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Title

Distinct growth responses to drought for oak and beech in temperate mixed forests

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Abstract

1. **Purpose**: Droughts are expected to become more intense and frequent. Mixed forests can be more resilient to extreme events, but are the individual trees in mixed forests also more resilient to drought?
2. **Methods**: We sampled 275 trees in 53 temperate forest stands in northern Belgium: monocultures, two-species mixtures, and the three-species mixture of *Fagus sylvatica*, *Quercus robur*, and *Q. rubra*. We related the annual basal area increment of individual trees to drought severity from 1955-2015 and calculated growth resistance, recovery, and resilience for six contrasting drought episodes (spring, summer, or full-year drought).
3. **Results**: Tree growth of the diffuse-porous *F. sylvatica* was more sensitive to drought, summer drought in particular. The ring-porous *Q. robur* and *Q. rubra* were mainly affected by spring drought. In general, a tree's growth response to drought was not affected by tree species diversity, but some identity effects emerged.
4. **Conclusion**: The asynchrony in drought responses among the tree species (a large and immediate decrease in growth followed by swift recovery in *F. sylvatica* vs a smaller delayed response in *Quercus*) might stabilize productivity in forests in which both are present. The impact of the predicted increasing drought frequency will depend on the timing of the droughts (spring vs summer).

Keywords

Biodiversity ecosystem functioning, Standardized Precipitation Evapotranspiration Index, tree rings, TREEWEB, X-ray Computed Tomography

1. Introduction

Mixed forests are promoted to ensure continued delivery of forest ecosystem services in case of changes in environmental conditions due to climate change (Messier & Puettmann, 2011). In Europe, climate models predict an increase in climate extremes such as heat waves and droughts (Kovats *et al.*, 2014). Drought can significantly affect forests through decreased productivity, increased vulnerability to pests, and increased subsequent mortality (Bréda *et al.*, 2006). The extreme 2003 summer drought in Europe, for instance, caused a marked decline in forest productivity and increase in tree mortality (Ciais *et al.*, 2005; Bréda *et al.*, 2006). Forests that are more resilient towards fluctuating resources such as water availability may show a higher and more stable productivity over time. Mixed forests, consisting of multiple tree species, have been shown to be more productive (Liang *et al.*, 2016), more resilient to pests (Guyot *et al.*, 2016), and less affected by climate extremes such as drought (Gazol & Camarero, 2016). Yet, the opposite has also been observed, with mixed forests showing lower growth than monocultures and a higher impact of drought stress (Grossiord *et al.*, 2014a). While there is evidence on the relationships between tree species diversity and forest growth, questions remain about the interactive effect of diversity and drought on forest growth. Changes in temperature or precipitation can alter the relationship between growth and diversity (Ratcliffe *et al.*, 2016). Diversity effects may decrease with drought or warming (Paquette *et al.*, 2017; Jactel *et al.*, 2018) or, on the contrary, be apparent only in dry years (Lebourgeois *et al.*, 2013). This lack of generality may result from differences in the species or local environmental conditions. Indeed, drought-sensitive species may benefit less from mixing during a dry year than drought-tolerant species (Jucker *et al.*, 2014b), and diversity may enhance resistance to drought events only in environments prone to drought (Grossiord *et al.*, 2014b). A lower stand-level impact of drought in mixed forests can be explained by the portfolio effect (*sensu* Thibaut & Connolly, 2013), which states that diversity reduces the risk that a specific ecosystem function or service (e.g. tree growth or wood production) is hugely affected by, for instance, drought. Such a positive diversity-stability relationship may result from facilitation and temporal or functional complementarity among the species present in a mixture (Loreau & de Mazancourt, 2013). Jucker *et al.* (2014a) indeed saw that asynchrony in species' responses to climate resulted in lower year-to-year variation in productivity in mixed forests across Europe. Niche complementarity, e.g. in the exploitation of water reserves through differences in rooting depth among species, may result in increased resilience towards drought stress in mixtures (cf. Ratcliffe *et al.*, 2016). On the other hand, tree species diversity may also increase the effect of drought because of higher competition for the limiting resource, i.e. soil water (cf. Grossiord *et al.*, 2014a). Higher transpiration in mixtures (Kunert *et al.*, 2012) may cause soil water resources in mixed stands to be more quickly depleted during droughts, which then results in a higher exposure to soil drought (Grossiord *et al.*, 2014a).

Up until now, forest growth studies on drought-diversity interactions have mostly focused on stand-level or species-level productivity (Vilà *et al.*, 2013; Ratcliffe *et al.*, 2016; Paquette *et al.*, 2017) and have mainly compared monocultures and two-species mixtures (but see the studies on FunDivEUROPE platforms: Grossiord *et al.*, 2014a,b; Jucker *et al.*, 2014a,b; Ratcliffe *et al.*, 2016). Yet, the performance of individual plants shapes plant communities (Violle *et al.* 2007). Gaining insight into the growth response of individual trees might help explain inconsistent stand-level observations (Jucker *et al.* 2014b) and provide valuable input for forest dynamics models, which usually work at the level of individual trees, predicting their fate through life (Pacala *et al.*, 1996).

To study the interplay of drought severity and tree species diversity with regard to tree-level growth in temperate forest, we sampled increment cores from monoculture stands, two-species mixtures, and three-species mixtures of three deciduous, broadleaved species (*Fagus sylvatica* L., *Quercus robur* L., *Q. rubra* L.). Through a retrospective study of tree-ring and meteorological data, we investigated whether the species composition of the studied stands modulates the growth response of individual trees to drought. We hypothesized drought to negatively affect tree growth in both monocultures and mixtures, and drought effects to differ among the three study species as they differ in drought sensitivity and drought-coping strategies. By investigating the impact of distinct droughts (spring, summer, all-year drought), we aimed to link the growth responses of the studied trees to the anatomy and physiology of the study species.

2. Materials and Methods

2.1. Study area

The TREEWEB platform consists of 53 forest plots in a 15 km x 30 km area in northern Belgium (50° 54' N 3° 35' E - 50° 59' N 3° 56' E). The climate is temperate with a mean annual temperature of 10.5°C and mean annual precipitation of 826 mm (1981-2010, Royal Meteorological Institute of Belgium). The plots were situated outside river valleys (at 7-77 m above sea level) on sites with a similar soil texture and drainage (i.e. well-drained sandy loam). All plots lay in mature forest stands of similar stand age that have been forest since at least 1850, had a canopy cover of at least 60%, and showed no apparent signs of recent forest management.

The plots were selected along a diversity gradient of monocultures, two-species mixtures, and three-species mixtures of *Fagus sylvatica*, *Quercus robur*, and *Q. rubra*. For each of the seven possible species combinations, six to eight plots were installed (see Figs A.1, B.1). In each 30 m x 30 m plot, all trees with a diameter larger than 15 cm were mapped, and the topsoil was sampled for chemical analysis. For more detailed information on the TREEWEB design and the plot inventory and soil sampling, see De Groote *et al.* (2017, 2018).

2.2. Study species

Fagus sylvatica is widespread in Europe across a broad climatic range, requiring moist summers and mild winters. Its northern distribution reaches up to southern Scandinavia; its eastern distribution is limited by the hot summers of the continental climate and extends to the Carpathians and the Balkan Mountains. *Fagus sylvatica* favours well-drained soils and does not tolerate flooding; its shallow rooting makes it susceptible to drought. Unless limited by drought or frost, *F. sylvatica* is a competitive species, tolerant to deep shade and casting a deep shade itself (Packham *et al.*, 2012; Houston Durrant *et al.*, 2016). The wood is diffuse-porous, with a clear maximum in density at the ring boundaries, mainly caused by a decrease in the number of vessels. The radial growth mostly depends on photosynthesis. Trees start to grow after budburst and show maximum growth when their leaf mass is at its maximum, in June (Michelot *et al.*, 2012).

Quercus robur occurs across most of Europe, extending further west and east than *F. sylvatica*. The climatic ranges of *F. sylvatica* and *Q. robur* overlap, but *Q. robur* appears to tolerate warmer conditions and higher levels of precipitation than *F. sylvatica*. Notwithstanding its large ecological amplitude, *Q. robur* prefers fertile and moist soils. The heart roots extend deeper than *F. sylvatica*'s roots, which enables *Q. robur* to withstand moderate droughts. As a light-demanding species, *Q. robur* is generally outcompeted by *F. sylvatica*, except on soils low in nutrients or high in soil moisture (Jones, 1959; Ellenberg, 1996; Eaton *et al.*, 2016). The ring boundaries in the ring-porous wood are defined by a minimum wood density, caused by the large-diameter early-wood vessels. Radial tree growth starts before leaf-out, using carbohydrate reserves stored during the previous year (Barbaroux & Bréda, 2002). The large early-wood vessels are formed early in spring to restore the xylem's water flow pathways after winter embolism has blocked most of the previously formed xylem (Tyree & Cochard, 1996). Consequently, *Quercus*' radial growth occurs mainly in spring, and its growth stops earlier than *Fagus*' (Michelot *et al.*, 2012).

Quercus rubra is native in the eastern United States and south-eastern Canada, where it grows on a variety of sites, from dry-mesic to mesic, and in diverse climatic conditions. The species was introduced in Europe in the 17-18th century as an ornamental tree and has been widely planted for wood production. *Quercus rubra* is more shade-tolerant than *Q. robur* and forms a denser canopy; it loses its taproot at an earlier age and has a more extensive superficial root system (Jones, 1959; Tirmenstein, 1991; Magni, 2004). The wood formation phenology and anatomy are similar to *Q. robur*.

2.3. Tree core data

We collected tree cores in August-September 2016. Per plot and study species, we sampled at least two (co)dominant trees (minimum diameter 30 cm, minimum height 22.5 m) (Appendix C). We took two cores per tree, perpendicular to each other, at breast height. The cores were stored in paper straws, dried at 103°C for 24 hours, and scanned at 110 µm with the Nanowood X-ray Computed Tomography facility (Dierick *et al.*, 2014) of the UGCT (Ghent University Centre of X-ray Computed Tomography, www.ugct.ugent.be). The scans were processed following De Mil *et al.* (2016). To ensure correctly dated tree-ring series, we graphically and statistically crossdated the two cores per tree and all cores of each species per plot, in CoreComparison (De Mil *et al.* 2016) and TSAP-Win (Rinntech, Heidelberg, Germany). We calculated a mean ring width series per tree by averaging the ring width series of the two cores. When a core did not contain the tree's pith, we estimated the number of rings missing until the pith based on the curvature of the last rings. For each sampled tree, we then determined the age of the tree at the height of coring. Most of the sampled trees had an age between 50 and 100 years, and we excluded the trees younger and older than this age cohort from our analyses (i.e. eight *F. sylvatica* trees of 100-125 years old; six *Q. robur* trees of 100-200 years old, eleven *Q. rubra* trees younger than 50 years). Old trees have been reported to be more sensitive to climate than young trees (e.g. Copenheaver et al., 2011; Primicia et al., 2013; Hacket-Pain et al., 2016). In restricting the age range (50-100 years), we aimed to limit the age effect on the climate response of the trees (cf. D'Amato et al. 2013). For each tree in the final dataset (Table 1), we transformed the mean ring width series to a basal area increment series (*dplR* library; Bunn *et al.*, 2017).

2.4. Meteorological data

We used monthly data of temperature and precipitation from a nearby meteorological station, at 1.5-13.5 km distance from the study plots (Lemberge-Merelbeke, Royal Meteorological Institute of Belgium). Data were only available from January 1951 (precipitation) and December 1953 (temperature) onwards. We used the Standardized Precipitation Evaporation Index (SPEI) as an integrative measure of drought intensity. SPEI combines precipitation and temperature and is therefore able to identify increases in drought severity caused by higher evapotranspiration, a key advantage over drought indices that only consider precipitation and may not reveal droughts caused by high temperatures (Vicente-Serrano *et al.*, 2010). SPEI can be calculated for relatively large integration timescales and can then cumulatively represent current-year and past-year drought. We calculated SPEI for different timescales (1-24 months) and for every month of the year (January to December) from 1955-2015 (*SPEI* library; Beguería & Vicente-Serrano, 2017), using the equation of Hargreaves (1994) modified by Droogers and Allen (2002) to calculate potential evapotranspiration. The calculated difference between a month's precipitation and potential evapotranspiration represents a water surplus or deficit during that month. These monthly values are then aggregated over a certain integration timescale (a number of months) and normalized. A 6-month SPEI value, for instance, represents the cumulative water deficit or surplus for a specific month and the five preceding months. Negative SPEI values indicate dry conditions: moderate drought (SPEI smaller than -1), severe drought (SPEI < -1.5), or extreme drought (SPEI < -2; Potop et al., 2014). For each tree species, we selected the SPEI time series that showed the highest correlation with the tree-level 1955-2015 time series of annual basal area increments (Fig. D.1): the 18-month SPEI for the month July for *F. sylvatica* and the 10-month SPEI for April for both *Quercus* species (Fig. 1). Note that the integration timescale (i.e. 18 and 10 months here) does not measure drought length (Schwalm *et al.*, 2017); it represents the time period across which monthly water balances are aggregated to quantify the hydrologic state at the end of this period (i.e. in July or April here).

To study the effect of exceptional drought on tree growth, we selected years with different types of droughts to gain insight into how specific drought characteristics may result in different drought responses. We listed years with (1) the most extreme drought events, using the SPEI best correlated with *F. sylvatica* and *Quercus* growth ($SPEI_{18}$-July, $SPEI_{10}$-April) similar to Sousa-Silva (2018) and (2) extreme spring and summer droughts following Merlin *et al.* (2015), who calculated SPEI for spring (3-month SPEI for June) and summer (2-month SPEI for August). For the listed years, we compared the monthly precipitation and mean temperature with the 1981-2010 climograph (Fig. D.2). We retained six drought episodes (Table D.1, Fig. D.2): 1959-1960 (1959: spring and summer drought; 1960: spring drought), 1976-1977 (1976: full-year drought), 1990 (summer drought), 1996 (dry spring, following a summer drought in 1995), 2004 (spring drought, following a summer drought in 2003), and 2010-2011 (spring drought in both years). We looked at these six different drought events rather than focusing only on the two most illustrious European drought events (cf. Pretzsch *et al.*, 2013) or selecting pointer years based on the basal area increment time series as is commonly done in dendroclimatology studies (cf. Nechita *et al.*, 2017; Perkins *et al.*, 2018).

2.5. Resilience

The resilience of an ecosystem can be influenced by both its resistance to and recovery from disturbance (Ingrisch & Bahn, 2018). For each drought episode and each tree, we calculated three components of resilience that capture different aspects of resilience (Lloret *et al.*, 2011), which allows more comprehensive insight into the effect of drought. *Resistance* quantifies the growth decrease due to drought as the ratio between the growth during the drought episode and the pre-drought period. *Recovery* is the ability to recover from the drought, estimated as the ratio between post-drought and during-drought growth. *Resilience* is the capacity to return to the pre-drought growth, i.e. the ratio between post-drought and pre-drought growth (see Appendix E for formulas and a graphic example). We calculated pre-drought and post-drought growth as the mean basal area increment of the three years before or the three years after the drought (cf. Pretzsch *et al.*, 2013), and during-drought growth as the basal area increment during the drought episode (two-year mean for the drought episodes consisting of two consecutive years).

2.6. Tree species diversity

The TREEWEB design, with each study species present across the full species richness gradient (Figs A.1, B.1), allows looking at the effects of species richness and species combination for all study species. We quantified the stand composition of the plots using (i) *tree species richness*, i.e. the number of study species in the plot (1, 2, or 3), (ii) *tree species combination*, i.e. the seven possible combinations of species (Figs A.1-B.1), and (iii) *tree species presence*, i.e. the presence of admixed study species in a plot (for *Q. robur*, for instance, we considered *F. sylvatica* an admixed study species, present in the Fsyl-Qrob mixture and absent in the Qrob-Qrub mixture).

2.7. Data analysis

To investigate how tree species diversity affected the impact of drought on the growth of individual trees in the plots, we investigated whether, overall, annual tree growth was related to drought intensity and tree species diversity. Next, we looked at the effects of specific, exceptional drought events, comparing growth resilience among study species and diversity levels (Fig. A.1).

First, we used the time series of annual basal area increment between 1955 and 2015 (at tree level) to link tree growth and drought severity over time and to investigate whether tree species diversity modulates the growth response of individual trees to drought. For each study species, we modelled the basal area increment of a tree *i* in year *t* (ln-transformed) as a function of the *size* (diameter) of the tree in the previous year (*t-1*), the *soil* condition (the first two axes of a principal component analysis of the available topsoil chemistry data; Fig. B.2) and tree species *div*ersity (tree species richness, combination, or presence) of plot *j*, and the drought severity of year *t* quantified by the Standardized Precipitation Evapotranspiration Index (*spei*).

$$ln(bai_{i,t}) = \beta_0 + \beta_{size} size_{i,t-1} + \beta_{soil} soil_j + \beta_{spei} spei_t + \beta_{div} div_j \quad (1)$$

We used *tree* nested within *plot* as a random factor to account for the nested structure of the data and the repeated measures in a tree, and we used a second-order autoregressive correlation structure (i.e. auto-regressive moving average ARMA[2,0]) to account for the temporal autocorrelation present in the basal area increment series.

Second, for the six selected drought episodes, we investigated whether growth resistance, recovery, and resilience were affected by the stand's tree species composition. We modelled each of the three resilience indices (*R*) as a function of the *species* (to look for differences in resilience between the three study species) and *size* of tree *i*, and the *soil* condition and tree species *div*ersity of plot *j*.

$$R_i = \beta_0 + \beta_{species} species_i + \beta_{size} size_i + \beta_{soil} soil_j + \beta_{div} div_j \tag{2}$$

We performed this analysis for the full dataset, including all six drought episodes, to investigate the overall effect of extreme drought (including *plot* nested within *drought episode* as a random factor) and for each drought episode separately to investigate the effect of the different types of drought (*plot* as random factor).

In addition, for each drought episode and study species, we modelled the basal area increment of tree *i* as a function of the pre-drought, during-drought, and post-drought *period*, and looked for interaction with tree species *div*ersity (*tree* nested within *plot* as random factor).

$$bai_i = \beta_0 + \beta_{period} period \ * \beta_{div} div_j \tag{3}$$

For each response variable, we fitted a model with and a model without the diversity variable and compared the models with Akaike's Information Criterion and the log likelihood ratio test (library *nlme*; Pinheiro *et al.*, 2018). We used Tukey's pairwise post-hoc comparisons to determine significant differences between diversity levels for the different response variables (library *emmeans*; Lenth, 2018). All analyses were done in R version 3.4.4 (R Core Team, 2018); graphs were made with *ggplot2* (Wickham, 2009).

3. Results

Overall, basal area increment was smaller for *Q. robur* than for *F. sylvatica* and *Q. rubra* (Table 1). *Quercus robur* growth tended to be higher in the monocultures than in the three-species mixture, while *Q. rubra* showed overall higher growth in the three-species mixture compared with the monoculture (Fig. 2). Yet, the tree species richness effect was not statistically significant. Drought intensity did decrease tree growth for all three species. Stand composition had an effect for *Q. robur* only, with *Q. robur* showing lower growth in stands in which *F. sylvatica* was present (Table 2). For *F. sylvatica* and *Q. robur*, little variation in growth was explained by tree diameter, drought severity, and stand composition (small R^2_m in Table 2); plot and tree identity (random effects) accounted for more variation. *Quercus rubra*, on the other hand, a considerable part of the variation in growth was explained by the explanatory variables ($R^2_m = 0.41$, Table 2). For all three species, the tree-to-tree variation was larger than the variation among plots (Table 2).

The study species responded differently to the selected drought episodes (Figs 3-4). Resistance was smaller in *F. sylvatica* than in *Q. robur* and *rubra* ($p < 0.001$; lowest Rt in Fig. 4); *F. sylvatica* showed a larger growth decrease during the droughts (Fig. 3). Recovery was largest in *F. sylvatica* ($p < 0.001$; highest Rc in Fig. 4), followed by *Q. rubra*, and then *Q. robur* ($p = 0.024$). *Fagus sylvatica* showed a steep growth increase after the droughts (Fig. 3). Resilience was generally higher in *Q. rubra* than in *Q. robur* ($p = 0.039$) and *F. sylvatica* ($p < 0.001$), but the pattern differed strongly among the drought episodes (Fig. 4). For 2004, the growth of both *Quercus* species decreased after (rather than during) the drought episode (Fig. 3), which resulted in lower resilience values for *Quercus* than for *F. sylvatica* (Fig. 4). For 2010-2011, *Q. robur* also showed a growth decrease after the drought and thus a lower resilience than *F. sylvatica* (Fig. 4). *Quercus rubra* growth did increase again after 2010-2011, contrary to 2004 (Fig. 3). The timing of the drought mattered. For example, summer drought (in the year 1990) affected *F. sylvatica* growth but had no clear effect on *Quercus* (Fig. 3).

The influence of stand composition (species richness and combination) on the growth response to the selected drought episodes was limited. The post-drought growth increase in *Q. rubra* monocultures was higher (1959-1960 episode) or lower (1976-1977) than in the mixtures, and *Q. rubra* growth in the two-species mixture with *Q. robur* increased less after the 1990 drought episode than in the other stands (Fig. 3). *Fagus sylvatica* was most affected by drought in the two-species mixture with *Q. robur*, with a larger growth decrease followed by a sharper growth increase (Fig. 3). Yet, the interaction between drought and diversity was only significant for the 2004 and 2010-2011 episodes (Fig. 3). *Quercus robur* showed the strongest decrease in growth due to the 1976-1977 episode in mixtures with *Q. rubra* (Fig. 3).

The 1959-1960 episode represented an extreme drought (Fig. 1), but had only limited effect on basal area increment when compared with the other episodes (Figs 3-4). The years 1959-1960 were preceded by several hot dry years (Fig. D.3), which may have negatively affected tree growth already before 1959-1960. The resilience to drought (Rs in Fig. 4) tended to decrease between 1976-1977 and 2010-2011, while drought frequency increased. Before 1990, there was a 15-year interval between the drought episodes; after 1990, the drought episodes were only 6-8 years apart.

4. Discussion

The response of tree growth to drought differed among the species of the TREEWEB platform. *Fagus sylvatica* appeared more sensitive to drought than the two *Quercus* species (*Q. robur* and *rubra*), but *F. sylvatica* also showed remarkable recovery after each drought. Overall, tree species diversity did not modulate the growth response to drought of individual forest trees. Tree species identity effects were present, but only for particular species and drought episodes. Our results support the notion that a future increase in drought frequency and severity may eventually lower the growth superiority of *F. sylvatica* on drought-prone sites (Scharnweber *et al.*, 2011). The timing of the drought is important though; frequent summer droughts will be particularly detrimental for *Fagus* while frequent spring droughts may be disadvantageous for *Quercus*. When considering the future impact of drought, it may be important to take the local soil conditions into account, as soils can differ considerably in water storage capacity and moisture conservation during drought. Yet, several studies found drought to be the main factor controlling drought sensitivity and growth of trees across large geographic regions (Kelly et al., 2002; Hacket-Pain et al., 2016), trumping the effect of local soil conditions (D'Orangeville et al., 2018). As our study plots had been selected to have similar soil conditions (cf. De Groote *et al.*, 2017), we could not investigate whether local soil conditions can modulate the drought response in tree growth.

4.1. Strongest drought effect for *Fagus*

Drought intensity was more closely related to basal area increment for *F. sylvatica* than for both *Quercus* species, and *F. sylvatica* showed the lowest resistance and resilience for the studied drought episodes. *Fagus sylvatica* has indeed been described as more sensitive to drought than *Q. robur* (Scharnweber *et al.*, 2011; Scherrer *et al.*, 2011). Yet, for the studied drought episodes, *F. sylvatica* also showed high recovery. The quick recovery in *F. sylvatica* may be aided by the positive xylem sap flow at the base of the tree trunk before bud break in early spring, which causes active refilling of embolized vessels and thus (partial) recovery of xylem conductivity (Cochard *et al.* 2001). In addition, even though stem growth may stop early due to drought, accumulation of non-structural carbohydrates can continue until October also in case of soil water deficit (Barbaroux & Bréda, 2002). These carbohydrate reserves may enable *F. sylvatica* to quickly regain growth after a drought, especially on soils well-suited for *F. sylvatica* growth (e.g. the well-drained sandy loam soils in our study area). The lower immediate impact of drought on *Quercus* may be related to ring-porous species keeping up transpiration during drought, while diffuse-porous species such as *F. sylvatica* quickly close their stomata in times of water stress and hence reduce their transpiration as well as carbon acquisition (Scherrer *et al.*, 2011). Yet, maintaining photosynthesis during drought may require *Quercus* trees to invest more carbohydrates, which will result in lower carbohydrate reserves and lower growth in the year after the drought (Michelot *et al.*, 2012). We indeed found a decrease in growth after, rather than during, the 2004 drought episode for *Q. robur* and *rubra*. The observed decrease in resilience over time, i.e. across the six studied drought episodes, for *F. sylvatica* and *Q. robur* may reflect a tree age effect, with trees becoming more sensitive to drought when they grow older (see e.g. Carrer & Urbinati, 2004).

The differences in wood formation phenology between *Quercus* and *Fagus* are reflected in our study. *Quercus* growth was correlated with the cumulative drought up until April ($SPEI_{10}$-April), when early-wood formation starts in these ring-porous species (Barbaroux & Bréda, 2002; Michelot *et al.*, 2012). The growth of *F. sylvatica* was best correlated with the cumulative drought up until July ($SPEI_{18}$-July), including drought during June, the month of main *F. sylvatica* growth (Bouriaud *et al.*, 2004). D'Orangeville *et al.* (2018) also found drought sensitivity to be highest during the months of main tree growth. Summer drought (in 1990) negatively affected the basal area increment of *F. sylvatica*, but neither *Quercus* species, with main diameter growth in spring (Michelot *et al.*, 2012), was affected. The negative effect of summer drought on *F. sylvatica* growth has been previously reported (Scharnweber *et al.*, 2011; Hacket-Pain *et al.*, 2016). Summer drought may cause *F. sylvatica* to stop its wood formation early, resulting in a lower basal area increment in the year of the summer drought (Bouriaud *et al.*, 2004; Michelot *et al.*, 2012). Dry springs (in 1996 and 2010-2011), on the other hand, did affect the two *Quercus* species. Spring water availability has indeed been shown to be more important than summer drought for *Q. robur* (Toïgo *et al.*, 2015; Nechita *et al.*, 2017).

For *F. sylvatica*, not only the present-year climatic conditions, but also the temperature and precipitation of the previous summer, have been shown to affect its radial growth (e.g. Di Filippo *et al.*, 2007; Čufar *et al*., 2008; Hacket-Pain *et al*., 2016), which may explain why the integration timescale of the SPEI for *F. sylvatica* was longer than for the *Quercus* species in our study (i.e. 18 vs 10 months). Most dendroclimatology studies of *Q. robur* indeed found correlations with current-year temperature and precipitation only (e.g. Drobyshev *et al*., 2008; Mette *et al*., 2013; Hacket-Pain *et al*., 2016). D'Orangeville *et al*. (2018) suggested that the magnitude and duration of the legacy effects of climatological drivers may vary among species. The lagged effect of growing season climatic conditions on *F. sylvatica* may be the result of a carry-over effect (i.e. lower carbohydrate production in the unfavourable year leading to lower growth the next year) or of weather-cued masting. Masting, i.e. the synchronous production of large seed crops across trees and forests, does result in low growth for *F. sylvatica* (Drobyshev *et al.*, 2010). A mast year generally follows a year with drought in early summer (June-July) after a year with a cool moist summer (Piovesan & Adams, 2001). Two of the studied drought episodes with low during-drought growth of *F. sylvatica* (1976-1977, 2004) followed a year with a rather dry early summer preceded by a year with a rather wet early summer. Yet, the exceptionally severe full-year 1976 drought most likely caused the observed low growth in 1976-1977. In 2004, masting may have played a role, but local masting data for *F. sylvatica* are only available from 2008 onwards.

4.2. Species identity effects prevail

The effect of stand composition on drought resilience was limited in the studied species and stands. Limited or no effects of tree species diversity with regard to climate responses have been shown before in European forests (Vilà *et al.*, 2013; Merlin *et al.*, 2015; Ratcliffe *et al.*, 2016; Bosela *et al.*, 2018). We saw the highest basal area increment and the most negative drought effects in two-species mixtures, for *F. sylvatica* when growing in mixture with *Q. robur* (significant for 2004 and 2010-2011) and for *Q. robur* in mixture with *Q. rubra* (1976-1977). Similarly, *Q. rubra* showed a stronger post-drought growth restraint in the two-species mixture with *Q. robur* (1990) and higher recovery in monocultures (1976-1977). Overall, the basal area increment of *Q. robur* and *rubra* was lower in stands in which *F. sylvatica* was present. The observed identity effects may result from differences in functional traits among the study species (cf. Loreau & de

Mazancourt, 2013; but see D'Orangeville et al. (2018), who found mean species traits, such as rooting depth, to have limited value for explaining local drought effects). *Fagus sylvatica* is decidedly more shade-tolerant and casts a deeper shade than *Q. robur*, with *Q. rubra* moderately shade tolerant and shade casting (Jones, 1959; Packham *et al.*, 2012). In addition, *F. sylvatica* is known for its s*hallow and intensive rooting, Q. robur for its deep taproot, and Q. rubra for its taproot with spreading laterals (Köstler et al., 1968*). *Fagus sylvatica* may therefore experience less competition for light when growing in mixture with *Q. robur*, which will result in higher basal area increment for *F. sylvatica*. Higher growth of *F. sylvatica* in mixtures has been reported before (Pretzsch & Schütze, 2009). *Quercus robur* and *rubra*, on the other hand, will suffer from the shade cast by neighbouring *F. sylvatica*, resulting in lower *Quercus* growth in mixtures with *F. sylvatica*. The complementary rooting of *F. sylvatica* and *Q. robur* may result in a more complete use of the available water resources and thus higher soil water depletion, resulting in a stronger negative effect of drought on *F. sylvatica* growing in mixture with *Q. robur*. Competition for water between the more similarly rooting *Q. robur* and *rubra* might be more intense when water is limited, resulting in stronger drought effects for both species when growing together. Grossiord *et al.* (2014a), also found lower growth and water use efficiency in mixed forests during dry years, in boreal forests. On the other hand, Pretzsch *et al.* (2013) and del Río *et al.* (2014) found overyielding of *F. sylvatica* in mixtures with *Q. petraea* during dry or low-growth years, and Grossiord *et al.* (2014b) observed lower soil water depletion in mixtures than in monocultures for temperate beech and thermophilous deciduous forest during dry years. The drought-diversity-productivity relationship clearly depends on the specific context of the studies. For instance, the trees studied by Pretzsch *et al.* (2013) were generally smaller than our study trees, and tree size has been shown to affect the response of tree growth to drought (Merlin *et al.*, 2015).

Although we saw no overall effect of tree species diversity on the drought response of individual trees, we can expect the stability of stand-level productivity to be higher in mixed stands consisting of *F. sylvatica* and one of the *Quercus* species. *Fagus sylvatica* showed an immediate negative response to the selected drought episodes, but its growth recovered quickly after the drought, while the *Quercus* species were more resistant (smaller immediate decrease in growth) and showed a lagged response to drought. Asynchrony in the response of species to changes in environmental conditions is always stabilizing (Loreau & de

Mazancourt, 2013), and tree species diversity can thus be expected to increase forest ecosystem stability in this case.

5. Conclusion

Mixing tree species to enhance ecosystem services, such as overall forest biodiversity or nutrient cycling, will not decrease the resilience of forest tree growth to drought, but an increase in the frequency of extreme drought events may eventually lower the recovery potential of forest tree growth. Taking into account the timing of the drought and the physiology and anatomy of the tree species helped to explain the observed drought responses. The ring-porous *Quercus* species were mainly affected by spring drought and showed a relatively small decrease in growth but a long recovery. The diffuse-porous *F. sylvatica* was strongly affected by summer drought, showing a large and immediate decrease in growth and a swift recovery. This asynchrony in the growth response to drought suggests a stabilization of productivity in forests consisting of *F. sylvatica* and one of the studied *Quercus* species.

Author contributions

MV and SREDG collected the data; JVdB and JVA enabled the X-ray scanning; MV conceived the ideas, analysed the data, and led the writing of the manuscript; RS-S, SLM, and LH contributed to the data analysis and presentation of the results. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

We intend to archive our data at https://www.ncdc.noaa.gov/data-access/paleoclimatology-data.

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Table captions

Table 1 Description of the dataset: the number of trees (*N trees*), plots (*N plots*), and tree rings (*N rings*) for each study species, and the mean with range between brackets of diameter at breast height (*dbh*), estimated age at breast height (*age*), and basal area increment (*bai*)

Table 2 The final models linking annual basal area increment and drought severity for the period 1955-2015 for the three study species, including tree size (the diameter of the previous year – dbh_{t-1}), drought severity expressed as the Standardized Precipitation Evapotranspiration Index (i.e. the 18-month *SPEI* for July for *Fagus sylvatica* and the 10-month *SPEI* for April for both *Quercus* species), and stand composition (i.e. presence or absence of *F. sylvatica* – *Fsyl 0_1*). Parameter estimates (*est*, with standard error *se*), the estimated auto-regressive parameters of the autocorrelation structure (*ARMA*), the standard deviation (*sd*) of the random terms, and the marginal and conditional R² (R^2_m, R^2_c)[a] are shown for each model.

[a] calculated following Nakagawa & Schielzeth (2013)

Figure captions

Fig. 1 The Standardized Precipitation Evapotranspiration Index (SPEI) for each year between 1955 and 2015, calculated for July using an 18-month timescale (best correlated with the basal area increment of *Fagus sylvatica*) and for April using a 10-month timescale (best correlated with both *Quercus* species). $SPEI_{18}$-July ($SPEI_{10}$-April) represents the water balance for the period from February (June) of the previous year to July (April) of the current year. Colour of the dots - conditions wetter or drier than the median for the period considered across all years between 1955 and 2015; size of the dots - the number of months during the year for which the water balance of the preceding year (i.e. $SPEI_{12}$ for that month) indicated dry, normal, or wet conditions (according to the colour of the dot); grey lines - the six selected drought episodes, i.e. single (full line) or consecutive drought years (dotted line). For example, 1996 was a year with eight dry months, with July the last month of a moderately dry 18-month period ($SPEI_{18}$-July), and April the end of a severely dry 10-month period ($SPEI_{10}$-April).

Fig. 2 Mean basal area increment per year (with standard deviation) for trees of the three study species growing in stands of one, two, or three tree species. The grey lines indicate the six selected drought episodes: single drought years (full lines) or consecutive drought years (dotted lines).

Fig. 3 The mean basal area increment before (*PreDr*, n = 3 years), during (*Dr*, n = 1 or 2 years), and after (*PostDr*, n = 3 years) each of the six studied drought episodes, for *Fagus sylvatica* (Fsyl), *Quercus robur* (Qrob), and *Quercus rubra* (Qrub) growing in monocultures or mixtures of different species combinations. Line thickness - tree species richness; line type - species combination; lowercase letters - significant differences between pre-drought, during-drought, and post-drought basal area increment for each drought episode; uppercase letters - differences in basal area increment between species combinations; grey background - significant differences between stand compositions for the patterns of basal area increment along the sequence pre-drought, during-drought, post-drought; dark grey lines - the stand composition for which the basal area increment pattern significantly differed from the other stand composition levels; grey italic letters - brief description of the six drought episodes: spring, summer, or full year drought (drought during the preceding year between brackets).

Fig. 4 Mean resistance (Rt), recovery (Rc), and resilience (Rs) with 95% confidence interval for the six studied drought episodes and the three study species: *Fagus sylvatica* (Fsyl), *Quercus robur* (Qrob), *Q. rubra* (Qrub). The letters indicate significant differences between species. The horizontal dotted lines indicate complete resistance (Rt = 1; the further Rt falls below 1, the lower the resistance), a similar growth during and after the drought (Rc = 1; Rc smaller than 1 indicates further growth decline after the drought), and a return to pre-drought growth levels following a drought (Rs = 1; Rs smaller than 1 indicates lower growth after the drought than before the drought and thus low resilience). The six drought episodes are briefly described by the grey italic letters at the top: spring, summer, or full-year drought (with a drought during the preceding year indicated between brackets).

Table 1

	Fagus sylvatica	***Quercus robur***	***Quercus rubra***
N trees	86	101	88
N plots	28	30	27
N rings	5242	6121	5211
dbh (cm)	63 [33 – 97]	52 [31 – 88]	61 [31 – 99]
age (yr)	82 [59 – 100]	82 [54 – 98]	71 [51 – 95]
bai ($cm^2 yr^{-1}$)	44.1 [1.5 – 242.3]	29.1 [0.0 – 152.0]	45.4 [0.5 – 215.2]

Table 2

	Fagus sylvatica			*Quercus robur*			*Quercus rubra*		
	est	**se**	**p**	**est**	**se**	**p**	**est**	**se**	**p**
(Intercept)	2.7295	(0.1223)	< 0.001	2.8106	(0.0887)	< 0.001	1.9186	(0.0956)	< 0.001
dbh_{t-1}	0.0361	(0.0047)	< 0.001	0.0118	(0.0018)	< 0.001	0.0647	(0.0043)	< 0.001
dbh_{t-1}^{2}	-0.0003	(0.00005)	< 0.001		-		-0.0005	(0.0001)	< 0.001
$SPEI_{18}$-July	0.1002	(0.0046)	< 0.001		-			-	
$SPEI_{10}$-April		-		0.0520	(0.0029)	< 0.001	0.0357	(0.0026)	< 0.001
Fsyl (0_1)		-		-0.2297	(0.0763)	0.006		-	
ARMA $\varphi 1$		0.64			0.66			0.73	
ARMA $\varphi 2$		0.10			0.21			0.16	
sd plot		0.193			0.0001			0.093	
sd tree		0.410			0.298			0.281	
sd residuals		0.446			0.485			0.446	
R^{2}_{m} [a]		0.07			0.12			0.41	
R^{2}_{c} [a]		0.55			0.36			0.59	

Highlights

- Drought effects similar in mixed and monoculture TREEWEB forest plots.
- Asynchrony in the response of *Quercus* and *Fagus* tree growth.
- *Fagus* more sensitive and more resilient to drought than *Quercus*.
- Spring drought relevant for *Quercus*, summer drought for *Fagus*.

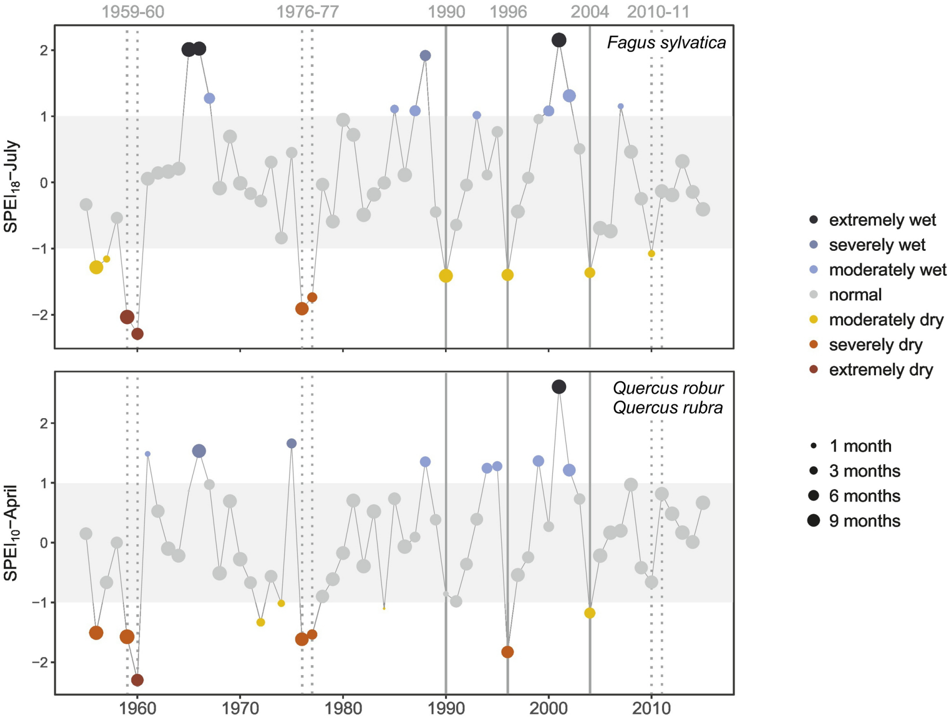
1959-60
1976-77
1990
1996
2004
2010-11
Fagus sylvatica
SPEI18−July
Quercus robur
Quercus rubra
SPEI10−April
2
1
0
−1
−2
1960
1970
1980
1990
2000
2010
extremely wet
severely wet
moderately wet
normal
moderately dry
severely dry
extremely dry
1 month
3 months
6 months
9 months

Figure 1

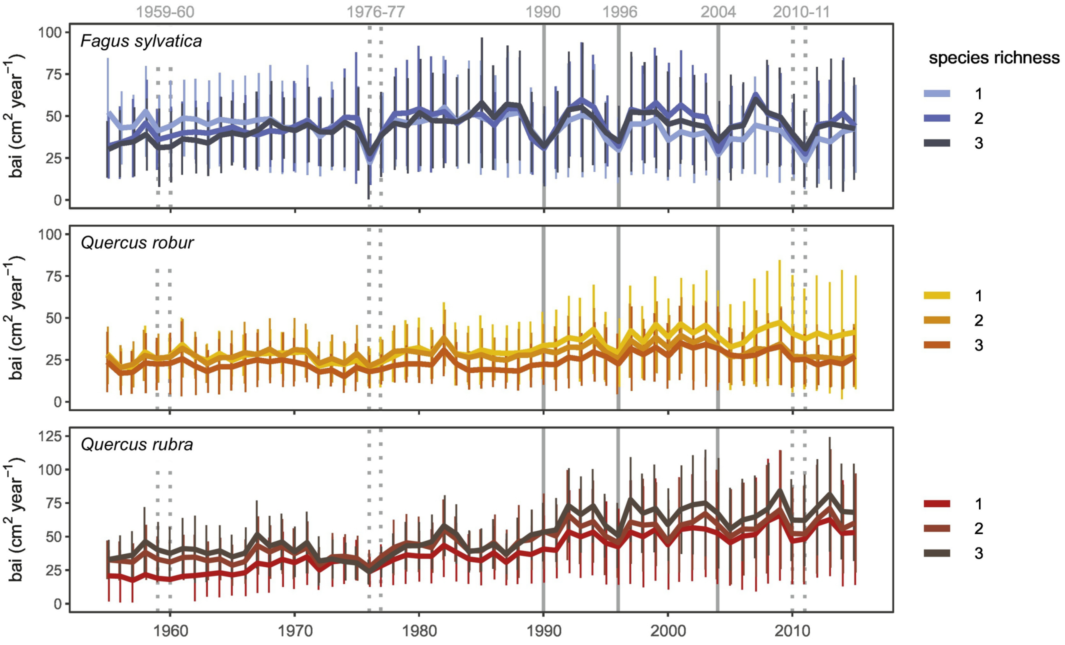
1959-60
1976-77
1990
1996
2004
2010-11
Fagus sylvatica
Quercus robur
Quercus rubra
bai (cm^2 year^{-1})
0
25
50
75
100
125
1960
1970
1980
1990
2000
2010
species richness
1
2
3

Figure 2

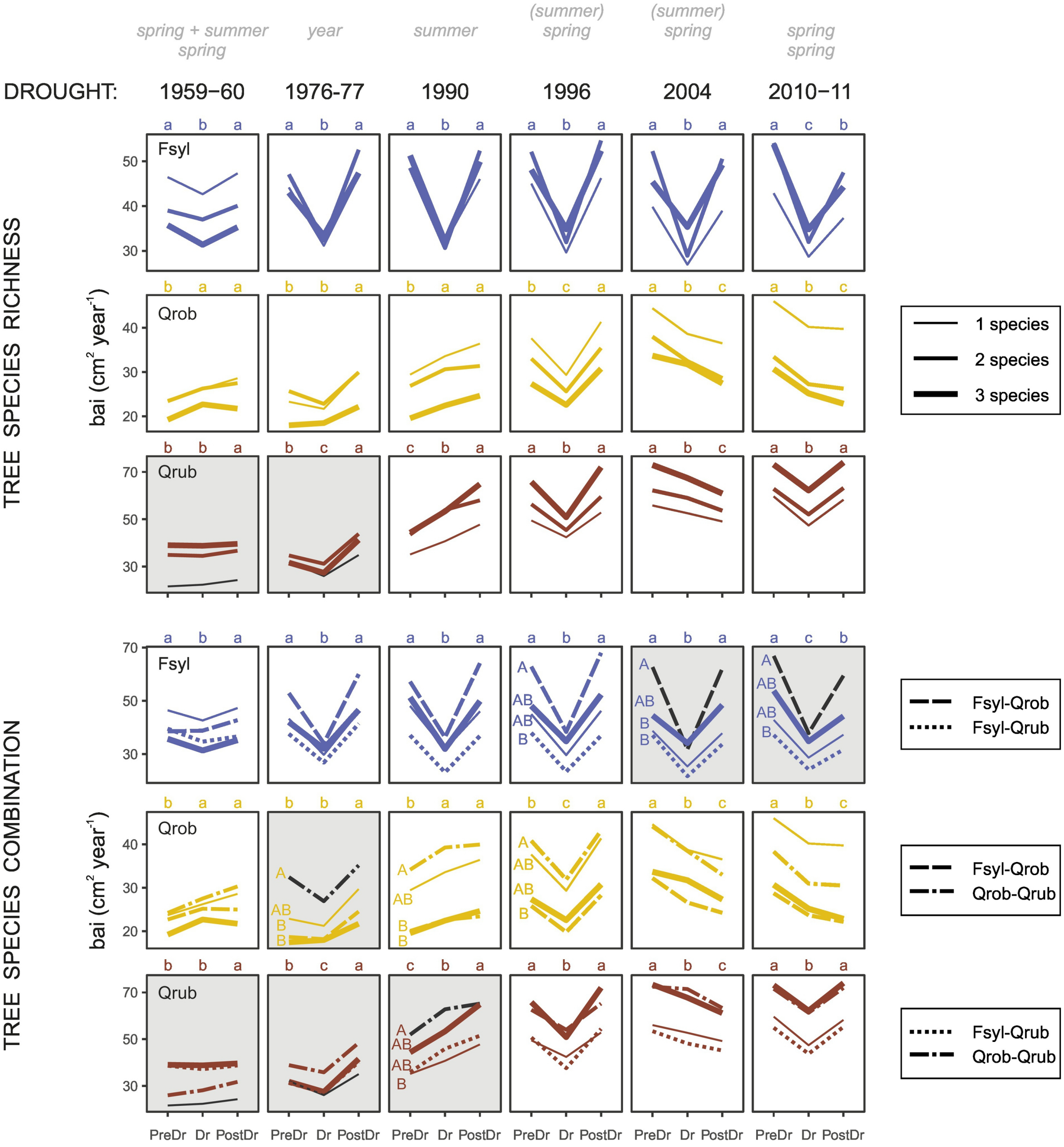
spring + summer
spring
year
summer
(summer)
spring
(summer)
spring
spring
spring
DROUGHT:
1959−60
1976-77
1990
1996
2004
2010−11
TREE SPECIES RICHNESS
TREE SPECIES COMBINATION
bai (cm^2 year^{-1})
Fsyl
Qrob
Qrub
a b a
b a a
b b a
b b a
b c a
b a a
c b a
a b a
b c a
a b a
a b a
a b c
a b c
a c b
a b c
a b a
A
AB
B
1 species
2 species
3 species
Fsyl-Qrob
Fsyl-Qrub
Qrob-Qrub
30
40
50
20
70
PreDr
Dr
PostDr

Figure 3

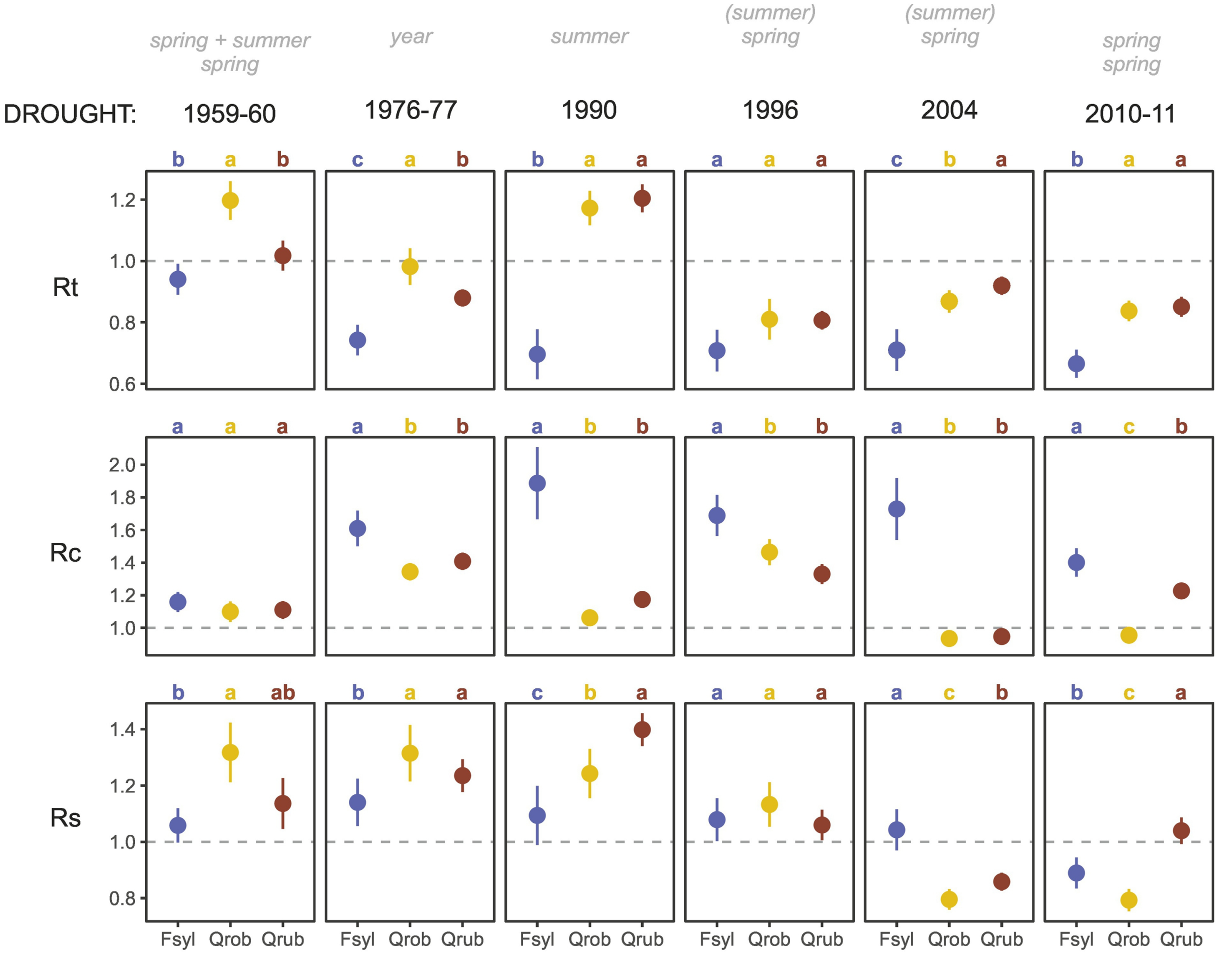
spring + summer
spring
year
summer
(summer)
spring
(summer)
spring
spring
spring
DROUGHT:
1959-60
1976-77
1990
1996
2004
2010-11
Rt
Rc
Rs
b a b
c a b
b a a
a a a
c b a
b a a
a a a
a b b
a b b
a b b
a b b
a c b
b a ab
b a a
c b a
a a a
a c b
b c a
1.2
1.0
0.8
0.6
2.0
1.8
1.6
1.4
1.2
1.0
1.4
1.2
1.0
0.8
Fsyl
Qrob
Qrub

Figure 4