esa ECOSPHERE

Disentangling the factors driving tree reproduction

Hendrik Davi,[1,†] Maxime Cailleret,[2] Gwendal Restoux,[3,4] Annabelle Amm,[5]
Christian Pichot,[1] and Bruno Fady[1]

[1]*Ecologie des Forêts Méditerranéennes, UR 629, INRA, URFM, Domaine Saint Paul, Site Agroparc, F-84914, Avignon, Cedex 9, France*
[2]*Forest Ecology, Department of Environmental Sciences, ETH Zurich, ETH-Zentrum, CHN G77,*
Universitätstrasse 16, CH-8092, Zürich, Switzerland
[3]*AgroParisTech, 16 rue Claude Bernard, F-75231, Paris 05, France*
[4]*INRA, UMR GABI, F-78350, Jouy-en-Josas, France*
[5]*GIP ECOFOR, 42, rue Scheffer, 75116, Paris, France*

Citation: Davi, H., M. Cailleret, G. Restoux, A. Amm, C. Pichot, and B. Fady. 2016. Disentangling the factors driving tree reproduction. Ecosphere 7(9):e01389. 10.1002/ecs2.1389

Abstract. Seed production is a strong indicator of plant fitness and plays a major role in population dynamics. However, the environmental and endogenous factors driving seed production are still poorly described and are often hard to disentangle. Consequently, we combined principal components analysis and mixed-effects linear models that can consider the multicollinearity of the explanatory variables and quantify their respective influence on the spatio-temporal variability in reproduction. We applied this method to analyze the relationships between cone production in *Abies alba* Mill. trees (6829 individual reports of cone production). We estimated the relationships between cone production and climate, elevation, tree size (diameter and height), age, crown defoliation rate, and past radial growth. We found that the distribution of annual cone production was highly skewed; 21% of the trees did not produce any cones, whereas 3.7% produced more than 100 cones in a single year. Among the endogenous factors, tree size explained 57% of the variation in cone production with large trees being the most productive. Low radial growth rates in previous years were mostly associated with higher cone production (14% of the variation), while elevation and crown defoliation had non-monotonic effects on reproduction. Finally, years of high cone production were strongly correlated with the difference between the April temperatures of the two previous years and were also associated with a dry spring 2 yr prior to cone production followed by a humid spring the previous year. These results highlight the complexity of the abiotic and biotic factors involved in reproduction and their respective and interactive influence on the interannual and interindividual variability in cone production.

Key words: *Abies alba*; cone; growth; mixed model; principal components analysis; reproduction; ring width; silver fir.

Received 8 December 2015; accepted 25 February 2016. Corresponding Editor: D. P. C. Peters.

† **E-mail:** hendrik.davi@avignon.inra.fr

INTRODUCTION

Understanding how populations will cope with global change is a major topic in ecology and evolution. The changes in climatic conditions forecasted over the next decades should induce shifts in the potential distribution of species due to the combined contraction and expansion of their habitats at their dry/hot and cold/wet edges, respectively (e.g., Morin et al. 2008). In addition to the role of interspecific interactions, the discrepancies between potential and realized distributions of species will depend on the ability of populations to (1) tolerate new environmental conditions through phenotypic plasticity, (2) genetically adapt to new environments through natural selection, and (3) migrate to track their climatic niches. The latter two abilities partially rely on seed production, which affects population regeneration and maintenance (Clark et al.

2007). In trees, rapid migration is likely to occur through rare, long-distance dispersal events (Petit et al. 1997, Clark et al. 2007), so if more seeds are produced, long-distance dispersal events will be more likely and lead to rapid rates of expansion, such as those that followed the last glaciation (Clark 1998). On the other hand, the ability of individuals to adapt to new climatic conditions depends on the natural selection of the most fit phenotypes, with high reproductive success thanks to a large production of pollen and seeds (Amm et al. 2012). Thus, the characterization of the determinants of the variation in seed production, both in time and in space, is critical if ecologists aim at better understanding and predicting forest dynamics (Clark et al. 1999), especially in the context of a changing climate, which will also affect tree physiological processes (Davi et al. 2006).

One important issue, which is often neglected despite its major effect on both tree physiology and the evolution of populations, is the variation in seed production among individual trees (Lamontagne and Boutin 2007). Indeed, the interindividual variability in seed production during a given year can be considerable and as high as two orders of magnitude (Dohrenbusch et al. 2002, Krouchi et al. 2004). This variation can be either due to the differences in microenvironmental conditions, such as light, water availability, and microclimate, or to endogenous factors, such as tree size, age, or vitality (e.g., recent growth or crown defoliation). These effects are often difficult to disentangle (Calama and Montero 2007, Thabeet et al. 2009). For instance, dominant trees have larger crowns that can hold a higher number of cones, but they also have more access to light and water resources and thus generally produce more seeds (Greene and Johnson 1994). Hence, a positive relationship is often found between tree size and absolute seed production (e.g., Amm et al. 2012), which serves as a basis for allometric models that predict annual reproductive biomass based on standing aerial biomass (e.g., the two-thirds power relationship in Niklas and Enquist 2003). Another example is the confounding effects of size and age on reproductive investment, as trees tend to produce more seeds as they become older (but also bigger; Debain et al. 2003, Viglas et al. 2013). However, these positive relationships can be altered by other factors such as competition intensity (Haymes and Fox 2012) or tree vitality (Innes 1994). Indeed, a trade-off may occur between the carbon allocated to growth and reproduction as there is a direct cost for the provisioning of pollen and seeds and accessory costs incurred for seeds to successfully mature and disperse (Obeso 2002, Lord and Westoby 2006). The presence of this trade-off has been discussed at the interspecific scale (Bazzaz et al. 1987, Barringer et al. 2013), but less so within species (but see Linhart and Mitton 1985 or Koenig and Knops 1998) despite its high influence on adaptive capacity.

Another important issue concerns the variation in reproduction between years. Masting (or mast-seeding) is a synchronized event of high seed production that occurs intermittently over many years, which is of considerable importance to forest management and has been extensively explored by ecologists (e.g., Isagi et al. 1997, Koenig and Knops 2000, Kelly and Sork 2002, Mutke et al. 2005, Kelly et al. 2013). Masting is now widely recognized as an adaptive reproductive strategy based on two non-exclusive mechanisms that can lead to greater reproductive success in populations of masting trees (Kelly and Sork 2002, Piovesan and Adams 2005). First, the synchronous production of seed crops may promote reproductive success through positive density-dependent effects on pollination (i.e., synchronous investment in male and female functions during mast years; Isagi et al. 1997), and empirical evidence from recent studies supported this hypothesis (Rapp et al. 2013, Moreira et al. 2014). Second, masting could also be an evolutionary response that controls the abundance of seed predators by severely limiting the resources available during consecutive years (Janzen 1971, Silvertown 1980, Lalonde and Roitberg 1992). The role of climate in masting is a matter for debate. Kelly et al. (2013) recently argued that climate is an environmental cue used by trees to synchronize their flowering. In contrast, others have argued that temperature is directly related to masting (Pearse et al. 2014) because years with favorable conditions are required for trees to establish sufficient carbohydrate reserves to produce seeds (Henkel et al. 2005). Furthermore, several climatic factors have been found to explain the variation in seed production. For example, drought during the early part of the preceding summer is a good predictor of masting in *Fagus sylvatica* and *Fagus grandifolia*, especially when preceded by a moist and cool summer 2 yr prior (Piovesan and Adams 2001). Similarly, Kelly et al. (2013) found that the difference in temperature between the two previous summers predicted seed crops better than the temperature of a given year.

The aim of this study was to assess the effects of endogenous (tree size, age, past growth, and crown defoliation) and environmental (spatial and temporal variation in climatic conditions) variables on seed production in natural populations, considering the variation in seed production at different levels, from individuals to populations, in both time and space. We focused on the forest tree *Abies alba* Mill., whose genus exhibits particularly strong masting behavior (Houle 1999, Politi et al. 2011). The cone production, as a proxy for seed production, of over 2000 trees was recorded annually from 1998 to 2014 at four sites in the southwestern French Alps. We then analyzed the variation in cone production with respect to climatic, altitudinal, and endogenous variables to identify the key determinants of reproductive output in forest trees.

Materials and Methods

Study species

Silver fir (*Abies alba* Mill.) is an evergreen conifer that covers a large area of the European mountains and is highly sensitive to edaphic and atmospheric drought in the summer as well as intense frost in the winter (Cailleret and Davi 2011). It is a monoecious species; that is, each tree bears male flowers at the bottom of the crown and female flowers at the top of the crown, and it is characterized by cone masting behavior. Cone growth lasts for 1 yr from the formation of reproductive buds to the opening of the cone, which contrasts with other conifers (e.g., 2 yr for *Cedrus* sp. and 3 yr for some *Pinus* sp.). Pollen is produced by yellow male flowers during vegetative budburst in early May (Davi et al. 2011). Cones are fertilized following pollination and become mature from late August to early September. On Mont Ventoux, cone length and dry weight averaged 13 cm and 13.2 g, respectively, and held 249.6 seeds on average (C. Pichot, *unpublished data*).

Study sites

Our four sampling sites (from west to east: Ventoux, Lure, Issole, and Vésubie; Fig. 1) are located at the southwestern tip of the Alps in France, where silver fir encounters the xeric edge of its distribution range. The sampled trees belong to different populations, for which crown defoliation, annual radial growth, seed dispersal, and genetic diversity have been studied (Sagnard et al. 2002, 2010, Cailleret and Davi 2011, Amm et al. 2012, Cailleret et al. 2014). Although the studied stands are subject to similar bioclimatic conditions, that is, a mountain climate under

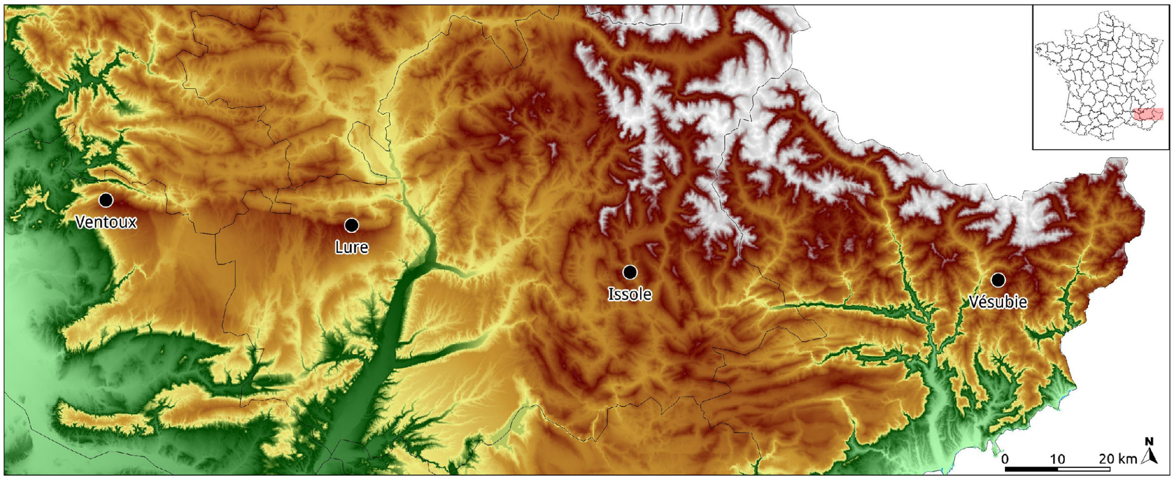

Fig. 1. Map of the four study sites.

Mediterranean influence, they experience different climatic conditions on average (Table 1). At intermediate altitude (approximately 1200 m) for the period from 1959 to 2013, the summer climate was wetter on Lure and Issole (187 and 189 mm, respectively, from June to August) than on Mont Ventoux (173 mm) and Vésubie (140 mm). Vésubie was also characterized by a higher mean annual temperature (+1.45°C, +1.78°C, and +1.22°C than Issole, Lure, and Ventoux, respectively; Table 1). Similarly, strong differences in soil properties among sites induced the variation in the amount of water available during the growing season. In Vésubie, the mother bedrock is sandstone schist, whereas it is calcareous clay in Issole and entirely calcareous on Mont Ventoux and Lure with higher expected water infiltration.

Climate

We estimated temperature, precipitation, and relative humidity from two different sources. First, in 2007, HOBO Pro V2 microloggers (Onset Computer, Cape Cod, Massachusetts, USA) were placed at each sampling site, and they registered daily maximum and minimum temperatures, the average relative humidity, and total precipitation (Cailleret and Davi 2011). Second, we used climate data from the French weather service ("SAFRAN" data set from Meteo France; Vidal et al. 2010), which are available at an 8-km grid scale for the period from 1959 to 2013, to estimate the long-term climatic variables at each site. We used linear models with daily time steps to correct the SAFRAN data for the local climatic conditions based on the relationship between the observed HOBO data and the SAFRAN data for the period of overlap (i.e., 2007–2013).

Cone production data sets

In this study, we compiled nine cone production data sets: six from Mont Ventoux and one each from Lure, Issole, and Vésubie (see Table 1). Brown, ripened cones were always counted using binoculars at the end of the summer prior to seed release; aborted cones were not included. This visual counting is a good approximation of the total number of cones, although this number may be underestimated (LaMontagne et al. 2005). The data set covers the period from 1998 to 2014 without interruption, except for the year 2001.

Table 1. Average tree and climate characteristics from the nine data sets by region and site.

Characteristics	Unit	Ventoux Contrat	Ventoux P34	Ventoux Mont Serein	Ventoux CLT	Ventoux CET	Ventoux DET	Lure	Issole DET	Vésubie DET
Latitude	°	44.18	44.18	44.18	44.18	44.18	44.18	44.11	44.02	43.97
Longitude	°	5.28	5.24	5.25	5.24	5.24	5.24	5.82	6.48	7.36
Elevation range	m	1399–1442	1310–1310	976–1424	1108–1142	965–1524	995–1340	1152–1747	1108–1585	1078–1586
Climate station elevation	m	–	–	–	1120	–	1225	1200	1280	1240
Annual Tav	°C	–	–	–	8.40	–	7.46	7.23	6.90	8.68
Annual RH	%	–	–	–	73.76	–	77.66	74.37	71.89	70.96
Annual P	mm	–	–	–	1045	–	1020	1144	947	1003
Summer Tav	°C	–	–	–	16.38	–	15.30	15.84	15.25	16.35
Summer RH	%	–	–	–	71.25	–	72.70	69.34	69.05	70.64
Summer P	mm	–	–	–	177	–	173	189	187	140
dbh	cm	34.25	14.15	39.96	31.35	27.34	30.06	33.29	36.05	39.89
Height	m	15.59	–	13.99	14.54	12.69	14.51	13.18	20.65	26.64
Ring width	mm	2.83	3.59	1.3	1.26	1.54	1.52	1.95	1.46	1.78
Mean sensitivity		0.2	0.16	0.25	0.25	0.23	0.24	0.18	0.25	0.23
Crown defoliation	%	–	–	–	44.72	–	31.92	–	25.8	20.23

Notes: CLT, contour line transect; CET, continuous elevation transect; DET, discontinuous elevation transect; RH, relative humidity; P, precipitation; dbh, diameter at breast height. The climate stations for the DET sites were chosen to allow for comparisons between sites.

1. On Mont Ventoux, we first used data from three different stands, in which cones were counted every year from 1998 to 2007 (Restoux 2009). We sampled 746, 221, and 47 firs on the stands named "P34" (1310 m a.s.l.), "Contrat" (1418 m), and "Mont Serein" (between 976 and 1424 m), respectively. Second, the cones of 73 trees located on a continuous elevation transect (Ventoux CET from 965 to 1524 m) were counted in 2006 and 2007 (see Davi et al. 2011 for a description of the trees). Third, 129 trees located inside or near five 400-m^2 plots at different altitudes (995, 1020, 1117, 1247, and 1340 m, collectively called the discontinuous elevation transect or Ventoux DET) were identified and mapped, and the cones were counted every year from 2007 to 2014. Fourth, the cones of 243 trees located along a contour line transect (Ventoux CLT with an average elevation of 1120 m) were counted in 2007, 2008, and 2012.
2. Two other DET were studied in Issole and Vésubie (Issole DET and Vésubie DET), where 113 and 154 trees were sampled, respectively. Cones were counted in 2007, 2008, 2009, 2013, and 2014.
3. Finally, on Lure, we used one data set of 52 trees sampled between 1152 and 1747 m a.s.l., and the cones were counted from 1998 to 2006.

Endogenous variables

We measured the diameter at breast height (dbh) and height (H) of each tree using a Forester VERTEX III (Haglöf, Langsele, Sweden). Using binoculars, we assessed the crown defoliation rate in the late summer of 2007, 2008, 2011, 2012, 2013, and 2014 along the Ventoux DET; in 2007, 2008, 2012, 2013, and 2014 along the Ventoux CLT; and in 2007, 2008, 2013, and 2014 along the Issole DET and the Vésubie DET (details in Cailleret et al. 2014). The interannual variability and the intertree variability in annual radial growth were assessed using classical tree-ring width analysis. All of the trees included in the Ventoux DET, Ventoux CLT, Issole DET, and Vésubie DET data sets were sampled with an increment borer at breast height in 2009, whereas only a subsample of the trees located in P34, Contrat, Mont Serein, and Lure were sampled in 2007. Cores were prepared with a razor blade and scanned at 1200 dpi, and ring limits were identified using CooRecorder v5.3 semiautomatic software (see Cailleret and Davi 2011, Cailleret et al. 2014). To express the level and variance in annual radial growth and the asymmetry in the ring width distribution, we calculated the mean ring width (rw), the mean sensitivity (MS), and the skewness of the ring width distribution, respectively; MS was calculated after detrending the raw chronology using smoothing splines (dplR package in R). Tree-ring data were also used to assess cambial age (at breast height), and because the trees differed in age and not all of the cores were sampled in the same year, all these variables were estimated for the common period 1974–2003 (all trees were born in 1974 and many trees died after 2003 because of repeated droughts) (Cailleret et al. 2014).

Statistical analyses

First, we estimated the average cone production across years and the relationship between cone production and its coefficient of variation using the Ventoux data set. Using all the different data sets, we then estimated the Spearman correlation coefficient between years to test whether the high producers remained the same between years.

Because of the multicollinearity between the variables used to characterize tree structure or function (e.g., dbh and H), we performed a principal component analysis (PCA) to reduce the number of variables and thus to perform the regression analysis on independent variables. This was carried out using the FactoMine package in R (Lê et al. 2008) with the following variables (hereafter termed endogenous factors): dbh, H, age, crown defoliation rate, mean rw, skewness of the ring width series, and MS. We used the first four principal axes obtained from this PCA in the subsequent analyses. These axes correspond to the main sources of variation and represent the endogenous factors related to cone production. We performed two PCA: one for DEG data sets and one for CLT data sets.

Next, a generalized linear mixed model (Littell et al. 2006) was used to disentangle the effects of the endogenous factors (using the *lme4* R package; Bates et al. 2014); the random effect for the intercept was grouped by tree to consider that trees may have different cone production irrespective of the factors included here (e.g., genetic variability). We chose a logarithmic link function to account for the cone production distribution and a Poisson distribution to describe the error distribution. We compared the effects of each variable using *F*-values obtained by ANOVA.

Model 1:

$$\log(Y) \sim \mathrm{Pois}(\lambda)$$

$$\begin{aligned}\lambda_{ise} =& \alpha_1 \mathrm{Axis1}_i + \alpha_2 \mathrm{Axis2}_i + \alpha_3 \mathrm{Axis3}_i \\ &+ \alpha_4 \mathrm{Axis4}_i + \beta \mathrm{SITE}_s + \gamma \mathrm{YEAR}_y \\ &+ \delta(\mathrm{ELV}|\mathrm{SITE})_{es} + \mathrm{v} \times \mathrm{Tree}_{i\mathrm{Tree}}\end{aligned}$$

$$\mathrm{Tree} \sim N(0, \sigma^2)$$

where λ_{ise} is the annual number of cones produced by each tree.

On the Ventoux CLT data set, all trees are at same elevation, and thus, we created a generalized linear mixed model with only the endogenous factors.

Model 2:

$$\log(Y) \sim \mathrm{Pois}(\lambda)$$

$$\begin{aligned}\lambda_{ise} =& \alpha_1 \mathrm{Axis1}_i + \alpha_2 \mathrm{Axis2}_i + \alpha_3 \mathrm{Axis3}_i \\ &+ \alpha_4 \mathrm{Axis4}_i + \mathrm{v} \times \mathrm{Tree}_{i\mathrm{Tree}}\end{aligned}$$

$$\mathrm{Tree} \sim N(0, \sigma^2).$$

For the DET data sets (pooling the Ventoux, Vésubie, and Issole sites), both models 1 and 2 were used; the residuals of model 2 were plotted against the elevation of every site and year to identify any potential non-monotonic effects of elevation and the complex interactions between site, year, and elevation. Indeed, two different limiting factors may constrain reproduction at the two edges of the elevation gradient: low temperature at high elevations and drought at low elevations, their intensity varying among sites and years. According to the Ventoux CLT data set, the axes obtained from the PCA could differ slightly, especially because we excluded some variables (SITE for CLT and CET and ELV for CLT) from model 2.

The role of climate in the interannual variability in cone production cannot be accurately assessed with short-term data (< 5 yr), so we estimated the variability at Ventoux using all of the existing data sets. We derived a third model that included dbh as a single endogenous explanatory variable because dbh explained the most the interindividual variability in cone production (see outputs of models 1 and 2 in *Results*):

Model 3:

$$\log(Y) \sim \mathrm{Pois}(\lambda)$$

$$\lambda_{ise} = \alpha_1 \mathrm{dbh}_i + \alpha_2 \mathrm{YEAR}_y + \mathrm{v} \times \mathrm{Tree}_{i\mathrm{Tree}}$$

$$\mathrm{Tree} \sim N(0, \sigma^2).$$

We then estimated the Kendall correlation coefficient between the estimates associated with the effect of year (α_2) and 207 variables that characterize the climate 2 yr prior to the cone count ($n - 2$ and $n - 1$ obtained from the weather station located at 1225 m a.s.l.). These variables included different combinations of average, minimum and maximum temperature (°C), daily global radiation (MJ), mean and minimum relative humidity (%), and total precipitation (mm) over annual, seasonal, or monthly time steps. We also tested the differences between the monthly temperatures of the two previous years (see Kelly et al. 2013) and kept only the climatic variables significantly correlated with α_2 ($P < 0.05$).

RESULTS

Variability in cone production

Focusing on all data sets (i.e., 6829 individual reports of cone production), we found a higher interindividual heterogeneity in cone production (average annual coefficient of variation $\mathrm{CV}_{\mathrm{intertrees}} = 160\%$) than the interannual variation ($\mathrm{CV}_{\mathrm{interyears}} = 95\%$). $\mathrm{CV}_{\mathrm{intertrees}}$ ranged between 82% in 1998 and 294% in 2010 and was negatively related to the average annual cone production (< 25 cones per tree on average; slope = −5.55 and $P < 0.01$; Fig. 2, top right).

Annual cone production averaged 20.6 cones per tree, but the median was close to eight cones per tree due to the positive skew of the distribution; 21% of the trees did not produce any cone in a given year, whereas 253 trees (3.7%) produced more than 100 cones in a single year. These rates also changed over time as the percentage of trees without cones was below 2.5% in 2009 (a high production year with 61.61 cones per tree on average) and above 81.5% in 2010 (the year of lowest production with 1.72 cones

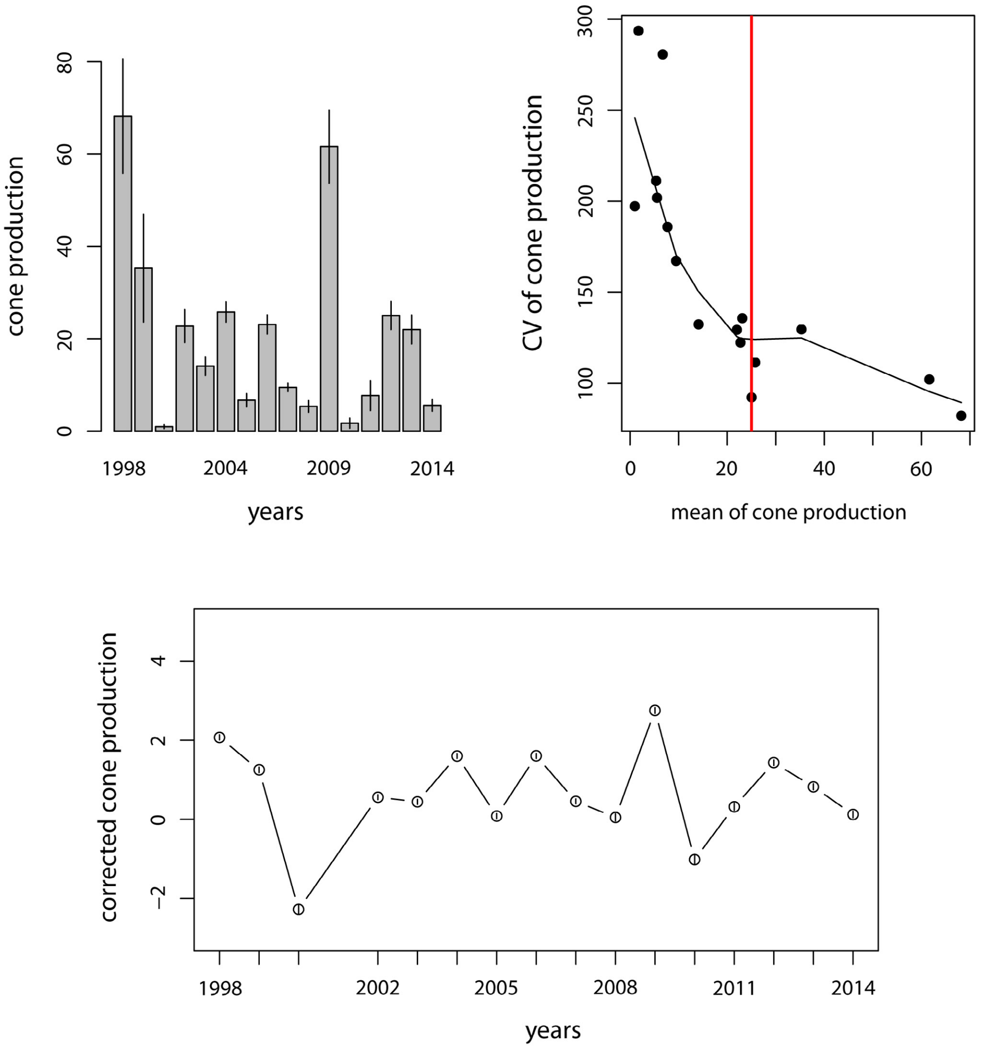

Fig. 2. Top left: average cone production across years in Mount Ventoux. Top right: the coefficient of variation (CV in %) in cone production vs. the average yearly cone production in Mount Ventoux (mean number from the count). Bottom: The coefficient associated with the effect of year on cone production in the model, including the effects of diameter at breast height on cone production (model 3; see text).

per tree on average). The high cone producers partly remained the same over time; for instance, cone production of trees from the DET data sets is correlated between both 2009 and 2013 mast years ($r^2 = 0.35$, $P < 0.01$), and between 2007 and 2014, both years of low production ($r^2 = 0.40$, $P < 0.001$).

Structure of the endogenous factors

The PCA of the endogenous factors revealed that 81.06% and 87.45% of the variation in cone production in the DET and CLT data sets, respectively, were explained by the first four axes (Fig. 3). In both data sets, tree dbh and height were the main components of the variability in the endogenous factors and were positively related to axis 1 (Fig. 3, $r = 0.85$ and $r = 0.88$ with dbh for the DET and CLT data sets, respectively). Mean rw was not related to tree size, but was negatively correlated with axis 2 (Fig. 3, $r = -0.7$ and $r = -0.61$ for the DET and CLT data sets, respectively). Finally, crown defoliation and the skewness index of rw distribution were the last components of the endogenous factors and were positively correlated

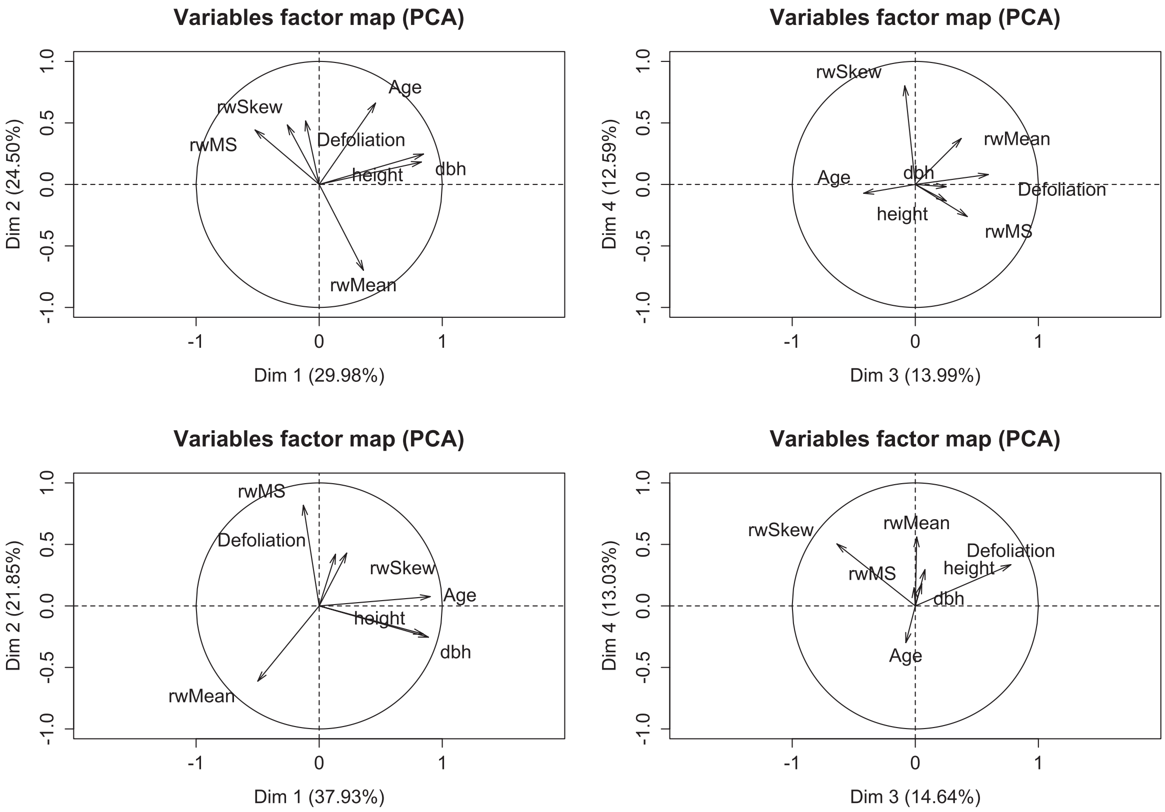

Fig. 3. Principal component analysis (PCA) of the (top) endogenous factors for trees in a three-site subsample (DET Ventoux, DET Vésubie, and DET Issole) and (bottom) the contour line transect (CLT Ventoux). Axis 1 vs. axis 2 is plotted on the left, and axis 2 vs. axis 3 is plotted on the right. The following endogenous factors were included: age, diameter at breast height (dbh), tree height (height), rate of crown defoliation (defoliation), mean ring width (rwMean), the mean sensitivity (rwMS), and the skewness of the ring width distribution (rwSkew).

with axis 3 (r = 0.59 and r = 0.78 for the DET and CLT data sets) and axis 4 (r = 0.80 and r = 0.50 for the DET and CLT data sets), respectively. Hereafter, we use the coordinates of the factors on the four PCA axes, which are named axis 1: size effect (+); axis 2: past growth (−); axis 3: defoliation (+); and axis 4: temporal heterogeneity of past growth (+).

Partitioning of the different effects on cone production

On the CLT data set (one site, same elevation), we used model 2 to disentangle the respective sources of variation in cone production (Table 2). The fixed effects (the effects of the endogenous variables and of the year) represented 60% of the total variance in the model, leaving 40% of the variability between trees unexplained. Tree size (axis 1; dbh and height) was the only variable significantly correlated with cone production, with a positive relationship revealing that the biggest/tallest trees produced more cones (Table 2). Tree size accounted for 30% of the total fixed effects, and the effect of the year explained the remaining 70%. We also compared the past growth of the trees producing low and high numbers of cones by separating young trees (< 82 yr old, i.e., the median of the age distribution) to old ones (> 82 yr old). For young trees, low cone producers exhibited lower growth rates in the past, but this effect was significant for only 1 yr (Fig. 4, top). For old trees, those producing high numbers of cones had higher growth rates between 1940 and 1979, but lower growth rates after 2000 (Fig. 4, bottom). For

Table 2. Summary of the results of model 2 (generalized linear mixed model) using the contour line transect data set (Ventoux CLT).

Effects	Variance	SD	Value	SE	Z	P	$\sqrt{F}$
Random effect (tree)	0.95	0.97					
Fixed effects	1.41	1.18					
Fixed effects							
Intercept			1.86	0.14	13.3	$< 2 \times 10^{-16}$	
Axis 1 (size)			0.30	0.04	6.9	$< 4 \times 10^{-12}$	7.47
Axis 2 (past growth)			0.06	0.08	0.7	0.50	0.31
Axis 3 (defoliation)			0.07	0.16	0.4	0.66	0.21
Axis 4 (skewness)			0.09	0.11	0.8	0.41	0.64
2008/2007			0.23	0.08	2.7	6.3×10^{-3}	
2012/2007			1.08	0.04	27.4	$< 2 \times 10^{-16}$	
2013/2007			0.60	0.05	11.7	$< 2 \times 10^{-16}$	17.80
2014/2007			−0.19	0.06	−3.0	$< 2 \times 10^{-16}$	

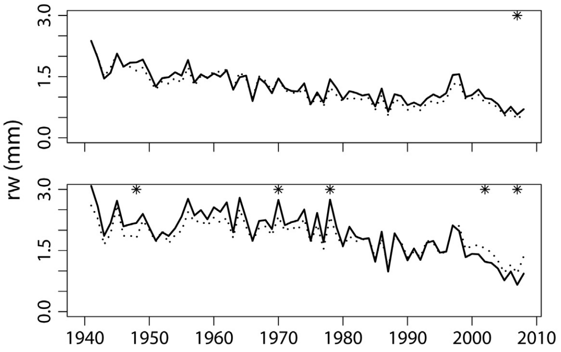

Fig. 4. Past ring width (rw in mm) of young (top) and old trees (bottom) producing low numbers (dashed line) and high numbers of cones (bold line) using the CLT data set. An asterisk indicates that the differences between low and high producers are significant.

this reason, the effect of past growth could be hidden when the entire period and both types of trees are considered, which explains why the effect of past growth was not significant using this data set and model 2.

The analysis of the DET data sets (three sites with five or six stands at different elevations) produced similar results (Table 3). When considering interindividual variability (model 1), tree size, elevation, and past growth were the main factors influencing cone production, and neither site nor axis 3 or axis 4 was significant. Among the endogenous variables, the positive effect of size corresponded to 57% of the variation, whereas the negative effect of past growth corresponded to 14%. The effect of elevation on cone production was nonlinear and changes among years and sites. For instance, in 2007, a non-mast year, cone production was significantly lower at high elevations in Ventoux, but significantly higher at high elevations in Issole and Vésubie (Fig. 5). During the mast year of 2013, there was only a slight effect of elevation with lower production in Issole at very high elevations.

We also observed non-monotonic relationships between defoliation and cone production by separating trees into different crown defoliation classes (Fig. 6). On the Ventoux CLT, the highest cone production was reported in trees with crowns that were 15–30% defoliated, while trees with 30–45% of defoliation were the most productive of the Ventoux DET, the Issole DET, and the Vésubie DET data sets.

Temporal variability

The interannual variability in cone production was examined by gathering all data sets from Ventoux and focusing on both (1) annual average cone production (Fig. 2, top left) and (2) coefficients associated with the year effect in model 3 that accounted for the dbh effects (Fig. 2, bottom). From 1998 to 2014, we recorded eight mast years with more than 20 cones per tree on average (1998, 1999, 2002, 2004, 2006, 2009, 2012, and 2013), two intermediate years (2003 and 2005), and 6 yr of low cone production (2000, 2007, 2008, 2010, 2011, and 2014).

The climate variables that correlated significantly with cone production included four monthly or seasonal variables calculated during the $n - 2$ yr (Table 4; maximum temperatures in

Table 3. Summary of the results of model 1 (generalized linear mixed model) using the three DET data sets (Ventoux DET, Vésubie DET, and Issole DET).

Effects	Variance	SD	Value	SE	Z	P	$\sqrt{F}$
Random effect (tree)	0.75	0.87					
Fixed effects	1.97	1.40					
Fixed effects							
Intercept			-5.64×10^{-1}	7.54×10^{-1}	−0.75	0.45	
Axis 1 (size)			4.56×10^{-1}	4.64×10^{-2}	9.83	$< 2 \times 10^{-16}$	8.55
Axis 2 (past growth)			8.34×10^{-2}	4.82×10^{-2}	1.73	0.08	2.08
Axis 3 (defoliation)			3.42×10^{-2}	6.81×10^{-2}	0.5	0.61	1.03
Axis 4 (skewness)			7.23×10^{-2}	5.59×10^{-2}	1.29	0.19	3.27
Site effect							4.82
Ventoux/Issole			2.18	1.38	1.58	0.11	
Vésubie/Issole			2.74	1.08	2.54	0.11	
Elevation effect							7.93
Elevation in Issole			2.38×10^{-3}	5.66×10^{-4}	4.2	2.71×10^{-5}	
Elevation in Ventoux			1.11×10^{-3}	8.50×10^{-4}	1.3	0.19	
Elevation in Vésubie			1.14×10^{-4}	5.31×10^{-4}	0.21	0.83	
Year effect							63.14
2008/2007			−1.49	3.08×10^{-2}	−48.26	$< 2 \times 10^{-16}$	
2009/2007			1.07	1.76×10^{-2}	60.66	$< 2 \times 10^{-16}$	
2013/2007			-6.66×10^{-2}	2.05×10^{-2}	−3.25	0.012	
2014/2007			−1.58	3.19×10^{-2}	−49.55	$< 2 \times 10^{-16}$	

February and April, precipitation in May, and relative humidity in July) and two monthly variables from the $n - 1$ yr (precipitation in May and minimum relative humidity in September). Years of high cone production were associated with (1) a cold winter and spring followed by a dry summer 2 yr before the cone crop of interest and (2) a humid spring and fall in the previous year. Finally, high difference between the April temperature 2 yr and 1 yr before the observation resulted in a high cone production.

DISCUSSION

Summarizing the endogenous factors using principal components analysis

Disentangling the exogenous and endogenous factors that affect cone production remains a difficult task. Exogenous factors correspond to the environmental conditions, such as the microclimate, light, and the availability of water and nutrients, that can be modified by competitors. These factors can directly impact reproduction by acting as a cue for masting (Kelly et al. 2013), but they can also be mediated by endogenous factors. With the exception of tree age, which is independent of exogenous factors, other endogenous factors, including the level of and variance in annual radial growth, crown health, and tree size, are the result of both a tree's historical development and its microenvironment.

We suggested using PCA to generate independent variables through the resulting axes to summarize all of these endogenous factors, and we found similar trends through a comparison of two of our data sets (Fig. 3). The only difference corresponded to the dependence of radial growth on tree age. Along the Ventoux CLT, young trees exhibit higher recent growth, but recent growth was independent of age in the DET data sets. This result was in line with the results given by Cailleret et al. (2014), who found that the relationships between age, defoliation, and recent growth differed according to the study site.

Effects of tree characteristics on cone production

A first key result is the large variability in cone production observed between trees. The coefficient of variation averaged 160% that was in line with the values found by Lamontagne and Boutin (2007) on *Picea abies* (between 184% and 215%). Using mixed-effects linear models allowed for decomposition between the various

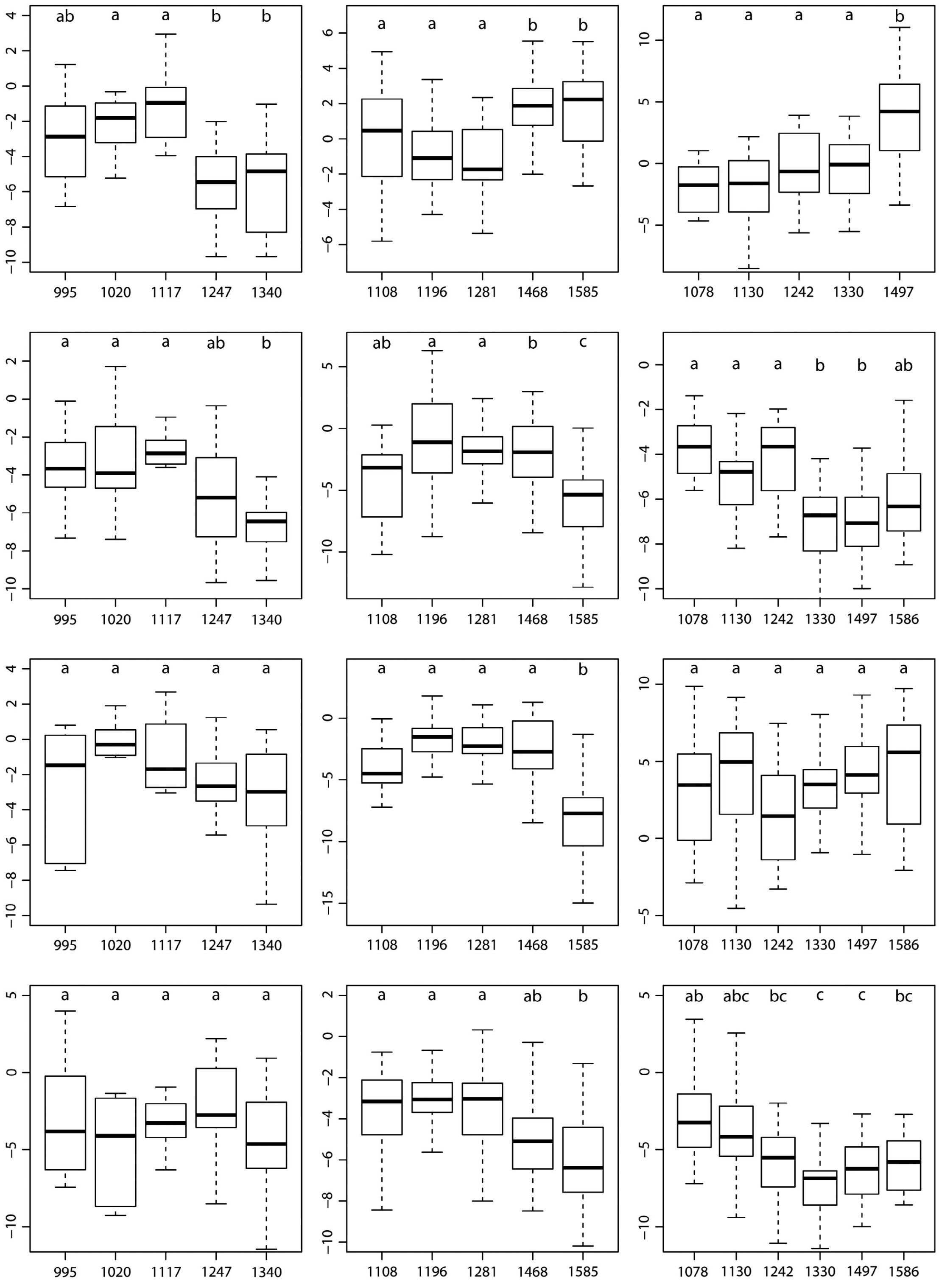

Fig. 5. The effect of elevation on cone production using the DET data sets: (from left to right) the residuals of model 2 against the elevation classes in Ventoux, Issole, and Vésubie (from top to bottom) in 2007, 2008, 2013, and 2014. Different letters above the boxplots indicate significant differences.

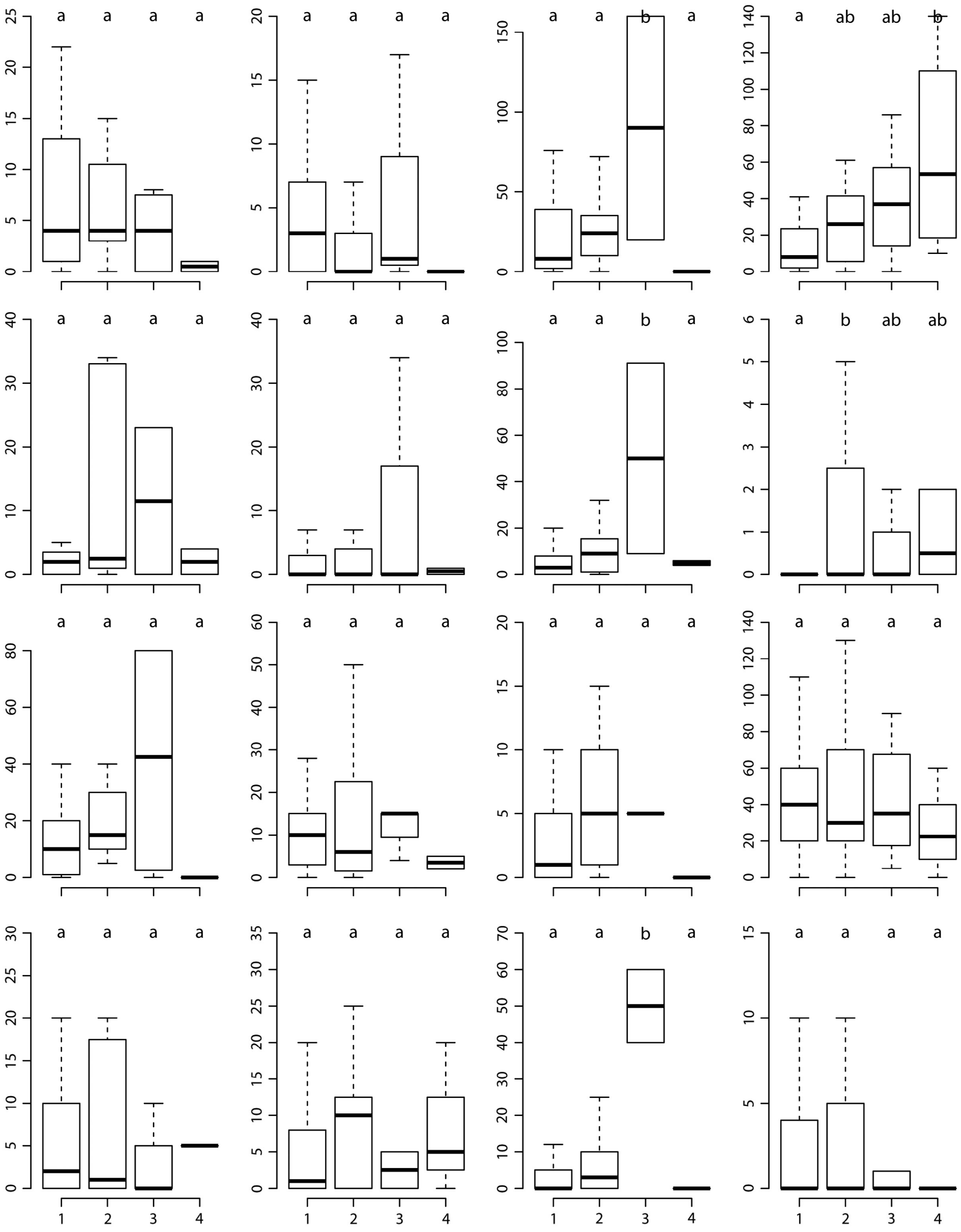

Fig. 6. The effect of crown defoliation on cone production using the DET and CET data sets: Boxplot of cone production for the four crown defoliation classes (1: 0–15%, 2: 15–30%, 3: 30–45%, and 4: 45–100%) for four data sets (Ventoux CET, Ventoux DET, Issole DET, and Vésubie DET from left to right) and 4 yr (2007, 2008, 2013, and 2014 from top to bottom). Different letters above the boxplots indicate significant differences.

Table 4. List of the climate variables significantly ($P < 0.05$) correlated with the coefficients associated with the year effect in model 3.

Variables	Year	Month	Cor	Pcor
Difference in temperature between years $n-1$ and $n-2$	–	April	0.85	7.6×10^{-5}
Max temperature	$n-2$	February	−0.60	2.6×10^{-2}
Max temperature	$n-2$	April	−0.64	1.7×10^{-2}
Precipitation	$n-2$	May	−0.55	2.9×10^{-2}
Relative humidity	$n-2$	July	−0.51	4.5×10^{-2}
Precipitation	$n-1$	May	0.53	3.5×10^{-2}
Minimal relative humidity	$n-1$	September	0.53	3.5×10^{-2}

Note: Cor and Pcor are, respectively, the Spearman coefficient and the associated P-value.

fixed effects (i.e., the environment and the endogenous effects summarized by the PCA) and the random effects not explicitly considered in the model (e.g., tree name as a grouping variable of the random effect on the intercept). For both CET and DET data sets, respectively, 30% and 40% of the variability between trees were not explained by the fixed effects. This variability likely includes the genetic variation among trees in terms of the allocation to reproduction, but also the interactions between endogenous factors (Barringer et al. 2013) and the endogenous factors that have been not measured (e.g., crown volume, local crown overlap, or the content of nonstructural carbohydrates).

If tree size and/or age were the most important drivers of cone production, trees being more productive as they become older and larger (Debain et al. 2003, Amm et al. 2012, Viglas et al. 2013), this study also demonstrates that other biotic effects must be considered. This size effect can be disentangled from the effect of recent radial growth. Indeed, recent growth was negatively related to cone production in the DET data sets. This negative relationship was also found in Ventoux CLT before 2000, for both old and young trees by comparing past growth of high-producing vs. low-producing trees. A negative correlation between radial growth and tree size (see Bowman et al. 2013) may explain this relationship, but the use of PCA invalidates this interpretation, as the two constructed axes were not correlated. It is more likely that a tradeoff between growth and reproduction occurred. Crown defoliation, which might characterize temporal changes in tree vitality (Dobbertin and Brang 2001), had a non-monotonic effect on cone production with an optimum for trees with intermediate rates of defoliation. On the one hand, trees with high crown defoliation rates (>45% in the present study) tend to allocate few resources to cone production to preserve them for root and foliage growth or defense (Innes 1994, Vilà-Cabrera et al. 2014). On the other hand, our results suggest that intermediate defoliated trees might also increase their carbon allocation to reproduction.

Effect of elevation

Elevation can be seen as a factor that integrates gradual changes in temperature and precipitation (Cailleret and Davi 2011). We found that the optimum in cone production occurred at intermediate elevations on both Ventoux and Issole in 2008, whereas in other cases, maxima were found at higher (e.g., Issole in 2007) or lower elevations (e.g., Vésubie in 2008). These contradictory effects were in line with the literature, from which no clear pattern emerges (e.g., Mencuccini et al. 1995, Van Mantgem et al. 2006). Indeed, the effect of elevation on cone production depends on the position of the elevation range studied within the species niche and on the importance of the factors that limit carbon uptake and carbohydrate reserves at both the lower and upper limits of the species distribution (drought and frost, respectively). Moreover, the way that these limiting factors varied across elevations changed over the years. On the one hand, the effect of elevation on tree carbohydrate reserves was not constant over time due to nonlinear changes in the rates of photosynthesis and respiration, which have recently been demonstrated by Oddou-Muratorio and Davi (2014) using a process-based modeling approach. On the other hand, as cone production during a mast year likely depends on the cone production of the previous years, due to their influence over carbohydrate reserves, the effect of elevation can change from 1 yr to another. This seems to indicate that endogenous factors (e.g., carbohydrate reserves), more than climatic cues, drive the variations in cone production with elevation.

Relationships between climate conditions and mast events

Only 16 yr were available in our data set, which limits the inference of strong climate impacts on cone production. However, we demonstrated that the use of separate data sets does not bias the conclusions because the year effect was similar when using raw data (average cone production per year) or when analyzing the coefficients associated with the year effect in a modeling approach. We tested many climatic variables (e.g., minimum monthly relative humidity or global radiation) that have never been tested in previous studies. The climatic variables that best explained the interannual variability in cone production and mast events included precipitation, temperature, and relative humidity. Moreover, in line with the recent study by Kelly et al. (2013), a large difference in mean temperature between two consecutive springs (April) induced high cone production during the third year.

As the cones were initiated 1 yr before their maturation, the majority of the significant climatic variables reflected the weather conditions from 1 to 2 yr prior to cone production. This result indicated that there was not only a direct climate signal during bud formation but also a delayed signal that was transmitted, for instance, through the carbohydrate reserves. In *Fagus sylvatica*, Piovesan and Adams (2001) found that drought in the preceding early summer (year $n-1$) is a very strong predictor of masting in Europe and eastern North America. Our study, in line with previous research, indicated that both spring and summer are important for determining the link between cone production and climate. However, our results also highlighted that the role of photosynthesis and the elaboration of carbohydrate reserves outside of summer (e.g., in winter) are probably very important for silver fir, especially at its dryer margin.

Research Perspectives

To strengthen our results, one important task would be to analyze whether cone production is always a good proxy for reproductive success. Indeed, when cone production is high, the seed mass can be lower and the rate of empty or predated seeds can be higher. These effects have to be considered to better estimate reproductive success. The next step will be to include data on carbohydrate reserves in such correlation analyses to analyze the potential trade-offs and synergies between radial growth, carbon storage, and cone production and to determine whether they are constant over time as trees grow (see Sala et al. 2012, Han et al. 2013, Hoch et al. 2013). Finally, a promising way to better understand all of these mechanisms is to adequately include the allocation to reproduction in process-based models and to test different hypotheses: “Is the carbohydrate reserves dynamics explained the mast years?” “How does the phenology of reproduction affect the level of seed production and the quality of seeds?”

Acknowledgments

We wish to thank N. Mariotte, W. Brunetto, F. Courdier, and the UEFM team (especially O. Gilg, N. Turion and F. Jean) for their contribution to field measurements and dendrochronological analyses. The French Research National Agency (ANR) and INRA supported research funding in the frame of the DRYADE project (ANR-06-VULN-004) and this work was also supported by the metaprogramme Adaptation of Agriculture and Forests to Climate Change (AAFCC) of the French National Institute for Agricultural Research (INRA). This were supported also by the ERAnet BiodivERsA project, LinkTree (ANR-08-Biodiversa-006-06) and was made possible by the grant, Conservation des Ressources Génétiques Forestières from the French Ministry of Agriculture to INRA-URFM. Financial support to Gwendal Restoux during his Ph.D. was provided by INRA-EFPA and The Provence Alpes Cotes dAzur Regional Government. The study was also partially funded by the European Network of Excellence EVOLTREE. HD conceived and designed the experiments, analyzed the data, and wrote the manuscript; MC performed the experiments and wrote the manuscript; GR analyzed the data and wrote the manuscript; AA performed the experiments; CP and BF conceived and designed the experiments.

Literature Cited

Amm, A., C. Pichot, P. Dreyfus, H. Davi, and B. Fady. 2012. Improving the estimation of landscape scale seed dispersal by integrating seedling recruitment. Annals of Forest Science 69:845–856.

Barringer, B., W. D. Koenig, and J. M. H. Knops. 2013. Interrelationships among life-history traits in three California oaks. Oecologia 171:129–139.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4

Bazzaz, F. A., N. R. Chiariello, P. H. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. BioScience 37:58–67.

Bowman, D. M., R. J. Brienen, E. Gloor, O. L. Phillips, and L. D. Prior. 2013. Detecting trends in tree growth: not so simple. Trends in Plant Science 18:11–17.

Cailleret, M., and H. Davi. 2011. Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient. Trees: Structure and Function 25:265–276.

Cailleret, M., M. Nourtier, A. Amm, M. Durand-Gillmann, and H. Davi. 2014. Drought-induced decline and mortality of silver fir differ among three sites in southern France. Annals of Forest Science 71:643–657.

Calama, R., and G. Montero. 2007. Cone and seed production from stone pine (*Pinus pinea* L.) stands in Central Range (Spain). European Journal of Forest Research 126:23–35.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. American Naturalist 152:204–224.

Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86:1–16.

Clark, J. S., J. R. Poulsen, D. L. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed augmentation experiments. American Naturalist 170:128–142.

Davi, H., E. Dufrêne, C. Francois, G. Le Maire, D. Loustau, A. Bosc, S. Rambal, E. Granier, and E. Moors. 2006. Sensitivity of water and carbon fluxes to climate changes from 1960 to 2100 in European forest ecosystems. Agricultural and Forest Meteorology 141:35–56.

Davi, H., M. Gillmann, T. Ibanez, M. Cailleret, A. Bontemps, B. Fady, and F. Lefèvre. 2011. Diversity of leaf unfolding dynamics among tree species: new insights from a study along an altitudinal gradient. Agricultural and Forest Meteorology 151:1504–1513.

Debain, S., T. Curt, J. Lepart, and B. Prevosto. 2003. Reproductive variability in *Pinus sylvestris* in southern France: implications for invasion. Journal of Vegetation Science 14:509–516.

Dobbertin, M., and P. Brang. 2001. Crown defoliation improves tree mortality models. Forest Ecology and Management 141:271–284.

Dohrenbusch, A., S. Jaehne, M. Bredemeier, and N. Lamersdorf. 2002. Growth and fructification of a Norway spruce (*Picea abies* L. Karst) forest ecosystem under changed nutrient and water input. Annals of Forest Science 59:359–368.

Greene, D. F., and E. A. Johnson. 1994. Estimating the mean annual seed production of trees. Ecology 75:642.

Han, Q., D. Kabeya, A. Iio, Y. Inagaki, and Y. Kakubari. 2013. Nitrogen storage dynamics are affected by masting events in *Fagus crenata*. Oecologia 174:679–687.

Haymes, K. L., and G. A. Fox. 2012. Variation among individuals in cone production in *Pinus palustris* (Pinaceae). American Journal of Botany 99:640–645.

Henkel, T. W., J. R. Mayor, and L. P. Woolley. 2005. Mast fruiting and seedling survival of the ectomycorrhizal, monodominant *Dicymbe corymbosa* (Caesalpiniaceae) in Guyana. New Phytologist 167:543–556.

Hoch, G., R. T. W. Siegwolf, S. G. Keel, C. Körner, and Q. Han. 2013. Fruit production in three masting tree species does not rely on stored carbon reserves. Oecologia 171:653–662.

Houle, G. 1999. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. Journal of Ecology 87:413–422.

Innes, J. L. 1994. The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. Trees 8:139–150.

Isagi, Y., K. Sugimura, A. Sumida, and H. Ito. 1997. How does masting happen and synchronize? Journal of Theoretical Biology 187:231–239.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: Why, how, where? Annual Review of Ecology and Systematics 33:427–447.

Kelly, D., A. Geldenhuis, A. James, E. P. Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, G. A. Harper, W. G. Lee, and M. J. Maitland. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. Ecology Letters 16:90–98.

Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. Nature 396:225–226.

Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. American Naturalist 155:59–69.

Krouchi, F., A. Derridj, and F. Lefèvre. 2004. Year and tree effect on reproductive organisation of *Cedrus atlantica* in a natural forest. Forest Ecology and Management 197:181–189.

Lalonde, R. G., and B. D. Roitberg. 1992. On the evolution of masting behavior in trees: Predation or weather? American Naturalist 139:1293–1304.

Lamontagne, J. M., and S. Boutin. 2007. Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. Journal of Ecology 95:991–1000.

LaMontagne, J. M., S. Peters, and S. Boutin. 2005. A visual index for estimating cone production for individual white spruce trees. Canadian Journal of Forest Research 35:3020–3026.

Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: an R package for multivariate analysis. Journal of Statistical Software 25:1–18.

Linhart, Y. B., and J. B. Mitton. 1985. Relationships among reproduction, growth rates, and protein heterozygosity in ponderosa pine. American Journal of Botany 72:181–184.

Littell, R. C., W. W. Stroup, G. A. Milliken, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. SAS Institute, Cary, North Carolina, USA.

Lord, J. M., and M. Westoby. 2006. Accessory costs of seed production. Oecologia 150:310–317.

Mencuccini, M., P. Piussi, and A. Zanzi Sulli. 1995. Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. Forest Ecology and Management 76:109–125.

Moreira, X., L. Abdala-Roberts, Y. B. Linhart, and K. A. Mooney. 2014. Masting promotes individual-and population-level reproduction by increasing pollination efficiency. Ecology 95:801–807.

Morin, X., D. Viner, and I. Chuine. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. Journal of Ecology 96:784–794.

Mutke, S., J. Gordo, and L. Gil. 2005. Variability of Mediterranean stone pine cone production: yield loss as response to climate change. Agricultural and Forest Meteorology 132:263–272.

Niklas, K. J., and B. J. Enquist. 2003. An allometric model for seed plant reproduction. Evolutionary Ecology Research 5:79–88.

Obeso, J. R. 2002. The costs of reproduction in plants. New Phytologist 155:321–348.

Oddou-Muratorio, S., and H. Davi. 2014. Simulating local adaptation to climate of forest trees with a physio-demo-genetics model. Evolutionary Applications 7:453–467.

Pearse, I. S., W. D. Koenig, and J. M. H. Knops. 2014. Cues versus proximate drivers: testing the mechanism behind masting behavior. Oikos 123:179–184.

Petit, R. J., E. Pineau, B. Demesure, R. Bacilieri, A. Ducousso, and A. Kremer. 1997. Chloroplast DNA footprints of postglacial recolonization by oaks. Proceedings of the National Academy of Sciences USA 94:9996–10001.

Piovesan, G., and J. M. Adams. 2001. Masting behaviour in beech: linking reproduction and climatic variation. Canadian Journal of Botany 79:1039–1047.

Piovesan, G., and J. M. Adams. 2005. The evolutionary ecology of masting: Does the environmental prediction hypothesis also have a role in mesic temperate forests? Ecological Research 20:739–743.

Politi, P. I., K. Georghiou, and M. Arianoutsou. 2011. Reproductive biology of *Abies cephalonica* Loudon in Mount Aenos National Park, Cephalonia, Greece. Trees 25:655–668.

Rapp, J. M., E. J. McIntire, and E. E. Crone. 2013. Sex allocation, pollen limitation and masting in whitebark pine. Journal of Ecology 101:1345–1352.

Restoux, G. 2009. Variabilité spatio-temporelle de la reproduction chez une espèce pérenne monoïque : Le cas du sapin pectiné, Abies alba Miller, en limite sud de son aire de répartition. Thèse de doctorat en sciences. Université Paul Cézanne Aix, Marseille, France.

Sagnard, F., C. Barberot, and B. Fady. 2002. Structure of genetic diversity in *Abies alba* Mill. from southwestern Alps: multivariate analysis of adaptive and non-adaptive traits for conservation in France. Forest Ecology and Management 157:175–189.

Sagnard, F., S. Oddou-Muratorio, C. Pichot, G. G. Vendramin, and B. Fady. 2010. Effects of seed dispersal, adult tree and seedling density on the spatial genetic structure of regeneration at fine temporal and spatial scales. Tree Genetics & Genomes 7:37–48.

Sala, A., K. Hopping, E. J. B. McIntire, S. Delzon, and E. E. Crone. 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytologist 196:189–199.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14:235–250.

Thabeet, A., M. Vennetier, C. Gadbin-Henry, N. Denelle, M. Roux, Y. Caraglio, and B. Vila. 2009. Response of *Pinus sylvestris* L. to recent climatic events in the French Mediterranean region. Trees 23:843–853.

Van Mantgem, P. J., N. L. Stephenson, and J. E. Keeley. 2006. Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecology and Management 225:391–399.

Vidal, J. P., E. Martin, L. Franchistéguy, M. Baillon, and J. M. Soubeyroux. 2010. A 50-year high-resolution atmospheric reanalysis over France with the Safran system. International Journal of Climatology 30:1627–1644.

Viglas, J. N., C. D. Brown, and J. F. Johnstone. 2013. Age and size effects on seed productivity of northern black spruce. Canadian Journal of Forest Research 43:534–543.

Vilà-Cabrera, A., J. Martínez-Vilalta, and J. Retana. 2014. Variation in reproduction and growth in declining Scots pine populations. Perspectives in Plant Ecology, Evolution and Systematics 16:111–120.