

How do mixing tree species and stand density affect seasonal radial growth during drought events?



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ABSTRACT

Forecasted climate change impacts on temperate forest ecosystems include increased summer drought. Forest managers can increase the resistance of forest stands against summer drought by reducing stand density and favoring tree species mixtures. These strategies have been studied separately, but their combined effect on increasing forest stand resistance to summer drought is unknown.

The main objective of our study was to quantify tree species interaction effects on radial growth during a water stress period and to determine whether these effects changed with different levels of competition reflected by stand density.

The study was based in the Orleans state forest (Central France) at a long-term triplet experimental site (OPTMix) with pure and mixed stands of mature *Quercus petraea* and *Pinus sylvestris*. The experimental design comprised three repetitions of two densities (low and medium) in each composition (pure oak, mixed stands, pure pine). We monitored tree radial growth with 216 manual dendrometers placed throughout 18 plots, on small, medium and large trees. We analyzed three consecutive years with contrasted water stress: no water stress, a summer stress period, and a late summer stress period.

We found that mixture did not improve tree growth of the either species during the summer water stress period. On the other hand, there was a mixture effect during the late summer water stress period but only in medium-density stands inversely for the two species studied. More growth occurred for oaks in mixtures while, inversely, more growth occurred for pines in monocultures. A density effect occurred only for oaks, which grew more in lower-density stands than in medium-density stands. Finally, tree size did not influence seasonal resistance to drought.

1. Introduction

The IPCC expert group has forecasted an increase in summer drought events in temperate regions with climate change (IPCC, 2014), and water is one of the most important resources for tree growth. When water resources become too scarce, the tree greatly reduces its growth to maintain vital processes at a basic minimum (Aussenac, 2000). Therefore, radial growth is a good proxy for water stress (Locosselli et al., 2013) and can be used to assess silvicultural management options designed to cope with climate change.

Reducing stand density and mixing tree species are two options that may help forest stands cope with the future climate (Loreau and Hector, 2001; Tilman et al., 2001; Puettmann, 2011). The former limits water

loss in the ecosystem by reducing stand leaf area index (LAI), and thus evapotranspiration. As a consequence, the decrease in soil water content is slower and sufficient soil water availability is maintained for the trees during water stress events (Bréda et al., 1995). Though dominant trees have the highest growth, it is also necessary to follow the growth of co-dominant and dominated trees to study the overall effect of lower stand density (Pape, 1999; Merlin et al., 2015). Moreover, researchers do not agree on how tree social status affects sensitivity to drought. Some studies have found large trees to be more sensitive (Castagneri et al., 2012; Zang et al., 2012) while in other studies, they appear to be less affected than small trees (Piutti and Cescatti, 1997; Zang et al.,

Abbreviations: CI, circumference increment; SP, summer period; LSP, late summer period; REW, relative extractable water

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Table 1

Dendrometrical characteristics of the 18 plots in 2015. For the mixtures, the quadratic mean diameter, the basal area, number of stems and RDI columns provide values by species. The total value for the stand is the sum of these values. Standard deviations are given in parentheses.

Density	Composition	Species	Dg (cm)	Basal area (m ² /ha)	Number of stems (/ha)	RDI
Low	Pure oak	Oak	23.5 (2.5)	14.8 (0.4)	347 (60)	0.41 (0.01)
		Mixture	23.5 (2.1)	8.9 (0.9)	209 (38)	0.24 (0.03)
	Pure pine	Pine	35.9 (3.6)	10.7 (1.5)	106 (19)	0.24 (0.03)
		Mixture	33.8 (1.2)	21.7 (3.2)	242 (45)	0.48 (0.07)
Medium	Pure oak	Oak	22.5 (2.4)	20.8 (1.6)	530 (75)	0.57 (0.05)
		Mixture	23.6 (1.9)	10.4 (1.1)	245 (60)	0.29 (0.03)
	Pure pine	Pine	36.0 (3.3)	15.7 (2.8)	154 (19)	0.35 (0.06)
		Mixture	33.6 (1.7)	30.7 (1.7)	348 (23)	0.68 (0.04)

2012). Finally, some studies found no influence of tree size on drought response (Lebourgeois et al., 2014).

The second silvicultural strategy – mixing tree species – can have several benefits, one of which is better tree growth (Richards et al., 2010) likely due to the complementarity effect, i.e. resource partitioning or positive interactions lead to increased resource use and thus greater growth (Loreau and Hector, 2001). Complementarity is widely found in herbaceous communities and in agriculture, and its growth response effect is now being transposed to forestry (Richards et al., 2010; Forrester and Bauhus, 2016). Many studies show higher productivity for tree mixtures compared to monocultures (Liang et al., 2016). However, contrasted results are observed and can depend on certain conditions. Some authors have shown that the greater growth in mixtures (i.e. over-yielding) is site-dependent (Toïgo et al., 2015a; Lu et al., 2016) and occurs mainly when site quality is poor (Condés et al., 2013; Toïgo et al., 2015a) or in drought-prone environments (Grossiord, 2014). Over-yielding has also been observed in associations of shade-tolerant and shade-sensitive species (Toïgo et al., 2017) and in evergreen-deciduous mixtures, though not in deciduous-deciduous mixed stands (Lu et al., 2016). The stand composition effect can even result in under-yielding during long water stress periods (Richards et al., 2010; Ge et al., 2011).

Studies on tree growth are most often carried out through comparisons of inter-annual radial increment (Pretzsch et al., 2008; Michelot et al., 2012a; Mina et al., 2016); ring width is correlated to different stand or climatic variables to assess their potential effects on radial growth (Lebourgeois et al., 2014; Toïgo et al., 2015b). In temperate forests, annual growth data is readily available and this makes studying a wide variety of situations relatively easy. However, the inter-annual scale only makes it possible to study the long-term effect of drought (i.e. retrospective studies); to study the short term effects of drought on tree growth the seasonal scale is more appropriate (Lloret et al., 2012). Other studies have focused on seasonal growth by monitoring tree ring formation dynamics linked to variations in environmental conditions (Mäkinen, 2000; Michelot et al., 2012b; Sohn et al., 2016). This approach can improve tree growth models for dryer and warmer conditions (Zweifel et al., 2005; McMahon and Parker, 2015) and provide more accurate predictions in a changing climatic context.

In this study, we tested whether stand density and stand composition affected the radial growth of trees during seasonal drought events for two tree species: sessile oak (*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.). We were particularly interested in determining whether stand density changed the intensity or type of interaction between the two species during a drought event. We also tested whether the results differed according to tree size.

We hypothesized that (1) growth would be greater in low-density stands compared to medium-density stands for both species, (2) mixing tree species would improve tree growth during a drought event, (3) the mixture effect on growth would be greater in the highest density, and finally (4) the smallest trees would be the most sensitive to drought events.

2. Materials and methods

2.1. Study site

This study took place in the Orléans state forest (France, 47° 49'N, 2°29'E). It is the biggest forest managed by the National Office of Forest (ONF) in metropolitan France, covering 35,000 ha. Two main species are represented: sessile oak (*Quercus petraea*) and Scots pine (*Pinus sylvestris*), in both pure and mixed stands. The study used the long-term experimental site OPTMix (Oak Pine Tree Mixture, <https://optmix.irstea.fr/>, (Korboulewsky et al., 2015), installed in even-aged adult stands (aged 60–80 years) over a total of 44 ha. The area has a temperate continental climate with an oceanic influence: the mean annual temperature is 10.6 °C and mean annual rainfall is 716 mm (1959–2017 data from the SAFRAN and ISBA analytical platforms, Météo-France (Durand et al., 1993)).

The soil is qualified as a primary planosol (IUSS Working Group WRB, 2015). This type of soil is poor and acidic (C < 1%, C/N < 20, pH = 4.5). The first horizon is loamy sand lying on a more or less impermeable clay horizon about 40 cm deep; this leads to temporarily waterlogged conditions in winter and spring.

2.2. Experimental design

OPTMix consists of three triplets of pure oak (*Quercus petraea*), pure pine (*Pinus sylvestris*) and mixed stands of both species (making nine stands overall) (Korboulewsky et al., 2015). In each stand, there are two 0.5 ha plots with two different tree target densities: low (Relative Density Index, target RDI = 0.4) and medium (target RDI = 0.7) (Reineke, 1933). The distance between two repetitions of the triplet is at least a few kilometers. The dendrometrical characteristics of the stands are given in Table 1. Some stands were thinned during the experiment. The data from the thinned plots were excluded from the analyses for the thinning year (two mixed plots in 2015 and the same two mixed plots plus a pure pine plot in the 2014, out of a total of 18 plots).

In each of the 18 plots, we selected nine individuals per species according to their relative size class (large, medium and small) based on their circumference at breast height. We measured the DBH of all the trees in the plot, then used the cumulated frequencies of the DBH values to divide the trees in the plot into three quantiles corresponding to three within-plot size classes. We rejected any trees whose circumference fell within a 10% margin between any two size classes to clearly differentiate among them. Species proportion and local stand density were checked within a 10-meter circle centered on each target tree. In mixed stands, a tree could be selected if the other species represented between 40 and 80% of the basal area of the neighboring trees. These thresholds were chosen to mark the contrast in composition between mixed and pure stands. Lastly, for low and medium density respectively, RDI ranged from 0.25 to 0.4 and from 0.5 to 0.75 within the 10-meter circle. We obtained a final stratified sampling of 216 trees as follows:

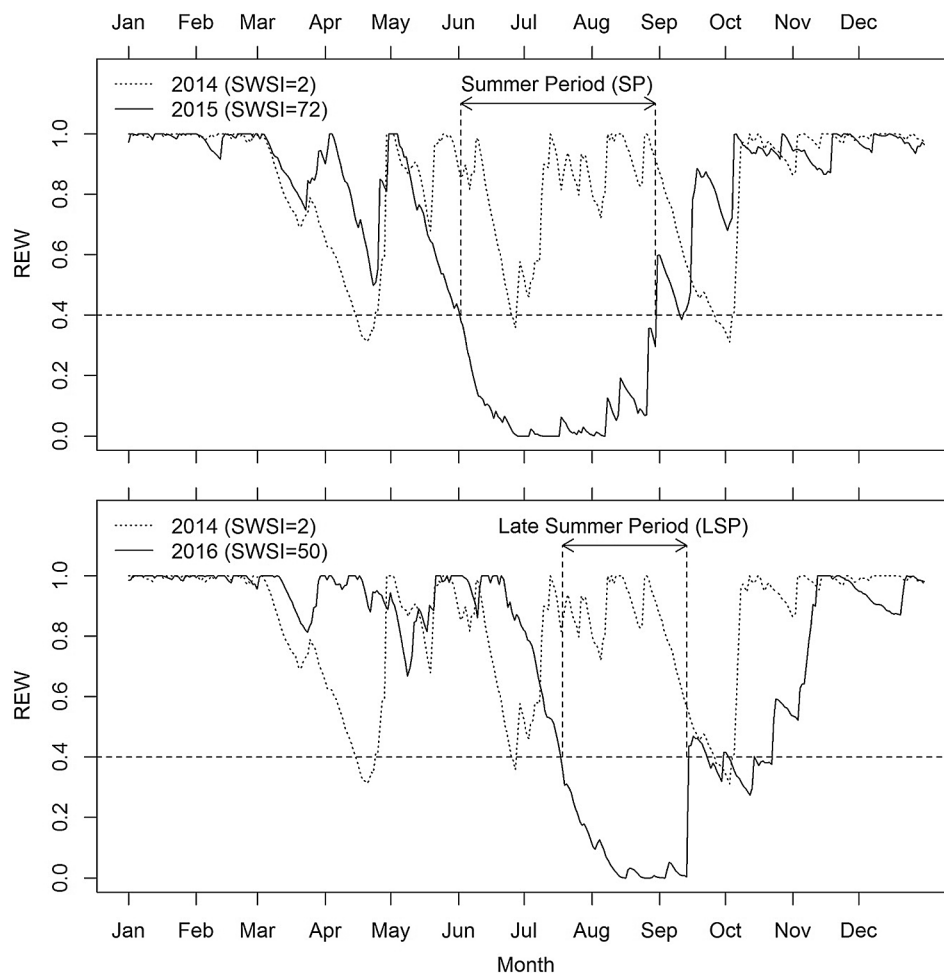


Fig. 1. Soil Relative extractable water (REW) for 2014 (dotted line, a and b), (a) 2015 (solid line) and (b) 2016 (solid line) for one year. The stress periods (summer period (SP) and late summer period (LSP)) are the periods when REW remained below the 0.4 threshold. SWSI is the Soil Water Stress Index of the year.

2 species × 2 compositions × 2 densities × 3 sizes × 3 individual replicates
 × 3 plot replicates = 216 trees

2.3. Drought periods

In order to compare the different years in term of water stress, we calculated the daily soil Relative Extractable Water (REW) using climate variables from the SAFRAN and ISBA analytical platforms (Météo-France, Durand et al., 1993); we also recorded the average soil characteristics of our plots. REW represents the water available for plants in the soil (Granier et al., 1999). Evapotranspiration (ETP) was estimated with the Penman-Monteith equation (Penman, 1948; Monteith, 1981). A soil water holding capacity (SWHC) of 85 mm was used to estimate REW. This value was calculated as in Toigo et al. (2015b) from the mean SWHC in our plots, which we measured by digging soil profile pits and describing the textural class of each horizon to determine the pedotransfert class for our soil (Al Majou et al., 2008). We considered that a stress event had occurred when the REW fell below the 0.4 threshold (Fig. 1); which the literature defines as the limit below which trees begin to acclimate to their environmental conditions, particularly to water availability (Granier et al., 1999). We considered that the stress period had ended when the REW moved back above the 0.4 threshold. In order to quantitatively describe the drought for each year, we calculated a Soil Water Stress Index (SWSI) following the stress index used in the Bijlou model (<https://appgeodb.nancy.inra.fr/biljou/>) from Granier et al. (1999):

$$SWSI = \frac{\sum (0.4 - REW_i)}{0.4} \tag{1}$$

where REW_i are the REW daily values for all days i of a given year where REW is below 0.4. Therefore the SWSI is a measure of the magnitude of the drought stress for a given year. It equaled 2 for the year 2014, 72 for the year 2015 and 50 for the year 2016. Given these contrasted values of REW and SWSI which are in accordance with the literature (Granier et al., 1999), we can consider that virtually no stress periods were observed for the year 2014, which we considered as an unstressed year. An intense stress period was observed during the 2015 summer, starting June 2nd and ending August 30th; we characterized this as the summer period (SP), which was stressed for 2015 and unstressed for 2014. A stress period also occurred during the year 2016, lasting from July 17th until September 13th; we characterized this period as the late summer period (LSP), which was stressed for 2016 and unstressed for 2014.

2.4. Tree radial growth

We used manual band dendrometers (DB20, Environmental Measuring Systems, Brno, Czech Republic) to monitor circumference increment at breast height. We left the bark on the tree in order to take as much as possible into account all variations in circumference and to monitor continuous growth (Deslauriers et al., 2003). The first measurements were taken one year after attaching the dendrometers to allow for a stabilization period (Drew and Downes, 2009). We recorded circumference variations as measured by the dendrometers every two

weeks during the growing season and monthly during the winter, for a total of 15,617 observations over the three years of the study (2014, 2015 and 2016).

To determine tree short-term response to a drought period, we also calculated the circumference increment between the beginning and the end of the drought period (Fig. 1).

We then defined resistance to drought as the ratio between the circumference increment during the stress period, when stomatal conductance should be minimal (Granier et al., 1999), and the increment during the same period for a year when water was not a limiting factor:

$$R_s = \frac{CI_{SP2015}}{CI_{SP2014}} \times 100 \quad (2)$$

where R_s is the Resistance to the drought event, $CI_{SP 2015}$ is the difference in circumference increment between June 2nd and August 30th in 2015 corresponding to the stress period and $CI_{SP 2014}$ is the circumference increment during the same period for the unstressed year 2014.

We did not calculate drought resistance for the LSP because the growth rate was very slow for both species during the LSP in 2014 and did not, in fact, differ from zero for pines.

2.5. Statistical analyses

To test density, stand composition and tree size effects, we performed an analysis of variance with linear mixed-effect models. We took into account the spatial structure of the sampling design (repetitions at the stand level and repetitions at the plot level in the stand) by introducing nested random effects into the model.

When the variance of the residuals was significantly different among groups (tree species, stand density, stand composition, tree size), we added a variance model to estimate the standard deviation per group (Pinheiro and Bates, 2000).

We performed all statistical analyzes with the R Software (R Core Team (2017)). We used the “lme” function of the “nlme” package (Pinheiro et al., 2017) to fit the linear mixed-effect models. We used model showed in Eq. (3) to assess the effects of the different factors for both species. We then applied the model showed in Eq. (4) for each species.

$$CI_{t,p,s} = m + S_i + G_j + D_k + C_l + SG_{ij} + SD_{ik} + SC_{il} + GD_{jk} + GC_{jl} + DC_{kl} + r_s + r_{s,p} + \varepsilon_{t,p,s} \quad (3)$$

$$CI_{species_t,p,s} = m + G_j + D_k + C_l + GD_{jk} + GC_{jl} + DC_{kl} + r_s + r_{s,p} + \varepsilon_{t,p,s} \quad (4)$$

where $CI_{t,p,s}$ and $CI_{species_t,p,s}$ are the circumference increment for tree t , in plot p , in stand s ; m is the intercept; S_i represents the effect of the species factor; G_j represents the effect of the size group factor; D_k is the effect of the density factor; and C_l is the effect of the composition factor. i, j, k and l stand for species, size group, density and composition factors, respectively; SG_{ij} , SD_{ik} , SC_{il} , GD_{jk} , GC_{jl} and DC_{kl} represent the interaction effects between the different factors; r_s represents the stand random effect and $r_{s,p}$ the plot random effect nested into the stand random effect; $\varepsilon_{t,p,s}$ are the residuals of the model. The interactions between factors were not significant and were removed from the model.

3. Results

In the first part of this section, we provide the overall results of the models. Then in a second part we detail these results according to the studied hypotheses.

3.1. Models outcomes

3.1.1. Circumference increment

Fig. 2 for sessile oak and Fig. 3 for Scots pine show the circumference increment (CI) for each stand density, composition and tree size categories. The two sub-figures on the left (Fig. 2a and c) correspond to the unstressed period (i.e. the year 2014), whereas the two sub-figures on the right (Fig. 2b and d) correspond to the stressed period (i.e. years 2015 for the summer period and 2016 for the late summer period). The two sub-figures at the top (Fig. 2a and b) correspond to the summer period, whereas the two sub-figures at the bottom (Fig. 2c and d) correspond to the late summer period.

Both oaks and pines had the same CI during the summer period without stress ($4.58 \text{ mm} \pm 0.23 \text{ SE}$). During the stressed summer period, oaks had higher CI than did pines ($+0.47 \text{ mm} \pm 0.23 \text{ SE}$). CI during the late summer stressed period was low for oaks ($0.53 \text{ mm} \pm 0.07 \text{ SE}$), and not significantly ($p\text{-value} > 0.05$) different from zero for pines (Figs. 2 and 3).

3.1.2. Drought resistance

We studied drought resistance only for the SP (Fig. 4). Indeed, during the LSP in 2014, for the unstressed year, average tree growth did not differ from zero and we could not estimate drought resistance since the annual growth had almost been completed by that period.

Mean drought resistance was $76.06\% \pm 5.9 \text{ SE}$ for both species (Fig. 4). Density alone did not change ($p\text{-value} > 0.05$) resistance for either species (Table 2). Tree size had no effect ($p\text{-value} > 0.05$) on pine resistance (Table 2). We did find a tree-size effect on resistance for oaks; medium-size oaks had 7.5% higher ($p\text{-value} < 0.05$) resistance than large ones. However, small oaks had a 17% greater but only marginally significant ($p\text{-value} = 0.057$), resistance than did large ones (Table 2).

Finally, stand composition had an effect on resistance, with opposite responses for the two species. Oak resistance was 98.6% in mixtures while it was only 72.1% in pure stands ($p\text{-value} < 0.05$) whereas pine resistance was 79.3% in mixtures and reached 84.2% in pure stands (marginally significant $p\text{-value} = 0.065$) (Table 2, Fig. 4).

3.2. Evaluation of the hypotheses

3.2.1. Stand density effect

Oaks had greater growth in lower density stands than in medium-density stands (Fig. 2). This result was found for both the SP and LSP periods of the unstressed year ($p\text{-value} < 0.05$) ($+1.52 \text{ mm} \pm 0.39 \text{ SD}$ and $+0.36 \text{ mm} \pm 0.11 \text{ SD}$, for summer period and late summer period, respectively), as well as for the two stressed periods (summer and late summer stress, $p\text{-value} < 10^{-2}$) ($+1.31 \text{ mm} \pm 0.30 \text{ SD}$ and $+1.02 \text{ mm} \pm 0.22 \text{ SD}$, for the summer and late summer stress periods, respectively) (Fig. 2). The statistics of the models are detailed in Appendix A.

For pine, density had no effect on growth in any of the periods, whether stressed or unstressed (Fig. 3).

3.2.2. Stand composition effect and interaction with density

The only case for which a composition effect was significant was for the late summer stressed period (2016) (Figs. 2d and 3d), see Appendix A for statistical values. During this period, a composition effect was found for both species, but in opposite directions: while oak CI was significantly greater ($p\text{-value} < 0.05$) in mixtures ($0.66 \text{ mm} \pm 0.24 \text{ SE}$) than in monocultures (Fig. 2d), pine CI significantly ($p\text{-value} < 0.05$) decreased in mixtures ($-1.43 \text{ mm} \pm 0.34 \text{ SE}$) compared to monocultures (Fig. 3d). These differences between mixtures and monocultures were modulated by the density effect: the stand composition effect was significant only in the medium-density stands for both species. For oaks, growth remained greater ($p\text{-value} < 10^{-2}$) in low-density stands compared to medium-density stands regardless of

Pinus sylvestris

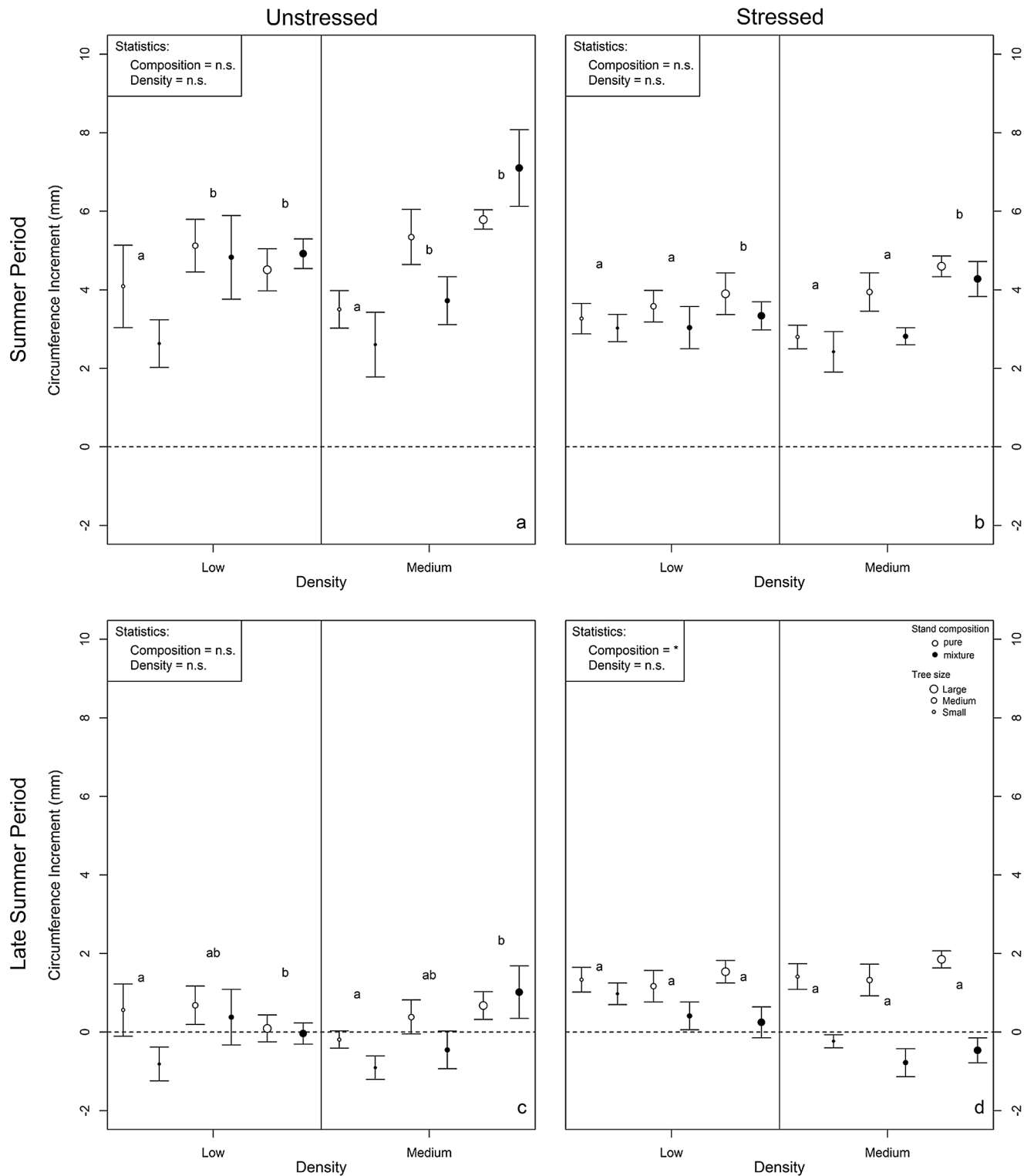


Fig. 3. Mean circumference increment (mm) for *Pinus sylvestris*. The lefthand figures (a, c) correspond to unstressed periods (year 2014), and the righthand figures (b, d) correspond to stressed periods (year 2015 (b) and 2016 (d)). The top figures (a, b) correspond to the summer period (the same Julian days between 2014 and 2015), and the bottom figures (c, d) to the late summer period (the same Julian days between 2014 and 2016). Values are given for the two densities (low and medium). Open circles are pure stands, solid circles are mixed stands. Circle sizes reflect tree size class and letters above the circles (a and b) show significance among them. The bars show standard errors.

difference between small and large trees reached $4.07 \text{ mm} \pm 0.47 \text{ SE}$ for oaks and $2.34 \text{ mm} \pm 0.48 \text{ SE}$ for pines, see Appendix A for statistical values. This size effect were also observed (p-value < 0.05) for

oak during the late summer period without stress, whatever the stand density (Fig. 2c). The difference between small and large trees was reduced during the summer stressed period (2015) compared to the

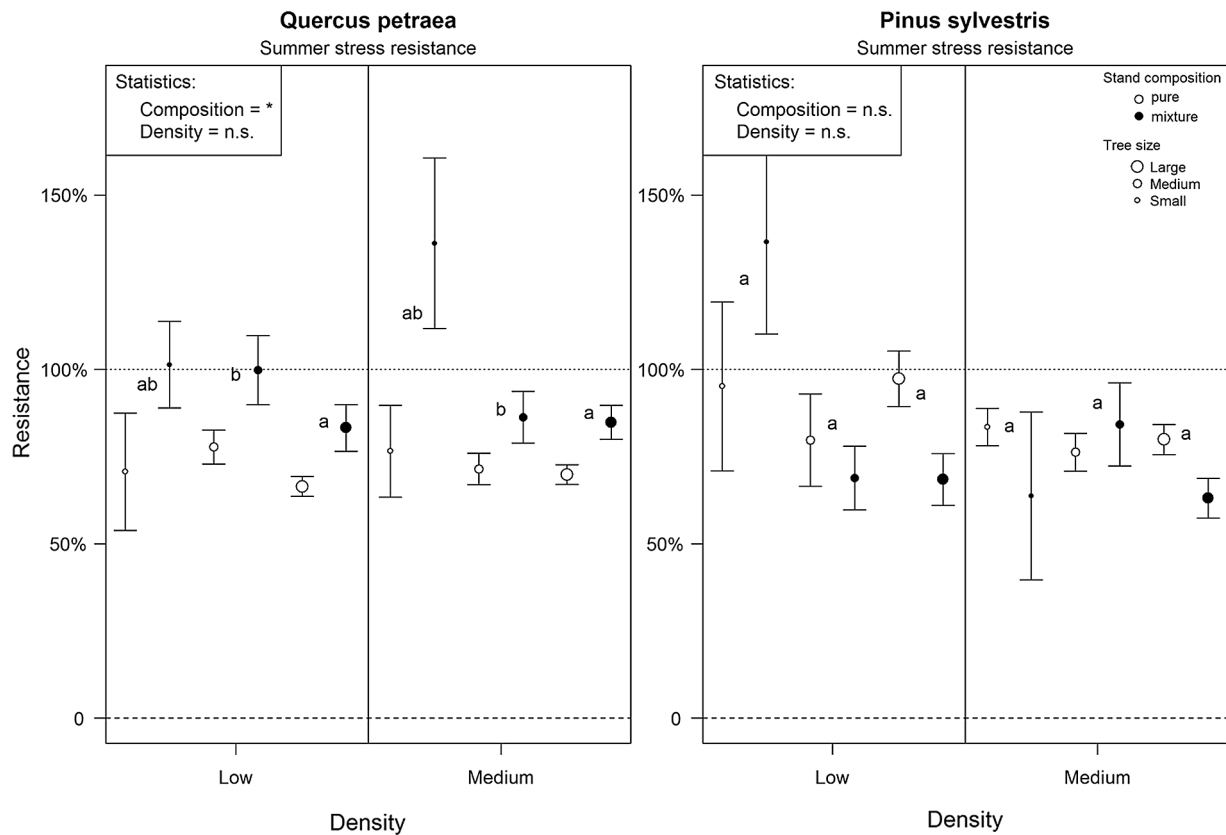


Fig. 4. SP mean resistance for *Quercus petraea* and *Pinus sylvestris* for the two different densities (low and medium). Open circles are pure stands and filled black circles are mixed stands. Circle sizes reflect tree size class and letters (a and b) show significance among them. The bars show standard errors.

Table 2

Estimated coefficients (Est.), standard errors (Std. error) and p-values for resistance during SP (2015 vs. 2014). The intercept of the model represents the resistance percentage of large trees in lower densities and pure stands.

	Resistance SP 2015		
	Value	Std. error	p value
<i>Quercus petraea</i>			
Intercept	67.517	3.540	0.000
Size_Medium	7.492	3.588	0.040
Size_Small	17.047	8.823	0.057
Density_medium	-0.092	4.128	0.983
Composition_mixture	17.534	4.212	0.025
<i>Pinus sylvestris</i>			
Intercept	89.169	4.966	0.000
Size_Medium	-0.341	5.891	0.954
Size_Small	14.197	10.534	0.182
Density_medium	-9.097	5.183	0.154
Composition_mixture	-14.818	5.183	0.065

unstressed period (2014): 2.52 mm ± 0.36 SE and 1.27 mm ± 0.29 SE for oaks and pines, respectively (Figs. 2a and b; 3a and b). The only case where tree size did not influence CI was for pines in pure stands during the late stressed period (Fig. 3d).

4. Discussion

4.1. Stand density effect

For sessile oak though not for Scots pine, our results show greater growth in low-density stands for every period. Our first hypothesis is therefore confirmed for oaks but rejected for pines.

Reducing stand density (i.e. thinning effect) decreases competition

and increases the water available for each tree (Bréda et al., 1995). Thanks to higher water availability, the growth rate can increase; this has already been observed at the annual scale and is a species-dependent response. Oak can show a relevant growth response while pine has weaker circumference increment after thinning in adult stands (Bréda et al., 1995; Dhôte et al., 2000; Mäkinen and Isomäki, 2004).

Our results at the seasonal scale, during a drought period, confirm that thinning effect is species dependent with a positive and significant response for oak, and a non-significant response for pine. Similarly, Primicia et al. (2013) found a weak thinning effect for Scots pine in adult stands at the seasonal scale. Pine seems to have a positive growth response when thinning is relatively intense (Mäkinen and Isomäki, 2004) and when the thinning occurred at least three years before (Primicia et al., 2013). In our experiment, thinning occurred two years before and did not exceed 30% of initial basal area, which was probably insufficient to stimulate any observable effect on pine growth.

4.2. Stand composition effect

Our second hypothesis was rejected for both species, as we did not find any overall effect of stand composition during the two drought periods for either of the two species. We found the same growth during drought periods in monocultures and mixed stands for both species in the lower density class, but not in the medium density class, for the late summer period.

This result highlights that there was no competition reduction in our mixed stands during any of the drought periods. In the case of competition reduction, at least one species should have shown greater growth compared to its corresponding monoculture, while the second species should have had at least the same growth rate as its corresponding monoculture (Loreau and Hector, 2001). The lack of mixture effect we observed could be explained by the presence of a clay layer in

the soil at around 40 cm in depth. Root penetration would likely be negatively affected by this layer which acts as physical barrier (Meinen et al., 2009). We do not know the total thickness of this layer, but it is present on our plots down to at least one meter (maximum depth of our soil pits). The fine root densities of oaks and pines are low (Bréda et al., 1995; Coomes and Grubb, 2000) below one meter in depth. This clay layer could have impaired efficient sharing of the root distribution space, necessary for niche complementarity, because, in the remaining upper 40 cm of soil, nutrient content drives the fine root density in temperate forests (Coomes and Grubb, 2000). On the other hand, our result does show that competition did not increase in the mixtures compared to the monocultures.

4.3. Stand composition effect in higher-density stand

We observed a pronounced mixture effect in the medium-density stands for both species during LSP, suggesting that competition pressure depends on both composition and stand density. Our third hypothesis is partially confirmed. The higher the density, the greater the growth in mixtures compared to monocultures, though this was true only for oaks. Indeed, for pines, the effect was opposite. What is more, growth was greater for pines in monocultures than in mixed stands with medium density.

As shown in other studies, depending on species associations or stand density, interaction can be competitive (i.e. negative interaction) or mutualistic (i.e. positive interaction) (Boyden et al., 2005; Forrester et al., 2013; Toigo et al., 2015a). Several processes simultaneously affect tree growth in mixtures and influence tree sensitivity to drought (Forrester, 2015). Indeed, nutrient or light availability can be greater in mixtures (Richards et al., 2010; Augusto et al., 2015) and species water use efficiency can increase compared to monocultures (Forrester, 2015). An optimal proportion of the other species should decrease the competition effect in case of complementarity (del Rio and Sterba, 2009; Perot and Picard, 2011; Manso et al., 2015; Lu et al., 2016; Prevosto et al., 2016). For instance, species can share soil root distribution space if their root prospection volume differs (Richards et al., 2010). When oaks grow with another species, they can prospect deeper soil layers for root distribution, and this decreases competition for water. Niche complementarity occurs in the above-ground component as well. Trees can have different degrees of shade tolerance (Niinemets, 2010) with the less shade-tolerant species occupying the upper canopy and the more shade-tolerant species the understory, each taking advantage of the neighboring stand structure to increase their light interception (Richards et al., 2010). In this way, competition is decreased by a physical complementarity mechanism.

Moreover, in lower-density stands, trees are more distant from each other and this limits their interactions (Balandier et al., 2008; Forrester and Tang, 2016). In sites where soil fertility is low, even if light availability is high, we can expect an increase in competition (e.g. for nutrients), but when competition decreases – for example, due to heavy thinning, neighborhood interactions become negligible or even absent (Baribault and Kobe, 2011). When stand density increases, neighborhood interactions become more important and mixed stands may be able to compensate for the increase in competition due to increasing stand density. Nevertheless, the complementarity effect is likely limited by an optimal stand density level.

4.4. Smaller trees are not more sensitive to drought

Our fourth hypothesis is rejected for both species. Resistance to the drought events was the same for all tree sizes for both species. However, circumference increment during all the periods studied was greater for large trees, independently of stand density or composition.

Lebourgeois et al. (2014) found that climate effects on growth were not dependent on tree size whereas others authors found similar drought resistance (annual scale) among tree sizes but a slower

recovery rate for small trees (Martinez-Vilalta et al., 2012; Trouvé et al., 2017).

In our study, drought sensitivity was the same for all tree sizes for both species; therefore, differences in tree size cannot be due to greater drought resistance. Size differences are more likely due to other factors such as light or nutrients (Coomes and Grubb, 2000; Baribault and Kobe, 2011; Augusto et al., 2015; Knapp et al., 2016). Small trees are expected to have smaller root biomass or at least lower root water uptake (Balandier et al., 2008); in other words, they are limited by the uptake capacity of their roots. In addition, small trees are in the lowest part of the canopy, and therefore have less accessibility to light (Niinemets, 2010). In an even-aged forest, light interception is greater in the upper part of the canopy (Niinemets, 2010), so the trees occupying that stratum benefit from increased photosynthesis and growth, thus amplifying size differences over time (Trouvé et al., 2017). This would explain size differences more than drought sensitivity.

4.5. Seasonal drought resistance differs among species and varies with stand composition

Even though we found a high level of resistance for both species during the SP, the stand composition effect was opposite between them. Indeed, resistance was enhanced by the mixture for oak and weakened for pine.

For some species associations, niche complementarity (Loreau and Hector, 2001) does not occur; tree diversity does therefore not necessarily enhance drought resistance (Grossiord, 2014).

Evergreens and broadleaved species do not function in the same manner (Richards et al., 2010; Sohn et al., 2016), and this is even truer for isohydric and anisohydric species (Farquhar et al., 1980; Buckley, 2005; Levesque et al., 2014). During a drought period, whereas pine (an isohydric species) reduces stomatal conductance to avoid embolism (Buckley, 2005), oak (an anisohydric species) maintains a significant level of transpiration (Epron and Dreyer, 1990; Grossiord et al., 2014; Page et al., 2016). Thus the carbon fixation rate for oak is higher than for pine during stressed periods and this leads to higher seasonal drought resistance values. Oaks in mixtures can take advantage of the pine's more conservative strategy and benefit from more water availability during drought than they would with conspecific neighbors (Loreau and Hector, 2001; Balandier et al., 2009; Pretzsch and Schütze, 2009). Whether or not pines are competing with oaks for the same water – as, for example, with certain soil constraints such as the presence of a clay layer (reduction in soil volume prospected by the roots), the oak's strategy to use more water during drought stress likely decreases water availability for the pines in the mixture. This leads to an increase in interspecific competition rather than complementarity, and would be beneficial to the more competitive species (oak) and detrimental to the other (pine).

Finally, there was no mixture effect at the annual scale for either species (data not shown), though, overall, pine trees suffered more than oaks from the drought events; indeed, pine annual growth dropped to the same level as oak growth in years with droughts, while it was greater than oak growth during the year without stress.

5. Conclusion

Mixing stand composition and reducing stand density are two of the strategies currently being considered to face climate change. In our study, growth was greater in the low-density stands for oaks only; pine growth did not differ between the two densities. No overall stand composition effect on growth was found for either species, though oaks in mixtures did show more growth than pines during LSP in the medium-density stands. Conversely, pines showed better growth in monocultures. Probably inter-specific competition increased with increasing stand density. Oaks were more resistant to summer drought than were pines, especially when they were growing in mixtures.

Summer drought resistance did not depend on tree size for either species. Further investigations are needed to better understand how the two species use water resources throughout the year when drought events occur in order to better understand the complexity of the interactions in mixtures compared to monocultures.

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Appendix A. Statistics results of models for circumferences increments during stress periods.

	SP 2014			LSP 2014			SP 2015			LSP 2016		
	Est.	Std. error	p value	Est.	Std. error	p value	Est.	Std. error	p value	Est.	Std. error	p value
<i>Quercus petraea</i>												
Intercept	7.96	0.46	< 10 ⁻³	1.13	0.16	< 10 ⁻³	5.63	0.34	< 10 ⁻³	2.24	0.21	< 10 ⁻³
Size_Medium	-2.03	0.53	< 10 ⁻³	-0.45	0.19	0.020	-1.15	0.40	0.005	-0.52	0.18	0.006
Size_Small	-4.07	0.47	< 10 ⁻³	-0.65	0.16	< 10 ⁻³	-2.52	0.36	< 10 ⁻³	-1.02	0.19	< 10 ⁻³
Density_medium	-1.52	0.39	0.012	-0.36	0.11	0.022	-1.31	0.30	0.007	-1.02	0.22	0.004
Composition_mixture	-0.45	0.40	0.341	-0.11	0.11	0.397	0.41	0.30	0.270	0.66	0.24	0.046
<i>Pinus sylvestris</i>												
Intercept	5.52	0.46	< 10 ⁻³	0.75	0.30	0.016	4.27	0.30	< 10 ⁻³	1.76	0.32	< 10 ⁻³
Size_Medium	-0.65	0.50	0.197	-0.20	0.34	0.563	-0.69	0.29	0.019	-0.29	0.21	0.168
Size_Small	-2.21	0.50	< 10 ⁻³	-0.78	0.31	0.014	-1.27	0.29	< 10 ⁻³	0.03	0.21	0.872
Density_medium	0.32	0.41	0.486	-0.08	0.26	0.766	0.15	0.24	0.570	-0.44	0.34	0.236
Composition_mixture	-0.42	0.43	0.400	-0.53	0.26	0.138	-0.55	0.32	0.181	-1.43	0.34	0.013

Estimated coefficients (Est.), standard errors (Std.Error) and p-value of the circumferences increment during stress periods (Summer Period (SP) for 2014 and 2015 and Late Summer Period for 2014 and 2016). The fixed effects were the size class, the density and the composition. Random effects were the site and the plot into the site.

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