



Meta-analysis Reveals Different Competition Effects on Tree Growth Resistance and Resilience to Drought

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ABSTRACT

Drought will increasingly threaten forest ecosystems worldwide. Understanding how competition influences tree growth response to drought is essential for forest management aiming at climate change adaptation. However, published results from individual case studies are heterogeneous and sometimes contradictory. We reviewed 166 cases from the peer-reviewed literature to assess the influence of stand-level competition on tree growth response to drought. We monitored five indicators of tree growth response: mean sensitivity (inter-annual tree ring width variability); association between inter-annual growth variability and water availability; resistance; recovery; and resilience to drought. Vote counting did not indicate a consistent effect of competition on mean sensitivity.

Conversely, higher competition for resources strengthened the association between water availability and inter-annual growth rates. Meta-analysis showed that higher competition reduced resistance ($p < 0.001$) and improved recovery ($p < 0.05$), but did not consistently affect resilience. Species, site and stand characteristics, and drought intensity were insignificant or poor predictors for the large variability among the investigated cases. Our review and meta-analysis show that competition does not affect the response of tree growth to drought in a unidirectional and universal way. Although density reduction (thinning) can alleviate growth declines during drought, the effects on growth after stress are uncertain. The large variability among investigated cases suggests that local-scale processes play a crucial role in determining such responses and should be explicitly evaluated and integrated into specific strategies for adaptation of forests to climate change.

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Key words: climate change adaptation; drought response; forest management; meta-analysis; resilience components; review; stand density; tree radial growth; tree rings.

HIGHLIGHTS

- It is often suggested that competition exacerbates drought influence on tree growth.
- We reviewed and ran meta-analysis on five descriptors of growth response to drought.
- Stand-level competition reduces tree growth resistance, but not growth resilience.

INTRODUCTION

Anthropogenic climate change is responsible for more frequent and intense droughts worldwide (IPCC 2013; Trenberth and others 2014). Chronic soil water deficits and extreme drought events are projected to increasingly affect most forest ecosystems at different spatio-temporal scales (Reyer and others 2015), influencing tree reproduction (Bogdziewicz and others 2020), regeneration (Clark and others 2016), primary productivity (Rita and others 2019), radial growth (Anderegg and others 2015), plant defenses (Anderegg and others 2016), and mortality (Allen and others 2015).

Tree responses to drought are species- and site-specific (Vitasse and others 2019; DeSoto and others 2020), but also depend on forest structure (tree size, number, and distribution in the stand), which regulate resource supply, uptake, and use efficiency (Pretzsch and others 2013; Tsamir and others 2019). Stand density and individual tree size, typically measured as stem diameter at breast height (in lieu of the desirable but more difficult measurement of leaf area, Forrester 2019), determine stand-level competition (Weigelt and Jolliffe 2003) and directly affect water availability and uptake (Krajicek and others 1961; Moreno-Gutiérrez and others 2012). A dense tree cover is associated with high rainfall interception by the canopy, subsequent evaporation of water before it reaches the soil, and reduced soil water storage (Molina and del Campo 2012). A dense canopy (high leaf area index) causes higher stand-level transpiration, which reduces soil water availability (Brèda and others 1995), yet it reduces daily maximum soil temperature and evaporation rates, particularly during dry-soil conditions (von Arx and others 2013). Notably, canopy influence on water evapotranspiration varies between tree species with different water-use behavior (anisohydric species have higher water-use than isohydric ones, Klein and others 2013) and crown architecture (for example, the decoupling of the canopy from the atmosphere is stronger for broadleaves than for conifers, Mag-

nani and others 1998). Stand density also affects belowground competition for water, whose intensity increases linearly with the number of trees in the stand (Casper and Jackson 1997). Finally, competition exacerbates the effects of drought on tree functional processes, such as stomatal conductance and photosynthetic rate (Brèda and others 1995; Moreno and Cubera 2008; Tsamir and others 2019)—even though intrinsic water-use efficiency (that is, the ratio between photosynthetic assimilation and stomatal conductance) was found unaffected (Moreno-Gutiérrez and others 2012; Fernández-de-Uña and others, 2016).

By influencing soil water availability and tree physiological responses to water stress, competition eventually affects tree radial growth. Some large-scale studies have shown a negative influence of stand density on growth during and after drought (Sohn and others 2016; Bottero and others 2017), and most literature on adaptive forest management recommends thinning as a tool to reduce drought constraints on tree growth (Brang and others 2014; Keenan 2015; del Río and others, 2017; Ammer 2016; Vilà-Cabrera and others 2018; Field and others 2020). Nevertheless, other studies show that the effect of competition on growth responses may vary widely in size and direction (Gazol and Camarero 2016; Serra-Maluquer and others 2018; Mausolf and others 2018; van Mantgem and others 2020). The large heterogeneity of results in the literature calls for a new synthesis of research. Identifying general patterns and specific drivers of the effect of competition on tree growth response to drought is critical to better understanding mechanisms of forest response to global warming. Furthermore, reviewing existing knowledge is key for planning effective management actions to maintain forest ecosystem services under climate change (Bolte and others 2009; Clark and others 2016).

In this paper, we investigated five widely used tree ring-based descriptors of growth response to drought: mean sensitivity, a measure of inter-annual tree ring width variability; association between inter-annual growth variability and water stress; growth resistance (Lloret and others 2011), which quantifies the growth reduction during a specific drought event; recovery, to assess the capacity to recover relative to the drought-induced growth reduction; and resilience, which measures the capacity of growth to return to the pre-disturbance performance. The three indices proposed by Lloret and others (2011) do not capture all aspects of tree response to drought, and recent papers have proposed integrations to evaluate tree responses to

environmental stress in a more comprehensive way (see Gessler and others 2020; Nikinmaa and others 2020; Schwarz and others 2020). Still, these indices have been and still are widely used (Vitasse and others 2019; Gillerot and others 2020; DeSoto and others 2020). We analyzed results and data reported in the literature with the aim of assessing the influence of stand-level competition on tree growth response to drought. Specifically, we expected that (1) competition differently affects the five response descriptors (mean sensitivity, association of growth variability with water stress, resistance, recovery and resilience); (2) moderators such as climate, species, and stand characteristics influence the relationship between competition and resistance, recovery and resilience; (3) literature biases, study design, and local factors within individual studies affect our understanding of competition–drought interactions in forest stands.

MATERIALS AND METHOD

Literature Search and Database Building

The literature search was performed using the Scopus database and the search engine Google Scholar, considering papers published until September 2020 included. The search keyword combination used was: “forest* OR tree*” AND “growth OR tree ring*” AND “competition OR density” AND “drought*”. An initial check of the title and abstract of several hundred papers allowed us to exclude irrelevant studies, that is, not related to competition and drought influence on tree radial growth. After screening of the full papers, we retained 69 studies (papers) that included analyses on the influence of stand-level competition on at least one of the five descriptors of growth response to drought. Each study included one or more cases (166 in total). A case corresponded to one species in one site. Each site included at least two stands with different basal area. Responses to different drought events were considered separately, but consecutive dry years were included in the same case. For each case, we recorded: bibliometric data, including the publication year; site location, including geographical coordinates; climate information, that is, annual mean temperature and precipitation sum; the reported drought year (or years); tree species; stand characteristics, such as species composition (mixed or pure), age, and basal area; the shade and drought tolerance of the species studied, measured on a 1–5 scale (from Niinemets and Valladares 2006); year of the last thinning (if any) before the drought; sample size (number of sampled trees);

study design, that is, “observational,” when stands of different basal area were investigated without density manipulation, or “treatment,” which involved comparisons among different thinning intensities (Supplementary Table 1). We characterized each of the investigated drought events (as identified by the reference study) using the Standardized Precipitation-Evapotranspiration Index (SPEI, Vicente-Serrano and others 2010), calculated for integration periods of 3, 6, 9, 12, and 15 months, from month 1 (January for the northern hemisphere; previous year July for the southern hemisphere) to month 12 (December for the northern hemisphere; June for the southern hemisphere). SPEI was calculated using Thornthwaite’s potential evapotranspiration computed from monthly air temperature and precipitation data at 0.5° resolution (period of coverage 1901–2017) from the CRU TS dataset v. 4.02 (Harris and others 2014).

Five Descriptors of Growth Response to Drought

To assess growth response to drought, we used five descriptors widely used in the literature: the mean sensitivity, the association between inter-annual growth variability and water availability/water stress indices, and the three resilience components, that is, resistance, recovery, and resilience to drought events (Lloret and others 2011). The mean sensitivity measures the inter-annual variability of tree ring width series. It does not directly assess the relationship between growth and climatic variability, nor the response to extreme events. Despite criticism (Bunn and others 2013), this index is still widely used to assess how much tree growth depends on external factors, including water availability (Weber and others 2013; Hoffmann and others 2018). The association between growth variability and precipitation or drought indices can be measured by correlation, uni- and multivariate regression, or mixed models (Fritts 1976; Guiot 1991). Strong associations with climate variability can be due to either growth reductions during stressful years, or growth increases in favorable years. Therefore, this method cannot discriminate the specific response to drought. The three components of resilience (Lloret and others 2011) assess the growth responses during and in the years immediately following the drought. In contrast to the mean sensitivity and growth association with precipitation variability, they distinguish between positive and negative responses. Furthermore, as they are measured on a specific period (in contrast

to mean sensitivity and response to climate, assessed over multi-decadal series), it is possible to reliably associate them with stand attributes (for example, stand density) measured in the same period.

When available, we retrieved mean sensitivity, growth-climate association, resistance, recovery and resilience values reported in the papers. When not available, resistance, recovery and resilience were calculated from data extracted from published graphics using WebPlotDigitizer v. 4.1 (Rohatgi 2011). Stand basal area was used as an indicator of stand-level competition intensity. Stand basal area depends on tree number and size (both influencing stand-level competition), is reported consistently in many papers, and has been often used to assess stand-level competition (Young and others 2017; Etzold and others 2019). In particular, to quantitatively assess competition for stands included in a case study, we calculated the relative basal area, that is, the ratio between the stand basal area and the maximum basal area for the species among the stands investigated in the study. The influence of competition on the five descriptors of growth response to drought was investigated using two different approaches: vote counting and meta-analysis.

Vote Counting

We used vote counting to assess the number of cases when competition had a negative or positive effect on the five descriptors of growth response to drought. We assigned the label “negative” to the cases where competition exacerbated the negative effects of drought, that is, when trees in stands with higher basal area exhibited: higher mean sensitivity, stronger association with inter-annual variability of drought or precipitation, lower resistance, recovery or resilience to drought events. The label “positive” was assigned to the opposite cases and “neutral” to cases where no differences were detected. When available, quantitative data on the resilience components were used to assess negative, positive, or neutral competition effects. However, qualitative information found in the papers could not be used for quantitative assessment. Therefore, vote counting on qualitative data allowed us to investigate more cases than the quantitative meta-analysis described below. Due to the low power of vote counting (Hunter and Schmidt 2004; Borenstein and others 2009; Cooper and others 2009), we did not use it to quantify the influence of competition on drought response descriptors, but to assess

whether the number of positive and negative cases was similar or not, using a sign (binomial) test.

Statistical Meta-analysis

Meta-analysis was performed to test for competition effects on resistance (79 cases with quantitative information, excluding outliers), recovery (56 cases), and resilience (58 cases). A much lower number of cases (27) reported competition effects on mean sensitivity, which we did not consider sufficiently robust for a statistical meta-analysis. The association between growth and precipitation/drought was not measured consistently: early studies used correlation or response function analysis (Fritts 1976), whereas most recent studies used more complex methods such as linear mixed models. Therefore, we did not perform a statistical meta-analysis on this descriptor either.

As an “effect size” for meta-analysis, we used the slope of the linear relationship between stand relative basal area and each resilience component, computed for each case. Negative (positive) slopes indicate that stands with higher relative basal area have lower (higher) resistance, or recovery or resilience (Figure 1). Relative basal area and resilience components were calculated using the same scale for all cases, and thus, the regression slope served as a comparable metric, indicating both the size and direction of the investigated effect (Hunter and Schmidt 2004). The meta-analysis was computed using the package Metafor (Viechtbauer 2010) for the R statistical framework (R Core Team 2019). We fitted a random-effects model to estimate the mean effect size of competition on resilience components, under the assumptions that the cases included in our analysis were a random sample of a greater population of cases and that the true effect size varied from case to case, and the mean effect was an estimator of the mean of the distribution of effect sizes (Borenstein and others 2009; Viechtbauer 2010). We computed separate models for resistance, recovery, and resilience. Outliers (cases with a slope ± 3 standard deviations from the mean slope across all cases) were removed (Viechtbauer and Cheung 2010), and the dependent variable (slope) was sin-transformed to reduce kurtosis and improve normality. In all models, weight argument was used to give more weight to studies with larger samples (more trees). A restricted maximum-likelihood estimator was used to assess the degree of heterogeneity in the effect sizes (Metafor’s default). Model outcomes included the grand mean effect size, its 95% confidence intervals, and heterogeneity measures.

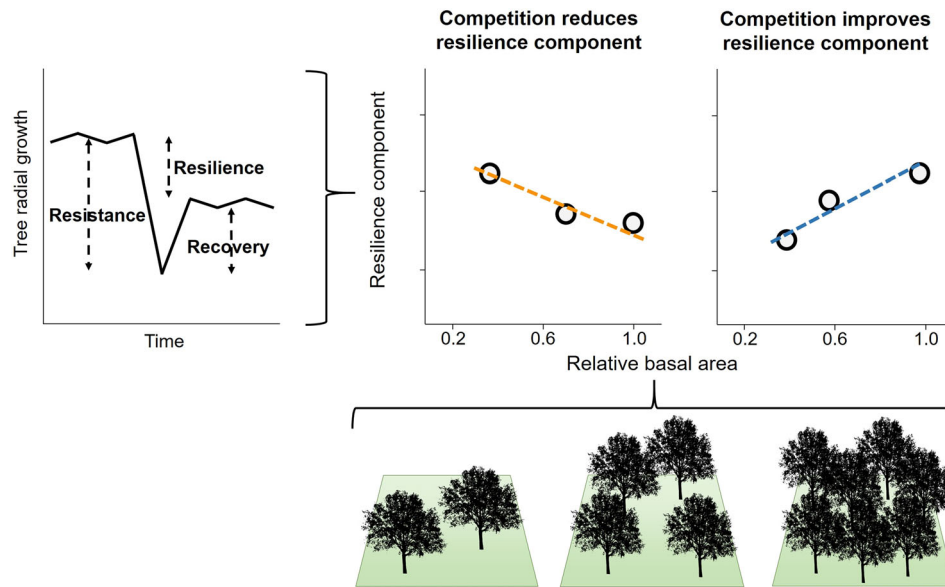


Figure 1. Schematic representation of the assessment of effect size in the meta-analysis. For each case, we computed the slope of the linear relationship between relative stand basal area (relative to the maximum basal area reported for the species by each study, x axis) and resilience component (growth resistance, recovery, and resilience separately, y axis). Negative (positive) slopes indicate that stands with higher relative basal area have lower (higher) resistance, recovery or resilience, that is, that competition reduces (improves) the resilience component.

Finally, we assessed the influence of different moderators on the effect size by meta-regression (Borenstein and others 2009). As fixed factors, we used tree species, functional type (conifer/broad-leaf), species-specific shade and drought tolerance, stand composition (pure/mixed), mean tree age, age structure (even/uneven-aged), year of the last thinning (if any) before the drought, the study design (observational with no treatment/stand density manipulation treatment), site mean annual temperature and precipitation sum. Site was assigned as a random factor. Since all SPEI timescales were strongly cross-correlated, we retained only the one providing the most consistent results for each resilience component in the final meta-regression model. Backwards selection of predictors was performed based on the corrected Akaike information criterion.

Sensitivity Analysis and Publication Bias

Sensitivity analysis was used to test robustness of the meta-analysis results, that is, if they were sensitive to effect size metrics and data structure (Koricheva and Gurevitch 2014). First, we ran the models using stand relative basal area calculated on the maximum absolute basal area for the species (species-specific), calculated as a function of mean wood specific gravity according to Woodall and others (2005). Furthermore, we used the *leave1out*

function in the *Metafor* package for R, which assesses the influence of each case on the model outcome by recalculating the models leaving out one observation at a time (Viechtbauer 2010). Finally, we ran the models without removing the outliers (Viechtbauer and Cheung 2010; Thabane and others 2013). To assess the potential bias of sample size (Hunter and Schmidt 2004) and time of publications (Koricheva and Gurevitch 2014) on meta-analytical models, we scrutinized scatterplots and calculated Kendall's correlation coefficient between effect size and (1) study sample size or (2) publication year.

RESULTS

Vote Counting and Relationships Between the Three Resilience Components

Our dataset comprised studies mostly from temperate regions of North America and Europe. Conifers were more represented than broadleaves, pure more than mixed stands, and even-aged more than uneven-aged stands (Figure 2, Supplementary Table 1). A similar number of cases showed positive (41%) and negative (37%) effects of stand-level competition on tree-ring mean sensitivity (binomial sign test, probability = 0.48, $p = 0.99$) (Figure 3). The association between growth and

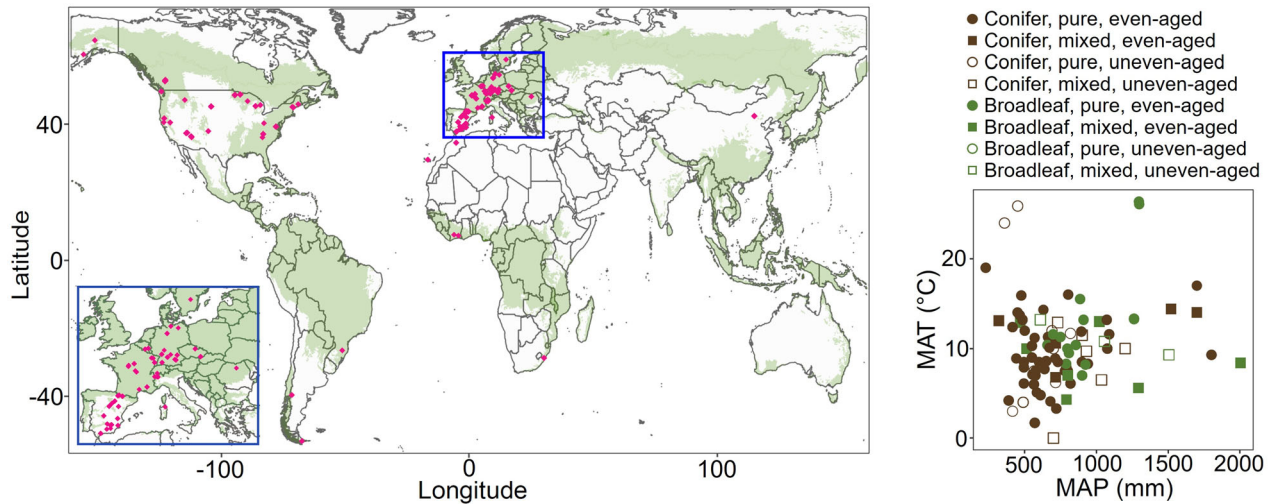


Figure 2. Locations of reviewed studies (left, magenta diamonds on the world forested land, in green) and scatterplot (right) of the corresponding mean annual temperature (MAT) and precipitation (MAP). See the key for correspondence between symbols and stand characteristics in the scatterplot.

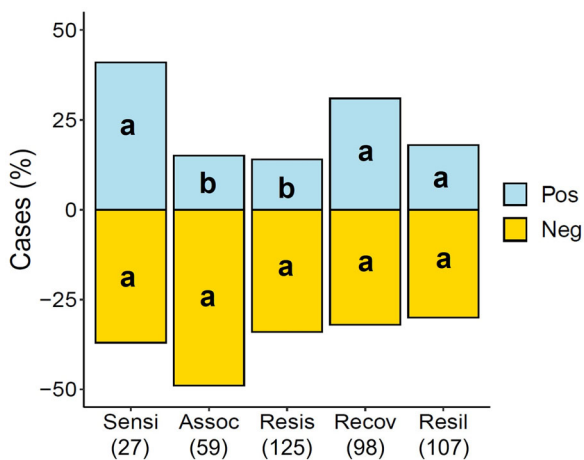


Figure 3. Relative frequency of cases with positive and negative effects of competition (stand basal area) on mean sensitivity (Sensi), climate-growth association (Assoc), resistance (Resis), recovery (Recov), and resilience (Resil). Neutral cases are not shown (positive, negative and neutral sum to 100%). The total number of cases is reported below each descriptor. Different letters in the bars indicate significant differences in counts of negative and positive cases within each descriptor according to the binomial sign test ($p < 0.05$).

inter-annual precipitation (or drought) variability was stronger in higher- versus lower-density stands in 49% of cases, while only 15% of cases showed the opposite pattern (probability = 0.76, $p < 0.01$). More than half of cases (52%) showed no significant competition effect on resistance to drought. However, when significant effects occurred, higher density stands had lower resistance in most cases

(probability = 0.72, $p < 0.01$). No significant difference occurred between positive and negative counts of cases that reported competition effects on recovery (probability = 0.51, $p = 0.99$) and resilience (probability = 0.63, $p = 0.09$). For cases with quantitative information, mean resistance was 0.70, mean recovery was 1.66, and mean resilience was 0.96. The three resilience components were significantly related to each other. In particular, recovery was strongly negatively related to resistance (Spearman's $\rho = -0.66$, $p < 0.001$), whereas resilience was less strongly but positively related to recovery ($\rho = 0.39$, $p < 0.001$) and resistance ($\rho = 0.36$, $p < 0.001$).

Meta-analysis on Growth Resistance

Resistance to drought was generally lower in denser stands. The overall mean effect size, that is, the average slope of the linear relationship between site-specific stand relative basal area and resistance to drought, was -0.133 ($p < 0.001$; Table 1, Figure 4). However, high variability occurred among the investigated cases, as indicated both by high variance of the true effect sizes ($\tau^2 = 0.089$), and high inconsistency across the different cases ($I^2 = 94.3$). Moderators that describe site, stand, or species characteristics were not able to further explain this variability (Table 1; Figure 5; Supplementary Table 2). However, the sampling design affected the size effect estimate ($p < 0.01$), with cases from treatment studies showing lower size effects compared to cases from observational studies. The 3-month SPEI at the end of summer

Table 1. Statistics for the Random-Effect and Meta-regression Models

	df	τ^2	τ	$I^2(\%)$	H^2	Estim	s.e	p	AICc
Random-eff. model									
Resistance	78	0.089	0.299	94.3	17.6	– 0.133	0.036	< 0.001	44.5
Recovery	55	0.209	0.458	97.5	40.2	0.132	0.063	0.037	78.3
Resilience	57	0.111	0.333	94.8	19.2	– 0.039	0.047	0.400	48.6
Meta-regr. model									
Resistance	76	0.076	0.276	93.1	14.5				37.4
Intercept						0.096	0.102	0.349	
SPEI						– 0.074	0.037	0.045	
Observ/treat						– 0.289	0.107	0.007	
Meta-regr. model									
Recovery	45	0.180	0.425	97.1	34.6				62.6
Intercept						0.204	0.140	0.146	
SPEI						0.141	0.069	0.041	
Thin. year						0.012	0.009	0.199	
Meta-regr. model									
Resilience	56	0.096	0.309	93.9	16.5				42.6
Intercept						– 0.136	0.054	0.012	
SPEI						– 0.124	0.042	0.003	

df are the degrees of freedom, τ^2 is the estimate of total amount of heterogeneity in the size effect, that is, the slope of the linear relationship between each resilience component (resistance, recovery, and resilience) and the stand relative basal area calculated on the maximum value for the species in the study (site-specific); τ is the square root of the estimate of total heterogeneity; $I^2(\%)$ is the percentage of total variability due to heterogeneity; H^2 is the ratio between total variability and within-study variance; estim. is the estimate of the mean size effect for random-effect models, and of moderators for meta-regression models; s.e. is the estimate standard error; p indicates the estimate significance; AICc is the corrected Akaike's information criterion of the model; intrcpt is the intercept; SPEI is the Standardized Precipitation-Evapotranspiration Index calculated for different periods (for resistance, from July to September for the northern hemisphere, from January to March for the southern hemisphere; for recovery, from January to September for the northern hemisphere, from previous year July to current year March for the southern hemisphere; for resilience, from previous year August to current year April for the northern hemisphere, from previous year February to previous year October for the southern hemisphere); Thin. year is the number of years from the last thinning (if any) before drought; Observ/treat is the study design, that is, "observational," for comparisons between non-manipulated stands with different basal areas, or "treatment," which involved comparisons between different thinning intensities.

(March for the southern hemisphere, September for the northern hemisphere) significantly improved the meta-regression model fit ($p < 0.05$), as the influence of competition on resistance was stronger for moderate, rather than for severe, droughts (Table 1; Supplementary Table 3). When using species-specific (instead of site-specific) relative basal area to assess competition influence on resistance, we obtained slightly more heterogeneous results (Supplementary Table 4), but the mean effect size and its significance were unchanged. Model outputs were robust to influential cases and outliers. Indeed, removal of one observation at a time did not affect mean effect size estimate (always negative at $p < 0.001$; Supplementary Table 5). Inclusion of outliers increased heterogeneity, but had a negligible effect on the mean effect size (Supplementary Table 6).

Meta-analysis on Growth Recovery

The average slope (mean effect size) of the relationship between relative stand basal area and recovery was + 0.132 ($p = 0.04$; Table 1, Figure 4), that is, recovery was generally higher in denser stands. The heterogeneity among the investigated

cases was higher than for resistance ($\tau^2 = 0.209$; $I^2 = 97.5$). The 9-month SPEI at the end of summer (March for the southern hemisphere, September for the northern hemisphere) and the number of years elapsed between the drought and the last thinning had a positive influence on the effect size (Table 1; Figure 5). As for resistance, using species-specific relative basal area resulted in slightly higher heterogeneity (Supplementary Table 4), but in this case, the mean effect size was not significant. Leaving out one observation at a time (Supplementary Table 5) slightly affected effect size estimates. Inclusion of outliers increased the heterogeneity statistics and the mean effect size (Supplementary Table 6).

Meta-analysis on Growth Resilience

The mean effect of competition on resilience was not significant (– 0.039, $p = 0.40$) (Table 1, Figure 4). Heterogeneity was intermediate between that of resistance and recovery ($\tau^2 = 0.111$; $I^2 = 94.8$). The 9-month SPEI at mid-spring (October for the southern hemisphere, April for the northern hemisphere) negatively affected the effect size ($p < 0.01$; Table 1). The model on species-

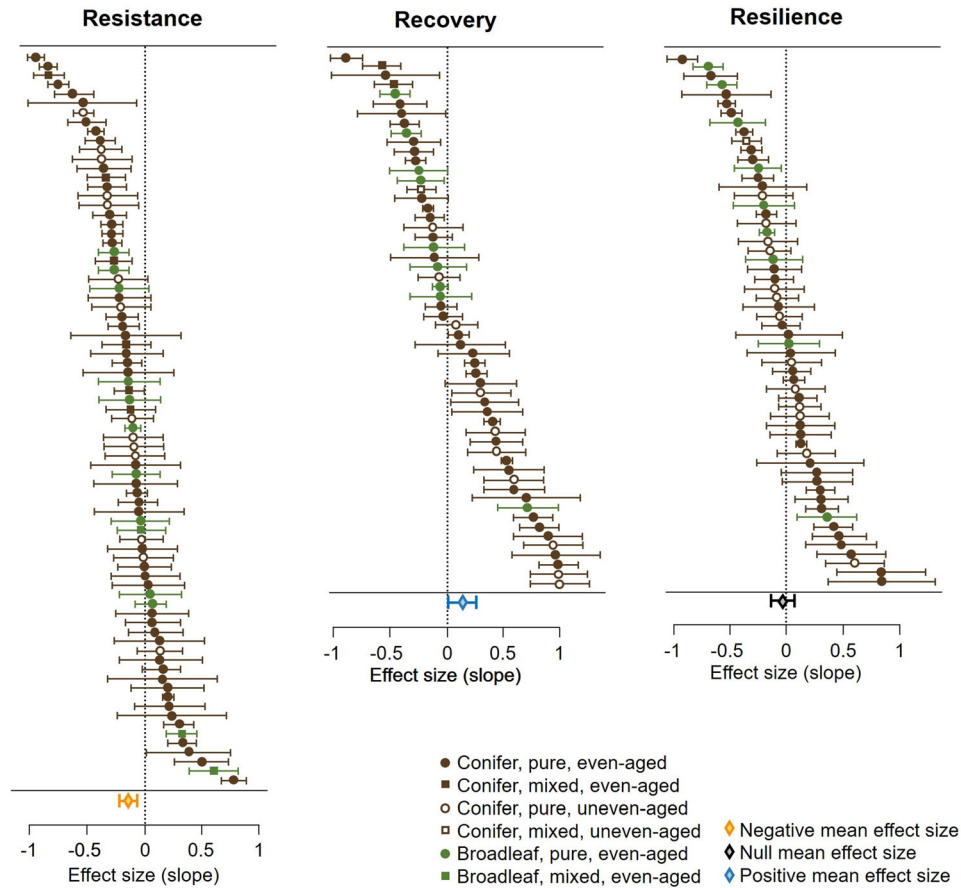


Figure 4. Graphical display (forest plots) of the estimated results of meta-analysis on resistance (left panel), recovery (central panel), and resilience (right panel). For each case, the circle or the square (see the key for symbol description) represents the effect size, that is, the slope of the linear relationship between site-specific relative basal area and resistance, recovery, and resilience, with confidence interval bars. Dotted vertical lines separate positive and negative slopes. Diamonds (see the key for symbol description) at the bottom of the plots display the mean effect size, with confidence interval bars, estimated in the random-effect meta-analysis model.

specific relative basal area provided similar size effect estimate (Supplementary Table 4). Removal of one observation at a time did not lead to significant effect size estimate, nor did the inclusion of outliers improve the model fit (Supplementary Tables 5 and 6).

Publication Bias

For resistance, recovery, and resilience, studies based on larger samples showed more negative effect sizes (for both models using species-specific or site-specific relative basal area, Supplementary Fig. 2 and Supplementary Table 7). Publication year did not affect the effect size in any model (Supplementary Fig. 3 and Supplementary Table 7).

DISCUSSION

General Patterns of Competition Effects on Tree Growth Response to Drought

Our synthesis of research shows that the influence of competition on tree growth response to drought is highly variable. Although the literature often assumes that high stand density exacerbates drought influence on growth (Ammer 2016; del Río and others 2017; Pretzsch 2020; van Mantgem and others 2020), our analysis demonstrates that such an effect is not universal and differs across the investigated response descriptors. Mean sensitivity, an estimate of growth dependency on environmental variability, was not consistently affected by competition (vote counting analysis). However, in most investigated cases, a tighter coupling of growth to water availability was observed in high-

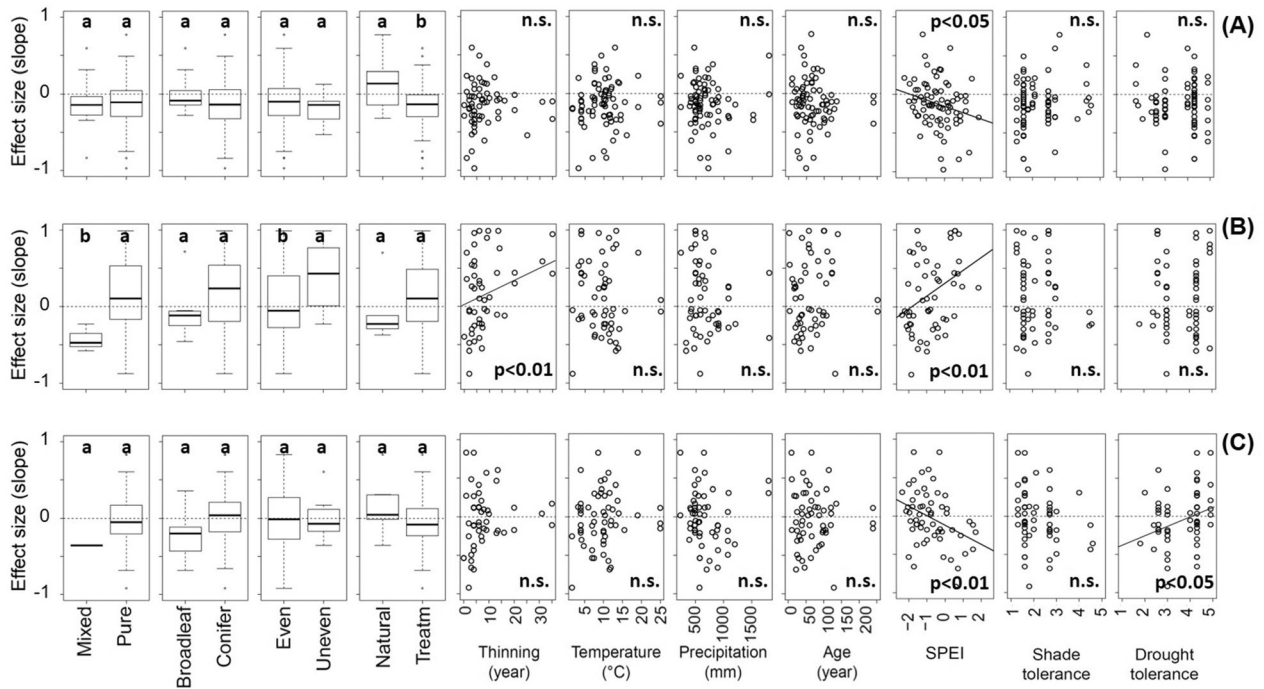


Figure 5. Resistance (A), recovery (B), and resilience (C) effect size across stand and climate characteristics, drought intensity (SPEI) and species shade and drought tolerance. For resistance, SPEI is computed from July to September in the northern hemisphere, from January to March in the southern hemisphere. For recovery, SPEI is computed from January to September in the northern hemisphere, from previous year July to current year March in the southern hemisphere. For resilience, SPEI is computed from previous year August to current year April in the northern hemisphere, from previous year February to previous year October in the southern hemisphere. In the boxplots, different letters correspond to significantly different means. In the scatterplots, regression line (solid line) is presented for significant models ($p < 0.05$).

er- versus lower-density stands, contradicting the classical idea that competition reduces inter-annual growth variability, and masks climate influence on radial growth (Schweingruber and others 1990).

The three components of resilience were differentially affected by competition. Overall resistance, which quantifies the growth reaction during drought events, was lower in stands with higher basal area. Trees in dense stands have higher rainfall interception, lower access to groundwater and faster water depletion (López and others 2003; Annighöfer 2018). Therefore, during dry years, soil water deficit starts earlier and becomes more severe for trees in denser stands, resulting in stronger growth reduction (Brèda and others 1995; Brown and others 2005; Moreno and Cubera 2008; Klein and others 2013). Although lower competition intensity generally mitigated tree growth reduction during drought, it did not systematically improve resilience. One possible explanation is that competition does not directly affect tree functional and structural traits that allow trees to return to pre-disturbance growth rates (Moreno-Gutiérrez and others 2012; Fernández-de-Uña and others 2016).

Also, drought carry-over effects are not always more severe in denser stands due to higher water depletion (Brown and others 2005; Clark and others 2016).

Somewhat unexpectedly, competition had a positive influence on recovery; however, before inferring possible ecological and physiological causes, we must consider interdependence between the resilience components (Lloret and others 2011; Pretzsch and others 2013). As calculated in our dataset, recovery was strongly and negatively related to resistance, as also found by Gazol and others (2018), Hoffmann and others (2018), and Schwarz and others (2020). Because denser stands had, on average, lower resistance than low-density stands, but resilience was on average constant, recovery was also inevitably higher in high-density stands. Such inter-relationships (particularly between resistance and recovery) should be considered before interpreting the outcome of this, or any analysis of resilience components.

Large Variability Among Cases

The lack of universal patterns of competitive influence on growth response to drought, in particular for recovery and resilience, was likely due to multiple causes. First, the assessment of the three resilience component indices was quite variable among studies (for example, different sampling design, reference period for the indices computation, criteria for drought identification), and this can lead to different results as extensively discussed by Schwarz and others (2020). The computation of resilience and recovery components is particularly problematic, as the time for recovery varies across species and site conditions (Anderegg and others 2015; Gessler and others 2020).

The observed variability could be also related to climate, site, and stand differences among cases, which we explored through meta-regression. Tree response to drought is certainly species-specific (McDowell and others 2008; Klein 2014; Anderegg and others 2015; DeSoto and others 2020), but we found that competition effects on the resilience components did not differ between conifers and broadleaves, and among species with different drought and shade tolerance. Yet, we cannot exclude differences among species at the local scale or for specific drought events, as they might depend on factors not investigated in our analysis, such as soil characteristics and site-specific phenology (Lévesque and others 2014; Merlin and others 2015; Gillerot and others 2020).

The intensity of drought can also play a critical role on tree response to water stress (Kannenbergh and others 2019). For moderate droughts, we found larger differences in resistance, recovery, and resilience between low- and high-density stands, whereas during intense drought events, all stands were similarly affected irrespective of density. This corroborates the idea that the stand-level competition influence on resistance is mostly related to soil water availability. Denser stands deplete water storage earlier (Simonin and others 2007; Cabon and others 2018; Andrews and others 2020), and thus soil moisture deficit occurs even during moderate droughts. However, during strong and prolonged dry periods, soil water is depleted even in low-density stands, which then experience significant growth reduction. Still, the intensity of drought depends not only on meteorological conditions (as assessed through the SPEI), but also on topography and soil characteristics. This information is inconsistently reported across studies (for example, different soil classification systems, different measures of soil water potential, and con-

tent), but future research ought to consider such factors at the stand scale (Field and others 2020).

The intensity and timing of thinning likely affects tree growth response to drought. Despite the general positive effects of density reduction on tree physiology (Giuggiola and others 2016), heavy thinning likely stresses the remaining trees for a few years. For example, canopy microclimate can be strongly altered, increasing individual tree transpiration in the immediate post-intervention period (Aussenac 2000; Tsamir and others 2019). This might explain why we observed both positive and negative effects of recent thinning on recovery. Furthermore, heavy crown cover reduction might increase soil evaporation and surface runoff for many years, especially at xeric sites, or promote colonization of shrubs that compete for water in the upper soil layers (Brown and others 2005; Raz-Yaseef and others 2010). In contrast, low reductions in density might be ineffective at increasing stand water availability during droughts (Stednick 1996). Intermediate densities could represent the best compromise between high stand leaf area, which rapidly exhausts water availability, and low crown cover, which exposes the soil to evaporation and understory transpiration (Gebhardt and others 2014; Cabon and others 2018). Such nonlinear influence of stand density on drought responses deserves more investigation in future studies. Furthermore, the effects of thinning are variable in time (D'Amato and others 2013; Sohn and others 2013). For example, any positive effect of light thinning might vanish after few years, due to canopy closure. A single thinning operation can improve stand conditions for just a few years, and regular management is needed to the maintenance of reduced stand densities in the long term (Pretzsch 2020).

Research Gaps and Indications for Future Studies

Our review revealed interesting geographical shortcomings within the available literature, knowledge gaps, and possible research biases. The majority of the studies we included came from pure conifer stands in temperate regions. Scant information was available for broadleaves, which respond differently to drought than conifers (Anderegg and others 2015; De Soto and others 2020), and for mixed forests, which might be more drought resistant than pure forests (Pretzsch and others 2013; Gillerot and others 2020). Unfortunately, there were few studies available from semiarid and tropical regions, the southern hemisphere, and Asia. This was partially due to the

shortage of species forming annual rings in these regions (Zhao and others 2019), which make impossible the calculation of tree ring-based descriptors of growth response to drought. Somewhat surprisingly, northern countries with long forestry tradition such as Canada, Russia, and Fennoscandian countries were also underrepresented. Future investigation in these areas, also susceptible to increasing drought (Allen and others 2015), is urgently needed.

The number of papers considered in our analysis increased in recent years, but the outcomes of these studies did not change over time (no temporal bias, Koricheva and Gurevitch 2014). However, we noted that some titles, abstracts and conclusions stress the negative effect of competition on the three resilience components, despite significant results that occurred for only some species, sites or drought events. The tendency to publish studies, or to highlight results, in agreement with current theories is a common pattern in many research fields (Dickersin 2005). Specifically, we argue that there is likely a risk to convey that high competition always reduces growth resistance and/or resilience to drought, while our meta-analysis clearly demonstrates that is not the case.

We also explored how the study design influenced research outcomes, to provide indications for future research. The cases from “treatment” studies, as well as those based on a larger number of sampled trees, showed more consistent size effects (especially for resistance) compared to “observational” studies and those based on few trees. Applying different silvicultural treatments to homogenous stands (“treatment” studies) is important if one wants to discern the effect of competition from other factors that can influence growth response to drought. Confounding factors cannot be ruled out when comparing stands differing in competition intensity for natural causes (as for “observational” studies).

Implications for Forest Management

The results of our review and meta-analysis have important implications for management strategies aimed at mitigating the negative impacts of drought on forest growth. Although most literature recommends thinning to improve growth resilience to drought, we did not find support for an overall negative effect of competition on this component. The unexpected positive influence of competition on recovery was likely due to the inverse relationship of this component with resistance. This calls into question not only current recommenda-

tions to improve tree growth after drought, but more generally, poses an issue with respect to how we assess forest capacity to return to the initial, or a new stable-state state, after disturbance (resilience and recovery), as discussed in recent papers (Gessler and others 2020; Nikinmaa and others 2020; Schwarz and others 2020; Albrich and others 2020). However, we showed that reducing competition in high-density stands can increase growth resistance to drought. Still, large and mostly unexplained variability among the investigated cases emphasizes the need for more extensive research, especially in underrepresented regions and for mixed and broadleaf stands, and an integration of mechanistic information to better understand tree-water relationships. We suggest that future studies seeking to determine the competition effects on growth response to drought should explicitly consider the particularities of the species, stand, stage of development and local climate. Identifying the factors acting on the interactions between competition and drought at the local scale can improve management strategies aimed at building forest adaptive capacity.

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DATA AVAILABILITY

The dataset used in this study is available as Supplementary material.

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