Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine

M. Merlin, Thomas Perot, Sandrine Perret, Nathalie Korboulewsky, P. Vallet

HAL Id: hal-01140201

https://hal.science/hal-01140201

Submitted on 8 Apr 2015

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

2   oak and Scots pine

3

4   Morgane Merlin, Thomas Perot, Sandrine Perret, Nathalie Korboulewsky, Patrick Vallet

5   Irstea, UR EFNO Ecosystèmes Forestiers, Centre de Nogent-sur-Vernisson, F-45290 Nogent-

6   sur-Vernisson, France

7   Corresponding author:

8   Morgane Merlin

9   morgane.merlin@orange.fr

10   Irstea, UR EFNO Ecosystèmes Forestiers, F-45290 Nogent-sur-Vernisson, France

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.

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 (Bréda *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 (Bréda

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; Vilà-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

3

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 (Dhôte, 1994). This hierarchy implies a differential

90   availability of resources such as water (Dawson, 1996), nutrients and light (Dhôte, 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 (Bréda *et al.*, 2006; Eilmann *et al.*, 2006; Bréda 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 Orléans 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, sylvicultural

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					
Stand	*Pure*			*Mixed*			*Pure*			*Mixed*		
Size	S	M	L	S	M	L	S	M	L	S	M	L
Age (*years*)	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)
Diameter (*cm*)	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*.
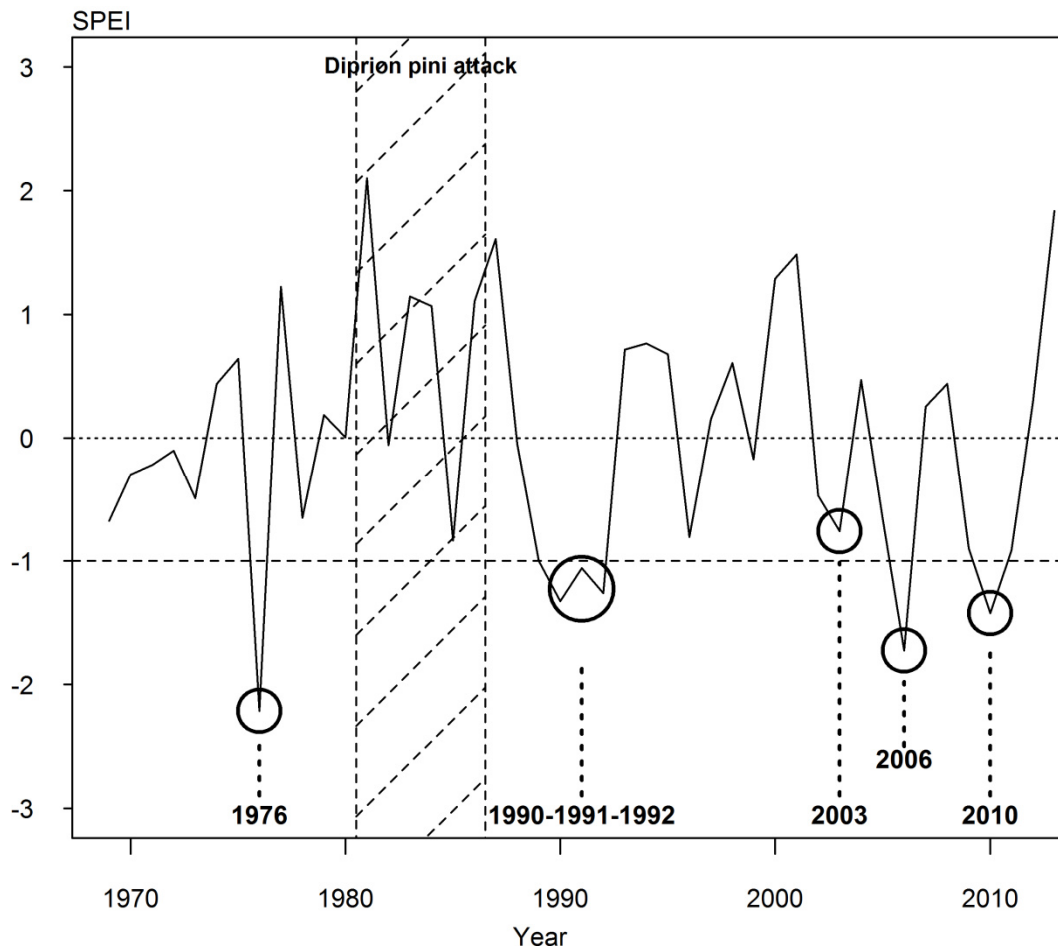
252

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

13
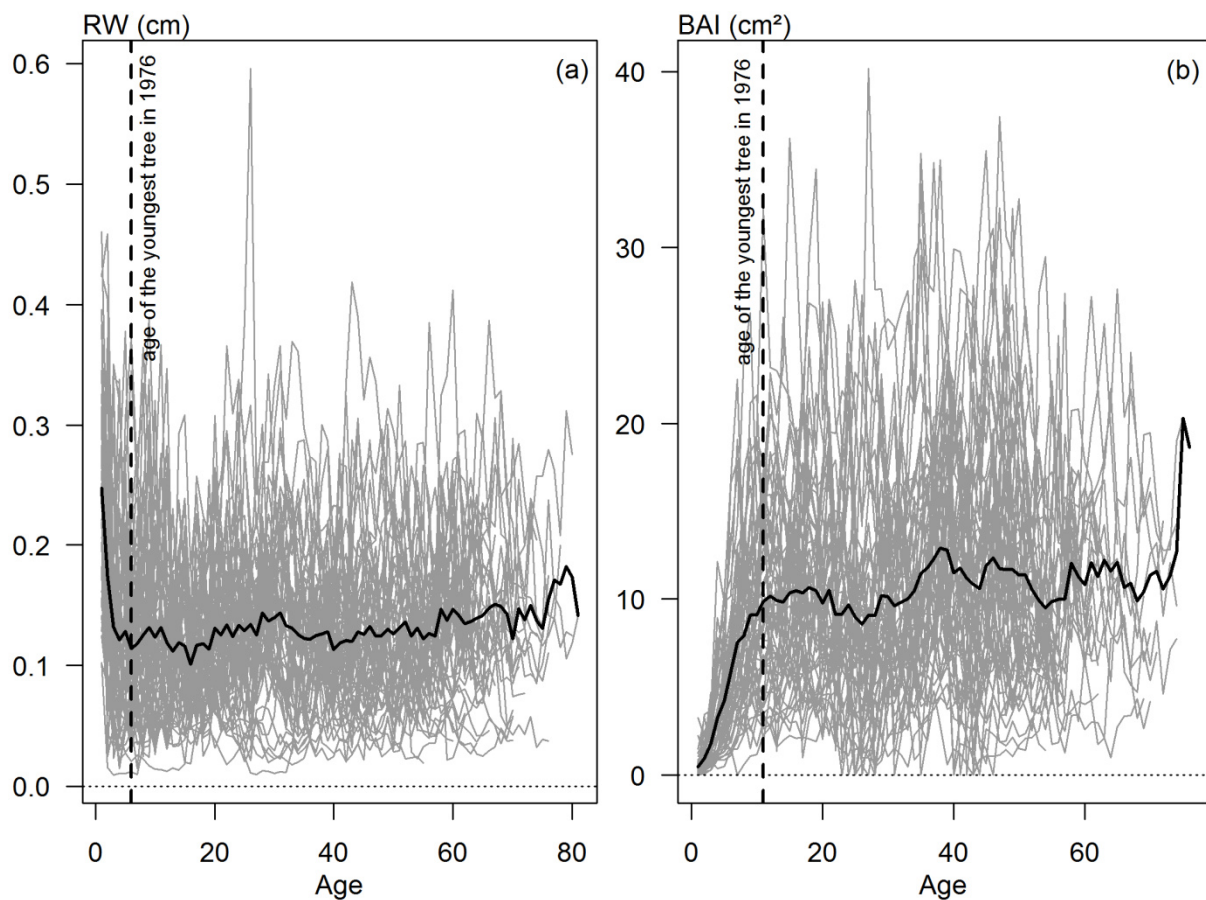
267   The absence of strong age-related trends (excluding the juvenile period) on these two growth

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 Rt, recovery Rc and resilience Rs 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.

297
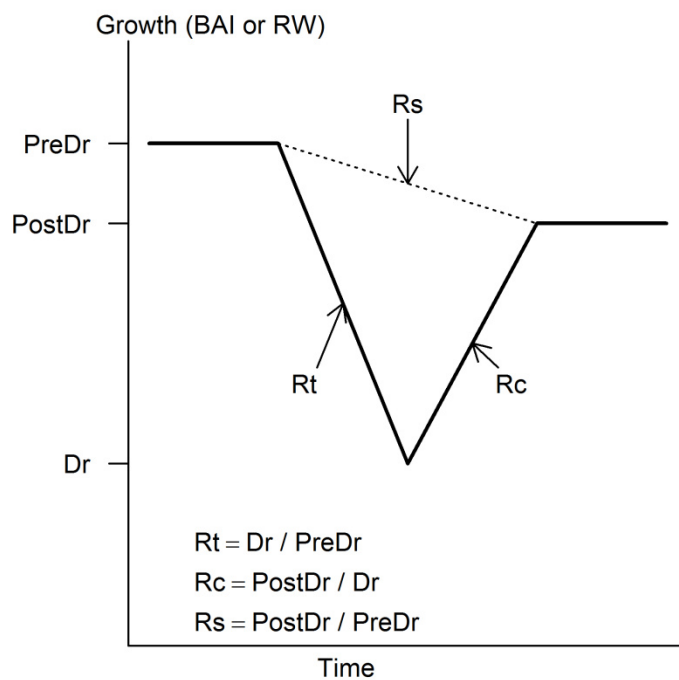
298   The post-disturbance period for 2003 and the pre-disturbance period for 2006 overlap. We

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.

15

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 ε_{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:

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

16

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   ε_{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 Rt		**Recovery Rc**		**Resilience Rs**	
	Oak	*Pine*	*Oak*	*Pine*	*Oak*	*Pine*
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 4**Erreur ! Source du renvoi introuvable.**).

348 Table 4. Results from the linear mixed models for species effect on resistance Rt, recovery Rc

349 and resilience Rs 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**
Rt			*ln*		*ln*	*ln*
Intercept	Estimation	**0.668**	**-0.405**	**0.951**	**-0.307**	**-0.305**
	s.d.	**0.018**	**0.038**	**0.034**	**0.057**	**0.043**
	p-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
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**
Rc		*ln*	*ln*	*ln*	*ln*	*ln*
Intercept	Estimation	**0.514**	**0.336**	**0.123**	**0.320**	**-0.272**
	s.d.	**0.073**	**0.035**	**0.038**	**0.057**	**0.066**
	p-value	**< 0.001**	**< 0.001**	**0.002**	**< 0.001**	**< 0.001**
Scots pine	Estimation				**0.235**	**-0.172**
	s.d.				**0.059**	**0.051**
	p-value				**< 0.001**	**< 0.001**
Rs		*ln*	*ln*	*ln*	*ln*	*ln*
Intercept	Estimation	**0.087**	-0.091	-0.046	-0.046	**-0.526**
	s.d.	**0.056**	0.061	0.038	0.038	**0.076**
	p-value	**0.126**	0.134	0.236	0.236	**< 0.001**
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 Rt, recovery Rc and resilience Rs 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 Rt, recovery Rc and resilience Rs 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 Rt, recovery Rc and resilience Rs 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 Rt, recovery Rc and resilience Rs 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
Rt				*ln*			*ln*
Intercept		Estimates	**0.654**	**-0.537**	**1.041**	**0.732**	**-0.304**
		s.d.	**0.022**	**0.059**	**0.063**	**0.023**	**0.062**
		p-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Composition	*Mixed*	Estimates					
		s.d.					
		p-value					
Size	*Medium*	Estimates		**0.155**	-0.121		
		s.d.		**0.071**	0.063		
		p-value		**0.034**	0.059		
	Small	Estimates		**0.241**	**-0.130**		
		s.d.		**0.071**	**0.063**		
		p-value		**0.001**	**0.043**		
Rc			*ln*		*ln*		
Intercept		Estimates	**0.624**	**1.443**	0.086	**1.572**	**0.850**
		s.d.	**0.090**	**0.071**	0.062	**0.079**	**0.064**
		p-value	**< 0.001**	**< 0.001**	0.175	**< 0.001**	**< 0.001**
Composition	*Mixed*	Estimates					
		s.d.					
		p-value					
Size	*Medium*	Estimates				**-0.262**	-0.068
		s.d.				**0.090**	0.043
		p-value				**0.005**	0.117
	Small	Estimates				-0.129	**-0.125**
		s.d.				0.090	**0.043**
		p-value				0.157	**0.005**
Rs			*ln*	*ln*			*ln*
Intercept		Estimates	0.169	-0.070	**1.052**	**1.052**	**-0.573**
		s.d.	0.010	0.062	**0.063**	**0.063**	**0.106**
		p-value	0.098	0.271	**< 0.001**	**< 0.001**	**< 0.001**
Composition	*Mixed*	Estimates					
		s.d.					
		p-value					
Size	*Medium*	Estimates					
		s.d.					

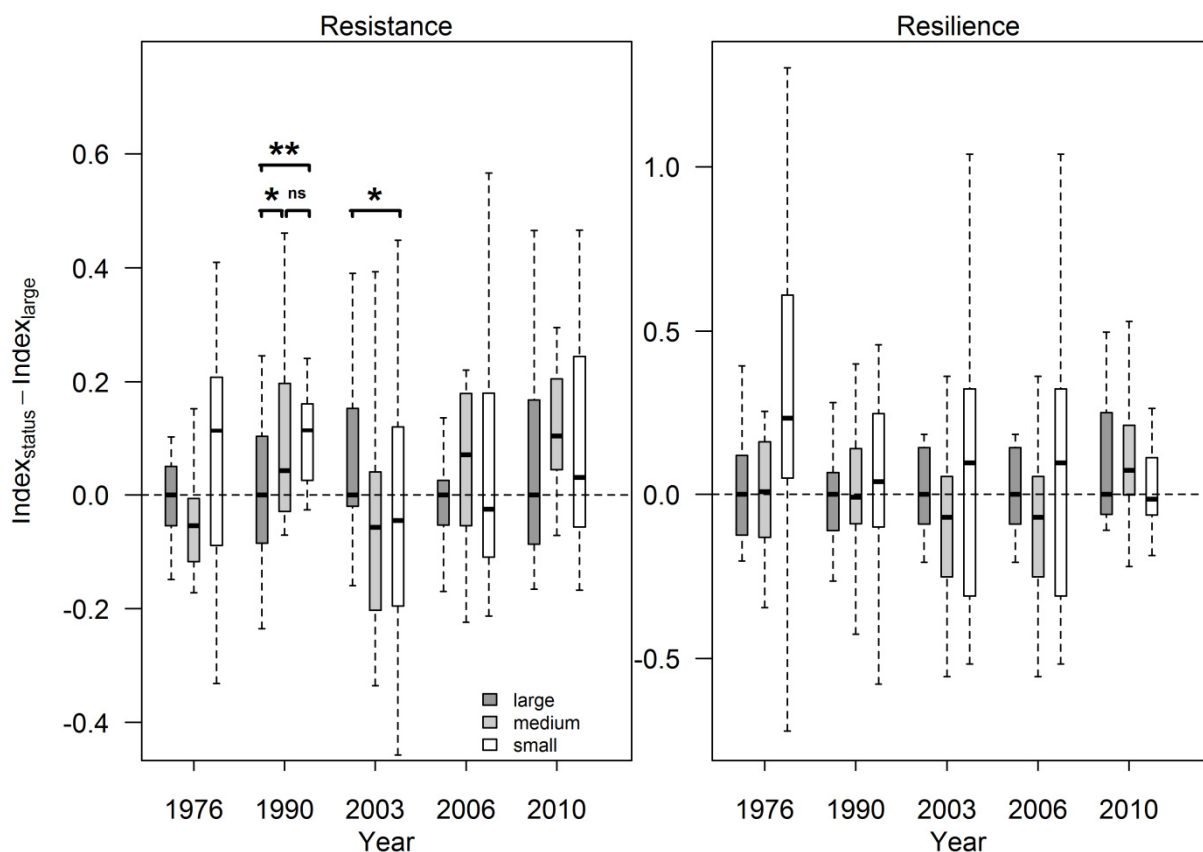|	p-value	
	Estimates	
Small	s.d.	
	p-value	

409

24

410   Table 6. Results from the linear mixed models for stand composition and tree size effects on

411   resistance Rt, recovery Rc and resilience Rs 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
Rt				*ln*			*ln*
Intercept		Estimates	**0.607**	**-0.148**	**0.790**	**0.481**	-0.029
		s.d.	**0.045**	**0.058**	**0.022**	**0.059**	0.032
		p-value	**< 0.001**	**0.014**	**< 0.001**	**< 0.001**	0.367
Composition	*Mixed*	Estimates					
		s.d.					
		p-value					
Size	*Medium*	Estimates	0.088			0.105	
		s.d.	0.052			0.065	
		p-value	0.095			0.112	
	Small	Estimates	**0.128**			**0.137**	
		s.d.	**0.052**			**0.065**	
		p-value	**0.017**			**0.041**	
Rc			*ln*	*ln*			*ln*
Intercept		Estimates	**0.425**	**0.334**	**1.220**	**1.801**	**-0.450**
		s.d.	**0.085**	**0.044**	**0.058**	**0.126**	**0.091**
		p-value	**< 0.001**	**< 0.001**	**< 0.001**	**<0.001**	**< 0.001**
Composition	*Mixed*	Estimates					
		s.d.					
		p-value					
Size	*Medium*	Estimates					
		s.d.					
		p-value					
	Small	Estimates					
		s.d.					
		p-value					
Rs			*ln*	*ln*	*ln*	*ln*	*ln*
Intercept		Estimates	**-0.220**	**0.186**	**-0.288**	**-0.253**	**-0.479**
		s.d.	**0.070**	**0.092**	**0.080**	**0.081**	**0.100**
		p-value	**0.003**	**0.049**	**0.001**	**0.003**	**< 0.001**
Composition	*Mixed*	Estimates					
		s.d.					
		p-value					

|						
Size	Medium	Estimates	**0.323**		0.219	0.149
		s.d.	**0.089**		0.113	0.115
		p-value	**< 0.001**		0.059	0.203
	Small	Estimates	**0.337**		**0.310**	**0.275**
		s.d.	**0.089**		**0.113**	**0.115**
		p-value	**< 0.001**		**0.009**	**0.021**

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. *: $p < 0.05$; **:

424 $p < 0.01$; ***: $p < 0.001$.; 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
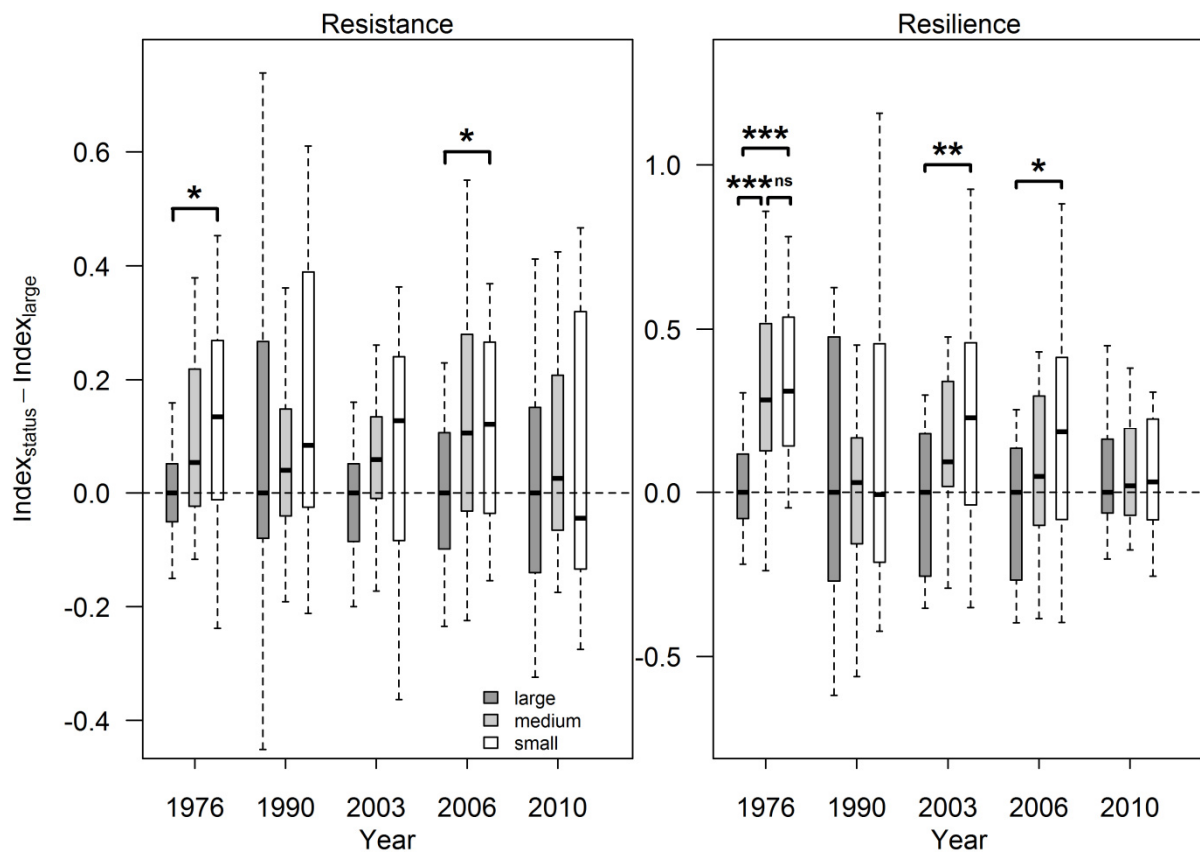
4. Discussion

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*.
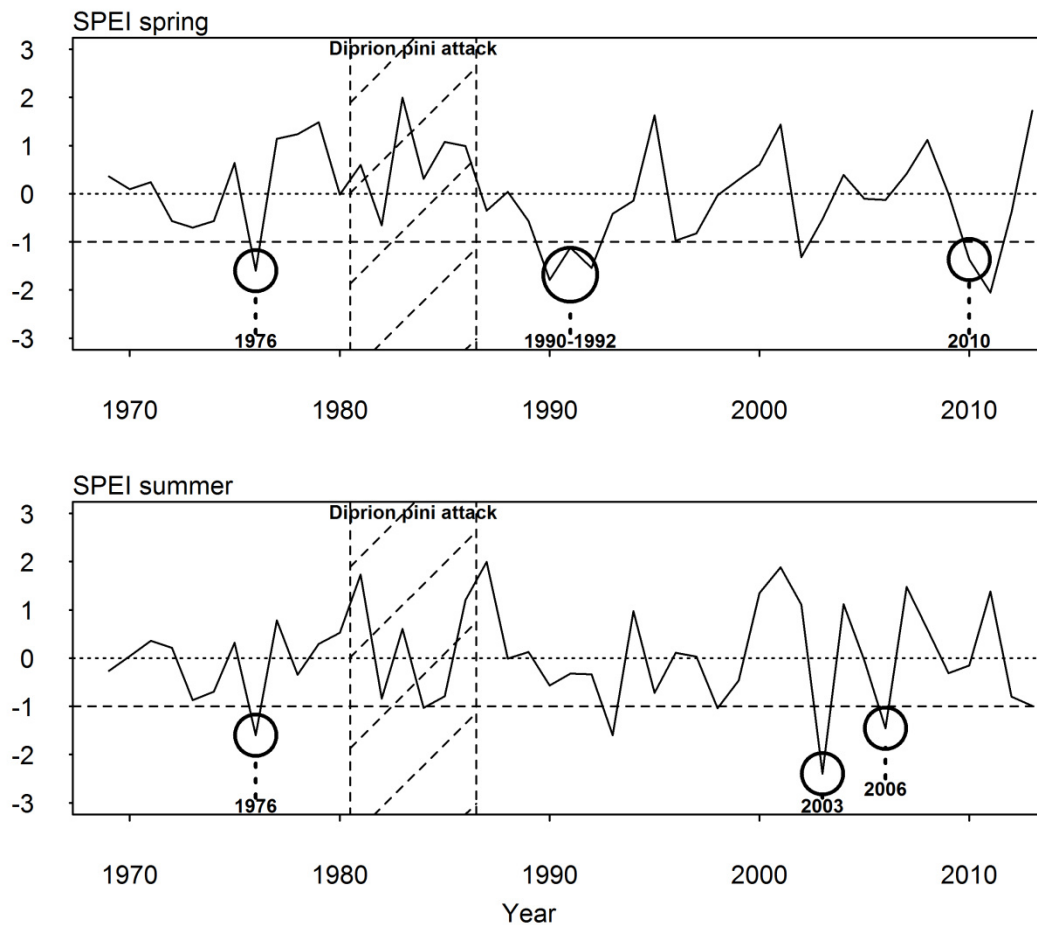
459

460   The 1976 drought was global throughout the whole growing season. The 1990-1992 and 2010

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   4**Erreur ! 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 photosynthesic 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 Piñol, 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 oppposite 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.

622   **Acknowledgements**

626   **References**

627   Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M.,

628   Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R.,

629   Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A.,

630   Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals

631   emerging climate change risks for forests. For. Ecol. Manage. 259, 660-684.

632   Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological

633   aspects and consequences for silviculture. Ann. Forest Sci. 57, 287-301.

634   Bréda, N., Badeau, V., 2008. Forest tree responses to extreme drought and some biotic events:

635   Towards a selection according to hazard tolerance? Comptes Rendus Geoscience 340, 651-

636   662.

637 Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under

638   severe drought: a review of ecophysiological responses, adaptation processes and long-

639   term consequences. Ann. Forest Sci. 63, 625-644.

640 Bunn, A.G., Jansma, E., Korpela, M., Westfall, R.D., Baldwin, J., 2013. Using simulations

641   and data to evaluate mean sensitivity (zeta) as a useful statistic in dendrochronology.

642   Dendrochronologia 31, 250-254.

643 Cavin, L., Mountford, E.P., Peterken, G.F., Jump, A.S., 2013. Extreme drought alters

644   competitive dominance within and between tree species in a mixed forest stand. Funct.

645   Ecol. 27, 1424-1435.

646 Charru, M., Seynave, I., Morneau, F., Rivoire, M., Bontemps, J.D., 2012. Significant

647   differences and curvilinearity in the self-thinning relationships of 11 temperate tree species

648   assessed from forest inventory data. Ann. Forest Sci. 69, 195-205.

649 Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant responses to drought -

650   from genes to the whole plant. Funct. Plant Biol. 30, 239-264.

651 Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E.S.,

652   Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P., 2012. Climate change impacts on

653   tree ranges: model intercomparison facilitates understanding and quantification of

654   uncertainty. Ecol. Lett. 15, 533-544.

655 Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann,

656   N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein,

657   P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca,

658   G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S.,

659   Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005.

660   Europe-wide reduction in primary productivity caused by the heat and drought in 2003.

661   Nature 437, 529-533.

662   Cochard, H., Tyree, M.T., 1990. Xylem dysfunction in Quercus: vessel sizes, tyloses,

663   cavitation and seasonal changes in embolism. Tree Physiol. 6, 393-407.

664   Corcuera, L., Camarero, J.J., Gil-Pelegrín, E., 2004. Effects of a severe drought on growth and

665   wood anatomical properties of Quercus faginea. Iawa Journal 25, 185-204.

666   Dawson, T.E., 1996. Determining water use by trees and forests from isotopic, energy balance

667   and transpiration analyses: The roles of tree size and hydraulic lift. Tree Physiol. 16, 263-

668   272.

669   Dhôte, J.F., 1994. Hypotheses about competition for light and water in even-aged common

670   beech (Fagus sylvatica L.). For. Ecol. Manage. 69, 219-232.

671   Eilmann, B., Dobbertin, M., Rigling, A., 2013. Growth response of Scots pine with different

672   crown transparency status to drought release. Ann. Forest Sci. 70, 685-693.

673   Eilmann, B., Weber, P., Rigling, A., Eckstein, D., 2006. Growth reactions of Pinus sylvestris

674   L. and Quercus pubescens Willd. to drought years at a xeric site in Valais, Switzerland.

675   Dendrochronologia 23, 121-132.

676   Eilmann, B., Zweifel, R., Buchmann, N., Fonti, P., Rigling, A., 2009. Drought-induced

677   adaptation of the xylem in Scots pine and pubescent oak. Tree Physiol. 29, 1011-1020.

678   Eilmann, B., Zweifel, R., Buchmann, N., Pannatier, E.G., Rigling, A., 2011. Drought alters

679   timing, quantity, and quality of wood formation in Scots pine. J. Exp. Bot. 62, 2763-2771.

680   Felton, A., Lindbladh, M., Brunet, J., Fritz,Ö., 2010. Replacing coniferous monocultures with

681   mixed-species production stands: An assessment of the potential benefits for forest

682   biodiversity in northern Europe. For. Ecol. Manage. 260, 939-947.

683   Forrester, D.I., Bauhus, J., Cowie, A.L., Vanclay, J.K., 2006. Mixed-species plantations of

684   Eucalyptus with nitrogen-fixing trees: A review. For. Ecol. Manage. 233, 211-230.

685   Galiano, L., Martínez-Vilalta, J., Lloret, F., 2010. Drought-Induced Multifactor Decline of

686   Scots Pine in the Pyrenees and Potential Vegetation Change by the Expansion of Co-

687   occurring Oak Species. Ecosystems 13, 978-991.

688   Galiano, L., Martínez-Vilalta, J., Lloret, F., 2011. Carbon reserves and canopy defoliation

689   determine the recovery of Scots pine 4 yr after a drought episode. New Phytol. 190, 750-

690   759.

691   Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: An inventory and

692   analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323-334.

693   Grissino-Mayer, H.D., 2001. Evaluating Crossdating Accuracy: A Manual and Tutorial for

694   the Computer Program COFECHA. Tree-Ring Research 57, 205-221.

695   Grossiord, C., Gessler, A., Granier, A., Pollastrini, M., Bussotti, F., Bonal, D., 2014.

696   Interspecific competition influences the response of oak transpiration to increasing drought

697   stress in a mixed Mediterranean forest. For. Ecol. Manage. 318, 54-61.

698   Gruber, A., Pirkebner, D., Florian, C., Oberhuber, W., 2012. No evidence for depletion of

699   carbohydrate pools in Scots pine (Pinus sylvestris L.) under drought stress. Plant Biol. 14,

700   142-148.

701   IPCC, 2013. : Summary for Policymakers. In, Climate Change 2013: The Physical Science

702   Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the

703   Intergovernmental Panel on Climate Change. [Stocker, T. F., D. Qin, G.-K. Plattner, M.

704   Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley (eds.)].

705   Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

706   IUSS Working Group, W.R.B., 2014. World Reference Base for Soil Resources 2014. In,

707   World Soil Resources Reports. International soil classification system for naming soils and

708   creating legends for soil maps. No. 106. FAO, Rome.

709   Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol.

710   Lett. 10, 835-848.

711   Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., Coomes,

712   D.A., 2014. Competition for light and water play contrasting roles in driving diversity–

713   productivity relationships in Iberian forests. J. Ecol.

714   Kelty, M.J., 2006. The role of species mixtures in plantation forestry. For. Ecol. Manage. 233,

715   195-204.

716   Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous

717   tree species: a review on yield, ecological stability and economics. Eur. J. Forest Res. 127,

718   89-101.

719   Korboulewsky, N., Balandier, P., Ballon, P., Boscardin, Y., Dauffy Richard, E., Dumas, Y.,

720   Ginisty, C., Gosselin, M., Hamard, J.P., Mace, S., Marell, A., NDiaye, A., Perot, T., Perret,

721   S., Rocquencourt, A., Seigner, V., Vallet, P., 2013. OPTMix - Oak Pine Tree Mixture -

722   Dispositif expérimental de long terme en forêt mélangée. Atelier Regefor, la gestion de la

723   fertilité de sols est-elle a un tournant ? In, 9ème Colloque d'Ecologie des Communautés

724   Végétales, Tours, France.

725   Lebourgeois, F., Eberlé, P., Mérian, P., Seynave, I., 2014. Social status-mediated tree-ring

726   responses to climate of Abies alba and Fagus sylvatica shift in importance with increasing

727   stand basal area. For. Ecol. Manage. 328, 209-218.

728   Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce Abies alba tree-

729   ring sensitivity to summer drought in the Vosges mountains, western Europe. For. Ecol.

730   Manage. 303, 61-71.

731   Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate

732   coniferous forests to climate variability and extreme events (Abies alba, Picea abies and

733   Pinus sylvestris). J. Veg. Sci. 21, 364-376.

734   Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J., Valladares, F., 2012. Extreme

735   climatic events and vegetation: the role of stabilizing processes. Global Change Biol. 18,

736   797-805.

737   Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive

738   low-growth episodes in old ponderosa pine forests. Oikos 120, 1909-1920.

739   Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient

740   hypothesis for competition and facilitation in plant communities. J. Ecol. 97, 199-205.

741   Martín-Benito, D., Beeckman, H., Cañellas, I., 2013. Influence of drought on tree rings and

742   tracheid features of Pinus nigra and Pinus sylvestris in a mesic Mediterranean forest. Eur.

743   J. Forest Res. 132, 33-45.

744   Martín-Benito, D., Cherubini, P., del Río, M., Cañellas, I., 2008. Growth response to climate and

745   drought in Pinus nigra Arn. trees of different crown classes. Trees-Struct. Funct. 22, 363-

746   373.

747   Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level

748   determinants of the drought response of Scots pine radial growth. Oecologia 168, 877-888.

749   Martinez-Vilalta, J., Piñol, J., 2002. Drought-induced mortality and hydraulic architecture in

750   pine populations of the NE Iberian Peninsula. For. Ecol. Manage. 161, 247-256.

751   Mérian, P., Lebourgeois, F., 2011. Size-mediated climate-growth relationships in temperate

752   forests: A multi-species analysis. For. Ecol. Manage. 261, 1382-1391.

753   Michelot, A., Bréda, N., Damesin, C., Dufrêne, E., 2012a. Differing growth responses to

754   climatic variations and soil water deficits of Fagus sylvatica, Quercus petraea and Pinus

755   sylvestris in a temperate forest. For. Ecol. Manage. 265, 161-171.

756   Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., Damesin, C., 2012b. Comparing the

757   intra-annual wood formation of three European species (Fagus sylvatica, Quercus petraea

758 and Pinus sylvestris) as related to leaf phenology and non-structural carbohydrate

759 dynamics. Tree Physiol. 32, 1033-1045.

760 Morán-López, T., Poyatos, R., Llorens, P., Sabaté, S., 2014. Effects of past growth trends and

761 current water use strategies on Scots pine and pubescent oak drought sensitivity. Eur. J.

762 Forest Res. 133, 369-382.

763 Niinemets, U., 2010. A review of light interception in plant stands from leaf to canopy in

764 different plant functional types and in species with varying shade tolerance. Ecol. Res. 25,

765 693-714.

766 Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of

767 temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521-547.

768 Olivar, J., Bogino, S., Spiecker, H., Bravo, F., 2012. Climate impact on growth dynamic and

769 intra-annual density fluctuations in Aleppo pine (Pinus halepensis) trees of different crown

770 classes. Dendrochronologia 30, 35-47.

771 Orwig, D.A., Abrams, M.D., 1997. Variation in radial growth responses to drought among

772 species, site, and canopy strata. Trees-Struct. Funct. 11, 474-484.

773 Palacio, S., Hoch, G., Sala, A., Körner, C., Millard, P., 2014. Does carbon storage limit tree

774 growth? New Phytol. 201, 1096-1100.

775 Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks as indicated by

776 growth prior to death. Ecology 79, 79-93.

777 Perot, T., Vallet, P., Archaux, F., 2013. Growth compensation in an oak-pine mixed forest

778 following an outbreak of pine sawfly (Diprion pini). For. Ecol. Manage. 295, 155-161.

779 Pichler, P., Oberhuber, W., 2007. Radial growth response of coniferous forest trees in an

780 inner Alpine environment to heat-wave in 2003. For. Ecol. Manage. 242, 688-699.

781   Potop, V., Boroneant, C., Mozný, M., Štěpánek, P., Skalák, P., 2014. Observed spatiotemporal

782   characteristics of drought on various time scales over the Czech Republic. Theor. Appl.

783   Clim. 115, 563-581.

784   Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress

785   in mixed versus pure forests: evidence of stress release by inter-specific facilitation. Plant

786   Biol. 15, 483-495.

787   R Development Core Team, 2014. R: A Language and Environment for Statistical

788   Computing. In. R Foundation for Statistical Computing, Vienna, Austria.

789   Regent, I., 2005. Windendro 2005a. In. Université du Quebec, Chicoutimi, Canada.

790   Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46,

791   627-638.

792   Smith, M.D., 2011. An ecological perspective on extreme climatic events: a synthetic

793   definition and framework to guide future research. J. Ecol. 99, 656-663.

794   Speer, J.H., 2010. Fundamentals of Tree-Ring Research, Tucson, Arizona.

795   Taeger, S., Zang, C., Liesebach, M., Schneck, V., Menzel, A., 2013. Impact of climate and

796   drought events on the growth of Scots pine (Pinus sylvestris L.) provenances. For. Ecol.

797   Manage. 307, 30-42.

798   Tardif, J.C., Conciatori, F., 2006. Influence of climate on tree rings and vessel features in red

799   oak and white oak growing near their northern distribution limit, southwestern Quebec,

800   Canada. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere

801   36, 2317-2330.

802   Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. Geogr.

803   Rev. 38, 55-94.

804   Tyree, M.T., Cochard, H., 1996. Summer and winter embolism in oak: Impact on water

805   relations. Ann. Forest Sci. 53, 173-180.

806   Vacchiano, G., Garbarino, M., Mondino, E.B., Motta, R., 2012. Evidences of drought stress

807   as a predisposing factor to Scots pine decline in Valle d'Aosta (Italy). Eur. J. Forest Res.

808   131, 989-1000.

809   Vallet, P., Perot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway

810   spruce: evidence based on large-scale inventory data and a generic modelling approach. J.

811   Veg. Sci. 22, 932-942.

812   van der Werf, G.W., Sass-Klaassen, U.G.W., Mohren, G.M.J., 2007. The impact of the 2003

813   summer drought on the intra-annual growth pattern of beech (Fagus sylvatica L.) and oak

814   (Quercus robur L.) on a dry site in the Netherlands. Dendrochronologia 25, 103-112.

815   Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index

816   Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J.

817   Clim. 23, 1696-1718.

818   Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2014. Xylogenesis of Pinus pinaster

819   under a Mediterranean climate. Ann. Forest Sci. 71, 71-80.

820   Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L., Retana, J., 2013. Patterns of Forest Decline

821   and Regeneration Across Scots Pine Populations. Ecosystems 16, 323-335.

822   Weber, P., Bugmann, H., Rigling, A., 2007. Radial growth responses to drought of Pinus

823   sylvestris and Quercus pubescens in an inner-Alpine dry valley. J. Veg. Sci. 18, 777-792.

824   Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time-

825   series, with applications in dendroclimatology and hydrometeorology. J. Climate Appl.

826   Meteorol. 23, 201-213.

827   Wiley, E., Huepenbecker, S., Casper, B.B., Helliker, B.R., 2013. The effects of defoliation on

828   carbon allocation: can carbon limitation reduce growth in favour of storage? Tree Physiol.

829   33, 1216-1228.

830   Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in

831   Scots pine, Norway spruce and common oak. Trees-Struct. Funct. 26, 557-569.

832   Zweifel, R., Zimmermann, L., Zeugin, F., Newbery, D.M., 2006. Intra-annual radial growth

833   and water relations of trees: implications towards a growth mechanism. J. Exp. Bot. 57,

834   1445-1459.

835

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.
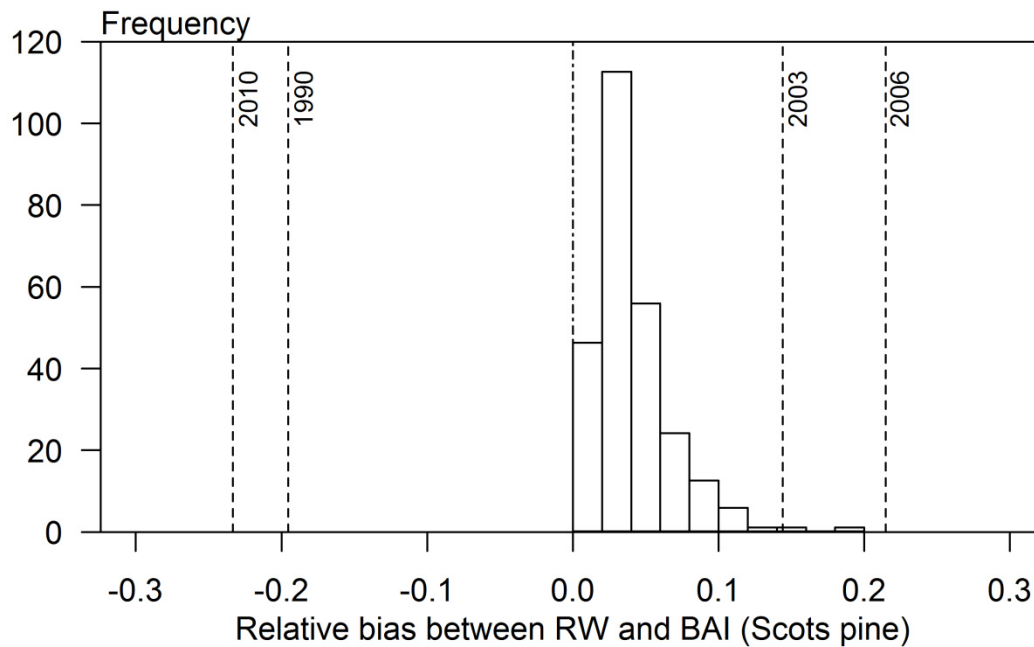
857

858

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

866

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

871