

# Drought-induced decline and mortality of silver fir differ among three sites in Southern France

Maxime Cailleret · Marie Nourtier · Annabelle Amm ·  
Marion Durand-Gillmann · Hendrik Davi

Received: 12 May 2012 / Accepted: 21 January 2013  
© INRA and Springer-Verlag France 2013

## Abstract

• **Context** In the Mediterranean area, numerous decline and mortality processes have been reported during recent decades, affecting forest dynamics. They are likely due to increases in summer drought severity and therefore especially affect drought-sensitive species, such as silver fir (*Abies alba* Mill.).  
• **Aims and methods** To understand the relationships between tree growth, crown condition and mortality probability, radial growth trends of healthy, declining (showing crown damages) and dead trees were compared using tree-ring analysis. Factors involved in determining this mortality were also examined at the plot and tree level using altitudinal gradients on three contrasted sites in southeastern France.

• **Results** Individuals with higher inter-annual variability in growth were more prone to dieback. At two sites, dead trees displayed lower growth rates over their entire lifetime, while, on the last site, their juvenile growth rate was higher. Trees with crown damage had higher growth rates than healthy trees on one site, and their radial growth trends over time always differed from those of dead trees. Mortality and crown damage were little related to altitude, but strongly differed between sites and among plots underlining the importance of local edaphic and topographic conditions.  
• **Conclusion** These results suggest that the relationships among mortality probability, crown condition and growth can differ among sites, and highlight the impact of soil conditions and the need to assess them in tree mortality studies.

**Handling Editor:** Nathalie Breda

**Contribution of the co-authors** All co-authors contributed to field measurements. Maxime Cailleret performed data analysis and wrote the manuscript. Marie Nourtier, Annabelle Amm and Marion Durand-Gillmann contributed to the revision and amelioration of the manuscript. Hendrik Davi wrote the manuscript and supervised the whole project.

**Electronic supplementary material** The online version of this article (doi:10.1007/s13595-013-0265-0) contains supplementary material, which is available to authorized users.

M. Cailleret · A. Amm · M. Durand-Gillmann · H. Davi  
UR629, Écologie des Forêts Méditerranéennes, INRA,  
Domaine Saint Paul, Site Agroparc,  
84914 Avignon, France

M. Nourtier  
UMR1114, Environnement Méditerranéen et Modélisation des  
AgroHydrosystèmes, INRA, Domaine Saint Paul, Site Agroparc,  
84914 Avignon, France

M. Cailleret (✉)  
Forest Ecology group, Institute of Terrestrial Ecosystems,  
Department of Environmental Sciences,  
Swiss Federal Institute of Technology ETH, Universitätstrasse 16,  
8092 Zürich, Switzerland  
e-mail: cailleret.maxime@gmail.com

**Keywords** Tree mortality · Drought · Decline · *Abies alba* Mill. · Tree-ring · Growth · Altitude

## 1 Introduction

Tree decline and mortality are main processes in forest dynamics. As they impact forest regeneration, timber production, carbon sequestration and biodiversity, they were the focus of an increasing number of studies. However, our knowledge on the processes leading to tree mortality is still limited (Allen et al. 2010; Mc Dowell 2011). The ability of a tree to overcome stress or to survive, i.e. the tree vitality, decreases with the occurrence of environmental stress (Dobbertin 2005). This decline can be reversible, but in the worst cases, when the stress is too long, intense or occurs too frequently, the process becomes irreversible, leading to death. Natural tree mortality can be either regular or irregular (Pedersen 1998). Regular mortality is associated with a progressive reduction in tree vitality and results from competition for light, water and soil nutrients or from a decrease in hydraulic conductance due to tree height. In contrast, irregular mortality

is caused by random events or hazards, such as insect attacks, fire, wind, snow, rock falls, browsing and severe drought, all of which are able to interact. A strong increase in the scientific interest in the mortality process has been observed in the last 40 years (Allen et al. 2010), which is mainly due to the rise in the number of mortality events. The recent increase in regular mortality has been assigned to rising temperatures (van Mantgem et al. 2009), and massive diebacks have usually been directly or indirectly induced by drought (Pedersen 1998; Bréda et al. 2006).

As climate change might increase the frequency and intensity of droughts, water-limited areas were expected to be affected by declines in tree vitality and by mortality events (Allen et al. 2010). The dry zones of North America already experienced high mortality rates. Similarly, forest dieback and decline were reported after severe droughts in the European-Mediterranean bioclimate and paralleled a decrease in tree growth (e.g. Cailleret and Davi 2011). As climate is predicted to become hotter and dryer in the future (Somot et al. 2008), we can expect that massive diebacks will occur more frequently and will affect a greater number of species and larger forest areas.

This decrease in water availability during the growth period especially affects drought-sensitive species. The genus *Abies* is an interesting case for mortality studies because this keystone species is economically important and is especially sensitive to drought. Since the beginning of the twenty-first century, high rates of mortality and crown defoliation have been observed for this *genus* in the southernmost European forests. In Spain, the relict *Abies pinsapo* species is declining (Linares et al. 2009), while many *Abies cephalonica* died in Greece due to a severe drought in 2000 (Tsopeles et al. 2004). Concerning silver fir (*Abies alba* Mill.), its entire xeric range was affected by tree decline and dieback (e.g. Linares and Camarero 2011).

The first aim of this paper is to build up reliable indicators of tree vitality for an improved assessment of the biotic and abiotic factors leading to tree decline and death. Radial growth is commonly used, as it is easily assessed by tree diameter or ring-width measurements, and it is associated with carbon assimilation and the drought level experienced by the tree (Dobbertin 2005). For instance, tree mortality can be predicted by models using radial growth data with a respectable performance (Bigler and Bugmann 2003; Cailleret 2011). In these models, survival probability decreases when growth rate falls under a given threshold and/or when the temporal growth trend is obviously negative. Radial growth can be compared to two other commonly used indicators: sapwood area (SA) and crown condition. SA approximates tree vitality because it is the area of living wood that contains carbohydrates reserves and the area of functional xylem conducting the sap flow. A higher SA indicates a higher hydraulic conductance within the tree, and we commonly assumed that it also indicates a higher leaf area (Granier 1981). Tree vitality can also be estimated by assessing crown

damages. Because needles act as storage organs for carbon and nitrogen (Hoch et al. 2003), defoliation and, in a lesser extent, chlorosis were usually reported as common decline symptoms in coniferous trees (Bréda et al. 2006) and used to indicate future mortality (Dobbertin and Brang 2001). Needle chlorosis can be caused by several factors, such as nutrient deficiency, atmospheric pollution (e.g. ozone), pathogens and drought, and reduces the photosynthetic capacities of the leaves (Dreyer et al. 1994). Defoliation is usually due to insect defoliators or to drought which induces premature shedding of green leaves due to petiole cavitation (Bréda et al. 2006) and limits the number and the size of active axes and needles produced during the following years (Girard et al. 2012).

To our knowledge, these three vitality indicators have not yet been compared by gathering both spatial and temporal data. If SA was related with growth trends for long-term growth decline (Becker 1987), the relationship may change for quick declines in tree vitality due to successive droughts. Concerning crown condition, temporal surveys of defoliation produced suitable indications of changes in tree vitality (temporal analysis), but few studies compared the growth of trees with different crown damages (spatial analysis).

The second aim was to use these indicators to obtain information identifying which trees are more prone to die, and areas where mortality and crown damages were particularly prevalent. Different biotic and abiotic factors predispose a tree to mortality. For drought-induced dieback, we commonly accept that a higher risk occurs in dry stations, e.g. at low latitude, at low altitude, on shallow or karstic soils, with high slope or located on south-facing slopes (Manion 1981). Similarly, pathogens, such as fungi, which induce a decrease in water uptake, bark beetles, which feed on phloem and which amplify hydraulic failure when water transport is interrupted by symbiotic fungi and mistletoe, which uses tree sap flow for its own photosynthesis, predispose a tree to mortality (Durand-Gillmann et al. 2012). At stand scale, different relationships can be found between tree size and mortality rate. In an undisturbed environment, intense competition for light and water especially affects small trees inducing a higher mortality probability (Coomes and Allen 2007), although large trees can be more affected by extreme events, such as storms. Similarly, it is commonly accepted that the probability of tree survival increases with large diameter increments (Cailleret 2011), but some studies recently showed a trade-off between tree growth rate and longevity (e.g. Bigler and Veblen 2009). Consequently, all these factors should be studied and organised into a hierarchy that strongly depends on the spatial scale of interest. Indeed, an important issue is how and why there is a large spatial variability in tree mortality or in crown condition, such as in the case of patchy mortality.

Experiments analysing tree mortality at several spatial scales will contribute to a better understanding of the various causes determining tree death (see Mc Dowell 2011 for a review). It can also be helpful to improve adapted management at the stand (to decide which tree should be thinned) and watershed levels (to choose where a species or a provenance might be planted).

Consequently, in this paper, we compared the decline and mortality process of silver firs in three Mediterranean mountain locations in Provence, in southeastern France, to assess (1) the relevance of growth, sapwood area and crown condition assessment as indicators of tree vitality; (2) if the relationships between these vitality indices and tree mortality vary between sites; and (3) which factors predispose and trigger trees to die.

## 2 Materials and methods

### 2.1 Study area and sample sites

This study was conducted on three Mediterranean mountains in Provence, France: Mont Ventoux (Dvx in Table 1), Issole forest (Diss) and Vésubie (Dves; Fig. S1). The sites were selected to represent contrasted climatic and edaphic conditions. Based on data from climate stations in southeastern France (see next section), we estimated for the period of 1964–2009 that mean annual temperature in Vésubie was 1.2 °C and 1.4 °C, respectively, higher than at Issole and on Mont Ventoux, at comparable altitudes ( $\approx$ 1,250 m above sea level). Climate was the wettest on Mont Ventoux

**Table 1** Main characteristics of the studied plots on Mont Ventoux (Dvx and TC), Issole (Diss) and Vésubie (Dves)

Plot	Altitude (ma.s.l.)	Slope (°)	Soil depth (cm)	Coarse elements (%)	BA (m <sup>2</sup> /ha)	Fir proportion (/tree)	Mortality rate (/tree)	Number of trees cored	Mean age	Mean circ. (mm)	Mean Gini index
Dvx1	995	25	35	50.0	42.5	0.11	0.39	20	75.4	497.8	0.120
Dvx2	1,020	36	20	80.0	53.6	0.46	0.26	30	63.3	542.6	0.127
Dvx3	1,117	22	65	82.5	50.8	0.28	0.13	25	62.9	428.0	0.119
Dvx4	1,247	29	32	48.0	44.2	0.82	0.25	16	160.8	591.4	0.130
Dvx5	1,340	27	60	58.3	32.6	0.62	0.07	25	156.0	626.8	0.120
TC1	1,138	35	62	86.5	34	0.40	0.13	9	65.4	496.1	0.106
TC2	1,108	37	67	81.9	19.5	0.27	0	7	57.1	312.8	0.095
TC3	1,125	41	62	76.1	35.5	0.57	0.33	18	65.9	493.3	0.120
TC4	1,110	41	72	72.8	28.4	0.34	0.20	11	73.7	519.1	0.124
TC5	1,122	37	65	80.8	32.2	0.56	0.48	19	75.9	483.3	0.121
TC6	1,128	39	67	61.2	40.2	0.53	0.54	22	75.0	496.9	0.130
TC7	1,128	42	60	61.3	41.9	0.53	0.16	13	83.5	474.4	0.143
TC8	1,123	45	20	60.0	31.1	0.66	0.23	15	73.7	405.0	0.136
TC9	1,131	44	43	83.0	35.9	0.52	0.21	15	82.3	421.7	0.124
TC10	1,124	47	45	40.0	40.2	0.48	0.46	12	104.9	595.4	0.134
TC11	1,121	45	25	65.0	49.2	0.51	0.36	16	107.9	524.9	0.143
TC12	1,134	42	58	79.7	35.3	0.36	0.12	11	108.6	614.9	0.136
TC13	1,143	40	20	75.0	54.7	0.59	0.05	16	148.4	610.4	0.124
TC14	1,137	47	16	40.0	29.0	0.67	0.06	10	102.9	551.7	0.131
TC15	1,132	46	34	75.0	61.1	0.70	0.11	17	142.1	677.7	0.132
TC16	1,128	45	50	71.0	48.3	0.55	0.16	16	106.3	598.4	0.131
Diss1	1,108	38	34	30.0	54.6	0.95	0	15	167.1	658.1	0.144
Diss2	1,196	39	30	43.5	56.9	0.93	0.08	27	101.3	492.0	0.165
Diss3	1,281	23	33	52.4	65.5	0.94	0.01	22	91.5	507.5	0.121
Diss4	1,468	25	36	56.9	44.7	0.79	0.06	21	79.8	578.7	0.130
Diss5	1,585	35	67	57.1	63.6	0.83	0.09	19	74.4	759.2	0.125
Dves1	1,078	43	61	56.6	55.9	0.23	0.01	17	78.6	699.4	0.112
Dves2	1,130	42	85	59.1	45.4	0.44	0.03	19	77.8	688.8	0.114
Dves3	1,242	47	73	56.6	43.9	0.52	0.25	26	96.8	637.9	0.128
Dves4	1,330	40.5	71	72.7	42.1	0.81	0.02	18	153.2	760.8	0.123
Dves5	1,497	39	59	40.0	49.9	0.87	0.02	21	138.7	726.7	0.122
Dves6	1,586	27	82	40.6	48.0	0.83	0.05	13	148.6	897.8	0.111

(1,126 mm), followed by Vésubie (954 mm) and Issole (856 mm). However, this order changed for summer rainfall: 243 mm for Mont Ventoux, 217 mm in Issole and 194 mm on Vésubie. Similarly, strong differences in soil properties induced inter-site differences in the amount of water available during the growing season. In Vésubie, the mother bedrock is sandstone schist, while in Issole, it is calcareous clay, and in Mont Ventoux, it is entirely calcareous. The soils on Mont Ventoux are karstic, likely leading to a higher water infiltration than on Issole and Vésubie, and infiltration intensified by the high slope (between 22° and 47°; Table 1).

On Mont Ventoux, Issole and Vésubie, five, five and six plots located along an altitudinal gradient were respectively studied with the consideration that a downward shift in altitude approximates climate change, i.e. decreasing rainfall and rising temperatures (Cailleret and Davi 2011). Elevational transects were located on the northern slopes of the mountains, had the same northern exposure (between ENE and WNW) and covered the entire distribution range of silver fir from low to high altitudes. The impact of local edaphic variations was studied using 16 plots distributed along a transect along a contour line (TC in Table 1) between 1,100 and 1,140 m on Mont Ventoux. On each 400-m<sup>2</sup> plot (20×20 m), all trees with a diameter at breast height (dbh, diameter at 1.30 m) above 10 cm were identified, mapped and measured for dbh. Soil water storage capacity was assessed by measuring soil depth and the percentage of coarse elements in one pedological pit situated at the centre of the plot. As karstic soils vary in space, soil depth was also measured on the four corners of the plot using a heal bar. The impact of competition on radial growth was calculated for all studied trees. As the forest inventory made within the 400-m<sup>2</sup> plot was not sufficient to correctly assess the impact of tree density, all trees and stumps with a dbh above 10 cm were measured and mapped within a 20-m radius around each studied tree. On Mont Ventoux, Issole and Vésubie, a previous study reveals that the highest determination coefficient between radial growth rate and competition was obtained using a distance-dependent index (equation of Martin and Ek 1984) and considering all neighbouring trees respectively located within a radius of 9, 15 and 14 m around the studied tree, as competitors (Cailleret 2011).

## 2.2 Climatic data

Long-term evolution of climatic conditions on the study sites was reconstructed using the closest long-term meteorological stations and hobos stations located on the plots. Meteorological data were gathered from stations of the French National Climatic Network (Météo-France). On Mont Ventoux, Issole and Vésubie, stations in Carpentras (1964–2009; 99 m a.s.l.), St André (1964–2009; 890 m a.s.l) and Moulinet (1961–2009; 780 m a.s.l), respectively, were

used. To compare the climate between sites, reconstruction was made using Hobos ProV2 micro-loggers located at comparable altitudes (1,225 m on Mont Ventoux, 1,281 m on Issole and 1,242 m on Vésubie). Climatic data were taken in 2008 and 2009, and were related month per month with long-term data using linear regression models. Relationships were reliable for temperature ( $R^2$  ranged between 0.95 and 0.99) and summer rainfall ( $R^2=0.93$  to 0.98), but not winter rainfall ( $R^2=0.77$  on Mont Ventoux, 0.28 in Issole and 0.84 in Vésubie). These discrepancies were caused by the amount of snow that fell on the site. However, as the amount of water that fell during the winter has little impact on silver fir growth (Cailleret and Davi 2011), we used this climatic reconstruction for radial growth analysis.

Temperature increased on all sites since the 1960s, particularly during summer. The increase respectively approximated +4.6 °C, +5.9 °C and +3.4 °C per century on Mont Ventoux, Issole and Vésubie (Cailleret 2011). No trend was found for annual rainfall, but summer rainfall was slightly reduced on Mont Ventoux (−177 mm per century;  $p<0.1$ ), while no change was detected in Issole and Vésubie (−69 mm per century).

The effect of elevation on temperature was recorded using Hobos ProV2 micro-loggers located on each sample plot. In 2008 and 2009, the altitude-related shift in temperatures was respectively 0.72 °C/100 m ( $R^2=0.99$ ), 0.51 °C/100 m ( $R^2=0.98$ ) and 0.71 °C/100 m ( $R^2=0.94$ ) on Mont Ventoux, Issole and Vésubie, but showed high temporal instability (Cailleret 2011). Hobos meteorological stations were also installed at the top of four trees along the transect in contour line. Climatic conditions were considered constant as differences in mean temperatures between plots did not exceed 0.25 °C and 0.65 % for relative humidity.

## 2.3 Tree-ring analysis

A total of 561 dominant or codominant firs were studied. Inter-annual and inter-tree variability of radial growth was analysed using classical tree-ring width analysis. Trees were sampled with an increment borer at dbh, and the cores were planed with a razor blade. Ring-widths (RW, millimetres per year) were measured at a precision of 0.01 mm using the CDendro v5.3 and Coorecorder 5.3 softwares (Cybis Elektronik & Data AB., Sweden). When a core did not reach the pith, the total missing width was estimated using the curvature of the innermost rings of the sample, which allows the calculation of basal area increments (BAI, square millimetres per year), assuming a circular outline of stem cross-sections. The number of years estimated to the pith was based on the growth rate after the missing segment (Esper et al. 2003).

To analyse the impact of climate on inter-annual growth variability, individual RW series were standardised in a

common two-step procedure using the ARSTAN software (Holmes 1994). First, the best model between a negative exponential curve and a linear regression line was fitted to remove long-term trend. Second, a more flexible detrending was made by a cubic smoothing line with a 50 % frequency response over 75 years. To obtain residual chronologies, autocorrelation was removed using autoregressive models for each individual series (Cook 1987). Individual residual chronologies were introduced into a principal component analysis (PCA; period 1900–2009) to elucidate the impact of climatic conditions on tree radial growth inter-annual variability and an ecological structure between trees. The relationships between climatic variables of the current and previous year as well as the inter-annual changes in PC scores for the first (PC1) and the second axes (PC2) were analysed using linear models. Following the results of a previous dendroclimatic analysis (Cailleret and Davi 2011), the selected input variables were the sum of rainfalls and the maximum and minimum temperatures of the previous end of summer (August to September), current winter (October to February), current spring (March and April) and current summer (May to July). The effect of tree age, size and altitude on inter-tree changes in PC1 and PC2 scores was also assessed. The sensitivity of each tree to environmental changes was assessed by calculating Gini indices (Biondi and Qeadan 2008). The package *ade4* of the statistical software R (R for Windows version 2.8.0; R Development Core Team 2008) was used for PCA analysis. MASS was used for the selection of models by Akaike information criterion in a stepwise algorithm (stepAIC) and *dplR* package for dendrochronological analysis (Bunn 2008).

The analysis of radial growth trends during the twentieth and twenty-first centuries was made after removing the age effect using the mean regional age curve (RC) of the BAI of the species ( $RC_{BAI}$ ; Regional Curve Standardisation method; Esper et al. 2003). This method was adapted to the study in a two-step procedure. First, BA (basal area=cumulative BAI, in square millimetres) curves were used considering that they include fewer medium frequency changes than  $RC_{BAI}$  curves when the sampling effort is not large enough (Cailleret 2011). These changes in growth are only due to a sampling effect, not to aging, and are therefore included in smoothing splines fitted to  $RC_{BAI}$  curves, transmitting an important bias to annual growth indices. Second, as the effect of tree age on radial growth strongly differs between altitudes, different mean plot age curves BA ( $PC_{BA}$ ) were used instead of the only one  $RC_{BA}$  curve. Gompertz functions were then fitted to each  $PC_{BA}$  curve considering that the increase in BA is less important when the tree is very old. Finally, annual growth indices were calculated as

$$GI_{i,t} = BAI_{i,t} / (BA_{PC,t} - BA_{PC,t-1})$$

where  $GI_{i,t}$  is the growth index of a tree  $i$  at the cambial age  $t$ , and  $BA_{PC,t}$  and  $BA_{PC,t-1}$  is the basal area predicted by the plot curve ( $PC_{BA}$ ) during the current and previous age, respectively. A GI greater than 1 indicates that the tree had a better growth than the average at same age. The mean growth index ( $GI_{i,mean}$ ) was calculated as the ratio  $BA_{i,u} / BA_{PC,u}$ , with  $u$  representing the age when the tree died or was cored.

## 2.4 Tree vitality

Tree vitality was assessed in 2008 using different methods. First, crown condition was assessed through the visual analysis of crown defoliation and chlorosis. The same two observers made all visual analyses to reduce and the subjectivity of both assessments (based on a reference tree growing on the same site which is considered as healthy) and the “observer effect” (Dobbertin and Brang 2001). Crown defoliation was preferred to crown transparency because trees with high shoot elongation rates usually showed high transparency levels—the number of branch per length unit is reduced—even if no needle loss occurred. In this way, the defoliation rate only depends on unexpected branch death and needle loss. Four crown condition classes were used: healthy trees with crown defoliation and chlorosis below 20 % (class 0); moderately declining trees with crown defoliation and/or chlorosis between 20 % and 40 % (class 1); severely declining trees with crown defoliation and/or chlorosis above 40 %, typically with a large number dead branches in the crown (class 2); and dead trees (class 3).

Sapwood area was assessed on 281 trees by differentiating heartwood and sapwood on each core using perchloric acid. This chemical reagent identifies living wood by reacting with chemical compounds in the heartwood and is the most adapted for firs (Becker 1987). For this study, the sapwood area was analysed as it is, but we also used an index of sapwood area (ResSA) in which tree age, tree size, altitude and competition effects were removed. To compare GI trends of trees with different sapwood areas, the “plot” effect should also be removed, as GI was performed at the intra-plot scale. ResSA were thus calculated as individual ResSA divided by the mean sapwood area of the neighbouring trees as follows:

$$ResSA_i = \left( \frac{SAMES_i}{SATH_i} \right) / \left[ \left( \sum_n \frac{SAMES_n}{SATH_n} \right) / n \right]$$

where the sapwood index calculated for a tree  $i$  ( $ResSA_i$ ) depends on the ratio between the measured SA ( $SAMES$ ) and the theoretical SA given by the generalised linear model ( $SATH$ ; Table S1; Cailleret 2011) for the tree  $i$ , and on this ratio averaged for the neighbouring trees  $n$  of the same plot.

### 3 Results

#### 3.1 Inter-annual variability of growth

PCA revealed that the inter-annual variability of tree-ring width was primarily explained by climatic conditions. PCA axes 1 and 2 explained more than 60 % of the total variance of the growth indices (GI; Table 2). The first axis differentiated years with high growth (positive PC1 scores) from those with low growth (negative PC1 scores) (Fig. 1). On each site, PC1 scores were negatively related with the previous PC1 scores, indicating that an increase in tree GI was mostly followed by a decrease in GI (Table 3). This inter-annual variation was not due to biological changes but rather to the standardisation method, which removed medium frequencies to highlight inter-annual growth variability. Summer rainfall positively impacted current radial growth (Table 3). The amount of rainfall in April and May seemed also to be positively related to growth at Issole site. Moreover, high maximum temperatures of previous year negatively affected the growth on Mont Ventoux and Issole, while a lack of water during this period had little impact on growth rates on Vésubie. For several years, low growth rates on Mont Ventoux were explained by low minimum temperatures during spring. On all sites, large reductions in ring-widths were observed in 1942, 1974, 1986 (dry summers) and 2004 (dry spring and dry summer during the previous year). In contrast, depending on the site, 1995 or 1996 was reported as a “good” year for growth especially due to a high amount of rainfall during the spring and early summer (Fig. 1).

PC scores along the first axis (PC1) increased with tree size but decreased with tree age and were not related to altitude (Table 2 and Fig. 1). The second axis discriminates years when growth trends strongly differed between altitudes. Positive PC2 scores indicated that growth rates during these years increased for trees at high altitude but decrease for those growing at low altitude. On the contrary, negative PC2 scores indicated an increase in growth rate at low altitude but not at high altitude. PC2 scores were less related

**Fig. 1** Principal components analysis (PCA) main plane (axis 1 and 2) calculated for the period 1900–2009 on Mont Ventoux (top), Issole (middle) and Vésubie (bottom). The size of the circles reveals the amount of rainfall during current summer (May–July), while crosses indicate that climatic data were not available for this year. Mean summer rainfalls for the period 1964–2009 (Mont Ventoux and Issole) or 1961–2009 (Vésubie) were indicated in the upper left boxes

to climatic conditions. On Issole, trees at high altitude were favoured by moderate temperatures in winter (elevated Tmax) and in spring (moderate Tmax) while the reverse trend can be expected at low altitude. On Mont Ventoux, summer maximum temperatures were positively correlated with GIs of trees growing at high altitude but not at low altitude.

#### 3.2 Comparison of three indicators of tree vitality

The comparison of the growth levels of trees with different sapwood areas (ResSA; Table S1) indicated that differences in ResSA were related with differences in GIs. Trees with high ResSA were also those with high GIs (Fig. 2). This trend was reported on Mont Ventoux during the period 1950–2000 (Fig. 2a, c) but was less clear on Issole, where only the GI of trees with a ResSA > 1.2 was higher than the GI of the others and not significant in Vésubie (Fig. 2b).

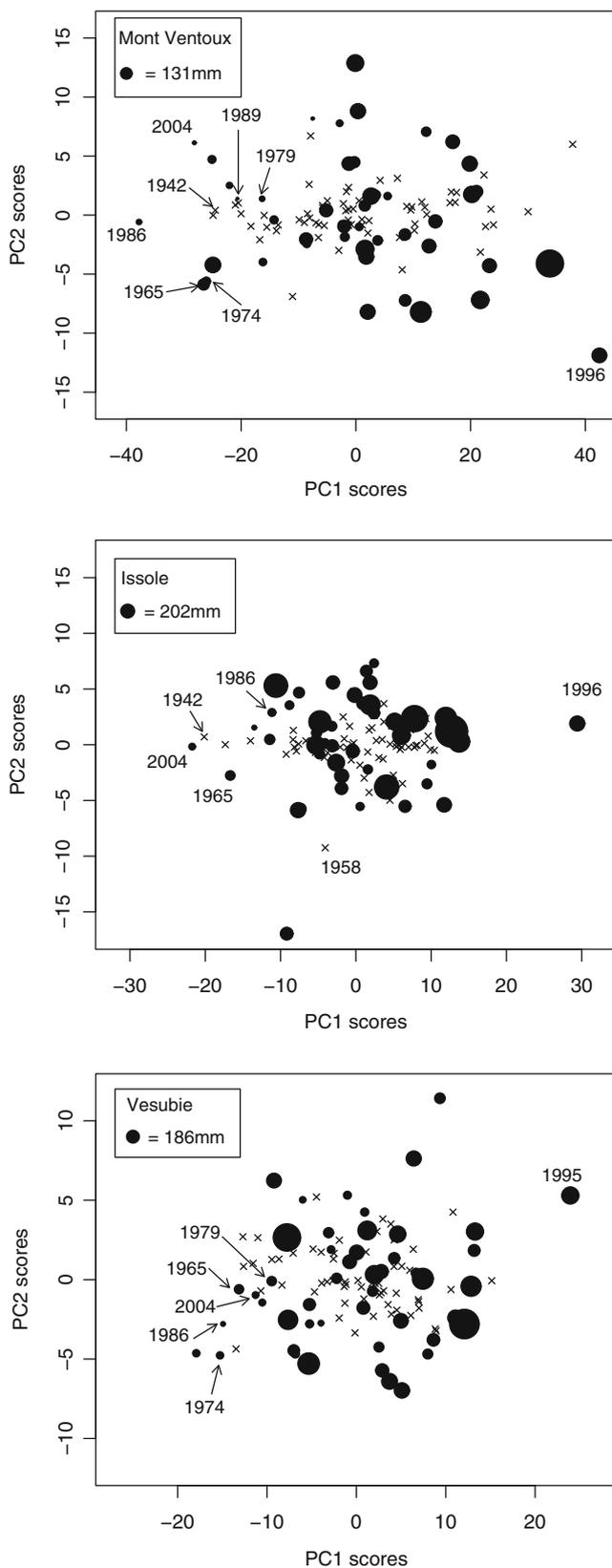
Approximately 10 %, 50 % and 30 % of the trees sampled in Ventoux, Issole and Vésubie, respectively, displayed a crown defoliation and/or discoloration rate above 20 %. The relationship between crown condition and current radial growth differed among sites (Fig. 3). On Mont Ventoux and Vésubie, growth rates of dead trees (class 3) and severely damaged trees (class 2) were lower than those of healthy (class 0) and moderately damaged trees (class 1; Fig. 3a, c). A different pattern was observed in Issole, where dead trees had the lowest growth rates, and trees with crown damages had unexpectedly higher growth rates than trees with healthy crowns (Fig. 3b). Similarly, on the three sites, trees with crown damages displayed different growth trends during their juvenile phase (Fig. 4) and reduced Gini indices than dead trees, indicating lower sensitivity to inter-annual

**Table 2** Regression coefficients of the linear models relating PC scores 1 (axis 1) and PC scores 2 (axis 2) and altitude, tree age and tree size

	Ventoux		Issole		Vésubie	
	Axis 1 (60.9 %)	Axis 2 (2.35 %)	Axis 1 (65.7 %)	Axis 2 (2.31 %)	Axis 1 (57.8 %)	Axis 2 (3.46 %)
Intercept	9.79e <sup>-01</sup> ****	-9.03e <sup>-01</sup> ****	9.31e <sup>-01</sup> ****	-2.22****	1.04****	-7.96e <sup>-01</sup> ****
Altitude	-2.38e <sup>-05</sup> NS	6.77e <sup>-04</sup> ****	1.79e <sup>-05</sup> NS	1.54e <sup>-03</sup> ****	-9.09e <sup>-05</sup> **	-5.72e <sup>-04</sup> ****
Age	-2.14e <sup>-03</sup> ****	2.05e <sup>-03</sup> ****	-1.69e <sup>-03</sup> ****	1.87e <sup>-03</sup> ****	-1.77e <sup>-03</sup> ****	3.45e <sup>-04</sup> NS
BA (mm <sup>2</sup> )	4.07e <sup>-07</sup> ****	-6.81e <sup>-07</sup> ****	2.17e <sup>-07</sup> *	-2.26e <sup>-07</sup> NS	2.76e <sup>-07</sup> ****	1.70e <sup>-07</sup> NS

NS not significant

\* $p < 0.1$ ; \*\* $p < 0.05$ ; \*\*\* $p < 0.01$ ; \*\*\*\* $p < 0.001$  (statistical significance)



environmental changes (Fig. 5c). Finally, there was no clear relationship between crown condition and sapwood area. Indeed, the sapwood area of dead trees was not significantly different to that of living trees ( $p>0.1$ ; Fig. 5a). In addition, in Issole, declining trees had a larger sapwood area than healthy trees, but this trend can be attributed to a tree size effect, as declining trees are the biggest ones on this site.

### 3.3 Characteristics of dead trees

Silver fir mortality rates were assessed using the forest inventory data. They reached important levels, especially on Mont Ventoux: on average, 20 % of the trees died during the last 10 years, up to 54 % on some plots. All tree sizes were affected, but medium-size trees were more predisposed to die (chi-squared test:  $p<0.001$ ; Table 1 and Fig. 6). On the other sites, the dieback process affected less than 10 % of the firs that were essentially small on Issole (chi-squared test:  $p<0.01$ ), while mortality rate was equally distributed with tree size in Vésubie (chi-squared test:  $p>0.1$ ). Our sampling was representative of this pattern except for a lack of large dead trees in Vésubie (Fig. 6).

The degree of competition had no impact on tree vitality on Mont Ventoux or Vésubie (Fig. 5b). In Issole, dead trees experienced a higher degree of competition than healthy trees, and declining trees showed the lowest competition indices.

According to the study site, dead trees showed different growth trends during their juvenile phase compared with living ones (Fig. 4). On Mont Ventoux, their growth rate was higher during the juvenile ages (until 35 years old; unpaired  $t$  test:  $p<0.05$ ), while the reverse pattern was found on Issole (greater than 12 years old;  $p<0.05$ ) and Vésubie (between 17 and 36 years old;  $p<0.05$ ). On each site, Gini indices were higher for dead trees than for living trees (Fig. 5c). This relationship was not biased by other explained variables, such as altitude, tree age and tree size, as the same result was obtained when removing all other effects (data not shown).

On Mont Ventoux, mortality rate clearly increased with the downward shift in altitude (Table 1). However, a high variability was also explained by variations in environmental conditions. The 16 plots located on the transect along a contour line on Mont Ventoux revealed that mortality rate ranged between 0 % and 54 % at the same altitude, and was not related to the slope and soil depth (linear regression model;  $p>0.1$ ). In Vésubie, 25 % of the firs located in Dves3 died, while this rate was below 5 % at the other sites (Table 1).

### 3.4 Climatic episodes triggering crown damages and tree death

On Mont Ventoux, the growth of severely declining trees was very low since the 1930s (Fig. 3a). Two slight divergences

**Table 3** Regression coefficients of the linear models relating PC scores 1 (axis 1) and PC scores 2 (axis 2) and rainfall (P), maximum (Tmax) and minimum (Tmin) temperatures during winter, spring and summer of the previous and current year

	PC1 scores			PC2 scores		
	Ventoux ( $R^2=0.51$ )	Issole ( $R^2=0.43$ )	Vésubie ( $R^2=0.35$ )	Ventoux ( $R^2=0.18$ )	Issole ( $R^2=0.22$ )	Vésubie ( $R^2=0.04$ )
Intercept	21.56 NS	5.09 NS	-16.66****	-16.01 NS	9.45**	1.73 NS
PC1 score, $n-1$	-0.19*	-0.30**	-0.35***	-0.06 NS		
P end summer, $n-1$		0.03 NS	0.03**	-0.01 <sup>NS</sup>		
Tmax end summer, $n-1$	-2.84***	-2.43**		-0.55 NS		
P winter		0.02*				-0.01*
Tmax winter				-1.34 NS	1.61***	
P spring		0.06**	0.02 NS			
Tmax spring					-1.78****	
Tmin spring	3.80**					
P summer	0.10****	0.04***	0.05***			
Tmax summer		1.24 NS		1.41***		

Variables from the previous year were indicated using  $n-1$ . The best linear models were chosen by AIC in a stepwise algorithm

NS not significant

\* $p<0.1$ ; \*\* $p<0.05$ ; \*\*\* $p<0.01$ ; \*\*\*\* $p<0.001$  (statistical significance)

occurred in 1979 and 1989, when decreases in GIs of dead trees were stronger than the one of the other trees. The year 1942 emerged regardless growth trends of trees with different ResSA (Fig. 2a). Afterwards, differences in GIs increased until the end of 1990s, when the GI curves of trees with ResSA<1.2 began to converge.

In Issole, considering crown damage classifications, temporal drops among GI curves occurred in 1942 (Fig. 3b), and in the early 1960s (1958 to 1965) which was confirmed by focusing on GI curves from different ResSA groups (Fig. 2b).

In Vésubie, dead trees exhibited lower GIs since the 1940s (Fig. 3c). No strong temporal drops were revealed in the analysis, except a decline in GIs of severely declining trees between 1974 and 1980 reaching a similar growth level than the one of dead trees. GI curves of trees with ResSA>1.2 diverged from those with ResSA<0.8 during the early 1960s, and in 1997 towards trees whose ResSA ranged between 0.8 and 1.2 (Fig. 2c).

As revealed by PCA, these years were mostly strong negative pointer years due to low amount of rainfalls during summer (Fig. 1). On Mont Ventoux, convergences or divergences between curves occurred in 1942, 1965, 1979 and 1989 when the PC1 scores were, respectively, the eighth, third, 16th and 11th lowest values of the twentieth and twenty-first centuries. In Issole, the years 1942, 1965 (second and fourth rank on PC1) and 1958 (second lowest value on PC2) emerged out of the analysis, while the years 1974, 1979 and 1997 (second, 13th and 20th on PC1) seemed to have an impact on tree decline on Vésubie.

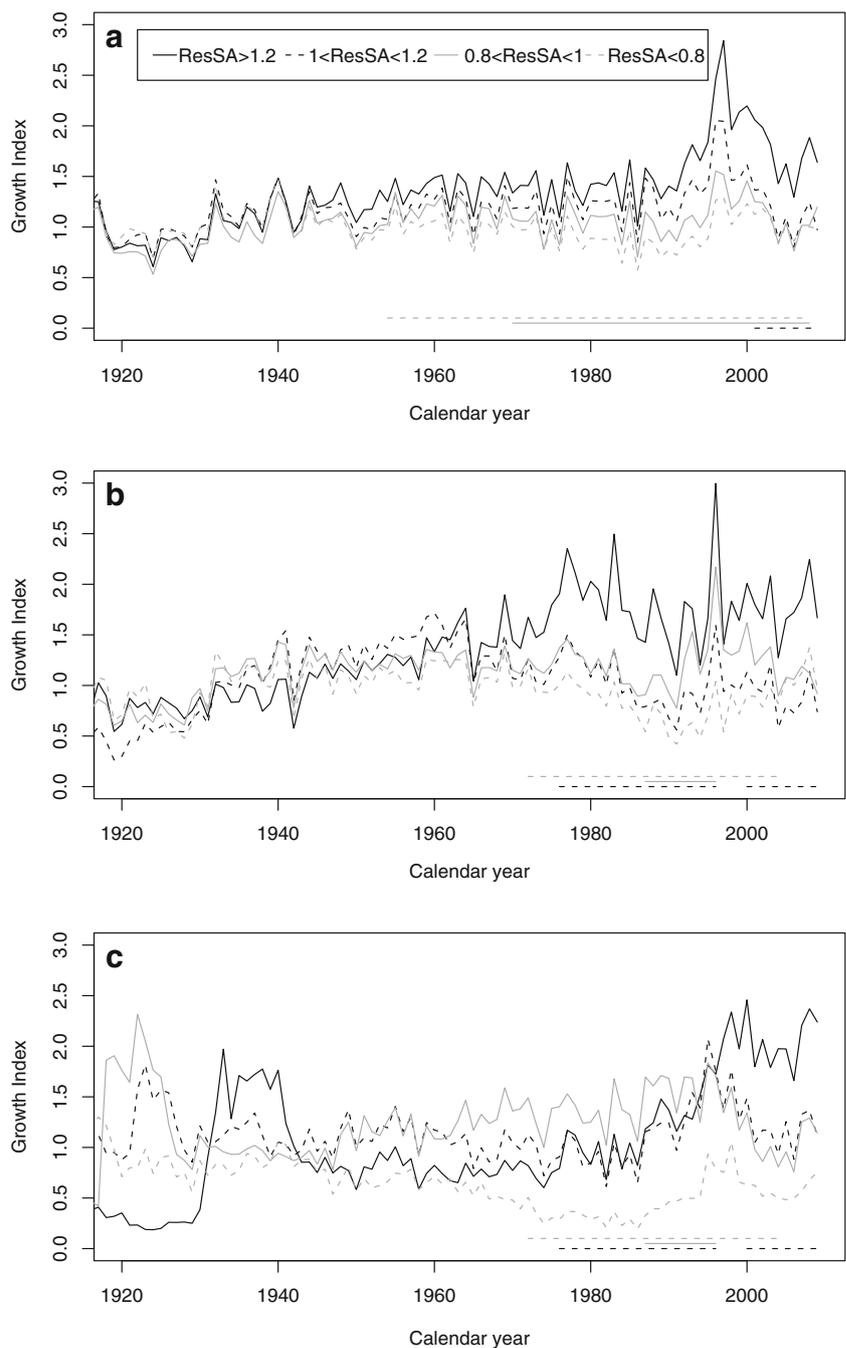
## 4 Discussion

### 4.1 Indicators of tree vitality

Recent tree radial growth is commonly used as an indicator of tree vitality and to predict tree mortality (Dobbertin 2005). On Mont Ventoux, we recently showed that the prediction accuracy of tree mortality models based on dendrochronological data was above 80 % (Cailleret 2011). GIs were studied instead of BAI as they consider the quantity of carbon needed to maintain metabolism, which mostly depends on tree size, and they better predict tree mortality (Chao et al. 2008; Cailleret 2011). GIs before death were at lower levels than GIs of living trees, but the timing of growth divergence differed. On Mont Ventoux, the divergence started approximately 30 years ago, while at Issole and Vésubie, it respectively started 60 and 70 years ago. Moreover, even if GIs were very low, silver fir can survive; this report was often made under dense canopies where young seedlings have needle traits to tolerate shade (Robakowski et al. 2004) and is likely when a tree grows on a very shallow soil.

After removing age and size effects, sapwood area (SA) discriminated trees with different current and past growth levels. However, surprisingly, there were no differences in SA between dead and living trees or between healthy and declining trees. As perchloric acid reveals heartwood, its use is reliable when the wood not transformed in heartwood (i.e. sapwood) really contains carbohydrates and is conducting sap. However, in the case of a rapid decline of carbon reserves and large

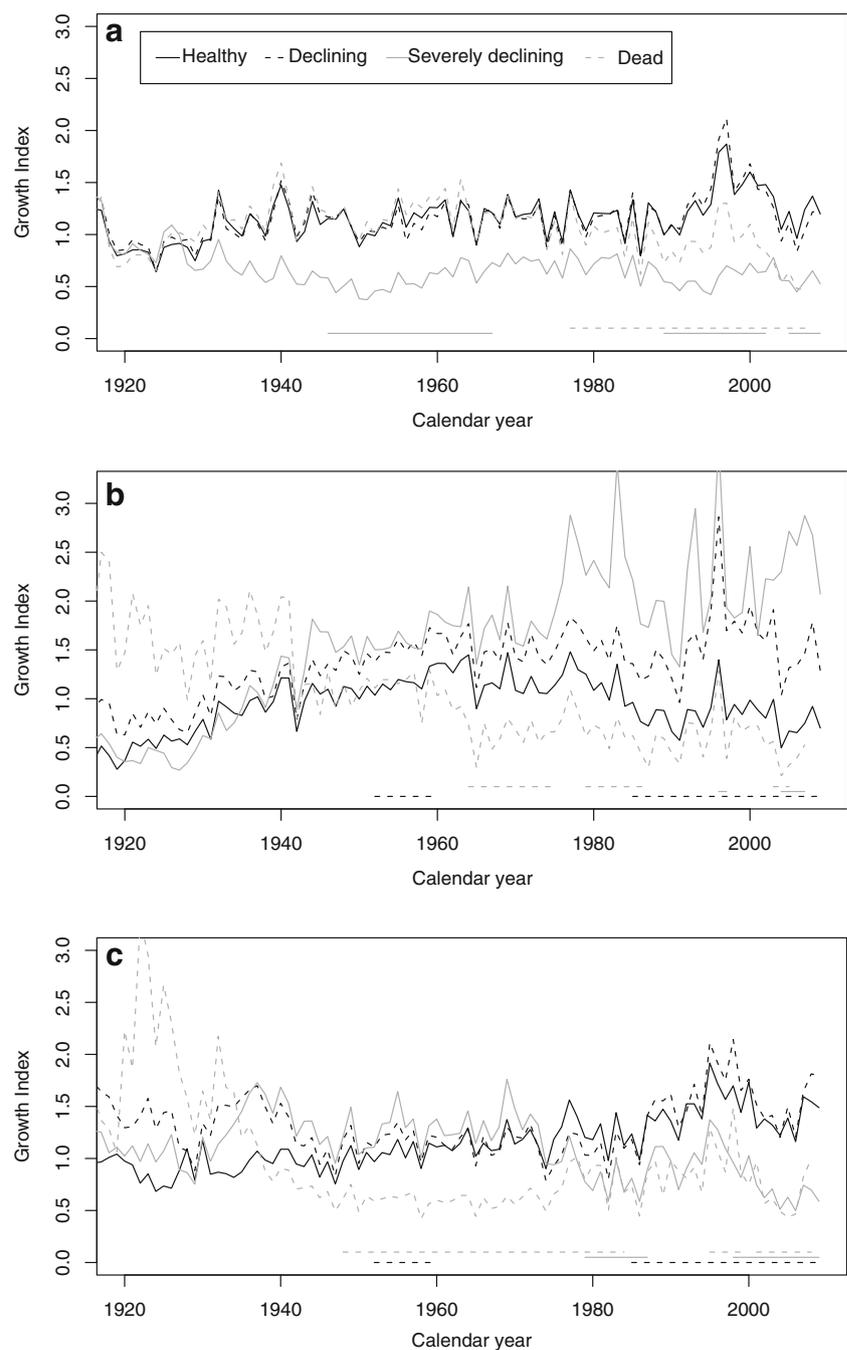
**Fig. 2** Time course of growth indices for trees with different sapwood areas on Mont Ventoux (a), Issole (b) and Vésubie (c). *Solid black line:* ResSA>1.2; *dashed black line:* 1<ResSA<1.2; *solid grey line:* 0.8<ResSA<1; *dashed grey line:* ResSA<0.8. *Horizontal bars* indicate significant differences between each class of crown damage and healthy trees (unpaired *t* test; *p*<0.1)



xylem embolism, heartwood formation may slow down, and the sapwood area may have been overestimated by perchloric acid. If this method can be used in the case of long-term growth declines (Becker 1987), other methods may be preferred when rapid tree dieback occur according to the aim of the study. For sap flow analysis, the sapwood length, i.e. the length of functional xylem, should be measured visually or using physical methods. The area of wood that contains carbohydrates should be analysed using specific reagents, such as Lugol for testing starch.

In our study, crown condition was not obviously related with tree radial growth. The dates when GI curve dropped differed between crown condition classes. Additionally, on Mont Ventoux, GI decreased with increasing crown damages, while the reverse trend was found in Issole. Leaf area deficit causes a reduction in carbon assimilation and is detrimental for a quick recovery of efficient crown development after a complete refilling of water resources (Limousin et al. 2009). However, it also can occur as an avoidance mechanism to maintain a favourable water balance by reducing transpiration and can induce higher growth efficiencies (per square metre

**Fig. 3** Time course of growth indices for trees with different crown condition on Mont Ventoux (a), Issole (b) and Vésubie (c): healthy trees (class 0; solid black line), declining trees (class 1; dashed black line), severely declining trees (class 2; solid grey line) and dead trees (class 3; dashed grey line). Horizontal bars indicate significant differences between each class of crown damage and healthy trees (unpaired *t* test;  $p < 0.1$ )

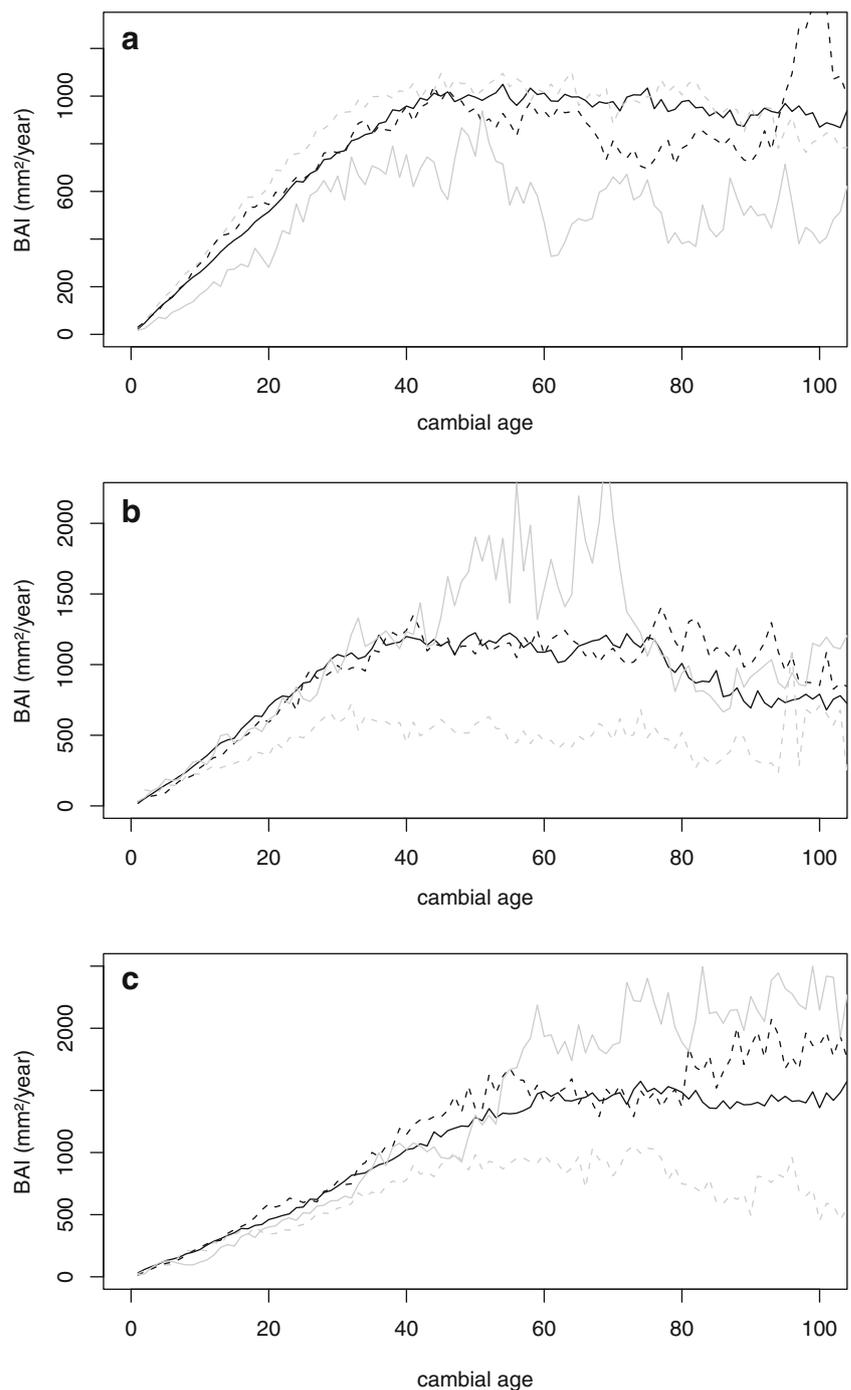


total leaf area; Kaufmann 1996). Even if crown damage is often related to the probability of tree mortality (Dobbertin and Brang 2001), severely declining trees showed a different GI evolution with time than dead trees, indicating that decline and mortality processes can be dissociated. Dead trees would not necessarily be those that had the most crown damages. Tree crown condition can be assumed to be a good indicator of the evolution of tree vitality with time (temporal analysis). However, comparing trees with different crown damages did not reveal differences in tree vitality or vulnerability to die-back (spatial analysis). Recent whole-tree architectural studies

revealed that drought effects and post-drought recovery differed according to branch vigour and position within the crown (Girard et al. 2012; Vennetier, personal communication). We suggest that protocols of crown condition assessment should integrate these results for a better accuracy, for instance by focusing only on the active part of the crown (one-third upper part).

For a better reliability, tree vitality should be assessed using structural and functional traits, such as xylem embolism vulnerability, the ratio between leaf area and root area and the ratio between carbon availability and demand. For

**Fig. 4** Evolution of tree basal area increment (BAI) with tree cambial age of trees with different crown conditions: healthy trees (class 0; *solid black line*), declining trees (class 1; *dashed black line*), severely declining trees (class 2; *solid grey line*) and dead trees (class 3; *dashed grey line*), on Mont Ventoux (a), Issole (b) and Vésubie (c)



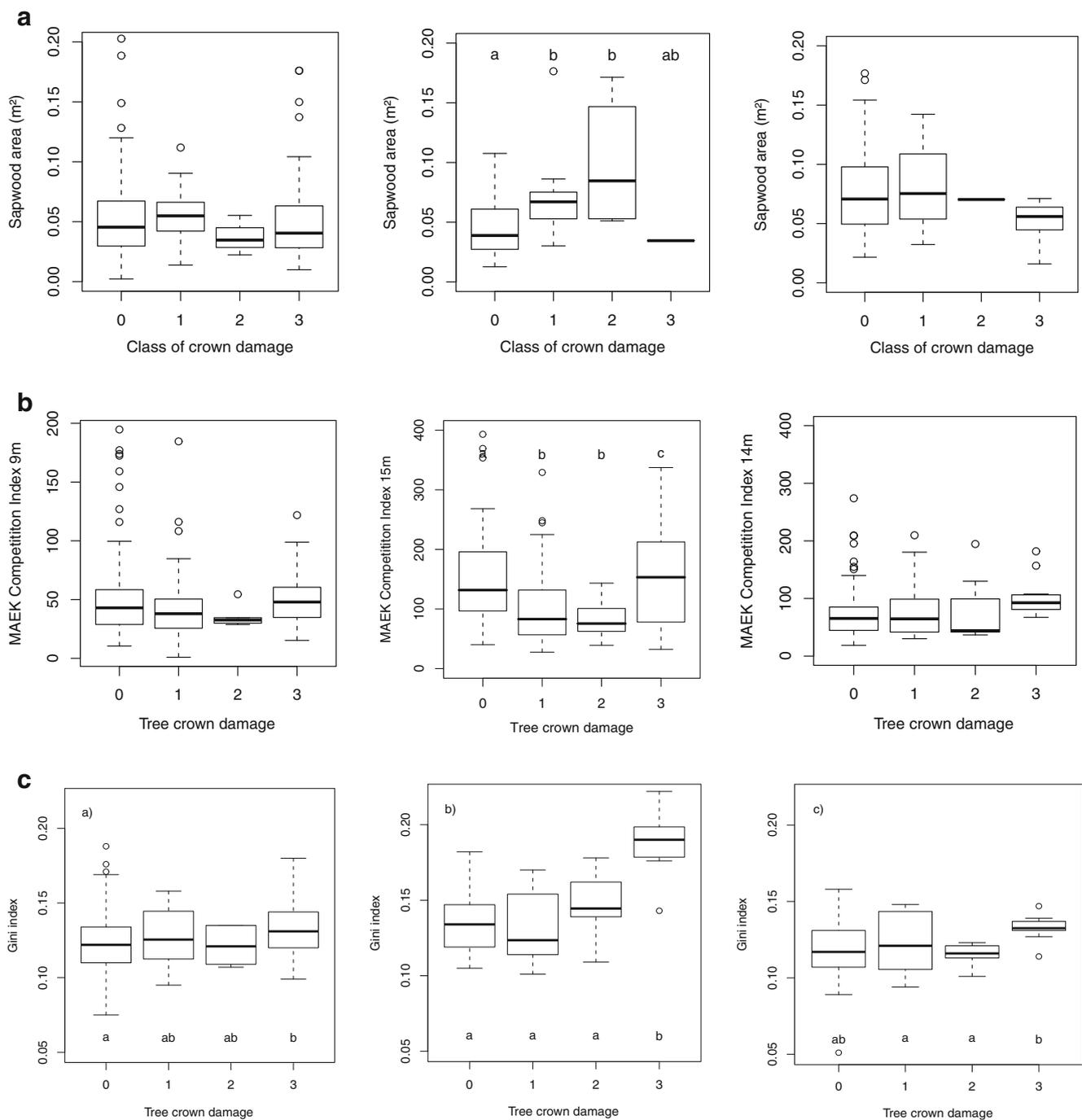
this aim, additional experimental data are needed to better understand the functional processes during drought by coupling whole-tree hydraulic and carbohydrate measurements (Mc Dowell 2011).

#### 4.2 Factors predisposing to mortality

In southeastern France, large areas of silver fir forests showed decline and dieback symptoms, but mortality was extremely patchy. The large heterogeneity in mortality rates

within a site and within a plot was explained by a combination of numerous stress factors that predispose trees to dieback.

Even if tree density was not sufficient to cause crown damages and tree mortality on Mont Ventoux and Vésubie, in Issole, dead trees were mainly small and experienced higher degree of competition than living trees. This result corresponds to a common trend in undisturbed stands (Coomes and Allen 2007) and is due to the decrease in light, water and nutrient availability. On the three sites, the



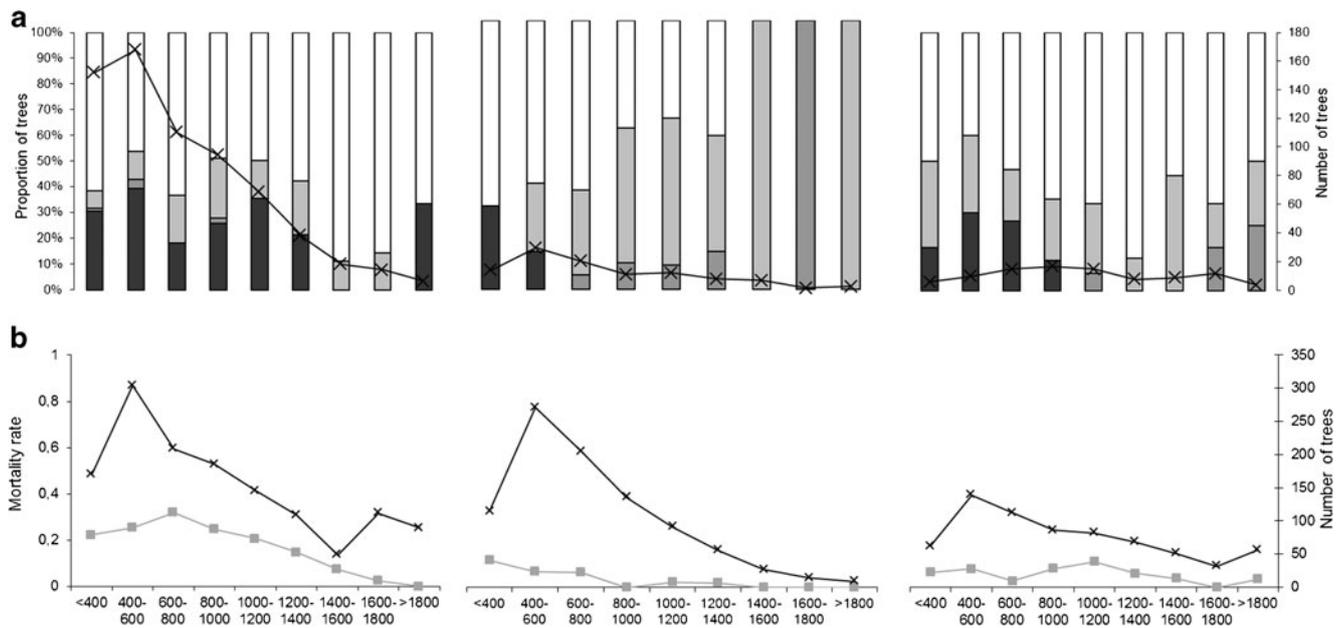
**Fig. 5** Relationship between tree crown damage and sapwood area (a), the relative degree of competition experienced by these trees ( $RCI_{on\_stumps}$ ; MAEK equation) (b), and the Gini index (c) on Mont

Ventoux (left), Issole (middle) and Vésubie (right). Different letters indicates significant differences between classes (Tukey HSD,  $p < 0.05$ )

strong relationship between the competition index and growth ( $R > 0.45$ ) was more due to competition for below-ground resources than for aboveground resources. Indeed, the optimised neighbouring radius used for the determination of competitors ranged between 9 to 15 m, which is quite high compared with the range 2–5 m found by Linares et al. (2009) on *A. pinsapo* using  $\Delta^{13}C_{wood}$  data. As silver fir of

Mont Ventoux exhibits an average crown projection diameter of approximately 5 m (Nourtier et al. 2012), the overlap rate can be neglected.

In the Mediterranean area, the main growth-limiting factor that can predispose trees to die is water availability. We found that the trees which are more prone to dieback are located in xeric conditions. They grow on specific topographic position



**Fig. 6** **a** (Top) Proportion of dead (black histogram), very declining (dark grey), declining (light grey) and healthy (white) trees for each circumference class, and the corresponding number of trees cored (black line with crosses) on Mont Ventoux (left), Issole (middle) and

Vésubie (right). **b** (Bottom) Number of firs mapped and measured during the forest inventory per circumference class (millimetres; black line with crosses), and corresponding proportion of dead firs (grey squares) on Mont Ventoux, Issole and Vésubie

(high slope in Dves3) or at low altitude (on Mont Ventoux). At larger spatial-scale, silver fir mortality in southeastern France was also observed to be more important on dry plots, i.e. at low altitude, on south-facing slopes and on dry edaphic conditions (e.g. high and convex slope; data not shown). This finding was confirmed on the three sites by focusing on the climate-growth relationships using PCA. PCA scores along the first axis were mainly related to rainfalls and high temperatures during the growing season. Inter-annual variability in radial growth was primarily explained by water availability during the vegetation period (Cailleret and Davi 2011). These results can be explained by a high vulnerability to drought-induced cavitation, which is counterbalanced by a rapid and complete stomatal closure when soil water potential decreases (Nourtier et al. 2012) and by an inhibition of cell division and enlargement (Zweifel et al. 2006). Moreover, a lack of water during summer also negatively impacts the growth of the following years by reducing both the quantity of carbohydrates stored in the tree and the fine root turnover, and by inducing needle loss (Bréda et al. 2006). Due to both rainfall and thermal gradients, altitude displayed a complex role. On Mont Ventoux, PCA revealed that high maximum temperatures during spring induced an increase in growth increment at high altitude but a decrease at low altitude. In high elevation sites, carbon assimilation was favoured due to an earlier budburst and higher photosynthesis rates as well as earlier cambium activation (Deslauriers et al. 2008), while drought stress intensity increased at lower

altitude due to stronger evapotranspiration rates. However, these trends were not found on the other sites.

Herbivorous insects and pathogens may also contribute to the loss of vitality and increased tree susceptibility to subsequent stress (e.g. drought). Although no herbivorous insects were reported on the study sites over the last decade, infestations by mistletoe (*Viscum album*) and bark beetles were especially important on Mont Ventoux and can partly explain the high mortality rates (Durand-Gillmann et al. 2012).

These long-term stress factors are often expressed as reduced tree growth rates contributing to an increase in tree vulnerability to dieback (Manion 1981; Pedersen 1998). This pattern was found in Issole and Vésubie, where dead trees showed very low growth rates. However, we also found on Mont Ventoux that dead trees had reached larger growth rates during the juvenile phase than living trees did. This trade-off between longevity and juvenile growth rate was not many observed within a species (Bigler and Veblen 2009). Fast growth rates during young ages can increase tree vulnerability to mortality, as it is related to high ratios of above- and below-ground biomass, reduced investment in secondary carbon compounds used for defence against pathogens (Loehle 1988) and higher respiration rates (Issartel and Coiffard 2011). Similarly, as revealed by tree-ring sensitivity to inter-annual changes in environmental conditions (e.g. climate), individuals with variable growth were more prone to die from drought than trees with more regular growth (Cailleret 2011; Suarez et al. 2004). These differences in trees

climatic sensitivity within a plot are likely caused by soil micro-heterogeneity and differences in tree size and ratios of above- and below-ground biomass.

The concept of predisposing factors, as described by Manion (1981), may be revised, as they differ between sites and even within a site. Predisposing factors induced higher tree vulnerability to drought events, which do not necessarily include weakening. Mortality can occur for trees with high level of defoliation and/or with low growth, but also for those without these symptoms. A better assessment of soil heterogeneity in depth is needed, for instance using geophysical methods (Nourtier et al. 2012). The structural traits of trees should also be integrated using allometric variables (total leaf area measurements using hemispherical photography, sapwood area) and xylem anatomy.

To conclude, this study highlights the importance of local site and stand conditions on mortality and decline processes, and reveals that both processes should be separated. As there were several factors predisposing mortality which differed among sites, different vitality indicators should be used. Relative radial growth trends, crown damage and sapwood area should be analysed, as these variables allowed the assessment of spatiotemporal changes in tree vitality, but they were not sufficient to assess the differences in tree vulnerability to dieback. An integration of functional processes is needed to understand the interaction of causes, for instance, by assessing the sensitivity of different carbon allocation rules to fine roots, growth, reproduction and defence as well as of different hydraulic parameters on tree mortality probability.

**Acknowledgments** The authors wish to thank N. Mariotte, W. Brunetto, F. Courdier, S. Rachedi and A. Fourrier for their contribution to field measurements and dendrochronological analyses. We are also grateful to anonymous reviewers and to the editors for valuable suggestions during the review process.

**Funding** M.C. received a Ph.D. student grant from the French Research National Agency (ANR), which also supported research funding in the frame of the DRYADE project (ANR-06-VULN-004).

## References

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage* 259:660–684
- Becker M (1987) Bilan de santé actuel et rétrospectif du sapin (*Abies alba* Mill.) dans les Vosges. Etude écologique et dendrochronologique. *Ann For Sci* 44:379–402
- Bigler C, Bugmann H (2003) Growth-dependent tree mortality models based on tree rings. *Can J For Res* 33:210–21
- Bigler C, Veblen TT (2009) Increased early growth rates decrease longevity of conifers in subalpine forests. *Oikos* 118:1130–1138. doi:10.1111/j.1600-0706.2009.17592.x
- Biondi F, Qeadan F (2008) Inequality in paleorecords. *Ecology* 89:1056–1067
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63:625–644. doi:10.1051/forest:2006042
- Bunn A (2008) A dendrochronology program library in R (dplR). *Dendrochronologia* 26:115–124. doi:10.1016/j.dendro.2008.01.002
- Cailleret M (2011) Causes fonctionnelles du dépérissement et de la mortalité du sapin pectiné en Provence. Thèse de doctorat de l'Université d'Aix-Marseille III
- Cailleret M, Davi H (2011) Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient. *Trees* 25:265–276. doi:10.1007/s00468-010-0503-0
- Chao KJ, Phillips OL, Gloor E, Monteagudo A, Torres-Lezama A, Vasquez-Martinez R (2008) Growth and wood density predict tree mortality in Amazon forests. *J Ecol* 96:281–292. doi:10.1111/j.1365-2745.2007.01343.x
- Cook ER (1987) The decomposition of tree-ring series for environmental studies. *Tree-Ring Bulletin* 47:37–59
- Coomes DA, Allen R (2007) Mortality and tree-size distributions in natural mixed-age forests. *J Ecol* 95:27–40
- Deslauriers A, Rossi S, Anfodillo T, Saracino A (2008) Cambial activity, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree Physiol* 28:863–871
- Dobbertin M, Brang P (2001) Crown defoliation improves tree mortality models. *For Eco Manage* 14:271–284
- Dobbertin M (2005) Tree growth as indicator of tree vitality and tree reaction to environmental stress: a review. *Eur J For Res* 124:319–333. doi:10.1007/s10342-005-0085-3
- Dreyer E, Fichter J, Bonneau M (1994) Nutrient content and photosynthesis of young yellowing Norway spruce trees (*Picea abies* L. Karst.) following calcium and magnesium fertilisation. *Plant Soil* 160:67–78
- Durand-Gillmann M, Cailleret M, Boivin T, Nageleisen LM, Davi H (2012) Individual vulnerability factors of silver fir (*Abies alba* Mill.) to parasitism by two contrasting biotic agents: mistletoe (*Viscum album* L. ssp. *abietis*) and bark beetles (Coleoptera: Curculionidae: Scolytinae) during a decline process. *Ann For Sci*. doi:10.1007/s13595-012-0251-y
- Esper J, Cook ER, Krusic PJ, Peters K, Schweingruber FH (2003) Tests of the RCS method for preserving low-frequency variations in long tree-ring chronologies. *Tree Ring Res* 59:81–98
- Girard F, Vennetier M, Guibal F, Corona C, Ouarmim S, Herrero A (2012) *Pinus halepensis* Mill. crown development and fruiting declined with repeated drought in Mediterranean France. *Eur J Forest Res* 131:919–931. doi:10.1007/s10342-011-0565-6
- Granier A (1981) Etude des relations entre la section du bois d'aubier et la masse foliaire chez le Douglas (*Pseudotsuga menziesii* Mirb. Franco). *Ann For Sci* 38:503–512
- Hoch G, Richter A, Körner C (2003) Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ* 26:1067–1081
- Holmes RL (1994) Dendrochronology program manual. Laboratory of Tree-Ring Research, Tucson
- Issartel J, Coiffard C (2011) Extreme longevity in trees: live slow, die old? *Oecologia* 165:1–5
- Kaufmann MR (1996) To live fast or not: growth, vigor, longevity of old-growth ponderosa pine and lodgepole pines. *Tree Physiol* 16:139–144
- Limousin JM, Rambal S, Ourcival JM, Rocheteau A, Joffre R, Rodriguez-Cortina R (2009) Long-term transpiration change with

- rainfall decline in a Mediterranean *Quercus ilex* forest. *Global Change Biol.* doi:10.1111/j.1365-2486.2009.01852.x
- Linares JC, Camarero JJ (2011) Growth patterns and sensitivity to climate predict silver fir decline in the Spanish Pyrenees. *Eur J For Res.* doi:10.1007/s10342-011-0572-7
- Linares JC, Delgado-Huertas A, Camarero JJ, Merino J, Carreira JA (2009) Competition and drought limit the response of water-use efficiency to rising atmospheric carbon dioxide in the Mediterranean fir *Abies pinsapo*. *Oecologia* 161:611–624. doi:10.1007/s00442-009-1409-7
- Loehle C (1988) Tree life history strategies: the role of defenses. *Can J For Res* 18:209–22
- Manion PD (1981) *Tree disease concepts*. Prentice-Hall, Inc, Englewood Cliffs
- Martin GL, Ek AR (1984) A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *For Sci* 30:731–743
- Mc Dowell N (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol* 155:1051–1059
- Nourtier M, Cailleret M, Yingge X, Chanzy A, Davi H (2012) Transpiration of silver fir (*Abies alba* Mill.) during and after drought in relation to soil properties in a Mediterranean mountain area. *Ann For Sci.* doi:10.1007/s13595-012-0229-9
- Pedersen BS (1998) The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. *Ecology* 79:79–93
- Robakowski P, Wyka T, Samardakiewicz S, Kierzkowski D (2004) Growth, photosynthesis, and needle structure of silver fir (*Abies alba* Mill.) under different canopies. *For Ecol Manag* 201:211–227. doi:10.1016/j.foreco.2004.06.029
- Somot S, Sevaut F, Déqué M, Crépon M (2008) 21st century climate change scenario for the Mediterranean using a coupled atmosphere–ocean regional climate model. *Global Planet Change* 63:112–126
- Suarez ML, Ghermandi L, Kitzberger (2004) Factors predisposing episodic drought-induced tree mortality in *Nothofagus*—site, climatic sensitivity and growth trends. *J Ecol* 92:954–966
- Tsopelas P, Angelopoulos A, Economou A, Soulioti N (2004) Mistletoe (*Viscum album*) in the forest of Mount Parnis, Greece. *For Ecol Manag* 202:59–65
- Van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009) Widespread increase of tree mortality rates in the Western United States. *Science* 323:521–524
- Zweifel R, Zimmermann L, Zeugin F, Newbery DM (2006) Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J Exp Bot* 57:1445–1459. doi:10.1093/jxb/erj125