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Mixing oak and pine trees does not improve the functional response to severe drought in central French forests

Damien Bonal¹ · Mathilde Pau² · Maude Toigo^{2,3} · André Granier¹ · Thomas Perot²

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Abstract

• **Key message** Mixing sessile oak and Scots pine in central France to reduce intraspecific competition for water resources did not improve the ability of these two species to withstand severe drought during the summer.

• **Context** In order to reduce the impact of increasingly extreme droughts on forests, managers must adapt their practices to future climate conditions. Maintaining a greater diversity of tree species in temperate forest ecosystems is one of the recommended options.

• **Aims** We addressed how interactions between sessile oak and Scots pine in mixed forests in central France affect their functional response to drought.

• **Methods** We characterized the carbon isotope composition ($\delta^{13}\text{C}$) in the tree growth rings formed during wet (2001, 2007) or dry (2003, 2004) summers for each of the two

species growing both in pure and in mixed stands in order to compare the effect of stand composition on variations in carbon isotope discrimination ($\Delta^{13}\text{C}$) among contrasted years.

• **Results** The severe drought in 2003 induced a strong decrease in $\Delta^{13}\text{C}$ for all trees and in all stands as compared to 2001. This decrease was greater in pine than in oak. There was no significant difference between pure and mixed stands in the response of either species to drought.

• **Conclusion** Mixing sessile oak and Scots pine in stands in central France does not improve the ability of either species to withstand severe drought during the summer.

Keywords Climate change · Carbon isotope composition · Carbon isotope discrimination · Community ecology · Functional ecology

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Contribution of the co-authors TP and DB initiated the project and designed the experiment. MT and TP collected the samples. MP and AG selected the years for the study period. MP prepared all samples. TP and MP carried out the statistical tests. MP, TP, AG and DB analysed the data, and all authors contributed to the manuscript.

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1 Introduction

Due to their longevity, trees must not only be adapted to their current climatic conditions, but also be able to adapt to future ones. Yet, in the context of climatic changes, a relatively sudden rise in temperatures accompanied by an increase in the frequency and intensity of droughts is expected at temperate latitudes in the northern hemisphere over the next decades (IPCC 2013) and this is likely to dramatically affect forests. Indeed, extreme droughts cause stomatal closure (Granier et al. 2007), leading to a decrease in both photosynthesis (Saxe et al. 2001) and secondary growth (Bréda and Badeau 2008; Toïgo et al. 2015). Droughts induce fine-root mortality (Jany et al. 2003) which further limits a tree's ability to absorb water. Finally, droughts can sometimes cause partial or total defoliation (Bréda et al. 2006) and ultimately tree death (Allen et al. 2010; McDowell et al. 2008).

In order to limit the impact of extreme droughts on forests, managers must adapt their practices to future climate conditions. Many studies have shown the benefits of species-diverse forests over mono-specific ones (Gamfeldt et al. 2013; Jactel and Brockerhoff 2007; Knoke et al. 2008; Perot et al. 2013; van der Plas et al. 2016). Some of these studies have suggested that mixed forests might be better adapted to soil drought, since the impact of drought on tree growth or tree transpiration was found to be lower in mixed forests than in pure ones (Grossiord et al. 2015a; Lebourgeois et al. 2013; Pretzsch et al. 2013). These results encourage forest managers to promote greater diversity of tree species in temperate forest ecosystems in order to limit the impact of extreme droughts on forests. However, other results suggest that this pattern cannot be generalized. Indeed, in various forest types across Europe, greater tree species diversity has not always been found to improve resistance to drought (Forrester et al. 2016; Grossiord et al. 2014c; Merlin et al. 2015). Negative effects have even been observed in some boreal and temperate forests (Grossiord et al. 2014b; Toïgo et al. 2015): drought affected tree growth more in mixtures than in pure stands. The effect of species mixture on drought resistance depends on species identity, forest type and local environmental conditions (precipitation, drought, soil characteristics etc.) (Grossiord et al. 2015b). Further work is therefore needed to address the effect of species mixture on the resistance of tree species and forest communities to drought with a view to developing forest management strategies adapted to climate change.

The impact of drought on tree function has been extensively studied over the past decades. Limited soil water availability induces a series of short- or long-term biophysical, physiological and morphological responses in trees, thus allowing them to acclimate and adapt to adverse conditions and, hopefully, survive (e.g. Bréda et al. 2006; Chaves et al. 2003; McDowell et al. 2008). Typical plant responses to drought stress include leaf stomatal regulation and reduced carbon assimilation rates. Of the two reactions, stomatal conductance for water vapour is affected to a greater extent than is carbon assimilation and a concomitant decrease in the ratio of internal leaf CO_2 to ambient CO_2 concentrations occurs during the period when the carbon is fixed (Farquhar et al. 1989). During photosynthetic assimilation of atmospheric CO_2 , it has been shown that plants discriminate against molecules of CO_2 containing ^{13}C , because the heavier isotope diffuses more slowly to the site of carboxylation and reacts less readily than does ^{12}C with the primary carboxylating enzyme (Farquhar et al. 1982). This leaf-level discrimination is proportional to the ratio of internal leaf CO_2 to ambient CO_2 concentrations (Farquhar et al. 1982), and carbon isotope discrimination during photosynthesis ($\Delta^{13}\text{C}$, ‰) is thus influenced by drought (Ehleringer and Cooper 1988; O'Leary 1995). When photosynthate products move from the sites of carboxylation in the leaf to woody tissues, post-

photosynthetic fractionation processes and a mixing of molecules with different compositions occur (Gessler et al. 2014). These processes modify the isotope composition of the woody tissues and cause a partial decoupling between leaf and wood carbon isotope signals. However, this decoupling remains moderate and estimates of $\Delta^{13}\text{C}$ in wood still provide an interesting integrated record of the functional response of trees to drought (e.g. Ehleringer and Farquhar 1993; Saurer et al. 1995; Stewart et al. 1995; Bert et al. 1997).

Sessile oak and Scots pine have contrasting growth characteristics, and Scots pine is more sensitive to summer drought than is sessile oak (Merlin et al. 2015). Furthermore, Toïgo et al. (2015) showed that tree ring density decreased more in mixtures than in pure stands under drought conditions for both species, even though there was no clear trend for ring width. Herein, we address how interactions between sessile oak (*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.) trees in mixed forests in central France affected the functional response of the two species to a severe drought. To estimate the effect of stand composition, we used a retrospective approach: we compared $\Delta^{13}\text{C}$ found in the rings of mature trees of the two species, growing in either pure or mixed stands, among years with different climatic conditions (wet or dry growing seasons). We tested whether the decrease in $\Delta^{13}\text{C}$ between a wet and a dry summer differed according to tree species (oak vs. pine) and stand composition (pure vs. mixed stands). We also tested whether stand composition influenced the resistance, the recovery and the resilience of the species to severe soil drought conditions. If complementarity for water use is occurring among the two species under drought conditions, $\Delta^{13}\text{C}$ values should decrease less between wet and dry soil conditions in mixed than in pure stands. We, therefore, hypothesized that

- (i) the $\Delta^{13}\text{C}$ for both species would strongly decrease from a wet summer to an extremely dry one,
- (ii) the $\Delta^{13}\text{C}$ response to drought would not be similar among species, and
- (iii) species interactions would affect the $\Delta^{13}\text{C}$ response of both species to severe drought with a lower decrease in $\Delta^{13}\text{C}$ expected in mixed stands than in pure ones.

2 Material and methods

2.1 Study site and species

A precise description of the study site is presented in Toïgo et al. (2015); only the most important features are given below. The site (47° 82' N, 2° 48' E) is located in north-central France in the Orléans forest, which covers 35,000 ha. The climate is semi-continental with mild rainy winters and warm dry summers. The mean annual temperature is 11.2 °C, with a mean maximum temperature of 24.0 °C during summer and a mean

minimum temperature of 1.5 °C during winter. The mean annual rainfall is 739 mm (data from the Irstea weather station at Nogent-sur-Vernisson from 1980 to 2010). The soil is composed of sand on a dense clay layer. The clay layer can cause waterlogging in winter while the top layer of sand severely constrains vegetation growth during summer drought events.

The species under study were Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.), both emblematic commercial species in Europe. These species grow in both pure and mixed stands in north-central France and have contrasting characteristics (Bréda and Badeau 2008; Bréda et al. 2006; Eilmann et al. 2006; Merlin et al. 2015; Michelot et al. 2012). Notably, they use different strategies to cope with periods of severe drought. Sessile oak has a deep root system with a large taproot and strong lateral roots (Zapater et al. 2011), whereas Scots pine roots are mainly superficial (Grossiord et al. 2014a). During summer drought periods, stomatal closure to minimize the risk of xylem cavitation is more marked in Scots pine than in oak (Tyree and Cochard 1996; Zweifel et al. 2009).

2.2 Sampling design and tree ring measurements

To conduct this study, we used tree cores that were sampled by Toïgo et al. (2015) in early 2013. The sampling design and collection methods of these cores are described in Toïgo et al. (2015) and are briefly recalled below.

Twenty-four plots with a 15-m radius were selected: eight plots in pure oak stands, eight in pure pine stands and eight in oak–pine mixtures. The mean basal area was $20.1 \pm 3.7 \text{ m}^2 \text{ ha}^{-1}$ in pure oak stands, $30.5 \pm 8.6 \text{ m}^2 \text{ ha}^{-1}$ in pure pine stands and $28.4 \pm 4.7 \text{ m}^2 \text{ ha}^{-1}$ in mixed stands. In the mixtures, the mean basal area ratio of oak represented $40.4 \pm 10.5\%$ of the total basal area (i.e. 59.6% for pines). The mean tree age was 66 years for oak in pure stands, 60 years for pine in pure stands and, respectively, 62 and 56 years for oak and pine in mixed stands. Finally, the mean tree height was 21 m for oak in pure stands, 20 m for pine in pure stands and, respectively, 20 and 23 m for oak and pine in mixed stands. In each plot, three dominant or co-dominant trees were sampled per species for a total of 48 oak and 48 pine trees.

A 5-mm internal diameter Pressler auger was used to collect a wood core at breast height on the north side of the trunk for each of the 96 trees. After drying, the cores were sawn into thin flat slices to make it possible to measure the X-ray density of each ring. Once prepared and radiographed, the cores were cross-dated and ring width measurements were taken (Toïgo et al. 2015).

2.3 Climate data and selection of the target years

Our objective was to conduct a retrospective analysis to compare tree response to drought during summer periods (July–

August) with different water limitation levels. To avoid a potential bias from tree ageing, the target period needed to be as short as possible; we, therefore, selected the 2001–2007 period which included an extreme drought in 2003. The selected years include (i) 1 year without water limitation in the late summer (wet year), taken as the reference year; (ii) 1 year with strong water limitations in summer (dry year) to test for drought effect and tree resistance to drought; (iii) 1 year that followed the dry year when water was also limited to test for the cumulative effect of drought and (iv) 1 year without water limitations after the dry year to test the trees' resilience and recovery ability to drought (resilient year).

To select our study period, the approach described in Grossiord et al. (2014c) was followed. We used the daily water balance model BILJOU© (Granier et al. 1999) to calculate the daily relative extractable soil water and the soil water stress index (SWSI) for each stand type. Stand characteristics used to parameterize the model (leaf area index, soil depth) were obtained from Toïgo et al. (2015). The daily relative extractable water is a dimensionless number and varies from 1 when the soil is at field capacity to 0 when the soil is at the wilting point. Water stress is assumed to occur when relative extractable water drops below a threshold of 0.4. It has been shown that below this threshold, the stomata close and radial growth stops (Granier et al. 1999). The SWSI reflects the intensity of soil water limitation for trees for a given day. To select the target years, we calculated the SWSI for the July–August period, i.e. during the heart of the summer drought.

Based on SWSI values, 2 years with extreme July and August droughts were identified: 2003 and 2006. However, 2006 followed several years with some level of water stress (2003 to 2005); we, therefore, discarded it as the target dry year because tree functioning might have been affected by the succession of previous dry years (Bréda and Badeau 2008). We selected 2001 as the wet year, 2003 as the dry year, 2004 as the year with an intermediate drought following the extreme drought in 2003 and 2007 as the resilient year without drought but which followed a series of years with water limitations (Fig. 1).

2.4 Selecting the part of the ring to analyse

For many species, including oak, the isotopic signature of the reserves accumulated during the year $n - 1$ strongly influences the isotopic signature of the wood formed during the spring of the subsequent year n (Lipp et al. 1991). Therefore, to avoid any delayed effects of accumulated reserves, it is essential to analyse the carbon isotope composition ($\delta^{13}\text{C}$) of the wood that was formed towards the end of the growing season and not the spring wood. Following Michelot et al. (2012), we analysed the last third of the ring for oak and the last quarter of the ring for pine for each selected year. This ensured that the

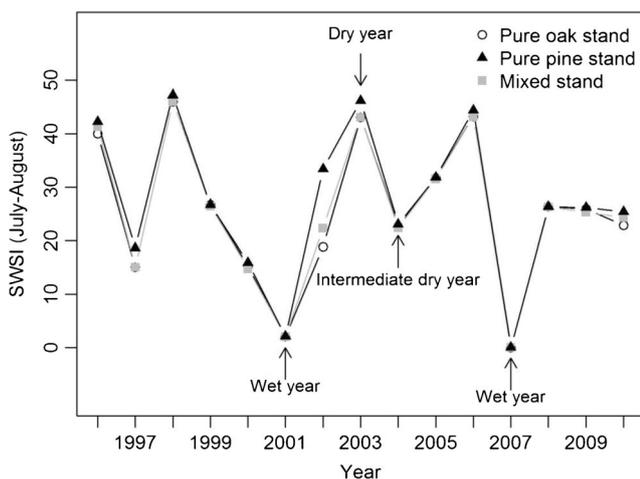


Fig. 1 Soil water stress index (SWSI) calculated with the BILJOU© model for the July–August period for the years 1999 to 2010. Arrows indicate years selected in this study

carbon isotope signature we obtained for each sample and each given year characterized the functioning of the selected trees during the second part of the growing season, i.e. under high soil water conditions during the wet years and under limited soil water conditions during the dry years.

2.5 Sample preparation

Sample preparation was conducted at the PTEF facility at INRA Nancy-Lorraine. For each core and each selected year, we oven-dried the cores at 50 °C for 48 h and then carefully separated the desired piece of wood from the rest of the ring with a scalpel. Of the 384 pieces initially planned (2 species × 2 stand composition types × 8 plots × 3 trees × 4 years), 56 were impossible to collect because the rings were not distinguishable. Each of the resulting 328 samples was then weighed.

For isotope analyses, around 1 mg of fine dry powder is needed. When the mass of the samples was above 4 mg, the whole piece of wood was ground into fine powder and put into tin capsules. However, since some powder is always lost during grinding, small samples were not ground. The following procedure was applied to avoid the risk of losing all the available biomass: When the dry mass of the ring samples was below 4 mg, the piece of wood was crushed into very small pieces with a scalpel; a subsample of 1 mg was then randomly selected and put into the tin capsules. Previous tests conducted at the PTEF facility showed that this procedure does not impact the results of the isotope analyses (N. Angeli, pers. comm.).

2.6 Isotopic analyses

Isotopic analyses were performed at the PTEF facility at INRA Nancy-Lorraine. The carbon isotopic ratio was measured in an IRMS isotope mass spectrometer (Isoprime 100,

Isoprime Ltd., Cheadle Hulme, UK) coupled with an elementary analyser (Elementar vario, ISOTOPE cube, Elementar Analysen Systeme GmbH, Hanau, Germany) and was expressed as the carbon isotope composition $\delta^{13}\text{C}$ (‰). Unfortunately, due to a temporary malfunction of the spectrometer, 44 samples were lost. Statistical analyses were therefore carried out on 284 samples (Table 1).

2.7 Carbon isotope discrimination

The carbon isotope discrimination for each sample and for each year ($\Delta^{13}\text{C}_y$, ‰) was calculated based on the $\delta^{13}\text{C}$ values of each year ($\delta^{13}\text{C}_y$, ‰) according to the following equation (Farquhar et al. 1982):

$$\Delta^{13}\text{C}_y = \frac{\delta^{13}\text{C}_{\text{ay}} - \delta^{13}\text{C}_y}{1 + 0.001 \times \delta^{13}\text{C}_y},$$

where $\delta^{13}\text{C}_{\text{ay}}$ (‰) is the mean annual atmospheric $\delta^{13}\text{C}$ of year y . We used $\delta^{13}\text{C}_{\text{ay}}$ data provided by GLOBALVIEW-CO2C13 (2008). $\delta^{13}\text{C}_{\text{ay}}$ changes continuously, becoming more and more negative independently of any other factor (GLOBALVIEW-CO2C13 2008). Our comparison of $\Delta^{13}\text{C}_y$ among years took these changes into account, thus making it possible to compare carbon and water use in plants among different years.

2.8 Statistical analyses

The resistance, recovery and resilience of trees to drought are influenced by a range of extrinsic and intrinsic factors. We evaluated these capacities based on variations in $\Delta^{13}\text{C}$ between 2 years ($\Delta^{13}\text{C}_{\text{year 2} - \text{year 1}} = \Delta^{13}\text{C}_{\text{year 2}} - \Delta^{13}\text{C}_{\text{year 1}}$, ‰) for each tree for the following pairs of years: 2001–2003, 2001–2004, 2001–2007, 2003–2004, 2003–2007 and 2004–2007. The year 2003 was considered representative of an extreme drought event. $\Delta^{13}\text{C}_{2003 - 2001}$ was then used as an indicator of the water stress suffered by a tree during the drought and, by extension, its degree of drought resistance: The more negative its $\Delta^{13}\text{C}_{2003 - 2001}$ value, the less a tree was resistant to drought. $\Delta^{13}\text{C}_{2007 - 2003}$ was used as an indicator of the recovery capacity of the tree after drought stress: The more positive its $\Delta^{13}\text{C}_{2007 - 2003}$, the more the tree recovered from drought. $\Delta^{13}\text{C}_{2007 - 2001}$ indicated the resilience capacity of the tree after drought stress: If $\Delta^{13}\text{C}_{2007 - 2001}$ was close to 0, there was high resilience; in contrast, if $\Delta^{13}\text{C}_{2007 - 2001}$ was negative, the tree was not resilient.

For each of the $\Delta^{13}\text{C}_{\text{year 2} - \text{year 1}}$ variables, we tested for species effect and stand composition effect separately. Species effect was tested only in pure stands. In order to check that our selection of target years was relevant in terms of the SWSI, we plotted the average $\Delta^{13}\text{C}$ with the variations in SWSI values (ΔSWSI) for each period and visually interpreted the data. We

Table 1 Number of observations by tree species, stand composition and selected year

Species	Stand composition	2001	2003	2004	2007
Sessile oak	Pure	15	14	10	15
	Mixed	19	15	14	17
Scots pine	Pure	24	23	21	22
	Mixed	21	18	18	18

could not statistically analyse the relationship between $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$ and ΔSWSI because of the strong correlations between the different periods. As 2004 was chosen because water stress was lower than in 2003, we, therefore, tested whether $\Delta^{13}\text{C}_{2003-2001}$ was indeed different from $\Delta^{13}\text{C}_{2004-2001}$ for each species.

For all analyses, we used linear mixed models to take into account the random effects related to our sampling structure (plot and tree random effects) (Pinheiro and Bates 2000). For some analyses, because the variance of the residuals was significantly different among groups (tree species or stand composition), we added a model variance to estimate the standard deviation per group (Pinheiro and Bates 2000). Simplified results without random-effect parameters or variance models are presented in the “Results” section. Detailed results are available in the supplementary material (see Tables S1, S2 and S3). All analyses were performed with the lme function of the nlme package (Pinheiro et al. 2016) in the R software, version 3.3.2 (R Core Team 2016).

3 Results

3.1 Intra- and inter-specific variabilities in $\Delta^{13}\text{C}$

For a given species, there was considerable variability in $\Delta^{13}\text{C}$ among individuals (Fig. 2) and this intraspecific variability was greater in oaks than in pines. On average, pine always had lower $\Delta^{13}\text{C}$ than oak (Fig. 2). For the year 2001 (a year without water limitation) and in pure stands (no species interactions), the average $\Delta^{13}\text{C}$ of pine (18.0‰) was significantly lower than that of oak (19.9‰) ($p < 0.001$).

3.2 Drought effect on $\Delta^{13}\text{C}$ and tree species effect in pure stands

The change in $\Delta^{13}\text{C}$ over time for both species in pure stands followed the expected pattern: $\Delta^{13}\text{C}$ was lower in dry years (2003, 2004) than in wet years (2001, 2007) (Fig. 2), with the lowest values in 2003 and the highest in 2007.

For pine, $\Delta^{13}\text{C}_{2007-2004}$ and $\Delta^{13}\text{C}_{2004-2001}$ did not significantly differ from 0 ($p > 0.10$), whereas $\Delta^{13}\text{C}_{2003-2001}$, $\Delta^{13}\text{C}_{2007-2001}$, $\Delta^{13}\text{C}_{2004-2003}$ and $\Delta^{13}\text{C}_{2007-2003}$ were

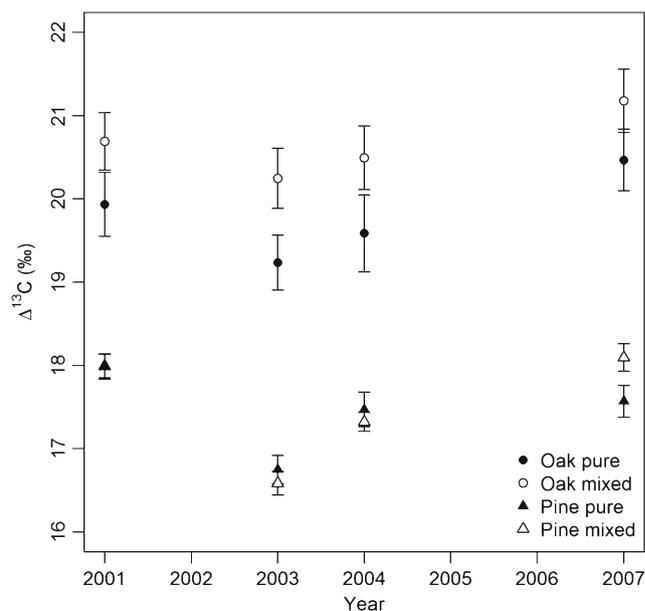


Fig. 2 Mean $\Delta^{13}\text{C}$ values for each year according to tree species and stand composition. Vertical bars represent standard errors of the mean

significantly different from 0 ($p < 0.05$, Table 3, Fig. 3). $\Delta^{13}\text{C}_{2003-2001}$ and $\Delta^{13}\text{C}_{2007-2001}$ were negative whereas $\Delta^{13}\text{C}_{2004-2003}$ and $\Delta^{13}\text{C}_{2007-2003}$ were positive. $\Delta^{13}\text{C}_{2003-2001}$ was significantly more negative than $\Delta^{13}\text{C}_{2004-2001}$ ($p < 0.001$, Table S3).

For oak, $\Delta^{13}\text{C}_{2007-2001}$, $\Delta^{13}\text{C}_{2007-2003}$ and $\Delta^{13}\text{C}_{2007-2004}$ were significantly different from 0 ($p = 0.020$, 0.003 and 0.048, respectively), whereas the other $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$ values were not ($p > 0.05$) (see results for pure oak stands in Table 3, Fig. 3). However, though $\Delta^{13}\text{C}_{2003-2001}$ did not significantly differ from 0 ($p = 0.064$, Table 3), when the stand composition effect was removed from the analysis (no mixture effect), the value did significantly differ from 0 ($\Delta^{13}\text{C}_{2003-2001} = -0.59$, $p = 0.004$). Finally, $\Delta^{13}\text{C}_{2003-2001}$ was more negative than $\Delta^{13}\text{C}_{2004-2001}$, but the difference was not statistically significant ($p = 0.226$, Table S3).

In pure stands, tree species effect was significant for $\Delta^{13}\text{C}_{2003-2001}$ and $\Delta^{13}\text{C}_{2007-2001}$ (Table 2): $\Delta^{13}\text{C}_{2003-2001}$ for oak was significantly less negative than the values for pine ($p < 0.01$), and $\Delta^{13}\text{C}_{2007-2001}$ for oak was significantly greater than the values for pine ($p < 0.01$).

3.3 Stand composition effect on $\Delta^{13}\text{C}$

For pine, mean $\Delta^{13}\text{C}$ values in pure and mixed stands in 2001, 2003 and 2004 did not significantly differ ($p > 0.10$). In 2007, the difference was around 0.5‰ but was still not significant ($p = 0.131$). We did observe a significant mixture effect on $\Delta^{13}\text{C}_{2007-2003}$ ($p = 0.003$) and $\Delta^{13}\text{C}_{2007-2004}$ ($p = 0.009$), but not on the other variations in $\Delta^{13}\text{C}$ between pairs of years ($p > 0.10$) (Table 3, Fig. 3).

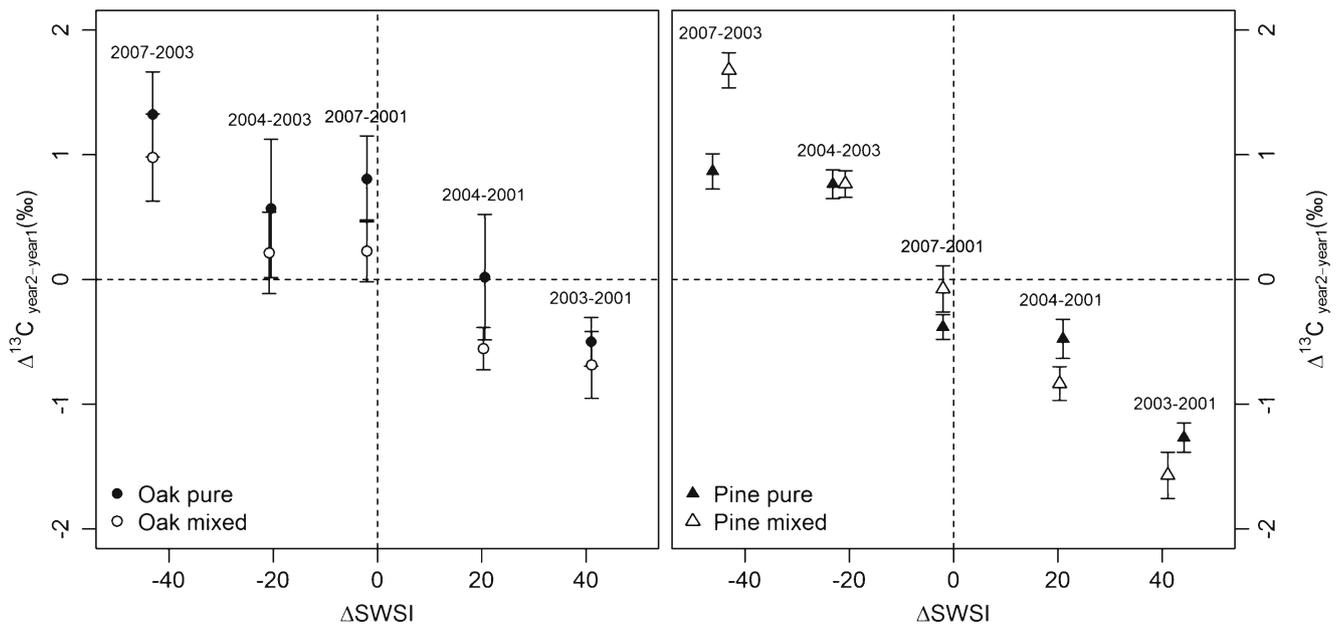


Fig. 3 Variations in carbon isotope discrimination between 2 years ($\Delta^{13}C_{\text{year 2-year 1}}$) according to variations in the soil water stress index between the 2 years (ΔSWSI) for each period (2003–2001, 2007–2003, 2007–2001, 2004–2003, 2004–2001) and each stand composition. For the sake of clarity, the values corresponding to 2007

–2004 are not shown. Horizontally, the upper part of the graph corresponds to an increase in $\Delta^{13}C$ between year 1 and year 2 and the lower part to a decrease. Vertically, the right side corresponds to an increasing drought intensity and the left side to a return to high soil moisture content

For oak, mean yearly $\Delta^{13}C$ values in pure stands were on average lower by about 1.0‰ than those in mixed stands (Fig. 2). Yet, this difference was not significant when all years were included in the model ($p = 0.132$) nor when the values for each year were tested separately: 2001 ($p = 0.153$), 2003 ($p = 0.058$), 2004 ($p = 0.237$) and 2007 ($p = 0.205$). We, therefore, conclude that there was no significant effect of stand composition on $\Delta^{13}C$ for oak (Table 3, Fig. 3).

4 Discussion

4.1 Intra- and inter-specific variabilities in $\Delta^{13}C$

The pine and oak trees differed strongly in carbon isotope discrimination, notwithstanding stand composition or year (Fig. 2). These results, which are consistent with previous studies that have shown a wide range of $\delta^{13}C$ values among

Table 2 Parameter estimates and associated p values for the model testing the effect of tree species on $\Delta^{13}C_{\text{year 2-year 1}}$. μ_0 is the value of $\Delta^{13}C_{\text{year 2-year 1}}$ estimated for pure pine stands. If μ_0 is significantly different from 0, then, $\Delta^{13}C_{\text{year 2-year 1}}$ is significantly different from 0 in pure pine stands. μ_1 is the difference in $\Delta^{13}C_{\text{year 2-year 1}}$ between pure

oak stands and pure pine stands. If μ_1 is significantly different from 0, then, the $\Delta^{13}C_{\text{year 2-year 1}}$ of pure oak stands is significantly different from that of pure pine stands. n = number of observations; Est. = parameter estimate; Std. err. = standard error of parameter estimate

$\Delta^{13}C_{\text{year 2-year 1}}$	Pine (n)	Oak (n)	Parameter	Est.	Std. err.	p value
2003–2001	23	13	Pine (μ_0)	-1.27	0.16	<0.001
			Oak–pine (μ_1)	0.79	0.25	0.007
2007–2001	22	13	Pine (μ_0)	-0.38	0.13	0.010
			Oak–pine (μ_1)	1.18	0.38	0.006
2007–2003	21	13	Pine (μ_0)	0.87	0.16	<0.001
			Oak–pine (μ_1)	0.45	0.38	0.254
2004–2001	21	10	Pine (μ_0)	-0.37	0.28	0.201
			Oak–pine (μ_1)	0.39	0.59	0.516
2004–2003	21	8	Pine (μ_0)	0.77	0.12	<0.001
			Oak–pine (μ_1)	-0.20	0.57	0.730
2007–2004	19	9	Pine (μ_0)	0.02	0.20	0.928
			Oak–pine (μ_1)	1.13	0.62	0.092

Table 3 Parameter estimates and associated p values for the model testing the effect of stand composition on $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$. μ_0 is the estimated value of $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$ for pure stands. If μ_0 is significantly different from 0, then, $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$ is significantly different from 0 in pure stands. μ_1 is the difference in $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$ between mixed stands and pure stands. If μ_1 is significantly different from 0, then, the $\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$ of pure stands is significantly different from that of mixed stands. n = number of observations; Est. = parameter estimate; Std. err. = standard error of parameter estimate

$\Delta^{13}\text{C}_{\text{year } 2 - \text{year } 1}$	Species	Pure (n)	Mixed (n)	Parameter	Est.	Std.err.	p value
2003 – 2001	Pine	23	17	Pure (μ_0)	-1.27	0.16	<0.001
				Mixed – pure (μ_1)	-0.32	0.25	0.226
	Oak	13	15	Pure (μ_0)	-0.44	0.22	0.064
				Mixed – pure (μ_1)	-0.25	0.39	0.538
2007 – 2001	Pine	22	17	Pure (μ_0)	-0.38	0.15	0.017
				Mixed – pure (μ_1)	0.32	0.26	0.237
	Oak	13	17	Pure (μ_0)	0.81	0.31	0.020
				Mixed – pure (μ_1)	-0.58	0.41	0.184
2007 – 2003	Pine	21	16	Pure (μ_0)	0.87	0.15	<0.001
				Mixed – pure (μ_1)	0.82	0.23	0.003
	Oak	13	15	Pure (μ_0)	1.32	0.36	0.003
				Mixed – pure (μ_1)	-0.35	0.49	0.495
2004 – 2001	Pine	21	17	Pure (μ_0)	-0.39	0.22	0.090
				Mixed – pure (μ_1)	-0.44	0.32	0.193
	Oak	10	14	Pure (μ_0)	0.02	0.5	0.972
				Mixed – pure (μ_1)	-0.57	0.53	0.303
2004 – 2003	Pine	21	16	Pure (μ_0)	0.78	0.12	<0.001
				Mixed – pure (μ_1)	0.01	0.18	0.974
	Oak	8	12	Pure (μ_0)	0.51	0.52	0.351
				Mixed – pure (μ_1)	-0.34	0.69	0.630
2007 – 2004	Pine	19	17	Pure (μ_0)	0.02	0.18	0.921
				Mixed – pure (μ_1)	0.79	0.26	0.009
	Oak	9	14	Pure (μ_0)	1.16	0.53	0.048
				Mixed – pure (μ_1)	-0.45	0.68	0.524

temperate tree species (Grossiord et al. 2014b; Michelot 2011; Ponton et al. 2001), point to clear differences between pine and oak related to the functional traits at play in the trade-off between carbon gain and water loss at the plant level (Ehleringer 1993).

One intriguing observation was that levels of intraspecific variability were greater in oak than in pine, notwithstanding stand conditions or year (Fig. 2). Micro-environmental and/or genetic factors could be the main causes of such variability (Leavitt 2010; Michelot 2011; Ponton et al. 2001). Since no information about the genetic structure of the pine and oak populations exists, the genetic origin of this variability cannot be precisely addressed. With regards to micro-environmental conditions, the greater intraspecific variability in oak $\Delta^{13}\text{C}$ could not have been related to soil water availability since the same variability patterns were found in both wet and dry years. Climatic variability among plots cannot explain the intraspecific variability observed for oak either: the studied plots are located in a lowland forest with little altitudinal variability and, consequently, little variability in micro-climatic parameters such as air temperature or air humidity.

Under wet conditions (2001), while pine $\Delta^{13}\text{C}$ did not differ between pure and mixed stands, for oak trees, there was a trend for slightly higher $\Delta^{13}\text{C}$ values in mixed stands

than in pure stands, though the effect was not significant (Fig. 2). Differences in soil water availability are known to explain gradients of $\Delta^{13}\text{C}$ among trees (Saurer et al. 1995; Stewart et al. 1995), but this effect should not have contributed to the trend for oak since water levels remained high in 2001 in all the stands (Fig. 1). Access to other resources, such as light or soil nutrients, may therefore have had an influence. It is well-known that gradients of light levels (Francey et al. 1985), carbon isotope composition in atmospheric CO_2 (Schleser and Jayasekera 1985) and air humidity (Winter et al. 1982) influence $\Delta^{13}\text{C}$ in trees. The greater mean basal area in the mixed stands as compared to the pure oak stands may indicate that a denser canopy in the mixed stands reduced light interception by oak trees, thereby inducing slightly higher $\Delta^{13}\text{C}$ values. However, in the same forest, Perot et al. (2017) demonstrated that despite differences in stand basal area among pure and mixed oak/pine stands, mean solar radiation transmittance did not differ between pure oak and mixed stands. Nevertheless, pines and oaks drastically differ in canopy shape. The dense pine canopy in the mixed stands might have created micro-climatic conditions where respired CO_2 could possibly be re-assimilated more easily and where higher air humidity might prevail. Such conditions influence $\Delta^{13}\text{C}$ in the same direction (higher $\Delta^{13}\text{C}$ values), and one cannot rule

out that they contributed to the slightly higher $\Delta^{13}\text{C}$ values for oaks in mixed stands.

4.2 Drought effect and differences in tree species responses

As expected, the severe drought in 2003 induced a strong decrease in $\Delta^{13}\text{C}$ for all the trees in both stand types (Figs. 2 and 3). This result is consistent with previous literature (Saurer et al. 1995; Stewart et al. 1995) and shows that in dry years, the decrease in photosynthesis is less than the decrease in stomatal conductance for water vapour (Farquhar et al. 1989). Our results confirm the literature on species differences in response to drought: On average, the decrease in $\Delta^{13}\text{C}$ from 2001 to 2003 was greater in pine than in oak (Table 2, Fig. 3), suggesting that the impact of drought on the trade-off of carbon and water flux was greater in pine trees than in oaks. Scots pine is known to regulate stomatal conductance for water vapour more than oak in order to minimize the risk of xylem cavitation (Tyree and Cochard 1996; Zweifel et al. 2009). The difference in the two species' response to drought could also be explained by the deep rooting system of oaks (Zapater et al. 2011), which allows them to access deeper soil water, whereas pine trees often have shallower root systems (Grossiord et al. 2014a). Our results are in line with those of Merlin et al. (2015) who evidenced that the 2003 summer drought caused a 5% reduction (compared to the 3 years before the drought event) in radial growth for sessile oak whereas the reduction was 20% for Scots pine.

It is interesting to note that the decrease in $\Delta^{13}\text{C}$ for both species was greater from 2001 to 2003 than from 2001 to 2004, although this difference was not significant for oak (Table S3). Soil drought was greater in 2003 than in 2004 (Fig. 1), and this trend is therefore consistent with the expected relationship between soil drought and $\Delta^{13}\text{C}$ (Saurer et al. 1995; Stewart et al. 1995): The greater the intensity of the drought, the stronger the decrease in $\Delta^{13}\text{C}$, if there are no carry-over effects of an extreme drought on the $\Delta^{13}\text{C}$ of the following year.

The wet growing season in 2007, where extractable water levels never fell below the critical threshold inducing stomatal closure in trees (Fig. S1), followed a series of five growing seasons with dry summers (Fig. 1). For oak, $\Delta^{13}\text{C}$ values in 2007 were close to the ones in 2001 (Figs. 2 and 3), pointing to this species' strong functional resilience in terms of carbon and water acquisition and use to a series of dry summers. However, for pine, the variation in $\Delta^{13}\text{C}$ between 2007 and 2001 in both pure and mixed stands was significantly greater than 0 (Table 3, Fig. 3), suggesting that there was no full recovery after several successive years with high drought. Though we studied resilience to the 2003 drought through $\Delta^{13}\text{C}$ only, in the same forest, Merlin et al. (2015) evaluated the resilience of tree growth to the same drought event based on tree ring width indices. In their study, both sessile oak and

Scots pine showed strong resilience to drought. This indicates that for pine at least, functional and growth resilience to a given drought event differed. Further exploration of resilience issues for both oak and pine is needed since research findings could have a strong impact on mixed forest management practices.

4.3 Effect of stand composition on tree functional response to drought

The main objective of this study was to test for interacting effects of drought and species mixture on pine and oak $\Delta^{13}\text{C}$. Our results clearly indicate a lack of significant interactions between abiotic and biotic factors. There was a trend towards a slightly greater decrease in $\Delta^{13}\text{C}$ in mixed stands as compared to pure ones for pine and a slightly lower decrease in mixed stands for oak (Fig. 3). However, statistical tests revealed no significant difference in $\Delta^{13}\text{C}$ between stand composition types (pure vs. mixed) for either species (Table 3). Thus, despite the extreme soil drought conditions which occurred at the study site in 2003, one cannot conclude that mixing the two species significantly altered their functional response to drought. Even though positive effects of mixed species stands on tree growth or transpiration respiration in reaction to drought have been found in some case studies (Grossiord et al. 2015a; Lebourgeois et al. 2013; Pretzsch et al. 2013), our results are consistent with the recently increasing body of literature indicating that greater tree species diversity in temperate forests does not always improve tree and forest ecosystem resistance to drought (Forrester et al. 2016; Grossiord et al. 2014c; Merlin et al. 2015).

The absence of any clear species interaction effect under drought conditions suggests that even though these two species strongly differ in ecological and functional characteristics (phenology, root systems, growth patterns, stomatal regulation etc.), the processes involved in species interactions were not strong enough to modify species response to drought. This contrasts with previously published results showing positive effects of mixing coniferous and broadleaf species (e.g. Grossiord et al. 2015a) and suggests that even though mechanisms of competition (negative interactions) and complementarity (positive interactions) for resource acquisition (light, water, nutrients) between conifers and broadleaves may be at play in mixed stands, mixing is neither beneficial nor harmful to the trees. Though mixing certainly contributes to greater biodiversity, it does not necessarily enhance future ecosystem survival in a context of more frequent and severe droughts.

Stand mixture did not influence oak resilience to the series of dry summers from 2002 to 2006. However, for pine, $\Delta^{13}\text{C}_{2007-2001}$ was negative for both pure and mixed stands and $\Delta^{13}\text{C}_{2007-2003}$ was much less positive in pure than in mixed stands (Fig. 3). This suggests that the pines in pure

stands were less resilient to the period of dry summers (2002–2006) than the pines in mixed stands and indicates a positive effect of the presence of oak trees on pine resilience to drought. Yet, it is important to note here that 2001 cannot be considered as a true reference year in terms of long-term tree functional response to soil water conditions. Indeed, the trees sampled were around 60 years old and had certainly suffered from several severe summer drought events over their lifespan. Furthermore, as previously pointed out, both 2001 and 2007 had been preceded by a series of dry summers (Fig. 1). In view of our results, the question of the long-term response of pine to successive drought years remains. The variability in $\Delta^{13}\text{C}$ values among individual pine trees in 2007 was low and exactly within the range of the values for individual pine trees in other years. The results of $\Delta^{13}\text{C}$ observed in 2007 in pure stands thus do not seem to be related to a few specific trees, but they rather seem to represent a true response of the pure-stand populations. Analysing $\Delta^{13}\text{C}$ values in tree rings over a longer period of time would be of great value in understanding the origin of the pine response to drought.

5 Conclusion

In conclusion, we show that in mixed forests in central France, summer droughts influence carbon isotope discrimination during photosynthesis in both Scots pine and sessile oak. Though managing for tree mixtures has been encouraged to reduce intraspecific competition for resources, the impact of summer drought on $\Delta^{13}\text{C}$ did not clearly differ for either species in mixed as compared to pure stands. This result is consistent with a recently increasing body of literature showing that greater tree species diversity in temperate forests does not necessarily improve the resistance of forest ecosystems to drought. Nevertheless, it is important to point out that the response to drought of the two species in our study was no worse in mixed stands than in pure ones. Therefore, even though mixing Scots pine and sessile oak may not avoid the negative effects of future severe droughts in the region, the practice would still contribute to improving other ecosystem services such as biodiversity and long-term productivity (Perot and Picard 2012).

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References

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EHT, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 259(4):660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Bert D, Leavitt SW, Dupouey JL (1997) Variations of wood delta C-13 and water-use efficiency of *Abies alba* during the last century. *Ecology* 78:1588–1596
- Bréda N, Badeau V (2008) Forest tree responses to extreme drought and some biotic events: towards a selection according to hazard tolerance? *Compt Rendus Geosci* 340(9-10):651–662. <https://doi.org/10.1016/j.crte.2008.08.003>
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63(6):625–644. <https://doi.org/10.1051/forest:2006042>
- Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought—from genes to the whole plant. *Funct Plant Biol* 30(3):239–264. <https://doi.org/10.1071/fp02076>
- Ehleringer JR (1993) In: Griffiths H, Smith J (eds) Gas-exchange implications of isotopic variation in arid-land plants. BIOS Scientific Publishers, London, pp 265–284
- Ehleringer JR, Cooper TA (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76(4):562–566. <https://doi.org/10.1007/BF00397870>
- Ehleringer JR, Farquhar GD (1993) Stable isotopes and plant-carbon water relations. Academic press, Inc., San Diego
- Eilmann B, Weber P, Rigling A, Eckstein D (2006) Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. *Dendrochronologia* 23(3):121–132. <https://doi.org/10.1016/j.dendro.2005.10.002>
- Farquhar G, O'Leary M, Berry J (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Funct Plant Biol* 9(2):121–137. <https://doi.org/10.1071/PP9820121>
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40(1):503–537. <https://doi.org/10.1146/annurev.arplant.40.1.503>
- Forrester DI, Bonal D, Dawud S, Gessler A, I A, Pollastrini M, Grossiord C (2016) Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *J Appl Ecol* 53(6):1725–1734. <https://doi.org/10.1111/1365-2664.12745>
- Francey RJ, Gifford RM, Sharkey TD, Weir B (1985) Physiological influences on carbon isotope discrimination in huon pine (*Lagarostrobos franklinii*). *Oecologia* 66(2):211–218. <https://doi.org/10.1007/BF00379857>
- Gamfeldt L, Snäll T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Fröberg M, Stendahl J, Philipson CD, Mikusiński G,

- Andersson E, Westerlund B, Andrén H, Moberg F, Moen J, Bengtsson J (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun* 4:1340. <https://doi.org/10.1038/ncomms2328>
- Gessler A, Ferrio JP, Hommel R, Treydte K, Werner RA, Monson RK (2014) Stable isotopes in tree rings: towards a mechanistic understanding of isotope fractionation and mixing processes from the leaves to the wood. *Tree Physiol* 34(8):796–818. <https://doi.org/10.1093/treephys/tpu040>
- GLOBALVIEW-CO2C13 (2008) Cooperative atmospheric data integration project—d13C of carbon dioxide. CD-ROM, NOAA ESRL, Boulder [ftp://ftp.cmdl.noaa.gov/ccg/co2c13/GLOBALVIEW]
- Granier A, Bréda N, Biron P, Vilette S (1999) A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecol Model* 116(2-3):269–283. [https://doi.org/10.1016/S0304-3800\(98\)00205-1](https://doi.org/10.1016/S0304-3800(98)00205-1)
- Granier A, Reichstein M, Bréda N, Janssens IA, Falge E, Ciais P, Grünwald T, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Facini O, Grassi G, Heinesch B, Ilvesniemi H, Keronen P, Knohl A, Köstner B, Lagergren F, Lindroth A, Longdoz B, Loustau D, Mateus J, Montagnani L, Nys C, Moors E, Papale D, Peiffer M, Pilegaard K, Pita G, Pumpanen J, Rambal S, Rebmann C, Rodrigues A, Seufert G, Tenhunen J, Vesala T, Wang Q (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agri For Meteorol* 143(1-2):123–145. <https://doi.org/10.1016/j.agrformet.2006.12.004>
- Grossiord C, Gessler A, Granier A, Berger S, Bréchet C, Hentschel R, Hommel R, Scherer-Lorenzen M, Bonal D (2014a) Impact of inter-specific interactions on the soil water uptake depth in a young temperate mixed species plantation. *J Hydrol* 519:3511–3519. <https://doi.org/10.1016/j.jhydrol.2014.11.011>
- Grossiord C, Granier A, Gessler A, Jucker T, Bonal D (2014b) Does drought influence the relationship between biodiversity and ecosystem functioning in boreal forests? *Ecosystems* 17(3):394–404. <https://doi.org/10.1007/s10021-013-9729-1>
- Grossiord C, Granier A, Ratcliffé S, Bouriaud O, Bruelheide H, Checko E, Forrester DI, Dawud SM, Finer L, Pollastrini M, Scherer-Lorenzen M, Valladares F, Bonal D, Gessler A (2014c) Tree diversity does not always improve resistance of forest ecosystems to drought. *P Natl Acad Sci USA* 111(41):14812–14815. <https://doi.org/10.1073/pnas.1411970111>
- Grossiord C, Forner A, Gessler A, Granier A, Pollastrini M, Valladares F, Bonal D (2015a) Influence of species interactions on transpiration of Mediterranean tree species during a summer drought. *Eur J For Res* 134(2):365–376. <https://doi.org/10.1007/s10342-014-0857-8>
- Grossiord C, Gessler A, Granier A, Bonal D (2015b) Les forêts tempérées face aux conséquences du changement climatique : est-il primordial de favoriser une plus forte diversité d'arbres dans les peuplements forestiers? *Revue Forestière Française* LXVII(2):99–110. <https://doi.org/10.4267/2042/57901>
- IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecol Lett* 10(9):835–848. <https://doi.org/10.1111/j.1461-0248.2007.01073.x>
- Jany JL, Martin F, Garbaye J (2003) Respiration activity of ectomycorrhizas from *Cenococcum geophilum* and *Lactarius* sp. in relation to soil water potential in five beech forests. *Plant Soil* 255(2):487–494. <https://doi.org/10.1023/A:1026092714340>
- Knoke T, Ammer C, Stimm B, Mosandl R (2008) Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *Eur J For Res* 127(2):89–101. <https://doi.org/10.1007/s10342-007-0186-2>
- Leavitt SW (2010) Tree-ring C-H-O isotope variability and sampling. *Sci Total Environ* 408(22):5244–5253. <https://doi.org/10.1016/j.scitotenv.2010.07.057>
- Lebourgeois F, Gomez N, Pinto P, Merian P (2013) Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For Ecol Manag* 303:61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>
- Lipp J, Trimbom P, Fritz P, Moser H, Becker B, Frenzel B (1991) Stable isotopes in tree ring cellulose and climatic change. *Tellus B* 43 B: 322–330
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yezzer EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178(4):719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Merlin M, Perot T, Perret S, Korboulewsky N, Vallet P (2015) Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *For Ecol Manag* 339:22–33. <https://doi.org/10.1016/j.foreco.2014.11.032>
- Michelot A (2011) Croissance et $\delta^{13}\text{C}$ des cernes de trois essences forestières tempérées (*Fagus sylvatica*, *Quercus petraea* et *Pinus sylvestris*) face aux variations climatiques à l'échelle interannuelle et saisonnière. Université Paris-sud 11 – UFR Sciences d'Orsay, Laboratoire Ecologie, Systématique et Evolution UMR 8079
- Michelot A, Bréda N, Damesin C, Dufrene E (2012) Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *For Ecol Manag* 265:161–171. <https://doi.org/10.1016/j.foreco.2011.10.024>
- O'Leary MH (1995) Environmental effects on carbon fractionation in terrestrial plants. In: Wada E, Yoneyama T, Minigawa M, Ando T, Fry BD (eds) Stable isotopes in the biosphere. Kyoto University Press, Kyoto, pp 78–91
- Perot T, Picard N (2012) Mixture enhances productivity in a two-species forest: evidence from a modelling approach. *Ecol Res* 27(1):83–94. <https://doi.org/10.1007/s11284-011-0873-9>
- Perot T, Vallet P, Archaux F (2013) Growth compensation in an oak-pine mixed forest following an outbreak of pine sawfly (*Diprion pini*). *For Ecol Manag* 295:155–161. <https://doi.org/10.1016/j.foreco.2013.01.016>
- Perot T, Mârell A, Korboulewsky N, Seigner V, Balandier P (2017) Modeling and predicting solar radiation transmittance in mixed forests at a within-stand scale from tree species basal area. *For Ecol Manag* 390:127–136. <https://doi.org/10.1016/j.foreco.2017.01.023>
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Statistics and computing. Springer, New York. <https://doi.org/10.1007/978-1-4419-0318-1>
- Pinheiro JC, Bates DM, DebRoy S, Sarkar D, the R Development Core Team (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1–128
- Ponton S, Dupouey JL, Bréda N, Feuillat F, Bodenès C, Dreyer E (2001) Carbon isotope discrimination and wood anatomy variations in mixed stands of *Quercus robur* and *Quercus petraea*. *Plant Cell Environ* 24(8):861–868. <https://doi.org/10.1046/j.0016-8025.2001.00733.x>
- Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol* 15(3):483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Saurer M, Siegenthaler U, Schweingruber F (1995) The climate-carbon isotope relationship in tree-rings and the significance of site conditions. *Tellus B* 47(3):320–330. <https://doi.org/10.1034/j.1600-0889.47.issue3.4.x>

- Saxe H, Cannell MGR, Johnsen Ø, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytol* 149(3):369–400. <https://doi.org/10.1046/j.1469-8137.2001.00057.x>
- Schleser GH, Jayasekera R (1985) Delta C-13-variations of leaves in forests as an indication of reassimilated CO₂ from the soil. *Oecologia* 65(4):536–542. <https://doi.org/10.1007/bf00379669>
- Stewart GR, Turnbull MH, Schmidt S, Erskine PD (1995) C-13 natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. *Aust J Plant Physiol* 22(1):51–55. <https://doi.org/10.1071/PP9950051>
- Toïgo M, Vallet P, Tuilleras V, Lebourgeois F, Rozenberg P, Perret S, Courbaud B, Perot T (2015) Species mixture increases the effect of drought on tree ring density, but not on ring width, in *Quercus petraea*-*Pinus sylvestris* stands. *For Ecol Manag* 345:73–82. <https://doi.org/10.1016/j.foreco.2015.02.019>
- Tyree MT, Cochard H (1996) Summer and winter embolism in oak: impact on water relations. *Ann Sci For* 53(2-3):173–180. <https://doi.org/10.1051/forest:19960201>
- van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L, Barbaro L, Bauhus J, Benavides R, Benneter A, Berthold F, Bonal D, Bouriaud O, Bruehlheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes D, Coppi A, Bastias CC, Muhie Dawud S, de Wandeler H, Domisch T, Finér L, Gessler A, Granier A, Grossiord C, Guyot V, Hättenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Jucker T, Koricheva J, Milligan H, Müller S, Muys B, Nguyen D, Pollastrini M, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielinski D, Fischer M (2016) Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. *Nat Commun* 7:11109. <https://doi.org/10.1038/ncomms11109>
- Winter K, Holtum JAM, Edwards GE, O'Leary MH (1982) Effect of low relative humidity on delta C13 value in two C3 grasses and in *Panicum milioides*, a C3–C4 intermediate species. *J Exp Bot* 33(1):88–91. <https://doi.org/10.1093/jxb/33.1.88>
- Zapater M, Hossann C, Bréda N, Bréchet C, Bonal D, Granier A (2011) Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. *Trees - Struct Func* 25(5):885–894. <https://doi.org/10.1007/s00468-011-0563-9>
- Zweifel R, Rigling A, Dobbertin M (2009) Species-specific stomatal response of trees to drought—a link to vegetation dynamics? *J Veg Sci* 20(3):442–454. <https://doi.org/10.1111/j.1654-1103.2009.05701.x>