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1 Effects of stand composition and tree size on resistance and resilience to drought in sessile

2 oak and Scots pine

3

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## 11 **Abstract**

12 The IPCC previsions for the upcoming decades include an increase in frequency and intensity  
13 of drought events in several regions worldwide, including Northern Europe. Drought  
14 significantly affects forest ecosystems through decreased productivity, increased vulnerability  
15 to biotic disturbances and increased subsequent mortality. How forest ecosystems maintain  
16 resistance and resilience to drought events are important questions. Our study aimed to assess  
17 whether species mixture or an individual tree size within a stand alters a given tree's  
18 resilience and resistance to drought. A retrospective study of tree-ring widths allowed us to  
19 calculate resistance, resilience and recovery indices for five recent drought events: 1976, the  
20 1990-1992 period, 2003, 2006 and 2010. These drought events were selected based on the  
21 SPEI (Standardized Precipitation Evapotranspiration Index) drought index. Our study sample  
22 consisted of 108 individual sessile oak (*Quercus petraea* (Matt.)) or Scots pine (*Pinus*  
23 *sylvestris* L.) trees sampled in 2012 and 2013 (Orleans forest, central France) in pure and  
24 mixed stands, divided into three diameter classes corresponding to three sizes: large, medium  
25 and small trees. Scots pine performed better than sessile oak during the 1990-1992 and 2010  
26 droughts while the contrary was observed for the 2003 and 2006 droughts. They performed  
27 equally in 1976. We suggest that the differing sensitivity of the two species to spring and  
28 summer drought explained this result. In our study, stand composition had no effect on  
29 resilience or resistance for either species. The size effect in oaks was unclear as small oaks  
30 displayed either a better performance or a worse performance than large oaks. Small pines  
31 displayed better resistance and resilience than pines of a larger size. This work stressed the  
32 importance of taking into account stand composition and trees size as well as soil and climatic  
33 conditions for each drought events to achieve a better understanding of the diversity of  
34 responses to climatic variations among forest ecosystems.

35 **Keywords:** drought; resistance; resilience; sessile oak; Scots pine; tree size; stand  
36 composition.

## 37 **1. Introduction**

38 In the recent decades, the long term increase in temperature and changes in precipitation  
39 patterns (IPCC, 2013) accompanied by an increase in the frequency and intensity of extreme  
40 climatic events such as droughts (Smith, 2011) have been the object of several studies. The  
41 events are major disturbances, both ecologically and socially. The intense 1976 and 2003  
42 droughts in Europe marked people's minds, and foresters were no exception. They were the  
43 first to witness forest decline and tree mortality following these droughts. The ability of forest  
44 ecosystems to face such climate changes and extreme events has become a major question for  
45 the scientific community. There is a large number of studies addressing this question (Breda *et*  
46 *al.*, 2006; Allen *et al.*, 2010; Lloret *et al.*, 2012). At the ecosystem level, the composition  
47 (Smith, 2011; Cavin *et al.*, 2013), structure and distribution of forests as well as the water,  
48 carbon and nutrient cycles are expected to be modified in the context of climate change (Breda  
49 *et al.*, 2006; Galiano *et al.*, 2011; Cheaib *et al.*, 2012). Impacts on tree growth and wood  
50 production are becoming significant with increasing forest decline and mortality in some parts  
51 of Europe, especially in Mediterranean environments (Martinez-Vilalta and Piñol, 2002;  
52 Vacchiano *et al.*, 2012; Vila-Cabrera *et al.*, 2013).

53 To assess ecosystem stability or species response, three basic aspects can be considered:  
54 resistance, recovery and resilience (Grimm and Wissel, 1997). Resistance is the capacity of an  
55 ecosystem, species or individual to remain basically unchanged when it is subjected to a  
56 disturbance. Recovery is the capacity to regain growth or any other characteristic negatively  
57 affected after a disturbance. Resilience is the ability to recover pre-disturbance structures and  
58 functions after a disturbance. In the perspective of climate change, these three aspects are

59 essential to conserving ecosystems and their functions, or at a smaller scale, species and even  
60 individuals.

61 Ecosystems involve several levels of complexity and diversity. Many studies have examined  
62 the benefits of mixed forests (Forrester *et al.*, 2006; Kelty, 2006). Interest in mixed stands is  
63 inspired by observations of increased biodiversity in the ecosystem (Felton *et al.*, 2010),  
64 better resistance to some biotic disturbances (Jactel and Brockerhoff, 2007; Perot *et al.*, 2013)  
65 and an increase in productivity in most cases when compared to monoculture stands (Knoke  
66 *et al.*, 2008; Vallet and Perot, 2011). Despite an increasing number of studies relative to  
67 mixed stands, we still know little about their functioning compared with pure stands. Niche  
68 complementarity, which enables a better use of the available resources – including water, is a  
69 common hypothesis to explain increased productivity in mixtures (Lebourgeois *et al.*, 2013).  
70 Therefore, studying the potential consequences of climate change – induced modifications in  
71 water availability on mixed and monoculture stands is crucial. Two hypotheses could be made  
72 for the response of mixed stands to drought. Firstly, mixed stands could improve individual  
73 tree species' performance during drought; a species might be mixed with another species  
74 which does not occupy the same water reserves. This would lead to a release of intraspecific  
75 competition combined with the possibility of facilitation alleviating drought stress through a  
76 partitioning of the water reserves between the species (Lebourgeois *et al.*, 2013; Pretzsch *et*  
77 *al.*, 2013). The involved species would be expected to benefit from this interaction. Secondly  
78 and reversely, mixed stands could decrease individual species' performance during drought as  
79 it has been observed depending on the tree species and soil conditions. This would result in an  
80 increased interspecific competition during drought stress (Jucker *et al.*, 2014). The involved  
81 species or the least competitive species would then suffer from mixing during water shortage  
82 periods, affecting tree growth and functions such as photosynthesis, transpiration or sap flow  
83 (Grossiord *et al.*, 2014).

84 Another level of complexity in forest ecosystems lies in the existence of varying individual  
85 tree size within a stand. The majority of studies conducted on the impact of drought on forest  
86 stands focus on dominant trees, i.e. the largest in diameter with generally more developed  
87 crowns and root systems. It is possible to hierarchically organize the trees in an even-aged  
88 stand according to their diameter, reflecting differences between individual tree functional  
89 statutes within an even-aged stand (Dlôte, 1994). This hierarchy implies a differential  
90 availability of resources such as water (Dawson, 1996), nutrients and light (Dlôte, 1994). It  
91 also affects the intensity of competition between individuals. Population hierarchy can  
92 consequently play an important role in an individual's responses to climatic and biological  
93 disturbances (Pichler and Oberhuber, 2007; Martín-Benito *et al.*, 2008; Mérian and  
94 Lebourgeois, 2011; Zang *et al.*, 2012). It is important to incorporate both stand composition  
95 (pure or mixed stands) and individual tree size in the stand as explanatory variables when  
96 studying tree species response to abiotic disturbances such as drought in order to assess the  
97 risks associated with climate change and to propose adapted forest management strategies.

98 We studied the effects of tree size and stand composition on resistance and resilience to  
99 drought in terms of radial growth for two species: a deciduous broadleaved species; sessile  
100 oak (*Quercus petraea* Matt.) and a conifer needled species; Scots pine (*Pinus sylvestris* L.).  
101 These two tree species have very different characteristics, suggesting they may have different  
102 responses to drought (Béda *et al.*, 2006; Eilmann *et al.*, 2006; Béda and Badeau, 2008;  
103 Michelot *et al.*, 2012a), and are widespread throughout European forests in both pure and  
104 mixed stands. Sessile oak is a mesophilic species with a deep root system which prefers semi-  
105 shady environments well adapted to occasional droughts. During periods of water deficit, leaf  
106 water potential is reduced, potentially leading to xylem cavitation. The large vessels in oak  
107 earlywood are very sensitive to winter embolism (Tyree and Cochard, 1996) and water  
108 circulation must be restored each spring by the formation of at least one new tangential row of

109 large vessels. Sessile oak is common in Western Europe and is the most widespread species  
110 in French forests (National Forest Inventory data). Scots pine is a light-demanding evergreen  
111 species. Its root system is more superficial than most broadleaved species but it does develop  
112 a strong first pivot and lateral roots. Water potential in the needles is maintained above a  
113 threshold level thanks to stomatal closure during periods of water deficit which minimizes the  
114 risk of xylem cavitation. Scots pine can stop its radial growth entirely when conditions are too  
115 harsh possibly leading to missing tree rings. Its drought tolerance as defined by Niinemets and  
116 Valladares (2006) is slightly higher than sessile oak. It is widely distributed throughout  
117 temperate and boreal Europe and is common in French forests and around the Mediterranean  
118 basin. Both species are present in pure or mixed stands at our study site in the Orléans National  
119 Forest in central France.

120 Radial growth is sensitive to biotic and abiotic disturbances (Lebourgeois *et al.*, 2010; Olivar  
121 *et al.*, 2012; Wiley *et al.*, 2013; Palacio *et al.*, 2014). It can be used for past climatic  
122 reconstructions or for retrospective analysis of tree performance during past known  
123 disturbances (Speer, 2010). We thus used radial growth to evaluate how individual trees  
124 responded to past climatic severe events such as drought using indices of resistance, recovery  
125 and resilience. We selected five drought events between 1970 and 2013 based on the SPEI  
126 (Standardized Precipitation Evapotranspiration Index), a drought index defined by Vicente-  
127 Serrano *et al.* (2010). We sought to answer the following three questions:

- 128 1. Do sessile oak and Scots pine respond differently to past drought events?
- 129 2. Does stand composition (mixed stand *versus* pure stand) improve or deteriorate  
130 individual tree's radial growth during drought events?
- 131 3. Does tree status represented by tree size affect individual tree's response to drought?

## 132 **2. Material and methods**

133 2.1. Study site and species

134 For simplification, it is reasonable to partitionate this continuum of tree diameter. Three  
 135 classes of tree size can thus be distinguished based on diameter: large trees, medium trees and  
 136 small trees, excluding understorey trees. The study site is located in the center of France, in  
 137 the Orleans National Forest (France, 48°00'N, 2°09' E) which extends over 35,000 hectares and  
 138 is managed by the National Forest Office. Elevation ranges from 107 m to 174 m a.s.l.  
 139 Throughout the forest the soil is relatively poor and acidic with a sandy clay-loam texture  
 140 (Table 1 **Erreur ! Source du renvoi introuvable.**), and is classified as a planosol (IUSS Working  
 141 Group, 2014). Superimposed layers of clay and sand lead to a temporary perched water table  
 142 in winter, but the low soil water storage capacity reduces available water for plants in  
 143 summer. The area has a temperate continental climate with an oceanic influence (mean  
 144 minimum temperature of 0.7 °C in February; mean maximum temperature of 25 °C in July).  
 145 The mean annual rainfall is 740 mm (1969 to 2013 data from the weather station at Nogent-  
 146 sur-Vernisson, France).

147 The species studied were sessile oak *Quercus petraea* (Matt.) and Scots pine *Pinus sylvestris*  
 148 L., managed in pure or mixed stands.

149 Table 1. Physico-chemical characteristics of the forest site soil (at 20-40 cm in depth, mean,  
 150 standard deviation (s.d.), n=30). Cation exchange capacity (CEC) is given in milli-equivalents  
 151 of hydrogen per 100 g (meq/100g).

	Clay	Fine silt	Coarse silt	Fine sand	Coarse sand	C	N	C/N	pH-KCl	CEC
	(%)	(%)	(%)	(%)	(%)	(%)	(%)			(meq/100g)
Mean	8.6	11.8	7.9	14.3	55.8	0.92	0.046	19.6	4.43	4.21
(s.d.)	(2.4)	(2.8)	(2.3)	(2.2)	(7.5)	(0.25)	(0.010)	(2.9)	(0.16)	(2.58)

152 2.2. Sampling design

153 Nine plots were selected on three sites in even-aged stands (50 – 80 years old) as part of the  
154 Oak Pine Tree Mixture Experiment (OPTMix) (Korboulewsky *et al.*, 2013). Each site has one  
155 plot of pure sessile oak, one plot of pure Scots pine and one plot with a mixture of the two  
156 species. All plots have similar soil conditions, floral compositions, tree age, silvicultural  
157 treatments and diameter distributions (Table 2). For each plot, a 1.5-2 ha area was delimited  
158 and the position of each tree was mapped before the individual tree selection process. Nine  
159 trees per species and per plot were chosen according to a stratified sampling design with  
160 constraints. We studied the following two factors:

161 - The local composition or mixing rate: the mixing rate in the local environment (a 10m-  
162 radius circle around each selected tree) was calculated as a percentage of the partial  
163 Relative Density Index, or RDI (Reineke, 1933). The calibration for both species of the  
164 self-thinning boundaries needed for the RDI calculation followed Charru *et al.* (2012)  
165 based on data from the National Forest Inventory for the northern half of France. In pure  
166 stands, the RDI proportion of the target species was 100%. In mixed stands, the RDI of  
167 the companion species was set between 40 and 80% to ensure that the sampled trees from  
168 pure and mixed stands had contrasted mixing rates.

169 - Tree size: this reflects the hierarchy in tree diameter between individual trees, related to  
170 the social status within the stand. We distinguished three tree size classes in our study:  
171 small trees, medium trees and large trees. Based on 2012 or 2013 tree diameters, the trees  
172 at each site were assigned to one of these classes. Understorey trees were excluded. For  
173 the selection process, we defined four quantiles from the diameter distribution for each  
174 species: 28% quantile, 38% quantile, 61% quantile and 71% quantile to obtain three  
175 intervals clearly separated. Small trees of a given species were sampled in the interval  
176 [minimum diameter; 28% quantile], medium trees were sampled in the interval [38%  
177 quantile; 61% quantile] and large trees were sampled in the interval [71% quantile;

178 maximum diameter]. However, individual tree-level dynamics may have changed during  
 179 the growing process due to modifications in the local environment or to genetics, and tree  
 180 size may also have changed. To refine the influence of the hierarchy on the individuals’  
 181 responses to each drought event, we redefined the tree size classes for each drought event  
 182 studied here (see section 2.4 for the selection of the drought events) based on three  
 183 relative diameter classes (smallest, intermediate, largest) reconstructed from tree ring  
 184 analyses.

185 The local density was estimated using the RDI. It was set between 0.5 and 0.75 to ensure  
 186 similar competition conditions among sample trees. We visually checked the general form of  
 187 the candidate trees to ensure that the selected trees were representative of the stand  
 188 population.

189 The final sample consisted of 108 trees from the two species, the two stand composition types  
 190 (pure or mixed) and the three tree size classes; three tree replicates per plot were included  
 191 (Table 2). In autumn 2012 and 2013, the selected trees were felled and a 10cm thick cross  
 192 section was cut 1.30m above the ground, or as close as possible to this level when defects  
 193 (branches, damage or sap pockets) were present.

194 Table 2. Mean age and mean diameter at 1.30m for each species, stand composition type and  
 195 tree size class. Age and diameter standard deviation are indicated in parentheses. Nine trees  
 196 were sampled for each species, stand composition and size. S: small ; M: medium ; L: large.

Species	Sessile oak						Scots pine					
	Pure			Mixed			Pure			Mixed		
Stand	S	M	L	S	M	L	S	M	L	S	M	L
<b>Age (years)</b>	63.0 (8.8)	65.6 (3.8)	65.9 (3.8)	65.1 (7.8)	68.7 (9.0)	72.0 (8.6)	55.0 (4.0)	56.0 (4.0)	56.2 (5.0)	57.6 (7.8)	61.8 (8.4)	68.0 (7.6)
<b>Diameter (cm)</b>	11.6 (1.5)	17.6 (1.9)	22.1 (2.2)	11.6 (1.8)	17.8 (2.4)	24 (3.6)	21.5 (2.0)	27.6 (1.1)	30.9 (3.1)	18.6 (2.8)	26.8 (1.1)	33.1 (2.8)

197        2.3. Tree-ring analyses

198        We used the WinDendro software (Regent, 2005) to measure tree-ring widths from pith to  
199        bark along two radii along a systematic north-south axis. The east-west axis was not used to  
200        avoid reaction wood or possible ovalization related to the prevailing east-west winds in this  
201        region. A visual crossdating was performed for known reference dates: – the 1976 drought  
202        and the *Diprion pini* attack on pine between 1981 and 1986 (Perot *et al.*, 2013). We used a  
203        DigiMicro 2.0 Scale USB camera (Mikroskop Digital Kamera, DNT), an SMZ745 wen  
204        (Nikon) and an Eclipse E200 microscope (Nikon) to help us clarify the position of a few tree  
205        rings close to the pith. Statistical crossdating was performed with the COFECHA software  
206        (Grissino-Mayer, 2001).

207        The following statistics from the COFECHA software output (see Appendix B for detailed  
208        result for each sampled tree) were used to verify the quality of the tree-ring series (Grissino-  
209        Mayer, 2001). Series intercorrelation (SI) is a measure of the strength of the signal common  
210        to all the trees sampled. Most chronologies have values between 0.550 and 0.750. In our  
211        sample, SI was 0.577 for oak and 0.631 for pine. These values indicate a good common signal  
212        among the individuals sampled. The Expressed Population Signal (EPS) ensures that the trees  
213        sampled accurately represent a hypothetical population. This is verified when  $EPS > 0.85$   
214        (Wigley *et al.*, 1984). This condition was verified in our study with an EPS of 0.96 for sessile  
215        oak, and 0.98 for Scots pine.

216        The analysis was restricted to the 1970-2013 period, which corresponds to the extent of the  
217        meteorological data available for the study sites. Moreover, tree growth dynamics are usually  
218        different during the juvenile stage and the adult and mature stages. The choice of the 1970-  
219        2013 period ensured that the sampled trees were not in the juvenile stage (

220 Figure 2). Two radial growth variables were calculated. Ring width (RW) per year was  
221 calculated as the average ring width over the two radii along the north-south axis. Tree basal  
222 area increment (BAI) was calculated per year as follows:

$$BAI_n = (d_n^2 - d_{n-1}^2) \times \pi/4$$

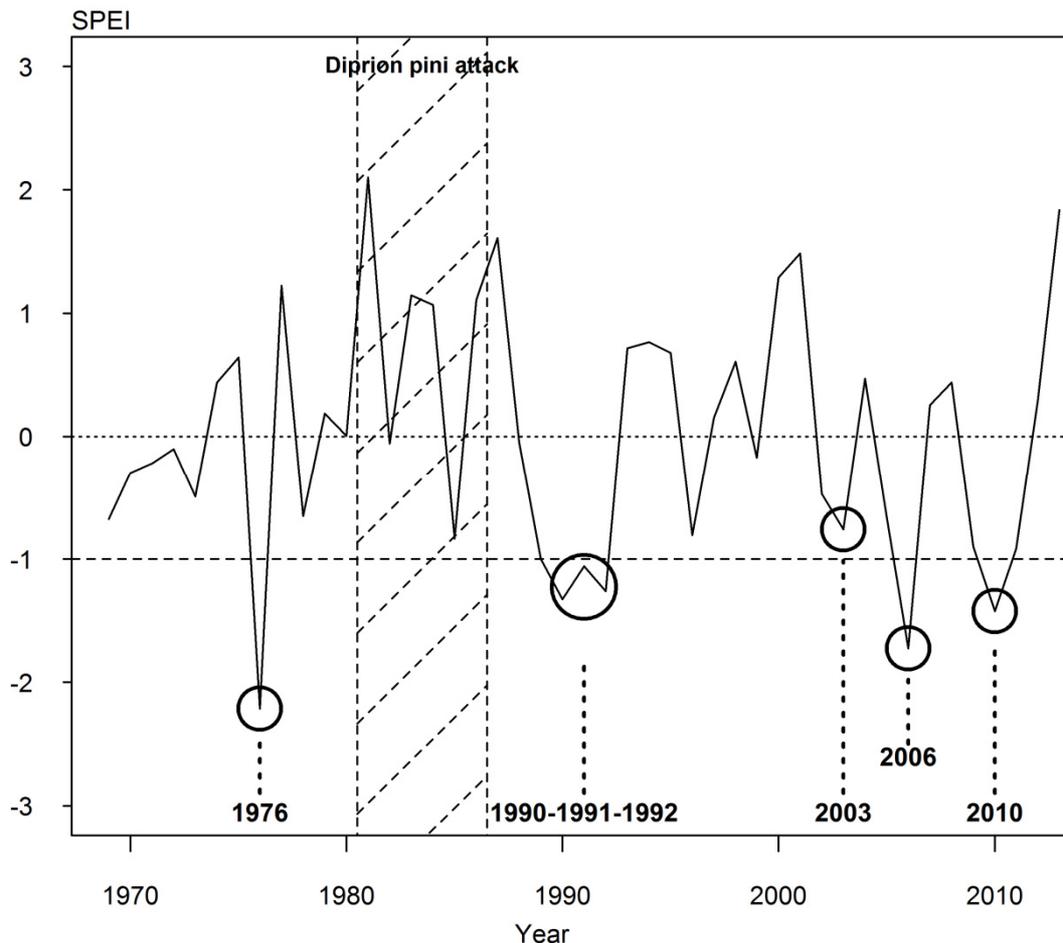
223 where  $d_n$  is tree diameter for year  $n$ .  $d_n$  was calculated from the cumulative ring widths of  
224 the tree ring series for each year.

#### 225 2.4. Climatic data and drought index

226 Daily minimum, maximum and average temperature and precipitation for the last 44 years  
227 (1969-2013) were collected from the Irstea weather station (France, 47°50' N, 2°44' E) located  
228 twenty kilometers from the study forest. Drought events were identified based on the SPEI  
229 (Standardized Precipitation Evapotranspiration Index) drought index (Vicente-Serrano *et al.*,  
230 2010) calculated with the *spei* CRAN package. This index has the advantage of incorporating  
231 the effects of temperature on drought and considering different time scales indicative of the  
232 chronic, long-term or exceptional character of each drought event and can be used to estimate  
233 changes in the dynamics and/or intensity of drought events over previous decades. Monthly  
234 SPEI is a standardized variable (see Vicente-Serrano *et al.* (2010) for details of the  
235 standardization). It is based on the degree of water surplus or deficit, defined as the difference  
236 between the monthly precipitation and the monthly Thornthwaite potential evapotranspiration  
237 (Thornthwaite, 1948). In this study, the SPEI for each year was calculated for the growing  
238 season spanning seven months from April to October. At this time scale, there is a fairly good  
239 correlation between the growth variables (RW for oak and BAI for pine, results not shown)  
240 and the SPEI values. When SPEI was under the value of -1, the year was considered a severe  
241 drought year (Potop *et al.*, 2014). Following this criterion, the selected drought events in our  
242 study were: 1976, 2006, 2010 and the period 1990-1991-1992 (Figure 1). We added the year

243 2003 since a short but intense summer drought event occurred then that has been largely  
244 studied as an important drought event in Europe (Ciais *et al.*, 2005; Pichler and Oberhuber,  
245 2007; van der Werf *et al.*, 2007; Lebourgeois *et al.*, 2010). Moreover, the SPEI during the  
246 summer months of 2003 was considerably below the threshold of -1, with a value of -2.4.

247 Figure 1. SPEI computed for the growing season (April to October) from 1970 to 2013. The  
248 selected drought events are indicated by a bold circle. The horizontal dotted line indicates the  
249 threshold of -1 below which a drought was considered severe. The 1981 to 1986 period  
250 (hatched zone) was removed from our analysis because of severe pine defoliation by *Diprion*  
251 *pini*.

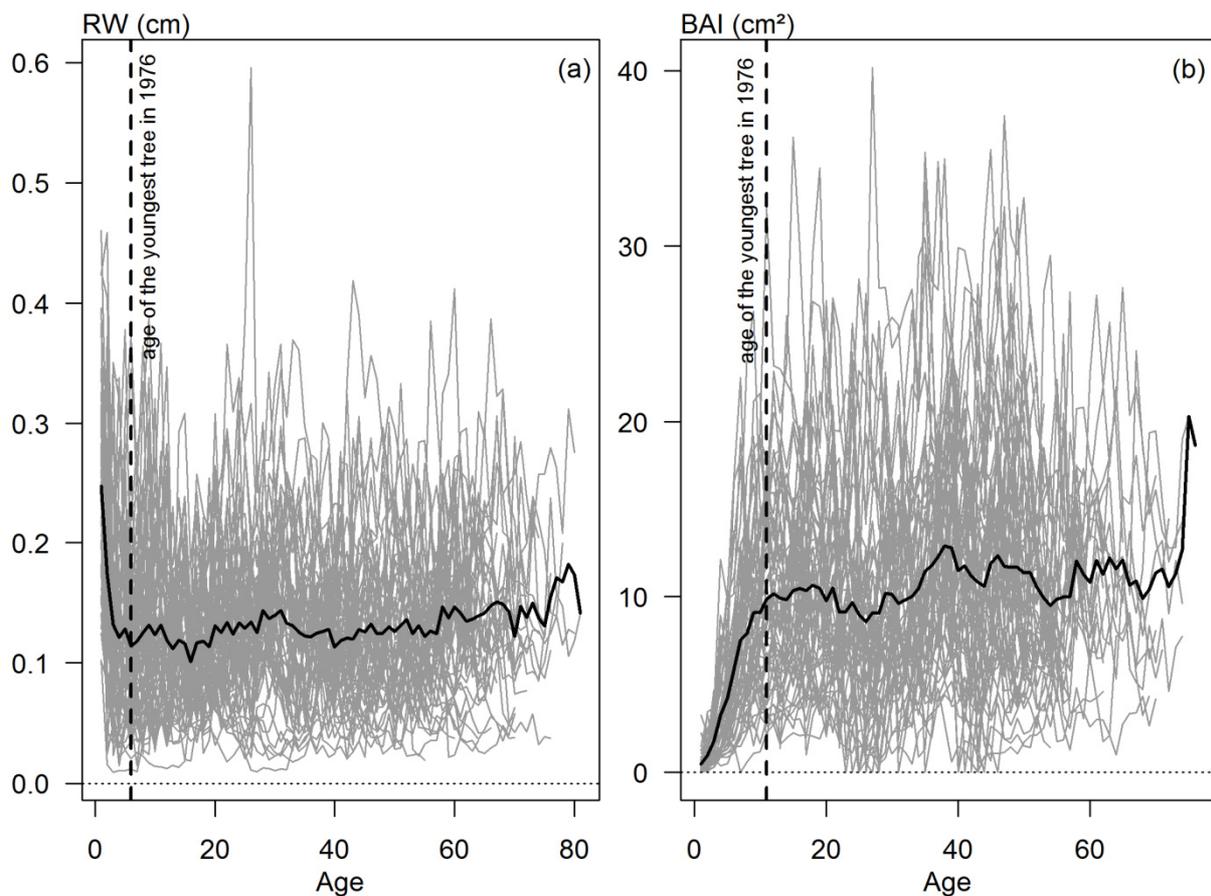


252

253 2.5. Resistance, recovery and resilience indices

254 We used the resistance, recovery and resilience indices defined by Lloret *et al.* (2011) to  
255 quantify individual tree responses to the drought events we selected. We hypothesized that  
256 pre-disturbance period reflect the expected growth missing during the year of the disturbance.  
257 To support this hypothesis, the growth variables on which the indices are based must not  
258 show any strong temporal trend, so we used RW for sessile oak and BAI for Scots pine (  
259 Figure 2).

260 Figure 2. Raw tree-ring growth series for sessile oak and Scots pine according to tree age.  
261 Each tree-ring series is printed in grey. The bold line represents the series mean averaged for  
262 all trees. (a) for sessile oak; the growth variable presented is RW, (b) for Scots pine: the  
263 growth variable presented is BAI. The vertical dotted line indicates the age in 1976 (oldest  
264 drought studied here) of the youngest tree sampled.



265

266

267 The absence of strong age-related trends (excluding the juvenile period) on these two growth  
268 variables allowed us to calculate the response indices with raw data (non-transformed or  
269 standardized data). Since comparing indices based on two different growth variables could be  
270 misleading when interpreting the species responses (see section 2.6 for the statistical models),  
271 we quantified the error resulting from using BAI for Scots pine for each drought event. We  
272 included a multiplying factor  $R$  to link the index calculated with BAI with the one calculated  
273 with RW (see Appendix A for further details):

$$Index_{BAI} = Index_{RW} \times R$$

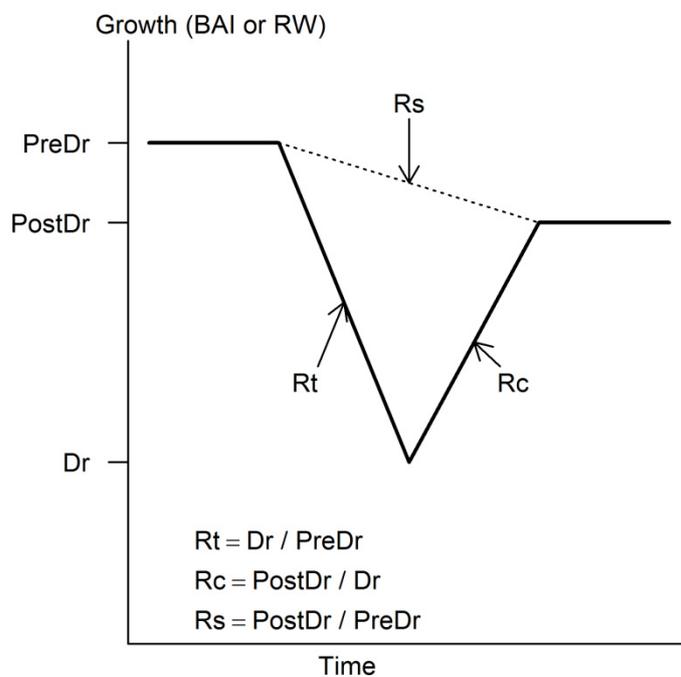
274 For the five drought events selected, the relative bias  $1 - R$  induced by the use of BAI for  
275 Scots pine is much smaller (around 4-9%) than the differences between the oak and pine  
276 responses (between 15-36%) for the same drought events (Appendix A, Figure A 1). The use  
277 of different growth indices for the two species does not influence the direction of the results  
278 obtained for the comparison of the two species (see Appendix A).

279 Growth during pre-and post-disturbance periods (*PreDr* and *PostDr*) was calculated as the  
280 average growth in the 3 years respectively before and after disturbance. There is a trade-off  
281 between retaining a long enough period to ensure a good estimation of the mean growth  
282 before and after the drought event and the risk of an overlap between the pre- or post-  
283 disturbance period and adjacent drought events. Growth during disturbance *Dr* is the growth  
284 observed the year of the drought event (or the average growth over the period of the  
285 disturbance in the case of a drought spanning several years, *i.e.* 1990 to 1992). Resistance,  
286 recovery and resilience are defined as follows (Figure 3):

- 287 - Resistance =  $Dr/PreDr$ : the individuals' ability to withstand harsh conditions  
288 (*e.g.* drought).

- 289 - Recovery =  $PostDr/Dr$ : the individuals' ability to restore a level of growth after  
290 disturbance relative to the damage during the disturbance.  
291 - Resilience =  $PostDr/PreDr$ : the ability of an individual to regain post-  
292 disturbance growth similar to pre-disturbance growth.

293 Figure 3. Resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices in a hypothetical case, adapted  
294 from Lloret *et al.* (2011). Resistance (solid line) and resilience (dotted line) correspond to the  
295 negative slopes, so the steeper the decline, the lower the resistance and resilience. Recovery  
296 (solid line) corresponds to the positive slope.



298 The post-disturbance period for 2003 and the pre-disturbance period for 2006 overlap. We  
299 therefore decided to use the 2006 post-disturbance period to calculate the 2003 indices and the  
300 2003 pre-disturbance period for the 2006 indices. This choice removes the immediate impact  
301 on growth of the 2003 drought event on individual tree responses to the 2006 drought. It  
302 should also be noted that resilience for the 2010 drought event is incomplete for the trees  
303 sampled in 2012 as only two years of data were available after the drought event to calculate  
304 the resilience index for these trees.

305 2.6. Statistical analyses

306 Our first question on species specific response to drought was tested for each drought event.  
307 We used linear mixed models where response indices (transformed with the natural logarithm  
308 when necessary to meet the assumptions of normality of the residuals) were dependent  
309 variables and species (fixed factor) and plot (random factor) were explanatory variables. The  
310 linear mixed model for a given drought event was as follows, with sessile oak as the  
311 reference:

$$I_{ijk} = m + m_i + E_j + \varepsilon_{ijk}$$

312 where  $I_{ijk}$  is one of the three indices calculated for a tree  $k$  of a species  $j$  in plot  $i$ ,  $m$  is the  
313 intercept representing the sessile oak average for the relevant index and year;  $m_i$  is the plot  
314 random effect;  $E_j$  is the species effect (*i.e.* the difference for the relevant index and year  
315 between Scots pine and the reference – sessile oak) and  $\varepsilon_{ijk}$  are the residuals of the model.  
316 For each drought event, the species effect was removed in the model if it was found to be not  
317 significant.

318 We also used linear mixed models to answer our second and third questions on stand  
319 composition and tree size effects on individual's performance during drought events for each  
320 species and each drought event. The dependent variables were the indices of response to  
321 drought (log-transformed when necessary). The explanatory variables were stand composition  
322 (mixed or pure, fixed effect), tree size (large, medium and small, fixed effect) and plot  
323 (random effect). The full linear mixed model used to test the effects of composition and tree  
324 size for a given drought event and one species was as follows, with large trees growing in  
325 pure stands as the reference:

$$I_{ijkl} = m + m_i + C_j + S_k + CS_{jk} + \varepsilon_{ijkl}$$

326 where  $I_{ijkl}$  is one of the three indices calculated for a tree  $l$  belonging to a size  $k$  in  
 327 composition  $j$  for the plot  $i$ ,  $m$  is the intercept representing the reference (large trees growing  
 328 in pure stands) average for the relevant index and year;  $m_i$  is the plot random effect;  $C$  is the  
 329 composition effect (*i.e.* the difference between the reference – pure – and mixed stands);  $S$   
 330 corresponds to the tree size parameter (*i.e.* the difference between the reference – large – and  
 331 each of the other two size classes);  $CS$  is the interaction between composition and size; and  
 332  $\varepsilon_{ijkl}$  are the residuals of the model. For each model, variables which were found to be not  
 333 significant were removed to improve the estimations of the significant variables. The  
 334 interaction parameter  $CS$  was consequently removed from all models as it was never  
 335 significant. All statistical analyses were performed with the *nlme* package of the R statistical  
 336 software (R Development Core Team, 2014). The significance threshold was set at 0.05.

### 337 3. Results

338 Growth decreased during the drought events for both sessile oak and Scots pine as resistance  
 339 values were less than 1 in average (Table 3). Mean index values showed relatively high levels  
 340 of resistance to drought and resilience for both species (Table 3).

341 Table 3. Mean values (and standard deviation s.d.) of the resistance, recovery and resilience  
 342 indices. Mean values are calculated for each species over the five selected drought events.

	Resistance $R_t$		Recovery $R_c$		Resilience $R_s$	
	<i>Oak</i>	<i>Pine</i>	<i>Oak</i>	<i>Pine</i>	<i>Oak</i>	<i>Pine</i>
Mean	0.759	0.787	1.361	1.366	0.994	0.985
s.d.	0.218	0.274	0.606	0.765	0.434	0.457

#### 343 3.1. Comparison between the two species' response to drought events

344 The species effect was significant for some drought events, and differs depending on the  
 345 index. Pine was more resistant than oak for 1990-1992 and 2010 droughts and more resilient

346 for the 1990-1992 drought only. Oak was more resistant for the 2003 and 2006 droughts,  
 347 recovered better after the 2010 drought (Table 4Erreur ! Source du renvoi introuvable.).

348 Table 4. Results from the linear mixed models for species effect on resistance  $R_t$ , recovery  $R_c$   
 349 and resilience  $R_s$  indices for the five selected drought events. For each model, when the  
 350 “species” variable was not significant, we chose to remove it completely. Parameters are  
 351 estimated with sessile oak as the reference. *ln* below a drought event indicates that logarithm  
 352 transformation of the response variable was used to fit the model. The estimates and standard  
 353 deviations (s.d.) were not back transformed when the logarithm was applied. Significant  
 354 results are shown in bold characters. Shading indicates the direction of the difference between  
 355 Scots pine and the reference, *i.e.* sessile oak; dark grey: positive difference; light grey:  
 356 negative difference.

		1976	1990-1992	2003	2006	2010
<b>R<sub>t</sub></b>			<i>ln</i>		<i>ln</i>	<i>ln</i>
Intercept	Estimation	<b>0.668</b>	<b>-0.405</b>	<b>0.951</b>	<b>-0.307</b>	<b>-0.305</b>
	s.d.	<b>0.018</b>	<b>0.038</b>	<b>0.034</b>	<b>0.057</b>	<b>0.043</b>
	p-value	<b>&lt; 0.001</b>				
Scots pine	Estimation		0.257	-0.155	-0.345	0.275
	s.d.		0.054	0.041	0.066	0.051
	p-value		< 0.001	< 0.001	< 0.001	< 0.001
<b>R<sub>c</sub></b>			<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>
Intercept	Estimation	<b>0.514</b>	<b>0.336</b>	<b>0.123</b>	<b>0.320</b>	<b>-0.272</b>
	s.d.	<b>0.073</b>	<b>0.035</b>	<b>0.038</b>	<b>0.057</b>	<b>0.066</b>
	p-value	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>0.002</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
Scots pine	Estimation				0.235	-0.172
	s.d.				0.059	0.051
	p-value				< 0.001	< 0.001
<b>R<sub>s</sub></b>			<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>
Intercept	Estimation	<b>0.087</b>	-0.091	-0.046	-0.046	<b>-0.526</b>
	s.d.	<b>0.056</b>	0.061	0.038	0.038	<b>0.076</b>
	p-value	<b>0.126</b>	0.134	0.236	0.236	<b>&lt; 0.001</b>
Scots pine	Estimation		0.287			
	s.d.		0.074			
	p-value		< 0.001			

357

358           3.2. Effects of stand composition on species responses to drought events  
359    The effect of stand composition (pure or mixed stands) on sessile oak or Scots pine responses  
360    was never significant for the selected drought events and was thus removed from all models  
361    (Table 5,

362 Table 6. Results from the linear mixed models for stand composition and tree size effects on  
363 resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices of Scots pine for the five selected drought  
364 events. Parameters are estimated with pure stands and large trees as the references. *ln* below a  
365 drought event indicates that logarithm transformation of the response variable was used to fit  
366 the model. Estimates and standard deviations (s.d.) were not back transformed when the  
367 logarithm was applied. Significant results are shown in bold characters. Shading indicates the  
368 direction of the difference between each factor level and the references, *i.e.* large trees and  
369 pure stands; dark grey: positive difference; light grey: negative difference.

370 ).

### 371 3.3. Effects of tree size on species responses to drought events

#### 372 3.3.1. Sessile oak

373 The effect of the tree size on the sessile oak response to drought was variable depending on  
374 the year and the index considered. In 2003, 2006 and 2010, small trees showed significantly  
375 lower resistance (2003) or recovery (2006, 2010) than did large trees. The opposite result was  
376 found for resistance for the 1990-1992 drought event (Table 5,  
377 Figure 4). There was no effect of tree size on sessile oak resilience for any of the five drought  
378 events considered.

#### 379 3.3.2. Scots pine

380 Several significant results were found. The general trend for Scots pine indicates better  
381 resistance and resilience among small individuals than among large individuals (

382 Table 6. Results from the linear mixed models for stand composition and tree size effects on  
383 resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices of Scots pine for the five selected drought  
384 events. Parameters are estimated with pure stands and large trees as the references. *ln* below a  
385 drought event indicates that logarithm transformation of the response variable was used to fit  
386 the model. Estimates and standard deviations (s.d.) were not back transformed when the  
387 logarithm was applied. Significant results are shown in bold characters. Shading indicates the  
388 direction of the difference between each factor level and the references, *i.e.* large trees and  
389 pure stands; dark grey: positive difference; light grey: negative difference.

390 , Figure 5). There were no significant effects of stand composition or tree size for some  
391 indices and drought events (

392 Table 6. Results from the linear mixed models for stand composition and tree size effects on  
393 resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices of Scots pine for the five selected drought  
394 events. Parameters are estimated with pure stands and large trees as the references. *ln* below a  
395 drought event indicates that logarithm transformation of the response variable was used to fit  
396 the model. Estimates and standard deviations (s.d.) were not back transformed when the  
397 logarithm was applied. Significant results are shown in bold characters. Shading indicates the  
398 direction of the difference between each factor level and the references, *i.e.* large trees and  
399 pure stands; dark grey: positive difference; light grey: negative difference.

400 ).

401 Table 5. Results from the linear mixed models for stand composition and tree size effects on  
 402 resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices of sessile oak for the five selected  
 403 drought events. Parameters are estimated with pure stands and large trees as the references.  $\ln$   
 404 below a drought event indicates that logarithm transformation of the response variable was  
 405 used to fit the model. Estimates and standard deviations (s.d.) were not back transformed  
 406 when the logarithm was applied. Significant results are shown in bold characters. Shading  
 407 indicates the direction of the difference between each factor level and the references, *i.e.* large  
 408 trees and pure stands; dark grey: positive difference; light grey: negative difference.

			1976	1990-1992	2003	2006	2010
<b>R<sub>t</sub></b>				<i>ln</i>			<i>ln</i>
Intercept		Estimates	<b>0.654</b>	<b>-0.537</b>	<b>1.041</b>	<b>0.732</b>	<b>-0.304</b>
		s.d.	<b>0.022</b>	<b>0.059</b>	<b>0.063</b>	<b>0.023</b>	<b>0.062</b>
		p-value	<b>&lt; 0.001</b>				
Composition	<i>Mixed</i>	Estimates					
		s.d.					
		p-value					
Size	<i>Medium</i>	Estimates		<b>0.155</b>	-0.121		
		s.d.		<b>0.071</b>	0.063		
		p-value		<b>0.034</b>	0.059		
	<i>Small</i>	Estimates		<b>0.241</b>	<b>-0.130</b>		
		s.d.		<b>0.071</b>	<b>0.063</b>		
		p-value		<b>0.001</b>	<b>0.043</b>		
<b>R<sub>c</sub></b>			<i>ln</i>		<i>ln</i>		
Intercept		Estimates	<b>0.624</b>	<b>1.443</b>	0.086	<b>1.572</b>	<b>0.850</b>
		s.d.	<b>0.090</b>	<b>0.071</b>	0.062	<b>0.079</b>	<b>0.064</b>
		p-value	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	0.175	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
Composition	<i>Mixed</i>	Estimates					
		s.d.					
		p-value					
Size	<i>Medium</i>	Estimates				<b>-0.262</b>	-0.068
		s.d.				<b>0.090</b>	0.043
		p-value				<b>0.005</b>	0.117
	<i>Small</i>	Estimates				-0.129	<b>-0.125</b>
		s.d.				0.090	<b>0.043</b>
		p-value				0.157	<b>0.005</b>
<b>R<sub>s</sub></b>			<i>ln</i>	<i>ln</i>			<i>ln</i>
Intercept		Estimates	0.169	-0.070	<b>1.052</b>	<b>1.052</b>	<b>-0.573</b>
		s.d.	0.010	0.062	<b>0.063</b>	<b>0.063</b>	<b>0.106</b>
		p-value	0.098	0.271	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
Composition	<i>Mixed</i>	Estimates					
		s.d.					
Size	<i>Medium</i>	Estimates					
		s.d.					

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	p-value
Estimates	
<i>Small</i>	s.d.
	p-value

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409

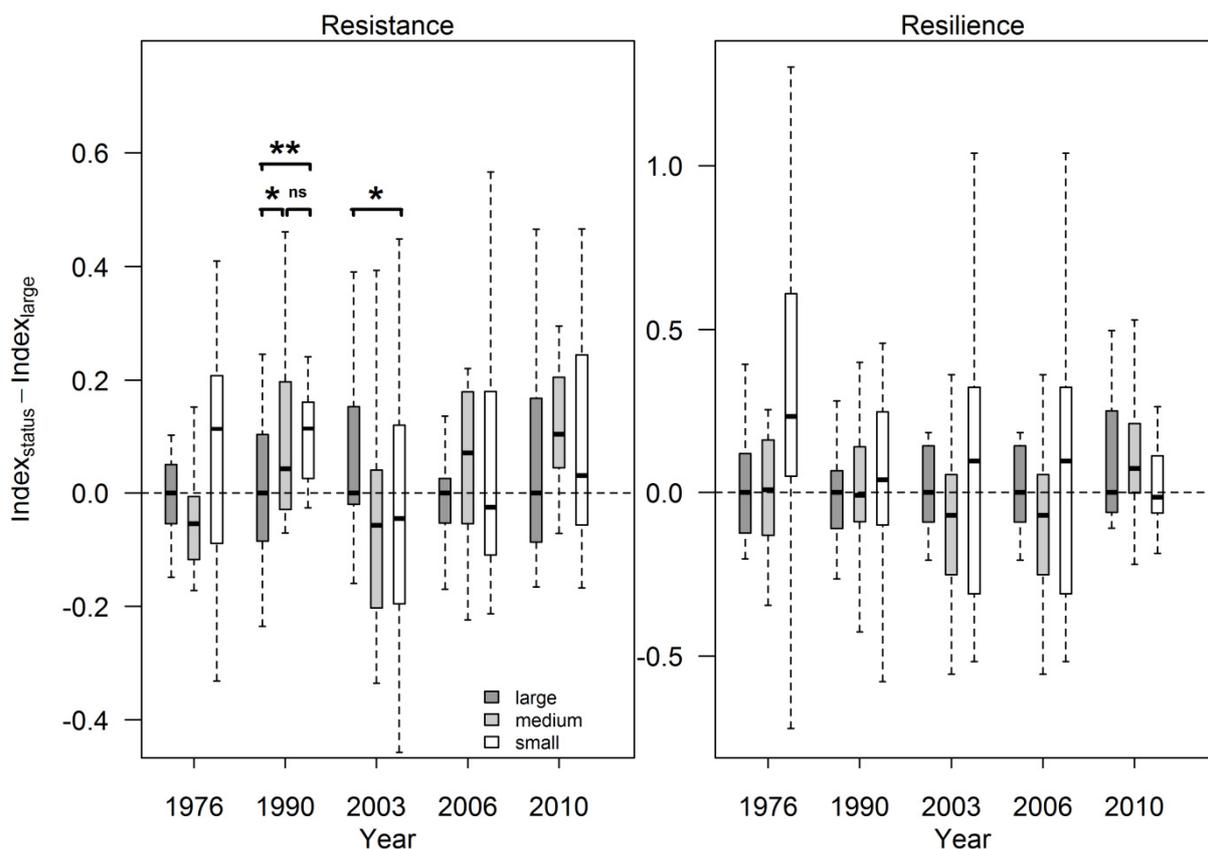
410 Table 6. Results from the linear mixed models for stand composition and tree size effects on  
 411 resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices of Scots pine for the five selected drought  
 412 events. Parameters are estimated with pure stands and large trees as the references. *ln* below a  
 413 drought event indicates that logarithm transformation of the response variable was used to fit  
 414 the model. Estimates and standard deviations (s.d.) were not back transformed when the  
 415 logarithm was applied. Significant results are shown in bold characters. Shading indicates the  
 416 direction of the difference between each factor level and the references, *i.e.* large trees and  
 417 pure stands; dark grey: positive difference; light grey: negative difference.

		1976	1990-1992	2003	2006	2010
<b><math>R_t</math></b>			<i>ln</i>			<i>ln</i>
Intercept	Estimates	<b>0.607</b>	<b>-0.148</b>	<b>0.790</b>	<b>0.481</b>	-0.029
	s.d.	<b>0.045</b>	<b>0.058</b>	<b>0.022</b>	<b>0.059</b>	0.032
	p-value	< <b>0.001</b>	<b>0.014</b>	< <b>0.001</b>	< <b>0.001</b>	0.367
Composition	<i>Mixed</i>	Estimates				
		s.d.				
		p-value				
Size	<i>Medium</i>	Estimates	0.088		0.105	
		s.d.	0.052		0.065	
		p-value	0.095		0.112	
	<i>Small</i>	Estimates	<b>0.128</b>		<b>0.137</b>	
		s.d.	<b>0.052</b>		<b>0.065</b>	
		p-value	<b>0.017</b>		<b>0.041</b>	
<b><math>R_c</math></b>		<i>ln</i>	<i>ln</i>			<i>ln</i>
Intercept	Estimates	<b>0.425</b>	<b>0.334</b>	<b>1.220</b>	<b>1.801</b>	<b>-0.450</b>
	s.d.	<b>0.085</b>	<b>0.044</b>	<b>0.058</b>	<b>0.126</b>	<b>0.091</b>
	p-value	< <b>0.001</b>				
Composition	<i>Mixed</i>	Estimates				
		s.d.				
		p-value				
Size	<i>Medium</i>	Estimates				
		s.d.				
		p-value				
	<i>Small</i>	Estimates				
s.d.						
p-value						
<b><math>R_s</math></b>		<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>
Intercept	Estimates	<b>-0.220</b>	<b>0.186</b>	<b>-0.288</b>	<b>-0.253</b>	<b>-0.479</b>
	s.d.	<b>0.070</b>	<b>0.092</b>	<b>0.080</b>	<b>0.081</b>	<b>0.100</b>
	p-value	<b>0.003</b>	<b>0.049</b>	<b>0.001</b>	<b>0.003</b>	< <b>0.001</b>
Composition	<i>Mixed</i>	Estimates				
		s.d.				
		p-value				

Size	<i>Medium</i>	Estimates	<b>0.323</b>	0.219	0.149
		s.d.	<b>0.089</b>	0.113	0.115
		p-value	<b>&lt; 0.001</b>	0.059	0.203
	<i>Small</i>	Estimates	<b>0.337</b>	<b>0.310</b>	<b>0.275</b>
		s.d.	<b>0.089</b>	<b>0.113</b>	<b>0.115</b>
		p-value	<b>&lt; 0.001</b>	<b>0.009</b>	<b>0.021</b>

418

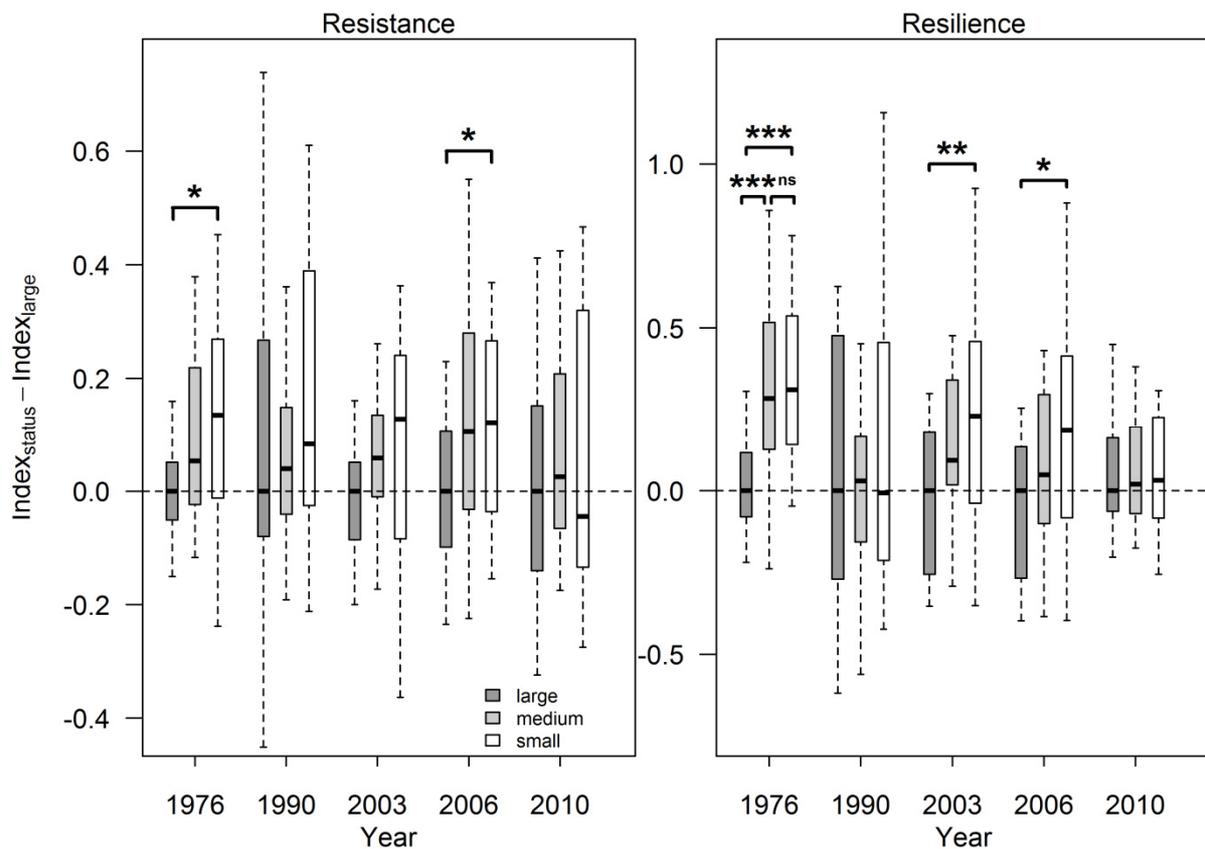
419 Figure 4. Difference between the resistance or resilience index value for large sessile oak trees  
 420 and the values for the other tree size classes for each drought event. For each year and tree  
 421 size, the segments and stars indicate the level of significance of the difference between large  
 422 Scots pine trees and other trees from the models. The models were re-run with the medium  
 423 size as the reference to test the difference between this size and the small size. \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .; ns: not significant.



425

426 Figure 5. Difference between the resistance or resilience index value for large Scots pine trees  
 427 and the values for the other tree size classes for each drought event. For each year and tree

428 size, the segments and stars indicate the level of significance of the difference between large  
429 Scots pine trees and other trees from the models. The models were re-run with the medium  
430 size as the reference to test the difference between this size and the small size. \*:  $p < 0.05$ ; \*\*:  
431  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .; ns: not significant.



432

#### 433 4. Discussion

434 As expected, both species reduced their radial growth during drought events. When drought  
435 occurs, photosynthesis is reduced leading to less carbon available for functions such as radial  
436 growth which in turn decreases (Chaves *et al.*, 2003; Palacio *et al.*, 2014).

437 Resistance and resilience to drought differed between oak and pine, as expected (Table 4),  
438 though the mean values for each species were close to each other (Table 3). Stand  
439 composition had no effect on the resistance indices of the species studied (Table 5, Table 6).

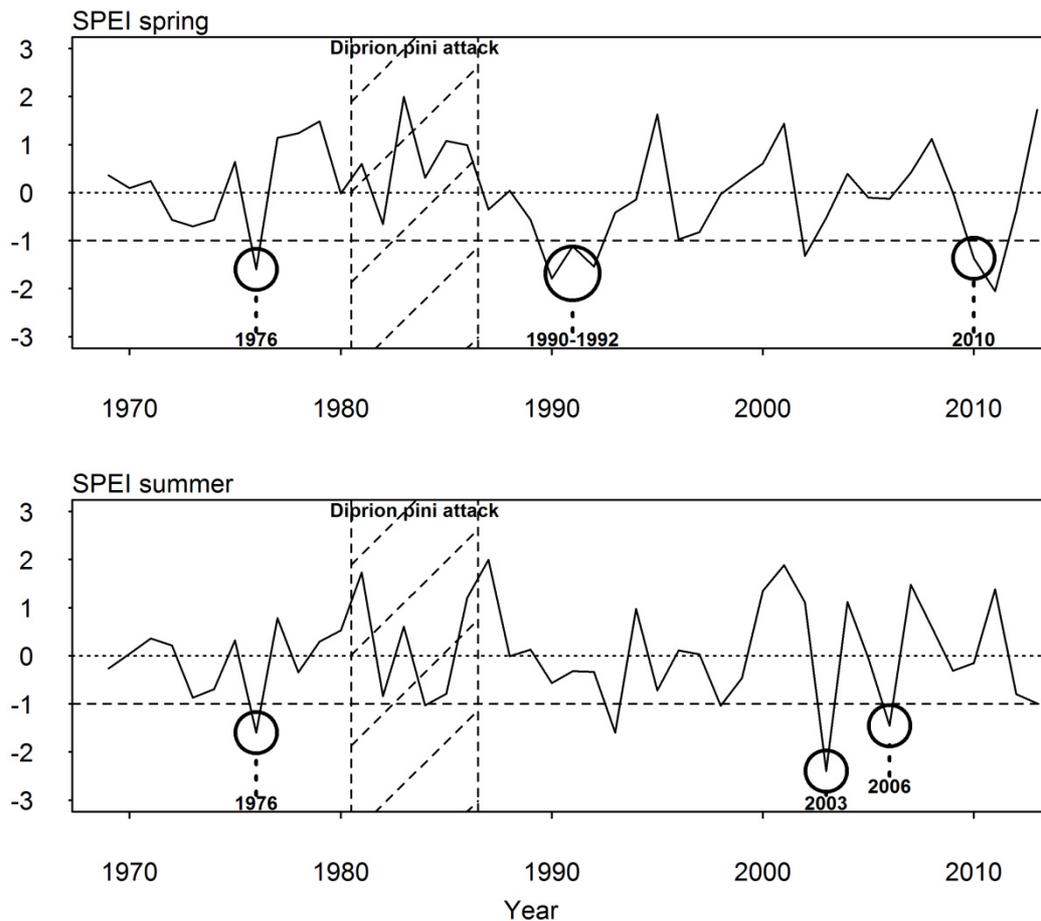
440 However, tree size did have an effect in some cases. The influence of tree size was

441 pronounced and unidirectional for resistance and resilience in Scots pine for several drought  
442 events. Results for sessile oak show that the size effect varied between drought events or  
443 indices.

#### 444 4.1. Oak and pine respond differently to drought events

445 We first showed that sessile oak and Scots pine responded differently to the five drought  
446 events studied. Pine was more resistant during the 1990-1992 drought period and the 2010  
447 drought while oak was more resistant during the 2003 and 2006 droughts. The drought events  
448 studied here occurred at different periods during the growing season and this could have  
449 influenced the responses of the two species. Indeed, several studies have shown that pine and  
450 oak species have different growth dynamics during the growing season (Weber *et al.*, 2007;  
451 Eilmann *et al.*, 2009; Michelot *et al.*, 2012b). Complementary analyses of the SPEI over the  
452 spring (March to May) and summer months (June to August) separately revealed different  
453 types of drought (Figure 6).

454 Figure 6. SPEI computed for spring (April to June) and for summer (July to August) from  
455 1970 to 2013. The selected drought events are indicated by a bold circle. The horizontal  
456 dotted line indicates the threshold of -1 below which a drought was considered severe. The  
457 1981 to 1986 period (hatched zone) was removed from our analysis because of severe pine  
458 defoliation by *Diprion pini*.



459  
460 The 1976 drought was global throughout the whole growing season. The 1990-1992 and 1010  
461 droughts occurred in the spring while the 2003 and 2006 droughts were intense summer  
462 droughts. Our results suggest that Scots pine was more resistant during spring droughts than  
463 sessile oak, and that sessile oak was more resistant during summer droughts (Table 4). The  
464 1976 drought, which lasted through spring and summer, should have affected both species;  
465 our results confirm this (we found no difference between the two species for any index, Table  
466 **4Erreur ! Source du renvoi introuvable.**). Their differing growth dynamics, particularly

467 how the two species form intra-annual wood, could explain this time-dependent resistance.  
468 Zweifel *et al.* (2006) showed that pubescent oak (*Quercus pubescens*) starts radial growth  
469 about one month before leaf expansion, achieving almost half of the annual radial increment  
470 by the time the leaves reach full expansion at the end of spring. Furthermore, oak species have  
471 been found to be more sensitive to spring conditions, and particularly to water availability  
472 during spring, than to summer conditions and droughts (van der Werf *et al.*, 2007; Weber *et*  
473 *al.*, 2007; Eilmann *et al.*, 2009; Zang *et al.*, 2012; Morán-López *et al.*, 2014). Earlywood vessels  
474 in oak are formed before and during budburst using stored reserves from the previous growing  
475 season (Corcuera *et al.*, 2004). These newly formed vessels are wide allowing such ring-  
476 porous species to transport more water during early growing season but at the expense of  
477 increased embolism risk. They rapidly become embolized as conditions become more stressful  
478 during the growing season (Cochard and Tyree, 1990). During spring droughts, the oak's  
479 newly formed vessels are exposed to the risk of cavitation leading to water deficit and  
480 reduced cell enlargement. Water stress during spring is thus the most important factor  
481 controlling radial growth for oak (Tardif and Conciatori, 2006). This phenomenon constrains  
482 ring width despite the potential activation of drought avoidance mechanisms (Eilmann *et al.*,  
483 2009). In contrast, summer drought would be of less consequence on oak radial growth as the  
484 radial increment would have mainly occurred during the months preceding the drought.  
485 However, a summer drought still reduces photosynthetic activity for oak through stomatal  
486 closure, which prevents further accumulation of reserves for the following year's growth  
487 (Chaves *et al.*, 2003). For Scots pine, on the other hand, needles only appear during the  
488 summer and the tree has achieved a mere fourth of its annual radial increment by the time  
489 needles reach full expansion (Zweifel *et al.*, 2006). This species' radial growth dynamics,  
490 which have been extensively studied in Europe, show a stronger dependency on conditions at  
491 the end of spring and during the summer months (Weber *et al.*, 2007; Eilmann *et al.*, 2009;

492 Eilmann *et al.*, 2011; Zang *et al.*, 2012; Taeger *et al.*, 2013). Spring droughts constrain pine  
493 growth and might lead to the cavitation of some xylem tracheids. However, pine can continue  
494 its radial growth when the conditions become better after the spring drought subsides,  
495 resulting in wider ring widths during spring drought years than for oak. Summer droughts, on  
496 the other hand, quite strongly affect pine growth because they hamper needle formation and  
497 reduce cell enlargement, consequently reducing the radial increment for that year, in contrast  
498 to oak.

499 Results for recovery were less pronounced than for resistance: for resistance, four out of five  
500 drought events showed significant differences between the two species while only two out of  
501 five drought events showed significant differences for recovery (Table 4). However, assuming  
502 that both resistance to and recovery from drought events depend on the amount of carbon  
503 reserves available, a compromise might be established between these two indices (Galiano *et*  
504 *al.*, 2011; Lloret *et al.*, 2011). As mentioned before, ring widths for oak show a strong  
505 relationship with climatic conditions of the previous year, even when the current year's  
506 conditions are favorable (Zweifel *et al.*, 2006; van der Werf *et al.*, 2007; Eilmann *et al.*, 2009;  
507 Michelot *et al.*, 2012b). A summer drought does not constrain oak ring width but does  
508 constrain its photosynthetic activity, thus reducing the amount of reserves stored for the  
509 establishment of the following year's tree ring. This was observed for 2004, following the  
510 2003 drought, for some individuals in our study (data not shown) and for 2007, following the  
511 2006 drought (van der Werf *et al.*, 2007). The longer growing season for Scots pine (Michelot  
512 *et al.*, 2012b) as well as its ability to maintain photosynthesis throughout autumn and winter  
513 thanks to its evergreen leaves limit its dependence on the previous year's accumulated  
514 reserves for recovery after a drought event (Gruber *et al.*, 2012). This compromise between  
515 resistance and recovery explains that in 2006 (summer drought) and 2010 (spring drought),  
516 we found opposite results for resistance and resilience (Table 4). However, this idea of a

517 potential compromise between resistance and recovery based on the amount of carbon  
518 reserves available needs further investigation.

#### 519 4.2. Stand composition has no effect on resistance and resilience

520 Neither pine nor oak responses to the selected drought events depended on stand composition  
521 (pure or mixed) (Table 5). This result was unexpected as results in the literature usually  
522 present various effects of species mixtures in forests in case of biotic and abiotic disturbances,  
523 whether they present benefits or drawbacks (Knoke *et al.*, 2008; Maestre *et al.*, 2009; Felton  
524 *et al.*, 2010; Lebourgeois *et al.*, 2013; Perot *et al.*, 2013; Pretzsch *et al.*, 2013).

525 Assuming equivalent stand density, lower growth in mixed stands associated to drought  
526 episodes would indicate stronger between-species competition (Grossiord *et al.*, 2014) than  
527 within-population competence. The absence of this pattern in our results indicates that  
528 drought conditions did not increase between-species competition, suggesting that water  
529 acquisition for each species was not disrupted by the presence of the other species. The  
530 absence of any benefits (higher growth) of the mixed stands also suggests the absence of any  
531 complementarity process (through root stratification for example e. g. Pretzsch *et al.* (2013))  
532 in our study sites during drought, which might be related to the type of soil encountered in the  
533 study plots prohibiting deep root extension (Table 1).

534 Moreover, the trees sampled in this study had all necessarily survived the selected drought  
535 events. Trees which died during these drought events might have had an impact at the stand  
536 level on the stand composition effect. A long-term survey including mortality is needed to  
537 more precisely define the effects of stand composition on individuals' response to drought.  
538 Lastly, the stand composition effect might be reflected in structural characteristics other than  
539 ring widths. There is a growing number of studies focusing on other wood characteristics such  
540 as the relative widths of earlywood and latewood, the number and size of vessels, and ring  
541 density. These parameters would add a degree of precision to the understanding of the

542 processes governing tree growth and cambial activity (Martinez-Vilalta and Pñol, 2002;  
543 Eilmann *et al.*, 2009; Martín-Benito *et al.*, 2013; Vieira *et al.*, 2014).

544

545 4.3. The tree size effect on individual tree response to drought varies between species

546 In *Pinus sylvestris* large trees were more sensitive than small trees to drought, while no clear  
547 trend was observed for *Quercus petraea* (Table 5, Table 6).

548 4.3.1. Small oak response seems better for older droughts than for recent droughts

549 The results obtained for sessile oak show varying effects of tree size depending on the  
550 drought event and the index (Table 5, Figure 4). We observed a better response of small trees  
551 for the 1990-1992 drought (resistance), and the opposite for the 2003 (resistance), and 2010  
552 droughts (recovery) while medium-sized trees responded better in terms of recovery for the  
553 2006 drought. Several hypotheses could be made to explain these results. As it has been  
554 suggested before, the type of drought could play a major role in shaping trees' responses to  
555 such disturbances. The 1990-1992 drought and the 2003 drought have very different  
556 characteristics: the first one was a drought spanning several years and more related to water  
557 stress than temperature stress while the second one was very short and intense and more  
558 related to temperature stress. The 2003, 2006 and 2010 droughts were frequent, happening  
559 only a few years apart from each other while the 1990-1992 drought happened 15 years after  
560 the previous drought which was in 1976. Small and large trees could reasonably respond  
561 differently to these varying characteristics of droughts, explaining the results we observed in  
562 our study. Processes related to drought hardening for example in small trees as suggested by  
563 Martín-Benito *et al.* (2008) might confer them an advantage while large trees might recover  
564 faster in the favorable years following a drought (Martín-Benito *et al.*, 2008; Martínez-Vilalta  
565 *et al.*, 2012). Moreover, we could imagine that oaks could respond differently to droughts as

566 they grow older (as suggested by Lloret et al. (2011) and Martínez-Vilalta et al. (2012) for pine  
567 species) leading to a potential change in the direction of the individual tree response to  
568 different drought effects, as we observed between the 1990-1992 drought and the following  
569 droughts. Unfortunately, very few references could be found and our results could not support  
570 one hypothesis more than another.

#### 571 4.3.2. Small pines' response to drought is better than large pines

572 The results for Scots pine are unambiguous: when tree size is significant, trees of lower size  
573 (e. g. medium or small) have better responses to drought than large trees in terms of  
574 resistance, and above all, resilience (Table 6, Figure 5). It can be noted that these differences  
575 are observed only for summer droughts (no tree size effect for the 1990-1992 and 2010 spring  
576 droughts). In our stands, the variability of Scots pine diameters is associated with a  
577 stratification of tree crowns (through different crown transparency and expansion). Thus,  
578 microsite climatic conditions (humidity, temperature or solar radiation) might be kept  
579 relatively favorable for small trees, providing them with better growing conditions despite the  
580 overall drought conditions (Aussenac, 2000). Small trees may also be drought-hardened due  
581 to their position in the stand. Their need for carbon, nutrients and water would thus be  
582 reduced while their efficiency to use these resources might be enhanced. These drought-  
583 hardening adaptations (Martín-Benito *et al.*, 2008) as well as the micro-climatic conditions  
584 could enable the small trees to sustain growth while conditions are too harsh for large trees  
585 with high resource and maintenance needs as found in the literature (Martín-Benito *et al.*,  
586 2008; Martínez-Vilalta *et al.*, 2012; Zang *et al.*, 2012).

587 However, other results in the literature contradict our results, showing that small trees are  
588 more affected by drought events than large trees (Orwig and Abrams, 1997; Pichler and  
589 Oberhuber, 2007) due to a shallower root system or increased intraspecific competition

590 (Martín-Benito *et al.*, 2008; Zang *et al.*, 2012), or no tree size effect at all (Mérian and  
591 Lebourgeois, 2011).

592 Variability in the definition and magnitude of the tree size classes analyzed and the indices  
593 used in other studies and in ours may play a role in these conflicting results. Different soil and  
594 climatic conditions at each study site can also modify the response thresholds of individual  
595 trees. Finally, our study shows that in the same environmental context, the tree size effect  
596 varies according to the species considered (Lebourgeois *et al.*, 2014), though we have yet to  
597 provide an explanation for this variation. Nevertheless, it is important to take into account the  
598 tree size classes within a stand in the study of the responses to climatic and/or biotic  
599 disturbances, as some previous studies have noted (Orwig and Abrams, 1997; Martín-Benito *et*  
600 *al.*, 2008; Mérian and Lebourgeois, 2011; Zang *et al.*, 2012; Eilmann *et al.*, 2013).

## 601 **5. Conclusion**

602 Our study confirms the differing responses of sessile oak and Scots pine to several specific  
603 drought events. Our results suggest that summer and spring droughts do not have the same  
604 impact on different species, though the limited number of drought events in our data did not  
605 enable us to test this hypothesis. The two species' contrasted growth dynamics and timing  
606 may lead to different consequences from a spring or a summer drought. Specific responses to  
607 different types of drought should be considered in future studies. Our results indicated no  
608 adverse or beneficial effects of mixture on the two species' resistance, resilience and recovery  
609 to drought. Tree size significantly affected both species, though the direction of this effect  
610 was not clear in sessile oak while it was for Scots pine, showing a better response of small  
611 trees to drought events. We hypothesize that intra-specific facilitation and/or physiological  
612 adaptations confer an advantage to small individuals during periods of water stress, though  
613 results from the literature are contradictory. The long-term monitoring of forest stands makes  
614 it possible to take into consideration mortality events following disturbances; a severe drought

615 can speed up the mortality process for weak trees (Pedersen, 1998; Galiano *et al.*, 2010) but  
616 less so for strongly growing trees. Such experiments are in progress in the research unit where  
617 the OPTMix experimental site is located. Our study provides support for good resilience  
618 among surviving individuals of sessile oak and Scots pine in this lowland forest, which is  
619 facing climate change and increased drought frequency. This research is essential to adapt  
620 forest management strategies to changing conditions, while taking economic requirements  
621 into account.

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836

837 **Appendices**

838 **A. Calculation of the relative bias in the index comparison between species**

839 In the following equations,  $d_{i,n}$  is the mean diameter at drought event  $n$  for the pre-drought,  
840  $RW_{i,n}$  or  $BAI_{i,n}$  is respectively the ring width or tree basal area increment at drought event  $n$ .  
841 The  $i$  or  $j$  subscript defines for which period – drought, pre-drought or post-drought – the  
842 variable is calculated depending on the relevant index.

843 The definition of BAI is as follows:

$$BAI_n = (d_n^2 - d_{n-1}^2) \times \frac{\pi}{4}$$

844 which can be simplified as:

$$BAI_n = \pi \times RW_n \times (d_{n-1} + RW_n)$$

845 Therefore, we may write any index based on BAI as:

$$Index_{BAI,n} = \frac{BAI_{i,n}}{BAI_{j,n}} = \frac{\pi \times RW_{i,n} \times (d_{i,n-1} + RW_{i,n})}{\pi \times RW_{j,n} \times (d_{j,n-1} + RW_{j,n})}$$

846 Using the index based on RW, the previous equation can be written as:

$$Index_{BAI,n} = Index_{RW,n} \times \frac{(d_{i,n-1} + RW_{i,n})}{(d_{j,n-1} + RW_{j,n})}$$

847 Therefore, the error  $R$  for each index based on BAI is:

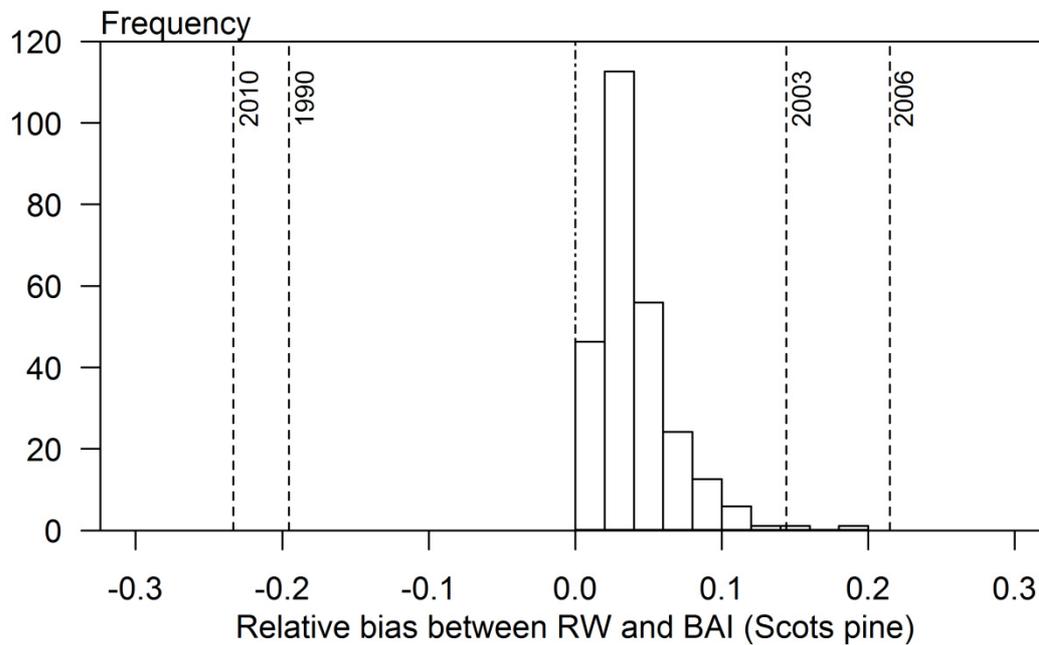
$$R_n = \frac{(d_{i,n-1} + RW_{i,n})}{(d_{j,n-1} + RW_{j,n})}$$

848 This error was calculated on the Scots pine data for each drought event. The relative bias

849  $1 - R$  thus defined can be compared with the modeled difference between the species for each

850 index. When the difference between species was significant, the relative bias was largely  
851 under the modeled difference, as is shown in Figure A 1 for the resistance index.

852 Figure A 1. Relative bias in the comparison between oak RW and pine BAI. The modeled  
853 difference in resistance to drought between oak and pine responses are plotted in dotted lines  
854 for the drought events for which the species effect was significant. These dotted lines are far  
855 beyond the mean relative bias, showing that the results we obtained are not confounded with  
856 the error induced by using two different growth variables to calculate the indices.



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859 **B. COFECHA outputs for Scots pine and sessile oak tree-ring cross-validation**

860 Mean sensitivities values were discarded as it has been shown not to be a good estimator of the characteristics of a time-series (Bunn *et al.*,  
 861 2013).

862 Table B 1. Selected COFECHA output for Scots pine individual tree series showing descriptive information on each individual (site, plot,  
 863 subplot, first year and last year of the measured tree rings, cumulative number of years). The statistics calculated by COFECHA are shown in the  
 864 following columns: correlation with master series (computed from the 54 individual series), the mean and maximum measurement (tree-ring  
 865 widths) along with the standard deviation (s.d.) associated and the autocorrelation of each series.

Site	Plot	Subplot	Individual	First year	Last year	Years	Correlation with Master Series	Mean	Max	s.d.	Autocorrelation
2	O200	2	1	1952	2012	61	0.768	1.84	6.31	1.244	0.802
2	O200	2	2	1950	2012	63	0.714	2.38	8.82	1.87	0.888
2	O200	2	3	1955	2012	58	0.726	1.86	5.54	1.292	0.834
2	O200	2	4	1957	2012	56	0.714	2.32	9.58	2.064	0.736
2	O200	3	5	1952	2012	61	0.739	1.79	4.12	0.769	0.78
2	O200	3	6	1951	2012	62	0.628	2.2	6.48	1.437	0.913
2	O200	3	7	1950	2012	63	0.722	2.17	8.08	1.67	0.832
2	O200	3	8	1950	2012	63	0.665	2.38	7.04	1.569	0.875
2	O200	3	9	1951	2012	62	0.69	2.32	6.23	1.074	0.772
2	O216	1	1	1955	2012	58	0.825	2.69	6.42	1.446	0.744
2	O216	1	2	1958	2012	55	0.736	1.75	4.49	0.866	0.636
2	O216	1	3	1952	2012	61	0.809	2.69	8.92	2.201	0.86
2	O216	1	4	1957	2012	56	0.791	2.77	7.11	1.559	0.746
2	O216	1	5	1960	2012	53	0.731	2.52	10.17	1.519	0.589
2	O216	2	6	1959	2012	54	0.722	1.53	5.1	1.191	0.875
2	O216	3	7	1959	2012	54	0.584	2.29	6.82	1.058	0.707

2	O216	3	8	1963	2012	50	0.714	2.64	6.28	1.168	0.592
2	O216	3	9	1960	2012	53	0.734	1.9	8.47	1.298	0.554
3	O333	1	1	1961	2013	53	0.733	2.57	5.28	1.254	0.756
3	O333	1	2	1963	2013	51	0.7	2.99	7.56	1.679	0.87
3	O333	1	3	1962	2013	52	0.747	2.22	6.68	1.269	0.84
3	O333	1	4	1961	2013	53	0.554	2.68	7.57	1.36	0.812
3	O333	1	5	1964	2013	50	0.45	1.71	3.86	0.82	0.788
3	O333	2	6	1962	2013	52	0.553	2.54	6.25	1.232	0.807
3	O333	2	7	1960	2013	54	0.646	2	5.16	1.013	0.776
3	O333	2	8	1960	2013	54	0.518	2.78	8.8	1.788	0.754
3	O333	2	9	1959	2013	55	0.766	2.41	6.41	1.486	0.848
3	O333	2	1	1944	2012	69	0.688	2.01	4.51	1.094	0.783
1	O57	3	2	1948	2012	65	0.763	2.2	4.88	0.961	0.697
1	O57	3	3	1944	2012	69	0.703	1.18	3.65	0.899	0.821
1	O57	3	4	1943	2012	70	0.702	1.96	5.64	1.334	0.854
1	O57	3	5	1951	2012	62	0.622	1.46	3.32	0.626	0.571
1	O57	3	6	1943	2012	70	0.744	1.71	5.29	1.632	0.864
1	O57	4	7	1942	2012	71	0.717	2.17	5.65	1.458	0.899
1	O57	4	8	1941	2012	72	0.739	2.46	5.34	1.466	0.802
1	O57	4	9	1943	2012	70	0.651	2.4	6.31	1.237	0.805
3	O598	1	1	1940	2013	74	0.736	1.82	3.93	0.701	0.519
3	O598	1	2	1966	2013	48	0.562	1.74	3.71	0.862	0.726
3	O598	1	3	1963	2013	51	0.74	2.1	4.74	1.148	0.832
3	O598	1	4	1940	2013	74	0.542	2.64	7.07	1.776	0.829
3	O598	1	5	1958	2013	56	0.556	1.37	2.34	0.533	0.552
3	O598	2	6	1940	2013	74	0.516	2.04	5.6	0.967	0.718
3	O598	2	7	1952	2013	62	0.704	2.07	5.08	0.933	0.31
3	O598	3	8	1955	2013	59	0.475	2.28	6.34	0.797	0.357
3	O598	3	9	1938	2013	76	0.517	2.21	4.76	0.897	0.756
1	O83	2	1	1960	2012	53	0.806	2.89	5.86	1.026	0.636

1 O83	2	2	1961	2012	52	0.592	2.15	4.86	0.889	0.685
1 O83	2	3	1959	2012	54	0.546	2.58	5.39	0.855	0.714
1 O83	2	4	1956	2012	57	0.638	2.55	9.65	2.007	0.855
1 O83	2	5	1960	2012	53	0.701	1.87	4.55	0.936	0.69
1 O83	3	6	1959	2012	54	0.459	2.22	5.35	1.209	0.846
1 O83	3	7	1960	2012	53	0.432	3.41	7.2	1.254	0.737
1 O83	3	8	1961	2012	52	0.71	3.41	6.31	0.906	0.468
1 O83	3	9	1959	2012	54	0.465	2.71	7.57	1.464	0.866

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867 Table B 2. Selected COFECHA output for sessile oak individual tree series showing descriptive information on each individual (site, plot,  
868 subplot, first year and last year of the measured tree rings, cumulative number of years). The statistics calculated by COFECHA are shown in the  
869 following columns: correlation with master series (computed from the 54 individual series), the mean and maximum measurement (tree-ring  
870 widths) along with the standard deviation (s.d.) associated and the autocorrelation of each series.

Site	Plot	Subplot	Individual	First year	Last year	Years	Correlation with Master Series	Mean	Max	s.d.	Autocorrelation
1	O12	1	1	1944	2012	69	0.805	1.31	3.16	0.577	0.367
1	O12	1	2	1942	2012	71	0.576	1.38	2.54	0.481	0.455
1	O12	1	3	1944	2012	69	0.682	1.34	2.73	0.411	0.249
1	O12	1	4	1941	2012	72	0.595	0.94	3.14	0.466	0.683
1	O12	1	5	1941	2012	72	0.667	1.63	2.94	0.488	0.543
1	O12	2	6	1942	2012	71	0.661	1.11	2.76	0.412	0.552
1	O12	2	7	1943	2012	70	0.652	0.78	3.96	0.615	0.764
1	O12	2	8	1943	2012	70	0.571	0.74	3.04	0.47	0.704
1	O12	2	9	1946	2012	67	0.688	1.59	3.72	0.649	0.559
2	O214	2	1	1948	2012	65	0.509	1.32	3.73	0.616	0.363
2	O214	2	2	1954	2012	59	0.612	1.32	3.38	0.461	0.447
2	O214	2	3	1951	2012	62	0.541	0.75	2.24	0.372	0.422
2	O214	2	4	1955	2012	58	0.5	0.91	3.41	0.569	0.686
2	O214	2	5	1947	2012	66	0.769	1.43	3.78	0.604	0.462
2	O214	3	6	1950	2012	63	0.812	1.24	3.2	0.471	0.405
2	O214	3	7	1950	2012	63	0.767	1.76	3.88	0.737	0.609
2	O214	3	8	1953	2012	60	0.713	1.74	3.65	0.67	0.602
2	O214	3	9	1951	2012	62	0.628	0.93	2.47	0.494	0.479
2	O216	1	1	1957	2012	56	0.718	1.05	1.79	0.368	0.506
2	O216	1	2	1956	2012	57	0.75	1.31	2.93	0.456	0.513
2	O216	1	3	1958	2012	55	0.433	0.91	3.83	0.671	0.612

2	O216	1	4	1952	2012	61	0.687	1.69	3.06	0.616	0.574
2	O216	1	5	1954	2012	59	0.724	1.75	2.86	0.607	0.583
2	O216	1	6	1958	2012	55	0.651	1.09	2.48	0.398	0.354
2	O216	2	7	1953	2012	60	0.608	1.38	3.35	0.64	0.653
2	O216	2	8	1950	2012	63	0.722	1.82	3.66	0.734	0.774
2	O216	2	9	1953	2012	60	0.708	1.2	2.61	0.517	0.62
1	O57	1	1	1938	2012	75	0.658	1.29	3.02	0.517	0.622
1	O57	2	2	1937	2012	76	0.46	1.04	2.69	0.507	0.724
1	O57	3	3	1944	2012	69	0.645	1.07	2.21	0.599	0.803
1	O57	3	4	1943	2012	70	0.584	0.95	2.1	0.514	0.626
1	O57	4	5	1940	2012	73	0.561	0.72	1.95	0.396	0.785
1	O57	4	6	1952	2012	61	0.718	1.49	3.85	0.749	0.517
1	O57	4	7	1937	2012	76	0.748	1.76	4.19	0.926	0.698
1	O57	4	8	1935	2012	78	0.75	1.67	2.99	0.694	0.763
1	O57	4	9	1937	2012	76	0.659	1.33	4.61	0.64	0.637
3	O593	2	1	1971	2013	43	0.866	1.57	3.13	0.441	0.352
3	O593	2	2	1950	2013	64	0.843	1.92	4.59	0.679	0.406
3	O593	2	3	1951	2013	63	0.556	1.4	3.09	0.601	0.597
3	O593	2	4	1948	2013	66	0.513	0.96	3.4	0.608	0.632
3	O593	2	5	1950	2013	64	0.596	1.64	3.14	0.543	0.577
3	O593	2	6	1948	2013	66	0.735	1.92	3.7	0.813	0.694
3	O593	3	7	1950	2013	64	0.752	1.76	4.26	0.673	0.516
3	O593	3	8	1950	2013	64	0.675	0.93	3.28	0.455	0.546
3	O593	3	9	1947	2013	67	0.708	1.45	3.46	0.54	0.54
3	O598	1	1	1933	2013	81	0.655	1.4	5.96	0.748	0.623
3	O598	1	2	1944	2013	70	0.235	0.73	1.74	0.412	0.628
3	O598	2	3	1942	2013	72	0.581	1.47	4.12	0.777	0.738
3	O598	2	4	1934	2013	80	0.301	1.26	2.08	0.328	0.491
3	O598	2	5	1937	2013	77	0.521	1.27	3.08	0.694	0.72
3	O598	2	6	1950	2013	64	0.37	0.73	1.64	0.422	0.634

3	O598	3	7	1940	2013	74	0.184	0.84	2.89	0.646	0.872
3	O598	3	8	1940	2013	74	0.646	1.66	3.27	0.642	0.614
3	O598	3	9	1934	2013	80	0.59	1.95	3.87	0.687	0.695

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