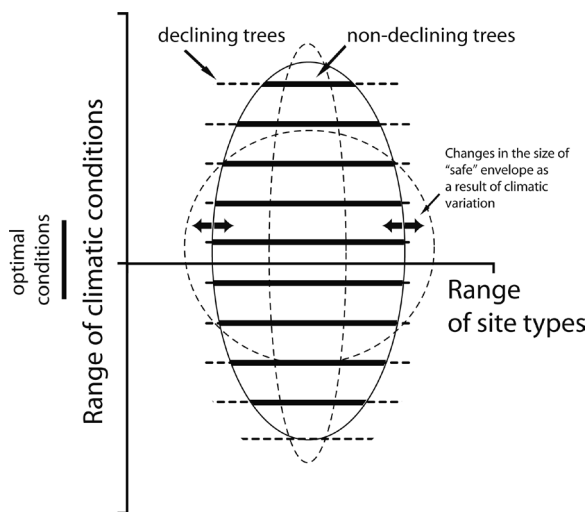

Figure 3. Conceptual model of interaction between climatic variation, site properties, and decline phenomena (Drobyshev et al. unpubl.). The model predicts variation in the proportion declining trees or, alternatively, a risk of decline for stands along gradients in climatic variation and a hypothetical gradient in site conditions. See further explanations of the model in the text.

control over expression of decline, which is understood as decline in crown conditions and/or decline in ring-width increment. Incidence or risk of decline effects is minimal during the periods with close-to-optimal conditions, since most of the gradient of site conditions can adequately support processes of nutrition and growth. Deviation of climatic conditions away from the optimal state reduces the part of the site conditions gradient where a majority of trees can be adequately supplied by resources. Larger deviation from the optimal range of growing conditions would then mean a higher percentage of trees being physiologically stressed and, eventually, being subject to secondary decline agents (e.g. insects or parasites). The model explicitly considers climatic variability as the main factor behind the decline. Further, we consider increased frequency of extreme events, i.e. events deviating from the typical range of climatic variability for the region, as the principal element in climate variability related to oak decline. Site conditions may uniquely modify expression of physiological stress in trees on a particular site. We consider this model, though relatively simple, as the most general representation of the state of our knowledge concerning oak decline in southern Sweden. The temporal component of the phenomena is represented by the changes in the area of the "decline-free" envelope in the multi-space of the site properties, as the result of climatic variability. The graphic version of the model lacks representation of time lags in the studied system.

Directions for future research

Although oak decline has been observed in southern Sweden since 1987 (Barklund and Wahlström 1998), its nature and driving mechanisms still require better mechanistic models to interpret its spatio-temporal dynamics. Building on completed and ongoing studies we propose a number of research topics, which should advance our knowledge in this field. We start by acknowledging the importance of regional field inventory data in providing information about the current state of oak forests. The size of the regional dataset (n_{trees} = 808, n_{sites} =123) allows complex interactions between tree- and site-properties to be tested statistically (Drobyshev et al. 2007a). Continued effort with such inventories would permit analysis of the time factor, i.e. temporal trends in forest conditions, at multiple spatial scales. In this context, temporal dynamics of oak crowns are to be analyzed as a function of tree-level variables (e.g. size, age, and past crown conditions), site conditions (e.g. soil conditions, stand density, stand composition, presence of *P. quercina*), and sub-regional differences in weather conditions (e.g. amount of precipitation and frequency of climatically extreme periods). Coupling existing inventories with remote sensing methods may bring further advantages by considerably expanding data on spatial coverage and providing opportunities for analyz-

ing crown inventory data in a spatially-explicit way with other gridded environmental datasets.

Extending our understanding of climatic influence on tree functioning is fundamental for interpreting the decline phenomena and, generally, for providing a mechanistic model of trees' responses to environmental variability. Long observational series are vital for parameterizinge such models. Tree-ring chronologies present the most readily available annual proxies of trees' past environmental conditions and therefore have a strong potential in modeling research. Our studies suggest that analysis of the regional networks of tree-ring width chronologies may considerably increase temporal resolution and extend the time perspective of forest condition studies. Additionally, annual ring-based chronologies of element concentrations and stable isotope chronologies may bring further important detail into this work.

Physiological conditions of the trees may be an important factor affecting dynamics of tree crowns. Studies of trees' nutrient status, as one of the measures of tree health status, should help evaluate the role of nutrient deficiencies and their interactions with adverse climatic conditions in shaping the pattern of oak decline. Results from such studies may also be instrumental in developing such silvicultural activities as soil liming and/or fertilization to mitigate negative crown dynamics.

Finally, detailed analysis of crown dynamics in other trees from the Fagaceae family should be of value in assessing the generality of patterns revealed in oak forests. In southern Sweden, European beech *Fagus sylvatica* has shown similar negative trends in crown conditions since the late 1980s (Sonesson and Anderson 2001). Both accumulating tree-ring chronologies and already available inventory data allow for a similar set of analyses to be performed for this species. With apparent differences in biology of these two species, e.g. in the patterns of root distribution (Rosengren and Stjernquist 2004) and mechanisms of stomatal control (Epron and Dreyer 1993), a comparative analysis may be of value in partitioning the effects of climatic variability and site conditions on decline dynamics.

References

Anonymous 2008. The condition of forests in Europe. – 2008 Executive Report, World Forestry, Hamburg.

Balci, Y. and Halmschlager, E. 2003a. Incidence of *Phytophthora* species in oak forests in Austria and their possible involvement in oak decline. – For. Pathol. 33: 157–174.

Balci, Y. and Halmschlager, E. 2003b. *Phytophthora* species in oak ecosystems in Turkey and their association with declining oak trees. – Plant Pathol. 52: 694–702.

Barklund, P. 2002. Ekskador i Europa. – National Board of Forestry, Report 2002:12, in Swedish.

Barklund, P. and Wahlström, K. 1998. Death of oaks in Sweden since 1987. – In: Cech, T. H. et al. (eds), Disease/environment interactions in forest decline. Proceedings of a workshop of the working party IUFRO 7.02.06, 16–21 March 1998, Federal Forest Research Centre, Vienna, p. 193.

Berger, T. W. and Glatzel, G. 1994. Deposition of atmospheric constituents and its impact on nutrient budget of oak forests (*Quercus petraea* and *Quercus robur*) in Lower Austria. – For. Ecol. Manage. 70: 183–193.

Blaschke, H. 1994. Decline symptoms on roots of *Quercus robur*. – Eur. J. For. Pathol. 24: 386–398.

Brasier, C. M. et al. 1995. *Phytophthora cinnamoni* and oak decline in southern Europe. Environmental constraints including climate change. – Ann. Sci. For. 53: 347–358.

Braun S. et al. 2007. Shoot growth of mature *Fagus sylvatica* and *Picea abies* in relation to ozone. – Environ. Pollut. 146: 624–628.

Bréda, N. 2000. Water shortage as a key factor in the case of the oak dieback in the Harth Forest (Alsatian plain, France) as demonstrated by dendroecological and ecophysiological study. – In: Oszako, T. and Delatour, C. (eds), Recent advances on oak health in Europe. Forest Research Inst., Warsaw, pp. 157–159.

Bridge, M. et al. 1996. Dendroclimatological observations on trees at Kew and Wakehurst Place: event and pointer years. – Forestry 69: 263–269.

Bridge, M. C. and Winchester, V. 2000. An evaluation of standard oak tree growth in Ruislip woods, West London. – Bot. J. Linn. Soc. 134: 61–71.

Bussotti, F. and Ferretti, M. 2009. Visible injury, crown condition, and growth responses of selected Italian forests in relation to ozone exposure. – Environ. Pollut. 157: 1427–1437.

Camy, C. et al. 2003. Relationships between soil factors, *Quercus robur* health, *Collybia fusipes* root infection and *Phytophthora* presence. – Ann. For. Sci. 60: 419–426.

Cater, M. and Levanic, T. 2004. Increment and environmental conditions in two Slovenian pedunculate-oak forest complexes. – Ekologia (Bratisl.) 23: 353–365.

De Vries, W. et al. 2003. Intensive monitoring of forest ecosystems in Europe. 1. Objectives, set-up and evaluation strategy. – For. Ecol. Manage. 174: 77–95.

Drobyshev, I. et al. 2007a. Crown condition dynamics of oak in southern Sweden 1988–1999. – Environ. Monit. Assess. 134: 199–210.

Drobyshev, I. et al. 2007b. Relationship between crown condition and tree diameter growth in southern Swedish oaks. – Environ. Monit. Assess. 128: 61–73.

Drobyshev, I. et al. 2007c. Temporal mortality pattern of pedunculate oaks in southern Sweden. – Dendrochronologia 24: 97–108.

Drobyshev, I. et al. 2008a. Lifespan and mortality of old oaks – combining empirical and modeling approaches to support their management in southern Sweden. – Ann. For. Sci. 65: 401, doi: 10.1051/forest:2008012.

Drobyshev, I. et al. 2008b. Influence of annual weather on growth of pedunculate oak in southern Sweden. – Ann. For. Sci. 65: 512, doi: 10.1051/forest:2008033.

Drobyshev, I. et al. 2009. Tree mortality in a mixed deciduous forest in northwestern Russia over 22 years. – Ann. For. Sci. 66: 411, doi: 10.1051/forest:2009018.

Epron, D. and Dreyer, E. 1993. Photosynthesis of oak leaves under water-stress – maintenance of high photochemical-II and occurrence of nonuniform CO_2 assimilation. – Tree Physiol. 13: 107–117.

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

Führer, E. 1992. Oak decline in central Europe: a synopsis of hypotheses. – In: McManus, M. L. and Liebhold, A. M. (eds), Proceedings: population dynamics, impacts and integrated management of forest defoliating insects. USDA Forest Service General Technical Report NE 247, pp. 7–24.

Gallego, F. J. et al. 1999. Etiology of oak decline in Spain. – Eur. J. For. Pathol. 29: 17–27.

Gibbs, J. N. and Greig B. J. W. 1997. Biotic and abiotic factors affecting the dieback of pedunculate oak *Quercus robur* L. – Forestry 70: 399–406.

Gieger, T. and Thomas, F. G. 2002. Effects of defoliation and drought stress on biomass partitioning and water relations of *Quercus robur* and *Q. petraea*. – Basic Appl. Ecol. 3: 171–181.

Greig, B. 1992. Occurrence of decline and dieback of oak in Great Britain. – Research Information Note 214, Forestry Commission, Alice Holt, Surrey.

Hagen-Thorn, A. et al. 2004. Macronutrients in tree stems and foliage: a comparative study of 6 temperate forest species planted at the same site. – Ann. For. Sci. 61: 489–498.

Hajji, M. et al. 2009. Impact of *Erysiphe alphitoides* on transpiration and photosynthesis in *Quercus robur* leaves. – Eur. For. Pathol. 125: 63–72.

Hansen, E. and Delatour, C. 1999. *Phytophthora* species in oak forests of north-east France. – Ann. For. Sci. 56: 539–547.

Hartmann, G. 1996. Ursachenanalyse des Eichensterbens in Deutschland – Versuch einer Synthese bisheriger Befunde. – Mitteilungen Aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem 318: 125–151, in German.

Hartmann, G. and Blank, R. 1992. Winterfrost, Kahlfrass und Prachtkäferbefall als Faktoren im Ursachenkomplex des Eichensterbens in Norddeutchland. – Forst Holz 47: 443–452, in German.

Hartmann, G. et al. 1989. Eichensterben in Norddeutchland: Verbreitung, Schadbilder, mögliche Ursachen. – Forst Holz 44: 475–487, in German.

Helama, S. et al. 2009. Oak decline in Helsinki portrayed by tree-rings, climate and soil data. – Plant Soil 319: 163–174.

Jones, M. E. et al. 2008. The effect of nitrogen addition on oak foliage and herbivore communities at sites with high and low atmospheric pollution. – Environ. Pollut. 151: 434–442.

Jönsson, U. 2004a. *Phytophthora* species and oak decline – can a weak competitor cause significant root damage in a nonsterilized acidic forest soil. – New Phytol. 162: 211–222.

Jönsson, U. 2004b. *Phytophthora* and oak decline – impact on seedlings and mature trees in forest soils. – Ph.D. thesis, Lund Univ., Sweden.

Jönsson, U. and Rosengren, U. 2005. Can *Phytophthora quercina* have a negative impact on mature pedunculate oaks under field conditions? – Ann. For. Sci. 63: 661–672.

Jönsson, U. et al. 2003a. First records of soilborne *Phytophthora* species in Swedish oak forests. – For. Pathol. 33: 175–179.

Jönsson, U. et al. 2003b. Pathogenicity of Swedish isolates of *Phytophthora quercina* to *Quercus robur* in two different soils. – New Phytol. 158: 255–264.

Jönsson, U. et al. 2003c. Acidification-induced chemical changes in coniferous forest soils in southern Sweden 1988–1999. – Environ. Pollut. 123: 75–83.

Jönsson, U. et al. 2005. Relationships between *Q. robur* health, occurrence of *Phytophthora* species and site conditions in southern Sweden. – Plant Pathol. 54: 502–511.

Jung, T. 2003. Effect of environmental constraints on *Phytophtora*-mediated oak decline in central Europe. – In: McComb, J. A. et al. (eds), *Phytophthora* in forests and natural ecosystems. 2nd international IUFRO working party 7.02.09 meeting, Albany, W. Australia, 30 Sept–5 Oct, 2001, Murdoch Univ. Print, pp. 89–98.

Jung, T. et al. 1996. Isolation, identification, and pathogenicity of *Phytophthora* species from declining oak stands. – Eur. J. Pathol. 26: 253–272.

Jung, T. et al. 1999. *Phytophthora quercina* sp. nov., causing root rot of European oaks. – Mycol. Res. 103: 785–798.

Jung, T. et al. 2000. Involvement of soilborne *Phytophthora* species in central European oak decline and the effect of site factors on the disease. – Plant Pathol. 49: 706–718.

Jung, T. et al. 2002. Three new species of *Phytophthora* from European oak forests. – Mycol. Res. 106: 397–411.

Karlsson, P. E. et al. 2006. Negative impact of ozone on the stem basal area increment of mature Norway spruce in south Sweden. – For. Ecol. Manage. 232: 146–151.

Karlsson, P. E. et al. 2007. Risk assessments for forest trees: the performance of the ozone flux versus the AOT concepts. – Environ. Pollut. 146: 608–616.

King, J. S. et al. 2005. Tropospheric O_3 compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO_2. – New Phytol. 168: 623–636.

Landmann, G. et al. 1993. Oak dieback in France: historical and recent records, possible causes, current investigations. – In: Anon. (ed.), Zustand und Gefährdung der Laubwälder 5. F. Pfeil, Munchen, pp. 97–113.

Manion, P. D. 1991. Tree disease concepts. – Prentice Hall.

Marcais, B. and Breda, N. 2006. Role of an opportunistic pathogen in the decline of stressed oak trees. – J. Ecol. 94: 1214–1223.

Marcais, B. and Caël, O. 2006. Spatial pattern of the density of *Armillaria* epiphytic rhizomorphs on tree collar in an oak stand. – For. Pathol. 36: 31–40.

Marcais, B. et al. 1999. Measuring the impact of *Collybia fusipes* on the root system of oak trees. – Ann. For. Sci. 56: 227–235.

Marcais, B. et al. 2000. Relationship between presence of basidomes, above-ground symptoms and root infections by *Collybia fusibes* in oaks. – For. Pathol. 30: 7–17.

Moraal, L. and Hilszczanski, J. 2000a. *Agrilus biguttatus* (Col.: Buprestidae) in relation with oak decline. – In: Oszako, T. and Delatour, C. (eds), Recent advances on oak health in Europe. Forest Research Inst., Warsaw, pp. 219–224.

Moraal, L. and Hilszczanski, J. 2000b. The buprestid beetle, *Agrilus biguttatus* (F.) (Col. Buprestidae), a recent factor in oak decline in Europe. – J. Pest Sci. 73: 134–138.

Nihlgård, B. 1997a. Relationship of forest damage to air pollution in the Nordic countries. – Agric. For. Meteorol. 50: 87–98.

Nihlgård, B. 1997b. Forest decline and environmental stress. – In: Chapman, D. (ed.), The global environment. VCH, pp. 422–440.

Olano, J. M. et al. 2009. Why and where do adult trees die in a young secondary temperate forest? The role of neighbourhood. – Ann. For. Sci. 66: 105, doi: 10.1051/forest:2008074.

Oleksyn, J. and Przybyl, K. 1987. Oak decline in the Soviet Union – scale and hypotheses. – Eur. J. For. Pathol. 17: 321–336.

Oosterban, A. and Nabuurs, G. J. 1991. Relations between oak decline and groundwater class in the Netherlands. – Plant Soil 136: 87–93.

Oszako, T. 2000. Oak declines in Europe's forest – history, causes and hypothesis. – In: Oszako, T. and Delatour, C. (eds), Recent advances on oak health in Europe. Forest Research Inst., Warsaw, pp. 11–40.

Pedersen, B. S. 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. – Ecology 79: 79–93.

Pilcher, J. and Gray, S. 1982. The relationships between oak tree growth and climate in Britain. – J. Ecol. 70: 297–304.

Rosengren, U. and Stjernquist, I. 2004. Gå på djupet! Om rotdjup och rotproduktion i olika skogstyper. – Rahms, Lund, in Swedish.

Roskams, P. and Sioen, G. 2000. The condition of *Quercus robur* L. in the Flemish Region. – In: Oszako, T. and Delatour, C. (eds), Recent advances on oak health in Europe. Forest Research Inst., Warsaw, pp. 117–119.

Schlyter, P. et al. 2002. Forest condition – a regional overview. – In: Sverdrup, H. and Stjernquist, I. (eds), Developing principles and models for sustainable forestry in Sweden. Kluwer, pp. 256–271.

Schmitthenner, A. F. and Canaday, C. H. 1983. Role of chemical factors in the development of *Phytophthora* diseases. – In: Erwin, D. C. et al. (eds), *Phytophthora*. Its biology, taxanomy, ecology and pathology. The American Phytophthora Society, pp. 189–196.

Seidling, W. 2007. Signals of climatic drought in crown condition data of the German level I network. – Eur. J. For. Res. 126: 529–544.

Simon, A. and Wild, A. 1998. Mineral nutrients in leaves and bast of pedunculate oak (*Quercus robur* L.) at different states of defoliation. – Chemosphere 36: 955–959.

Siwecki, R. and Ufnalski, K. 1998. Review of oak stand decline with special reference to the role of drought in Poland. – Eur. J. Pathol. 28: 99–112.

Skeffington, R. A. and Wilson, E. J. 1988. Excess nitrogen deposition: issues for consideration. – Environ. Pollut. 54: 159–184.

Somogyi, Z. 2000. Oak decline in Hungary: case study. – In: Oszako, T. and Delatour, C. (eds), Recent advances on oak health in Europe. Forest Research Inst., Warsaw, pp. 91–103.

Sonesson, K. 1999. Oak decline in southern Sweden. – Scand. J. For. Res. 14: 368–375.

Sonesson, K. 2000. Short term effects of nitrogen-free fertilization in three oak stands in southern Sweden. – In: Ozako, T. and Delatour, C. (eds), Recent advances on oak health in Europe. Forest Research Inst., Warsaw, pp. 207–214.

Sonesson, K. and Anderson, S. 2001. Forest condition of beech and oak in southern Sweden. – National Board of Forestry, Report 2001:12.

Stjernquist, I. et al. 2002. Acid deposition and soil activity. – In: Sverdrup, H. and Stjernquist, I. (eds), Developing principles and models for sustainable forestry in Sweden. Kluwer, pp. 222–236.

Stribley, G. H. and Ashmore, M. R. 2002. Quantitative changes in twig growth pattern of young woodland beech (*Fagus sylvatica* L.) in relation to climate and ozone pollution over 10 years. – For. Ecol. Manage. 157: 191–204.

Sverdrup, H. et al. 2006. Assessing nutrient sustainability of forest production for different tree species considering Ca, Mg, K, N and P at Björnstorp Estate, Sweden. – Biochemistry 81: 219–238.

Thomas, F. M. and Kiehne, U. 1995. The nitrogen status of oak stands in northern Germany and its role in oak decline. – In: Nilsson, L. O. et al. (eds), Nutrient uptake and cycling in forest ecosystems. Proceedings of the CEC/IUFRO Symposium in Halmstad, Sweden, 7–10 June, 1993. Kluwer, pp. 671–676.

Thomas, F. M. and Blank, R. 1996. The effect of excess nitrogen and of insect defoliation on the frost hardiness of bark tissue of adult oaks. – Ann. Sci. For. 53: 395–406.

Thomas, F. M. and Büttner, G. 1998. Nutrient relations in healthy and damaged stands of mature oaks on clayey soils: two case studies in northwestern Germany. – For. Ecol. Manage. 108: 301–319.

Thomas, F. M. and Hartmann, G. 1998. Tree rooting patterns and soil water relations of healthy and damaged stands of mature oak (*Quercus robur* L. and *Quercus petraea* [Matt.] Liebl.). – Plant Soil 203: 145–158.

Thomas, F. M. and Ahlers, U. 1999. Effects of excess nitrogen on frost hardiness and freezing injury of above-ground tissue in young oaks (*Quercus petraea* and *Q. robur*). – New Phytol. 144: 73–83.

Thomas, F. M. and Schafellner, C. 1999. Effects of excess nitrogen and drought on the foliar concentrations of allelochemicals in young oaks (*Quercus robur* and *Q. petraea*). – J. Appl. Bot. 73: 222–227.

Thomas, F. M. et al. 2002. Abiotic and biotic factors and their interactions as causes of oak decline in central Europe. – For. Pathol. 32: 277–307.

Throop, H. L. and Lerdau, M. T. 2004. Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. – Ecosystems 7: 109–133.

Vansteenkiste, D. et al. 2004. Predisposition and symptoms of *Agrilus* borer attack in declining oak trees. – Ann. Sci. For. 61: 815–823.

Vettraino, A. M. et al. 2002. Occurence of *Phytophthora* species in oak stands in Italy and their association with declining oak trees. – For. Pathol. 32: 19–28.

Wargo, P. M. 1996. Consequences of environmental stress on oak: predisposition to pathogens. – Ann. Sci. For. 53: 359–368.

Yakovlev, I. A. and Yaklovlev, A. S. 2000. Oak decline in the Middle Povolzhje region of Russia. – In: Oszako, T. and Delatour, C. (eds), Recent advances on oak decline in Europe. Forest Research Inst., Warsaw, pp. 73–82.

Zierl, B. 2002. Relations between crown condition and ozone and its dependence on environmental factors. – Environ. Pollut. 119: 55–68.