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Relationship Between Crown Condition and Tree Diameter Growth in Southern Swedish Oaks

Igor Drobyshev · Hans Linderson · Kerstin Sonesson

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Abstract We studied correlation between crown conditions and tree-ring widths in 260 trees of pedunculate oak (*Quercus robur* L.) growing on 33 sites in southern Sweden. The tree-ring increment over 1998–2002 was highest in trees with healthy crowns, intermediate in trees with moderately declined crowns, and lowest in trees with heavily declining crowns. The time period with significant correlation between crown status and tree-ring increment varied between 10 years (given autocorrelation in tree-ring chronologies preserved) and 4 years (autocorrelation removed). In pairwise comparisons of three crown classes, differences in tree-ring increment between trees with healthy crowns and trees with heavily declining crowns were the most pronounced, Fisher LSD *P* value staying below 0.05 over 13 years (autocorrelation preserved) or 4 years (autocorrelation removed). Over two 5-year periods (1993–1997 vs. 1998–2002) the cumulative increment increased significantly for trees with healthy crowns, did not change in trees with moderately declining crowns, and significantly decreased in trees with heavily declining crowns. For trees with healthy crowns, this dynamics may represent growth recovery after 1992 drought. Instead, oaks with defoliation above 60% appear to reach a threshold in their ability to recover growth. At sites on nutrient-poor soils cumulative increments over 1998–2002 differed significantly among trees with different crown condition and no differences were observed at sites on nutrient-rich soils. Analyses and interpretation of the oak growth trends as recovered from tree-ring chronologies may be improved by controlling for the crown status of the trees sampled, e.g., by using sampling strategy that would represent the average crown and growth conditions of the sites.

Keywords Climate variation · Defoliation · Dendrochronology · Drought · Forest health · Hardwood · Forest monitoring · Inventories · Oak decline · *Quercus robur*

1 Introduction

Assessment of crown condition has been widely used to study impact of various environmental factors on tree health. In Europe the Intensive Forest Monitoring Programme (Level II monitoring), which started in

I. Drobyshev (✉) · K. Sonesson
Sustainable Management in Hardwood Forests,
Southern Swedish Forest Research Centre,
P.O. Box 49, 230 53 SLU, Alnarp, Sweden
e-mail: Igor.Drobyshev@ess.slu.se

K. Sonesson
e-mail: Kerstin.Sonesson@ess.slu.se

H. Linderson
Laboratory for Wood Anatomy and Dendrochonology,
Department of Quaternary Geology, Lund University,
Sölvegatan 12, 223 62 Lund, Sweden
e-mail: Hans.Linderson@geol.lu.se

1994, relies on the repeated inventories of about 850 permanent plots to document variation in crown conditions of major leaved and coniferous species (De Vries et al., 2003; Seidling, 2004). The main focus of monitoring programs has been on (a) correlations between site factors and the risk of decline (De Vries et al., 2003; Seidling, 2004; Solberg, Kvindesland, Aamlid, & Venn, 2002; Zierl, 2002) ; (b) temporal trends in stress factors (De Vries et al., 2003; Sonesson, 1999); and (c) identification of the critical loads of air pollutants (Solberg et al., 2002; Zierl, 2002) and nutrient deposition (Matzner & Murach, 1995; Neirynck & Roskams, 1999; Raben, Andreae, & Meyer-Heisig, 2000). In Europe, two major decline phenomena have been reported recently. Decline of coniferous forests was expressed as a temporal trend towards higher crown transparency during 1970–1980 (Thomsen & Nellemann, 1994). Deterioration in the forest condition of deciduous stands, primarily oak, has been regularly reported since late 1960s (Greig, 1992; Selochnik, 1989; Sonesson, 1999; Thomas, Blank, & Hartmann, 2002).

The penduculate oak (*Quercus robur* L.) is an important tree species in the Swedish forest industry (Löf, 2001). There is a need for empirical knowledge to support stand management and to get a better insight into pattern of decline phenomenon and its relation to the site properties. The knowledge about the factors controlling the status of oak stands is currently limited (Luisi, Lerario, & Vannini, 1993; Thomas et al., 2002). In Sweden, this knowledge gap became apparent as the evidence of regional decline of hardwood forests started accumulating since late 1980s and attempts were made to interpret this phenomenon (Sonesson, 1999; Wijk, 1989).

Relationship between tree crown status and its growth has been studied on a number of tree species both in Europe (Dobbertin, 2005; Eckmullner & Sterba, 2000; Fischer et al., 2004) and in North America (Dushesne, Ouimet, & Morneau, 2003; Dwyer, Cutter, & Wetteroff, 1995; Payette, Fortin, & Morneau, 1996). As to pedunculate oaks in Sweden, until recently no data were available to couple visually observed changes in crown conditions with more quantitative measures of tree performance, e.g., tree growth. To fill up this gap we analysed interactions between crown and diameter growth for pedunculate oak (*Q. robur* L.) across a range of site types within an area below 60°N (Figure 1). The main study question was whether oaks' crown condition represented their tree-ring increment, and if so, what is the time frame of this correlation? Additionally, we tried to find out if this correlation vary with site type and tree age.

2 Materials and Methods

2.1 Field sampling

The field data were collected in the counties of Scania, Blekinge, Halland, Jönköping, Kronoberg, Västra Götaland, and county of Stockholm (Figure 1, Table I), in the nemoral and boreo-nemoral vegetation zones (Ahti, Hämet-Ahti, & Jalas, 2004). Study sites sampled were selected to reflect a range of site types and stand ages, and at the same time, to cover the most of the oak distribution range in the southern Sweden. The network of sites was a product of newly established sites and existing sites (HJ, EL, and TR) being part of another forest monitoring studies (Sonesson, 2000). It should be noted, however, that this network can not be considered 'representative' in an objective manner, since site selection was non-random. During site selection we attempted to eliminate bias towards a particular stand and site type while coupling with logistical constrains (possibilities to get sampling permissions from the forest owners). We also avoided sites where thinning operations were carried out recently (within about two decades prior to the year of sampling). Large number of sites sampled ($n=33$) and trees analysed (total $n=260$) should ensure the results being representative for the region. Sites were inventoried during autumn 2002 and winter-spring 2003. On each site a study plot was established (20×10 or 25×15 m^2) and between 7 and 15 trees were randomly sampled with an increment borer. Two samples were taken from each tree, extending in to the pith. In cases when pitch of the tree were not met, the pith age was estimated by identifying projected position of the pitch and using increment over the first five tree rings in the core, located closest to the pith. Since trees were cored at the DBH (diameter at breast height, 140 cm above ground), tree ages reported in this paper refer to the age at this level. For each tree we recorded crown vitality, DBH, and height. Based on the analysis of tree cores, each tree was assigned one of three age

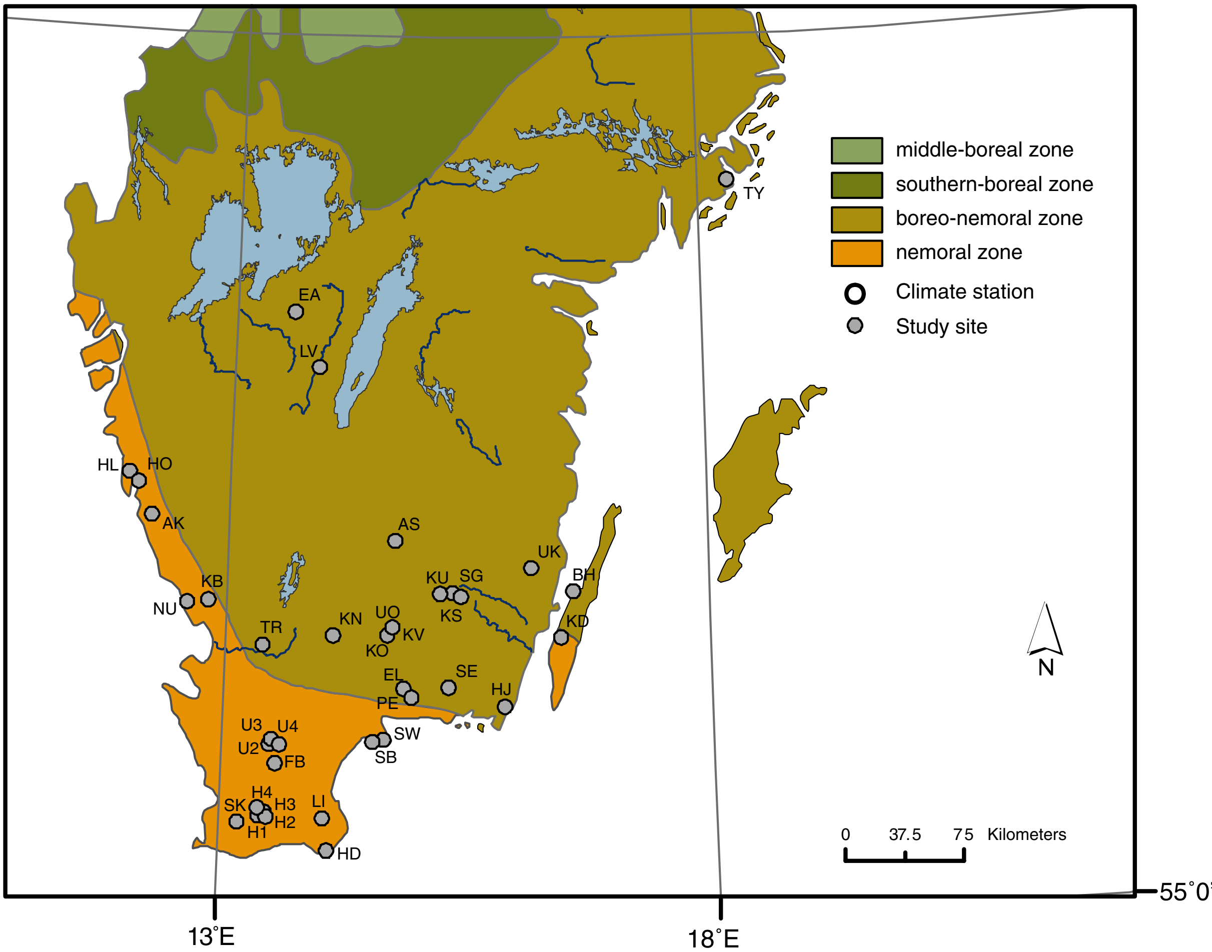


Figure 1 Location of study sites and climatic stations. Boundaries of vegetation zones are according to Swedish National Atlas (SNA, 2001).

classes: younger than 70 years, between 70 and 140 years old, and older than 140 years. Crown vitality was evaluated through the analysis of crown defoliation, amount and size distribution of dead branches, and the branching pattern of young shoots (Sonesson, 1999). Three vitality classes were used: (1) healthy trees with crown defoliation less than 25%, single dead branches with a diameter not exceeding 2–4 cm and fully developed young shoots exceeding 10 cm in length; (2) moderately declining trees with crown defoliation between 25% and 60%, commonly with a number of dead branches whose diameter was 4–8 cm and reduced length of the young shoots; and (3) severely declining trees with crown defoliation above 60%, typically with a large number of thick (>8 cm in diameter) dead branches in the crown, and severely reduced rosette-like appearance of young shoots.

2.2 Soil sampling and analysis

To characterize soil conditions at the sites, soil samples were taken with the Haglöf soil-borer at 25–30 random points within the plot. The borer was inserted into the soil down to a depth of 30 cm and samples from three soil layers (0–10, 10–20, and 20–30 cm) were collected for chemical analyses. The samples were combined in the field to give one sample per plot for each layer. At three sites (HJ, TR and EL) the soil sampling was originally done with respect to the visually identified soil layers which approximately corresponded to the 10-cm depth classes. 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 were extracted in 100 ml 0.1 M $BaCl_2$ at room temperature for 2 hours. The pH of the $BaCl_2$ filtrate was measured. Concentrations of aluminium (Al), calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), manganese (Mn), and iron (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. A LECO instrument was used for the determination of total soil carbon. The concentration of C was normalized to the dry matter content at 40°C. Base saturation (BS) was calculated for three soil layers (0–10, 10–20, and 20–30 cm) for each site. K-mean version of cluster analysis (Hartigan, 1975) was used to classify sites into two groups according to their soil conditions. pH, C/N ratio, and BS variables representing each soil layer were the input variables. They were standardized before the analysis. Based on the

Table I Characteristics of the sites studied

Site ID	Coordinates	Canopy composition	DBH ± SD, cm	Height ± SD, m	Age ± SD, years	Soil type
AA	57° 15′ 37″ 12° 13′ 55″	Oak	66 ± 29.0	19.3 ± 0.8	142 ± 94.8	1
AS	57° 09′ 02″ 14° 46′ 51″	Oak, aspen	63 ± 12.4	23.4 ± 3.1	156 ± 20.4	1
BH	56° 52′ 04″ 16° 38′ 05″	Oak	37 ± 7.6	17.3 ± 0.9	166 ± 11.4	2
EA	58° 26′ 23″ 13° 40′ 25″	Oak, beech, elm	75 ± 25.0	27.6 ± 2.2	126 ± 14.8	1
EL	56° 18′ 48″ 14° 53′ 18″	Oak	30 ± 7.2	21.2 ± 3.6	99 ± 14.0	1
FB	55° 54′ 57″ 13° 38′ 02″	Oak, beech	38 ± 5.2	18 ± 2.1	107 ± 3.2	1
H1	55° 34′ 28″ 13° 27′ 37″	Oak, beech	89 ± 25.5	21.2 ± 3.0	143 ± 46.0	1
H2	55° 34′ 30″ 13° 26′ 58″	Oak	18 ± 2.9	13.1 ± 2.2	35 ± 1.7	1
H3	55° 34′ 30″ 13° 26′ 60″	Oak	23 ± 3.4	16.4 ± 1.6	35 ± 2.9	1
H4	55° 34′ 37″ 13° 26′ 08″	Oak	18 ± 3.3	16.5 ± 1.4	39 ± 1.3	1
HD	55° 23′ 11″ 14° 08′ 24″	Oak	49 ± 13.6	17.4 ± 1.5	99 ± 16.0	2
HJ	56° 12′ 57″ 15° 55′ 11″	Oak	26 ± 5.7	17.2 ± 1.2	54 ± 2.6	1
HL	57° 29′ 48″ 11° 58′ 34″	Oak, maple, aspen	54 ± 22.8	19.6 ± 1.1	127 ± 36.9	1
KB	56° 47′ 35″ 12° 51′ 53″	Oak, beech, hornbeam	28 ± 14.3	15.5 ± 3.6	139 ± 61.5	1
KD	56° 36′ 33″ 16° 30′ 13″	Oak	36 ± 6.5	17.2 ± 0.4	102 ± 9.3	2
KN	56° 36′ 33″ 14° 09′ 18″	Oak, beech, ash, hornbeam	50 ± 11.3	24.9 ± 1.5	147 ± 9.0	2
KO	56° 36′ 59″ 14° 42′ 56″	Oak	35 ± 10.7	19.5 ± 1.5	102 ± 39.1	1
KS	56° 51′ 31″ 15° 22′ 58″	Oak	75 ± 20.3	19.5 ± 1.8	145 ± 56.5	1
LI	55° 34′ 22″ 14° 05′ 19″	Oak	46 ± 9.0	21.4 ± 0.5	128 ± 9.7	1
LV	58° 07′ 45″ 13° 56′ 37″	Oak, pine	40 ± 19.4	17.5 ± 2.3	159 ± 52.2	1
NU	56° 49′ 44″ 12° 38′ 23″	Alder, oak, ash	46 ± 16.4	23.2 ± 2.9	131 ± 23.1	1
PE	56° 15′ 40″ 14° 58′ 32″	Oak, beech, aspen, birch, spruce	33 ± 13.8	22.2 ± 5.5	109 ± 16.9	1
SB	56° 01′ 11″ 14° 41′ 31″	Oak, beech	64 ± 31.0	20.9 ± 1.2	91 ± 32.0	1
SE	56° 19′ 15″ 15° 21′ 14″	Oak, beach	44 ± 4.6	22.2 ± 0.3	156 ± 5.7	1
SK	55° 32′ 25″ 13° 14′ 09″	Oak, beech, spruce, hornbeam	74 ± 37.6	22.6 ± 3.4	134 ± 75.2	1
SW	56° 01′ 21″ 14° 41′ 49″	Oak, hornbean	45 ± 9.1	19.8 ± 1.7	101 ± 6.5	2
TR	56° 32′ 51″ 13° 26′ 27″	Oak	28 ± 6.7	18.4 ± 2.2	130 ± 5.3	1
TY	59° 11′ 06″ 18° 22′ 40″	Oak	80 ± 27.8	14.8 ± 3.5	214 ± 84.4	2
U2	55° 59′ 07″ 13° 32′ 16″	Oak	27 ± 9.7	16.9 ± 1.5	49 ± 10.6	1
U3	55° 59′ 03″ 13° 32′ 07″	Oak	24 ± 4.4	16.8 ± 0.7	39 ± 0.8	1
U4	55° 58′ 47″ 13° 32′ 42″	Oak	35 ± 10.1	19.8 ± 1.2	77 ± 8.0	1
UK	56° 59′ 58″ 16° 11′ 54″	Oak, pine	26 ± 7.8	14.7 ± 4.8	109 ± 6.8	1
UO	56° 39′ 47″ 14° 46′ 08″	Oak	31 ± 6.4	21.7 ± 1.5	70 ± 2.5	1

Soil types: 1, soils with low nutrient status; 2, soils with high nutrient status. Detailed characteristics of soils classes are given in Table II. Age refers to the age at the breast height (140 cm above ground).

results of chemical analyses, soils of the sites were classified as soils with low nutrient status (lower pH and base saturation, and higher C/N ratio) or soils with high nutrient status (higher pH and base saturation, and lower C/N ratio (see Section 3 and Table II).

2.3 Tree-ring analyses

Oak cores were dried, mounted on wooden plates, and polished up to 400 grid polishing band. The cores were measured using an ANIOL measuring stage controlled by the CATRAS software (Aniol, 1983). Single-tree chronologies were cross-dated and verified by use of signature years (Stokes & Smiley, 1968) and through the application of two computer programs: CATRAS (Aniol, 1983) and COFECHA. The latter program is a part of the International Tree-Ring Data Bank Program Library (version 2.1, Grissino-Mayer, Holms, & Fritts, 1997). We did not detrend chronologies to filter out eventual decrease of increment with age (age trend) since this operation could partly remove growth signal related to more short-term changes in trees' crown status.

Tree-ring chronologies typically contain a considerable amount of autocorrelation between years which is a product of tree's ability to buffer the effects of environmental variation on growth (Schweingruber, 1996). In the context of the present study, this autocorrelation represented a meaningful factor, which might extend back in time the correlation between *current* year tree-ring increment and *current* crown conditions. In other words, the relationship between *current* tree crown conditions and a tree-ring increment during *previous years*, if present, could be a result of (1) complacency in tree-ring chronology, (2) complacency in crown conditions, or (3) interaction of two above-mentioned factors. Here "*complacency"* is understood as a lack of sensitivity to the variation in external factors (e.g., to the annual variation in growing conditions). Complacency in growth can be directly estimated by analysing autocorrelation in tree-ring chronologies and crown-growth correlation on filtered (autocorrelation removed) data. Assessment of the complacency in crown conditions would require a reinventory of trees, which was not available for this study. The combined effect of factors (1) and (2) could, however, be estimated by analyzing the absolute (with no autocorrelation removed) values of tree-ring chronologies. From a practical perspective, assessment of correlation between *current* crown conditions and absolute growth *in the past* may be helpful for obtaining the retrospective estimates of tree biomass accumulation. It was also of interest to evaluate the same effect on autocorrelation-removed data to assess possible role of the crown complacency.

Following this reasoning, we calculated Pearson r correlation coefficients within every tree ring chronology for the time lags 1 to 30 years. One-factor ANOVA with Type VI (unique) sum of squares (Sokal & Rolf, 1995) was run for every year for the period 1973–2002 with ring-width increment as dependent variable and crown class code as independent factor. These analyses were run first on the chronologies with autocorrelation present, and then on the same chronologies with autocorrelation removed in ARSTAN program (version 2.1, Grissino-Mayer et al., 1997) with each series treated separately and with no force rewhitening of residual chronology. For each ANOVA run, we recorded Fisher statistics for the whole model, and post hoc Fisher LSD tests for each pair of contrasts of independent factor (crown class, three levels).

Repeated-measure ANOVA with Type VI sum of squares was used to study the change in the cumulative tree-ring increments between two 5-year

Table II Site classification based on the chemical analyses of upper 30 cm of the mineral soil

Soil layer	Soil type	
	1 (Low nutrient status)	2 (High nutrient status)
0–10 cm		
C/N	19.1 ± 6.15	13.6 ± 1.05
pH	3.4 ± 0.34	4.4 ± 0.53
BS	44.6 ± 21.48	94.2 ± 8.01
10–20 cm		
C/N	20.1 ± 9.38	12.8 ± 1.10
pH	3.8 ± 0.24	4.5 ± 0.80
BS	19.5 ± 17.27	86.5 ± 16.96
20–30 cm		
C/N	19.9 ± 8.49	12.4 ± 1.33
pH	4.1 ± 0.26	4.6 ± 0.75
BS	14.2 ± 10.82	88.1 ± 15.61
Replication (n)	27	6

pH was measured in the $BaCl_2$ filtrate. Data mean ± SD.

periods (1993–1997 and 1998–2002), separately for trees belonging to different crown classes. In this case, repeated measures factor was represented by cumulative increment during these two periods, and crown class represented independent factor.

Influence of soil type and tree age on crown-growth interactions was studied by three-factor nested ANOVA with Type 3 sum of squares. Dependent variable was the cumulative 5-year increment over the period 1998–2002, and crown class, age class, and soil type represented independent factors. Both crown class and tree age class were nested inside soil type factor since soil data represented soil conditions of the whole stand and not of particular tree. To account for the absolute differences in the growth rate among sites, prior to ANOVA analyses tree-ring data was transformed as $G'_{ij} = G_{ij}/G_{average\ j}$, where G_{ij} was the cumulative diameter increment of the tree i at site j , and $G_{average\ j}$ was the average increment for the site j for a particular year. During the analyses we controlled for the form of distribution of the dependent variable and for the interaction between cell means and variances.

3 Results

Sites sampled were both pure and mixed oaks stands (Table I). The average age of trees in a site did not exceed 170 years with the exception of the site Tyresta (214 years). Some sites, typically belonging to the age class 2 (70–140 years), showed considerable variation in the age of the trees. Clustering of the sites with respect to the soil properties produced two distinct groups of sites with low (soil type 1) and high (soil type 2) nutrient status. Majority of the sites had low nutrient status (Table I). In such soils the upper 0–20 cm appeared strongly acidified with pH values falling below 3.9. Clear differences in C/N ration and base saturation between two types of soils paralleled those in pH values.

Tree ring chronologies contained a considerable amount of autocorrelation (Figure 2). All trees considered, mean correlation coefficient stayed above 0.2 for about a decade since the focal year and effectively declined to zero value over the second decade since the focal year. Mean site-weighted chronologies suggested differences in tree-ring increment among trees assigned to different three crown defoliation classes (Figure 3). Indeed, one-way ANOVAs showed significant differences in the effect of crown class factor on tree-ring increment. This effect extended 10 years back in time (Figure 4a) for chronologies with autocorrelation preserved, and four years for chronologies with autocorrelation removed. Post hoc Fisher LSD test showed significant differences between crown class 1 and class 2 for 6 years in unfiltered data set (with autocorrelation preserved), whereas no significant differences were found in filtered data (autocorrelation removed, Figure 4b). In case of differences between class 1 and class 3 trees, post hoc Fisher LSD test revealed differences over 13-year period on unfiltered data set, and 4 years on filtered data set (Figure 4c). For the last pair of contrasts, significant crown class 2 vs. crown class 3, the differences were found for 3 years if using unfiltered data set, and for 2 years on filtered data set. The level of significance naturally decayed with time, although there were situations (e.g., class 1 vs. class 2, unfiltered data), where the years nearest to the sampling date did not show significant results.

Considering cumulative increments over two 5-year periods, crown class factor was found to be highly significant (Table III), with all crown classes showing significant differences between each other (post hoc Fisher LSD $P < 0.027$). Trees belonging to

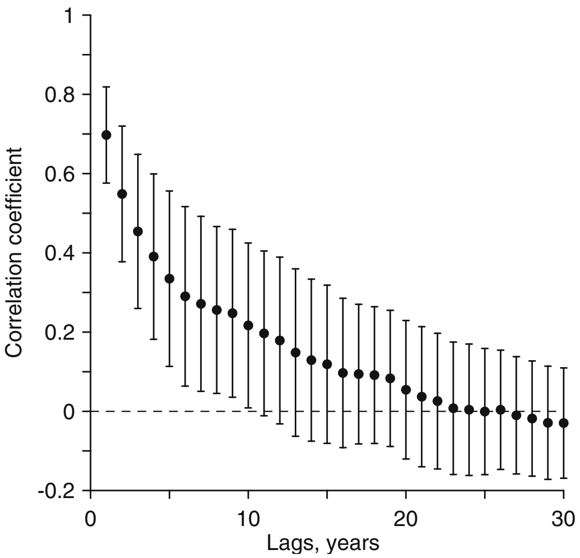


Figure 2 Autocorrelation structure of the tree-ring data. Error bars refer to ±1 SE of correlation coefficient distribution for respective lag.

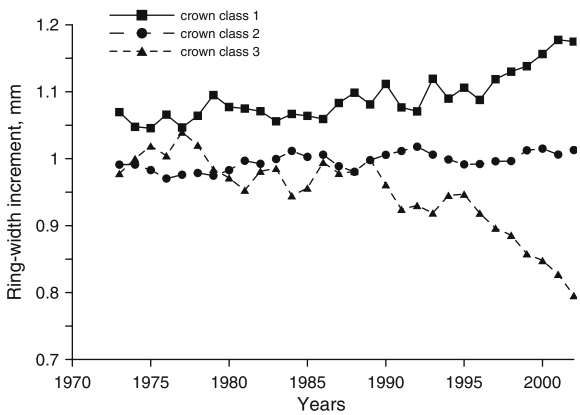


Figure 3 Growth pattern of trees belonging to different classes of crown condition over the period 1973–2002. To account for the variation in the proportion of trees of different crown classes among sites chronologies were weighted against site average for a particular year. Total n = 260; crown classes 1, 2, and 3 were represented by 63, 137, and 60 trees, respectively.

different crown classes grew differently as demonstrated by repeated measured ANOVA with cumulative increment for two 5-year periods (Figure 5, Table III). Cumulative increment increased significantly in trees with healthy crowns (post hoc Fisher LSD $P = 0.011$), did not changed in trees with moderately declining crowns ($P = 0.158$), and decreased in trees with heavily declining crowns ($P = 0.0038$).

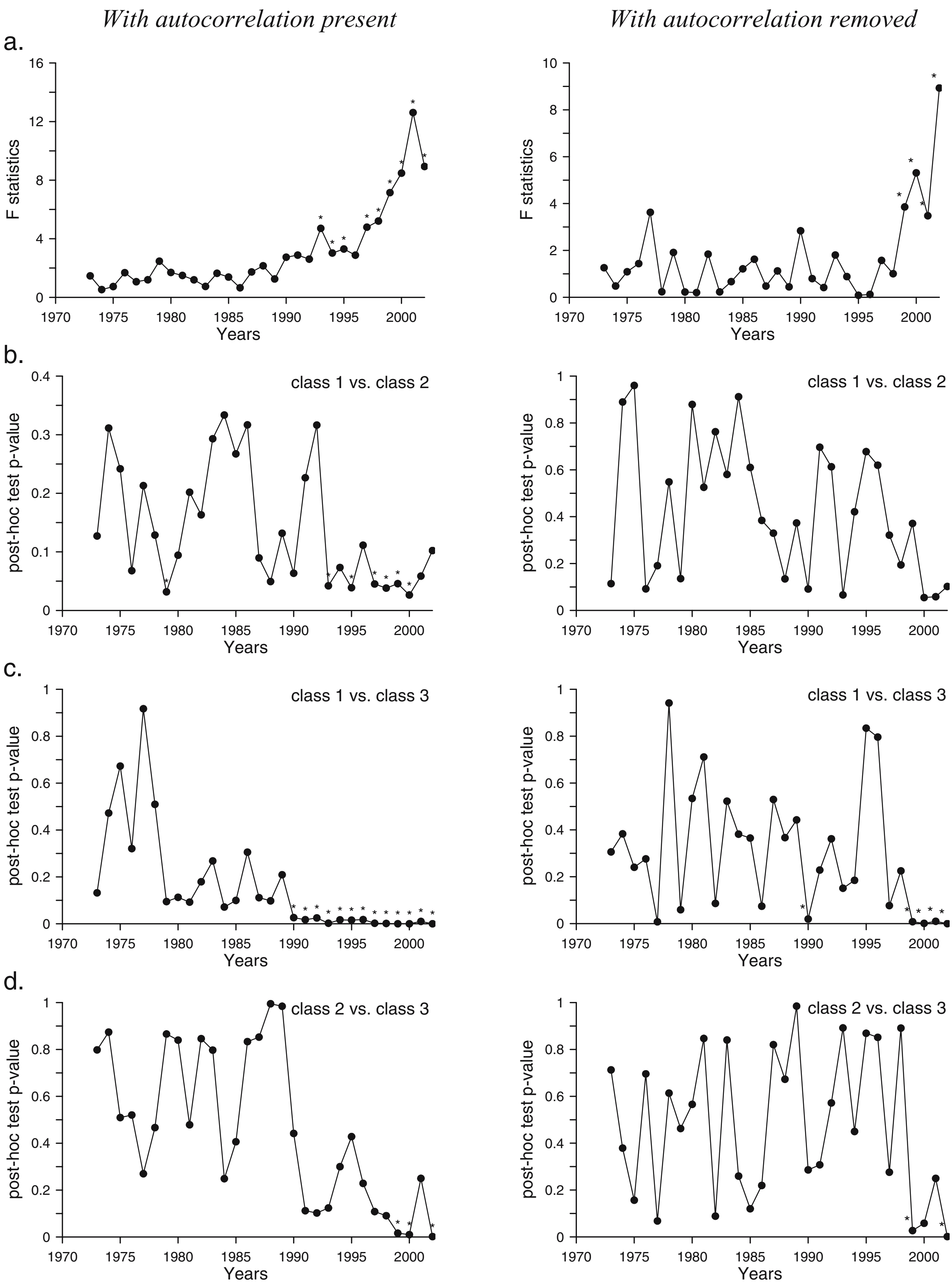
We found significant interaction between cumulative increment over 5-year period preceding sampling and site soil type (Figure 6, Table IV). Nested three-factor ANOVA showed highly significant differences on nutrient-poor soils (P varying between 0.008 and 0.0001 for three pairs of contrasts), but found no differences between crown classes on nutrient-rich soils (post hoc Fisher LSD $P > 0.16$). The effect observed could, however, be a result of the confounding effect of tree age: trees on soils with low nutrient status were younger than trees on soils with high nutrient status, mean ages and SE being 107 ± 3.3 and 146 ± 9.0 years, respectively. In an attempt to evaluate the role of age factor, separate ANOVA analyses with cumulative increment over 1998–2002 were run within two subsamples of sites on nutrient-poor (soil type 1) and nutrient-rich soils (soil type 2). In both cases, effects of age factor and of interaction between age and crown class were non-significant with P levels staying between 0.23 and 0.87.

4 Discussion

4.1 Crown conditions and growth

Which sign of correlation is reasonable to expect between diameter increment and crown conditions? In this study we found a positive correlation that would imply that a change in crown condition is positively related to the ability of the tree to accumulate biomass in the main stem (see reviews in Waring, 1987; Waring, Thies, & Muscato, 1980). There are, however, theoretical reasons for this correlation to be negative and be affected by relocation mechanisms within tree. Presence of negative correlation may arise from the fact that summer precipitation is an important factor that controls growth of oak across Europe (Kelly, Leuschner, Briffa, & Harris, 2002; Pilcher & Gray, 1982; Smelko & Scheer, 2000). Amount of water conducting sapwood determines the ability of the trees to withstand the water vapour pressure deficit. A shift in the accumulation pattern, favouring investments into sapwood formation at the expense of crown's photosynthetic potential, may, therefore, have an adaptive meaning. A literature review of the leaf/sapwood area (LSA) in several European and North American pine species has indicated that it can significantly decrease LSA in response to a higher vapour pressure deficit (DeLucia, Maherali, & Carey, 2000). Although the relationship between leaf area and sapwood area is not necessarily related to stem growth, a negative correlation may nevertheless exist between crown condition and diameter increment. Evidence supporting this possibility have been reported in the study of sugar maple (*Acer saccharum* Marsh.) in eastern USA (Elvir, Wiersma, White, & Fernandez, 2003). However, a study of young sessile oaks (*Quercus petraea* L.) in France has found similar growth patterns in stems and roots (Drexhage, Huber, & Colin, 1999), suggesting no signs of reallocation mechanisms. Up till the present this effect has not been studied in penduculate oak (but see a study of sessile oak; Standovar and Somogyi, 1998). Our results did not support the importance of relocation mechanisms within the tree, significantly affecting interactions between crown conditions and tree-ring increment.

Tree-ring increments were highest in trees with healthy crowns, intermediate in trees with moderately declined crowns, and lowest in trees with heavily


With autocorrelation present
With autocorrelation removed
a.
F statistics
Years
b.
class 1 vs. class 2
post-hoc test p-value
Years
c.
class 1 vs. class 3
post-hoc test p-value
Years
d.
class 2 vs. class 3
post-hoc test p-value
Years

◀**Figure 4** Results of one-factor ANOVA analyses of ring increments and crown defoliation class, run for each year in 30-year time period and on two data sets—with autocorrelation present and removed. (a) Dynamics of F statistics; (b)–(d) results of post hoc Fisher LSD tests of differences between (b) crown class 1 trees and crown class 2 trees, (c) class 1 and class 3 trees, and between (d) class 2 and class 3 trees.

declining crowns (Figure 3, Table III). However, considered with annual resolution the significance of these differences varied depending on the (a) time lag since sampling date, and (b) a particular combination of crown defoliation classes. Crown status was related to the absolute values of tree-ring increment over 10 years (Figure 4a), partly resulted from autocorrelation effects within tree-ring chronologies (Figure 2). Controlling for autocorrelation decreased the time period with significant differences to four years, suggesting that crown conditions in oak represented a proxy for the past growth as recorded in tree rings. Not surprisingly, the largest number of significant differences in annual growth (number of years = 13 for unfiltered and number of years = 4 for filtered data) was observed between trees with healthy crowns (<25% defoliation) and heavily declining crowns (>60% defoliation) (Figure 4c), than in other pairs of contrasts. Class two trees (25%–60% defoliation) showed fewer significant differences in annual growth with other two classes both on unfiltered and filtered data set. Generally, significant differences in growth between crown 2 and other classes were mostly observed on unfiltered data set which pointed to autocorrelation in tree-ring chronologies being responsible for the effect.

Table III Details of the repeated measures ANOVA with two repeated measure factors (cumulative increments during 1998–2002 and during 1993–1997) and one independent factor (crown defoliation class), see Figure 5)

	SS	df	MS	F	*P*
Intercept	458.09	1	458.09	1,886.40	$<10^{-6}$
Crown class	3.74	2	1.87	7.70	$<10^{-3}$
Error	62.41	257	0.24		
RMF	0.00	1	0.00	0.11	0.739
RMF and crown class	0.33	2	0.17	8.158	$<10^{-3}$
Error	5.20	257	0.02		

Type VI decomposition of SS.

RMF Repeated-measures factor.

It is likely that both crown conditions and ring increment acclimate to the changes in environment and thus parallel to a certain degree each other. Several studies have previously confirmed the relation between crown condition and tree rings. Growth of spruce (*Picea abies* (L.) H. Karst), pine (*Pinus sylvestris* L.), and beech (*Fagus sylvatica* L.) has been shown to significantly correlate with degree of crown defoliation across Europe (Fischer et al., 2004). Black and scarlet oaks (*Quercus velutina* Lam. and *Quercus coccinea* Muenchh., respectively) with more than 30% crown dieback had significantly lower increment than trees with less than 30% dieback in southeastern Missouri (Dwyer et al., 1995). A study of Norway spruce in Austria has shown that the proportion of sapwood may serve as a good proxy of crown conditions (Eckmullner & Sterba, 2000).

4.2 Crown conditions and growth trends

Growth of oaks reported healthy in 2002 (<25% of crown defoliation) improved from earlier (1993–1997) to the later (1998–2002) period, while no growth trend was found in the moderately declining trees, and negative growth trend occurred in heavily declining oaks (Figure 5). General amelioration of growth conditions could be a factor behind positive change in the growth of healthy trees. In the southern Sweden the year 1992 is known as year with severe drought during May–June (Karlström, 1993). This year was followed by wetter and somewhat cooler conditions towards the end of the decade (Tuomenvirta et al., 2001). Although oak can sustain periods of prolonged drought due to a complex system of stomatal (Dickson & Tomlinson, 1996) and non-stomatal responses of carbon fixation (Epron & Dreyer, 1990), it is sensitive to lack of precipitation in early summer (Bridge & Winchester, 2000; Siwecki & Ufnalski, 1998; Thomas et al., 2002). Drought period in 1992 resulted in growth decline in southern Swedish oaks (Drobyshev et al., unpublished MS). A positive change in growth of healthy looking trees that followed might therefore reflect a post-drought recovery of growth. Ring increments of trees with moderately declining crowns did not change significantly over the 10-year period, which we attribute to the compensating effects of recent weather variation (acting towards better growth) and factors causing crown defoliation. Class 3 trees (>60%

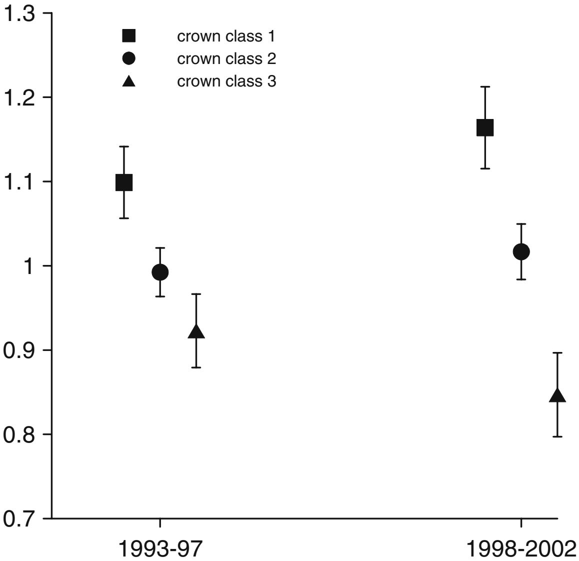


Figure 5 Results of repeated measures ANOVA with index of cumulative 5-year increments for 1993–1997 and 1998–2004 as repeated factors, and crown defoliation class as the independent factor. Data mean for each combination of factors ±1 SE. Numerical details of the analysis are given in Table III.

defoliation) appear to reach a threshold in their ability to recover growth. Trees in this group would be probably the first to contribute to the future oak mortality. A study of German oaks has demonstrated that trees with crown defoliation exceeding 60% had disproportionately increased mortality rates (Paar et al., 1999). Dobbertin and Brang (2001), analysing Swiss Forest Health Inventory database, reported an exponential increase of mortality probability with increasing crown transparency over the whole range of defoliation classes.

4.3 Role of soil conditions

In this study differences in growth trend among crown classes were more pronounced in trees growing on soils of low nutrient status, as compared with trees on more fertile soils (Figure 6, Table IV). Independent analysis of soil type and tree age on the growth–crown relationship was hindered by the unbalanced nature of the data set used, in which oaks growing on soils with low nutrient status were younger than oaks on more nutrient-rich soils. However, we found no significant impact of age on growth–crown relationship within two subsamples of sites (on poor and rich soils). This suggested that the effect observed could be a product of (a) unique contribution of the soil type factor, (b) interaction between age and soil type. In several previous studies, little correlation has been found between oak growth or crown conditions, on one hand, and element concentrations in the soil (Halmschlager & Kowalski, 2004; Thomas & Buttner, 1998) or their input through deposition (Berger & Glatzel, 2001), on the other.

Stronger growth differentiation among crown classes on more nutrient-poor soils could be explained by the link between crown conditions and tree roots. Crown conditions in oak may reflect the status of the fine roots (Blaschke, 1994) and trees with severely reduced crown vitality have been shown to exhibit extensive fine root mortality (Thomas & Hartmann, 1996). Under more limiting soil conditions, the differences in the amount and performance of fine roots, expressed as differences in crown conditions, may stronger differentiate the growth of trees. This effect would translate into better possibilities for growth recovery in trees with healthy crowns (and supposedly with better roots) than for declining trees. Differences in age might further enhance variation in growth responses between two site types. It is reasonable to suggest that more developed root system of older oaks may buffer

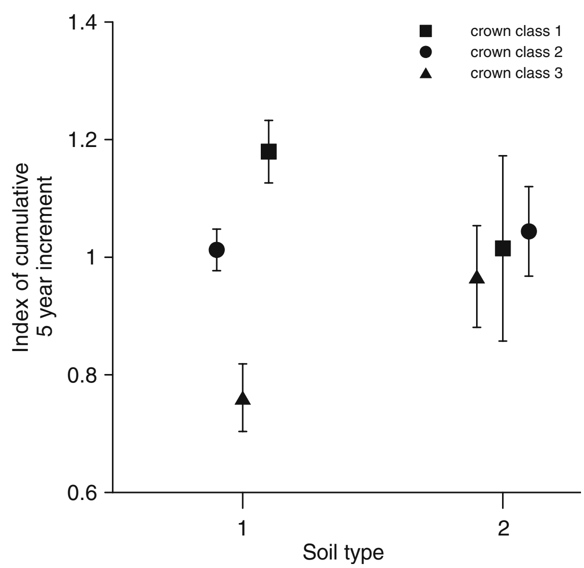


Figure 6 Index of cumulative 5-year increment as a function of crown defoliation class and soil type (1, nutrient-poor soils; 2, nutrient-rich soils, see Table II). Results of the nested two-factor ANOVA with crown class factor being nested in the soil factor. Data average for each combination of independent factors ± 1 SE. Numerical details of the analysis are given in Table IV.

Table IV Details of the nested three-factor ANOVA with 5-year cumulative increment as a function of crown defoliation class, tree age, and soil. Type III decomposition of SS

	SS	df	MS	F	*P*
Intercept	29.25	1	29.25	196.97	$<10^{-6}$
Soil type	0.07	1	0.07	0.488	0.486
Soil type and crown class	3.27	4	0.82	5.504	$<10^{-3}$
Soil type and age class	0.34	4	0.08	0.570	0.685
Error	37.12	250	0.15		

more efficiently changes in annual weather variability as compared to younger trees.

4.4 Methodological considerations

Dendrochronological data serve as a valuable complement to visual inventories, providing an advantage of retrospective analysis of growth conditions with annual resolution. Although being a relatively laborious technique, dendrochronological method is useful in considerably extending the time period studied and, thus, getting insight into more long-term picture of the changes in the forest conditions (Payette et al., 1996; Pedersen, 1999). In the study of relationship between vitality and basal area increment in sugar maple (*Acer saccharum* Marsh.) Dushesne et al. (2003) have found that the decrease in slope of basal area increment predated the observed symptoms of sugar maple decline by at least one decade. The authors have suggested that measuring tree's increment trend, an indicator that precedes the emergence of visible canopy symptoms, can assess the vigor of maple trees and their health. An interesting application of tree-ring analysis was presented by Bigler et al., who used tree ring series to model past tree mortality probability in silver fir, *Abies alba* Mill. (Bigler, Gricar, Bugmann, & Cufar, 2004) and in Norway spruce, *P. abies* (L.) Karst. (Bigler & Bugmann, 2003).

It is important to note that in this study we operated with the estimates of crown conditions, taken on only one occasion. Found differences in the past growth among crown classes did not prove that crown conditions remain constant over time. Continuous monitoring of oak crown vitality at three southern Swedish sites (EL, HJ, and TR in Figure 1) revealed that 248 out of 279 trees (89%) trees changed their crown class identity at least once during the period of nine years (Sonesson, unpublished MS). Acknowledging possible inaccuracies in the visual assessments among years, a certain annual variation in the appearance of oak crowns seems nevertheless to occur. Our study, however, demonstrated that the condition of oak crowns at the moment of sampling did reflect trees' growth over the preceding decade.

The results of the current study also have implications for climatic reconstructions based on tree-ring data. Such reconstructions make use of a parameterized relationship between a climate variable (typically precipitation or temperature) and tree-ring record, which extends beyond the time period covered by instrumental data (Fritts, 1976). Moving backward in time would most likely result in systematic changes in the properties of the trees used to build up chronology (Cherubini, Dobbertin, & Innes, 1998). For example, most recent rings in a chronology typically come from older trees since these trees are normally cored first in search for the longest tree-ring record. It is also likely that trees sampled represented healthier part of the population in the past since they survived till the moment of sampling. In our study oak trees demonstrated different growth trends, depending on their crown defoliation class. This implies that adjusting for the crown status of the trees sampled should help improve the parameterization of climate-growth relationship and avoid loss of sensitivity of chronologies to recent environmental variability.

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