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Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status

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Abstract

Key message: Tree resilience to drought was higher in drier sites and lower for suppressed trees grown in higher-density stands, highlighting the role of acclimation and selection in tree responses to drought.

Context: Ongoing climate change will drive more frequent drought events in the future, with potential impacts on tree community structure and functioning. Growth responses of tree communities may depend on their past water status and on competition pressure.

Material and methods: We investigated the effects of site water status, population density and tree social status on tree growth resistance and resilience following the severe drought of 1976 in even-aged stands of sessile oak (*Quercus petraea*). We used retrospective growth data collected in permanent plots experiencing contrasted climatic and stand density conditions. We used boosted regression trees to calibrate a tree growth model over 1960-1975, which was then used to provide a baseline of expected tree growth following 1976. Growth dynamics during and after 1976 was examined using the ratio between observed and expected growth over 1976-1983.

Results: Tree radial growth was on average 0.6 times its expected values in 1976 and was still 0.63 times its expected value in 1977. Despite experiencing higher summer soil water deficit in 1976, trees growing in drier sites exhibited remarkably faster growth recovery than those in moister sites. Suppressed trees grown in higher-density stands recovered their normal growth rate slower than dominant trees.

Conclusions: Forest growth is evidenced to be more vulnerable to drought in moister than in drier sites. Competitive pressures also alter tree capacity to recover from a severe drought, accelerating suppression of smaller trees in high-density stands. These results highlight the role of acclimation and selection processes in tree community responses to present and future climates.

Keywords: resistance; recovery; boosted regression trees; acclimation; adaptation; *Quercus petraea*.

1   Introduction

Global and increased climate variability is expected to drive more frequent heatwave and drought events in the future (Schar *et al.*, 2004; Sterl *et al.*, 2008). Ecological research has long used climate variables averaged over long periods of time as surrogates for climatic site conditions (Jentsch *et al.*, 2007), while most tree-ring research has focused on studying seasonal climate-growth relationships (Fritts, 1976). Accordingly, they have placed emphases on the consequences of mean climatic temporal trends and on progressive change in climate-growth relationships (D'Arrigo *et al.*, 2008) on ecosystem functioning. Yet, ecologists increasingly recognize that extreme climatic events can trigger important biotic responses (Bigler *et al.*, 2007; Jentsch *et al.*, 2007) and play a key role in shaping forest ecosystems

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(Allen *et al.*, 2010; Bréda *et al.*, 2006; Gutschick & BassiriRad, 2003).

Organism and community responses to extreme climatic events are usually classified as either immediate (resistance) or delayed (resilience) effects (Pimm, 1984). While several definitions of these phenomena exist, we use Pimm's definition, where resistance describes the degree to which a function is changed during a disturbance and resilience describes the time needed to recover to pre-disturbance conditions. In tree species, growth is a widely used indicator of individual vigor (Dobbertin, 2005). For climatic disturbances such as drought, radial growth is commonly used to assess the degree to which individuals are affected by the event. While most studies have focused on the immediate effect of drought on tree growth, delayed effects have received much less attention (Lloret *et al.*, 2011; Orwig & Abrams, 1997), despite their importance in driving changes in ecosystem functioning (Gutschick & BassiriRad, 2003).

Several factors are likely to condition the growth response of individuals to a given climatic drought event, one obvious factor being site water status. With less water resource available, drier sites will reach critical thresholds of drought conditions faster than moister sites and will experience higher water deficit and longer drought duration (Zang *et al.*, 2014). However, locally adapted ecotypes may demonstrate higher resistance and resilience than ecotypes from moister sites, as shown in several provenance trials (Eilmann *et al.*, 2013; Jansen *et al.*, 2013; Rozenberg, 1993; Taeger *et al.*, 2013). One approach to embrace these two counteracting processes is to evaluate forest growth resistance and resilience to drought along a gradient of site water availability, as determined by local climate and soil characteristics.

Most European temperate forests are managed and experience stand density reduction through thinning operations. Stand thinning has been shown to increase stand level water availability (Aussenac & Granier, 1988; Bréda *et al.*, 1995). As a result, trees growing in low-density stands have been shown to have higher climatic drought resistance (Misson *et al.*, 2003; Sohn *et al.*, 2013) and higher resilience (Kohler *et al.*, 2010; Sohn *et al.*, 2013, 2012) than trees growing in high-density stands. Still, longer term responses to stand thinning are not trivial to understand, as trees grown in lower-density stands have larger leaf area and thus higher individual water requirement than others (D'Amato *et al.*, 2013; McDowell *et al.*, 2006). Stand density management as an approach to mitigating negative growth responses to climatic drought and adapting forest management to climate change is therefore a crucial issue.

Within tree communities, trees of different social status may display a range of responses to severe droughts. While few studies report on dominant trees being less resistant (Liu & Muller, 1993; Martin-Benito *et al.*, 2008; Martinez-Vilalta *et al.*, 2012; Pichler & Oberhuber, 2007) and less resilient (Liu & Muller, 1993; Martinez-Vilalta *et al.*, 2012; Zang *et al.*, 2012) than intermediate and suppressed trees, other studies suggest that dominant trees are more resistant (Pichler & Oberhuber, 2007; Vose & Swank, 1994) and more resilient (Martin-Benito *et al.*, 2008) than suppressed trees. A more comprehensive view on competition-driven effects is therefore needed, and this requires to encompass both stand density and tree social rank as drivers of tree response to drought along gradients of water status. We are, however, not aware of any such integrative study on growth resistance and resilience to date.

In the present study, we aimed to explore the effects of site water status, stand density and tree social status on tree growth resistance and resilience to a severe drought. The 1976 drought event was chosen as one of the most severe and most documented droughts in Europe in the past recent decades (Cavin *et al.*, 2013). Investigation of resistance and resilience require a comparison of observed growth to an expected growth baseline. Most studies estimate this expected growth from simplistic models (e.g. 5 or 10 years mean growth preceding the drought) (Lloret *et al.*, 2011). Yet, climatic and dendrometric conditions of a given year strongly affect tree growth during that same year Fritts (1976); Pretzsch (2009). In order to suppress potential confounding factors, these conditions should be accounted for when estimating the expected growth baseline. We thus calibrated a climatic and dendrometric tree growth model from the 15 years preceding the 1976 drought (1960-1975), and used it to predict the expected growth during drought to assess resistance to the drought (1976) and the subsequent resilience (1977-1983). We considered trees grown in different sites with contrasting site water status and stand density, and belonging to different social ranks.

We based our study on *Quercus petraea* Liebl. (sessile oak) as one of the major broadleaved species in Europe (Koeble & Seufert, 2001) and the second most important broadleaved tree species in France in terms of growing stock with 281 Mm^3 (IFN, 2013). Annual growth data were collected by coring trees belonging to a network of silvicultural experiments with inclusive survey of stands and individuals characteristics.

The hypotheses tested were: (1) trees grown in drier sites have a lower resistance and lower resilience than trees grown in moister sites, as they experience higher summer soil water deficit

(*summer SWD*) during the drought; (2) trees grown at greater stand density level have a lower resistance and lower resilience than trees grown at a lower density level; and (3) suppressed trees have a lower resistance and lower resilience than dominant trees.

2 Material and methods

2.1 Experimental design

Our data originated from a long-term experimental network designed to explore the effect of density treatments on the dynamics of even-aged sessile oak stands in the species production area in France (Oudin, 1930). Each site contains several experimental plots of the same age that have been subject to contrasted thinning regimes. All trees in the plots were inventoried and their circumference measured (every 4-10 years). Stand thinning was triggered after each measurement campaign, whenever the stand density of the plot was above the stand density defined in its thinning regime.

From this network, three sites with contrasted water availability conditions were selected. These three sites are referred to as hygric, mesic and xeric sites. Note that while we tried to select sites of similar age, there remains a 20 years difference between youngest and oldest site which correlates with the site water status gradient. While this age gradient is relatively small compared to sessile oak's life cycle and to the site water status gradient, we cannot completely rule out the fact that site responses might be influenced by site age in addition to site water status. Each site contained two plots of the same age and area, one experiencing a medium and the other a high stand density. For the 1960-1983 study period, these three sites (six plots) cover a range of stand age from 71 to 92 years in 1960 to 94-115 years in 1983 and plot area from 0.47 to 1 ha. Table 1 provides general information on these trials.

Data for monthly precipitation (P) and monthly mean temperature (T) were estimated for each site, year and month from the Safran spatial climatic analysis that covers the 1960-2013 period (Quintana-Seguí *et al.*, 2008; Vidal *et al.*, 2010). Soil water content (SWC) and soil water deficit (SWD) were calculated as indices of belowground water availability (Appendix A). These indices of water stress are expected to be better indicators of the influence of climate on tree growth than raw climatic data (Lebourgeois *et al.*, 2013; Piedallu *et al.*, 2013). Monthly climatic data were then aggregated by season (December–February for winter, March–May for spring, June–August for summer and September–November for autumn) for a given running year (in this definition, December is taken from the preceding year). For autumn, data from the previous year were used, as indicated by the subscript -1 (e.g. *autumn* T_{-1}).

In the three study sites, the year 1976 was characterized by particularly high *summer SWD* conditions compared to the rest of the 1960-1983 period (Fig.1). For the hygric, mesic and xeric sites, mean *summer SWD* for the 1960-1983 period were 26, 35 and 48 mm, respectively. For the 1976 drought, *summer SWD* values were 76, 85 and 94 mm, respectively, that is, 2.9, 2.4 and 1.9 times their 1960-1983 mean values.

2.2 Annual tree growth

For each plot, annual growth data were collected from increment cores in thirty trees evenly distributed along the diameter distribution in 1990. This allowed each diameter class to be represented, based on their diameter value during the studied period. Ring-width chronologies were recorded using the LINTAB platform at 0.01 mm resolution and cross-dated at the site level using TSAP-Win (Rinn, 2003). Visual inspection of raw time series of individual basal area increment reveals negative effects of the 1976 drought on radial growth (Fig.2).

2.3 Stand variables and tree diameter rank

Relative Density Index (RDI, dimensionless) describes the current density (N, in stems/ha) relative to the threshold self-thinning density ($Nmax$, in stems/ha) at the current quadratic mean diameter (dg, in cm). We used RDI to express plot stand density on a relative scale. RDI was calculated as $RDI = N/N_{max}$, using $N_{max} = 125242/dg^{1.566}$ from Le Goff *et al.* (2011), so that $RDI = N \times dg^{1.566}/125242$. The 6 selected plots cover a range of RDI from 0.52 to 1.01. Thinning intensity (TI, dimensionless, between 0 and 1) in each plot was calculated for each thinning operation as a ratio between RDI removed and RDI before thinning.

RDI, TI and *time since thinning* (years) were together used to give a comprehensive representation of stand management. Tree size was characterized by individual tree basal area (g, m2) and tree age by *cambial age* (years). We used relative tree *diameter rank* (dimensionless) for a given year as a proxy for individual tree social status within each plot. *Diameter rank* was computed by first ranking trees by increasing size. This raw rank was then divided by the number of trees of the plot (hence, *diameter rank* spans the whole (0, 1] range). Individual *diameter rank* was therefore represented as a continuous variable. To ease the manuscript's
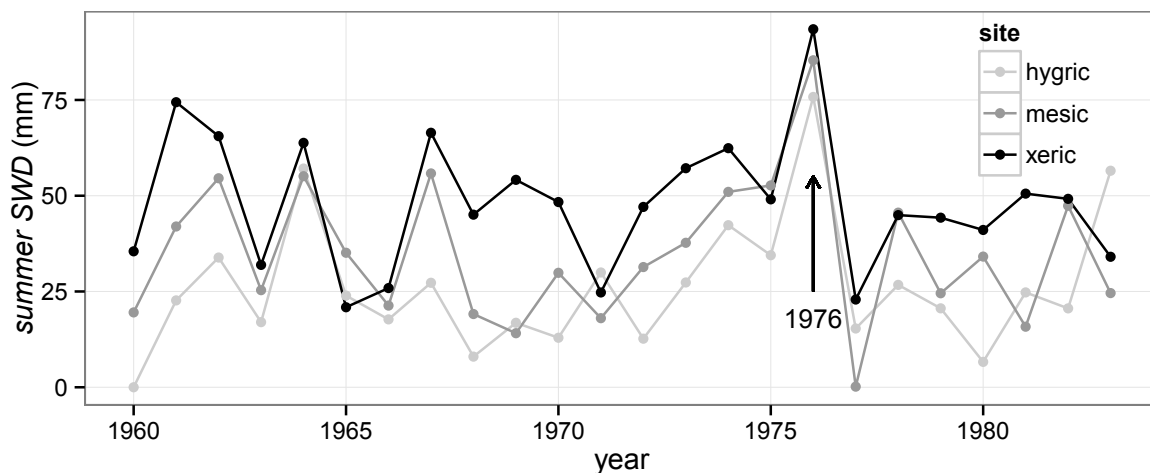
Figure 1: *Summer SWD* for the 1960-1983 period. Different lines represent different sites with a moisture gradient. Mean *summer SWD* for the 1960-1983 period were respectively equal to 26, 35 and 48 mm for the hygric, mesic and xeric sites. *Summer SWD* in 1976 were respectively equal to 2.9, 2.4 and 1.9 times their 1960-1983 mean value for the hygric, mesic and xeric sites

readability and to better answer our hypotheses, it was sometime preferable to group *diameter rank* into two categories: trees with diameter rank below 0.5 in 1983 were considered to be suppressed trees, while trees with diameter rank above 0.5 were considered to be dominant trees. This threshold was chosen because it objectively splits the population in two (0.5 is the median within-plot diameter) and avoid introducing any subjective selection bias. Analyzing the effect of social status as a continuous variable (Appendix B) provided results that were highly consistent with those obtained by analyzing the effect of social status as a categorical variable (this manuscript). Yearly values for *RDI* and *diameter rank* were obtained by linear interpolation between two successive measurement dates.

2.4 Modelling expected tree growth

Analyzing immediate and delayed effects of the 1976 drought requires comparing observed growth to an expected baseline. This baseline was constructed using the tree-ring chronology covering the 1960-1975 period (1960 being the first year covered by the Safran climatic model). The 1960-1975 period was used to calibrate the growth model, while the 1976-1983 period was used to predict expected tree growth during and after the drought year. The end year 1983 was selected to study drought recovery over a sufficient period (resilience studies usually analyze growth responses up to 3-5 years after drought (Lloret *et al.*, 2011; Martinez-Vilalta *et al.*, 2012; Orwig & Abrams, 1997; Zang *et al.*, 2014); yet, 1983 is not too far from the calibration period, reducing the risk of having dendrometric and

climatic conditions that are too different from the calibrations period (extrapolations).

Boosted Regression Trees (BRT), a non-parametric method able to fit nonlinear relationships and explore interactions among predictors (Aertsen *et al.*, 2014; De'ath, 2007; Elith *et al.*, 2008; Kint *et al.*, 2012), were used to build our growth model. In BRT, the boosting algorithm (Friedman, 2001) iteratively calls the regression tree algorithm (Breiman *et al.*, 1984) to construct a collection of regression trees. New regression trees are iteratively fitted to the residual errors of the existing regression trees collection. The final model is therefore an additive combination of all the regression trees in the collection. Elementary BRT models are characterized by the number of regression trees in their collection (nt) and the number of splits in each of the individual regression trees (tree complexity tc). Note that tc also defines the maximum interaction order that can be fitted (no interaction with tc=1, a two-way interaction with tc=2, etc.). To prevent overfitting, we applied several widely used extensions to these elementary BRT: at each iteration, 1) the contribution to the model of the newly fitted regression tree is reduced by a learning rate (lr); 2) stochasticity is incorporated by randomly subsampling the data on which the new regression tree was fitted (bag fraction, often set up at 50% of the data) (Elith *et al.*, 2008).

A BRT growth model was fit to the 1960-1975 period, with individual annual basal area increment (Δg) as the response variable and stand variables (*RDI, TI, time since thinning*), tree variables (*cambial age, g, diameter rank*)
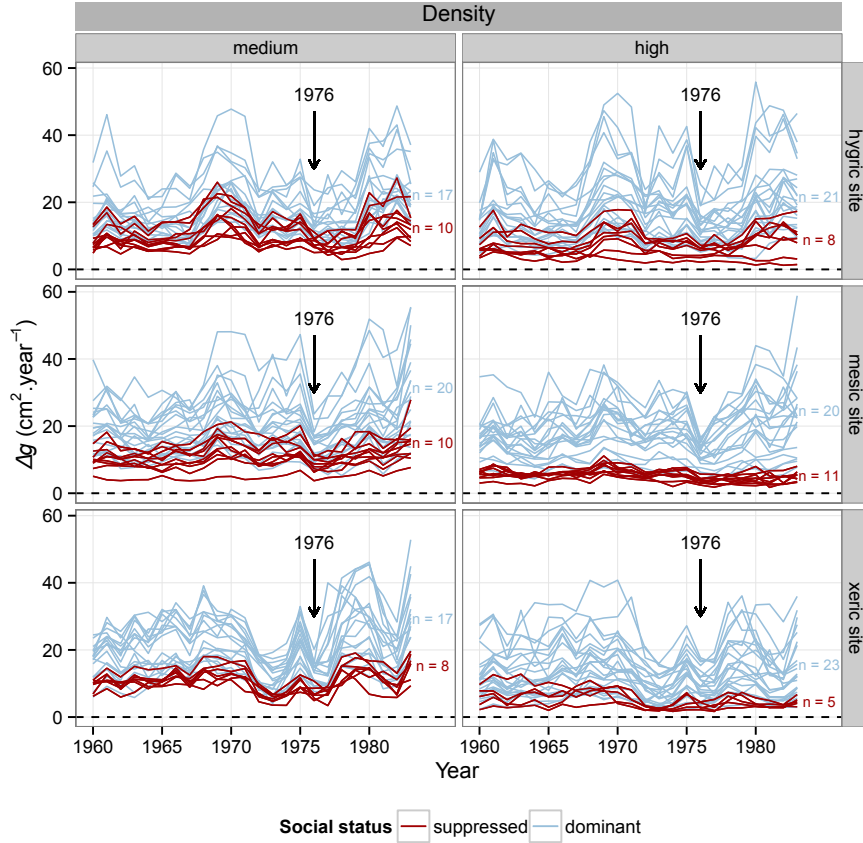
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Figure 2: Individual tree growth time series. Thin lines represent the basal area increment of individual trees over the 1960-1983 period. The number of trees per group is shown on the right side of the plot. Arrows highlight the year 1976

and seasonal climatic variables (seasonal P and T, and *autumn SWC_{-1}*, *spring SWC* and *summer SWD*) as potential predictors. In our sample, suppressed trees were less abundant than dominant trees. To balance the quality-of-fit of suppressed and dominant trees in each plot, a higher weight was applied to suppressed than to dominant trees: with a total of 168 trees split up in 6 plots and 2 social status groups, a balanced number of trees per group per plot was equal to 14. The weight of a tree (data point) in the model was calculated by dividing 14 by the number of trees present in a given group and a given plot (i.e. in the medium density plot of the hygric site, the weight applied was equal to 14/17 for dominant and 14/10 for suppressed trees). The R software (R, 2015), the 'gbm' package (Ridgeway, 2015) and its extension the 'dismo' package (Hijmans *et al.*, 2013) were used to fit the BRT models. We followed a cross-validation procedure similar to Elith *et al.* (2008) to select the most suitable number of trees (nt), tree complexity (tc) and learning rate (lr) (Appendix C). The final BRT model has a nt of 5000, a tc of 3, a lr of 0.001 and a bag fraction of 0.5. Goodness-of-fit of the final BRT model was evaluated by computing the coefficient of determination (R2, Eq.1), root mean squared error (RMSE, Eq.2) and relative RMSE (rRMSE; Eq.3), calculated from the calibration data.

$$R^2 = 1 - \frac{\sum (\Delta g_i - \widehat{\Delta g_i})^2}{\sum (\Delta g_i - \overline{\Delta g_i})^2} \quad (1)$$

$$RMSE = \sqrt{\frac{\sum (\Delta g_i - \widehat{\Delta g_i})^2}{n}} \quad (2)$$

$$rRMSE = \frac{\sqrt{\frac{\sum (\Delta g_i - \widehat{\Delta g_i})^2}{n}}}{\overline{\Delta g_i}} \quad (3)$$

Where Δg_i and $\widehat{\Delta g_i}$ are observed and predicted basal area increment of observation i, respectively. $\overline{\Delta g_i}$ is the mean basal area increment, and n is the total number of observations. Prediction R2p, RMSEp and rRMSEp of the BRT for the chosen set of parameter values were also calculated during the cross-validation procedure (Appendix C).

Table 1: Dendrometric and environmental description of the experimental sites

Site	Plot description					Dendrometrical variables[a]						Environmental variables[b]							
	Latitude-Longitude (decimal degrees)	Density treatment	Installation date	Plot size (ha)	Mean period (year)	age (years) 1960	1983	dg (cm) 1960	1983	RDI (dimensionless) 1960	1983	$SWHC^{c}$ (mm)	T (°C)	P (mm)	SWC (mm)	SWD (mm)	SWD_{1976} (mm)	SWD_{1976}/SWD (dimensionless)	pH^{d} (dimensionless)
Hygric	48.7236 − 6.3470	medium	1937	1	4 ±3.3	92	115	24	33	0.66	0.6	118	9.5 ±0.59	808 ±143	49 ±21	26 ±17	75	2.9	5.6
	48.7236 − 6.3470	high	1937	1	4 ±3.3	92	115	26	33	0.82	0.82	118	9.5 ±0.59	808 ±143	49 ±21	26 ±17	75	2.9	5.6
Mesic	46.6703 − 2.7223	medium	1932	1	10 ±1.4	81	104	24	34	0.63	0.52	99	10 ±0.5	797 ±118	32 ±19	35 ±18	85	2.4	5.3
	46.6703 − 2.7223	high	1932	1	10 ±1.4	81	104	21	29	0.88	0.87	99	10 ±0.5	797 ±118	32 ±19	35 ±18	85	2.4	5.3
Xeric	47.5713 − 1.2581	medium	1925	0.47	6 ±2.6	71	94	24	32	0.64	0.54	110	10.4 ±0.44	658 ±97	25 ±9	48 ± 16	94	1.9	5
	47.5713 − 1.2581	high	1945	0.47	6 ±2.6	71	94	17	21	0.98	1.01	110	10.4 ±0.44	658 ±97	25 ±9	48 ± 16	94	1.9	5

[a] Age, quadratic mean diameter (dg) and relative density index (RDI) values for each plot are those at the beginning and the end of the 1960-1983 period

[b] Averages and standard deviation per trial. Temperature (T) and precipitations (P) are yearly mean and sum values over the 1960-1983 period, respectively. Soil water content (SWC) and soil water deficit (SWD) are mean summer values over the 1960-1983 period. SWD_{1976} is the summer SWD value in 1976

[c] Soil water holding capacity (SWHC) for a soil down to a depth of 1 m. They are GIS interpolation of NFI data extracted from Piedallu et al. (2011)

[d] Soil pH values are GIS interpolation of pH values bioindicated from NFI floristic data (Coudun et al., 2006)

2.5 Analyzing BRT models for tree growth

In BRT, graphical and statistical tools allow to assess model behaviour in ways similar to more traditional modeling methods. For a single regression tree, variable importance of a predictor is computed by summing the number of times the predictor is selected for splitting, weighted by the sum of squared improvements resulting from those splits (Breiman et al., 1984). In BRT models, variable importance of a given predictor is simply the average of variable importance over all regression trees (Friedman & Meulman, 2003). For purposes of comparison, variable importances for all predictors were normalized to sum to 100%.

The main effect of each predictor was assessed using partial response plots (Friedman, 2001), which present the relationship between tree growth and the predictor, marginalized over all other predictors. Two-way interactions between pairs of predictors were detected using the 'gbm.interactions' function (Hijmans et al., 2013), which calculates the discrepancy to additivity of the response variable along a grid of values of the two predictors (Appendix D). Important two-way interactions were visualized by varying the value of one predictor of the pair, while fixing the second predictor to different contrasted values (and keeping the remaining predictors to their mean value).

2.6 Tree resistance and resilience to the 1976 drought

Individual tree resistance to drought was estimated for each tree as the ratio between its observed growth in 1976 and its expected growth for a year with average climatic conditions ($resistance = \Delta g_{obs\ 1976}/\Delta g_{exp\ under\ average\ climatic\ conditions}$). Expected tree growth under average climatic conditions was predicted from the BRT model with stand and tree predictors held at their 1976 values and climatic predictors held at their mean value in the 1960-1975 period.

Delayed effects of the drought on individual tree growth were estimated by computing for each tree the ratio of its observed and its expected growth ($resilience = \Delta g_{obs}/\Delta g_{exp}$), for each year from 1977 to 1983. Expected tree growth for each year during the 1977-1983 period was predicted from the BRT model with stand, tree and climatic predictors observed in that year. Using such a ratio allows trees with different growth baselines to be compared on the same scale. It also allows the year to year climate variability to be taken into account in our baseline.

For each site and each year from 1976 to 1983, t-tests were used to assess the significance of the dif-

ference in the ratios between suppressed and dominant trees for a given stand density level, and the significance of the difference in the ratios between medium and high-density stands for a given tree social status level. Because we did multiple t-tests, p-values given by individual t-tests should be regarded with caution. Still, it seems reasonable to look at the consistency and trends per group these t-tests describe.

Mortality rates for each site and treatment were calculated from pluri-annual dendrometrical measurements. As expected, most of the mortality occurred in suppressed trees growing in stands of high density. However, our data showed no evidence of increased mortality rates following the 1976 drought. This might be due to the coarse resolution of our mortality data (Appendix E).

3 Results

3.1 BRT growth model

Analysis of the BRT growth model highlights the strong positive effects of g (with variable importance equal to 58.6%) and *diameter rank* (15%), as well as the negative effects of RDI (6%) and *cambial age* (5.8%) on tree growth (Fig.3a). The most important climatic variables were *autumn* SWC_{-1} (3.2%) and *autumn* T_{-1} (3.2%), which had positive effects, and *summer* SWD (1.8%), which had negative effect on tree growth. Other predictors only had marginal effects. The positive effect of *autumn* SWC_{-1} and the negative effect of *summer* SWD were larger for larger trees, suggesting a multiplicative effect of climate and size on tree growth (Fig.3b). The effect of *cambial age* was larger for medium-sized trees, while *diameter rank* was maximal for small-sized trees. The goodness-of-fit ($R^2 = 0.81$, $RMSE = 3.5cm^2.year^{-1}$, $rRMSE = 0.23$), predictive performance ($R_p^2 = 0.71$, $RMSE_p = 4.3cm^2.year^{-1}$, $rRMSE_p = 0.29$) of the BRT model and the stability of the $\Delta g_{obs}/\Delta g_{exp}$ ratio in the calibration period around a value of one (Appendix F) indicated the robustness of the BRT model used to predict expected tree growth.

3.2 Immediate and delayed effects of the 1976 drought

Mean tree resistance was equal to 0.6. We found no evidence of significant differences in resistance between density treatment, social status, or sites (Fig.4). Since growth reduction in 1976 was proportional to growth baseline, fast-growing individuals (dominant trees) lost more absolute growth than slow growing individuals (suppressed trees). There

was however no rank reversal and dominant trees still maintained higher absolute growth rates than suppressed trees.

Delayed drought effects in 1977 were equal to 0.63 for all sites, stand density, and social statuses. We observed a progressive recovery of all but the suppressed trees grown in high-density stands after 1977. Delayed drought effects were significantly more severe in suppressed than in dominant trees grown in high-density stands (Fig.5), and also significantly more severe in suppressed trees grown in high-density stands than in medium-density stands (Fig.6). This was especially true in the mesic and xeric sites, where suppressed trees grown in high-density stands did not recover from the 1976 drought at the end of the period of observation (1983).

Among the trees that fully recovered before 1983, those grown in the xeric site recovered their normal growth rate faster (1978, 2 years) than trees grown in the mesic or hygric sites (1980, 4 years, with a more progressive recovery for the mesic site) (Fig.5 and 6). In the mesic site and hygric site, observed growth was below its expected values in 1981 and 1982, respectively.

4 Discussion

This research allowed to analyze the combined effects of site water status, stand density and tree social status on the immediate and delayed effect of a severe drought in even-aged stands of sessile oak. Note that since only one extreme drought event was studied, we cannot completely rule out the fact that trees might respond differently under different or successive drought conditions. In our study, tree resistance was found to be similar across sites, density treatments and social status (contradicting hypotheses 1-3). Among trees that recovered, trees grown in drier sites had a faster recovery than trees grown in moister sites (contradicting hypothesis 1). Suppressed trees grown in high-density stands took longer to recover than suppressed trees in medium-density stands and dominant trees in both density treatments (partially confirming hypotheses 2-3 and highlighting their interaction).

4.1 Analyzing the BRT growth model

The BRT model provided a baseline for estimating individual tree growth rate which compared favorably with the 10 years growth average prior to drought classically used to estimate resistance and resilience indices (Appendix F). Still, growth models can fail when used outside their calibration
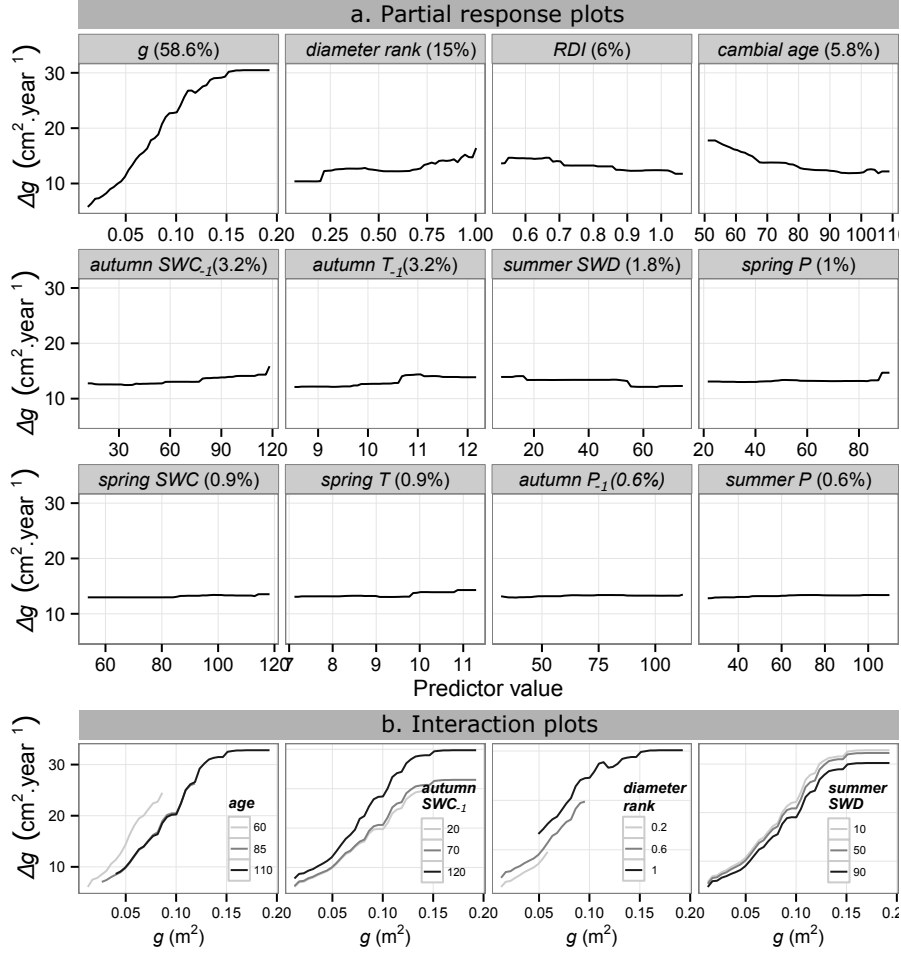
Figure 3: a. Partial response-plot for the twelve most influential variables of the BRT growth model calibrated on the 1960-1976 period. Variables are ordered according to their importance in the model. Percentages under brackets indicate variable importance. b. Interaction plots for the four most important two-way interactions. For each predictor pair, the predictor with the largest variable importance (g) is evenly distributed along its range, the second predictor is fixed at its 5%, 50% and 95% quantile values and remaining variables are fixed at their mean value. Note that the range of observed value for ba can vary with the value of the second predictor.

range, which can arise when they are used for temporal extrapolation. As an example, growth observations in 1981 in the mesic site are lower than BRT predictions for the same year, so that the ratio $\Delta g_{obs}/\Delta g_{exp}$ is ≤ 1 (Figs.5 and 6). This can be explained because *spring T* values in 1981 were above the range of the calibration period. A similar observation can be made for the 1982 observation in the xeric site (Figs.5 and 6).

The BRT model predicted strong positive effects of tree size and social status on tree growth, in accordance with tree size directly conditioning resource acquisition and ontogenetic growth (Enquist, 2002; Zeide, 2003). In crowded populations however, potential light and water resources acquisition may also be constrained by preemptive competition from larger neighbors (Schwinning & Weiner, 1998;

Trouvé *et al.*, 2014; Weiner, 1990). The interaction between tree size and diameter rank highlights this pattern. Sessile oak growth was also sensitive to summer SWD and previous autumnal conditions, which is consistent with previous studies (Friedrichs *et al.*, 2009; Lebourgeois *et al.*, 2004; Merian *et al.*, 2011; Trouvé *et al.*, 2014).

4.2 Effect of stand density and social status on tree growth resistance and resilience

We found little evidence for an effect of stand density and social status on sessile oak resistance to drought: All trees were affected the same way by the 1976 drought event and tree growth was equal to 0.6 times its expected value. One year after
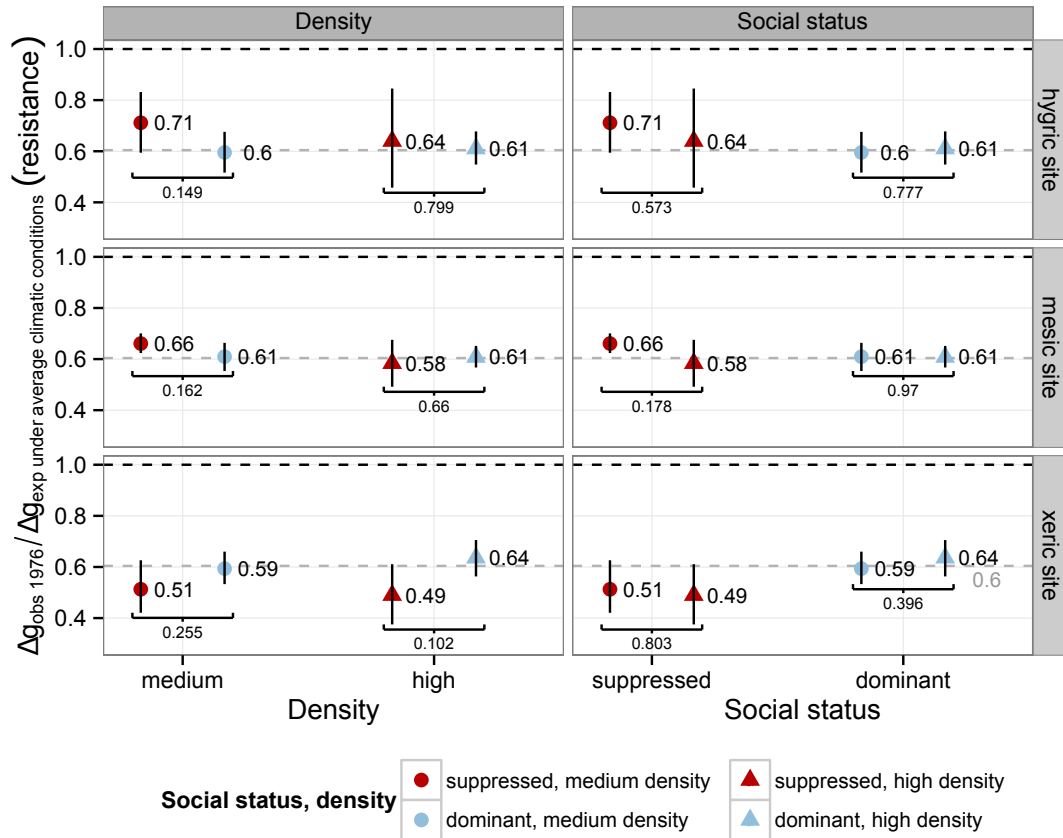
Figure 4: Effect of site water status, stand density and social status on mean tree growth resistance. Vertical bars indicate 95 % confidence interval. P-values for the effect of density (left panel) and social status (right panel) are shown below brackets. Significant p-values (p < 0.05) are shown in bold

the drought, tree growth had changed little and was 0.63 times its expected value on average for both density treatments and social status classes. However, two years after the drought event, differences in growth responses began to appear among trees with different social statuses. While dominant trees from all density levels and suppressed trees from medium-density stands gradually recovered from the 1976 drought, suppressed trees grown in high-density stands never completely returned to their pre-drought growth level (Figs.5 and 6) (except in the hygric site, where density treatments were not as different as in the mesic and xeric sites). Our results highlight an interaction between stand density and social status (Lebourgeois et al., 2014), which may partly explain differences in the effect of social status on tree recovery found in previous studies (Liu & Muller, 1993; Martin-Benito et al., 2008; Martinez-Vilalta et al., 2012; Merlin et al., 2015; Zang et al., 2012). A simple explanation for this interaction is that suppressed trees grown in high-density stands are more 'suppressed' than suppressed trees grown in medium-density stands.

High competition pressure appears to limit their ability to cope with drought stress. Suppressed trees grown in the higher-density stand had lower resource acquisition capacity than other trees, smaller crowns (Sumida et al., 2013), shallower and lower root densities (Bolte et al., 2004; Le Goff & Ottorini, 2001) and lower carbohydrate reserve (Miller & Kelman, 1966). All these features are known to possibly hinder tree recovery to pre-drought growth levels (Galiano et al., 2011). This situation for the suppressed trees will persist and even deteriorate with time, as they will be competing with fully recovered dominant trees, eventually leading to higher mortality rates (Berdanier & Clark, 2016).

From a demographic point of view, drought events are likely to amplify size-hierarchy and social status discrepancy in high-density stands and will hasten tree selection and eventually population adaptation to climate change. From a forest production point of view, the contribution of suppressed trees to stand growth remains minor, particularly in high-density stands (Trouvé et al., 2014) and management decision should be made with dominant − not suppressed − trees in mind. As reducing stand density did not improve drought resistance and recovery of dominant trees and as

Figure 5: Effect of social status on mean tree growth recovery for a given stand density and for different sites. Vertical bars indicate 95 % confidence interval. P-values for the effect of social status are shown below brackets. Significant p-values (p < 0.05) are shown in bold
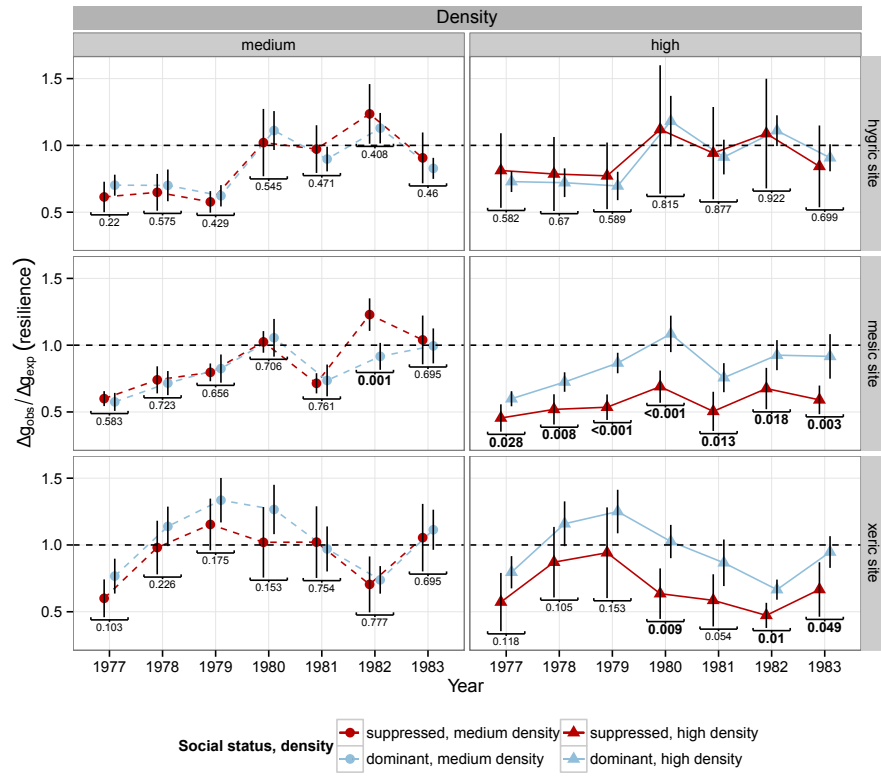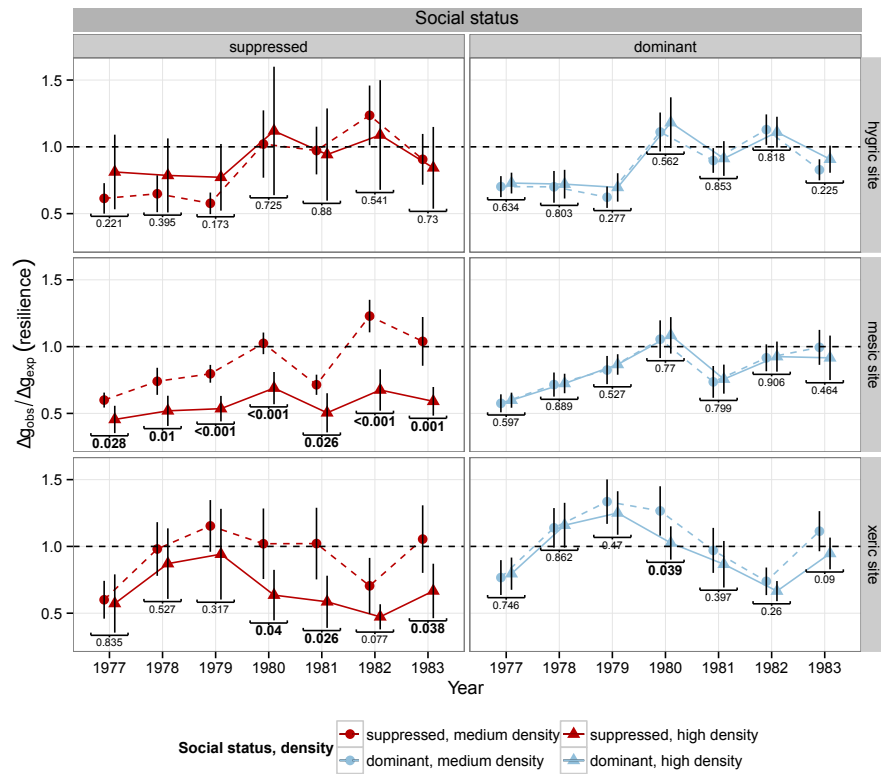

Figure 6: Effect of stand density on mean tree growth recovery for a given social status and for different sites. Vertical bars indicate 95 % confidence interval. P-values for the effect of density are shown below brackets. Significant p-values (p < 0.05) are shown in bold

stand growth is mainly determined by dominant tree growth, reducing stand density does not seem, in our case, to be a valuable option to adapt forest management to drought events.

4.3 Effect of site water status on tree growth resilience

Despite experiencing higher *summer SWD* during the 1976 drought (Fig.1), dominant trees at the xeric site exhibited faster recovery than dominant trees grown in the mesic and hygric sites (Figs.5 and 6). Remarkably, increase in *summer SWD* in 1976 relative to mean site conditions was lowest in the xeric site (1.9 times its mean site value; against 2.4 and 2.9 times for the mesic and hygric sites, respectively). This suggests that tree resilience is more closely related to the relative increase in *summer SWD* (higher in the hygric site) than to absolute *summer SWD* conditions (higher in the xeric site). This confirms that drought intensity should be defined in relation to mean climatic conditions, highlighting the importance of acclimation and adaptation of tree population to local climate.

Drier sites are more likely to favour individual acclimation and cross-generation adaptation of trees to drought (Bréda & Badeau, 2008). As suggested in previous studies (Martin-Benito *et al.*, 2008; Martinez-Vilalta *et al.*, 2012) and supported by our results, trees growing on wetter sites appear to be more vulnerable to drought events than drier ones. As a consequence, the strongest relative impact of climate change on forest growth might not necessarily appear at the southern margin of species distribution, but in areas where the species is less well adapted or acclimated to drought conditions.

5 Conclusions

While we could not detect any effect of site water status, stand density and social status on drought resistance, these factors had complex effects on drought resilience. This highlights the importance of studying not only immediate, but also delayed impacts of extreme events on tree growth.

Our study suggests that a tree's capacity to recover from drought events depends on mean site water status, and is typically greater in xeric sites. Relative increase in *summer SWD*, which is often lower in xeric sites, seems to be more relevant than absolute *summer SWD* to determine drought intensity and explain patterns of resilience.

Competition pressure was also shown to alter tree capacity to recover from a severe drought, with accelerated suppression of subordinate trees in high-density stands, highlighting an interaction between stand density and social status. These two results point to the important role of acclimation and selection processes in tree community responses to present and future climate.

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