






RESEARCH ARTICLE

Timing and duration of drought modulate tree growth response in pure and mixed stands of Scots pine and Norway spruce

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Abstract

1. Climate change is increasing the severity and frequency of droughts around the globe, leading to tree mortality that reduces production and provision of other ecosystem services. Recent studies show that growth of mixed stands may be more resilient to drought than pure stands. The two most economically important and widely distributed tree species in Europe are Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.), but little is known about their susceptibility to drought when coexist.
2. This paper analyses the resilience (resistance, recovery rate and recovery time) at individual-tree level using a network of tree-ring collections from 22 sites along a climatic gradient from central Europe to Scandinavia. We aimed to identify differences in growth following drought between the two species and between mixed and pure stands, and how environmental variables (climate, topography and site location) and tree characteristics influence them.
3. We found that both the timing and duration of drought drive the different responses between species and compositions. Norway spruce showed higher vulnerability to summer drought, with both lower resistance and a longer recovery time than Scots pine. Mixtures provided higher drought resistance for both species compared to pure stands, but the benefit decreases with the duration

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of the drought. Especially climate sensitive and old trees in climatically marginal sites were more affected by drought stress.

4. *Synthesis*. Promoting Scots pine and mixed forests is a promising strategy for adapting European forests to climate change. However, if future droughts become longer, the advantage of mixed stands could disappear which would be especially negative for Norway spruce.

KEYWORDS

drought period, drought resilience, forest adaptation, mixing effect, tree-ring data

1 | INTRODUCTION

Drought kills trees across Europe, affecting carbon balance and other ecosystem functions (Anderegg et al., 2015; Senf et al., 2020). Climate change is increasing the frequency of droughts, their intensity and duration around the globe, and European forests have recently endured unprecedented drought events (Buras et al., 2020; Spinoni et al., 2018). Drought stress predisposes trees to forest fires and damage from pest and diseases, leading to an emerging vulnerability of European forests (Forzieri et al., 2021). Therefore, new management strategies to increase forest drought resilience are urgently needed (DeSoto et al., 2020).

Drought frequency, intensity, duration and timing all affect tree growth (Anderegg et al., 2020; Bose et al., 2021; D'Orangeville et al., 2018), but their interactions are poorly understood. Huang et al. (2018) found that droughts during the dry season (DS) normally last longer and have larger impacts compared to droughts during other seasons. Trees with greater pre-drought growth can be more affected by long and intense droughts (Bose et al., 2020). In addition, other intrinsic and environmental drivers could modulate the impact of drought on growth (D'Orangeville et al., 2018). Intrinsic attributes include tree size, population age structure, species richness, evenness and diversity of communities. Extrinsic drivers are characteristics of the trees' environment such as topography and soil (Nimmo et al., 2015). Recent studies show that the tree response to extreme climate events may vary based on individual characteristics such as tree size or competition pressure (Nepstad et al., 2007; Pretzsch et al., 2018), while others point to minor or species-specific importance (Serra-Maluquer et al., 2021). Therefore, more evidence is needed in this regard.

Recent studies reveal several advantages of mixed over pure stands, including enhanced drought resilience (Fichtner et al., 2020; Jactel et al., 2017). In mixed stands, trees use water and light more efficiently than in single-species stands (Fichtner et al., 2017; Grossiord, 2019). This may result in higher growth and yield (Jactel et al., 2018; Pretzsch & Schütze, 2021), more stable growth (Schnabel et al., 2021), greater ecosystem service provision (Felton et al., 2020) and reduced disturbance impact (Jactel et al., 2017). On average, mixed stands are more resilient to drought than monospecific stands (Jansen et al., 2021), but exceptions are common (del Río et al., 2021; Forrester et al., 2016). Tree growth response to drought

depends on the identity of neighbouring species and forest structure (Pardos et al., 2021). Therefore, which species combinations are more resilient to drought is an important question that needs more investigation.

Understanding the effects of perturbations on ecosystems requires the simultaneous measurement of multiple components of stability (Ingrisch & Bahn, 2018). Various indices used to characterize tree growth resilience to drought have been widely discussed in literature (van der Maaten-Theunissen et al., 2021). The most commonly used indices for this purpose have drawbacks and limitations which may lead to misleading results or misinterpretation of observed patterns (Schwarz et al., 2020). Therefore, the way in which growth-based resilience indices are calculated and how intrinsic and environmental predictors are considered are important factors for correctly evaluating tree growth response to drought.

Forests in most of Europe are dominated by two coniferous tree species: Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.). They are widely distributed (Figure SM1), have great ecological significance and are of major commercial importance for European forestry. Low summer water availability combined with high temperatures strongly reduces growth for both of these species, suggesting that they may be unable to cope with prolonged and frequent dry conditions in Europe (Lévesque et al., 2014; Zang et al., 2012). In fact, there is clear evidence that extreme growth reductions (GRs) due to drought in Europe increased after 1990 for both species (Trembl et al., 2021). Norway spruce is regarded as more vulnerable to drought than other coexisting species (Pretzsch et al., 2020; Vitasse et al., 2019; Zang et al., 2014), with significant wood damage and economic loss (Rosner et al., 2018). Accordingly, Trembl et al. (2021) showed that Norway spruce is more vulnerable to drought than Scots pine at low altitudes in Central Europe. Other studies have shown that both Scots pine and Norway spruce can benefit from mixtures with other species (Pardos et al., 2021; Pretzsch et al., 2020), but it is still not known how these two species will respond to drought when growing together.

In this study, we used tree-ring data from 22 sites covering a large part of the distribution ranges of Scots pine and Norway spruce in Europe. We analysed their tree-level growth responses to drought in mixed and pure stands to identify: (1) differences in species-specific growth responses, (2) differences in tree-growth response to drought between mixed and pure stands and (3) how

drought characteristics (intensity, duration and timing) and other environmental and intrinsic factors influence tree growth responses. Our ultimate goal is to better understand and identify the individual tree, site and environmental conditions which influence growth resilience to drought in Scots pine and Norway spruce.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

This study focuses on Scots pine and Norway spruce in temperate, hemiboreal and boreal Europe (Figure SM1). The study area spans 47°–64°N, and 10°–27°E, covering the natural overlap of these species' distributions. Within this area, we used data from 22 sites in 10 countries, representing different climate conditions (Table SM1). The experimental design was based on the 'triplet' concept (Pretzsch et al., 2015), which consists of three plots per site: one monospecific stand each of Scots pine and Norway spruce, plus a stand mixing the two species. The three plots were located no more than 1 km from each other, with similar soil and topographical conditions to minimize site and stand effects. Thus, the study uses a total of 66 plots with a mean size of 0.12 ha and stand ages varying from 45 to 115 years (average age: 60 years). The species' proportions by basal area in mixtures ranged from 32% to 67% with an average close to 50%, and in the pure plots, additional tree species were always below 10%.

In each plot, 20 dominant living trees and 10 trees representing the rest of the diameter distribution were sampled for increment cores in 2017. In the mixed plots, both tree species were sampled for a total of 60 trees. Annual radial growth increments were measured for every core with an accuracy of 0.01 mm and cross-dated using the COFECHA software (Grissino Mayer, 2001).

2.2 | Tree ring dataset, weather and drought identification

We calculated tree-ring width (TRW) chronologies using the mean of the two cores per tree. The raw ring-width measurements were converted to a standardized TRW index (TRWI) by removing low-frequency ring-width fluctuations related to increasing tree size and age or to stand dynamics such as harvest or self-thinning (Anderegg et al., 2015). Each measured ring width was divided by its expected value, which was estimated based on a 30-year cubic smoothing spline approach with a 50% frequency cut-off using the 'dplR' R package (Bunn et al., 2022). Individual TRWI series were preserved for each site preserving the climate signal and the complex environment-tree growth interactions (Wilmking et al., 2020). We calculated the coefficient of variation (CV) for the TRWI at tree level, considering all the recorded years, and included this as predictor in the models described below. This procedure allowed us to check whether the tree growth response to drought depends on

recent past growth conditions, particularly climate sensitivity (Bose et al., 2020; Pretzsch, 2021). In most cases, weather data came from meteorological stations close to each study site. When meteorological stations were not available, national meteorological services' 0.5° resolution gridded datasets were used. Monthly water balance (WBAL) and monthly standardized precipitation–evapotranspiration index (SPEI) values were calculated from the weather data (Vicente-Serrano et al., 2010).

We used a climate-based approach for drought identification to avoid overestimating the effect of the explanatory variables (Schwarz et al., 2020). The first step was to compute the monthly SPEI from the previous September to August of each year at each site. In addition, we estimated the water availability for the same time period via WBAL to identify the periods in which there was a deficiency of water (resulting from rainfall and evapotranspiration deficit). A drought event was identified for a target year when both of the following criteria were met for one or more months: (a) an SPEI value more than one standard deviation (SD) below the mean, indicating moderate to extreme drought (McKee et al., 1993; Vicente-Serrano et al., 2010), during the previous September to current August period, and (b) a negative WBAL for the same period. We finally selected those drought events in which TRWI was also lower than the mean tree growth value during the target year or the following one. The latter condition allowed us to check the site sensitivity of the tree growth–climate relationship (Bose et al., 2021; Huang et al., 2018) and to consider the lagged drought responses in relation to the species-specific growth dynamics (Schwarz et al., 2020). The identified and analysed drought events are shown in the supplementary material (Table SM2). We calculated the duration (number of months with a negative WBAL and SPEI more than one SD below the mean), intensity (mean SPEI value during the months of drought) and seasonal timing to characterize each drought episode. We divided all drought events into three seasonal groups (Huang et al., 2018): (a) years with drought only in the DS, (b) years with drought only in the wet season (WS) and (c) years with drought in both the dry and wet seasons (DS+WS). The DS was defined as months when the mean value of the historical monthly WBAL was negative (June–August), and vice versa for the WS (all other months).

2.3 | Resilience to drought events

Since there is evidence of non-independence of the resilience components (Hodgson et al., 2015; Ingrisich & Bahn, 2018; Schwarz et al., 2020), we decided to use three variables simultaneously to better understand the trees' ability to return to equilibrium after a drought: resistance, recovery rate and recovery time (Figure SM2). We use more suitable alternative resilience indices than those commonly used and defined by Lloret et al. (2011) to correct some of their limitations (Schwarz et al., 2020; Thurm et al., 2016). We used a baseline normalized tree growth rate, which allowed comparison of the growth response relative to the pre-drought state of the respective tree (Ingrisich & Bahn, 2018). The pre-drought baseline was

defined by the mean tree growth value from the detrended data series (TRWI).

According to the terminology used by Thurm et al. (2016), we defined the total GR as the cumulative growth decrease in the drought year plus all years during the recovery period, that is, the total growth loss due to drought (Figure SM2). From this value, we calculated the resistance component of resilience as the inverse of total GR ($1/GR$), a measure of the overall ability to avoid drought impact, which primarily quantifies aspects of perturbation (Ingrisch & Bahn, 2018). The recovery period or recovery time was defined as the time needed to reach pre-drought growth levels after the disturbance (Schwarz et al., 2020; Thurm et al., 2016; Figure SM2). Accordingly, recovery time quantifies the endogenous processes that return the disturbed system back to the initial equilibrium (Hodgson et al., 2015), that is, capacity of trees to regain the growth rate of non-stress conditions. The maximum length of the recovery period to be considered in defining the recovery time was 10 years. The recovery rate component was calculated as the magnitude of total GR divided by the length of the recovery period, expressed as the mean magnitude of GR recovered annually after the drought episode. This quantifies the ecosystem state change per unit time after the disturbance (Ingrisch & Bahn, 2018). The three growth response indices were computed for drought events at different sites from 1940 to 2017, with a minimum continuous period of 40 years within this window (Table SM2). Data are open and free available in Zenodo public digital repository (Aldea, 2022).

2.4 | Statistical analysis

We used generalized mixed effect models to evaluate the influence of intrinsic and extrinsic environmental factors on the three tree-level resilience components. These types of models account for the hierarchical structure of the data and correct for the degree of correlation between the residuals due to spatial and temporal dependence, avoiding misleading inferences. Multiple tree, stand, site and climate variables and their interactions were included as predictors in the models (Table SM3). Triplet, plot and tree (hierarchically nested) and year (as a crossed factor) were included in the random effects, considering spatial and temporal observation's structure. The optimal model was calculated by comparing different random and fixed structures and selecting the model with the lowest value of Akaike's information criterion (AIC) following Zuur et al. (2009). The 'resistance' response variable was log transformed before analysis to correct for heteroscedasticity, and 'recovery time' was modelled following a Poisson distribution with logarithm as link function. Finally, differences between levels of some predictor variables (species, composition and drought seasonality) were evaluated post-hoc in the final models using Sidak tests for multiple comparisons. We used the 'lme4' R package (Bates et al., 2015) for model fitting, 'AICcmodavg' (Mazerolle, 2017) for model selection and 'emmeans' (Lenth, 2020)

to estimate the differences in marginal means between predictor levels. All analyses were performed in the R statistical environment version 4.1.2. (R Development Core Team, 2022).

3 | RESULTS

3.1 | Species-specific tree response

We observed that the number of trees which presented a GR due to drought was similar regardless of species composition and site (Figure SM3), although their response differed. Accordingly, tree growth responses to drought varied among species and stand compositions, but their interaction was not significant (Table 1). Scots pine resistance was on average higher than Norway spruce (Figure 1a), although it was dependent on the timing of the drought (Table 1). On the other hand, Norway spruce recovered 22.5% of mean growth per year after drought, compared to 20.2% per year for Scots pine (Figure 1b). Thus, the species' contrasting resistance and recovery rate patterns show a clear trade-off. Scots pine also showed a lower recovery time compared to Norway spruce (Figure 1c), although the average difference was <1 year, which reflects the similarity of the species' responses. In summary, the higher recovery rate of Norway spruce was not enough to compensate for the greater GR it suffered due to drought, evincing a slightly higher recovery time compared to Scots pine.

3.2 | Tree responses in pure versus mixed stands

Tree resistance and recovery rate varied between stand compositions. In general, trees in pure stands showed a lower resistance to drought compared to mixtures (Table 1). Norway spruce in pure stands had the largest average GR, while Scots pine in mixed stands had the lowest (Figure 1a). However, trees in pure stands recovered faster than in mixtures (Figure 1b). These two trends balanced one another out, so no recovery time differences were found between pure and mixed stands (Figure 1c). Therefore, mixtures could reduce tree vulnerability to drought by increasing resistance.

3.3 | Effect of drought characteristics and other environmental factors on tree growth response

The species' response to drought was controlled by the timing of the drought, and the differences between stand compositions were modulated by the duration of the drought (Table 1). Trees had higher resistance in mixed than in pure stands, but only during shorter drought events. The difference between trees growing in different stand compositions decreased with duration of drought and became similar during droughts longer than 2 months (Figure 1a). Timing of drought also affected species' performance. Norway spruce was less resistant to summer drought than Scots

TABLE 1 Summary of the results from modelling the three resilience components. dbh: Diameter at breast height (mm); Age: Tree age at the drought event; CV: Coefficient of variation for the TRWI; S.pine: Dummy variable for species (scots pine = 1); Pure: Dummy variable for stand composition (pure stands = 1); Latitude (°N); Longitude (°E); Elevation (m); SPEI: Monthly average standardized precipitation–evapotranspiration index during the drought event; Duration: The number of months that the drought lasted; WS: Wet season level for the timing of the drought; DS + WS: Dry and wet season level for the timing of the drought; triplet: Triplet random factor; plot: Plot random factor nested in triplet; tree: Tree random factor nested in plot and triplet; year: Year crossed random factor; error: Variance of residual error. The interactions Pure: Duration, S.pine: Duration, S.pine: Drought season were also included in the model. AIC: Akaike's information criterion; RMSE: Root-mean-square error

Model components	Variables	Resistance		Recovery rate		Recovery time	
		Coefficient	p-value	Coefficient	p-value	Coefficient	p-value
Fixed parameters	<i>Intercept</i>	1.879	<0.001	0.623	<0.001	0.790	<0.001
	<i>dbh</i>	–	–	$4.5 \cdot 10^{-5}$	0.045	–	–
	<i>Age</i>	–0.008	<0.001	–	–	0.005	<0.001
	<i>CV</i>	–0.019	<0.001	–	–	–	–
	<i>S.pine</i>	0.337	<0.001	–0.023	<0.001	–0.041	0.002
	<i>Pure</i>	–0.174	0.007	0.014	<0.001	0.023	0.065
	<i>Latitude</i>	–	–	–0.006	<0.001	–	–
	<i>Longitude</i>	–	–	–0.002	<0.001	–	–
	<i>Elevation</i>	–	–	-7.9×10^{-5}	<0.001	–	–
	<i>SPEI</i>	0.236	<0.001	–	–	–0.067	0.045
	<i>Duration</i>	–0.075	<0.001	–	–	–	–
	<i>WS</i>	0.525	<0.001	–	–	–0.112	0.002
	<i>DS + WS</i>	0.211	<0.001	–	–	0.004	0.841
	<i>Pure:Duration</i>	0.049	0.021	–	–	–	–
	<i>S.pine:WS</i>	–0.530	<0.001	–	–	–	–
	<i>S.pine:DS + WS</i>	–0.282	<0.001	–	–	–	–
Variance parameters	triplet	0.137	–	–	–	0.113	–
	plot	0.140	–	–	–	–	–
	tree	0.119	–	0.015	–	–	–
	year	0.364	–	0.018	–	0.302	–
	error	1.006	–	0.115	–	0.106	–
Fit statistics	AIC	2762.2	–	–1394.8	–	3613.7	–
	RMSE	0.996	–	0.115	–	1.028	–

pine, but more resistant to droughts occurred during the WS (Figure 2a). Scots pine showed little variation in resistance between seasons. Drought intensity, measured as SPEI, also reduced tree resistance (Table 1). Old trees and trees with a high growth variation showed a lower resistance.

Features of trees (species and diameter at breast height), stands (composition) and sites (latitude, longitude and elevation) all influenced post-drought recovery rate (Table 1). Trees further north and east and at lower elevations recovered more slowly. Timing of drought events also influenced the recovery time (Figure 2b). Droughts occurred in the WS needed the shortest recovery time for both species, but Scots pine always recovered faster than Norway spruce regardless of drought timing (Figure 2b). Drought intensity (SPEI) and tree age prolonged tree recovery (Table 1). In summary, Norway spruce showed a higher sensitivity to summer droughts, with lower resistance and longer recovery times compared to Scots pine.

4 | DISCUSSION

4.1 | Tree growth response to drought in pure and mixed stands

Scots pine was the more drought tolerant species, with higher resistance to drought and shorter recovery times, compared to Norway spruce. Dry summers have been shown to strongly reduce photosynthesis, stomatal conductance, carbohydrate transfer and growth for Norway spruce (Lévesque et al., 2014; Tremblé et al., 2021). Later termination of shoot elongation and later radial growth above-ground and below-ground make Norway spruce more sensitive to summer water stress than Scots pine (Zang et al., 2012). A higher specific leaf area of Norway spruce (compared to pine) would involve high transpiration rates longer into drought episodes, probably impairing tree water status (Greenwood et al., 2017). It increases drought damage risk and

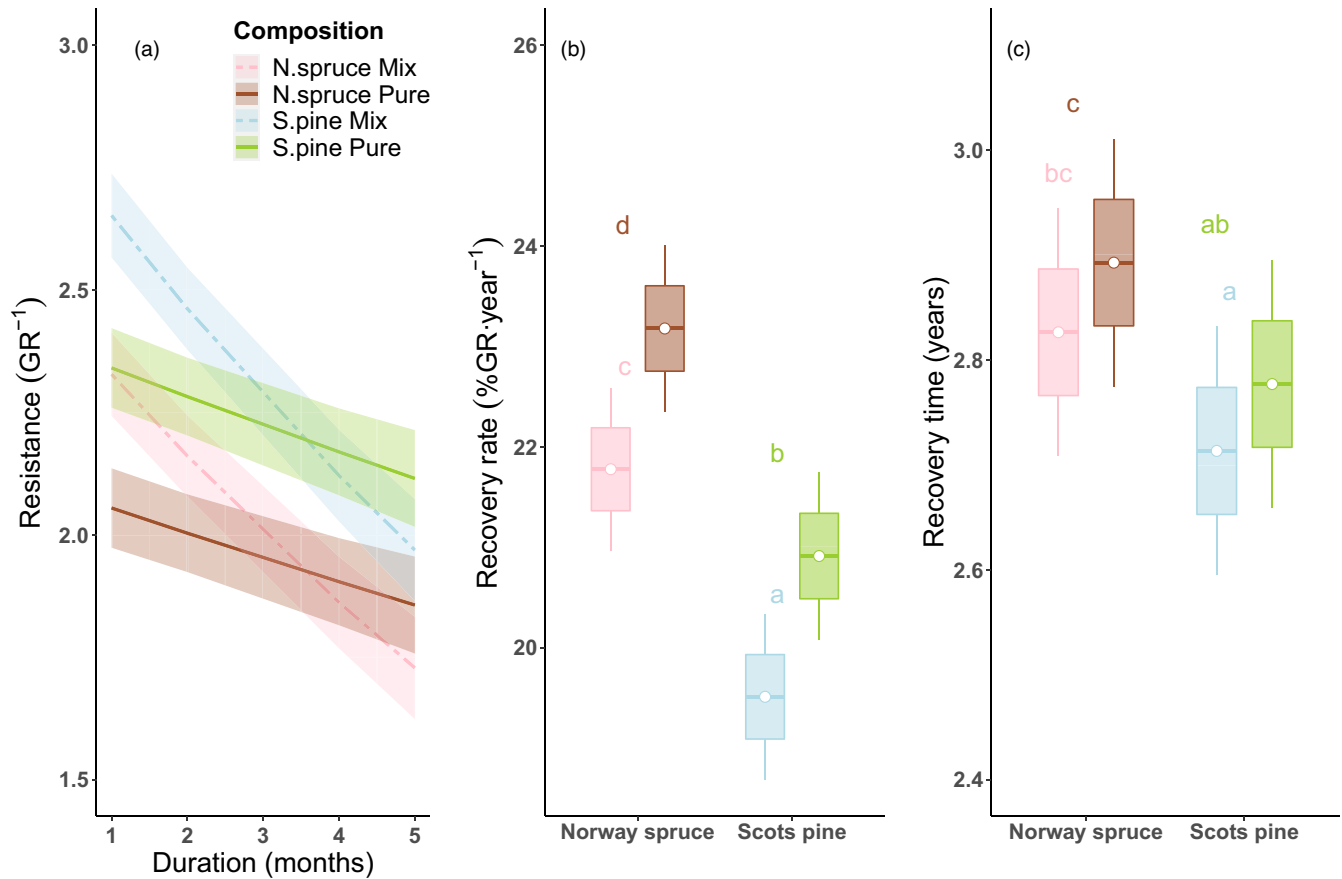


FIGURE 1 Differences between species and stand compositions in resistance to drought (a), recovery rate (b) and recovery time (c). Values were averaged according to the mean value of other predictors in the model (Table 1). Letters denote significant differences corrected for multiple comparisons using a Sidak test at $p < 0.05$. Shaded areas show 95% confidence intervals for the estimated trend lines in panel (a) and boxes and whiskers in panels (b, c) show standard error and 95% confidence intervals of estimated means, respectively

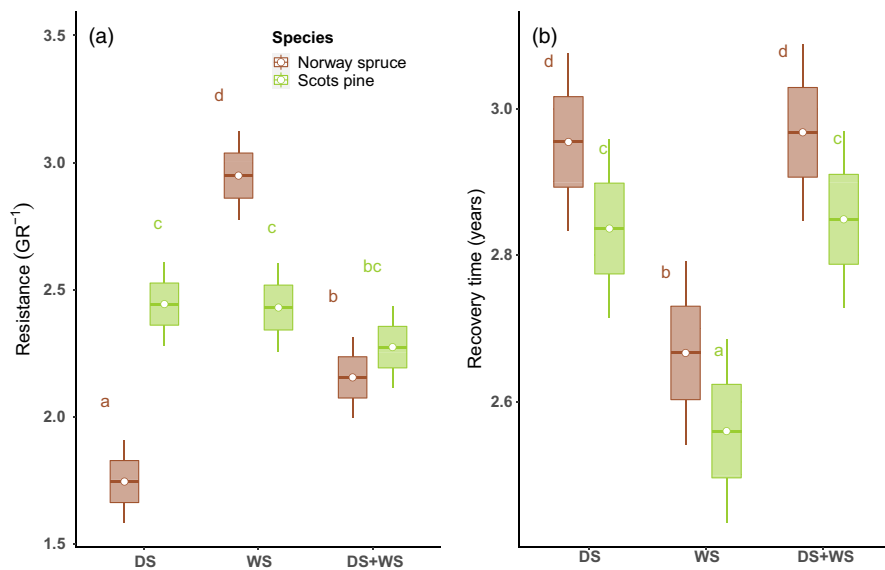


FIGURE 2 Species differences in resistance (a) and recovery time (b) as a function of drought seasonality: dry (DS), wet (WS) and, dry and wet (DS+WS) season. Values assume mean values of all other predictors in the model (Table 1). Letters denote significant differences using Sidak tests at $p < 0.05$. Boxes and whiskers show standard error and 95% confidence intervals of estimated means, respectively

mortality for this species (Rosner et al., 2018; Zang et al., 2014). On the other hand, Norway spruce's faster recovery rate could come from prioritizing investment of assimilates below ground, probably to regain root functions after drought (Hagedorn et al., 2016).

Scots pine showed a lower resistance to droughts occurred in WS compared to Norway spruce (Figure 2a), in agreement with previous findings (Camarero et al., 2016; Voltas et al., 2013). The earlier onset of cambial activity of Scots pine compared to Norway spruce

(Mäkinen et al., 2018) could be a disadvantage during droughts of WS. Scots pine's strict stomatal control to reduce hydraulic failure risk (Zang et al., 2014) could lead to high sensitivity regardless of drought timing, leading to similar resistance levels in DS and WS, but different recovery times (Figure 2). We observed that Scots pine was less vulnerable to drought compared to Norway spruce, which may result in a better adaptation to warmer and drier summers (Trembl et al., 2021).

Mixtures of Scots pine and Norway spruce may provide an option to reduce drought vulnerability because of increased resistance (Figure 1a). Resistance to drought of mixed forests may result from complementary use of below-ground resources, predominantly via root stratification (Jactel et al., 2017), potentially reducing soil water competition in mixtures (Grossiord, 2019). Norway spruce has shallower root systems than Scots pine, potentially reducing intraspecific competition for water in mixed stands (Fichtner et al., 2017). In contrast, Lutter et al. (2021) found that these species' roots overlap in mixed stands at boreal sites, suggesting competition for resources among trees of both species. They also showed that both species enlarged their root system in mixed stands. This increased root surface area may lead to more efficient water uptake during drought events compared to pure stands (Jansen et al., 2021). In addition, these species' contrasting crown structures might modify the proportion of precipitation that is intercepted by the canopy (Pretzsch, 2022). Another reason for better performance of mixtures could be Scots pine acting as a hydraulic lift, redistributing deep water to the drier surface soil layers (Jactel et al., 2017). There are strong indications that both Scots pine and Norway spruce improve performance during drought when they are mixed with other species (Pardos et al., 2021; Pretzsch et al., 2020). However, differences in density and basal area between pure and mixed stands may complicate explanation of mixture performance (Castagneri et al., 2021; Forrester et al., 2016). Another question for future research is the role of species' proportion and the spatial configuration of the species (intermingling vs. clustering), since it may affect the results. Here, we observed that in mixtures, trees of both species were less vulnerable to drought, making mixtures a preferable smart forest strategy to reduce drought stress.

Timing of drought was a crucial factor determining impacts on growth, which agrees with recent studies (Bose et al., 2021; D'Orangeville et al., 2018; Huang et al., 2018), who highlight the stronger effects of drought in summer seasons. Our results show that droughts occurred in DS require longer recovery times for both species, with Norway spruce having the lowest resistance during this time of year (Figure 2). Previous research has also shown that low summer water availability strongly reduces growth in both of these species (Lévesque et al., 2014; Vitasse et al., 2019). Nevertheless, Norway spruce seems to be much more sensitive to drought even in boreal forest (Gutierrez Lopez et al., 2021). In our study, resistance was reduced and recovery times prolonged when drought intensity increased, which has been reported as a promoter of tree mortality (Allen et al., 2015; Greenwood et al., 2017). According to our results, if future droughts become longer the advantage of mixed stands

could disappear, which would be especially negative for Norway spruce.

We also found other environmental and intrinsic factors which modulated tree growth response to drought. A low recovery rate was observed for trees at high latitude and elevation (Table 1), where growth is often limited by low temperatures (Gutierrez Lopez et al., 2021; Wilmking et al., 2020). Similarly, a high vulnerability to drought for both species has also been confirmed at dry sites in central and southern regions of Europe (Serra-Maluquer et al., 2021; Trembl et al., 2021), with a trend towards higher resilience in mixed stands at hotter sites (Pardos et al., 2021). Despite large trees having a higher recovery rate (Table 1), probably due to more extensive root systems, they may experience stronger GRs (Pretzsch et al., 2018; Zang et al., 2012), lower drought resilience (Bennett et al., 2015; Grote et al., 2016) and possibly increasing tree mortality risk (DeSoto et al., 2020; Ryan, 2015). High variation in TRWI during pre-drought conditions, which indicates that a tree has great climate sensitivity, can reduce tree resistance to drought stress (Bose et al., 2021; Pretzsch, 2021). These trees typically would occupy a dominant social position (Grote et al., 2016; Stovall et al., 2019). Senescence could also reduce drought tolerance since trees show lower resistance and higher recovery times as they age (Andivia et al., 2020; Zang et al., 2014). Therefore, dominant and old trees in sites with climate limitations could be more susceptible to drought and other damage (Drössler et al., 2018).

4.2 | Ecological, management and policy implications

Careful selection of tree species is a smart forest management strategy to face drought. Intensive production forestry has promoted the conversion of Scots pine and broadleaved forests to more profitable Norway spruce monocultures (Felton et al., 2020). This comes at the cost of large negative outcomes for biodiversity, aesthetic and recreational values, as well as increased stand vulnerability to disturbances such as drought, pests and pathogens. For single-species stands, Scots pine would be a safer choice to adapt forests to droughts. As conifers may be more susceptible to extreme weather events broadleaved species could be another forest management alternative (DeSoto et al., 2020).

Replacing pure Norway spruce plantations with the mixtures studied here would increase drought resilience and biodiversity (Felton et al., 2020; Messier et al., 2021) and reduce diseases (Lindén & Vollbrecht, 2002) without a significant loss in stand production (Drössler et al., 2018; Pretzsch & Schütze, 2021; Ruiz-Peinado et al., 2021). Since droughts can greatly reduce stand production, mixtures may help to alleviate it to some extent (Schnabel et al., 2021). However, mixtures are more complicated to manage than monocultures although useful examples of silvicultural prescriptions can be found in northern latitudes (Drössler et al., 2015; Huuskonen et al., 2021; Lindén & Agestam, 2003). Furthermore, some steps have recently been taken towards introducing

methodological approaches for steering European mixed forests (Pretzsch et al., 2021; Pretzsch & Del Río, 2020).

Our results also showed that tree and site features can modulate growth responses to drought. Bigger trees, for example, showed higher recovery rates, so stand density reduction to produce fewer but larger trees could be desirable to face drought (Castagneri et al., 2021; Sohn et al., 2016). On the other hand, a competition release due to thinning may increase water evaporation and tree climate sensitivity (CV), consequently reducing drought resistance (Table 1) which is consistent with recent studies (Pretzsch et al., 2018; Stovall et al., 2019). Mortality of large trees would be particularly concerning because they have an important ecological and carbon storage role (Lutz et al., 2018; Ryan, 2015). Managing the higher drought vulnerability of dominant and old trees does not necessarily require shorter rotation periods. In our view, it would be preferable to maintain a range of tree ages and sizes within stands. Shelterwood systems or continuous cover forestry may be promising strategies in this regard (Drössler et al., 2015). Finally, the revealed greater tolerance to drought stress of Scots pine-Norway spruce mixtures compared with neighbouring pure stands substantiates the benefits of mixed stands in the face of observed and forecasted climate change, and may help stem the ongoing dieback of Norway spruce monocultures across Europe.

5 | CONCLUSIONS

This research aimed to examine differences between species (Scots pine vs. Norway spruce) and compositions (pure vs. mixed stands) in terms of tree growth responses to drought along a climatic gradient in Europe. We showed that drought characteristics, tree and site conditions modulated the tree growth response. Drought seasonality modulated the differences of the species' responses, whereas the longer drought duration reduced the differences between mixed and pure stands. Summer droughts required longer recovery times compared to droughts occurred in the WS, with Norway spruce being more vulnerable than Scots pine. Thus, Norway spruce should be avoided at sites with water limitations. Since mixed stands increased drought resistance for both species, mixtures are a promising strategy for adaptation of forest management to climate change. However, more research is needed to develop concise and specific silviculture prescriptions for this type of mixtures. The findings of this study have a number of important implications for future forest management in Europe. Scots pine and Norway spruce mixtures could reduce tree drought vulnerability and therefore reduce the impact on forests from ongoing climate change. Furthermore, such forests would increase the value of several ecosystem services without a significant loss of forest productivity.

AUTHOR CONTRIBUTIONS

Jorge Aldea contributed to the methodology, formal analysis and writing the original draft. Ricardo Ruiz-Peinado contributed to data curation. Miren del Río and Hans Pretzsch conceived the main idea,

designed the methodology and improved critically the manuscript. Michael Heym, Gediminas Brazaitis, Aris Jansons, Marek Metslaid, Ignacio Barbeito, Kamil Bielak, Gro Hysten, Stig-Olof Holm, Arne Nothdurft and Roman Sitko provided logistical support, data collection and intellectual input. Magnus Löf supervised the data analysis, reviewed the main text and contributed in funding acquisition. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare they have no conflict of interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are open and free available in Zenodo public digital repository at <https://doi.org/10.5281/zenodo.6736276> (Aldea, 2022).

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REFERENCES

- Aldea, J. (2022). Tree growth response to drought in pure and mixed stands of scots pine and Norway spruce in Europe. *Zenodo*. <https://doi.org/10.5281/zenodo.6736276>
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from

- hotter drought in the Anthropocene. *Ecosphere*, 6, art129. <https://doi.org/10.1890/ES15-00203.1>
- Anderegg, W. R. L., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Shevliakova, E., Williams, A. P., Wolf, A., Ziaco, E., & Pacala, S. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349, 528–532. <https://doi.org/10.1126/science.aab1833>
- Anderegg, W. R. L., Trugman, A. T., Badgley, G., Konings, A. G., & Shaw, J. (2020). Divergent forest sensitivity to repeated extreme droughts. *Nature Climate Change*, 10, 1091–1095. <https://doi.org/10.1038/s41558-020-00919-1>
- Andivia, E., Ruiz-Benito, P., Díaz-Martínez, P., Carro-Martínez, N., Zavala, M. A., & Madrigal-González, J. (2020). Inter-specific tolerance to recurrent droughts of pine species revealed in saplings rather than adult trees. *Forest Ecology and Management*, 459, 117848. <https://doi.org/10.1016/j.foreco.2019.117848>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bennett, A. C., McDowell, N. G., Allen, C. D., & Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1, 15139. <https://doi.org/10.1038/nplants.2015.139>
- Bose, A. K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarero, J. J., Haeni, M., Hereş, A. M., Hevia, A., Lévesque, M., Linares, J. C., Martínez-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. *Global Change Biology*, 26, 4521–4537. <https://doi.org/10.1111/gcb.15153>
- Bose, A. K., Scherrer, D., Camarero, J. J., Ziche, D., Babst, F., Bigler, C., Bolte, A., Dorado-Liñán, I., Etzold, S., Fonti, P., Forrester, D. I., Gaviñet, J., Gazol, A., de Andrés, E. G., Karger, D. N., Lebourgeois, F., Lévesque, M., Martínez-Sancho, E., Menzel, A., ... Rigling, A. (2021). Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe. *Science of The Total Environment*, 784, 147222. <https://doi.org/10.1016/j.scitotenv.2021.147222>
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., & Zang, C. (2022). dplR: Dendrochronology program library in R. R package version 1.7.4. <https://CRAN.R-project.org/package=dplR>
- 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>
- Camarero, J. J., Guada, G., Sánchez-Salguero, R., & Cervantes, E. (2016). Winter drought impairs xylem phenology, anatomy and growth in Mediterranean Scots pine forests. *Tree Physiology*, 36, 1536–1549. <https://doi.org/10.1093/treephys/tpw077>
- Castagneri, D., Vacchiano, G., Hacket-Pain, A., DeRose, R. J., Klein, T., & Bottero, A. (2021). 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>
- del Río, M., Löf, M., Bravo-Oviedo, A., & Jactel, H. (2021). Understanding the complexity of mixed forest functioning and management: Advances and perspectives. *Forest Ecology and Management*, 489, 119138. <https://doi.org/10.1016/j.foreco.2021.119138>
- DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E. M. R., Aakala, T., Amoroso, M. M., Bigler, C., Camarero, J. J., Čufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L. J., Hereş, A. M., Kane, J. M., Kharuk, V. I., Kitzberger, T., Klein, T., ... Martínez-Vilalta, J. (2020). Low growth resilience to drought is related to future mortality risk in trees. *Nature Communications*, 11, 545. <https://doi.org/10.1038/s41467-020-14300-5>
- 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., ... Phillips, R. P. (2018). Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Global Change Biology*, 24, 2339–2351. <https://doi.org/10.1111/gcb.14096>
- Drössler, L., Agestam, E., Bielak, K., Dudzinska, M., Koricheva, J., Liziniewicz, M., Löf, M., Mason, B., Pretzsch, H., Valkonen, S., & Wellhausen, K. (2018). Over- and underyielding in time and space in experiments with mixed stands of scots pine and Norway spruce. *Forests*, 9(8), 495. <https://doi.org/10.3390/f9080495>
- Drössler, L., Ekö, P. M., & Balster, R. (2015). Short-term development of a multilayered forest stand after target diameter harvest in southern Sweden. *Canadian Journal of Forest Research*, 45, 1198–1205. <https://doi.org/10.1139/cjfr-2014-0471>
- Felton, A., Petersson, L., Nilsson, O., Witzell, J., Cleary, M., Felton, A. M., Björkman, C., Sang, Å. O., Jonsell, M., Holmström, E., Nilsson, U., Rönnberg, J., Kalén, C., & Lindblad, M. (2020). The tree species matters: Biodiversity and ecosystem service implications of replacing scots pine production stands with Norway spruce. *Ambio*, 49, 1035–1049. <https://doi.org/10.1007/s13280-019-01259-x>
- Fichtner, A., Härdtle, W., Li, Y., Bruelheide, H., Kunz, M., & von Oheimb, G. (2017). From competition to facilitation: How tree species respond to neighbourhood diversity. *Ecology Letters*, 20, 892–900. <https://doi.org/10.1111/ele.12786>
- Fichtner, A., Schnabel, F., Bruelheide, H., Kunz, M., Mausolf, K., Schuldt, A., Härdtle, W., & von Oheimb, G. (2020). Neighbourhood diversity mitigates drought impacts on tree growth. *Journal of Ecology*, 108, 865–875. <https://doi.org/10.1111/1365-2745.13353>
- Forrester, D. I., Bonal, D., Dawud, S. M., Gessler, A., Granier, A., Pollastrini, M., & Grossiord, C. (2016). Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *Journal of Applied Ecology*, 53, 1725–1734. <https://doi.org/10.1111/1365-2664.12745>
- Forzieri, G., Girardello, M., Ceccherini, G., Spinoni, J., Feyen, L., Hartmann, H., Beck, P. S. A., Camps-Valls, G., Chirici, G., Mauri, A., & Cescatti, A. (2021). Emergent vulnerability to climate-driven disturbances in European forests. *Nature Communications*, 12, 1081. <https://doi.org/10.1038/s41467-021-21399-7>
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R., Laughlin, D. C., Kattge, J., Bönsch, G., Kraft, N. J. B., & Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 20, 539–553. <https://doi.org/10.1111/ele.12748>
- Grissino Mayer, H. D. (2001). For the computer program covecha. *Tree*, 57, 205–221.
- Grossiord, C. (2019). Having the right neighbors: How tree species diversity modulates drought impacts on forests. *The New Phytologist*, 228, 42–49. <https://doi.org/10.1111/nph.15667>
- Grote, R., Gessler, A., Hommel, R., Poschenrieder, W., & Priesack, E. (2016). Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees*, 30, 1467–1482. <https://doi.org/10.1007/s00468-016-1446-x>
- Gutierrez Lopez, J., Torngern, P., Oren, R., Kozii, N., Laudon, H., & Hasselquist, N. J. (2021). How tree species, tree size, and topographical location influenced tree transpiration in northern boreal forests during the historic 2018 drought. *Global Change Biology*, 27, 3066–3078. <https://doi.org/10.1111/gcb.15601>
- Hagedorn, F., Joseph, J., Peter, M., Luster, J., Pritsch, K., Geppert, U., Kerner, R., Molinier, V., Egli, S., Schaub, M., Liu, J. F., Li, M., Sever, K., Weiler, M., Siegwolf, R. T. W., Gessler, A., & Arend, M. (2016). Recovery of trees from drought depends on belowground sink control. *Nature Plants*, 2, 16111. <https://doi.org/10.1038/NPLANT.2016.111>

- Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology & Evolution*, 30, 503–506. <https://doi.org/10.1016/j.tree.2015.06.010>
- Huang, M., Wang, X., Keenan, T. F., & Piao, S. (2018). Drought timing influences the legacy of tree growth recovery. *Global Change Biology*, 24, 3546–3559. <https://doi.org/10.1111/gcb.14294>
- Huuskonen, S., Domisch, T., Finér, L., Hantula, J., Hynynen, J., Matala, J., Miina, J., Neuvonen, S., Nevalainen, S., Niemistö, P., Nikula, A., Piri, T., Siitonen, J., Smolander, A., Tonteri, T., Uotila, K., & Viiri, H. (2021). What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? *Forest Ecology and Management*, 479, 118558. <https://doi.org/10.1016/j.foreco.2020.118558>
- Ingrisch, J., & Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution*, 33, 251–259. <https://doi.org/10.1016/j.tree.2018.01.013>
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagnérol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017). Tree diversity drives forest stand resistance to natural disturbances. *Current Forestry Reports*, 3, 223–243. <https://doi.org/10.1007/s40725-017-0064-1>
- Jactel, H., Gritti, E. S., Drössler, L., Forrester, D. I., Mason, W. L., Morin, X., Pretzsch, H., & Castagnérol, B. (2018). Positive biodiversity–productivity relationships in forests: Climate matters. *Biology Letters*, 14, 20170747. <https://doi.org/10.1098/rsbl.2017.0747>
- Jansen, K., Von Oheimb, G., Bruelheide, H., Härdtle, W., & Fichtner, A. (2021). Tree species richness modulates water supply in the local tree neighbourhood: Evidence from wood $\delta^{13}\text{C}$ signatures in a large-scale forest experiment. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20203100. <https://doi.org/10.1098/rspb.2020.3100>
- Lenth, R. V. (2021). emmeans: Estimated marginal means, aka least-squares means. R package version 1.7.1-1. <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. *Agricultural and Forest Meteorology*, 197, 1–12. <https://doi.org/10.1016/j.agrfor.2014.06.001>
- Lindén, M., & Agestam, E. (2003). Increment and yield in mixed and monoculture stands of *Pinus sylvestris* and *Picea abies* based on an experiment in southern Sweden. *Scandinavian Journal of Forest Research*, 18, 155–162. <https://doi.org/10.1080/02827580310003722>
- Lindén, M., & Vollbrecht, G. (2002). Sensitivity of *Picea abies* to butt rot in pure stands and in mixed stands with *Pinus sylvestris* in southern Sweden. *Silva Fennica*, 36(4), 519. <https://doi.org/10.14214/sf.519>
- 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>
- Lutter, R., Henriksson, N., Lim, H., Blaško, R., Magh, R.-K., Näsholm, T., Nordin, A., Lundmark, T., & Marshall, J. D. (2021). Belowground resource utilization in monocultures and mixtures of Scots pine and Norway spruce. *Forest Ecology and Management*, 500, 119647. <https://doi.org/10.1016/j.foreco.2021.119647>
- Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., Anderson-Teixeira, K. J., Andrade, A., Baltzer, J., Becker, K. M. L., Blomdahl, E. M., Bourg, N. A., Bunyavejchewin, S., Burslem, D. F. R. P., Cansler, C. A., Cao, K., Cao, M., Cárdenas, D., Chang, L. W., ... Zimmerman, J. K. (2018). Global importance of large-diameter trees. *Global Ecology and Biogeography*, 27, 849–864. <https://doi.org/10.1111/geb.12747>
- Mäkinen, H., Jyske, T., & Nöjd, P. (2018). Dynamics of diameter and height increment of Norway spruce and Scots pine in southern Finland. *Annals of Forest Science*, 75, 28. <https://doi.org/10.1007/s13595-018-0710-1>
- Mazerolle, M. J. (2017). AICcmovavg: Model selection and multimodel inference based on (Q)AIC(c). R Package. Version 2.1-1 R package.
- McKee, T. B., Doesken, N. J., & Kleist, J. (1993). The relationship of drought frequency and duration to time scales. In *8th Conference on Applied Climatology, Anaheim, 17–22 January 1993*, pp. 179–184.
- 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., ... Zemp, D. C. (2021). For the sake of resilience and multifunctionality, let's diversify planted forests! *Conservation Letters*, 15(1), e12829. <https://doi.org/10.1111/conl.12829>
- Nepstad, D. C., Tohver, I. M., David, R., Moutinho, P., & Cardinot, G. (2007). Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, 88, 2259–2269. <https://doi.org/10.1890/06-1046.1>
- Nimmo, D. G., Mac Nally, R., Cunningham, S. C., Haslem, A., & Bennett, A. F. (2015). Vive la résistance: Reviving resistance for 21st century conservation. *Trends in Ecology & Evolution*, 30, 516–523. <https://doi.org/10.1016/j.tree.2015.07.008>
- Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defosse, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., ... Calama, R. (2021). The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. *Forest Ecology and Management*, 481, 118687. <https://doi.org/10.1016/j.foreco.2020.118687>
- Pretzsch, H. (2021). Trees grow modulated by the ecological memory of their past growth. Consequences for monitoring, modelling, and silvicultural treatment. *Forest Ecology and Management*, 487, 118982. <https://doi.org/10.1016/j.foreco.2021.118982>
- Pretzsch, H. (2022). Facilitation and competition reduction in tree species mixtures in Central Europe: Consequences for growth modeling and forest management. *Ecological Modelling*, 464, 109812. <https://doi.org/10.1016/j.ecolmodel.2021.109812>
- Pretzsch, H., & Del Río, M. (2020). Density regulation of mixed and mono-specific forest stands as a continuum: A new concept based on species-specific coefficients for density equivalence and density modification. *Forestry*, 93, 1–15. <https://doi.org/10.1093/forestry/cpz069>
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D. I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., ... Bravo-Oviedo, A. (2015). Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research*, 134, 927–947. <https://doi.org/10.1007/s10342-015-0900-4>
- Pretzsch, H., Grams, T., Häberle, K. H., Pritsch, K., Bauerle, T., & Rötzer, T. (2020). Growth and mortality of Norway spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally extended drought. Results of the KROOF throughfall exclusion experiment. *Trees*, 34, 957–970. <https://doi.org/10.1007/s00468-020-01973-0>
- Pretzsch, H., Poschenrieder, W., Uhl, E., Brazaitis, G., Makrickiene, E., & Calama, R. (2021). Silvicultural prescriptions for mixed-species forest stands. A European review and perspective. *European Journal of Forest Research*, 140, 1267–1294. <https://doi.org/10.1007/s10342-021-01388-7>
- Pretzsch, H., & Schütze, G. (2021). Tree species mixing can increase stand productivity, density and growth efficiency and attenuate the trade-off between density and growth throughout the whole

- rotation. *Annals of Botany*, 128, 767–786. <https://doi.org/10.1093/AOB/MCAB077>
- Pretzsch, H., Schütze, G., & Biber, P. (2018). Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest Ecosystems*, 5, 20. <https://doi.org/10.1186/s40663-018-0139-x>
- R Development Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rosner, S., Gierlinger, N., Klepsch, M., Karlsson, B., Evans, R., Lundqvist, S. O., Světlík, J., Børja, I., Dalsgaard, L., Andreassen, K., Solberg, S., & Jansen, S. (2018). Hydraulic and mechanical dysfunction of Norway spruce sapwood due to extreme summer drought in Scandinavia. *Forest Ecology and Management*, 409, 527–540. <https://doi.org/10.1016/j.foreco.2017.11.051>
- Ruiz-Peinado, R., Pretzsch, H., Löf, M., Heym, M., Bielak, K., Aldea, J., Barbeito, I., Brazaitis, G., Drössler, L., Godvod, K., Granhus, A., Holm, S.-O., Jansons, A., Makrickienė, E., Metslaid, M., Metslaid, S., Nothdurft, A., Otto Juel Reventlow, D., Sitko, R., ... del Río, M. (2021). Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) karst.) productivity along a climatic gradient across Europe. *Forest Ecology and Management*, 482, 118834. <https://doi.org/10.1016/j.foreco.2020.118834>
- Ryan, M. (2015). Tree mortality: Large trees losing out to drought. *Nature Plants*, 1, 15150. <https://doi.org/10.1038/nplants.2015.150>
- 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. *Science Advances*, 7, 1643. <https://doi.org/10.1126/SCIADV.ABK1643>
- 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. *Current Forestry Reports*, 6, 185–200. <https://doi.org/10.1007/s40725-020-00119-2>
- Senf, C., Buras, A., Zang, C. S., Rammig, A., & Seidl, R. (2020). Excess forest mortality is consistently linked to drought across Europe. *Nature Communications*, 11, 6200. <https://doi.org/10.1038/s41467-020-19924-1>
- Serra-Maluquer, X., Granda, E., Camarero, J. J., Vilà-Cabrera, A., Jump, A. S., Sánchez-Salguero, R., Sangüesa-Barreda, G., Imbert, J. B., & Gazol, A. (2021). Impacts of recurrent dry and wet years alter long-term tree growth trajectories. *Journal of Ecology*, 109, 1561–1574. <https://doi.org/10.1111/1365-2745.13579>
- Sohn, J., Saha, S., & Bauhus, J. (2016). Potential of forest thinning to mitigate drought stress: A meta-analysis. *Forest Ecology and Management*, 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? *International Journal of Climatology*, 38, 1718–1736. <https://doi.org/10.1002/joc.5291>
- Stovall, A. E. L., Shugart, H., & Yang, X. (2019). Tree height explains mortality risk during an intense drought. *Nature Communications*, 10, 4385. <https://doi.org/10.1038/s41467-019-12380-6>
- Thurm, E. A., Uhl, E., & Pretzsch, H. (2016). Mixture reduces climate sensitivity of Douglas-fir stem growth. *Forest Ecology and Management*, 376, 205–220. <https://doi.org/10.1016/j.foreco.2016.06.020>
- Tremli, V., Mašek, J., Tumajer, J., Rydval, M., Čada, V., Ledvinka, O., & Svoboda, M. (2021). Trends in climatically driven extreme growth reductions of *Picea abies* and *Pinus sylvestris* in Central Europe. *Global Change Biology*, 28, 557–570. <https://doi.org/10.1111/gcb.15922>
- van der Maaten-Theunissen, M., Trouillier, M., Schwarz, J., Skiadaresis, G., Thurm, E. A., & van der Maaten, E. (2021). pointRes 2.0: New functions to describe tree resilience. *Dendrochronologia*, 70, 125899. <https://doi.org/10.1016/j.dendro.2021.125899>
- Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling, A., & Wohlgemuth, T. (2019). Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. *Global Change Biology*, 25, 3781–3792. <https://doi.org/10.1111/gcb.14803>
- Voltas, J., Camarero, J. J., Carulla, D., Aguilera, M., Ortiz, A., & Pedro, F. J. (2013). A retrospective, dual-isotope approach reveals individual predispositions to winter-drought induced tree dieback in the southernmost distribution limit of Scots pine. *Plant, Cell & Environment*, 36, 1435–1448. <https://doi.org/10.1111/pce.12072>
- Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., Smiljanic, M., & Trouillier, M. (2020). Global assessment of relationships between climate and tree growth. *Global Change Biology*, 26, 3212–3220. <https://doi.org/10.1111/gcb.15057>
- Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., & Menzel, A. (2014). Patterns of drought tolerance in major European temperate forest trees: Climatic drivers and levels of variability. *Global Change Biology*, 20, 3767–3779. <https://doi.org/10.1111/gcb.12637>
- Zang, C., Pretzsch, H., & Rothe, A. (2012). Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees*, 26, 557–569. <https://doi.org/10.1007/s00468-011-0617-z>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. <https://doi.org/10.1007/978-0-387-93837-0>

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