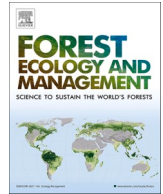


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Species stratification and weather conditions drive tree growth in Scots pine and Norway spruce mixed stands along Europe

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ABSTRACT

Mixed forests are suggested as a strategic adaptation of forest management to climate change. Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) are tree species of high economic and ecological value for European forestry. Both species coexist naturally in a large part of their distributions but there is a lack of knowledge on the ecological functioning of mixtures of these species and how to manage such stands. This paper analyses these species' intra- and inter-specific competition, including size-symmetric vs. size-asymmetric competition, and explore the effect of weather conditions on tree growth and competition. We studied basal area growth at tree level for Scots pine and Norway spruce in mixed versus pure stands in 22 triplets of fully-stocked plots along a broad range of ecological conditions across Europe. Stand inventory and increment cores provided insights into how species mixing modifies tree growth compared with neighbouring pure stands. Five different competition indices, weather variables and their interactions were included and checked in basal area growth models using a linear mixed model approach. Interspecific size-asymmetric competition strongly influenced growth for both tree species, and was modulated by weather conditions. However, species height stratification in mixed stands resulted in a greater tree basal area growth of Scots pine ($10.5 \text{ cm}^2 \text{ year}^{-1}$) than in pure stands ($9.3 \text{ cm}^2 \text{ year}^{-1}$), as this species occupies the upper canopy layer. Scots pine growth depended on temperature and drought, whereas Norway spruce growth was influenced only by drought. Interspecific site-asymmetric competition increased in cold winters for Scots pine, and decreased after a drought year for Norway spruce. Although mixtures of these species may reduce tree size for Norway spruce, our results suggest that this could be offset by faster growth in Scots pine. How inter-specific competition and weather conditions alter tree growth may have strong implications for the management of Scots pine-Norway spruce mixtures along the rotation period into the ongoing climate change scenario.

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1. Introduction

Currently, mixed stand management has been proposed as preferable to monocultures due to their potential to provide a reasonable combination of timber production, ecological functions and forest ecosystem services (Forrester, 2017; Jonsson et al., 2019). Mixed stands can lead to over-yielding (Pretzsch et al., 2015; Pretzsch and Schütze, 2009) and enhance temporal stability (Bauhus et al., 2017; del Río et al., 2017). In addition, mixed forests may be more resilient and resistant to biotic and abiotic disturbances and stresses resulting from climate change (Guyot et al., 2016; Pretzsch et al., 2013). For example, mixed forest stands may improve resilience to extreme and increasingly frequent drought events in Europe (Jactel et al., 2017), although contrasting results were found depending on species composition (Grossiord, 2019; Steckel et al., 2020). Trees may exhibit different climate-growth responses depending on the species of neighbouring trees. Such differences are crucial for understanding the effects of climate change on the growth and vulnerability of forests.

Coniferous stands in Europe dominate forest production on mineral soils, where site productivity does not allow economically-feasible wood production from broadleaved species (Löf et al., 2019; Nilsson et al., 2012). Scots pine (*Pinus sylvestris* L) and Norway spruce (*Picea abies* L. Karst) are very common on these types of sites. Both species are widely distributed from central to boreal and eastern Europe (Fig. 1). In addition, they are of major economic importance and great ecological significance for the European forestry sector (Coyette and Schenk, 2019). Consequently, they have been often cultivated in monocultures. Spontaneously-formed mixed stands have routinely been neglected due to an absence of clear forest management guidelines for mixtures and the belief that mixed stands are economically uninteresting (Agestam et al., 2005). Although previous studies analysed the interaction between both species locally (Jonsson, 2001, 1999; Yanai, 1992), Scots pine-Norway spruce mixed forests have received currently more attention in central and northern Europe (Holmström et al., 2018;

Wellhausen et al., 2016), since there is some scientific evidence that they can provide a wider range of ecosystem services than monocultures (Bielak et al., 2014; Felton et al., 2016).

Simplified forest structures in models, parameterized with data from monocultures, have been used in decision support to circumvent the limited knowledge of mixing effects between species (Shanin et al., 2019). Nonetheless, the main difference between monocultures and mixed stands is the inherent complexity of tree species interactions, resulting in a species-specific response, e.g. modifying growth or resilience to biotic and abiotic disturbances (Ammer, 2019; Grossiord, 2019; Jactel et al., 2017). Competition and facilitation (i.e. one or more species may influence other species positively) have been identified as key mechanisms driving species interaction in mixed stands (Ammer, 2019). If facilitation or competition reduction occurs, then, an increase of growth or resilience to abiotic events is expected in mixed stands compared to monospecific ones (Ammer, 2019; Grossiord, 2019).

Individual tree growth models can characterize the specific competitive situation between a subject tree and its neighbourhood (Larocque, 2018). Usually, this is based on competition indices, which are the most appropriate way to understand how growth is affected by competition between individuals of different species and sizes (Porté and Bartelink, 2002). The mode of competition, i.e., size-symmetric or size-asymmetric, allow to identify possible interaction between trees according to their size. Completely size-symmetric competition occurs where resource uptake among competitors is independent of their relative sizes, and size-asymmetric competition occurs where the largest plants obtain more of the disputed resources (Schwinning and Weiner, 1998). The use of spatially-explicit competition indices, which considers information about the physical location of individual trees, species identity and often the tree's dimension, has proven very useful when studying growth and yield of mixed-species stands (Brunner and Forrester, 2020; Houtmeyers and Brunner, 2020; Riofrío et al., 2019). Empirical growth and yield models commonly include stand, site, and management effects and have been developed based on forest

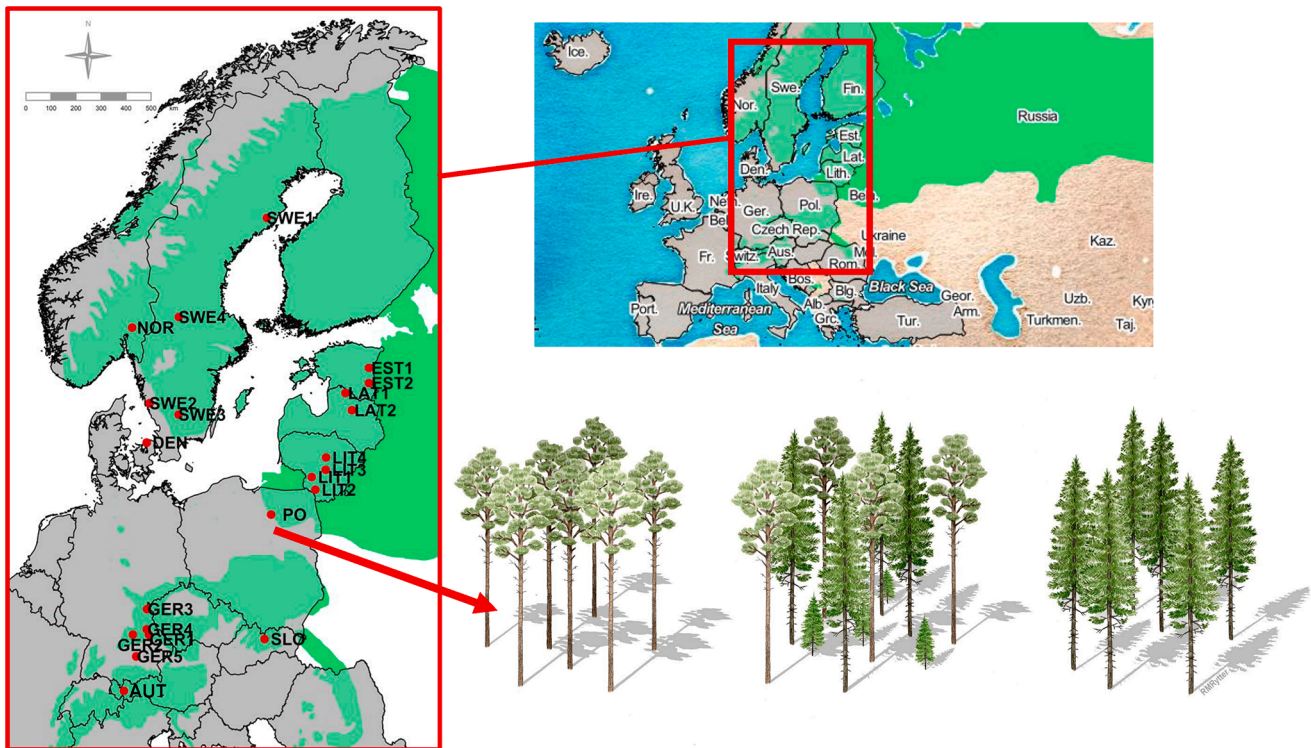


Fig. 1. Location of the Scots pine-Norway spruce triplets in Europe (top-right). Red dots are triplet locations and the green area is the overlap of the two species' distributions according to the EUFORGEN programme (<http://www.euforgen.org/>). Stand plot representation of a triplet (below-right). Drawing of pure and mixed stands by Rose-Marie Rytter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inventories or tree ring chronologies from local experiments. However, such models were originally designed to be climate-independent and, hence, they fail to evaluate future scenarios since they do not include causal relationships (Larocque, 2018; Rohner et al., 2016). On the other hand, tree ring chronologies used to assess the climate forcing of tree growth generally exclude tree competition or species interaction (Büntgen et al., 2007). Some studies have shown tree growth sensitivity to climate, increasing with decreasing competition intensity (Sánchez-Salguero et al., 2015), so studies based only on a dendrochronological approach may not be adequate to estimate tree-level growth. Process-based models are generally considered powerful tools to improve understanding of the processes that regulate forest ecosystems, as they are based on the description of cause–effect relationships. However, their predictions may be not necessarily accurate or biased (Larocque, 2018) at typical management scales in comparison to traditional empirical approaches (Calama et al., 2019). Therefore, competition and tree-level climate–growth sensitivity should be explicitly taken into account (Sánchez-Salguero et al., 2015). However, the combination of climate and competition structures in tree-growth models remains scarce (Calama et al., 2019; Sánchez-Salguero et al., 2015), and is rarer still in studies of mixed stands (González de Andrés et al., 2018; Houtmeyers and Brunner, 2020; Manso et al., 2014; Mina et al., 2018; Navarro-Cerrillo et al., 2020; Schwarz and Bauhus, 2019). In this study, we go one step further and use annual weather information and spatial competition structures to model species-specific growth. The interaction of competition and climate on tree growth has been the focus of some recent studies (Fernández-de-Uña et al., 2015; Ford et al., 2017; Rollinson et al., 2016). Although it is well known that interactions between species vary with climatic conditions (del Río et al., 2014), previous research on mixtures is limited (Oboite and Comeau, 2020).

There are a few sufficiently randomized and replicated experiments comparing Scots pine and Norway spruce in monocultures and mixtures (Holmström et al., 2018), whose results cannot be generalized beyond the study location. While Drössler et al., (2018) and Ruiz-Peinado et al., (2020) used large scale data from Northern and Central Europe for the Scots pine and Norway spruce mixtures, their research focused on stand-level productivity. Here, we used information from 22 triplets (monocultures and mixture of both species in each location), established along a broad range of ecological conditions throughout Europe, to evaluate the differences in tree radial growth of Scots pine and Norway spruce in mixed versus monospecific stands. We fitted an individual-based and spatially-explicit model to account for the relative positions and properties of all competing trees for each target tree. The main objective was to improve our understanding of the interactions between species and to identify the main drivers of Scots pine and Norway spruce growth in mixed stands. To achieve this, we adopted two specific aims: 1) to explore intra/inter-specific and size-symmetric/asymmetric competition effects, and 2) to identify weather conditions that influence tree growth for the two species.

2. Material and methods

2.1. Study sites and sampling design

The experimental design was based on the ‘triplet’ concept (Pretzsch et al., 2014). At each location, three plots were established: one in a mixed-species stand of Scots pine and Norway spruce and one in a monoculture of each species (Fig. 1). In total 22 triplets (66 plots) were installed along a comprehensive ecological gradient across ten countries in Europe. The study area covers the natural overlap of the species’ distributions in Europe, reaching from the south-western region in Austria to the northern and eastern regions in Sweden and Latvia, respectively (Fig. 1). The three plots of each triplet had similar soils and topography to allow meaningful comparisons between mixtures and monocultures, and were within 1 km of each other. The stands were even-aged, fully stocked with approximately maximum density and not

thinned in the last 10 years. We chose this design to minimize residual site and stand effects such as soil, microclimate, tree genetics and management effects (Steckel et al., 2019). Individual plot size ranged from 0.03 to 0.55 ha (mean = 0.12 ha) and stand age from 45 to 115 years (mean = 60 years). In the mixed plots the minimum proportion (based on basal area) of either of the two species was 10%, although the average was close to 50% (Table 1). The proportion of additional tree species was low in pure plots (on average < 10% of total basal area) and consisted of suppressed trees when present.

Stand elevations ranged between 35 and 995 m.a.s.l. (mean = 260 m.a.s.l., see Table S1). This study intentionally included a range of climatic conditions from dry and warm to moist and cold sites. The mean annual temperature ranged from 1.8 to 8.4 °C (mean = 6.2 °C), with an annual precipitation between 586 and 1,037 mm (mean = 708 mm) according to 1988–2017 data. Site productivity was reflected in the site index values, here defined as the quadratic mean tree height at age 100 (Elfving and Nyström, 2010; Wikström et al., 2011), which ranged from 24.4 to 39.0 m (mean = 32.0 m) in the monospecific stands studied (Table S1).

2.2. Data collection and preparation

The plots were established and measured in 2018, except the triplets located in Germany which were set up in 2013, following the same standardised protocol described in Pretzsch et al., (2015). All living and dead trees with a diameter at breast height larger than 70 mm were measured. Diameter at breast height (dbh), tree height (h), crown base height (cbh) and crown radii of all living trees were measured in the four cardinal directions (N, E, S, W). The crown length (cl), mean crown width (cw) and crown projection area (cpa) were also inferred from the former variables. The position of each tree was recorded relative to the central point of the plot. Two increment cores (from north and east cardinal directions) were taken from at least 20 dominant living trees plus 10 additional living trees covering the rest of the diameter distribution for each species and plot. Tree annual radial growth increments were measured for every increment core with an accuracy of 0.01 mm. Crossdating was performed for each species and plot using the COFECHA software (Grissino Mayer, 2001). We discarded cores that were broken, unreadable or minimally correlated with the master chronology (coefficient < 0.423, based on the critical inter-series correlation according to the sample length at the 99% confidence level; see Grissino Mayer, 2001). This left a total of 2,924 increment cores for further analysis. Tree basal area increment (BAI, cm² year⁻¹) for each year of the tree chronologies was calculated based on the annual ring width to reduce bias, as BAI is more related to volume growth than one-dimensional tree ring widths (Biondi and Qeadan, 2008). To avoid changes in stand structure which could modify tree competition status, only the 5 years before the sampling date were considered for the BAI calculation. The stand basal area surrounding each cored tree was measured using the Spiegel Relascope based on the Angle Count Method (Bitterlich, 1948). Mean tree and stand characteristics for the triplets included in the study are summarized in Table 1.

Weather data were obtained from meteorological stations near each triplet (monthly mean, maximum and minimum temperature, and total monthly precipitation) for the last five years before the sampling date. When they were not available, the data were provided by national meteorological services via 0.5° resolution gridded data. Monthly values of the water balance (WBAL) and of the standardised precipitation–evapotranspiration index (SPEI, Vicente-Serrano et al., 2010) were calculated from the weather data. Finally, the monthly weather variables (mean, minimum and maximum temperature, precipitation, WBAL, evapotranspiration and SPEI) were aggregated to seasonal averages, i.e. for periods of two, three, six, nine months, and a complete year, beginning at the previous year’s August and ending at September of each sample year. Table 2 shows the main weather variables included in the analysis for the study period.

Table 1

Tree and stand characteristics and competition status by species and composition in the dataset. BAI: Tree basal area increment. dbh: diameter at breast height. h: mean height. cbh: crown base height. cl: crown length. cw: crown width. cpa: crown projection area. BA: stand basal area. BAP: Species mixing proportion based on basal area. N: density. AL_{intra}: size-asymmetric competition index for larger trees of the same species according to the Hegyi index in an influence zone of 20 m from target tree. AL_{inter}: size-asymmetric competition index for the larger trees of the different species according to the Hegyi index in an influence zone of 20 m from target tree. SCI: Structure-based Competition Index.

Variable	Scots pine				Norway spruce			
	Pure		Mixed		Pure		Mixed	
	mean	range	mean	range	mean	range	mean	range
Tree variables								
BAI (cm ² year ⁻¹)	9.2	2.3–39.1	10.6	2.7–67.0	10.1	3.9–58.1	9.7	1.2–58.2
dbh (cm)	23.9	7.0–72.2	27.7	8.0–58.3	22.9	7.0–77.4	19.7	7.0–57.3
h (m)	21.3	6.6–32.3	24.1	10.1–37.0	21.7	4.1–34.8	19.3	3.4–40.3
cbh (m)	15.5	2.0–24.4	16.1	2.4–27.3	11.1	1.5–25.4	8.8	0.5–21.8
cl (m)	7.4	0.5–17.8	7.7	1.0–22.0	10.6	0.9–27.6	10.5	1.4–29.3
cw (m)	3.7	0.5–8.3	4.0	0.7–9.5	3.7	0.7–8.1	3.6	0.8–10.4
cpa (m ²)	12.1	0.2–54.1	13.8	0.3–70.1	12.0	0.4–50.9	11.0	0.6–84.3
AL _{intra}	5.3	0–29.8	2.2	0–15.9	8.0	0–34.6	3.9	0–20.0
AL _{inter}	0.3	0–4.1	1.5	0–17.1	0.5	0–10.6	4.7	0–18.9
SCI	0.2	0–0.8	0.2	0–0.7	0.2	0–0.8	0.3	0–0.9
Stand variables								
Age (years)	53	45–78	57	41–85	60	45–93	55	45–93
BA (m ² ha ⁻¹)	42.8	18.5–60.3	23.8	6.9–40.9	49.7	20.8–63.4	24.5	9.1–42.8
BAP (%)	95.8	90.2–100	49.0	32.2–63.5	93.2	90.1–100	49.5	36.4–67.6
N (stems.ha ⁻¹)	854	305–1400	411	105–872	1154	480–1930	775	170–1870

Table 2

Weather variables considered in the analysis. P_a: Mean annual precipitation (mm). T_a: Mean annual temperature (°C). T_{maxAP-sp}: mean daily maximum temperature from April to September (°C); T_{maxDec}: mean daily maximum December temperature (°C); WBAL_{JNJLAG}: mean monthly climatic water balance (precipitation minus potential evapotranspiration) from June to August (mm); SPEI_{JNJLAG}: mean of monthly Standardized Precipitation-Evapotranspiration Index from June to August; SPEI_{MyJnJl}: mean of monthly Standardized Precipitation-Evapotranspiration Index from May to July.

	P _a	T _a	T _{maxAP-SP}	T _{maxDec}	WBAL _{JNJLAG}	SPEI _{JNJLAG}	SPEI _{MyJnJl}
Mean	708	6.0	16.7	1.6	-22.5	0.2	0.2
range	410–1122	3.0–8.9	3.2–24.2	(-9.5)–11.2	(-89.7)–73.6	(-1.8)–2.1	(-1.9)–2.1

2.3. Competition indices

Competition indices allow us to quantify the spatial structure of a forest stand by describing the spatial relationships between the core tree and its immediate neighbouring trees (Pretzsch and Biber, 2010). For that, we used five types of competition indices based on different concepts (Table 3): the basal area (Wykoff et al., 1982), Hegyi's competition index (Hegyi, 1974), angle count sampling estimate (ACS; Bitterlich, 1948), the KKL position dependent competition index (Pretzsch, 2009), and the Structure-based Competition Index (SCI, Hui et al., 2018). For the first two indices the zone of influence was defined in advance, so we used 5, 10, 15 and 20 m from the target tree. Note that basal area is distance-independent while Hegyi index is a distance-dependent index which weights the competition based on distance from the target tree. ACS computes the stand basal area surrounding the

Table 3

Features of the competition indices used in the analysis.

Index	Source	Competitor identification	Size competition mode	Species identification
BA	Wykoff et al., 1982	Influence zone pre-fixed	symmetric/asymmetric	inter/intra competition
Hegyi's	Hegyi, 1974	Influence zone pre-fixed	symmetric/asymmetric	inter/intra competition
ACS	Bitterlich, 1948	Size and distance to target tree	symmetric	inter/intra competition
KKL	Pretzsch, 2009	Crown overlap	symmetric	inter/intra competition
SCI	Hui et al., 2018	Crown overlap	asymmetric	inter-species competition

target tree based on Bitterlich's relascope, hence, is unable to define basal area for larger or smaller trees than the subject one (compared to the first competition index). ACS was recorded during the field work as mentioned previously. For KKL and SCI competition is assessed from crown overlapping, by a vertical search cone or by horizontal distance respectively. However, SCI only considers trees larger than the target one, i.e., it is a size-asymmetric competition index. This competition index includes mingling to describe the species spatial heterogeneity; dominance, to reflect the size difference; aggregation, to describe the regularity of neighbourhood distribution; and crowding, to describe the degree of crown adjacency between the reference tree and its neighbouring trees (see Hui et al., 2018 for more detail). The edge effect for all competition indices was minimized by the construction of a 10 m wide exterior buffer zone around the sample plots. In addition, we used the "mirror technique" to correct tree competition indices when the influence zone ranged outside the buffer zone, by shifting the stand structure for each plot, which is then surrounded by eight identical stand sections (Pretzsch, 2009).

The basal area and Hegyi's competition indices were subdivided considering size-symmetric and/or size-asymmetric competition. Thus, four different competition structures were tested for the inclusion in growth modelling combining both size-symmetric and asymmetric indices (del Río et al., 2014):

S – only size-symmetric index.

AL – only size-asymmetric competition from larger trees index.

S + AL – combining size-symmetric and asymmetric indices.

AL + AS – combining both size-asymmetric indices (larger and smaller trees).

These indices assume that the species compete in a similar way, i.e. intra- and inter-specific competition are similar. Therefore, in addition to all the previous competition indices and structures, we also considered the basal area and Hegyi's competition indices split into intra- and inter-specific competition components. The KKL competition index was also split by species identification into intra- and inter-competition indices, but ACS was not since data were not always available for species identity from the inventory. SCI only considers larger trees from species different from the target tree, so it was only possible to consider size-asymmetric and inter-specific competition (Table 3). Finally, we used 100 different combinations of competition indices (48 each for BA and Hegyi's by considering 4 influence zones, 2 for KKL and one each for ACS and SCI), which were included and tested in the growth model approach for each species.

2.4. Modelling

2.4.1. Data assessment

Stand structure in terms of tree size was considered to explain single-tree growth in mixed and pure stands. For that, we evaluated differences in BAL, dbh and tree height in mixed vs. monospecific stands, according to the following model:

$$y_{ijl} = \alpha_0 + \alpha_1 \text{Pure}_{ijl} + u_i + v_{ij} + \rho_{ijl} + \varepsilon_{ijl} \quad (1)$$

where y_{ijl} is the tree variable studied for a species from triplet i , plot j and tree l ; Pure is a dummy variable representing pure stand composition; α_0 and α_1 are the regression coefficients for mixed and pure stands respectively; random effects were $u_i \sim N(0, \sigma_i)$ for triplet, $v_{ij} \sim N(0, \sigma_{ij})$ for plot and $\rho_{ijl} \sim N(0, \sigma_{ijl})$ for tree and $\varepsilon_{ijl} \sim N(0, \sigma_\varepsilon)$ is the error term.

2.4.2. Tree growth modelling

The annual basal area increment of the individual trees ($\text{cm}^2 \text{ year}^{-1}$) obtained from core measurements was modelled to test the hypotheses that the basal area growth of a species depends on its size (following the Huggershoff (1936) growth curve) and is modified by its competition status and weather conditions (del Río et al., 2014; Dyer and Fritts, 2006; Mina et al., 2018). The current and previous year's weather variables were included in the tree-growth model. To analyse how weather conditions could modify the competition status, we also included interactions between weather and competition indices in the model.

We used a linear mixed model to represent the hierarchically grouped data structure with correlated observations within the triplets, plots, and trees. We also included the sample core as additional grouping level to consider the increment variance between the tree-ring series from different sample cores (Lara et al., 2013). Although it would have been technically possible to introduce additional random effects on the slope coefficients for the competition and climate covariates, the random-effects structure of our modelling approach only considered the intercept variance. Candidate models different in their random-effects structures were fitted by restricted maximum log-likelihood techniques (REML) (Zuur et al., 2009). Goodness-of-fit of the different models was compared by means of Akaike information criterion (AIC). The fixed part of the model was fitted by using the ML (maximum likelihood) method, which allows comparison of the models according to AICc (Second-order Akaike Information Criterion), ΔAICc (difference of AICc values between the best and the i^{th} model) and Akaike weight (w_i) (Russell, 2016). The model with the lowest AICc and greater w_i was considered the best and most parsimonious model. Finally, the final best model for each species was fitted by the REML method. To obtain normally-distributed residuals and reduce heteroscedasticity, the original dependent variable was natural-log transformed after adding 1 to

avoid undefined values. The final model was constructed as follows:

$$\begin{aligned} \ln(\text{BAI}_{ijl} + 1) = & \alpha_0 + \alpha_1 \text{dbh}_{ijl} + \alpha_2 \ln(\text{dbh}_{ijl}) + \alpha_n \text{tree}_{ijl} + \beta_n \text{weather}_{in} \\ & + \sum \gamma_k \text{CI}_{ijk} + \delta_1 \text{weather}_{in} * \text{CI}_{ijk} + u_i + v_{ij} + \rho_{ijl} + \tau_{ijlm} \\ & + \varepsilon_{ijl} \end{aligned} \quad (2)$$

where BAI_{ijl} is the basal area increment observation in the year n (within the 5 years before the sampling date) of the core m from tree l on plot j of triplet i ; dbh_{ijl} is the diameter at breast height of tree l on plot j of triplet i ; tree is a linear function of tree allometry variables other than dbh (see Table 1); weather is a linear function of site and weather variables for current and previous years n (see Table 2 and Table S1); CI_{ijk} are the k different terms of the competition index for tree l according to the abovementioned size-symmetric and/or size-asymmetric and species composition structures (see Table 3); α_n is a vector for the intercept and regression coefficients of tree variables; β_n is a vector of the regression coefficients for the weather variables; γ_k are the regression coefficients for the competition index variables; δ_1 is the regression coefficient for the interaction between the weather variable and competition index; $u_i \sim N(0, \sigma_i)$ is the triplet random effect, $v_{ij} \sim N(0, \sigma_{ij})$ is the plot random effect; $\rho_{ijl} \sim N(0, \sigma_{ijl})$ is the tree random effect; $\tau_{ijlm} \sim N(0, \sigma_{ijlm})$ is the core direction random effect and $\varepsilon_{ijl} \sim N(0, \sigma_\varepsilon)$ is the error term. Multicollinearity of weather and predictor variables was assessed by means of the variance inflation factor, heteroscedasticity was checked by visual residual plots inspection (Zuur et al., 2009), and partial autocorrelation function plots were inspected for serial correlation. Accordingly, we used an Autoregressive Model AR(1) to consider the time-growth varying processes. The R package 'nlme' (Pinheiro et al., 2015) was used to fit the linear mixed models and 'AICcmovag' (Mazerolle, 2017) for model selection. All analyses were performed in the R statistical environment (R Development Core Team, 2020).

3. Results

3.1. Influence of species-mixing in tree growth

Basal area increment was on average higher in mixed stands than in pure for Scots pine trees, but no differences were found for the increments of Norway spruce growth (Fig. 2 and Table S2). In mixed stands, Scots pine forms the dominant height stratum at the expense of Norway spruce (Fig. 2). Accordingly, there were significant differences in tree height and diameter between mixed and pure stands for both species, with Scots pine bigger and Norway spruce smaller in mixed stands. This could indicate a release from competition for Scots pine in mixed stands at the expense of Norway spruce growth. A higher density of Norway spruce in mixed stands compared to pine (Table 1, $P < 0.001$) may also decrease the competition situation for Scots pine (because spruce is generally smaller and intra-specific competition decreases), but not for Norway spruce.

3.2. Basal area growth models with the best competition index

A model with the Hegyi index and the SCI had the lowest AIC and were selected as final models (Table S3). The Hegyi index had the highest relevance when the zone of influence was defined by a 20 m radius and when only size-asymmetric competition was considered for Scots pine. However, the importance of the Hegyi index and the BA indices was only slightly different. Similarly, the differences were not clear for the first three models in the case of Norway spruce, but the parsimony, and the absence of non-significant parameters clearly

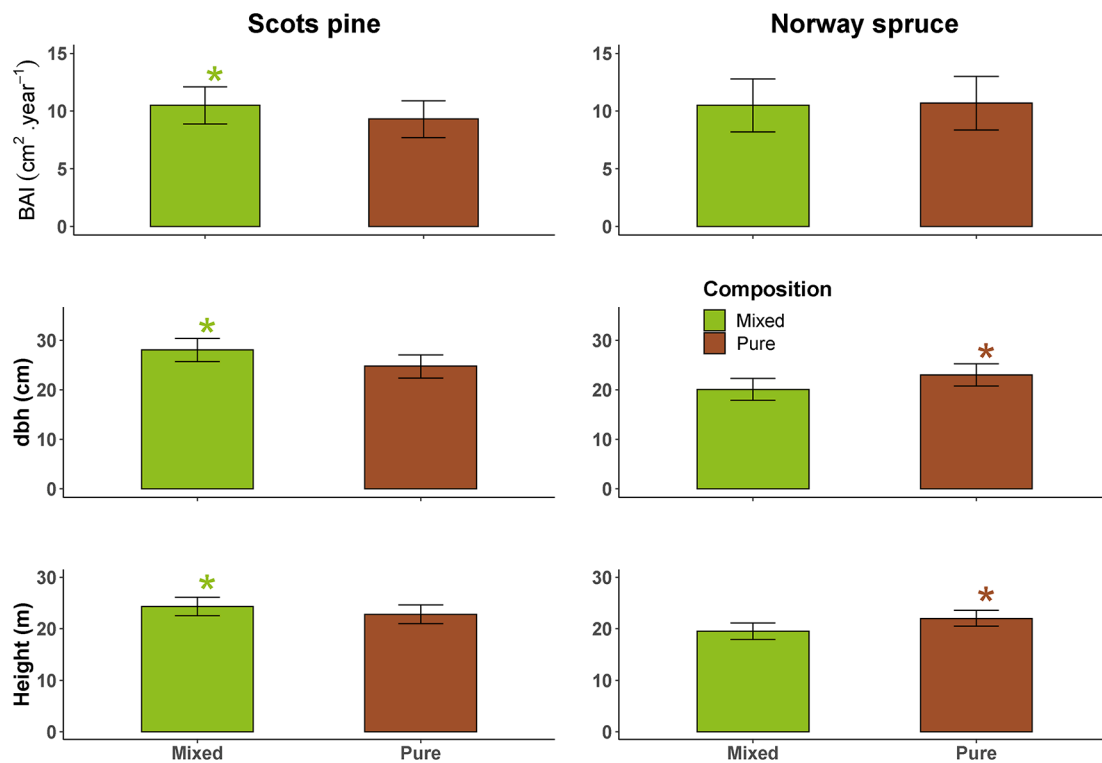


Fig. 2. Main differences in growth and tree size by stand composition (left: Scots pine, right: Norway spruce). Trees were measured in 2018 and the annual BAI growth was calculated for the last 5 years. Error bars show 95% confidence intervals. Asterisks (*) denote significant differences at $p < 0.05$.

Table 4

Parameter estimations and fit statistics for the best growth model for each species (Eq. (1)). dbh_{ij} : tree diameter at breast height (mm); cw: crown width (m); $Tmax_{AP-SP}$: mean maximum daily temperature from April to September of the current year ($^{\circ}C$); $WBAL_{JNJLAG}$: mean monthly climatic water balance (precipitation minus potential evapotranspiration) from June to August of the current year (mm); $SPEI_{JNJLAG}$: mean monthly Standardized Precipitation-Evapotranspiration Index from June to August of the current year; $Tmax_{Dec}$: mean of maximum December temperature of the previous year ($^{\circ}C$); $SPEI_{JnJAg}$: mean monthly Standardized Precipitation-Evapotranspiration Index from June to August of the previous year; $SPEI_{MyJnJl}$: mean monthly Standardized Precipitation-Evapotranspiration Index from May to July of the previous year. Latitude: geographic latitude coordinate ($^{\circ}$). AL_{intra} : size-asymmetric competition index for the larger trees of the same species according to Hegyi (1974) in an influence zone of 20 m from the target tree. AL_{inter} : size-asymmetric competition index for larger trees of the other species according to Hegyi (1974) in an influence zone of 20 m from target tree. SCI: Structure-based Competition Index. Variance parameters as explained in Eq. (1). Asterisks (*) denote interaction between variables. n.s.: not significant. —: not included into the model. AIC: Akaike's information criterion; RMSE: root mean square error.

Model components	Parameter	Scots pine		Norway spruce	
		Coefficient	p-value	Coefficient	p-value
Fixed parameters	α_0 (int.)	-4.223	<0.001	-2.035	<0.001
	α_1 (dbh_{ij})	n.s.	n.s.	n.s.	n.s.
	α_2 ($\ln(dbh_{ij})$)	1.478	<0.001	1.259	<0.001
	α_3 (cw)	0.055	0.002	0.087	<0.001
	β_1 ($Tmax_{AP-SP}$)	0.015	<0.001	—	—
	β_2 ($WBAL_{JNJLAG}$)	—	—	0.001	<0.001
	β_3 ($SPEI_{JNJLAG}$)	0.027	<0.001	—	—
	β_4 ($Tmax_{Dec}$)	0.011	<0.001	—	—
	β_5 ($SPEI_{JnJAg}$)	0.013	<0.001	—	—
	β_6 ($SPEI_{MyJnJl}$)	—	—	0.036	<0.001
	β_7 (Latitude)	0.021	0.0438	—	—
	γ_1 (AL_{intra})	n.s.	n.s.	—	—
	γ_2 (AL_{inter})	-0.056	<0.001	—	—
	γ_3 (SCI)	—	—	-0.212	0.015
	δ_1 ($Tmax_{Dec} * AL_{inter}$)	0.002	0.008	—	—
δ_2 ($SPEI_{MyJnJl} * SCI$)	—	—	-0.043	<0.001	
Variance parameters	σ_i (triplet)	0.145	—	0.231	—
	σ_{ij} (plot)	0.114	—	0.097	—
	σ_{jl} (tree)	0.250	—	0.340	—
	σ_{jlm} (core)	0.192	—	0.138	—
	σ_e (error)	0.288	—	0.334	—
	ϕ (AR(1))	0.646	—	0.661	—
Serial correlation parameter	AIC	665.7	—	3211.1	—
	RMSE	0.244	—	0.288	—
	R^2 marginal	0.460	—	0.463	—
	R^2 conditional	0.791	—	0.807	—

justified the use of SCI. The best model for each species, when different combinations of competition structures were examined (i.e., allowing each size-symmetric and size-asymmetric term to be calculated either with all trees or splitting into intra- and inter-specific competition terms) are shown in Table 4. Both models showed a good fit, with R^2 close to 0.8 when all effects were included and 0.46 when only fixed effects were considered. The tree component explained more basal area increment variance, which emphasizes the importance of the tree's local conditions in the stand. Our results also showed the importance of considering the variance between the sample cores, since it proved to be higher than the variance between the different plots.

Only the logarithmic term of tree diameter in the model was significant (Table 4). This means an almost quadratic increment due to diameter, which is greater for Scots pine than Norway spruce (1.4 and 1.2 power respectively). Accordingly, a higher tree size, measured by diameter or crown width, resulted in a higher basal area increment for both species (Fig. 3). In this sense, differences in crown width for the same diameter size would indicate tree dominance within the stand. For both species, size-asymmetric and inter-specific competition, i.e., competition from larger trees of the other species, was the most important effect in explaining tree basal area growth reduction due to competition (Table 4). However, size-asymmetric and inter-specific competition could be much more important for Scots pine growth than Norway spruce (Fig. 3 and Fig. 4).

Unexpectedly, Scots pine was found to grow faster at higher latitudes. Higher temperature during the growing season and winter time (December) increased annual growth for Scots pine, while Norway spruce was insensitive to temperatures during the time studied (Table 4 and Fig. S1). On the contrary, summer drought in the current and previous years, measured by WBAL or SPEI, reduced the increments of both species; weather effects of the current year were greater than those of the previous year (Figs. S1 and S2). In addition, weather conditions modified the competition status for both species (Fig. 4 and Table 4). Low temperatures during winter (specifically in December of the previous year) decreased tree growth but also increased the inter-specific competition for Scots pine. This would result in a greater growth reduction ratio in mixed stands during cold years, although trees in mixture could continue to grow faster due to a bigger size compared to trees in pure stands (Fig. 4). On the other hand, drought during late

spring and summer of the previous year decreased tree growth and also the inter-specific competition for Norway spruce, i.e., growth reduction was not so pronounced when coexisting with Scots pine during a drought episode. Accordingly, tree growth in mixtures would approximate that seen in pure stands when unfavourable weather conditions occurred for both species (Fig. 4). Therefore, Scots pine would be harmed in mixtures by cold winter temperatures but Norway spruce would release the negative effect of inter-specific competition after drought periods in mixed stands.

4. Discussion

In this study, we analysed competition between Scots pine and Norway spruce through growth models and indices which estimate tree competition status. Our approach also included weather variables and their interactions with competition indices. This combination of variables should be considered in growth predictions, especially given the future climatic changes projected for Europe. We provide insights into species interactions, which could serve as guidelines for designing forest management decisions to alleviate stress and enhance growth of Scots pine-Norway spruce mixed stands. We observed that distance-dependent competition indices (Hegyi's index) had a similar importance as the distance-independent indices (BA) for Scots pine. However, a competition index based on crown overlap (SCI) was found to outperform those based on basal area variables as surrogates for size-asymmetric competition for Norway spruce. This could suggest that individual tree growth is primarily controlled by light availability in the study sites since water disposal is not commonly limited (Bergh et al., 1999). The consideration of the between-core variance in the model, properly controlled tree growth variation in samples, hence, it is recommended for similar future studies. Since only the logarithmic term of tree diameter in the model was significant (Table 4), the relationship between BAI and tree size could be modelled also by a ln-ln relation using tree basal area as predictor. One limitation of this approach is that considering only a five year-old period of tree growth may prevent detecting extreme climatic events, which could have important implications for the results. Accordingly, further research focusing on these extreme climatic events would be necessary to understand tree species interaction in Scots pine-Norway spruce mixtures. Besides, the results

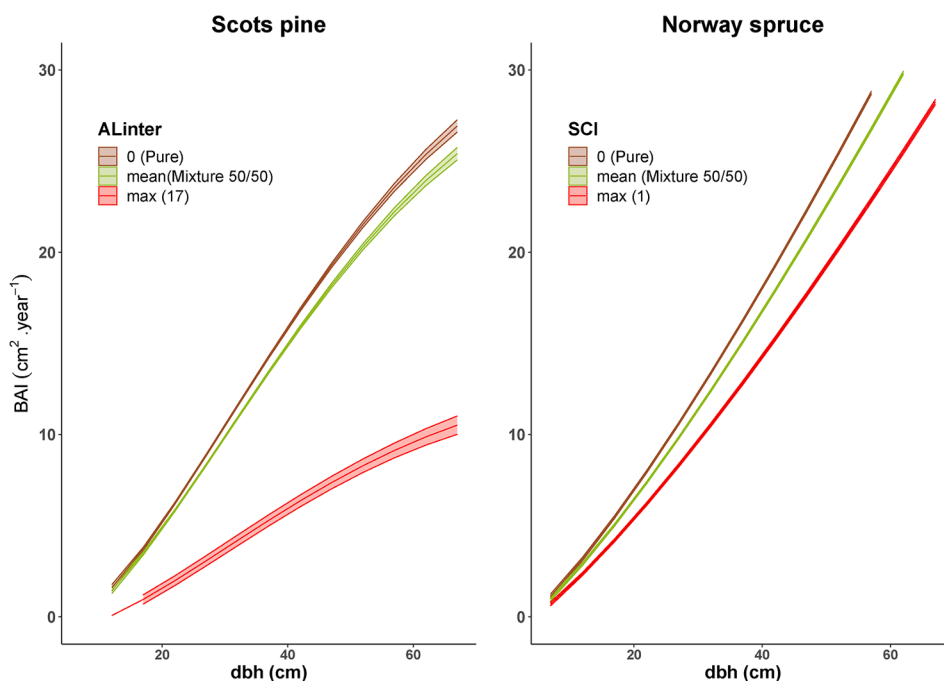


Fig. 3. Effects of initial size and size-asymmetric competition on tree growth according to the model in Table 4 for Scots pine (Pure: $AL_{inter} = 0$, Mixed: AL_{inter} is assigned the mean value for mixed plots, and max: is the maximum value of AL_{inter} observed in mixed plots) and Norway spruce (Pure: $SCI = 0$, Mixed: SCI is assigned the mean value for mixed plots, and max: $SCI = 1$). The other variables in the models took the average value according to the type of stand and species (mixed vs. pure, see Tables 1 and 2). Shaded areas show the 95% confidence intervals of the estimated mean response model.

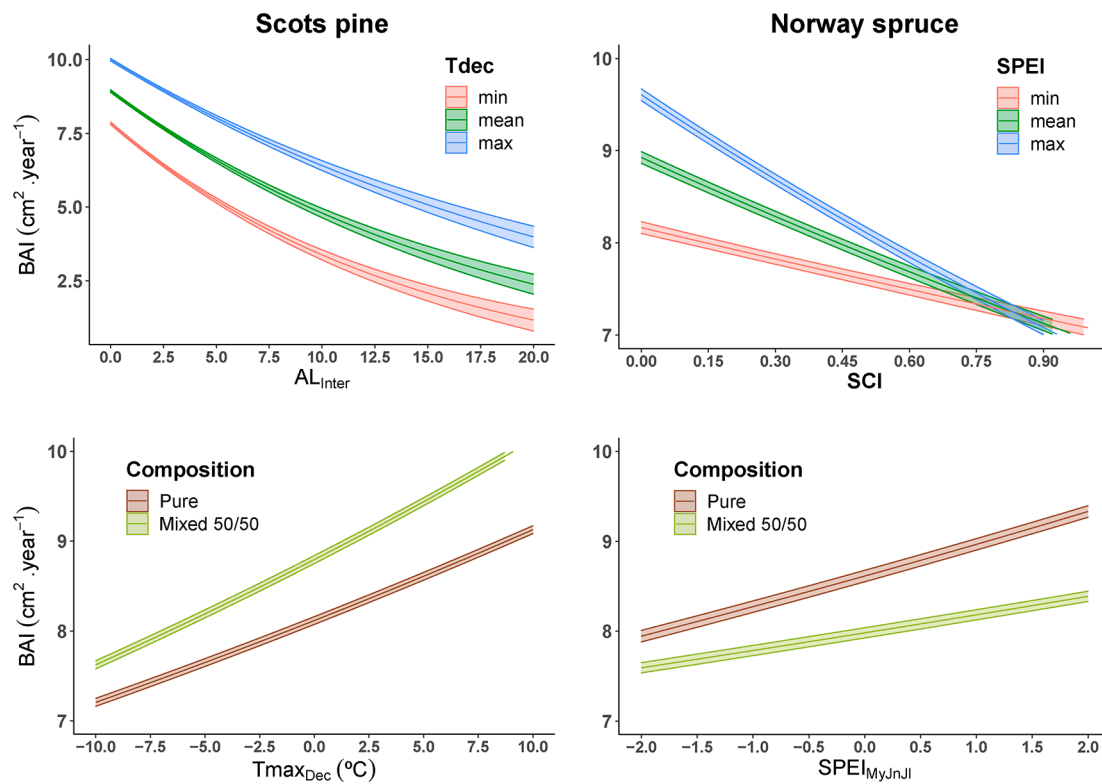


Fig. 4. Influence of weather conditions as a modifier of competition status and tree growth for both species according to the fitted models from Table 4 (left Scots pine; right Norway spruce). “min”, “mean” and “max” are the minimum, average and maximum values of T_{maxDec} and $SPEI_{MyJnJl}$ variables (see Table 2). Stand composition was computed as Pure: AL_{inter} and $SCI = 0$; Mixed: AL_{inter} and SCI take the mean value for mixed plots for Scots pine and Norway spruce respectively. The mean value was used for the rest of the variables in the growth model according to the type of stand and species (mixed vs. pure, see Tables 1 and 2). Shaded areas show the 95% confidence intervals of the estimated mean response model.

could be restricted by the experimental design, since the historical forest management practices carried out in the studied stands are unknown and they could have differed between triplets. In other words, we do not know the way in which the stand structure has been achieved up beyond ten years to the sampling date. However, the present study allows us to evaluate the species interaction along a broad range of ecological conditions according to current forest management practices in Europe.

4.1. Tree growth in mixed versus monospecific stands

According to our results, size-asymmetric and inter-specific competition are key drivers of the basal area increment rates in Scots pine-Norway spruce mixed stands. The mixed-stand situation clearly promoted the growth performance of Scots pine, as a consequence of the vertical (height) stand structure (Fig. 2). As a light-demanding pioneer species, Scots pine may take advantage of the earlier development stages to occupy the dominant crown layers, thus growing faster in mixtures. Under these conditions, young Scots pine trees could grow faster than in pure stands due released intra- and inter-specific competition, and maintain this growth for a long time. In addition, we demonstrated that competition between species was modulated by weather conditions, causing relatively similar increment rates between mixed and pure stands during unfavourable conditions (Fig. 4).

The reduction of the intra-specific competition in mixtures was greater for Scots pine than the increase of inter-specific competition caused by Norway spruce. In other words, the near absence of competition due to low density of the same tree species (intra-specific competition) and the dominance of the upper height stratum (i.e. avoidance of inter-specific competition) increased the growing space of Scots pine trees. This result may be caused by a quicker juvenile growth of Scots pine (Nilsson et al., 2019), which benefited from being ahead of

Norway spruce and without lateral or vertical competition (Jonsson, 1999). The consequence is that Scots pines were bigger than Norway spruces in mixed stands (Fig. 2), since the former grew faster than the latter in both height and diameter (Jonsson, 2001; Yanai, 1992). Similar results were found for Scots pine and European beech mixtures, where the pine had higher diameters and heights than beech when both co-existed in a mixed stand (González de Andrés et al., 2018; Pretzsch et al., 2015). Our findings agree with those who argue that the growth induced by mixtures is not only a matter of species proportion but also depends on stand structure (Brunner and Forrester, 2020; Houtmeyers and Brunner, 2020; Manso et al., 2014b). In this sense, the diameter and crown size variables in the growth models represent the dominance of the target tree, regardless of the species identity. In addition, they also play an important role in explaining tree growth, becoming more important than the intra-specific competition index in pure stands.

Although individual structural variables like size inequality might not be useful to correctly understand all the factors that influence growth process (Forrester, 2019), we hypothesize that Scots pine’s advantage in mixed stands is mainly caused by reduced light competition due to canopy stratification. Scots pine may have superior growth compared to Norway spruce at some sites regardless soil fertility (Nilsson et al., 2012), when they are regenerated by the same procedure (Nilsson et al., 2006). Pine trees likely intercept more light, since they occupied the dominant height strata (Forrester, 2017), leading to bigger crowns in mixed compared to pure stands (Ruiz-Peinado et al., 2020).

Although no differences in tree growth were found for Norway spruce between mixtures and monocultures (Fig. 2), slower growth was induced as the interspecific competition increases (Fig. 3 and Fig. 4), becoming even lower in mixtures than pure stands (Mina et al., 2018). Once again, stand structure may explain those differences (Brunner and Forrester, 2020); Norway spruce density in mixtures was almost double

that of Scots pine, so that the SCI inter-species competition did not vary too much between pure and mixed stands for Norway spruce (Table 1). Accordingly, Holmström et al., (2018) found that the same stem density proportion in the mixture caused a lower mean diameter for Norway spruce compared to the monoculture, while the diameter of Scots pine simultaneously benefitted from the mixture. Simulations based on individual tree growth have also proved that Norway spruce grows faster in pure stands than in otherwise comparable mixed stands (Sterba et al., 2002), although there could also be exceptions due to site-specific limitations (Pretzsch and Biber, 2010).

Our results demonstrated that asymmetric competition influenced the increment rates of both species; this is seen in the importance of tree size in pure stands and by the size-asymmetric competition index in mixtures. This is likely because the examined stands were even-aged and fully stocked, whereas a greater density or height variation may involve symmetrical tree competition. Although strong light competition prevails for both species (Pretzsch and Biber, 2010), it could be much more important for Scots pine growth than Norway spruce (Figs. 3 and 4), which could be related to the species' shade tolerance. In addition, our results may be also affected by light-, water- or nutrient-related interactions, with different importance depending on circumstances. Physiological differences and hydraulic redistribution among spatially-stratified root systems could imply that the species use different strata of available resources in spite of growing together. For example, Norway spruce can grow under the canopy of Scots pine, but the latter with deeper root systems may access water from lower soil layers and, thus, be less sensitive to drought. Tree properties developed in interspecific competition, in contrast to intraspecific competition, may originate from crown expansion (wider crowns), higher packing density or both reactions combined, producing denser stands and canopy filling by crowns (Pretzsch, 2014; Riofrío et al., 2017), leading to more efficient light interception (Shanin et al., 2019). This agrees with the findings of Ruiz-Peinado et al., (2020), who showed that the crown ratio was higher for Norway spruce in mixed than pure stands. Changes in crown characteristics for Norway spruce have also been seen depending on stand species composition and forest management system (Bianchi et al., 2020; Pretzsch and Schütze, 2009).

4.2. The influence of weather and competition interaction on growth

Since the two examined species coexist in large areas of Europe, much variation can be found in the relationships between tree growth and climate variables in the literature, from no significant relationship (Cermák et al., 2017; Cuny and Rathgeber, 2016), to those related to temperature (Büntgen et al., 2007; Misi et al., 2019) or precipitation/water availability as the main growth driver (Cermák et al., 2017; Drössler et al., 2018; González de Andrés et al., 2018). In our study, we observed that Scots pine growth increases with latitude and growing-season temperature. Latitude is correlated with growing season length and temperature, so decreased growth at northern latitudes should be expected. Although we observed this particular pattern in the triplet located at 64°N, the lack of replicates at similar northern latitudes meant the relationship was not significant here. Thus, we hypothesize that the positive relationship between growth and latitude is due to site fertility, which is commonly greater in the Baltic countries than in central Europe (Table S1). The effects of higher temperatures could be attributed to a longer frost-free period, and thus a longer growing season (Oboite and Comeau, 2019). On the other hand, cold winters may negatively affect Scots pine, and improve growth conditions for pine's competitors. Moreover, our findings concur with previous findings that current and previous year summer water availability is an important factor controlling Scots pine and Norway spruce growth in Europe (Misi et al., 2019; Primić et al., 2015). We demonstrated that drought conditions from the previous year may also modify competitiveness of Norway spruce in mixed stands.

In this regard, our study shows that competition can interact with

climate to influence growth, but this effect varies between species as previously mentioned. This finding is in conformance with Pretzsch and Biber (2010) who found that competition of both species can vary from size-asymmetric to size-symmetric depending on site conditions. The negative interaction between inter-specific competition and temperature suggests that cold winters could lead to a stronger growth decline for Scots pine in mixtures compared to trees of the same size in pure stands. In this case, the reduction in growth due to low temperatures might be attributed to greater frost damage to needles. Several studies have shown that Scots pine is quite vulnerable to late-winter and early-spring frosts (Misi et al., 2019), even in the southern range of the species (Camarero et al., 2016; Camarero et al., 2015). Since winter photosynthesis can be appreciable during mild periods in conifers, winter drought is unfavourable. The latter phenomenon likely occurs when anticyclonic conditions with bright sunshine cause a high evapotranspiration and the soil is frozen (Grace and Norton, 1990). Large-scale winter needle loss reduces the radial growth increment in the following summer, as old needles make a substantial contribution to total photosynthesis (Grace and Norton, 1990). Accordingly, low winter minimum temperatures cause dieback or increase mortality in pure Scots pine stands (Camarero et al., 2016). Winter drought could be much more prevalent in the continental climate and at high elevation sites, which are more typical for the central inland European region than Baltic areas with an oceanic climate influence. Conversely, a higher winter temperature reduces the duration and the deepness of snow cover and promote infiltration of moisture into the soil, which leads to greater photosynthesis at the beginning of the growing season (Misi et al., 2019).

On the other hand, temperature did not influence Norway spruce growth, probably because the temperature range of the studied area was not large enough to observe significant differences. Norway spruce can likely benefit from a reduction of drought stress in mixed stands, since it has a demonstrated low drought tolerance in monospecific stands (Rosner et al., 2018; Vitali et al., 2018). Cavin et al., (2013) found similar results showing that the effects of extreme drought can cascade beyond slowed growth of a dominant species resulting in the temporary release from suppression of a co-dominant competitor. Water scarcity has also been shown to constrict light-related complementarity for shade intolerant species (such as Scots pine) in mixtures at drought-prone sites (González de Andrés et al., 2018). We hypothesize that species differences in growth reaction to drought may clarify these patterns, since Scots pine trees show slow recovery after a drought year compared to Norway spruce (Pretzsch et al., 2013; Zang et al., 2012). Additionally, there is evidence that Norway spruce changes competition mode from a size-asymmetric when sufficient soil water is available to a size-symmetric competition under dry conditions (Pretzsch et al., 2018; Pretzsch and Biber, 2010; Zang et al., 2012).

Future growth trends for both species will depend on the location: in northern Europe, the increment rates will most likely increase, while in the central and southern Europe, a reduced productivity is expected (Bauwe et al., 2016). Although climate change could amplify the negative effects of cold winters by inducing winter drought (Camarero et al., 2016), the negative impact of more frequent summer droughts on tree-ring formation is continuously increasing even in northern latitudes (Misi et al., 2019). We hypothesize that under such a scenario, Scots pine-Norway spruce mixtures would be more resilient to extreme drought events than monocultures. The rationale is simply the competition release in mixed stands compared to pure stands.

4.3. Forest management implications

Our results showed that Scots pine benefits from a competitive reduction in mixtures, since interspecific competition is weaker than the intraspecific competition in pure stands. In contrast, the productivity of Norway spruce remains unchanged, at least for the species ratios, which were examined in our study (mostly 50/50% in basal area). The vertical and fast growing Scots pine could profit from above- and below-ground

asymmetric competition, but Norway spruce shows a better adaptation to asymmetric competition for light (Fig. 3). Mixed stands with two strata, with Scots pine taller than Norway spruce, may be easily established in the regeneration phase, leading to lower costs compared to monocultures of any of the tree species (Agestam et al., 2005). However, the establishment of a mixed stand might require careful tending during the early years to avoid problems due to species-specific seed production and responses to regeneration methods (Löf et al., 2018; Nilsson et al., 2006). The mixture of these two species could be an option in locations where the uncertainty in choice of species is high (Holmström et al., 2018). Since these species coexist over a wide area, it should not be very complex to keep the mixture by pre-commercial thinning, although more research is needed to adjust species density, frequency of interventions and stand structure through the rotation cycle to optimise yield and incomes (Agestam et al., 2005). According to our results, the size-asymmetric competition affected the increment rates of Scots pine within an influential zone of 20 m radius, whereas the increment rates of Norway spruce were only influenced when a crown overlap occurred (Table 4). This suggests that mixtures with large pines in small clusters of Norway spruce could be regarded as an optimum environment. This hypothetical scenario is common in the mixed stands studied here, and can be seen in the basal area proportions and density of both species (Table 1). Accordingly, Ruiz-Peinado et al., (2020) found a stand overyielding in 55% of cases and only detected a transgressive underyielding in 15% of cases in mixed stands compared to monocultures. Although at certain sites, pure stands may provide higher standing volumes than mixtures (Agestam et al., 2005; Holmström et al., 2018), the lower density of Scots pine could be compensated by an accelerated growth that is mainly induced by the competition release due to the stand structure. Hence, stand-level productivity may not differ much or is even superior for the mixtures compared to the pure stands (Bielak et al., 2014; Drössler et al., 2018; Ruiz-Peinado et al., 2020). In fact, higher incomes may be expected from the bigger tree sizes and the more valuable timber of the Scots pine trees. In any case, the relationship between species' growth and yield could be only temporary and may vary over the time with a changing stand structure. Accordingly, Norway spruce trees can outcompete and become higher than Scots pine in older ages (60–80) and force managers to prematurely harvest the pine. This often decrease density and reduces stand growth by 20–40% (Wellhausen et al., 2016). Therefore, it is important to establish adequate forest management plans for this type of mixture.

Despite the commonly-seen trade-off between production and other services (Coll et al., 2018), Scots pine and Norway spruce can also deliver a wider variety of positive outcomes for biodiversity, ecosystem services, and additional considerations compared to monocultures (Bielak et al., 2014; Felton et al., 2016). Positive effects of mixing for both species have been observed, for instance due to a reduced risk of pest and pathogen damage (Lindén and Vollbrecht, 2002). Scots pine-Norway spruce mixtures could slightly reduce windthrow damage (Chapin et al., 2007; Ruiz-Peinado et al., 2020) and enhance biodiversity, aesthetics, and outdoor recreation (Felton et al., 2016). According to our findings, inter-specific competition may be released for Norway spruce during late spring and summer droughts. This would make the mixture a preferable option to adapt the forests to climate change in central Europe, as has already been demonstrated with other species mixtures (Pretzsch et al., 2013; Steckel et al., 2020). On the other hand, fire propagation and ungulate browsing might be drawbacks of a mixed-stand forest management. In any case, the examined pine-spruce mixture achieves many positive externalities which, depending on forest owner priorities, might be preferable to monoculture outcomes (Felton et al., 2016).

5. Conclusions

Despite the broad coexistence of Scots pine and Norway spruce in Europe, monocultures of these species currently dominate the European forestry. However, it has been proven that intensive forestry involves trade-offs between timber yield and other forest goods and services which should be considered especially in a scenario of climate change. Mixtures of Scots pine and Norway spruce could achieve many of the benefits from a broad portfolio of ecosystem services, and they could also be compatible with forest owners focusing on wood production.

Competition for light, especially for Norway spruce trees growing in dense and dominated neighbourhoods, is the key driver of productivity changes in mixed stands studied here. We have also shown that stand structure must be considered to understand and correctly interpret the growth induced by this type of mixture. The way in which inter-specific competition alters tree growth response to weather conditions may have strong implications for the future management of Scots pine-Norway spruce mixtures. Trees in pure stands may suffer high competition pressure, whereas on the other hand, trees in mixed stands may be less stressed and less vulnerable to drought through competition release. However, further research is necessary to understand the underlying mechanisms behind these effects and to develop forest management plans suitable throughout the rotation period of the Scots pine-Norway spruce mixtures.

CRedit authorship contribution statement

Jorge Aldea: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - original draft. **Ricardo Ruiz-Peinado:** Investigation, Data curation, Writing - review & editing. **Miren del Río:** Conceptualization, Methodology, Writing - review & editing, Project administration. **Hans Pretzsch:** Investigation, Resources, Writing - review & editing. **Michael Heym:** Investigation, Resources. **Gediminas Brazaitis:** Investigation, Resources. **Aris Jansons:** Investigation, Resources. **Marek Metslaid:** Investigation, Resources. **Ignacio Barbeito:** Investigation, Resources. **Kamil Bielak:** Investigation, Resources. **Aksel Granhus:** Investigation, Resources. **Stig-Olof Holm:** Investigation, Resources. **Arne Nothdurft:** Investigation, Resources. **Roman Sitko:** Investigation, Resources. **Magnus Löf:** Investigation, Resources, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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

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