REGULAR ARTICLE

Soil chemical properties and dieback of *Quercus robur* in Atlantic wet forests after a weather extreme

Vicente Rozas · Luis Sampedro

Abstract

Background and Aims The dependence of oak decline on climatic stressors is fairly well documented, but little is known about the impact of soil properties on growth plasticity and as predisposing factors to decline. Here we investigate if oak dieback and individual responses to climatic stresses are related to soil nutrient availability.
Methods Chemical properties of surrounding soil and tree-ring series of healthy, declining, and dead oaks were analysed in four replicated forest stands under Atlantic wet climate conditions in NW Spain, where massive death has occurred.
Results Current nutrient availability significantly predicted oak death risk. Lower concentrations of macronutrients (N, Ca, Mg, and Na) were found in soil surrounding dead trees than living trees. Water excess before the growing season negatively affected growth, and trees showing declining symptoms were more responsive to climate. Trees with greater Ca availability in the surrounding soil were able to respond more plastically to the stress caused by water excess, while trees with lower Ca levels were less responsive to the stress and more predisposed to die.
Conclusion This work revealed that both climatically-induced dieback and the individual dendroclimatic

response of oaks may be linked to the uneven distribution of soil resources in declining Atlantic forests.

Introduction

Pedunculate oak (*Quercus robur* L.) is a dominant forest tree in the Atlantic European region that recurrently shows symptoms of decline (Gibbs and Greig 1997; Führer 1998). Oak decline is a complex syndrome in which the combined effects of several causal agents acting sequentially or simultaneously on oak vitality cause massive tree death over local or regional scales (Thomas et al. 2002). Summer drought as a limiting factor for carbon assimilation during the active period, and winter-spring frosts as a cause of damage to the growing tissues, have been considered relevant climatic stresses triggering oak decline in Europe (Helama et al. 2009; Di Filippo et al. 2010; Doležal et al. 2010). However, soil water saturation derived from increasing rainfall frequency and intensity could be also involved in the dieback, as reported by a recent study on oak decline in a wet Atlantic forest (Rozas and García-González 2012).

The dependence of oak decline on climatic stresses is fairly well documented, but relatively little is known about the potential influence of soil properties, which can act synergistically with climate to speed up or increase the level of decline. Soil properties such as

V. Rozas (✉) · L. Sampedro
Misión Biológica de Galicia, Consejo Superior de Investigaciones Científicas (MBG-CSIC), Apdo. 28, 36080 Pontevedra, Spain
e-mail: vrozas@mbg.csic.es

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depth, gas permeability, and nutrient imbalances have been suggested to be prominent factors associated with the oak decline syndrome (Thomas and Büttner 1998; Gaertig et al. 2002; Helama et al. 2009). Soil nutritional deficiencies can be limiting for carbon gain, and a minor deficiency of one resource may increase tree sensitivity to deficiencies of other resources, and can predispose trees to the detrimental effects of further superimposed stresses (Carlton and Bazzaz 1998; Niinemets 2010). An earlier study revealed different nutrient distributions in soils and leaves of healthy and declining oak stands, but concluded that soil nutrient imbalances have a minor impact on the decline at the stand level (Thomas and Büttner 1998). Nevertheless, differences in soil properties occur locally across a site, and local heterogeneity of nutrient distribution in forest soils can modulate growth, performance, and survival at the level of individual tree (Sheppard et al. 2001; Long et al. 2009).

Soil nutrient budget may not just be a predisposing factor for oak decline; it may also modulate the response of declining oaks to constraining climatic conditions. This question can be evaluated through a retrospective assessment of tree-ring growth and its response to climate (Dobbertin 2005; Friedrichs et al. 2009; Di Filippo et al. 2010). There is evidence that tree-ring growth plasticity and climatic responsiveness may be dependent on different site features, such as topography, soil water regime or soil nutrient content (Oberhuber et al. 1998; Oberhuber and Kofler 2000; Sheppard et al. 2001). In fact, the effect of local environmental heterogeneity on individual tree-ring growth response to climate has recently been established (Rozas and Olano 2013). Therefore, the hypothetical association between soil heterogeneity and individual sensitivity of declining oaks to climate can potentially be evaluated by tree-ring analysis.

Here we studied the association of tree health status and death risk with soil chemical properties, and assessed whether the individual sensitivity to climatic factors limiting radial growth is related to local variation in the soil nutrient budget. This was carried out in a mature oak forest in NW Spain, under wet Atlantic climate conditions, and where massive tree death has occurred over the last decade. The limited nutritional availability to oaks in this forest would have been exacerbated by seasonal soil water excess during recent decades, and in particular by the extremely rainy conditions in 2001 that first triggered the decline (Rozas

and García-González 2012). We hypothesized that heterogeneity of available belowground resources can modulate tree vitality and survival, and the individual susceptibility to soil water excess. The aims of this study were to: (1) evaluate the nutrient availability in the soil around trees differing in their degree of decline; (2) determine the variability in individual tree-ring growth response to climate between healthy trees, declining trees and trees that eventually died; and (3) assess the extent to which the tree-ring growth response to climate in individual trees is dependent on local levels of soil nutrients.

Materials and methods

Study area

The Serra do Suido is a moderately elevated (1,150 m), north-to-south oriented mountain range located in Galicia, NW Spain, that directly intercepts wet westerly fronts from the Atlantic Ocean. This range is largely deforested, and oak woodlands are fragmented within a matrix dominated by heathland, predominantly occupying ravines and valley-bottom sites where soils are deeper. The canopy in these wooded areas is almost exclusively composed of pedunculate oak, with a sparse understorey of *Ilex aquifolium* L., *Pyrus cordata* Desv., and *Crataegus monogyna* Jacq. Soils are Lithic and Umbric Leptosols and Epileptic Umbrisols on granite bedrock (Calvo de Anta and Macías Vázquez 2002). Climate is temperate and humid Atlantic, with a mean annual temperature of 12.0 °C for 1901–2006, ranging between 6.0 °C in January and 18.7 °C in August. Mean annual precipitation is 1,315 mm, with a maximum of 911 mm in October-March, and a minimum of 125 mm in June-August. Mean annual precipitation in the study area has significantly increased during the past century, from 1,194 mm in 1901–1959 to 1,458 mm in 1960–2006, and particularly rainy conditions were recorded in 2001, with 2,163 mm (Rozas and García-González 2012).

Sampling

We selected for this study a wooded sector of 385 ha on the windward slope of the Serra do Suido range (42°22′ 40″–42°23′50″ N, 08°21′10″–08°23′45″ W) where exceptionally high mortality rates of pedunculate oak have

been noticed for the last decade (Rozas and García-González 2012). We selected four representative stands located at elevations ranging between 610 and 770 m and mainly facing north (Table 1). In late spring 2007, one study plot of 40 m×50 m was randomly established within every stand. All living and dead oaks found within the study plots were tagged, and their crown status registered following a rating that considers three decline classes: healthy, declining, and dead (Balci and Halmschlager 2003). Healthy trees were those without symptoms of decline or only slightly damaged, with dieback of some tips of branches, and slight crown transparency. Declining trees were moderately to severely damaged, with apparent dieback of twigs and branches, yellowing or wilting of leaves, epicormic shoots, and conspicuous crown transparency. Dead trees had lost the majority of small branches, but conserved all their main branches, without erosion of the external sapwood in the stem. All trees classified as declining in 2007 did in fact survive, and have since recovered their vigour; at the time of this report (autumn 2012) all would now be classified as healthy.

Ten healthy, ten declining, and ten dead trees were randomly selected within each study plot for soil sampling. Three soil samples comprising the first 10 cm of soil were randomly taken at 1.5 m from the stem base around each of the 30 selected trees per stand with a 5-cm diameter soil core sampler. This depth was selected because the bedrock was intercepted within the upper 20 cm in the majority of samples, which indicate reduced thickness in the soil in most of the area. In addition, there is previous evidence that the great majority of nutrient uptake by oak roots normally occurs in the uppermost soil layer, from 0 to 10 cm depth (Göransson et al. 2006). The three cores around each tree were pooled into a single composite soil sample per tree. Ten healthy, ten declining, and ten dead trees were also randomly selected within each study plot for wood core sampling. Five of the cored trees per decline class were common to the trees previously selected for soil sampling. Two wood cores were collected along opposing radii oriented parallel to the slope contour line from each of the 30 selected trees per plot, using increment borers at breast height.

Soil analyses

Soil samples were sieved at 2 mm and air-dried, organic matter content was determined by combustion (500 °C, 4 h), and soil pH measured in distilled water (water:

Table 1 Traits of study stands and soils in the Serra do Suido range, NW Spain

	Stand 1	Stand 2	Stand 3	Stand 4
Site traits				
Elevation (m)	770	750	690	610
Aspect	N	NE	N-NE	N-NW
Total tree density (ha^{-1})	305	360	430	455
Healthy tree density (%)	21.3	27.8	18.6	46.2
Declining tree density (%)	41.0	16.7	27.9	29.7
Dead tree density (%)	37.7	55.5	53.5	24.1
Soil traits[a]				
CEC (mmol$_c$ kg^{-1})	109.5±6.0 [A]	105.1±11.4 [A]	121.3±14.8 [B]	120.6±27.1 [B]
pH (H$_2$O)	3.7±0.2 [A]	3.8±0.2 [A]	3.8±0.2 [A]	3.7±0.3 [A]
Organic matter (g kg^{-1})	22.6±2.9 [AB]	23.8±2.6 [A]	20.6±4.2 [B]	20.5±5.5 [B]
Total N (mg kg^{-1})	86.6±18.0 [AB]	88.9±22.5 [A]	86.5±20.8 [AB]	73.2±33.0 [B]
Extractable P (mg kg^{-1})	5.6±1.9 [A]	7.3±2.7 [A]	6.9±4.0 [A]	10.3±3.5 [B]
Extractable Ca (mg kg^{-1})	56.9±22.3 [A]	48.4±20.9 [A]	65.5±43.4 [A]	26.9±20.3 [B]
Extractable Mg (mg kg^{-1})	26.9±9.1 [A]	25.1±10.7 [A]	31.7±22.2 [A]	35.3±21.8 [A]
Extractable K (mg kg^{-1})	18.3±2.7 [AB]	14.9±2.8 [A]	17.1±6.4 [A]	20.8±7.1 [B]
Extractable Na (mg kg^{-1})	4.6±0.7 [A]	5.2±0.9 [AB]	5.9±1.7 [B]	5.9±1.6 [B]
Extractable Al (mg kg^{-1})	209.2±24.6 [A]	206.7±33.1 [A]	229.1±40.8 [AB]	246.8±54.6 [B]

[a] Mean ± SD, based on soil samples taken from a depth of 0–10 cm around 30 sampled trees per stand. Different uppercase letters for each soil trait indicate significant differences ($p<0.05$) among stands, according to Tukey's HSD *post hoc* test

soil, 1:2.5). Total nitrogen (N) was determined by the semimicro-Kjeldahl method (Bremner 1996), and extractable phosphorus (P) by the Olsen method (Olsen et al. 1954). Soil samples were extracted in a 1 N ClNH$_4$ solution, the suspension was filtered through 0.45 μm Millipore filter, and the concentration of exchangeable cations (Ca^{2+}, Mg^{2+}, K$^+$, Na$^+$, and Al^{3+}) in the extracts measured by atomic absorbance spectrometry. The cation exchange capacity (CEC) was calculated as the sum of concentrations of all exchangeable cations. Besides chemical analyses, the presence of *Phytophthora* zoospores (a major exotic oak forest pathogen in Europe) was analyzed in half of the soil samples surrounding healthy, declining and dead trees (*N*=60) by the Official Provincial Laboratory of Agricultural and Forest Pathology (Estación Experimental de Areeiro, Galician Forest Service) following the standard soil baiting method proposed by Jung et al. (2000). All samples were confirmed as negative for *Phytophthora* zoospores.

Statistical analysis of soil properties

We were interested in specific differences among decline classes, but also among stand replicates, since these would reflect local variation in soil properties. Two-way ANOVA was used to compare soil traits among decline classes, stands, and their interaction, considering decline class as a fixed factor and stand as a random factor. Data were log-transformed when necessary to achieve the requirements of normality and homoscedasticity. The differences among means were tested with the Tukey's HSD *post hoc* test. Statistical analyses were performed with the SPSS v.15.0 package (SPSS Inc., Chicago IL, USA).

Dendrochronological procedures

We used dendrochronological techniques based on the retrospective study of annual tree rings in order to assess the individual response of growth to climate during the past decades. The wood cores were air dried, glued onto wooden mounts, and polished until the xylem cellular structure was visible in the transverse plane, and tree-ring series were absolutely dated by assigning calendar years to the rings following the standard procedures in dendrochronological studies (see Rozas and García-González (2012) for a more complete routine description). Series of total tree-ring

width were measured on each wood core to the nearest 0.001 mm with a Velmex sliding-stage micrometer interfaced with a computer. The software COFECHA was used to quantitatively check for crossdating errors in the ring width series (Grissino-Mayer 2001). Tree-ring widths, measured from two cores for each tree, were averaged on a year-by-year basis for the period held in common by both cores. Individual ring-width series were then separately averaged into three mean ring-width chronologies for healthy, declining, dead trees with the purpose of growth comparison among decline classes.

Every raw ring-width series was standardized with the ARSTAN program (Cook and Holmes 1996). The series were fitted to a spline function with a 50 % frequency response of 32 year, which was flexible enough to minimize the non-climatic variance and maximize the high-frequency climatic signal (Helama et al. 2004). The residuals obtained showed a high serial autocorrelation that violates the statistical requisite of independence among observations in time series. Then, these residuals were pre-whitened with ARSTAN by autoregressive modelling, giving dimensionless indices that represent independent, normalized, and homogenized records of annual growth for each measured series. The year-by-year arithmetic mean of the two series of tree-ring indices from each tree, for the period held in common by both cores of the tree, was calculated to obtain an individual chronology. In addition, individual tree-ring indexed chronologies were separately averaged into three decline-class chronologies for healthy, declining, and dead trees.

Climate data

The climate data used in this study were monthly gridded time series for total precipitation (Prec), mean minimum (Tmin) and maximum (Tmax) temperatures, and Palmer drought severity index (PDSI), obtained from the Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl/), for the 0.5° longitude×0.5° latitude sector in which the study area is located. Series for Prec, Tmin and Tmax were obtained from the CRU TS 3 data set, period 1901–2006, and series for PDSI were obtained from the CRU self-calibrating PDSI data set, period 1901–2002. The PDSI is a standardized measure of soil moisture content computed from air temperature records,

cumulated rainfall, and field water-holding capacity (Dai et al. 2004). Monthly time series of water balance (WB) were also calculated as WB=Prec−PET, where PET is the potential evapotranspiration, estimated as a function of monthly mean temperatures and geographical latitude (Thornthwaite 1948). Monthly data from June of the previous year (Jun(−1)) to September of the current growth year (Sep) were used, and also averaged (Tmin, Tmax, PDSI) or summed (Prec, WB) in periods of 2 and 3 months to identify their main effects on tree-ring growth at monthly, bimonthly, and seasonal time scales.

Climate sensitivity assessment and its association with soil properties

Pearson's correlations were used to estimate the climatic responsiveness of the three decline-class chronologies to monthly, bimonthly, and seasonal climate time series in the period 1971–2000. This represents the most recent 30-year period common to all individual tree-ring chronologies prior to 2001, the wettest year within the studied period and following which a period of massive oak death took place (Rozas and García-González 2012). Most significant correlations were considered as indicative of the most limiting climatic factors for oak growth on our study site. Individual climatic responses to the main limiting climatic factors were calculated as bootstrapped correlations of these climatic time series with individual tree-ring indexed chronologies in 1971–2000. Bootstrapped correlations and their statistical significance were computed with the software DendroClim2002 (Biondi and Waikul 2004).

Individual correlations of growth with climate were not normally distributed, according to the Kolmogorov-Smirnov test of normality. We normalized these data with the Fisher's transformation, also called the inverse hyperbolic tangent transformation, which allows the application of regression techniques on normally distributed correlations (Faller 1981). Individual normalized correlations were separately averaged for healthy, declining, and dead trees, and mean response of the decline classes compared with one-way ANOVA and the Tukey's HSD post hoc test. Linear regression was used to explore the association between soil properties and the previously calculated normalized correlations of individual growth indices with climatic variables in 1971–2000.

Results

Decline incidence and soil chemical properties

Tree density ranged between 305 and 455 ha^{-1} (Table 1), and tree mortality ranged from 24.1 % to 55.5 % of the total number of individuals, with greater incidence in stands 2 and 3. Soils were acidic (mean pH 3.7–3.8), with a high organic matter content (20.5–23.8 g kg^{-1}), and relatively high cation exchange capacity (109.5–121.3 mmol$_c$kg^{-1}). The amount of nutrients in the soil varied among stands, with a mean concentration of total N higher in stand 2 than in stand 4. In stand 4, a higher concentration of P, K and Al, and a lower concentration of Ca, was found (Table 1).

Soil chemical properties as related to tree decline classes

CEC, pH, organic matter content and Al concentration did not differ among decline classes, while significant differences among decline classes were found for the concentrations of total N, and extractable P, Ca, Mg, K, and Na (Table 2). In general, nutrient levels in the surrounding soil decreased with increasing levels of tree decline, with lower concentrations of N, Ca, Mg, and Na in soils next to dead trees than living trees, lower P concentration around dead than declining trees, and

Table 2 Summary of F values from two-factor ANOVA for differences among decline classes, stands, and their interactions (D × S), in soil cation exchange capacity (CEC), pH, organic matter content (OM), and concentration of total N, and extractable P, Ca, Mg, K, Na, and Al. Error term df=108

	Decline class (D)	Stand (S)	D × S	Model
df	2	3	6	11
CEC	2.81	7.15***	0.89	2.95**
pH	1.81	2.65	1.26	1.94*
OM	2.12	5.39**	2.31*	3.11**
N	5.38**	2.86*	1.36	2.50**
P	4.19*	13.17***	1.75	5.31***
Ca	5.00**	10.62***	0.63	4.15***
Mg	7.86***	2.45	1.06	2.68**
K	5.50**	7.28***	1.44	3.77***
Na	5.13**	7.25***	1.47	3.71***
Al	1.95	6.68***	0.79	2.55**

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

lower K concentration around dead than healthy trees (Fig. 1). CEC, organic matter content, and the soil concentration of total N, and extractable P, Ca, K, Na, and Al differed among stands, while pH and extractable Mg level did not differ among stand replicates. No significant effect of the interaction term "decline class × stand" was noticed, except for the organic matter content (Table 2), evidencing a similar pattern of variation of soil chemical properties among decline classes in all study stands.

Tree-ring growth patterns and dendroclimatic responses

The number of trees included in the mean tree-ring chronologies varied depending on the decline class and

period (14–18 in the 1870s, 38–40 for 1955–2001) (Fig. 2a). Since 2001, the number of healthy and declining trees was 40 and 39, respectively, while the number of dead trees gradually decreased up to 20 in 2007. Long-term variation of mean annual growth rate showed a slightly decreasing trend for all decline classes (Fig. 2b). Trees that had died by 2007 had in fact shown lower growth rates since the 1940s, and a marked growth rate reduction since 2001 compared with healthy and declining trees. All decline classes showed very similar high frequency variation of radial growth throughout the complete period 1870–2007, as the chronologies of tree-ring growth indices revealed (Fig. 2c). All indexed chronologies showed the highest replication
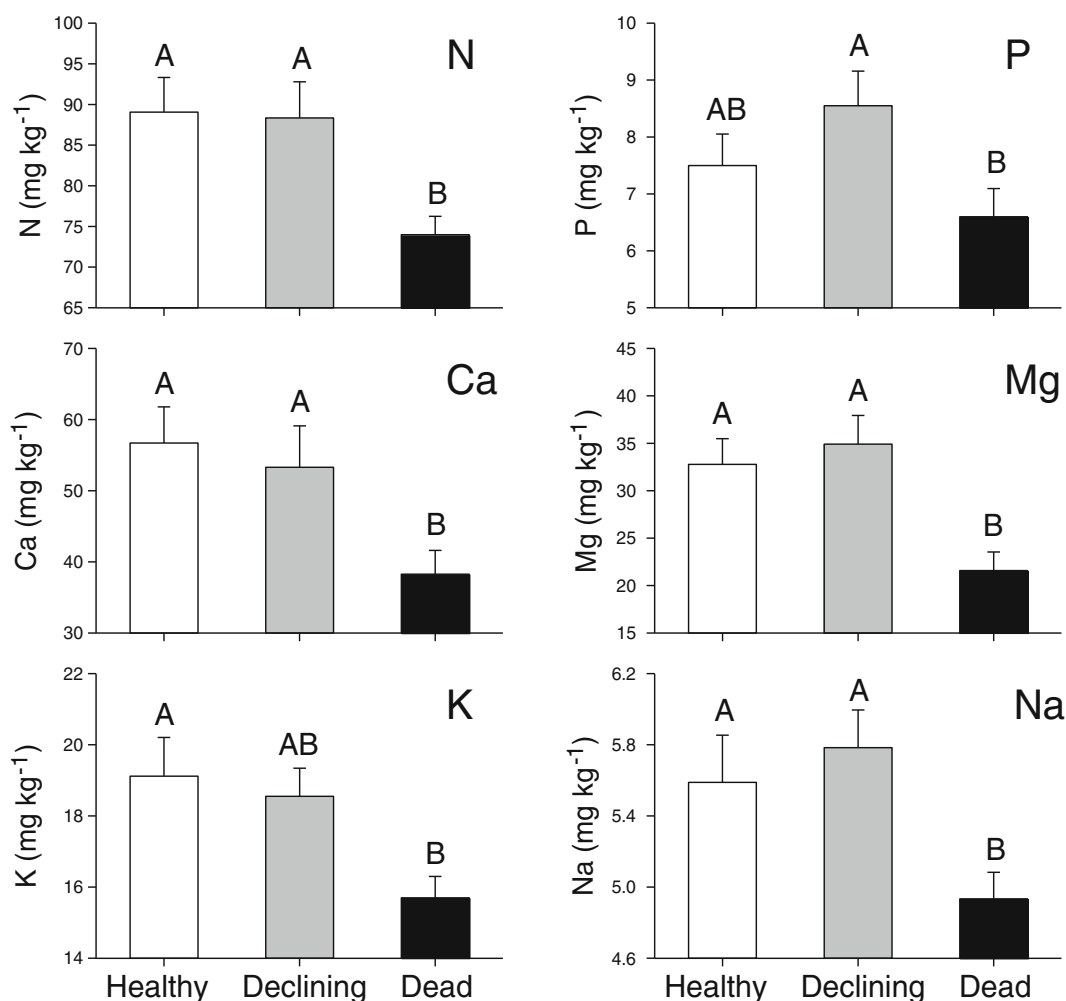

Fig. 1 Concentration of total N, and extractable P, Ca, Mg, K, and Na (mean + SE) in the soil surrounding healthy, declining, and dead oaks. Different *uppercase letters* indicate significant differences ($p<0.05$) among decline classes for every element, according to Tukey's HSD *post hoc* test. Soil CEC, pH, organic matter content, and Al concentration, did not significantly differ ($p>0.05$) among decline classes

Fig. 2 Trees sample size (**a**), chronologies of mean ring widths (**b**), and mean tree-ring growth indices (**c**) for healthy, declining and dead oaks in all study stands together. *Vertical dashed line* highlights the wettest year 2001
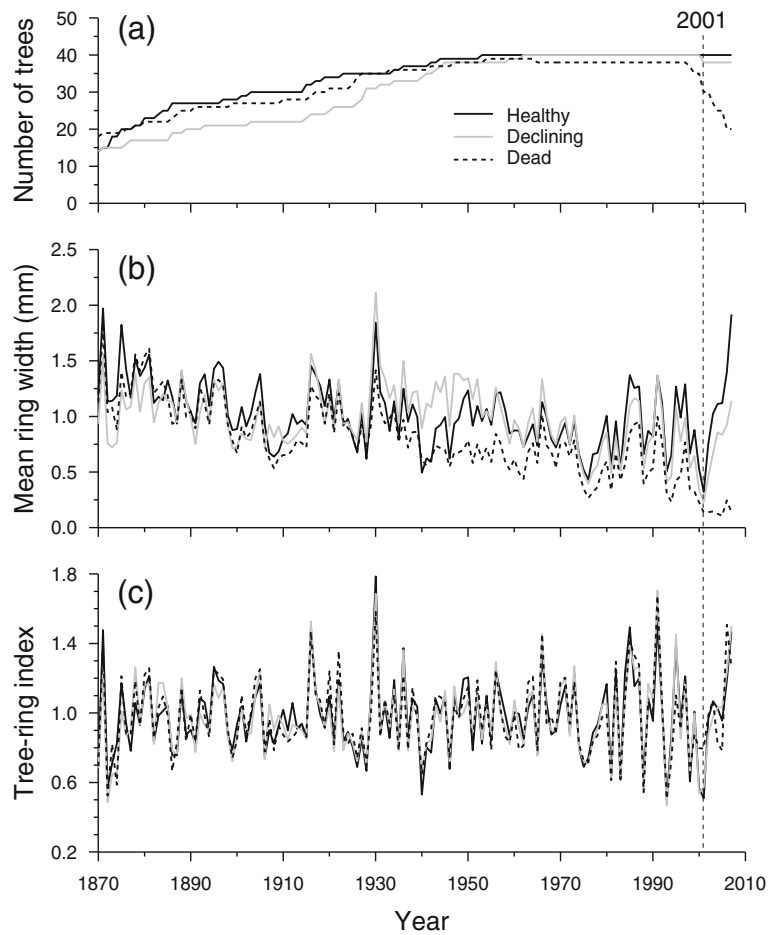
level and optimum common signal in the period 1971–2000, with values of expressed population signal of 0.944 for healthy trees, 0.949 for declining ones, and 0.903 for trees that died.

Previous summer precipitation (Jun-Aug(–1) Prec), soil water content in the previous autumn (Sep-Oct(–1) PDSI) and spring water balance (Apr-May WB) had a negative effect on growth, whereas mean minimum temperature in September (Sep Tmin) had a positive correlation (Table 3). Individual response to previous summer precipitation, soil water content in previous autumn, and September minimum temperature did not differ among tree classes (Fig. 3a; one-way ANOVA, $p>0.05$ in all cases), whereas the negative response to spring water balance was lower for dead than healthy and declining trees ($F_{2,55}=4.16$, $p=0.021$). In addition, a greater proportion of declining trees showed a significant relationship between individual tree-ring growth and climate, particularly for previous summer precipitation and September minimum temperature (Fig. 3b),

suggesting a stronger individual response to climate among declining trees.

Relationships between soil properties and individual dendroclimatic responses

Extractable Ca and Al were the only soil properties that showed significant relationships with individual dendroclimatic responses of oaks (Fig. 4), which could be related to the unbalanced and inversely related availability of soil Ca and Al ($r=-0.471$, $p<0.001$). Ca concentration was negatively correlated with individual responses to water availability in previous summer-autumn and spring, while Al concentration was positively correlated with soil water content (PDSI) in previous autumn. No significant relationships between soil properties and the individual dendroclimatic response to September minimum temperature was found. Trees with higher Ca levels in the surrounding soil showed a stronger negative response to spring water balance than trees with lower Ca

Table 3 Correlation coefficients (r) between the variation of tree-ring growth indices from healthy, declining, and dead oaks, and the most significant climatic predictors for precipitation (Prec), Palmer's drought severity index (PDSI), water balance (WB), and mean minimum temperature (Tmin), in the period 1971–2000. Statistical significances (p) of correlation coefficients are also shown

Climatic predictor	Healthy		Declining		Dead	
	r	p	r	p	r	p
Jun-Aug(−1) Prec	−0.434	0.013	−0.405	0.021	−0.415	0.018
Sep-Oct(−1) PDSI	−0.299	0.096	−0.370	0.037	−0.432	0.013
Apr-May WB	−0.502	0.003	−0.489	0.004	−0.458	0.008
Sep Tmin	0.403	0.022	0.431	0.013	0.479	0.005

levels (Fig. 5). By contrast, trees with low Al concentration in the surrounding soil showed a stronger negative response to soil water content (PDSI) in previous autumn than trees with high Al levels.

Fig. 3 Normalized bootstrap correlations (mean + SE) of individual tree-ring growth chronologies of healthy, declining, and dead trees with Jun-Aug(-1) Prec, Sep-Oct (-1) PDSI, Apr-May WB, and Sep Tmin (**a**). Different *uppercase letters* for each climate variable indicate significant differences ($p<0.05$) among decline classes, according to Tukey's HSD *post hoc* test. Proportion of trees showing significant correlations of tree-ring growth with climate for healthy, declining, and dead oaks (**b**). Trees showing declining symptoms (*grey bars*) appeared as the most plastic in their responses to climate
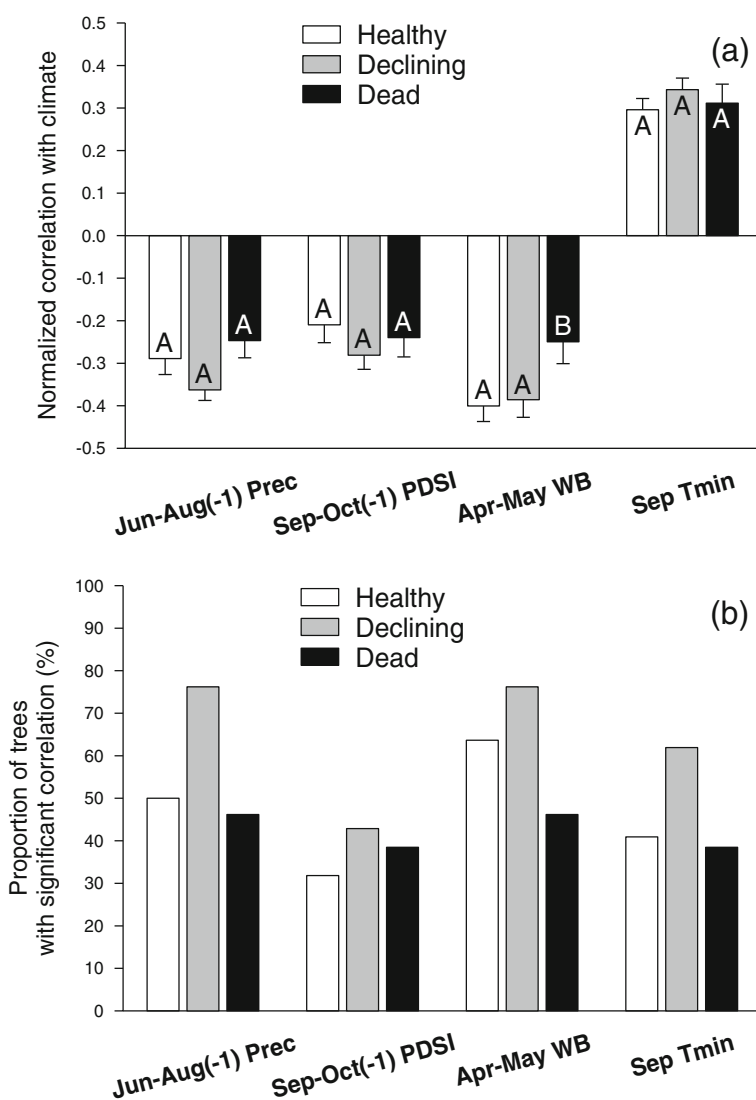
Fig. 4 Relationships of soil properties with normalized correlations of individual tree-ring growth chronologies with Jun-Aug(-1) Prec, Sep-Oct (-1) PDSI, Apr-May WB, and Sep Tmin. Horizontal *dashed lines* indicate the significance boundary ($p < 0.05$) for correlation coefficients. Only Ca and Al concentrations in the surrounding soil were significantly related to the individual dendroclimatic response
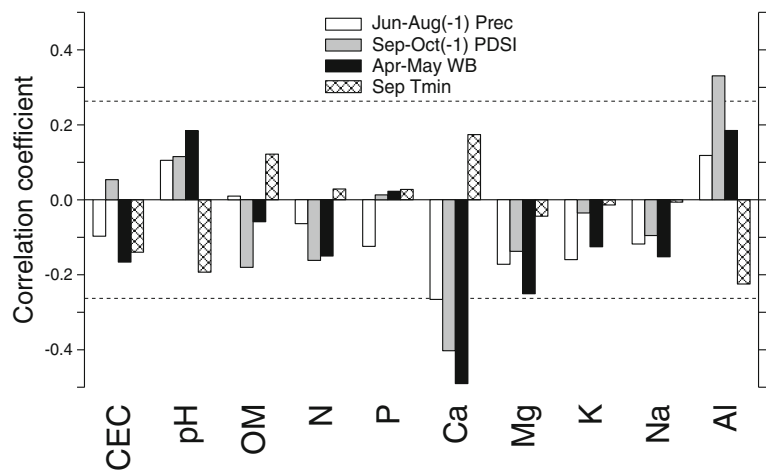
Discussion

Mean pH of our soils was below the range of 3.9–6.1 usually reported for typical *Quercus robur* forest soils in NW Spain, whereas organic matter content was near the upper range limit of 23.3 g kg^{-1} (Díaz-Maroto et al. 2012). Overall, studied soils are nutrient poor in comparison to other oak woodlands in NW Spain. Mean concentrations of total N, and extractable P, Ca, and K, were considerably lower than mean concentrations expected, and only concentrations of Mg fitted well to the expected mean values for soils beneath oak forests in NW Spain (Díaz-Maroto et al. 2012). Since the studied soils are narrow and most of the soil processes, such as biological pumping of nutrients and nutrient uptake by roots, are actually more strongly expressed in the topsoil and in the rhizosphere (Lucas 2001; Göransson et al. 2006) we assumed that soil chemical properties measured in this work were indicative of the pool of available nutrients at the individual level.

Belowground levels of N, Ca, Mg, and Na were even lower in soils surrounding trees that died than surrounding surviving (healthy and declining) trees. This evidence would suggest that the extremely rainy event in 2001 caused a higher mortality rate in oaks with low soil resources. Forest soils are heterogeneous in nature (Farley and Fitter 1999; Gallardo 2003), and the uneven distribution of nutrients could affect the individual tree performance differentially, since the spatial variation of nutrient concentration in oak tissues is strongly linked to the variation in soil resources (Gallardo and Covelo 2005). Nevertheless, soil nutrient availability can change through time, being modulated by processes such as tree growth and herbivore

grazing (Gallardo 2003; Harrison and Bardgett 2004), but also by disturbances such as tree felling or tree death (Guo et al. 2004; Kohlpaintner et al. 2009). Therefore, it is possible that the reduced concentration of soil nutrients around dead trees could be a consequence, rather than a cause, of tree death.

Nitrogen is mainly cycled through biological process, such as leaf fall and turnover of fine roots, and leaching of this element after tree death has been well documented (Knight et al. 1991; Jenkins et al. 1999). Other nutrients like Ca, Mg, K, and Na are mainly cycled through mineral weathering (Gallardo 2003), but also by biological pumping through leaf litter decomposition (Lucas 2001). It could be then possible that the reduced nutrient concentration of the soil beneath dead trees could be due to a reduced nutrient input via leaf fall. However, strong winds in autumn and winter normally redistribute the leaf litter throughout the forest floor in the study site. In addition, soil nutrient levels have in fact been shown to increase strongly after tree death, only returning to pre-death levels after a number of years. For instance, decline of *Tsuga canadensis* (L.) Carrière resulted in elevated concentrations of nitrate and most cations in soil water within 2 to 3 months of tree death, with maximum concentrations after 12 to 18 months, but nutrient concentration remained high for 3 to 4 years after death (Yorks et al. 2003). Similarly, death of *Pinus elliottii* Engelm. trees after experimental girdling also induced a rapid increase of soil nutrient availability up to a maximum 1 or 2 years after death, and then decreased returning to pre-death levels in 4 years (Guo et al. 2004). Considering that dead oaks died between 2002 and 2006, i.e. 1 to 5 years prior to soil sampling, nutrient content in soils surrounding dead trees should be similar
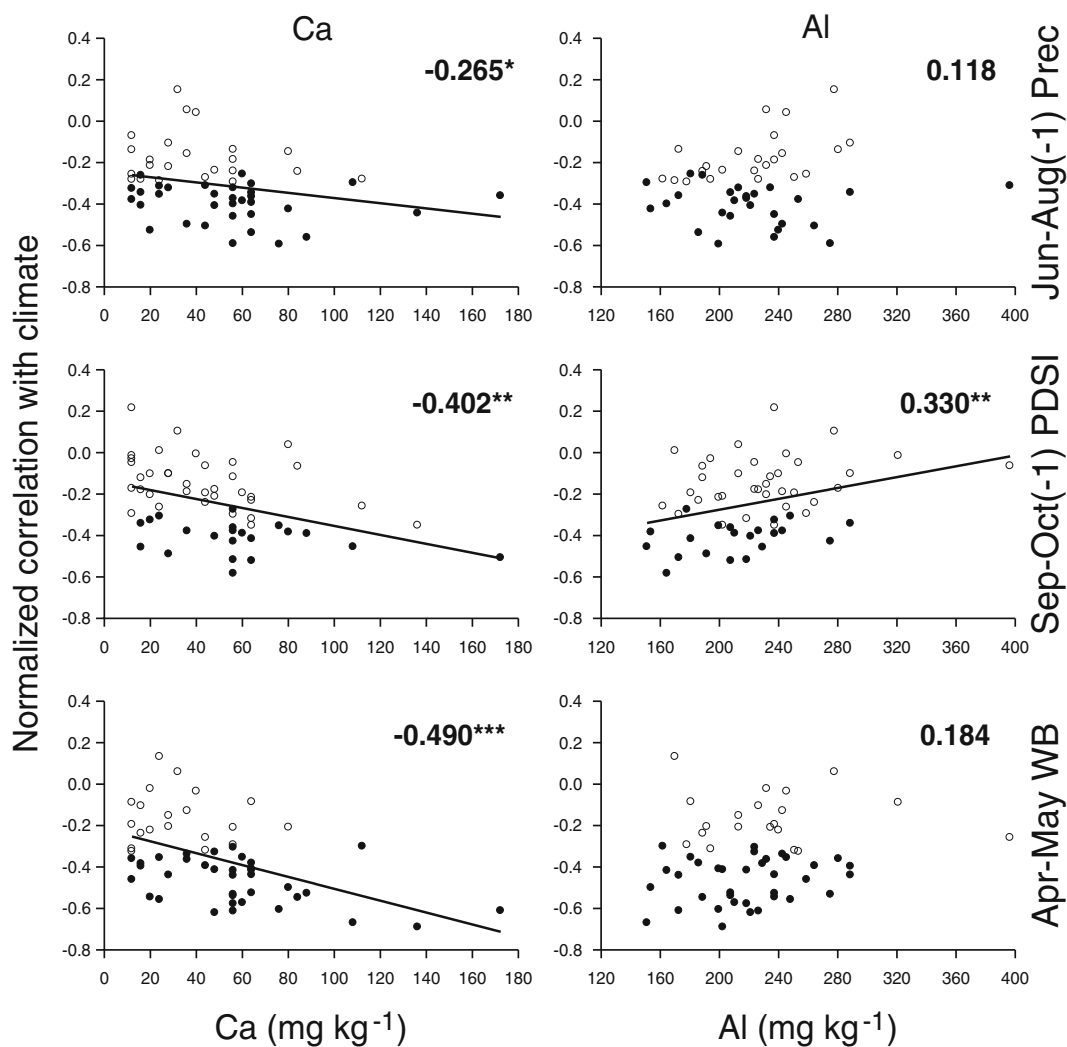
Fig. 5 Relationships of extractable Ca and Al concentrations in the surrounding soil, with normalized correlations of individual tree-ring growth chronologies with Jun-Aug(-1) Prec, Sep-Oct(-1) PDSI, and Apr-May WB. *Solid dots* indicate statistically significant ($p<0.05$) bootstrapped correlations, *empty dots* indicate non-significant correlations. Significant linear relationships, correlation coefficients, and their statistical significances (* $p<0.05$; ** $p<0.01$; *** $p<0.001$) are shown

to, or even higher than, pre-death concentrations. Thus, we assumed that the reduced concentration of soil nutrients around dead trees was likely to have been a cause, and not a consequence, of tree death.

This pattern of soil nutrients has been attributed to the sudden decomposition of litter and fine roots immediately after tree death. Reduced evapotranspiration when a tree dies increases soil moisture, and the greater amount of sunlight reaching the forest floor leads to increased soil temperature (Guo et al. 2002; Stoffel et al. 2010). A combination of increased soil moisture and temperature induces greater microbial activity and

accelerates decomposition and mineralization rates (Jenkins et al. 1999). In fact, localized nutrient-rich areas around dead trees may be important sources of nutrients for surviving trees, especially when the general levels of nutrient availability are low (Farley and Fitter 1999). Density of fine roots from neighbouring trees typically increases after tree death because of reduced competition and increased soil moisture and nutrient availability (Sucre and Fox 2009), which induce a fast reduction of nutrients to concentrations similar to pre-death levels. Trees that died in our study stands had experienced higher competition intensities

than surviving (healthy and declining) trees (Rozas and García-González 2012). Higher competition levels would probably have led to reduced availability of essential nutrients, and this is likely to have amplified the vulnerability to additional stresses among the trees that eventually died.

Our finding that soil Ca and Al availability are unbalanced and inversely related can be expected under acidic conditions, since Al is mobilized in the forest floor in a reactive form that reduces Ca storage, and thus its availability for root uptake (Lawrence et al. 1995). The soil Ca/Al molar ratio provides a valuable indicator for identification of thresholds beyond which the risk of forest damage from Al stress and nutrient imbalances increases (Cronan and Grigal 1995). It has been estimated that there is a 50 % risk of adverse impact on tree nutrition and growth when the soil Ca/Al ratio is as low as 1.0, a 75 % risk when the ratio is as low as 0.5, and a 100 % risk when the ratio is as low as 0.2 (Cronan and Grigal 1995). In our case, Ca/Al molar ratios for healthy and declining trees (0.31 ± 0.24 and 0.26 ± 0.13, respectively; mean $\pm$ SD) were significantly greater (one-way ANOVA, $F_{2,108}=12.60$, $p<0.001$) than for dead trees (0.09 ± 0.07). This finding supports that soil nutrient deficiencies, and probably also Al toxicity related to the quite acidic conditions of our study stands, might have contributed to oak decline and death.

The negative impact of water excess on tree-ring growth found in our study is exceptional within the dendroecological literature on *Quercus robur*. Wet spring-summers, and more specifically high rainfall between March-May and June-August, usually had beneficial effects on oak growth in Northern, Central, and Southern Europe (Friedrichs et al. 2009; Helama et al. 2009; Rozas et al. 2009). However, the particular conditions of our study site (i.e., a windward slope on a north-to-south oriented range that directly intercepts wet westerly fronts from the Atlantic Ocean), and the particular changes in local climatic conditions experienced over recent decades (i.e., a trend of rising rainfall throughout the 20th century, persistent soil water excess since the 1960s, and extremely rainy conditions in 2001), are likely to have led to water excess having a detrimental impact on tree growth and vitality (Rozas and García-González 2012). In addition, elevated minimum temperatures in September may delay the end of cambial activity and extend the active growing period, leading to the formation of wider rings, as has been observed across Europe in relation with global climate warming (Chmielewski and Rötzer 2001).

Climatic response of all decline classes was very similar, even considering that declining trees were the most responsive to climate at an individual level. The fact that trees that eventually died had shown lower growth rates ever since the 1940s would indicate a sustained stress (Dobbertin 2005), probably due to long-term competition and/or soil nutrient depletion. This work reveals a link between the local availability of nutrients in the soil and tree biological response, i.e., that soil chemical properties, and particularly Ca and Al concentrations, may modulate the individual dendroclimatic response. Cronan and Grigal (1995) and Lawrence et al. (1995) found that an increase in soil Al causes a reduced availability of Ca for tree uptake, and in our study we found trees growing under these conditions showed a less plastic response to water excess. Trees require a steady supply of Ca for wood formation and protection, since Ca is an essential regulator in many processes related to growth and responses to environmental stresses. Calcium regulates stomatal function, cell division, cell wall synthesis, and signalling functions in plant defence, repairs damage from biotic and abiotic stresses, contributes to the structural chemistry and function of woody tissues, and is needed to form protective layers in wood and bark (McLaughlin and Wimmer 1999; Lautner and Fromm 2010). This requirement for Ca may become problematic for soils with a naturally low base saturation (Shortle et al. 2012). Since Ca plays a major role during lignification in the cambial region and chemical signalling in responses to environmental stresses (McLaughlin and Wimmer 1999), we hypothesized that the individual response to the water excess that caused the decline was modulated by Ca concentration in oak tissues. Probably, low Ca availability diminished the individual physiological plasticity of oaks under the particularly acidic and nutrient-poor conditions of our study stands. The coincidence of stressful anoxic conditions with other biotic stressors such as root pathogens, would also aggravate the carbon starvation of trees, thus reducing its vitality and increasing death risk. High soil moisture may have increased the production and dispersion of *Phytophthora* zoospores in the past, thereby increasing the probability of root infection and damage (Jönsson et al. 2005). However, soil chemical traits in our study stands, such as low pH and relatively high Al content, are particularly unfavourable for *Phytophthora* infection (Jung et al. 2000; Jönsson et al. 2005). In addition, the presence of *Phytophthora* was checked in the sampled trees with negative results. Then, we think that the role of

Phytophthora as a significant triggering factor for massive tree death can be discarded in our case study. Furthermore, seasonal water excess can cause a massive impact on nutrient uptake and consequently on whole tree metabolism, since soil water saturation inhibits both the release of mineral nutrients and their uptake by the roots (Rennenberg et al. 2009).

Our results suggest that trees with higher Ca availability responded more plastically to the stressful conditions caused by water excess, particularly in spring, while trees with lower Ca levels were less responsive to the stress and more predisposed to die. Declining trees were able to overcome the stressful conditions, probably because they were under less competitive conditions (Rozas and García-González 2012), and showed higher levels of available nutrients in the surrounding soil than those trees that died. Additional research on the potential modulation of individual dendroclimatic responses of trees by soil chemical heterogeneity, under a wider variety of site conditions and on different tree species, is essential to reach more general inferences on this substantial and innovative field of study.

References

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

Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput Geosci 30:303–311

Bremner JM (1996) Nitrogen–total. In: Sparks DL (ed) Methods of soil analysis, part. 3. Chemical methods. Soil science society of America book series number 5. American Society of Agronomy, Madison, pp 1085–1121

Calvo de Anta R, Macías Vázquez F (2002) Mapa de solos de Galicia, Escala 1:50,000. Ponte Caldelas 186:5–10. Consellería de Medio Ambiente, Xunta de Galicia

Carlton GC, Bazzaz FA (1998) Resource congruence and forest regeneration following an experimental hurricane blow-down. Ecology 79:1305–1319

Chmielewski FM, Rötzer T (2001) Response of tree phenology to climate change across Europe. Agric For Meteorol 108:101–112

Cook ER, Holmes RL (1996) Guide for computer program ARSTAN. In: Grissino-Mayer HD, Holmes RL, Fritts HC (eds) The International tree-ring data bank program library version 2.0 user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, pp 75–87

Cronan CS, Grigal DF (1995) Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. J Environ Qual 24:209–226

Dai A, Trenberth KE, Qian T (2004) A global data set of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. J Hydrometeorol 5:1117–1130

Di Filippo A, Alessandrini A, Biondi F, Blasi S, Portoghesi L, Piovesan G (2010) Climate change and oak growth decline: dendroecology and stand productivity of a Turkey oak (*Quercus cerris* L.) old stored coppice in Central Italy. Ann Forest Sci 67:706

Díaz-Maroto IJ, Vila-Lameiro P, Vizoso-Arribe O, Alañón E, Díaz-Maroto MC (2012) Natural forests of oak in NW Spain: soil fertility and main edaphic properties. In: Whalen J (ed) Soil fertility improvement and integrated nutrient management: a global perspective. InTech Europe, Rijeka, pp 3–18

Dobbertin M (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. Eur J Forest Res 124:319–333

Doležal J, Mazůrek P, Klimešová J (2010) Oak decline in southern Moravia: the association between climate change and early and late wood formation in oaks. Preslia 82:289–306

Faller AJ (1981) An average correlation coefficient. J Appl Meteorol 20:203–205

Farley RA, Fitter AH (1999) Temporal and spatial variation in soil resources in a deciduous woodland. J Ecol 87:688–696

Friedrichs DA, Büntgen U, Frank DC, Esper J, Neuwirth B, Löffler J (2009) Complex climate controls on 20th century oak growth in Central-West Germany. Tree Physiol 29:39–51

Führer E (1998) Oak decline in central Europe: a synopsis of hypotheses. In: McManus ML, Liebhold AM (eds) Proceedings of population dynamics, impacts and integrated management of forest defoliating insects. USDA General Technical Report NE-247, pp 7–24

Gaertig T, Schack–Kirchner H, Hildebrand EE, Wilpert K (2002) The impact of soil aeration on oak decline in southwestern Germany. Forest Ecol Manage 159:15–25

Gallardo A (2003) Spatial variability of soil properties in a floodplain forest in Northwest Spain. Ecosystems 6:564–576

Gallardo A, Covelo F (2005) Spatial pattern and scale of leaf N and P concentration in a *Quercus robur* population. Plant Soil 273:269–277

Gibbs JN, Greig BJW (1997) Biotic and abiotic factors affecting the dying back of pedunculate oak *Quercus robur* L. Forestry 70:399–406

Göransson H, Wallander H, Ingerslev M, Rosengren U (2006) Estimating the relative nutrient uptake from different soil

depths in *Quercus robur*, *Fagus sylvatica* and *Picea abies*. Plant Soil 286:87–97

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res 57:205–221

Guo D, Mou P, Jones RH, Mitchell RJ (2002) Temporal changes in spatial patterns of soil moisture following disturbance: an experimental approach. J Ecol 90:338–347

Guo D, Mou P, Jones RH, Mitchell RJ (2004) Spatio-temporal patterns of soil available nutrients following experimental disturbance in a pine forest. Oecologia 138:613–621

Harrison KA, Bardgett RD (2004) Browsing by red deer negatively impacts on soil nitrogen availability in regenerating native forest. Soil Biol Biochem 36:115–126

Helama S, Lindholm M, Timonen M, Eronen M (2004) Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. Theor Appl Climatol 79:239–254

Helama S, Läänelaid A, Raisio J, Tuomenvirta H (2009) Oak decline in Helsinki portrayed by tree-rings, climate and soil data. Plant Soil 319:163–174

Jenkins JC, Aber JD, Canham CD (1999) Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Can J Forest Res 29:630–645

Jönsson U, Jung T, Sonesson K, Rosengren U (2005) Relationships between health of *Quercus robur*, occurrence of *Phytophthora* species and site conditions in southern Sweden. Plant Pathol 54:502–511

Jung T, Blaschke H, Oßwald W (2000) Involvement of *Phytophthora* species in Central European oak decline and the effect of site factors on the disease. Plant Pathol 49:706–718

Knight DH, Yavitt JB, Joyce GD (1991) Water and nitrogen outflow from lodgepole pine forest after two levels of tree mortality. Forest Ecol Manage 46:215–225

Kohlpaintner M, Huber C, Weis W, Göttlein A (2009) Spatial and temporal variability of nitrate concentration in seepage water under a mature Norway spruce [*Picea abies* (L.) Karst] stand before and after clear cut. Plant Soil 314:285–301

Lautner S, Fromm J (2010) Calcium-dependent physiological processes in trees. Plant Biol 12:268–274

Lawrence GB, David MB, Shortle WC (1995) A new mechanism for calcium loss in forest-floor soils. Nature 378:162–165

Long RP, Horsley SB, Hallett RA, Bailey SW (2009) Sugar maple growth in relation to nutrition and stress in the northeastern United States. Ecol Appl 19:1454–1466

Lucas Y (2001) The role of plants in controlling rates and products of weathering: importance of biological pumping. Annu Rev Earth Planet Sci 29:135–163

McLaughlin SB, Wimmer R (1999) Calcium physiology and terrestrial ecosystem processes. Tansley review no. 104. New Phytol 142:373–417

Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants:

past stress history, stress interactions, tolerance and acclimation. Forest Ecol Manage 260:1623–1639

Oberhuber W, Kofler W (2000) Topographic influences on radial growth of Scots pine (*Pinus sylvestris* L.) at small spatial scales. Plant Ecol 146:231–240

Oberhuber W, Stumbock M, Kofler W (1998) Climate–tree–growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. Trees 13:19–27

Olsen SR, Cole CV, Watanabe FS, Dean LA (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. 939. U.S. Govt. Printing Office, Washington

Rennenberg H, Dannenmann M, Gessler A, Kreuzwieser J, Simon J, Papen H (2009) Nitrogen balance in forest soils: nutritional limitation of plants under climate change stresses. Plant Biol 11:4–23

Rozas V, García-González I (2012) Too wet for oaks? Inter-tree competition and recent persistent wetness predispose oaks to rainfall-induced dieback in Atlantic rainy forest. Global Planet Chang 94–95:62–71

Rozas V, Olano JM (2013) Environmental heterogeneity and neighbourhood interference modulate the individual response of *Juniperus thurifera* tree-ring growth to climate. Dendrochronologia 31:105–113

Rozas V, Lamas S, García-González I (2009) Differential tree-growth responses to local and large-scale climatic variation in two *Pinus* and two *Quercus* species in northwest Spain. Ecoscience 16:299–310

Sheppard PR, Casals P, Gutiérrez E (2001) Relationships between ring-width variation and soil nutrient availability at the tree scale. Tree-Ring Res 57:105–113

Shortle WC, Smith KT, Jellison J, Schilling JS (2012) Potential of decaying wood to restore root-available base cations in depleted forest soils. Can J Forest Res 42:1015–1024

Stoffel JL, Gower ST, Forrester JA, Mladenoff DJ (2010) Effects of winter selective tree harvest on soil microclimate and surface CO_2 flux of a northern hardwood forest. Forest Ecol Manage 259:257–265

Sucre EB, Fox TR (2009) Decomposing stumps influence carbon and nitrogen pools and fine-root distribution in soils. Forest Ecol Manage 258:2242–2248

Thomas FM, Büttner G (1998) Nutrient relations in healthy and damaged stands of mature oaks on clayey soils: two case studies in Northwestern Germany. Forest Ecol Manage 108:301–319

Thomas FM, Blank R, Hartmann G (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. For Pathol 32:277–307

Thornthwaite DW (1948) An approach toward a rational classification of climate. Geogr Rev 38:55–94

Yorks TE, Leopold DJ, Raynal DJ (2003) Effects of *Tsuga canadensis* mortality on soil water chemistry and understory vegetation: possible consequences of an invasive insect herbivore. Can J Forest Res 33:1525–1537