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Drought timing, intensity, and consecutiveness have more influence on Douglas fir growth response than site conditions and stand density in European temperate climate

Camille Guisset[a,*], Morgane Dendoncker[a,b], Caroline Vincke[a], Quentin Ponette[a]

[a] Earth and Life Institute, Environmental Sciences, Université catholique de Louvain (UCLouvain), Croix du Sud, 2 box L7.05.24, Louvain-la-Neuve 1348, Belgium
[b] Département des sciences naturelles, Institut des sciences de la Forèt Tempérée (ISFORT), Université du Québec en Outaouais (UQO), Ripon, QC J0V 1V0, Canada

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ABSTRACT

Douglas fir is a largely introduced species in Europe and is often presented as a promising alternative to more drought-sensitive species. However, the observed and predicted increase in drought frequency and intensity could undermine its ability to cope with drought. This study aims to investigate the radial growth response of Douglas fir to drought in its climatic optimum in Europe, considering a number of drought characteristics (in terms of timing during the growing season, intensity, and consecutive occurrence), site conditions (average climatic water balance, maximal extractable soil water), and stand densities. Using growth data from 360 trees sampled across 24 sites in Wallonia (Belgium), we fitted linear mixed models to investigate the influence of drought, site, and stand characteristics on three commonly used resilience indices, as well as on an integrated index comparing observed resilience with a theoretical full resilience reference. On average, radial growth was reduced during droughts regardless of drought characteristics and site conditions. Trees always recovered to some extent, but not always to full resilience. Drought characteristics had a stronger influence on drought response than site and stand characteristics. Under the most intense droughts, trees were less resistant and less resilient to early droughts than to late droughts. Higher intensity and consecutive droughts increased the negative impact of a drought on resistance and resilience. Resistance was slightly higher on sites that were wetter and had higher maximal extractable soil water. In contrast, resilience to non-consecutive droughts was higher on drier sites. Finally, we did not detect any significant impact of stand density on Douglas fir growth response. The integrated index showed that Douglas fir has the best chance to be completely resilient to droughts when droughts are later, not very intense, and not consecutive and when trees are located on more water-limited sites. In conclusion, Douglas fir radial growth may not be as drought-resilient as expected. It is therefore advisable to avoid an overreliance on this species, and increase species diversity to strenghten forest stability. In this context, future research avenues could involve the comparison of drought response of Douglas fir with other species.

1. Introduction

Forest ecosystems are increasingly threatened around the globe by climate change, invasive insects and pests, in addition to threats from human activities (Anderegg et al., 2022; Hartmann et al., 2022; Trumbore et al., 2015). Natural disturbance impacts on European forests have significantly increased since 1950 (Patacca et al., 2023) and are projected to persist on this trajectory (Seidl et al., 2017). Among these disturbances, drought is of particular concern. In Europe, temperatures are rising faster than the global average and changes in precipitation patterns such as reduced precipitation in summer have been observed (IPCC, 2021). Heat extremes and droughts are also becoming more frequent and intense (Spinoni et al., 2018).

The recent drought of 2018 was described as unprecedented (Buras et al., 2020) with severe impacts on forest ecosystems: widespread canopy decline, increased mortality, and secondary drought impacts such as insect attacks (Schuldt et al., 2020; Senf and Seidl, 2021). Droughts can lead to carbon starvation, hydraulic failure and increased exposure to pests, negatively affecting forest productivity and vitality, eventually leading to mortality (Allen et al., 2010; McDowell et al., 2008). Forest decline and mortality due to warm and dry conditions have already been reported worldwide, including in regions not

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* Corresponding author.
E-mail addresses: camille.guisset@uclouvain.be (C. Guisset), quentin.ponette@uclouvain.be (Q. Ponette).

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normally considered to be at high risk for droughts such as the temperate zone in Europe (Choat et al., 2012; Hartmann et al., 2022; Szegleti et al., 2020).

The increasing, widespread negative impacts of drought on forest ecosystems are raising concerns about forest resilience (Forzieri et al., 2022; Reyer et al., 2015), defined in this study as “the ability of a forest to recover after disturbances and regain its pre-disturbance structure and function” (Holling, 1996; Lloret et al., 2011). Resilience can be divided into three components: resistance which is related to the reduction in ecological performance during the event; recovery which refers to the ability to recover relative to the damage estimated during disturbances; and resilience per se, which is the capacity to reach pre-disturbances performance levels (Lloret et al., 2011).

The impacts of drought, along with the expected responses of European forests to ongoing climate changes, have sparked debates about species composition of future European forests. Potential solutions to help forests adapt to climate change involve assisted migration and selection of more resilient varieties of native species, as well as the use of non-native species more tolerant to warmer and drier conditions (Felton et al., 2023; Vacek et al., 2021). For this reason, we need to understand how widely planted non-native tree species in Europe respond to drought.

Douglas fir (*Pseudotsuga menziesii var. menziesii* (Mirb.) Franco) is one of the most common non-native species planted in European forests (Brus et al., 2019), covering more than 830,000 ha (Nicolescu et al., 2023). It is regularly cited as a promising alternative to less drought-tolerant species such as the Norway spruce (*Picea abies* (L.) H. Karst.) (Stangler et al., 2022; Vacek et al., 2021; Vitali et al., 2017). Douglas fir is highly appreciated for its high productivity, adaptability, and valuable wood (Eckhart et al., 2019; Thomas et al., 2022). To cope with droughts, this species has a deep taproot system and a sensitive stomatal regulation (Thomas et al., 2022). Stomatal closure and cessation of growth in the early stages of droughts, known as the isohydric strategy, allows Douglas fir to avoid hydraulic failure by reducing the water loss. However, this strategy can become detrimental in cases of prolonged droughts, as it can lead to carbon starvation (McDowell et al., 2008). In Europe, recent studies have highlighted an increasing sensitivity of Douglas fir to summer temperatures (Vejpustková and Čihák, 2019), a severe impact of drought on its radial growth (Wrzesiński et al., 2024), and a trend towards decreasing resilience to drought over time (Bose et al., 2020). It is essential to document and assess the resilience of Douglas fir in the context of increasing drought frequency and intensity.

Radial growth response to past drought events is often studied using dendrochronological methods (e.g., Eilmann and Rigling, 2012; Wrzesiński et al., 2024). For a given drought event, tree ring chronologies can be used to calculate indices linked to the three components of resilience: resistance, recovery, and resilience (Lloret et al., 2011). Based on drought response indices, dendrochronological studies have shown that the impact on tree growth can be significantly influenced by several drought characteristics (Gao et al., 2018). For example, drought response is influenced by the onset timing of the drought. When it occurs late in the growing season, after growth has reached its maximum, the impact on growth is weaker (D’Orangeville et al., 2018). The growing season of Douglas fir extends on average from mid-April to mid-September, with a peak in radial growth rate in June (Miller et al., 2022). The minor impact of a late drought could be due to the fact that most radial growth is achieved before this period, even though cell wall lignification is not yet complete (Rossi et al., 2006). In addition to onset timing, drought intensity and frequency, as well as climate conditions in previous and subsequent years can influence drought response. More severe impacts on radial growth have been observed for more intense and more frequent droughts (Bohner and Diez, 2021; Bose et al., 2020; Jiang et al., 2024). In addition, studies have shown that wetter post-drought conditions can improve recovery and resilience (Jiao et al., 2021; Schmied et al., 2023). This highlights the importance of taking into account drought characteristics while studying their impacts.

Site and stand conditions can also influence drought response, by mitigating or exacerbating its effects. For example, the capacity of trees to withstand drought can be improved by more fertile soil conditions (Lévesque et al., 2016; Schmied et al., 2023; Sergent et al., 2012). Higher water availability, in terms of average local climate or soil water availability, can also buffer drought impacts on radial growth by reducing the exposure of trees to water shortages (Carnwath et al., 2012; Pardos et al., 2021). Finally, some studies have shown a positive impact of reduced stand density on drought response, probably due to a greater accessibility to resources such as light or water (Carnwath and Nelson, 2017; Sohn et al., 2016). Yet, other studies have shown divergent results (Castagneri et al., 2022). Understanding the impacts of site and stand characteristics on drought response is therefore crucial for implementing adaptive forest management to maintain the ecosystem services provided by forests in Europe (Keenan, 2015).

In this study, we investigated Douglas fir radial growth response to climatic drought in Wallonia (Belgium), a region with a temperate oceanic climate matching the climatic optimum of Douglas fir in Europe. We sampled 360 trees across 24 sites covering a wide range of both site water availability and tree density encountered by the species in our study area. We applied a dendrochronological approach and computed resistance, recovery, and resilience indices (Lloret et al., 2011), as well as an integrative approach of these three indices to assess the ability of the trees to fully recover when their growth was impacted by a drought event (Schwarz et al., 2020) Our first objective was to investigate the radial growth response of Douglas fir to climatic drought events of different timing, intensity, and consecutive occurrence. We hypothesized that droughts occurring late in the growing season would have a less negative impact on growth, that trees would be less resilient to the more intense droughts, and that trees would be less resilient to consecutive droughts (H1). Second, we assessed the extent to which site conditions (climate, soil) modulate Douglas fir growth response to drought. We hypothesized that trees growing on wetter sites (climate x soil water reserves) would be less sensitive to drought (H2). Third, we aimed to evaluate the influence of stand density on radial growth response to drought. We hypothesized that a higher stand density, and the subsequent higher competition for resources, would exacerbate the negative effects of drought on radial growth (H3).

2. Materials and methods

2.1. Study sites and sampling design

Our study area was located in Belgium, in the Walloon region (Fig. 1), where the temperate oceanic climate is favorable for Douglas fir growth. We sampled 24 mature, even-aged Douglas fir stands that were between 48 and 67 years old at the time of sampling (2021). The stands were selected to cover a wide range of site and stand density conditions encountered in the region. All sites were located on plateaus, at elevations ranging from 340 to 600 m. Mean annual temperatures vary between 7 and 9°C and mean annual precipitation varies between 980 and 1300 mm (Table 1).

Soils were well drained stony loam soils (cambisols in the WRB classification). We categorized the 24 sites in two groups of estimated maximal extractable soil water reserve (MEW). MEW was approximated based on soil depth and stoniness inferred from the Belgian soil map and then visually confirmed in the field using a soil auger. The “High MEW” category corresponds to soils with depths of at least 80 cm and stoniness less than 15 %, while “low MEW” category corresponds to shallow soils with less than 80 cm depth and more than 15 % stoniness.

The stands covered a wide density gradient, with stand basal areas (SBA) from 30 to 53 m^2/ha with at least 80 % being Douglas fir. The SBA represents the basal area (BA) at half of the silvicultural thinning interval and was calculated using the BA measured during sampling, the average annual increment (Perin et al., 2016), and the year of the last thinning obtained from forest managers. A more detailed description of

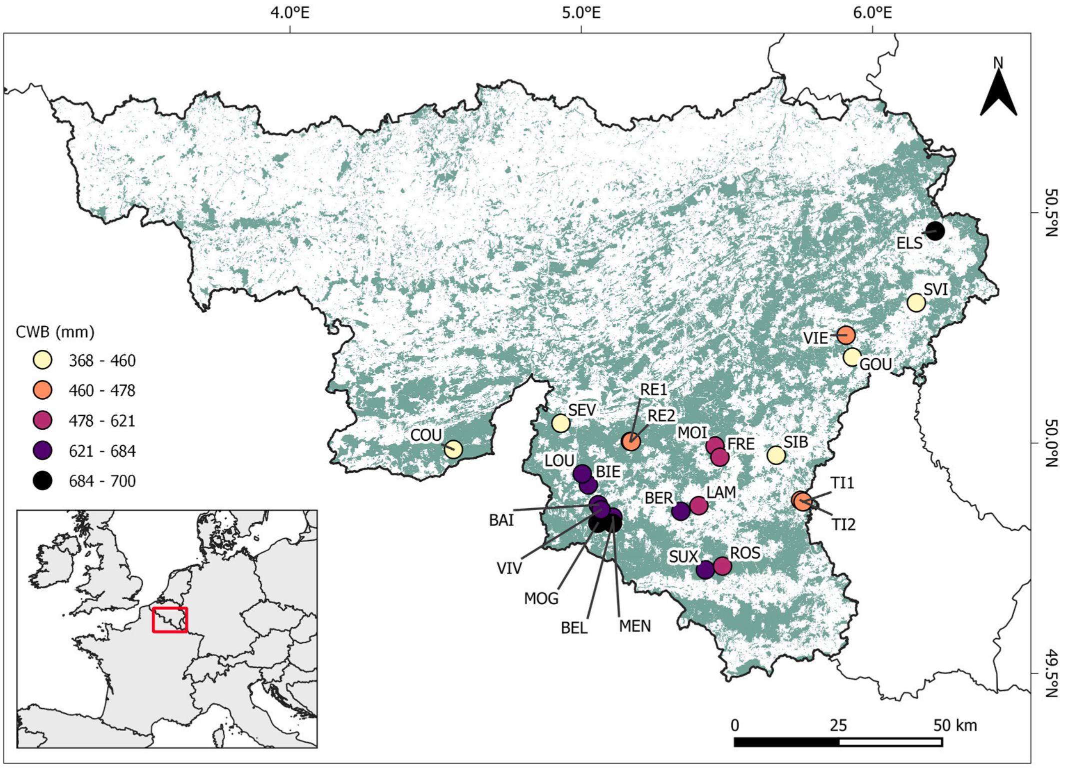

Fig. 1. Location of the 24 study sites in Wallonia (Belgium). The colored dots indicate the average climatic water balance (CWB) for the period 1961–2020, calculated as the difference between the annual sum of precipitation and evapotranspiration. The green color in the background corresponds to the Walloon forest cover (FAO definition) in 2018 (geoportail.wallonie.be).

Table 1
Characteristics of the 24 study sites (see Fig. 1 for site location). T is the mean annual temperature and P is the mean annual precipitation for the period 1961-2020. CWB corresponds to the mean annual climatic water balance (1961-2020) defined as the difference between annual precipitation and reference evapotranspiration. MEW is the estimated maximal extractable soil water, and SBA the stand basal area as defined in Section 2.1. The sites are listed in increasing CWB.

Site code	Altitude (m)	T (°C)	P (mm)	CWB (mm)	MEW	SBA (m^2/ ha)	Year of plantation
SEV	348	8.9	984	368	High	50.2	1963
GOU	483	8.0	1016	411	High	37.4	1969
SIB	541	7.7	1008	414	High	48.8	1969
COU	347	8.8	1036	431	Low	35.1	1973
SVI	492	7.7	1050	456	High	37.2	1960
RE1	403	8.5	1066	462	Low	35.9	1968
RE2	416	8.5	1066	462	Low	39.3	1965
VIE	500	7.8	1070	468	Low	41.7	1973
TI1	475	8.1	1075	468	Low	52.7	1964
TI2	466	8.1	1075	468	Low	35.8	1972
MOI	547	7.8	1101	518	High	39.2	1958
FRE	475	7.9	1139	550	High	51.0	1954
ROS	451	8.5	1210	593	Low	44.8	1958
LAM	439	8.2	1216	615	High	50.0	1963
LOU	396	8.3	1225	622	High	41.0	1958
SUX	405	8.5	1239	623	Low	30.3	1965
BER	460	8.2	1233	634	High	48.4	1959
BIE	395	8.2	1278	677	High	39.1	1966
BAI	422	8.2	1286	684	High	46.0	1970
MEN	401	8.2	1286	684	High	33.9	1968
VIV	402	8.2	1286	684	Low	44.9	1966
BEL	431	8.5	1298	690	Low	33.2	1958
MOG	391	8.5	1298	690	Low	41.1	1970
ELS	591	7.0	1270	700	Low	38.6	1966

site selection and characteristics can be found in Guisset et al. (2023, PREPRINT).

2.2. *Tree ring data*

At each study site, we selected 15 healthy (less than 20 % defoliation) dominant or co-dominant trees, separated by a distance of at least 10 m, with independent crowns, and not located at the edges of the stand. Defoliation was visually estimated according to the ICP forests methodology (Eichhorn et al., 2020). Each of these 360 trees was cored at height of 1.3 m at two locations perpendicular to the tree using a 5 mm Pressler borer between May and November 2021. The cores were then cut with a microtome, air dried, and scanned at a resolution of 2400 dpi. Ring-widths were measured on the scanned images using CooRecorder software (Maxwell and Larsson, 2021). Chronologies were crossdated using the COFECHA software (Holmes, 1983).

We constructed individual tree-ring series by averaging ring widths of the two cores of each tree. These series were then combined using a bi-weighted robust mean to compute site-level chronologies, starting from the year when data for at least 6 trees were available (Cook and Kairiukstis, 1991). The site level chronologies began between 1962 and 1976, and ended in 2020 which was the last fully formed tree ring for all sites at sampling time. We detrended individual tree-ring series, first by using a negative exponential function to remove the long-term, age-related, growth decline we observed on most trees. We then used a 20-year cubic smoothing spline with a 50 % frequency response cut-off to remove the mid-term signal that can be related, for example, to silvicultural interventions (Cook and Peters, 1981). The detrended ring-width indices were used to identify negative pointer years and assess tree growth responses to drought. The Expressed Population Signal (EPS) was computed to check if the sampled trees accurately represented the population and then compared to the 0.85 threshold suggested by Wigley et al. (1984). Other complementary statistics (average ring width, standard deviation, coefficient of variation, first autocorrelation, and interseries correlation) were calculated to characterize the chronologies (See Supplementary Material,Table S1). These analyses were done using the dplR package in R software (Bunn, 2008; R Core Team, 2022).

2.3. *Climate data and drought events*

Daily climatic data (minimum and maximum temperatures, precipitation, reference evapotranspiration) were obtained from the Royal Meteorological Institute of Belgium (RMI) for the period 1961–2020. The RMI data cover a 5 ×5 km grid. We extracted climate data for each site from the closest grid centroid. Reference evapotranspiration (ET0) was computed from radiation, air temperature, air humidity and wind speed data using the FAO Penman-Monteith equation (Allen et al., 1998). To characterize the average climate of the study sites, we calculated the mean annual climatic water balance (CWB; 1961–2020) as the mean difference between the annual precipitation and reference evapotranspiration (P-ET0). The CWB of the 24 study sites ranged between 360 and 700 mm for this 40-year period (Table 1).

Drought events were identified for each study site using the Standardized Precipitation and Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). The standardized nature of this index allows for the identification of abnormally dry conditions at each site, considering the entire available data period from 1961 to 2020. Radial growth of Douglas fir extends from mid-April to mid-September (Miller et al., 2022), but in the studied area, the species begins to photosynthesize after the winter break in February (Aubinet et al., 2016), and the February-March period has been shown to be a key period for Douglas fir radial growth (Guisset et al., 2023, PREPRINT). Therefore, we considered the February-September period as the “growing season” for the SPEI calculation, and divided it into two periods of four months to account for the impact of drought timing on tree response (Merlin et al., 2015; Vitali et al., 2018a). The first period corresponds to the first half of the growing season (from February to May), before the foliage of Douglas fir trees has fully matured and the trees have reached their maximum growth rate (Devine and Harrington, 2009; Miller et al., 2022) and is represented as the SPEI (4-month period) of May. The second period corresponds to the second half of the growing season (from June to September) and is represented by the SPEI (4-month period) of September. A year was identified as “early drought” when the SPEI of May was below −1 and as “late drought” when the SPEI of September was below −1 (Fig. S1-S2). We chose this threshold because SPEI values below −1 correspond to dry conditions outside of the range of normal climatic variability (Slette et al., 2019). When the SPEI was below −1 for both periods, a new SPEI was calculated for the two periods together (February to September) to measure drought intensity over the whole growth period. In our analyses, we included only trees that were at least 10 years old at the time of the drought event. In addition, we did not study drought events that occurred after 2018, to ensure a minimum of two years of post-drought growth.

For each study site, we calculated Bootstrapped Correlation Coefficients (BCCs) between the ring-width indices (RWI) and the SPEI for the early (February-May), late (June-September), and whole (February-September) growing seasons to investigate how they were related to radial growth, and how the relationship between radial growth and SPEI varied among sites. The BCCs were calculated for the period common to all study sites (1976–2020), using the “treeclim” R package (Zang and Biondi, 2015). The results of this analysis are presented in the Supplementary Material.

2.4. *Douglas fir growth response to drought*

2.4.1. *Negative pointer year*

For each site, we identified negative pointer years, which are defined as years for which a majority of trees exhibit remarkably negative growth responses (Jetschke et al., 2019). The Relative Growth Change (RGC) method was used to identify these years by comparing the ring width index of each year with the average indices of the four previous years for each individual chronology (Jetschke et al., 2019; Schweingruber et al., 1990). In this study, a year was considered as a negative pointer year for a study site if at least 70 % of the trees of this site exhibited a growth reduction of at least 10 %. For a given site, the analysis was performed from the year in which growth data were available for at least 10 trees. This analysis was performed in R software using the pointRes package (van der Maaten-Theunissen et al., 2015). Drought years identified by the SPEI and negative pointer years were compared to check for correspondence between negative growth response and drought events. However, we did not restrict the analysis of growth response to drought in Douglas fir to these negative pointer years. This approach could indeed have induced bias by excluding droughts that did not result in growth reductions (Schwarz et al., 2020).

2.4.2. *Resistance, recovery, and resilience*

The radial growth response in Douglas fir to identified drought events was assessed using resistance, recovery and resilience indices (Lloret et al., 2011). These indices were calculated from individual ring-width indices (RWI) and expressed in percentage (%). Resistance and resilience indices are defined relative to a reference growth level (RWI_{ref}; Bohner and Diez, 2021), which is calculated for each tree by averaging its RWI of all years except those corresponding to drought years, as identified by the SPEI (See Section 2.3). The resistance index (Rt, Eq. 1) is the ratio between the RWI of the drought year (RWI_{dr}) and the reference growth level (RWI_{ref}). It reflects the tree’s ability to maintain its growth during drought. The recovery index (Rc, Eq. 2) is the ratio between the average RWI of the two years that follow the drought year (RWI_{post}), and the RWI of the drought year (RWI_{dr}). It expresses the tree’s capacity to restore a certain growth level after the drought. Finally, the resilience index (Rl, Eq. 3) is the ratio between the average of the two post-drought years (RWI_{post}) and the reference growth level (RWI_{ref}). It describes the capacity of the tree to recover its “reference” growth level after the drought (Lloret et al., 2011; Steckel et al., 2020). The three indices were averaged and checked for deviation from 100 % using a t-test.

$$Rt = (RWI_{dr} \ / \ RWI_{ref}) \times 100 \tag{1}$$

$$\mathrm{Rc} = (\mathrm{RWI}_{\mathrm{post}} \ / \ \mathrm{RWI}_{\mathrm{dr}}) \times 100 \tag{2}$$

$$\mathrm{Rl} = (\mathrm{RWI}_{\mathrm{post}} \ / \ \mathrm{RWI}_{\mathrm{ref}}) \times 100 \tag{3}$$

Linear mixed models (Bates et al., 2015) were used to assess the effects of drought characteristics, site, and stand conditions on the radial growth. A model was fitted for each index (resistance, recovery, and resilience), with the index value for each tree and each selected drought event as the response variable, and drought characteristics, stand, and site conditions as the fixed effects. Drought characteristics considered in the models are timing (early/late/whole), intensity (SPEI), and consecutive occurrence (yes/no). For the resistance model, a drought year was considered as consecutive if another drought year occurred within the two previous years. For the recovery and the resilience models, a drought was considered as consecutive if another drought occurred within the two previous or the next two years. We used a two-year period to define consecutiveness to be consistent with the two-year post-drought period used to calculate the recovery and resilience indices. The determination of timing and the computation of SPEI to evaluate the intensity are described in Section 2.3. Site and stand characteristics used in the models are average climatic water balance (CWB), estimated maximal extractable soil water (MEW - high/low), and stand density (SBA). These parameters are explained in Section 2.1, and their values for each study site are presented in Table 1. Continuous variables (SPEI, CWB, SBA) were standardized by subtracting the mean of each variable and then dividing by its standard deviation, in order to enable the comparison between predictors (Schielzeth, 2010). Site effect was included in each model as a random effect. We did not include a random effect on trees because it did not improve the model based on AIC (Akaike Information Criterion; Akaike, 1981).

All these parameters were included in the models. We then selected the most relevant interactions for each model based on the AIC (Burnham and Anderson, 2004) and biological plausibility of the results. The three selected models were visually checked for homoscedasticity and normal distribution of the residuals. The variance inflation factor (VIF) was calculated to check for correlation between predictors (Fox and Monette, 1992). Estimated marginal means (emmeans) of the significant interactions were calculated and then compared using post hoc Tukey tests. All analyses were performed using the following R packages: lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), MuMIn (Bartoń, 2023), emmeans (Lenth, 2022) and ggplot2 (Wickham, 2016).

2.4.3. Integrated approach of resistance, recovery, and resilience

We adapted the « full resilience » approach proposed by Schwarz et al. (2020) to conduct complementary analyses that offer an integrated perspective on the resistance, recovery, and resilience indices of Lloret et al. (2011). This approach is based on the inherent relationship between the three indices: recovery corresponds to the ratio between resilience and resistance (see Eqs. 1, 2 and 3). Setting the resilience value to one, i.e., assuming that the trees recover completely, the theoretical recovery equals the inverse of resistance (Eq. 4).

$$\text{Recovery} = \text{Resilience}/\text{Resistance} = 1/\text{Resistance} \tag{4}$$

We compared this theoretical relationship (hereafter called “full resilience”) with the actual relationship between recovery and resistance for Douglas fir in Wallonia. As there is a generally observed trade-off between resistance and recovery of radial growth to drought, this relationship is expected to follow a negative power function (Schwarz et al., 2020). Therefore, we fitted the nonlinear function of Eq. (5) to the data, using the nls R function (R Core Team, 2022).

$$\text{Recovery} = \text{a} \times \text{Resistance}^{\text{-b}} \tag{5}$$

For the following analysis, only the observations with a resistance level below 100 % were considered to assess whether trees had the capacity to fully recover, taking into account their reduced growth during the drought. We plotted the theoretical “full resilience” curve (Eq. 4) and the curve fitted to our data and calculated a 95 % confidence interval using a bootstrap method (10,000 replications). An F-test was performed on the residuals to determine if the fitted curve was significantly different from the full resilience curve. We then calculated the intersection between these two curves to identify the resistance level threshold above which the fitted curve surpassed the theoretical full

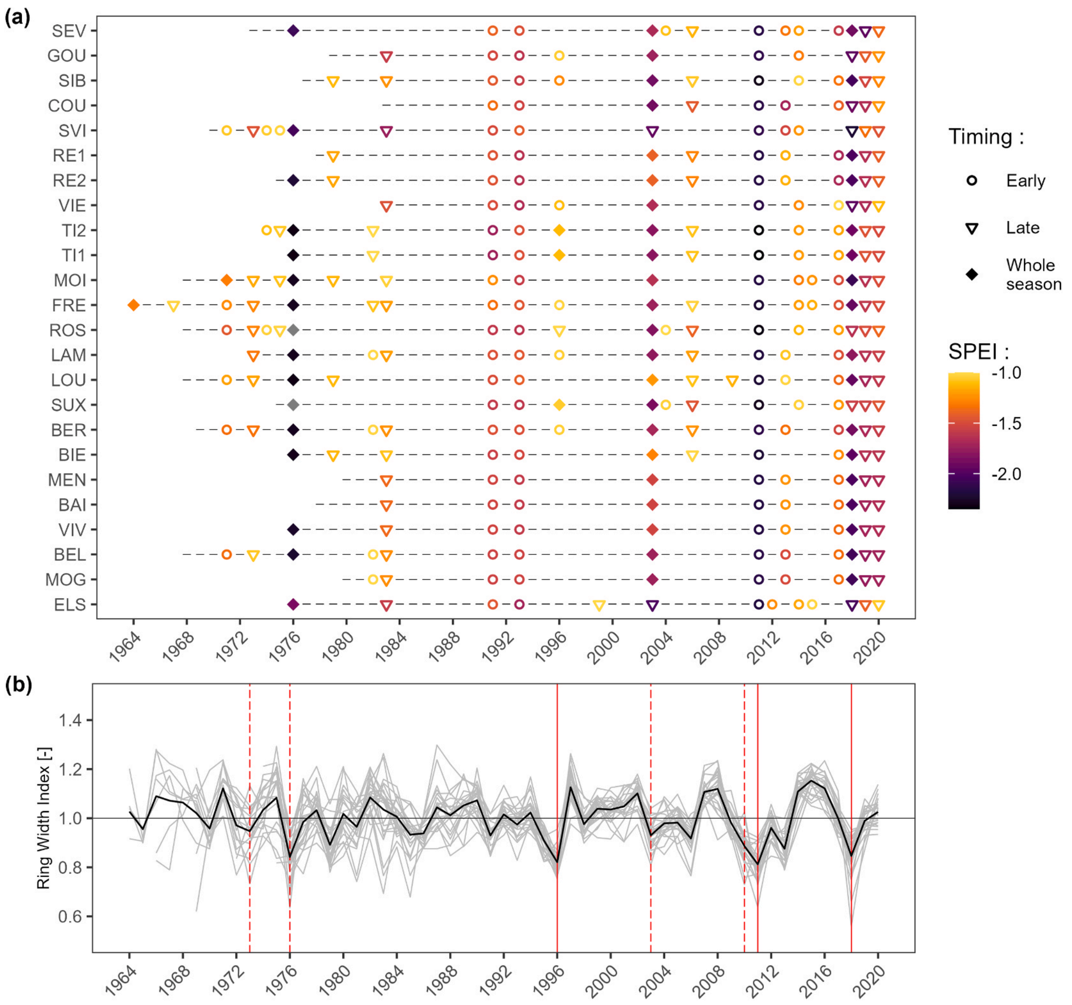

Fig. 2. **(a)** Drought years identified by SPEI for each study site from the year the trees were 10 years old. Point shape indicates the drought timing (“early” for the period February to May, “late” for the period from June to September, and “whole season” for February to September). Point color shows intensity based on SPEI. **(b)** Detrended site-level chronologies (grey) and overall average chronology (black). Negative pointer years identified from ring width indices using RGC method, are shown from the year data is available for at least 6 sites (1972): red solid lines when they have been identified for at least 50 % of the study sites, and red dashed lines when identified for at least one third of the study sites.

resilience curve. An intersection before a resistance level of 1 indicates the resistance level that the trees must present to fully recover. To assess the influence of drought, stand, and site characteristics on the achievement of full resilience, we built a linear mixed model of the distance to full resilience (same method as described in Section 2.4.2). The distance was calculated as the difference between the actual recovery (Eq. 2) and the theoretical recovery (i.e., the necessary level to reach the theoretical full resilience; Eq. 4). A negative distance indicates that trees failed to reach full resilience.

3. Results

3.1. Drought events and negative pointer years

Since the early 2000s, both the frequency and intensity of droughts have been increasing (Fig. 2a). Between 2011 and 2020, a drought (SPEI <-1) occured in at least half of the years, and from 2017 to 2020, a drought was detected each year. The most important early droughts occurred in 1991, 1993, 2011 for all study sites, and in 2017 for 21 out of 24 sites. In particular, the year 2011 corresponded to a remarkably dry year with SPEI values below −2 (from −2.4 to −2.1) for all study sites. These values represented return periods of more than 50 years (Svoboda et al., 2012). Additionally, the years 2013 (for 14 out of 24 sites) and 2014 (11 out of 24) also correspond to generalized early dry conditions. 2019 and 2020 were the most generalized late droughts, identified across all study sites. Drought response indices could not be calculated for these two years because growth data after 2020 were not available. The years 1973 (for 8 out of 9 sites), 1983 (15 out of 24), and 2006 (14 out of 24) are also important late droughts. Three years were identified as whole growing season droughts for almost all study sites: 1976, 2003 and 2018. The year 1976 was the most severe drought of the three, with SPEI values between −2.3 and −2.

The ring width indices were positively correlated with the SPEI used to identify early (February-May) and late (June-September) droughts (Fig. S3). In other words, the radial growth was lower when the conditions were drier. These correlations were significant for respectively 9 and 11 out of 24 sites. Fewer significant correlations were observed for the 12 wetter sites, based on their CWB. Correlations with the SPEI of the whole growing season were globally lower, and significant for only one study site.

Negative pointer years were identified from ring width indices (Fig. 2b) to check if they corresponded to dry years identified by the SPEI (Fig. 2a). The years 1996, 2011 and 2018 were identified as negative pointer years for at least half of the study sites, while the years 1973, 1976, 2003 and 2010 were identified for at least one third of the sites. All these years coincide with dry years identified in Fig. 2a, except for 2010. Despite its significant negative impact on growth, the year 1996 did not appear as an intense and generalized drought year. This could be explained by the important precipitation deficit at the end of the winter 1995–1996 in Belgium (IRM, 2022, 2015), which could not be detected by the SPEI for the chosen period (February-September). The main droughts identified in this study, such as those of 1976, 2003, 2011 and 2018, appeared to have a greater impact on growth in the year of the drought itself than in the subsequent years. Finally, the standardized average chronologies of the study sites tended to synchronize from the early 2000s (Fig. 2b). Most of the negative pointer years (5 out of 7) were identified in the second part of the chronology, from 1996 onwards. Details of the negative pointer years identified by study site can be found in the Supplementary Material (Fig. S4).

3.2. Influence of drought, site, and stand characteristics

On average, the sampled trees were affected by droughts, as the observed mean resistance value (92.4 %) was significantly different from 100 % ($p < 0.001$). They recovered in the two years following the drought, as the mean recovery was above 100 % (109.4 %, $p < 0.001$). However, post-drought growth level was on average slightly lower than the reference growth level as the mean resilience was 98 % and significantly lower than 100 % ($p < 0.001$).

The linear mixed models showed that the indices of resistance, recovery, and resilience were influenced by the three drought characteristics (timing, intensity, consecutiveness) as they were all involved in at least one significant interaction ($p < 0.001$). Overall, drought characteristics appeared to have a stronger effect on drought response than site and stand characteristics (Fig. 3, Table S2). The predicted values of resistance (< 100 %) and recovery (> 100 %) by linear models confirmed that Douglas fir was affected by drought regardless of drought, site, or stand characteristics, but always recovered some growth within two years since recovery values were always over 100 % (Fig. 4, Fig. 5). The species did not always return to its reference growth level, as resilience values were not always above 100 %. However, it has the best chances of being fully resilient (100 %) when the droughts were not consecutive, not very intense (SPEI > −1.5), and the site had a drier average climate (CWB between 360 and 550 mm) (Fig. 4, Fig. 5).

3.2.1. Drought characteristics

First, the timing of droughts had a significant impact on the three indices, in interaction with drought intensity for resistance and resilience, but not for recovery ($p < 0.001$, Fig. 4a). Drought response to early droughts depends more on drought intensity than drought response to whole growing season droughts and late droughts. As the intensity increased, resistance and resilience to early droughts decreased: the difference in resistance between a drought with an intensity of –1 (SPEI value) and −2 is 15 % for the resistance ($p < 0.001$), and 11 % for the resilience ($p < 0.001$). The opposite trend was observed for the recovery, with increasing values for more intense droughts, regardless of the timing of the droughts. For the most intense droughts (e.g., at SPEI = −2), resistance to early and whole season droughts were 6 % and 9 % lower, respectively, than resistance to late droughts ($p < 0.01$). Resilience to early droughts was 7 % and 5 % weaker than resilience to late and whole season droughts ($p < 0.001$). For the less intense droughts (e.g., SPEI = −1), resistance to early droughts was 7 % and 12 % higher than resistance to late and whole season droughts ($p < 0.001$). Resilience to early droughts was 6 % and 8 % higher than to late and whole season droughts ($p < 0.001$).

Second, the interaction between drought timing and consecutive occurrence of droughts also had a significant impact on the three indices ($p < 0.001$, Fig. 4b). Consecutive occurrence had a significant negative effect on recovery and resilience to early droughts (−17 % and −6 %, $p < 0.001$). Recovery from early consecutive droughts was the lowest, being 9 % and 14 % lower than for late and whole season consecutive droughts, respectively ($p < 0.001$). The effect of consecutive occurrence on late droughts was less pronounced, with an impact only on recovery, which was slightly higher for consecutive droughts (+6 %, $p < 0.01$). For whole season droughts, resistance and resilience were 10 % and 3 % lower when droughts were preceded or followed by another drought ($p < 0.01$).

Finally, the interaction between consecutiveness and drought intensity was significant for the three indices ($p < 0.001$, Fig. 4c). The negative effect of consecutive occurrence of droughts on resistance, recovery, and resilience was indeed less pronounced with increasing drought intensity. It was no longer significant when the SPEI was −2. We also observed that resistance decreased with increasing drought intensity and that this trend was less pronounced for consecutive droughts than for non-consecutive droughts. Resistance to non-consecutive droughts was 11 % lower for an SPEI value of −2 compared to an SPEI value of −1 ($p < 0.001$), while the difference was not significant for consecutive droughts. The opposite trend was observed for the recovery from consecutive droughts: as drought intensity increased, recovery also increased (+13 % between SPEI −1 and −2, $p < 0.001$). Regarding resilience, drought intensity only affected non-consecutive droughts: as intensity increased, resilience decreased (−8 % between SPEI −1 and

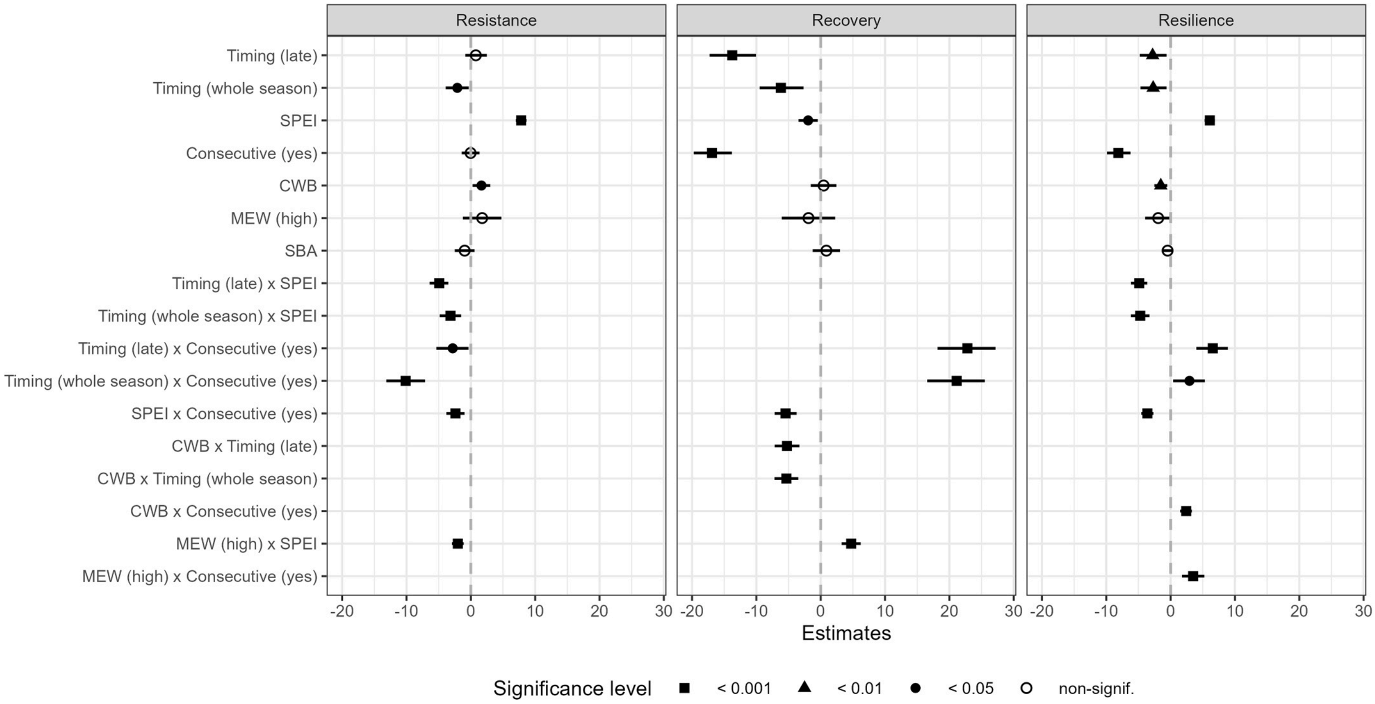

Fig. 3. Coefficient estimates of the mixed effects models explaining the resistance, recovery, and resilience indices. The three models included all the following explanatory variables: timing (early/late/whole season), intensity (SPEI, continuous and standardized), consecutive occurrence (consecutive yes/no), mean climatic water balance (CWB, continuous and *standardized), maximal extractable soil water (MEW, high/low), and stand density (SBA, continuous and standardized). Interactions were selected based on AIC for each model. The level of significance is shown by the different shapes (see legend). Confidence intervals (95 %) are represented by the horizontal bars for each estimate. As continuous variables are standardized, the distance to zero is related to the effect size. The outputs of the models are presented in Table S2.

−2, $p < 0.001$).

3.2.2. *Site and stand characteristics*

Climatic water balance (CWB) had a significant effect on resistance ($p < 0.05$), on recovery when in interaction with drought timing ($p < 0.001$), and on resilience alone ($p < 0.05$) and when in interaction with drought consecutiveness ($p < 0.001$, Fig. 3, Table S2). When the average climate was drier (CWB of 400 mm), resistance was slightly weaker by 5 % ($p < 0.05$) than when it was wetter (CWB of 700 mm) (Fig. 5a). On the other hand, recovery from late and whole season droughts was 13 to 14 % higher ($p < 0.01$) on drier sites (CWB of 400 mm) compared to wetter sites (CWB of 700 mm). In addition, resilience to non-consecutive droughts was also slightly higher by 4 % ($p < 0.05$) on drier sites (CWB of 400 mm).

Soil maximal extractable water (MEW) had a significant effect on the three indices in interaction with drought consecutiveness and intensity ($p < 0.001$, Fig. 3, Table S2). Resistance to the most intense droughts (SPEI of −2.3) was 6 % lower ($p < 0.05$), and recovery was 12 % higher ($p < 0.01$) on sites with low MEW compared with sites with high MEW (Fig. 5b). There was no significant difference in resilience between low and high MEW. However, the resilience of trees growing on low MEW sites was more impacted by the consecutive occurrence of droughts (−5 %, $p < 0.001$) than the resilience of trees growing on high MEW sites (no significant difference).

In contrast with CWB and MEW, stand density (SBA) had no significant effect on drought response indices (Fig. 3, Table S2).

3.3. *Integrated approach of the resistance, recovery, and resilience indices*

The curve fitted on our data always lies below the theoretical full resilience curve, the two curves being significantly different (Fig. 6a, $p < 0.001$). There was no intersection of the curves below the resistance value of 1, which means that, on average, trees affected by droughts (i.e., trees presenting a growth reduction during the drought) did not fully recover.

The distance to full resilience was influenced by all the drought characteristics tested (timing, intensity, consecutive occurrence), as they were included in at least one significant interaction in the linear mixed model (Fig. 6b, Table S3). Site and stand characteristics had a weak impact on the distance to full resilience, with only the average climatic water balance (CWB) being significant ($p < 0.05$).

The timing of drought affected the potential of Douglas fir to achieve full resilience, in interaction with drought intensity ($p < 0.001$, Fig. 6c). Trees that experienced severe early droughts were 10 % from full resilience (estimated distance for an SPEI = −2), while trees that experienced late or whole season droughts were on average 2 % and −2 %, respectively, from achieving full resilience for the same drought intensity. The distance to full resilience for early droughts tended to decrease as drought intensity decreased, with a distance of 4 % for an SPEI value of −1. The consecutiveness of drought events also affects the ability of trees to fully recover, in interaction with drought intensity ($p < 0.001$). Consecutive droughts always lead to a negative distance from full resilience. However, for non-consecutive droughts, trees could reach full resilience if the drought is of low intensity (mean distance of +3 % at SPEI = −1).

Regarding site and stand characteristics, CWB influenced the distance to full resilience in interaction with the consecutive occurrence of droughts ($p < 0.01$). Trees on the driest sites were able to reach full resilience when droughts were not consecutive (distance of +1 % for CWB = 400 mm). For trees on the wettest sites, the distance to full resilience remained negative for both consecutive and non-consecutive droughts (−3 and −4 % for CWB = 700 mm). Finally, stand density (SBA) had no significant effect on the distance to full resilience.

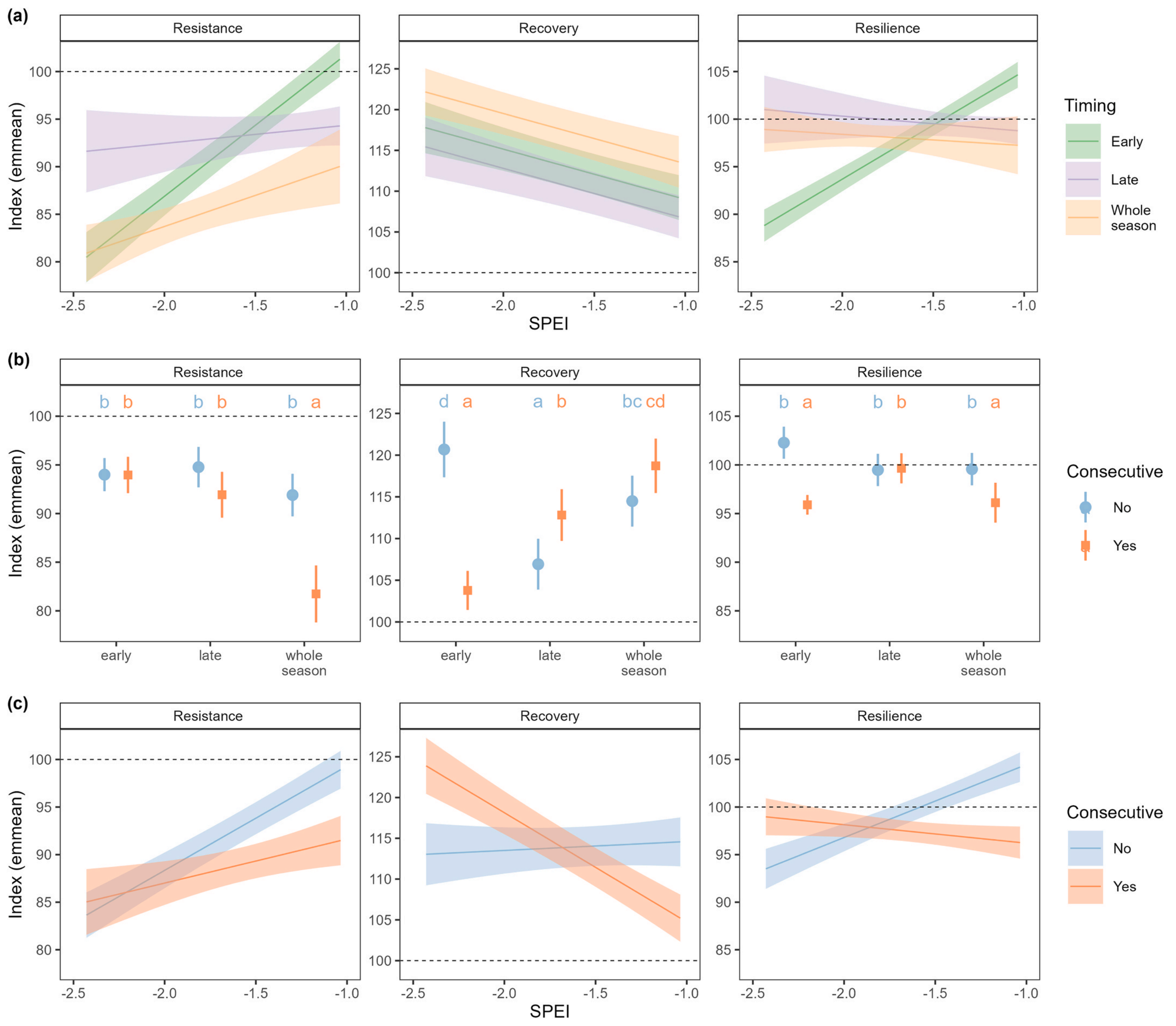

Fig. 4. Crossed effects of the studied drought characteristics on resistance, recovery, and resilience: (a) timing and intensity measured by the SPEI, (b) timing and consecutive occurrence, (c) intensity and consecutive occurrence. "Early" timing corresponds to the February-May period, "Late" to June-September, and "Whole season" to February-September. The y-axes show the estimated marginal means predicted by the model. Colored bands in (a) and (c), and vertical lines in (b) represent the 95 % confidence intervals. The coefficient estimates of the models are presented in Fig. 3 and **Table S2**.

4. Discussion

To investigate Douglas fir response to climatic droughts, we relied on radial growth data from 360 trees sampled from 24 study sites in Wallonia (Belgium). Drought response was studied through the computation of resistance, recovery and resilience (Lloret et al., 2011). We also applied an integrative approach using the concept of full resilience proposed by Schwarz et al. (2020). The influence of drought characteristics (timing, intensity, consecutive occurrence), site, and stand characteristics (average local climate, maximal extractable soil water, stand density) was investigated using linear mixed models. Overall, drought characteristics appeared to have a stronger influence than site and stand characteristics on Douglas fir radial growth response to droughts (Fig. 3). On average, Douglas fir trees did not reach full resilience, as the curve fitted to our data was below the theoretical full resilience curve (Fig. 6a). This means that the trees could not fully recover from the drought events studied between 1964 and 2018.

4.1. Drought characteristics significantly influence Douglas fir response

In line with our first hypothesis (H1), early droughts had a stronger negative effect than late droughts on resistance, recovery, and resilience, as well as on the distance to full resilience (Fig. 4; Fig. 6c). This was particularly the case when the droughts were more intense (SPEI < -1.5) and, in the case of recovery, when they were consecutive. Similarly, D'Orangeville et al. (2018) identified drought timing as a strong driver of drought sensitivity in temperate forests of Eastern North America, with early droughts having the strongest effect. For Douglas fir, Sergent et al. (2012) also showed a greater negative impact on radial growth when water deficits occurred early in the season, but Vitali et al. (2018a) highlighted a stronger impact of summer droughts. In contrast to the results obtained for Douglas fir in our study, Aldea et al. (2022) showed a greater sensitivity to summer droughts for Norway spruce, and no variation between seasons for Scots Pine (*Pinus sylvestris* L.). Differences in sensitivity to early and late droughts result from the cambial

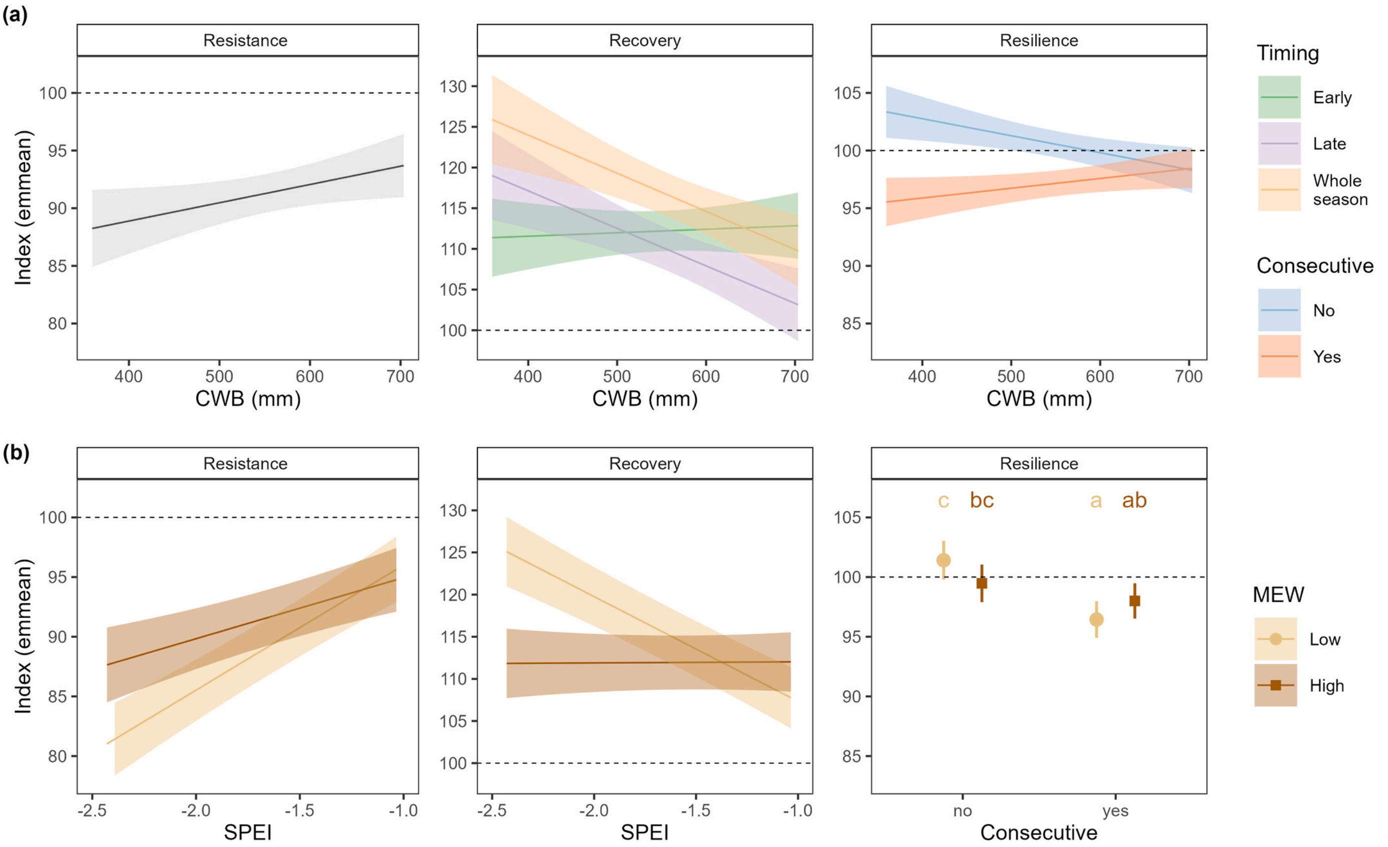

Fig. 5. Effects of climatic water balance (CWB) (a) and maximal extractable soil water (MEW) (b) on the resistance, recovery, and resilience indices. Only significant effects and significant interactions with drought are presented. "Early" timing corresponds to the February-May period, "Late" to June-September, and "Whole season" to February-September. The y-axes show the estimated marginal means calculated for each model. Vertical lines in (b) and colored bands represent the 95 % confidence intervals. The coefficient estimates of the models are presented in Fig. 3 and Table S2.

phenology, carbon allocation strategy and wood anatomy of the species (Schwarz et al., 2020). Low sensitivity to late droughts could be related to species having already achieved most of their annual radial growth before drought occurs (D'Orangeville et al., 2018; Rossi et al., 2006). It would indeed mitigate the effects of early growth cessation that can be induced by very high temperatures associated with summer droughts (Ford et al., 2017). Another explanation for the stronger impact of early droughts could be related to adaptative changes in wood anatomy during drought events. Water shortages during the early growing season induce a decrease in the lumen-to-wall thickness ratio which results in an increase in the minimum wood density (Camarero et al., 2017). An increase in wood density make trees less vulnerable to xylem cavitation, but at the cost of a reduction in ring width (Gazol et al., 2022).

We considered a relatively wide range of drought intensities, starting from SPEI < -1, which allowed us to investigate Douglas fir drought response not only to exceptional drought events with return periods of several decades, but also to moderate drought events that occur much more regularly. Instead of focusing on extreme drought events as most researchers have done, we included a range of drought intensities that allowed us to test for a drought intensity effect in our model. As we hypothesized (H1), our results show that the effects of climatic drought increased with increasing drought intensity, particularly on resistance, resilience, and distance to full resilience for the early droughts (Fig. 4; Fig. 6c). This is consistent with the results of Bohner and Diez (2021) for other conifers in the native range of Douglas fir in North America, and with the results of Sergent et al. (2012), who identified drought intensity, assessed in terms of soil water deficit, as an important driver of Douglas fir growth.

Consecutive occurrence of droughts had a significant negative effect on the resistance and resilience of Douglas fir (Fig. 4), supporting our first hypothesis (H1). Consecutiveness are defined here as the occurrence of another drought year within the two years before a drought event for the resistance, and within the two years before or after the drought for the recovery and resilience. When a drought is preceded by another drought, the negative effect on growth could be related to the legacy effect of the first drought, leading to delayed onset of growth and a reduced growth rate in the years following the drought (Miller et al., 2023). Indeed, recurring droughts can reduce the amount of carbohydrates stored by the tree, which can have a negative effect on growth, as the tree has to use available stored reserves for repair, maintenance, and defense in addition to growth (Bréda et al., 2006). Regarding the effects of dry conditions in the years following the drought, it can have the effect of reducing and delaying recovery (Serra-Maluquer et al., 2018; Thurm et al., 2016). Schmied et al. (2023) confirmed the influence of climatic conditions in the years preceding and following the droughts, showing increased recovery and resilience under wetter climatic conditions for *Picea abies* and *Fagus sylvatica* L.

4.2. Site conditions have a minor influence on radial growth response to drought

In line with our second hypothesis (H2), the drought resistance of Douglas fir was slightly higher on wetter sites, i.e., presenting a higher mean climatic water balance (CWB; Fig. 5a). Other studies have shown similar results for Douglas fir in Europe (Thom et al., 2023) and in its native range in North America (Carnwath et al., 2012). However, this is not always the case as Martínez-Vilalta et al. (2012), Lévesque et al. (2014) and Serra-Maluquer et al. (2018) showed little or no effect of the local mean climate on growth sensitivity. These divergent results could be due to a difference in the indicator used (CWB, ratio between

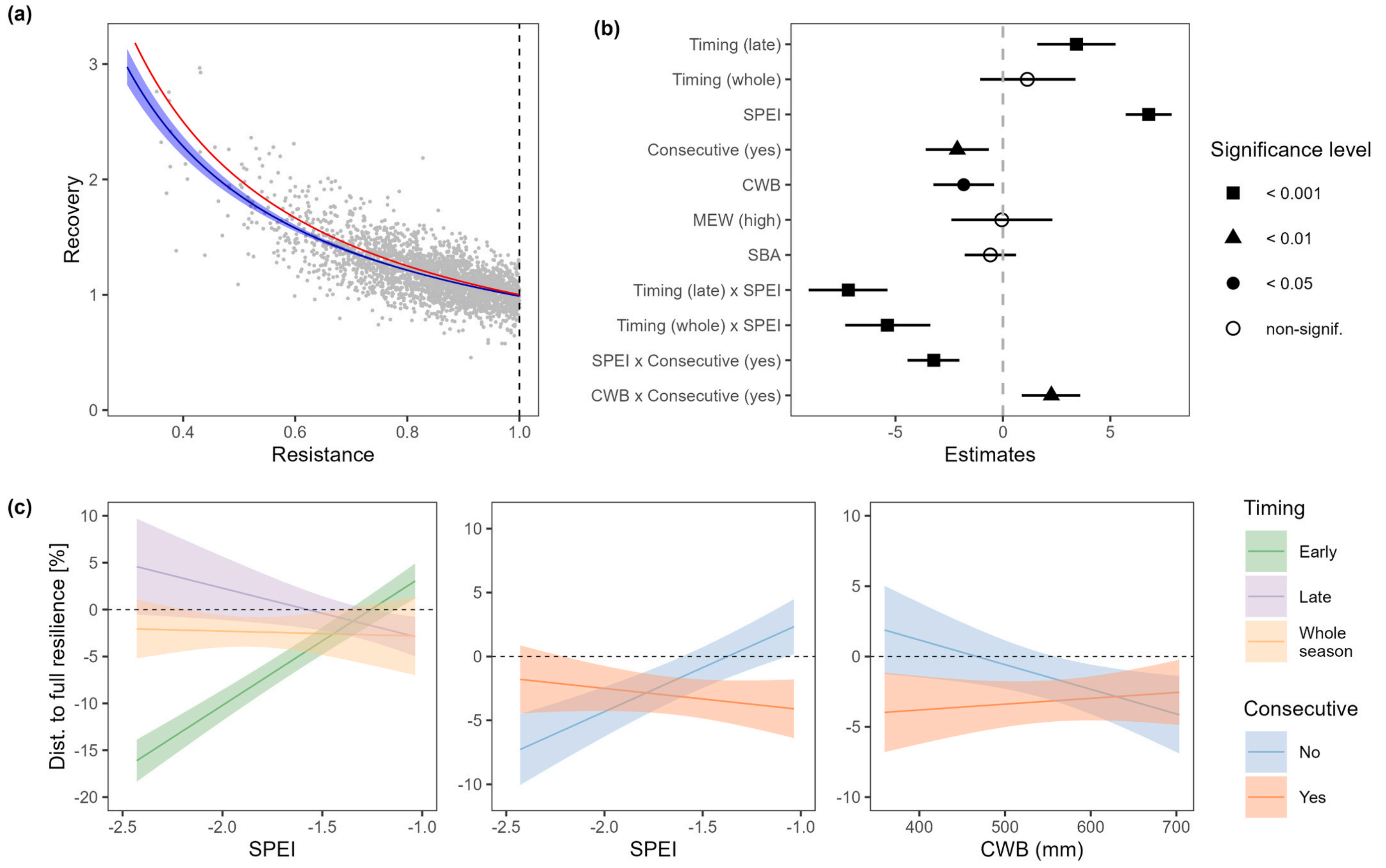

Fig. 6. Results of the integrated “full resilience” approach proposed by Schwarz et al. (2020). (a) Comparison of the fitted curve (in blue, with 95 % confidence interval) and the theoretical full resilience curve (in red) that corresponds to a resilience value of 1. (b) Coefficient estimates of the linear mixed model on the distance to full resilience. Point shapes indicate significance levels, and horizontal lines represent the 95 % confidence intervals. (c) Estimated marginal means of the distance to full resilience for the interactions, from left to right, between drought intensity and timing, drought intensity with consecutiveness, and Climatic Water Balance (CWB) with consecutiveness, with 95 % confidence intervals. “Early” timing corresponds to the February-May period, “Late” to June-September, and “Whole season” to February-September.

precipitation and evapotranspiration), in the time scale considered (annual or seasonal), or in the type of growth data (basal area increment instead of ring width index; Schwarz et al., 2020) used to calculate the resilience indices. Moreover, annual indicators may mask seasonal differences (Schmied et al., 2023).

In our study, the observed positive effect of CWB on resistance was consistent with the slightly higher resistance to the most intense droughts observed for the sites with a higher maximal extractable soil water (MEW; Fig. 5b). The higher resistance of Douglas fir on wetter sites and sites with higher MEW may be related to the trees being exposted to a lower level of water stress. As pointed out by Jarecke et al. (2024), it seems important to further investigate the effect of soil water storage on drought sensitivity of Douglas fir. We estimated MEW using simple soil descriptors (stoniness and soil depth) as proxies of soil water availability. A promising avenue for future research could be to better characterize the water stress experienced by trees by quantifying the soil water reserve based on soil and stand characteristics (e.g., texture, root depth, leaf area index). Sergent et al. (2012) used the Biljou © daily water balance model (Granier et al., 1999) for this purpose. However, estimating soil water reserves on stony soils remains quite challenging.

Drought recovery tended to be higher on sites with lower CWB and lower MEW, especially for the more intense droughts ($\text{SPEI} < -1.5$). As for resilience, it was higher (and above 100 %) for the sites with low CWB when the droughts were not consecutive (Fig. 5). This higher recovery could be explained by the fact that trees with lower resistance also have higher recovery potential. Sergent et al. (2012) and Thurm et al. (2016) also showed higher recovery for Douglas fir in Europe on sites with higher water constraints. Pardos et al. (2021), who studied other species along a wide ecological gradient across Europe, showed the same effect for resilience. A possible explanation is that the trees on wetter sites are less acclimated to droughts, because they have allocated fewer resources to root growth and non-structural carbon storage (Sergent et al., 2012). Favorable climate conditions in the past can also stimulate growth, leading trees to develop beyond what they can sustain when conditions become more challenging. This phenomenon, known as “structural overshoot”, increases ecosystem vulnerability to climate stress (Zhang et al., 2021).

Our third hypothesis (H3) was not verified, as we did not detect any significant effect of stand basal area on any of the indicators studied (Fig. 3; Fig. 6b). This is consistent with the results of Charlet de Sauvage et al. (2023), who found no impact of competition on the resilience of Douglas fir. As summarized in the meta-analysis of Castagneri et al. (2022), the effect of competition on drought response is not systematic and can be diverse. Some studies have shown an overall positive impact of reduced stand density and competition on the drought response of Douglas fir (Carnwath and Nelson, 2017; Dagley et al., 2023). However, in other studies on coniferous species, this positive effect was limited to recovery and/or resilience, but didn’t affect resistance (Serra-Maluquer et al., 2018; Sohn et al., 2016). This positive effect can be explained by a greater availability of resources due to a higher access to light, nutrients, and especially water (Aussenac and Granier, 1988; Rais et al., 2014). The absence of effects in our study could indicate that the density gradient sampled (30–53 m^2/ha) is not limiting in our study area. Other possible explanations are that these densities were measured at the time of sampling and therefore may not accurately represent the actual density experienced by the trees at the time of the drought, or that the sampled trees, being dominant or co-dominant, might be less affected by stand density.

The overall weaker impact of site and stand characteristics (CWB, MEW, stand density) compared to drought characteristics (timing, intensity, consecutive occurrence) must be put into perspective with the use of standardized growth data instead of raw tree ring widths to calculate the resilience indices. Indeed, the detrending procedure aims to maximize the climatic response of the trees, which in turn may reduce some site and stand effects. For example, Rais et al. (2014) showed a less important impact of thinning on resistance and resilience when calculated from detrended growth data.

4.3. Is Douglas fir radial growth resilient to droughts?

Our study showed that Douglas fir was always susceptible to being affected by drought as the predicted resistance was less than 100 % regardless of the consecutive occurrence, timing, or intensity of the drought (Fig. 4; Fig. 5). The trees generally manage to recover some growth, as the predicted recovery is always greater than 100 %. However, this level of growth does not systematically reach the reference growth level, as the predicted resilience is not always above 100 %. This result is confirmed by the full resilience analysis (Fig. 6), which shows that on average when the trees are affected by drought, the level of recovery is not sufficient to reach full resilience. In our study, Douglas fir has the best chances of reaching full resilience when droughts occur later in the season, are not consecutive, are not very intense and when trees are located on more water-limited sites.

This pattern (lower resistance, higher recovery) can be partly explained by the isohydric behavior of Douglas fir (Thurm et al., 2016), which is characterized by a strict stomatal control (McDowell et al., 2008). Stomatal closure under unfavorable conditions limits photosynthetic activity, leading to low carbon availability and allocation for cell division (Eilmann et al., 2011). Growth is therefore lower during droughts, but trees are able to better recover when the conditions become favorable again. The trade-off between resistance and recovery is a generally observed trend (Gazol et al., 2017; Hoffmann et al., 2018), which was highlighted in our study by the full resilience analysis (Fig. 6a). The limit of the isohydric strategy is that repeated or prolonged droughts can lead to carbon starvation and other effects such as reduced resistance to biotic agents (McDowell et al., 2008). The recent reports of significant biotic attacks on Douglas fir in Wallonia (André et al., 2023) may be a symptom of the increased vulnerability of the species.

4.4. Implications for forest management

Although Douglas fir is often cited as a promising alternative to Norway spruce due to its higher drought resistance (e.g., Eilmann and Rigling, 2012; Lévesque et al., 2014), our study has shown that it is nevertheless sensitive to droughts in Wallonia, a region so far identified as providing optimal climatic conditions for Douglas fir in Europe (Eckhart et al., 2019; Nicolescu, 2019). Moreover, this sensitivity is likely to increase as droughts become more frequent and more intense (IPCC, 2021). Our results confirmed that these two drought characteristics had a negative effect overall on the radial growth response of Douglas fir to droughts. In addition, the increase in the synchrony of the tree ring chronologies from the early 2000’s (Fig. 2a) suggests a stronger dependence on climate, which could be related to the increase in drought events (del Río et al., 2021).

Given the observed sensitivity of Douglas fir to drought, it seems advisable to minimize the risk of generalized forest decline by increasing diversity (e.g., in terms of species, origin, age) at both stand and landscape scales rather than relying solely on Douglas fir in monoculture stands (Messier et al., 2022). Mixing species can have various effects depending on the species and the context (Grossiord, 2020). For Douglas fir, Charlet de Sauvage et al. (2023) and Thurm et al. (2016) showed a positive effect of mixed-species under dry conditions while Vitali et al. (2018b) showed the opposite. Combining species with different drought-related functional traits could still ensure a better stability and improve adaptive potential of forest ecosystems (Schnabel et al., 2021). For example, Douglas fir in our study area could be mixed with a species which does not present the same higher sensitivity to early droughts.

Reducing competition by reducing stand density is another frequently suggested measure to mitigate the effects of drought (Bottero et al., 2017; Sohn et al., 2016). However, the absence of effect of stand basal area on Douglas fir response to drought questions the efficiency of this stand management option where average climatic conditions are at the species optimum, as in Wallonia. Regarding climate and soil, our study showed that on the sites with higher CWB and MEW, resistance to droughts was slightly higher. These situations should therefore be favored to minimize drought impact, yet this should be balanced with the slightly higher resilience observed on sites with lower CWB.

5. Conclusion

Overall, we have shown that drought characteristics have a stronger influence on drought response than site and stand characteristics. This highlights the importance of taking timing, intensity, and consecutive occurence into account when studying drought response. On average, Douglas fir was affected by drought regardless of drought, site, and stand characteristics. Trees didn’t systematically fully recover but had the best chances of doing so when droughts occurred in the second half of the growing season, were not very intense, were not consecutive, and when trees were located on more water-limited sites (within the range of conditions in our study area). Stand density had no significant impact on any of the indicators studied (resistance, recovery, resilience, and distance to full resilience).

Douglas fir has generally been considered a promising alternative for drought-sensitive species, but in the context of increasing drought intensity and frequency, our results raise concerns about the future of the species. However, it remains difficult to assess the extent to which the response of Douglas fir differs from that of other species. Further studies comparing the drought response of Douglas fir to the response of other species in the same context would therefore be an interesting complement to this study.

Another perspective could be to perform microdensity or seasonal wood measurements in order to get a complementary insight into the effects of drought on carbon allocation (Schwarz et al., 2020). Microdensity can also be linked to the hydraulic properties of Douglas fir wood (Dalla-Salda et al., 2011), allowing for a better understanding and prediction of its response to drought (Martinez-Meier et al., 2008; Ruiz Diaz Britez et al., 2014).

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CRediT authorship contribution statement

Camille Guisset: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Morgane Dendoncker:** Methodology, Writing – review & editing. **Quentin Ponette:** Conceptualization, Writing – review & editing, Supervision. **Caroline Vincke:** Conceptualization, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122177.

References

Akaike, H., 1981. Likelihood of a model and information criteria. J. Econ. 16, 3–14. https://doi.org/10.1016/0304-4076(81)90071-3.

Aldea, J., Ruiz-Peinado, R., del Río, M., Pretzsch, H., Heym, M., Brazaitis, G., Jansons, A., Metslaid, M., Barbeito, I., Bielak, K., Hylen, G., Holm, S.-O., Nothdurft, A., Sitko, R., Löf, M., 2022. Timing and duration of drought modulate tree growth response in pure and mixed stands of Scots pine and Norway spruce. J. Ecol. 110, 2673–2683. https://doi.org/10.1111/1365-2745.13978.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, Adaptation of Forests and Forest Management to Changing Climate. Selected papers from the conference on “Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health: A Review of Science, Policies and Practices”, Umeå, Sweden, August 25-28, 2008. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., et al., 1998. Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56. Rome Food Agric. Organ. U. N. 300, D05109.

Anderegg, W.R.L., Wu, C., Acil, N., Carvalhais, N., Pugh, T.A.M., Sadler, J.P., Seidl, R., 2022. A climate risk analysis of Earth’s forests in the 21st century. Science 377, 1099–1103. https://doi.org/10.1126/science.abp9723.

André, A., Bay, E., Bologna, A., Fesler, M., Goosse, J.-L., Gruslin, P., Lesenfants, C., Leroy, Q., Noiret, O., Pietequin, D., Ramelot, F., Vaïanopoulos, C., 2023. La lettre d’info de l’OWSF n° 10. Données 2022. Observatoire Wallon de la Santé des Forêts, Gembloux, Belgium.

Aubinet, M., Vincke, C., Heinesch, B., Hurdebise, Q., Manise, T., 2016. Vingt ans de mesures des échanges de CO2 et de vapeur d’eau à l’Observatoire Terrestre de Vielsalm. êt Nat. 139, 17–28.

Aussenac, G., Granier, A., 1988. Effects of thinning on water stress and growth in Douglas-fir. Can. J. . Res. 18, 100–105. https://doi.org/10.1139/x88-015.

Bartoń, K., 2023. MuMIn: Multi-Model Inference. R package version 1.47.5. ⟨https://cran.r-project.org/web/packages/MuMIn⟩.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bohner, T., Diez, J., 2021. Tree resistance and recovery from drought mediated by multiple abiotic and biotic processes across a large geographic gradient. Sci. Total Environ. 789, 147744 https://doi.org/10.1016/j.scitotenv.2021.147744.

Bose, A., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarero, J.J., Haeni, M., Hereş, A., Hevia, A., Lévesque, M., Linares, J.C., Martinez-vilalta, J., Matías, L., Menzel, A., Sánchez-salguero, R., Saurer, M., Vennetier, M., Ziche, D., Rigling, A., 2020. Growth and resilience responses of Scots pine to extreme droughts across Europe depend on predrought growth conditions. Glob. Change Biol. 26, 4521. https://doi.org/10.1111/gcb.15153.

Bottero, A., D’Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614. https://doi.org/10.1111/1365-2664.12847.

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63, 625–644. https://doi.org/10.1051/forest:2006042.

Brus, R., Pötzelsberger, E., Lapin, K., Brundu, G., Orazio, C., Straigyte, L., Hasenauer, H., 2019. Extent, distribution and origin of non-native forest tree species in Europe. Scand. J. For. Res. 34, 533–544. https://doi.org/10.1080/02827581.2019.1676464.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.

Buras, A., Rammig, A., Zang, C.S., 2020. Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. Biogeosciences 17, 1655–1672. https://doi.org/10.5194/bg-17-1655-2020.

Burnham, K.P., Anderson, D.R. (Eds.), 2004. Model Selection and Multimodel Inference: a practical information-theoretic approach, 2nd ed. Springer, New York, NY. https://doi.org/10.1007/b97636.

Camarero, J.J., Fernández-Pérez, L., Kirdyanov, A.V., Shestakova, T.A., Knorre, A.A., Kukarskih, V.V., Voltas, J., 2017. Minimum wood density of conifers portrays changes in early season precipitation at dry and cold Eurasian regions. Trees 31, 1423–1437. https://doi.org/10.1007/s00468-017-1559-x.

Carnwath, G., Nelson, C., 2017. Effects of biotic and abiotic factors on resistance versus resilience of Douglas fir to drought. PLoS One 12. https://doi.org/10.1371/journal.pone.0185604.

Carnwath, G.C., Peterson, D.W., Nelson, C.R., 2012. Effect of crown class and habitat type on climate–growth relationships of ponderosa pine and Douglas-fir. For. Ecol. Manag. 285, 44–52. https://doi.org/10.1016/j.foreco.2012.07.037.

Castagneri, D., Vacchiano, G., Hacket-Pain, A., DeRose, R.J., Klein, T., Bottero, A., 2022. Meta-analysis reveals different competition effects on tree growth resistance and resilience to drought. Ecosystems 25, 30–43. https://doi.org/10.1007/s10021-021-00638-4.

Charlet de Sauvage, J., Bugmann, H., Bigler, C., Lévesque, M., 2023. Species diversity and competition have minor effects on the growth response of silver fir, European larch and Douglas fir to drought. Agric. For. Meteorol. 341, 109664 https://doi.org/10.1016/j.agrformet.2023.109664.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688.

Cook, E.R., Kairiukstis, L.A., 1991. Methods of Dendrochronology: Applications in the Environmental Sciences. Springer Science & Business Media.

Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bull. 41, 45–53.

R. Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

D’Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., Houle, D., Arseneault, D., Beier, C.M., Bishop, D.A., Druckenbrod, D., Fraver, S., Girard, F., Halman, J., Hansen, C., Hart, J.L., Hartmann, H., Kaye, M., Leblanc, D., Manzoni, S., Ouimet, R., Rayback, S., Rollinson, C.R., Phillips, R.P., 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Glob. Change Biol. 24, 2339–2351. https://doi.org/10.1111/gcb.14096.

Dagley, C.M., Berrill, J.-P., Fraver, S., 2023. Forest restoration mitigates drought vulnerability of coast Douglas-fir in a Mediterranean climate. Can. J. For. Res. 53, 210–216. https://doi.org/10.1139/cjfr-2022-0119.

Dalla-Salda, G., Martinez-Meier, A., Cochard, H., Rozenberg, P., 2011. Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (Pseudotsuga menziesii (Mirb.)). Ann. For. Sci. 68, 747–757. https://doi.org/10.1007/s13595-011-0091-1.

del Río, M., Vergarechea, M., Hilmers, T., Alday, J.G., Avdagić, A., Binderh, F., Bosela, M., Dobor, L., Forrester, D.I., Halilović, V., Ibrahimspahić, A., Klopcic, M., Lévesque, M., Nagel, T.A., Sitkova, Z., Schütze, G., Stajić, B., Stojanović, D., Uhl, E., Zlatanov, T., Tognetti, R., Pretzsch, H., 2021. Effects of elevation-dependent climate warming on intra- and inter-specific growth synchrony in mixed mountain forests. For. Ecol. Manag. 479, 118587 https://doi.org/10.1016/j.foreco.2020.118587.

Devine, W.D., Harrington, C.A., 2009. Relationships among foliar phenology, radial growth rate, and xylem density in a young Douglas-fir plantation. Wood Fiber Sci. 41, 300–312.

Eckhart, T., Pötzelsberger, E., Koeck, R., Thom, D., Lair, G.J., van Loo, M., Hasenauer, H., 2019. Forest stand productivity derived from site conditions: an assessment of old Douglas-fir stands (Pseudotsuga menziesii (Mirb.) Franco var. menziesii) in Central Europe. Ann. For. Sci. 76, 19. https://doi.org/10.1007/s13595-019-0805-3.

Eichhorn, J., Roskams, P., Potočić, N., Timmermann, V., Ferretti, M., Mues, V., Szepesi, A., Durrant, D., Seletković, I., Schröck, H.- V, Nevalainen, S., Bussotti, F., Garcia, P., Wulff, S., 2020. Part IV: Visual Assessment of Crown Condition and Damaging Agents. Version 2020-3, in: UNECE ICP Forests Programme Co-Ordinating Centre (Ed.). Manual on Methods and Criteria for Harmonised Sampling, Assessment, Monitoring and Analysis of the Effect of Air Pollution on Forests. Thünen Institute of Forest Ecosystems, Eberswalde, Germany, pp. 49 [http://www.icp-forests.org/manual.htm].

Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species’ drought tolerance. Tree Physiol. 32, 178–187. https://doi.org/10.1093/treephys/tps004.

Eilmann, B., Zweifel, R., Buchmann, N., Graf Pannatier, E., Rigling, A., 2011. Drought alters timing, quantity, and quality of wood formation in Scots pine. J. Exp. Bot. 62, 2763–2771. https://doi.org/10.1093/jxb/erq443.

Felton, A., Belyazid, S., Eggers, J., Nordström, E.-M., Öhman, K., 2023. Climate change adaptation and mitigation strategies for production forests: Trade-offs, synergies, and uncertainties in biodiversity and ecosystem services delivery in Northern Europe. Ambio. https://doi.org/10.1007/s13280-023-01909-1.

Ford, K.R., Harrington, C.A., St. Clair, J.B., 2017. Photoperiod cues and patterns of genetic variation limit phenological responses to climate change in warm parts of species' range: modeling diameter-growth cessation in coast Douglas-fir. Glob. Change Biol. 23, 3348–3362. https://doi.org/10.1111/gcb.13690.

Forzieri, G., Dakos, V., McDowell, N.G., Ramdane, A., Cescatti, A., 2022. Emerging signals of declining forest resilience under climate change. Nature 608, 534–539. https://doi.org/10.1038/s41586-022-04959-9.

Fox, J., Monette, G., 1992. Generalized collinearity diagnostics. J. Am. Stat. Assoc. 87, 178–183. https://doi.org/10.1080/01621459.1992.10475190.

Gao, S., Liu, R., Zhou, T., Fang, W., Yi, C., Lu, R., Zhao, X., Luo, H., 2018. Dynamic responses of tree-ring growth to multiple dimensions of drought. Glob. Change Biol. 24, 5380–5390. https://doi.org/10.1111/gcb.14367.

Gazol, A., Camarero, J.J., Anderegg, W.R.L., Vicente-Serrano, S.M., 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests. Glob. Ecol. Biogeogr. 26, 166–176. https://doi.org/10.1111/geb.12526.

Gazol, A., Valeriano, C., Cantero, A., Vergarechea, M., Camarero, J.J., 2022. Douglas fir growth is constrained by drought: delineating the climatic limits of timber species under seasonally dry conditions. Forests 13. https://doi.org/10.3390/f13111796.

Granier, A., Bréda, N., Biron, P., Villette, S., 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol. Model. 116, 269–283. https://doi.org/10.1016/S0304-3800(98)00205-1.

Grossiord, C., 2020. Having the right neighbors: how tree species diversity modulates drought impacts on forests. N. Phytol. 228, 42–49. https://doi.org/10.1111/nph.15667.

Guisset, C., Ponette, Q., Vincke, C., 2023. Assessing the growth response to climate of Douglas fir under European temperate oceanic conditions. PREPRINT (Version 1) available at Research Square. 〈https://doi.org/10.21203/rs.3.rs-3671830/v1〉.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J., McDowell, N.G., Powers, J.S., Pugh, T.A.M., Ruthrof, K.X., Allen, C.D., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annu Rev. Plant Biol. 73, 673–702. https://doi.org/10.1146/annurev-arplant-102820-012804.

Hoffmann, N., Schall, P., Ammer, C., Leder, B., Vor, T., 2018. Drought sensitivity and stem growth variation of nine alien and native tree species on a productive forest site in Germany, 256–257 Agric. For. Meteorol. 431–444. https://doi.org/10.1016/j.agrformet.2018.03.008.

Holling, C.S., 1996. Engineering resilience versus ecological resilience. In: Engineering Within Ecological Constraints, 31. National Academies Press, Washington, D.C, p. 32.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.

IPCC, 2021. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press.

IRM, 2015. Evénements météorologiques remarquables depuis 1901. Institut Royal Météorologique [WWW Document]. URL https://www.meteo.be/fr/climat/climat-de-la-belgique/evenements-remarquables-depuis-1901 (accessed 7.27.22).

IRM, 2022. Bilans climatologiques. Institut Royal Météorologique [WWW Document]. URL 〈https://www.meteo.be/fr/climat/climat-de-la-belgique/bilans-climatologiques/2022/juillet〉.

Jarecke, K.M., Bladon, K.D., Meinzer, F.C., Wondzell, S.M., 2024. Impact of rainfall and vapor pressure deficit on latewood growth and water stress in Douglas-fir in a Mediterranean climate. For. Ecol. Manag. 551, 121529 https://doi.org/10.1016/j.foreco.2023.121529.

Jetschke, G., van der Maaten, E., van der Maaten-Theunissen, M., 2019. Towards the extremes: a critical analysis of pointer year detection methods. Dendrochronologia 53, 55–62. https://doi.org/10.1016/j.dendro.2018.11.004.

Jiang, Y., Marchand, W., Rydval, M., Matula, R., Janda, P., Begović, K., Thom, D., Fruleux, A., Buechling, A., Pavlin, J., Nogueira, J., Dušátko, M., Málek, J., Knír, T., Veber, A., Svoboda, M., 2024. Drought resistance of major tree species in the Czech Republic. Agric. For. Meteorol. 348, 109933 https://doi.org/10.1016/j.agrformet.2024.109933.

Jiao, T., Williams, C.A., De Kauwe, M.G., Schwalm, C.R., Medlyn, B.E., 2021. Patterns of post-drought recovery are strongly influenced by drought duration, frequency, post-drought wetness, and bioclimatic setting. Glob. Change Biol. 27, 4630–4643. https://doi.org/10.1111/gcb.15788.

Keenan, R.J., 2015. Climate change impacts and adaptation in forest management: a review. Ann. For. Sci. 72, 145–167. https://doi.org/10.1007/s13595-014-0446-5.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Lenth, R.V., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.4-1. https://CRAN.R-project.org/package=emmeans.

Lévesque, M., Rigling, A., Bugmann, H., Weber, P., Brang, P., 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agric. For. Meteorol. 197, 1–12. https://doi.org/10.1016/j.agrformet.2014.06.001.

Lévesque, M., Walthert, L., Weber, P., 2016. Soil nutrients influence growth response of temperate tree species to drought. J. Ecol. 104, 377–387. https://doi.org/10.1111/1365-2745.12519.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.

Martinez-Meier, A., Sanchez, L., Pastorino, M., Gallo, L., Rozenberg, P., 2008. What is hot in tree rings? The wood density of surviving Douglas-firs to the 2003 drought and heat wave. For. Ecol. Manag. 256, 837–843. https://doi.org/10.1016/j.foreco.2008.05.041.

Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. Oecologia 168, 877–888. https://doi.org/10.1007/s00442-011-2132-8.

Maxwell, R.S., Larsson, L.-A., 2021. Measuring tree-ring widths using the CooRecorder software application. Dendrochronologia 67, 125841. https://doi.org/10.1016/j.dendro.2021.125841.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? N. Phytol. 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.

Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. For. Ecol. Manag. 339, 22–33. https://doi.org/10.1016/j.foreco.2014.11.032.

Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., Bruelheide, H., Caldwell, B., Cavender-Bares, J., Dhiedt, E., Eisenhauer, N., Ganade, G., Gravel, D., Guillemot, J., Hall, J.S., Hector, A., Hérault, B., Jactel, H., Koricheva, J., Kreft, H., Mereu, S., Muys, B., Nock, C.A., Paquette, A., Parker, J.D., Perring, M.P., Ponette, Q., Potvin, C., Reich, P.B., Scherer-Lorenzen, M., Schnabel, F., Verheyen, K., Weih, M., Wollni, M., Zemp, D.C., 2022. For the sake of resilience and multifunctionality, let's diversify planted forests! Conserv. Lett. 15, e12829 https://doi.org/10.1111/conl.12829.

Miller, T.W., Stangler, D.F., Larysch, E., Honer, H., Seifert, T., Puhlmann, H., von Arx, G., Fonti, P., Fonti, M.V., Rathgeber, C.B.K., Kahle, H.-P., 2022. Longer and faster: Intra-annual growth dynamics of Douglas fir outperform Norway spruce and silver fir over wide climatic gradients. Agric. For. Meteorol. 321 https://doi.org/10.1016/j.agrformet.2022.108970.

Miller, T.W., Stangler, D.F., Larysch, E., Honer, H., Puhlmann, H., Schindler, D., Jung, C., Seifert, T., Rigling, A., Kahle, H.-P., 2023. Later growth onsets or reduced growth rates: what characterises legacy effects at the tree-ring level in conifers after the severe 2018 drought? Sci. Total Environ. 854, 158703 https://doi.org/10.1016/j.scitotenv.2022.158703.

Nicolescu, V.-N., 2019. Natural range, site requirements and shade tolerance, in: Spiecker, H., Lindner, M., Schuler, J. (Eds.), Douglas-Fir – an Option for Europe, What Science Can Tell Us. European Forest Institute, pp. 33–39.

Nicolescu, V.-N., Mason, W.L., Bastien, J.-C., Vor, T., Petkova, K., Podrázský, V., Đodan, M., Perić, S., La Porta, N., Brus, R., Andrašev, S., Slávik, M., Modranský, J., Pástor, M., Rédei, K., Cvjetkovic, B., Sivacioğlu, A., Lavnyy, V., Buzatu-Goanţă, C., Mihăilescu, G., 2023. Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in Europe: an overview of management practices. J. Res. https://doi.org/10.1007/s11676-023-01607-4.

Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defossez, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E., Calama, R., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: analysis along a climate gradient across Europe. For. Ecol. Manag. 481, 118687 https://doi.org/10.1016/j.foreco.2020.118687.

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., Linkevičius, E., Mahnken, M., Milanovic, S., Nabuurs, G.-J., Nagel, T.A., Nikinmaa, L., Panyatov, M., Bercak, R., Seidl, R., Ostrogović Sever, M.Z., Socha, J., Thom, D., Vuletic, D., Zudin, S., Schelhaas, M.-J., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Glob. Change Biol. 29, 1359–1376. https://doi.org/10.1111/gcb.16531.

Perin, J., Hebert, J., Lejeune, P., Claessens, H., 2016. Nouvelles normes sylvicoles pour les peuplements purs équiennes d'épicéa et de douglas.

Rais, A., van de Kuilen, J.-W.G., Pretzsch, H., 2014. Growth reaction patterns of tree height, diameter, and volume of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) under acute drought stress in Southern Germany. Eur. J. For. Res 133, 1043–1056. https://doi.org/10.1007/s10342-014-0821-7.

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J., Vanderwel, M.C., Verbeeck, H., Villela, D.M., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J. Ecol. 103, 5–15. https://doi.org/10.1111/1365-2745.12337.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. N. Phytol. 170, 301–310. https://doi.org/10.1111/j.1469-8137.2006.01660.x.

Ruiz Diaz Britez, M., Sergent, A.-S., Martinez Meier, A., Bréda, N., Rozenberg, P., 2014. Wood density proxies of adaptive traits linked with resistance to drought in Douglas fir (Pseudotsuga menziesii (Mirb.) Franco). Trees 28, 1289–1304. https://doi.org/10.1007/s00468-014-1003-4.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1, 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x.

Schmied, G., Hilmers, T., Mellert, K.-H., Uhl, E., Buness, V., Ambs, D., Steckel, M., Biber, P., Šeho, M., Hoffmann, Y.-D., Pretzsch, H., 2023. Nutrient regime modulates drought response patterns of three temperate tree species. Sci. Total Environ. 868, 161601 https://doi.org/10.1016/j.scitotenv.2023.161601.

Schnabel, F., Liu, X., Kunz, M., Barry, K.E., Bongers, F.J., Bruelheide, H., Fichtner, A., Härdtle, W., Li, S., Pfaff, C.-T., Schmid, B., Schwarz, J.A., Tang, Z., Yang, B., Bauhus, J., von Oheimb, G., Ma, K., Wirth, C., 2021. Species richness stabilizes productivity via asynchrony and drought-tolerance diversity in a large-scale tree biodiversity experiment. Sci. Adv. 7, eabk1643 https://doi.org/10.1126/sciadv.abk1643.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl. Ecol. 45, 86–103. https://doi.org/10.1016/j.baae.2020.04.003.

Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought—a critique of commonly used resilience indices and recommendations for future studies. Curr. For. Rep. 6, 185–200. https://doi.org/10.1007/s40725-020-00119-2.

Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., Bräker, O.U., 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 9–38.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Change 7, 395–402. https://doi.org/10.1038/nclimate3303.

Senf, C., Seidl, R., 2021. Persistent impacts of the 2018 drought on forest disturbance regimes in Europe. Biogeosciences 18, 5223–5230. https://doi.org/10.5194/bg-18-5223-2021.

Sergent, A.-S., Rozenberg, P., Bréda, N., 2012. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Ann. For. Sci. 71, 697–708. https://doi.org/10.1007/s13595-012-0220-5.

Serra-Maluquer, X., Mencuccini, M., Martínez-Vilalta, J., 2018. Changes in tree resistance, recovery and resilience across three successive extreme droughts in the northeast Iberian Peninsula. Oecologia 187, 343–354. https://doi.org/10.1007/s00442-018-4118-2.

Slette, I.J., Post, A.K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M.D., Knapp, A.K., 2019. How ecologists define drought, and why we should do better. Glob. Chang Biol. 25, 3193–3200. https://doi.org/10.1111/gcb.14747.

Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: a meta-analysis. For. Ecol. Manag. 380, 261–273. https://doi.org/10.1016/j.foreco.2016.07.046.

Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P., Dosio, A., 2018. Will drought events become more frequent and severe in Europe? Int. J. Climatol. 38, 1718–1736. https://doi.org/10.1002/joc.5291.

Stangler, D.F., Miller, T.W., Honer, H., Larysch, E., Puhlmann, H., Seifert, T., Kahle, H.-P., 2022. Multivariate drought stress response of Norway spruce, silver fir and Douglas fir along elevational gradients in Southwestern Germany. Front. Ecol. Evol. 10 https://doi.org/10.3389/fevo.2022.907492.

Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. For. Ecol. Manag. 461, 117908 https://doi.org/10.1016/j.foreco.2020.117908.

Svoboda, M., Hayes, M., Wood, D., 2012. Standardized Precipitation Index: User Guide. World Meteorological Organization Geneva, Switzerland.

Szegleti, Z., Czóbel, S., Zimmermann, Z., Horváth, F., 2020. How do central european forest stands respond to climate change - review. COLUMELLA: J. Agric. Environ. Sci. 7, 35–46.

Thom, D., Buras, A., Heym, M., Klemmt, H.-J., Wauer, A., 2023. Varying growth response of Central European tree species to the extraordinary drought period of 2018 – 2020. Agric. For. Meteorol. 338, 109506 https://doi.org/10.1016/j.agrformet.2023.109506.

Thomas, F.M., Rzepecki, A., Werner, W., 2022. Non-native Douglas fir (Pseudotsuga menziesii) in Central Europe: Ecology, performance and nature conservation. For. Ecol. Manag. 506, 119956 https://doi.org/10.1016/j.foreco.2021.119956.

Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. For. Ecol. Manag. 376, 205–220. https://doi.org/10.1016/j.foreco.2016.06.020.

Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. Science 349, 814–818. https://doi.org/10.1126/science.aac6759.

Vacek, Z., Cukor, J., Vacek, S., Linda, R., Prokůpková, A., Podrázský, V., Gallo, J., Vacek, O., Šimůnek, V., Drábek, O., Hájek, V., Spasić, M., Brichta, J., 2021. Production potential, biodiversity and soil properties of forest reclamations: Opportunities or risk of introduced coniferous tree species under climate change? Eur. J. For. Res 140, 1243–1266. https://doi.org/10.1007/s10342-021-01392-x.

van der Maaten-Theunissen, M., van der Maaten, E., Bouriaud, O., 2015. pointRes: An R package to analyze pointer years and components of resilience. Dendrochronologia 35, 34–38. https://doi.org/10.1016/j.dendro.2015.05.006.

Vejpustková, M., Čihák, T., 2019. Climate response of douglas fir reveals recently increased sensitivity to drought stress in Central Europe. Forests 10, 97. https://doi.org/10.3390/f10020097.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1.

Vitali, V., Büntgen, U., Bauhus, J., 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. Glob. Change Biol. 23, 5108–5119. https://doi.org/10.1111/gcb.13774.

Vitali, V., Büntgen, U., Bauhus, J., 2018a. Seasonality matters—the effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe. Dendrochronologia 48, 1–9. https://doi.org/10.1016/j.dendro.2018.01.001.

Vitali, V., Forrester, D.I., Bauhus, J., 2018b. Know your neighbours: drought response of norway spruce, silver fir and douglas fir in mixed forests depends on species identity and diversity of tree neighbourhoods. Ecosystems 21, 1215–1229. https://doi.org/10.1007/s10021-017-0214-0.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteor. 23, 201–213.

Wrzesiński, P., Klisz, M., Niemczyk, M., 2024. Looking for a drought-tolerant tree species among native and introduced mountain conifers. Trees. https://doi.org/10.1007/s00468-024-02491-z.

Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436. https://doi.org/10.1111/ecog.01335.

Zhang, Y., Keenan, T.F., Zhou, S., 2021. Exacerbated drought impacts on global ecosystems due to structural overshoot. Nat. Ecol. Evol. 5, 1490–1498. https://doi.org/10.1038/s41559-021-01551-8.