Species composition modulates seedling competitiveness of temperate tree species under hemiboreal conditions

Roberts Matisons[a,*], Annija Kārkliņa[a], Oskars Krišāns[a], Didzis Elferts[a,b], Āris Jansons[a]

[a] Latvian State Forest Research Institute 'Silava', 111 Rigas str., Salaspils LV-2169, Latvia
[b] University of Latvia, Faculty of Biology, Jelgavas str. 1, Riga LV-1010, Latvia

A B S T R A C T

Mixed stands are advised for reduction of impacts of natural hazards, and species composition can largely affect sustainability and productivity of the stands. Early development of a stands after a stand-replacing disturbance can have considerable legacy effects on growth via alterations in the diversity-productivity relationships. Accordingly compatibility of growth and competitiveness of different species is one of the key issues for susceptibility of mixed stands. A two-year chamber experiment was conducted to assess early growth and intra- and inter-specific competition for light and soil resources among the seedlings of temperate tree species simulating the predicted effect of warming (presuming optimal moisture regime). Five species, which have high economic importance or potential to become so in the eastern Baltic region (Scots pine, Norway spruce, silver birch, red oak, and European beech) were studied. Among the studied species, European beech had the fastest height growth and competitiveness, suggesting ability to concur a stable niche outside its natural range, particularly under increased temperature. Beech also maintained high competitiveness despite the damages suffered during the overwintering, supporting legacy effects of early development and suggesting invasive properties. Among the studied, Norway spruce had the slowest growth and suffered the highest competition, which is in line with predicted changes in forest composition. Scots pine, silver birch, and red oak showed intermediate growth and competitiveness, particularly when growing together, suggesting balanced development and optimal productivity of such mixed stands. Nevertheless, growth and competitiveness of these species was reduced by increased temperature, indicating negative effects of warming.

1. Introduction

Climatic changes cause growing economic consequences in forestry (Hanewinkel et al., 2013), hence plasticity and adaptability of management systems are essential for reduction of losses in the future (Nabuurs et al., 2018; Yousefpour et al., 2017). In Northern Europe, climatic changes (warming) are shifting vegetation zones and altering composition of forests favouring deciduous trees, yet impending conifers (Buras and Menzel, 2019). Under such conditions, the ability to agilely adjust management (e.g. composition of stands) mimicking natural processes is one of the key aspects of sustainable forestry (Yousefpour et al., 2017; Koivula et al., 2014; Pakarinen et al., 2010; Bolte et al., 2009).

Structural and species diversity of forests has been related to their sustainability and resistance to disturbances (Vilà et al., 2013). Higher structural diversity of mixed forests can aid to reduce growing environmental risks (Fares et al., 2015); however, the interactions between species are complex (e.g., competition or complementarity), hence should be considered (Forrester and Bauhus, 2016; Pretzsch et al., 2015). Naturally regenerating stands can be highly resistant to natural hazards, however they can also be less productive (Ratcliffe et al., 2015). Accordingly, the balance between stand structure and management intensity is crucial for the sustainability of commercial forests (Condés et al., 2013; Vilà et al., 2013). This requires comprehensive information about diverse ecological effects, particularly species interaction (Forrester and Bauhus, 2016).

During their life, trees encounter intensive competition, which influences their sensitivity to environmental changes (Ratcliffe et al., 2015; Vilà et al., 2013). Accordingly, the trade-offs in height growth and the inter-specific competition affect distribution and productivity of tree species (Forrester and Bauhus, 2016; Loehle, 1998). Considering temporal correlation of growth (Hong et al., 2015, Isik et al., 2010; Cundall et al., 2003), such process occurs through various stages of stand development. Height increment of trees is sensitive to

meteorological conditions (Jansons et al., 2015; Salminen and Jalkanen, 2007), hence even slight climatic changes can alter the trade-offs in height growth and competitiveness (Forrester and Bauhus, 2016; Nakashizuka, 2001; Loehle, 1998), causing disproportional growth responses (Way and Oren, 2010). Such alterations can have substantial effect on the abundance of species/genotypes in long-term, particularly considering local specialization of populations (Moran et al., 2017). Accordingly, competitiveness could be thought as proxy for sustainability of species/populations, particularly under intensifying natural disturbances (Seidl et al., 2017; Ratcliffe et al., 2015).

Early development, particularly after stand-replacing disturbances (e.g., clear-cuts), is a crucial process affecting growth and development of stands (Chmura et al., 2017; Collet et al., 2017; Brown et al., 2015), depending on species composition and structure (Forrester and Bauhus, 2016). At this stage, seedling competitiveness determines the amount of resources and space available (niche) for each individual (Chmura et al., 2017; van Couwenberghe et al., 2013; Picon-Cochard et al., 2006), affecting further growth and sustainability of the regenerating stand (Forrester and Bauhus, 2016; Brown et al., 2015). Early development of seedlings after the germination is affected by micro-climate and micro-topography (Montagnoli et al., 2016; Picon-Cochard et al., 2006), which are influenced by the surrounding seedlings (sheltering) (Brown et al., 2015; Zapater et al., 2011; Langvall and Örlander, 2001), thus forming a feedback loop.

The competition among trees has been firstly thought as an easily observable contest for light, which also shapes the canopies and promotes height growth (del Río et al., 2019; Chmura et al., 2017). However, the competition for soil nutrients and water, which is hidden, can have major effect on stand structure and growth (Bockstette et al., 2017; Montagnoli et al., 2016; Picon-Cochard et al., 2006; Schenk, 2006). Diverse intra- and inter-species interactions among roots, as in mixed stands (Wang et al., 2018; Kalliokoski et al., 2010), can alter sensitivity of trees (Schiffers et al., 2011; Bolte et al., 2009; Picon-Cochard et al., 2006). For instance, stand structure and composition affect the susceptibility of trees to drought (Zapater et al., 2011). The plasticity of root development can optimize the interactions among trees facilitating productivity of stands (Schiffers et al., 2011).

To minimize inter-specific competition, plants have evolved diverse life and reproductive strategies, which affect growth, lifespan, and reproduction (Moles and Westoby, 2006; Fynn et al., 2005). However, if mixed stands are intended, compatibility of trees with different life strategies is crucial (Nagel et al., 2014; Nakashizuka, 2001). For instance, if a pioneer species is outcompeting late-successional species, additional management might be necessary, increasing management costs (Forrester and Bauhus, 2016). In contrast, growth facilitation has been observed for mixture of Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*) due to compartmentalization of soil resources (Pretzsch et al., 2015). Under hemiboreal conditions, conifers and birch (*Betula* spp.) show different rooting strategies optimizing resources, thus suggesting resilience of such mixtures (Kalliokoski et al., 2010).

The accelerating climatic changes are apparently exceeding the adaptive capacity of local tree populations, hence assisted gene flow and/or assisted migration have been advised (Aitken and Bemmels, 2016; Williams and Dumroese, 2013). The introduction of a novel species/genotypes can minimize climatic hazards by matching the requirement of the trees with future climates. This, however, increase the biotic risks, as the novel trees, if superior to native ones (Ni et al., 2018), might become invasive, shattering interactions among the native species at all stages of stand development (Bucharova, 2017; Bradley et al., 2010; Mueller and Hellmann, 2008). Accordingly, the competitiveness of the potentially introduced trees already at young age can provide insight in their behaviour in the future (Ni et al., 2018, Bradley et al., 2010), projecting necessity for management and its costs (Mueller and Hellmann, 2008).

The aim of the study was to experimentally evaluate early inter- and intra-specific competitiveness and its effect on growth of seedlings of native and introduced tree species under current and future climatic conditions in the eastern Baltic region. We hypothesized that increase of temperature, as projected for Northern Europe during the 21st century, would improve the competitiveness of deciduous trees, particularly the north-transferred ones. Accordingly, we assumed that the seedlings of coniferous trees would suffer stronger competition under mixed stand structure.

2. Material and methods

2.1. Experimental design

A two-year climate chamber experiment was conducted during 2018–2019 in the central part of Latvia (56.681° N; 25.964° E). The climate at the study site was temperate; the 30-year mean annual temperature (± standard deviation) was 6.5 ± 0.7 °C, yet the monthly mean temperature ranged from −4.2 ± 2.7 to 17.9 ± 1.6 °C in January and July, respectively (Harris et al., 2014). The mean annual precipitation was 686 ± 83 mm, yet the highest monthly precipitation occurred during the summer months (78 ± 31 mm), resulting in pre-vailingly positive water balance. In 2018, temperature was above the long-term mean, while it was similar to it in 2019 (Fig. 1). During the study period, summer precipitation, particularly in June and July 2018, was below the long-term mean.

The experiment was initiated at the end of April 2018. Five species: native Scots pine, Norway spruce (*Picea abies*), and Silver birch (*Betula pendula*); introduced European beech, and exotic red oak (*Quercus rubra*) were analysed. Such species were chosen as they can often be found in mixed stands in the eastern Baltic region. Due to projected range shifts (Buras and Menzel, 2019), beech was chosen as potential commercially important species; red oak was selected as a substitute for the local oak species, which recently suffered decline. The studied species thought had different reproductive (beech and oak represented trees with large seeds, birch those with small seeds, while conifers trees with intermediate seeds; cf. Moles and Westoby, 2006) and life strategies (birch represent ruderals; beech, oak, and spruce represent competitive stress tolerant; while pine – the intermediate plants; cf. Brzeziecki and Kienast, 1994). For all except beech, the seed material was obtained from open-pollinated plus-trees located within the 50 km distance from the experiment site. Beech seeds were collected from a stand in the north-western Latvia (57.251° N; 22.700° E), where is the northeasternmost stand of the species occurring outside its natural range. Seeds from the second generation beech trees, which, apparently, have adapted to the local (harsher) conditions (Matisons et al., 2017), were collected in 2017.

To assess the effects of intra- and inter-species competition for light and soil on the early development of seedlings, seeds were sown in three types of seedling boxes. Standard 5 × 8 container boxes with the 4.4 cm spacing between 125 cm^3 lots were used to imitate competition for light. To imitate the competition for light and soil, seeds were sown in 25 × 40 cm seedling boxes (without separating walls), maintaining 5 × 8 lot grid with 4.4 cm spacing between the lots; the amount of substrate was maintained equivalent to 125 cm^3 per seed lot. As the control, seeds were sown in 3 × 5 container boxes with the spacing of 7.5 cm (two boxes per replication, i.e., 30 seed lots) and volume of 400 cm^3. Pre-fertilized peat "NPK 16–4–17" was used as the substrate. For the first two weeks, sown boxes were maintained under increased temperature (~ 4 °C above the ambient), providing abundant irrigation to ensure germination.

In total, 10 species compositions were tested. Among those, single species compositions were used to assess the intra-specific competition. Additionally, for the assessment of inter-species competition, five species compositions: 1) pine, spruce, and birch; 2) spruce, birch, and red oak; 3) spruce, birch, and beech; 4) birch, beech, and red oak; and 5) all five species together, which are, or might become common in the region or might become so under warming (Buras and Menzel, 2019),
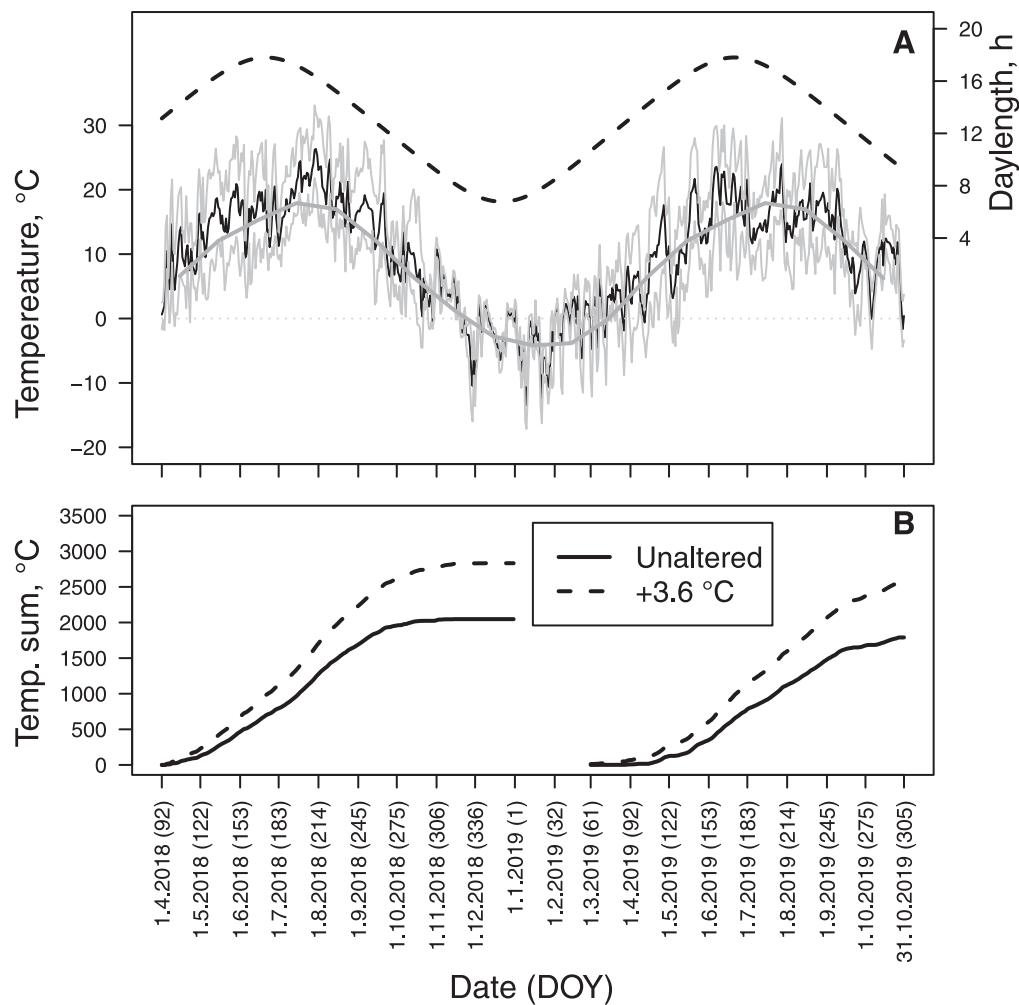
Fig. 1. Mean (solid bold black line), minimum and maximum (fine solid grey lines) daily ambient air temperature and photoperiod (daylength) (dotted line) during the greenhouse experiment and overwintering (A) and the accumulated temperature ($> +5°C$) sums during the growing period according to the temperature regime in the greenhouse (B). In (A), solid bold grey line represents smoothened 30-year mean daily temperature. DOY – day of year.

were tested. In the mixed compositions, the proportions of the viable sown seeds was similar for the species. Germination rates of the seed material were tested prior to the experiment and accounted during sowing (three birch seeds, which showed lower germination rates, were sown in each lot, and redundant seedlings were removed ten days after germination).

To assess the effects of warming climate, as predicted by the intermediate scenarios (IPCC, 2013), on the early competition, seedlings were subjected to two temperature regimes in separate transparent (transparency > 80%) climate chambers (controlled climate greenhouse). In one chamber, the temperature was maintained 3.6 °C above the ambient, while the ambient temperature was maintained in another chamber as the control. Temperature was manipulated by the automated system in the real time regime (i.e. 24/7). Soil moisture level was monitored by an automated system. Automated irrigation system was used to provide optimum soil moisture during the climate chamber experiment when the ambient temperature exceeded 0 °C. Photoperiod was not altered. Temperature manipulation was applied from May 7 to October 22 in 2018 and from April 8 to October 21 in 2019. After the temperature manipulation, seedlings were transferred to winter storage, where they received ambient temperature and precipitation, yet the temperature did not drop below ca. –18 °C (Fig. 1). Each of the 60 combinations of the treatments (Supplementary material, Fig. S1) was represented in three replications (6600 seed lots in 240 boxes sown in total), which were randomly distributed on 14 tables (seven tables per

temperature regime). Tables were used for maintenance purposes. The position of the boxes on the tables remained constant during the entire study period. The spacing between the tables was 50 cm. Survival and seedling/sampling height (uppermost bud) was determined in 2018 and 2019 after the temperature manipulation.

2.2. Data analysis

To assess the competitiveness of seedlings/samplings and its relation to growth under the studied treatments, competition index (CI) was calculated for each tree based height as:

$$CI_i = \sum \frac{h_n - h_i}{l_n} [h_n \geq h_i \bigwedge l_n \leq 200] \tag{1}$$

where h_n is the height of neighbouring seedlings, h_i the height of the seedling $_i$ and l_n distance to neighbouring seedlings in mm. The distances among the seedlings were calculated considering the spacing between seed lots, position of the boxes on the tables, and positions of the tables. Calculation of the competition index was based on seedling height at the end of temperature manipulation. The height of dead seedlings was considered zero. Competition index vas calculated for each year.

The effects of the studied treatments and species on competitiveness (CI), height in the end of the first growing season, relative height increment (RHI) of the second season, and survival of seedlings were

determined by a mixed model:

$$y_{ijklmn} = \mu + t_i + s_j + t_i \times s_j + s_j \times c_k + T_l + x_{ijk} + e_{im(n)} + \varepsilon_{ijklmn,} \quad (2)$$

where t is temperature (two levels (i): unaltered and increased by 3.6 °C), s tree species (five levels (j): pine, spruce, birch, beech, and red oak), $t \times s$ is the interaction between temperature and species, $s \times c$ is the interaction between species and composition (10 levels (k): pine; spruce; birch; beech; red oak; pine, birch, and spruce; spruce, birch, and red oak; spruce, birch, and beech; birch, beech, and red oak; and all five species together), T is the type of competition (three levels (l): light; light and soil; and control), x_{ijk} numeric covariate (tree height for CI and CI for tree height, RHI, and survival), $e_{i(m(n))}$ random effect (intercept) of replication (l) nested within table (m). Unfortunately, the scope of the study did not allow to study full model, i.e., with all possible interactions. Models were fit using the restricted maximum likelihood approach. For survival, a generalized model with the binomial distribution of residuals and 'logit' link function was used. The significance of the effects was evaluated by the likelihood-ratio χ^2 test. Tukey's HSD test was used to compare the marginal means according to the levels of the significant factors. Data analysis was conducted in R (R Core Team, 2020) using packages "lme4" (Bates et al., 2015) and "emmeans" (Lenth, 2019).

3. Results

After the first growing season, 5975 seedlings (from the 6600 seeds planted) survived, resulting in the overall survival of 90.5%. The mean (± standard deviation) height of the seedlings was 98.0 ± 71.2 mm, indicating high variability; the mean CI was 10.9 ± 11.2, suggesting that seedling suffered various degree of competition (Table 1). The overall survival after the second growing season remained high, as 5693 (86.3%) seedlings had survived. The mean height increment formed during the second growing season was 33.6 ± 42.4 mm, yet negative increment was observed for beech, which suffered some cold desiccation during the overwintering. Still, the mean RHI was 64.6 ± 89.1%, and likely caused slightly stronger competition among the seedlings, as suggested by the increase of CI after the second growing season reaching 11.9 ± 12.9.

The statistical models relating the experimental treatments with the studied response variables were strictly significant, and for most of them, except RHI, showed good fit (marginal $R^2 > 0.60$; Table 2). Among the random effects, variance of replication (box) exceed that of a table; however, they were considerably lower compared to the residual variance. The strength of the fixed effects differed among the studied response variables, though survival was less affected by the experimental design, as suggested by generally lower χ^2 values. Species showed the strongest individual effect on tree height after the first growing season, as well as on RHI and competitiveness after the second season. Among the fixed effects, type of competition (box) had the strongest effect on survival in both years. Individual effect of temperature was significant for CI after the second growing season, yet significant species-by-temperature interaction was estimated for tree height and CI after the first growing season.

During the first growing season, deciduous species, particularly

beech and birch, had reached the tallest height, (Fig. 2 A), while the height growth of conifers was considerably (by ca. 30–50%) and significantly (p-value < 0.001) slower. The increase of temperature by 3.6 °C resulted in a decreased height of all species, except beech, which showed slight improvement of growth (Table S1), thus explaining the temperature-by-species interaction (Table 2). Still, considering the experimental design, the effect of the interaction was rather small. Among the competition types, competition for light and soil, when seedlings were growing in common substrate, caused notable (ca. two fold) and significant (p-value < 0.001) increase of tree height (Fig. 2 B). The significant species-by-composition interaction (Table 2) indicated the effects of inter-specific competition on height growth of seedlings (Fig. 2 C). Stand mixture had a positive effect on height of coniferous trees, particularly Norway spruce, yet the effects were generally similar among the tested compositions. For silver birch, taller seedlings occurred in the compositions featuring European beech, while seedlings grew slightly slower in presence of Norway spruce and red oak. European beech favoured pure stands and its height decreased with the number of admixture species. Among the tested, composition containing birch and beech tended to facilitate growth of red oak during the first season.

Species had the strongest individual effect on RHI after the second growing season (Table 2). The differences in RHI among the species (Fig. 3 A) were inverse to tree height before the second growing period (Fig. 2 A). The highest RHI (ca. 140%) was observed for Scots pine (Fig. 3 A), which was growing slowly during the first season. The RHI of Norway spruce was lower, still, its height nearly doubled during the second season. Silver birch and red oak formed lower RHI, yet beech showed close to zero increment likely due to winter desiccation of tops. Among the competition types, only the control treatment was associated with increased RHI (Fig. 3 B; Table S1). The inter-specific competition had a negative effect on RHI of conifers, particularly pine (Fig. 3 C; Table S1), which was inverse to that observed for height in the first growing season. The RHI of silver birch tended to be higher if beech was present in the composition, yet the differences were weak, as observed for tree height. For red oak, RHI showed positive relation with species richness of the composition.

The competitiveness of seedlings after the first season was mainly affected by species composition, as suggested by the highest χ^2 estimate (Table 2), while the differences among the species mostly were non-significant (Fig. 4 A), highlighting the importance of the inter-specific interactions. Still, red oak and, particularly, Scots pine showed the lowest CI, implying that they have been subjected to lower competition from the neighbouring seedlings. Red oak, however, was subjected to increased competition when growing in combination with birch and beech (Fig. 4 C; Table S1). Among the tested species, spruce was subjected to the strongest competition when growing in any of the tested species compositions, yet showed minimal intra-specific competition if growing without admixture. Similar trend was observed also for Scots pine. European beech, which was the tallest (Fig. 2 A), obviously outcompeted others, especially when growing in the most diverse composition (Fig. 4 C). Accordingly, birch also suffered the highest competition when growing in the compositions containing beech, though it showed high intra-specific competition as well. As expected, among the

Table 1
Descriptive statistics of the response variables (tree height, competition index, height increment) after the first and second growing period. Height of the seedlings were measured to the uppermost living bud.

	Min	Mean	Median	Max	St. dev.
Tree height after the first growing season, mm	3.0	98.0	80.0	520.0	71.2
Tree height after the second growing season, mm	7.1	131.7	121.0	689.0	78.1
Height increment after the second growing season, mm	−134.0	33.6	29.0	370.0	42.4
Relative height increment after the second growing season, %	−81.8	64.6	42.9	1820.0	89.1
Competition index after the first growing season	0.1	10.9	7.1	73.2	11.2
Competition index after the second growing season	0.1	11.9	7.5	89.6	12.9

Table 2

Model statistics and the estimated effects of the experimental treatments (fixed effects) on random effects (table and box) on height, survival and competitiveness (completion index) of seedlings after the first and second growing seasons. NA- not available; df- degree of freedom; CI- competition index. Tree height and competition index used as covariates. Significance code, *p*-values: * < 0.05, ** < 0.01, and *** < 0.001.

	After the first growing season			After the second growing season		
	Tree height	CI	Survival	Relative height increment	CI	Survival
Fixed effects, χ^2						
Species (df = 4)	1254.6***	174.4***	123.5***	1083.6***	305.7***	120.6***
Temperature (df = 1)	2.5	1.6	0.2	0.1	28.32***	0.1
Competition (df = 2)	199.9***	278.3***	132.4***	14.6***	220.6***	180.2***
Covariate (df = 1)	4082.8***	4007.3***	445.6***	3.0	4042.3***	670.8***
Species-by-temperature (df = 4)	18.8***	17.4***	2.4	5.8	5.8	4.6
Species-by-composition (df = 19)	115.1***	296.7***	51.2***	46.7***	240.5***	51.7***
Random effects, variance						
Replication (box)	711.4	16.3	3.6	474.4	22.7	6.2
Table	11.9	0.9	< 0.1	128.3	2.0	< 0.1
Residual	1098.1	37.6	NA	5171	49.4	NA
Overall model statistics						
Marginal R^2	0.66	0.61	0.69	0.29	0.61	0.74
Conditional R^2	0.79	0.73	0.85	0.37	0.74	0.91
Model significance, p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

competition treatments, the highest and lowest CI were observed under the completion for soil and light and the control treatments, respectively (Fig. 4 B; Table S1). Increase in temperature reduced competition (CI) for most species except beech, (Fig. 4 A) similarly to seedling height, explaining the species-by-temperature interaction (Table 2).

The variation of CI of the seedling after the second growing season according to the experimental treatments showed highly similar pattern as observed after the first growing season (Fig. S2). The CI of seedlings was primarily affected by the species and composition (Table 2). Norway spruce suffered the strongest inter-specific competition (Fig. S2 C), which had increased, compared to the first growing season. The estimated CI for pine showed some increase, particularly if growing without an admixture (Table S1); for birch and oak, the pattern remained the same. Beech was the only species, for which CI tended to decrease during the second growing season, particularly if grown without admixture or together with spruce and birch. The competition for light and soil resulted in the highest competition (Fig. S2 B), yet the differences between the other two levels were non-significant. Temperature had a weaker effect, which however, was not interacted by species (Table 2), hence CI for all species was decreased if temperature was maintained 3.6 °C above the ambient (Fig. S2 B; Table S1).

Although survival of seedlings after both growing seasons was high, still it was affected by competition type and species-by-composition interaction (Table 2). Among the studied species, beech had the lowest survival, particularly during the first season and if grown alone or in combination with birch and oak (Figs. S3, S4). For red oak, survival was decreased in response to intra-specific competition. Competition type had a weaker effect, yet survival was decreased under the completion for light and control treatments.

4. Discussion

Mixed forests have been advised to increase sustainability of forests under changing climate (Nabuurs et al., 2018; Forrester and Bauhus, 2016; Bolte and Villanueva, 2006), and competitiveness of trees with different life strategies is a key issue for productivity of stands (Pretzsch et al., 2015; Nagel et al., 2014; Nakashizuka, 2001). The variances of the studied random effects, which were lower than the residual variances, the estimated R^2 values (Table S1), as well as higher CI under the competition treatments (particularly for both soil and light) (Fig. 4 B, S2 B) indicated sufficiency of the study design for assessment of inter- and intra-specific relationships among the seedling. Considering that trees of diverse systematic affiliations and life strategies were studied (cf. Moles and Westoby, 2006; Fynn et al., 2005; Nakashizuka, 2001), differing competitiveness of seedlings according to species, as

well as the experimental treatments (Table S1) indicated varying growth potential in a mixed stand (Forrester and Bauhus, 2016; Ratcliffe et al., 2015). Nevertheless, the deciduous trees showed generally superior growth, particularly during the first growing period (Fig. 2), which corresponds to the predicted changes in forest composition within the region (Buras and Menzel, 2019).

Competition for light causes reallocation of resources to height growth of trees (del Río et al., 2019; Chmura et al., 2017; Langvall and Örlander, 2001), which can explain increased height, RHI, and CI under the competition treatments (Fig. 2 B). In turn, faster height growth resulted in higher CI, enhancing the effects of the trade-offs in increment of individuals according to their growth rate (Loehle, 1998). Faster growth under more intense competition (Fig. 2 B, 4B) also implies that trees could be subjected to increased stress (Curt et al., 2005), though mortality was still low (Figs. S3, S4). The decreased RHI of the deciduous species in the second growing season might be explained by faster growth in the previous year, hence size-dependence of height growth (King, 1990). This might also be related to faster growth of trees and earlier reaching of the ecological capacity of soil resources under the restricted conditions. In contrast, the conifers, which showed slower growth in the first season (Fig. 2 A), enhanced their increment in the second year (Fig. 3 A).

The increase of temperature, which was hypothesized to alter growth and interactions among the seedlings (cf. Loehle, 1998), resulted only in slight trade-offs in competiveness among the species (beech vs. others) during the first growing season (Fig. 4 A), which followed the same pattern as tree height (Fig. 2 A). Considering that seed material represented population of trees (except beech), which have evolutionary adapted to local hemiboreal conditions (Aitken and Bemmels, 2016), increase of temperature burdened their growth (Fig. 2 A), likely as a result of increased evapotranspiration (Trajkovic, 2005), and physiological water deficit (Moran et al., 2017), though direct effect of irrigation regime was not analysed. In contrast, increased temperature showed positive effect on growth of beech, which is adapted to a warmer climate and more frequent water deficit conditions (Zapater et al., 2011). Such differences implied alterations in the trade-offs in height growth (Forrester and Bauhus, 2016; Loehle, 1998), suggesting disproportional changes in growth responses and competitiveness in the future (Way and Oren, 2010). Even small changes in the trade-offs in biotic relationships can have considerable effect (Nakashizuka, 2001; Loehle, 1998), supporting changes in early competitiveness of seedlings hence development and productivity of stands (Chmura et al., 2017; Collet et al., 2017; Fynn et al., 2005). The significant individual effect of temperature on CI after the second growing season (Table 2), which indicated systematic response of species (Fig. S2 A), however, implied
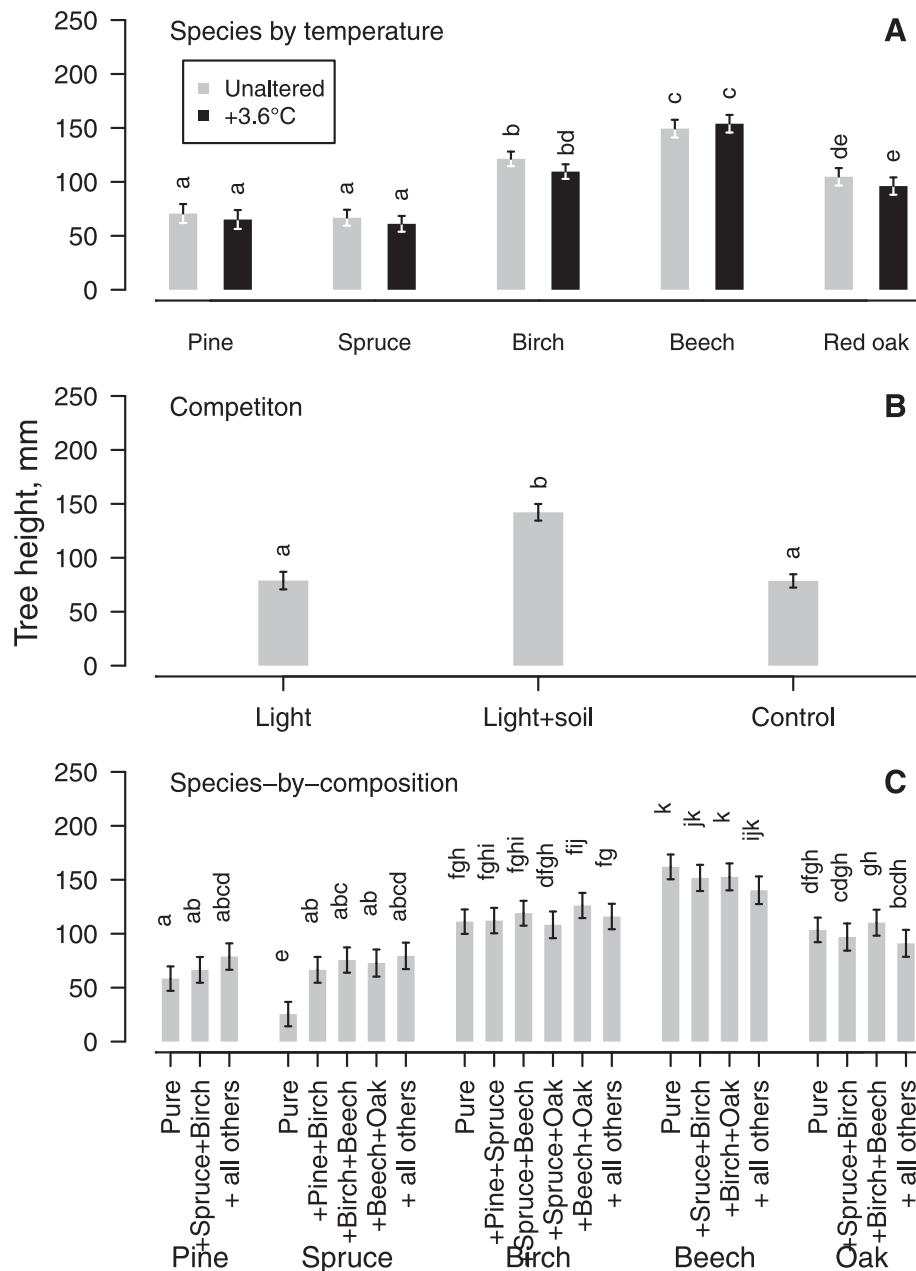
Fig. 2. Estimated marginal means and their 95% confidence intervals (whiskers) of tree height after the first growing season according to species and temperature (A), type of competition (B), and species- by-composition (C). Similar letters above the bars indicate lack of significant differences between the groups as determined by Tukey's HSD test (in C, for lettering α set to 0.1 for clarity).

temporal variability of the temperature related trade-offs among the species, hence shifting inter-species relationships (Kalliokoski et al., 2010; Fynn et al., 2005).

The increased height growth and CI during the first growing season under competition for light and soil (Fig. 2 B, 4B) can be explained by increased necessity for saplings to concur space, if the resources are not compartmentalized (Bockstette et al., 2017; Picon-Cochard et al., 2006; Schenk, 2006). Alternatively, such faster height growth might be related to the biotic relationships among roots (niche differentiation), which optimize available resources, thus facilitating productivity (Wang et al., 2018; Montagnoli et al., 2016; Schiffers et al., 2011; Kalliokoski et al., 2010). The inter- and intra-specific interactions among roots have been related to the coexistence of species with differing ecological demands and life strategies within a stand via segregation of resources increasing structural diversity (Wang et al., 2018; Schiffers et al., 2011; Kalliokoski et al., 2010; Bolte et al., 2009; Picon-Cochard et al., 2006).

The explicit species-by-composition interactions observed for CI and increment (Fig. 2 C, 4C, S2C; Table 2) indicated varying diversity-productivity relationships (Forrester and Bauhus, 2016), implying plasticity of growth responses of the species. Although conifers have been predicted to decrease abundance in the eastern Baltic region (Buras and Menzel, 2019), the estimated CIs (Fig. 4 C, S2C) indicated that such scenario is particular for Norway spruce, which suffered increasing competition if growing in a mixture with other species. Still, spruce is a highly shade-tolerant species, which can survive long time in advanced regeneration (Bolte and Villanueva, 2006), awaiting for a release by a disturbance, meanwhile providing little contribution to productivity of stand. In contrast, Scots pine (progenies of plus-trees), which is light demanding, was able to compete, as indicated by the intermediate CIs, suggesting adaptability of the local population (Aitken and Bemmels, 2016; Bucharova, 2017). Sheltering by other
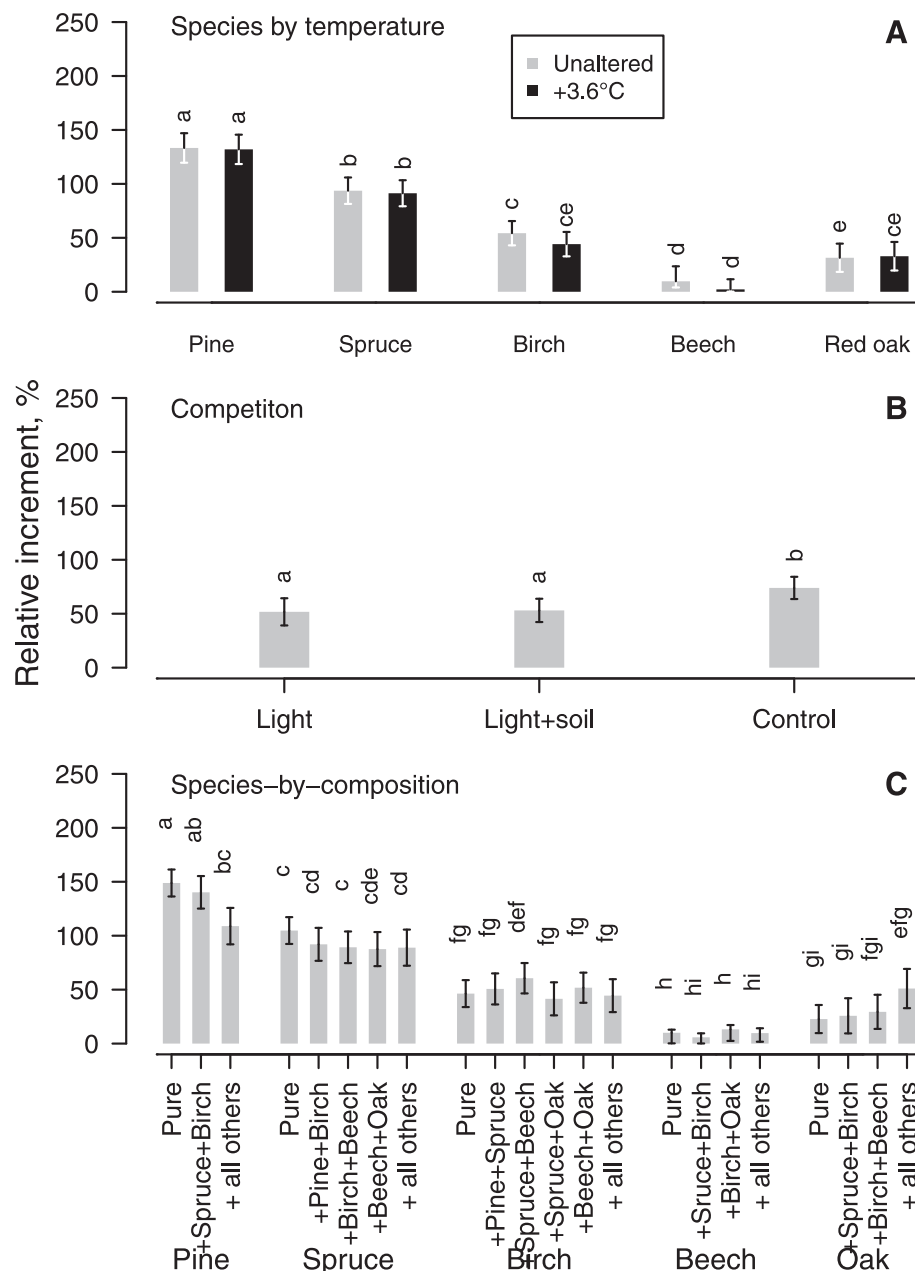
Fig. 3. Estimated marginal means and their 95% confidence intervals (whiskers) of the relative height increment of trees after the second growing season according to species and temperature (A), type of competition (B), and species- by-composition (C). Similar letters above the bars indicate lack of significant differences between the groups as determined by Tukey's HSD test (in C, for lettering α set to 0.1 for clarity).

species, apparently, had a positive effect on height growth of conifers during the early development (Fig. 2 C) likely via improved moisture and thermal micro-climates (Brown et al., 2015; Langvall and Örlander, 2001), although such effect is expected to change with ageing (Strand et al., 2006).

Among the studied species, seedlings of beech, which has large seeds (Moles and Westoby, 2006), showed superior growth and tended to outcompete others, particularly if competing for light and soil (Fig. 4, S2, Table S1) suggesting some invasive properties (Ni et al., 2018; Mueller and Hellmann, 2008; Fynn et al., 2005). On the other hand, invasive properties, such as rapid development (Bradley et al., 2010; Mueller and Hellmann, 2008) in combinations with high wood value, might be considered as an advantage in forestry, reducing establishment and maintenance costs. Accordingly, improved height growth and competitiveness supports growing commercial potential of beech outside its considered native range in the Baltic States, thus implying

positive effects of assisted migration (Aitken and Bemmels, 2016; Williams and Dumroese, 2013). Although beech, which is adapted to a warmer climate of the nemoral forest zone (Weigel et al., 2018), suffered damage during the overwintering, still it was still able to restore previous height, thus showing minimal, yet still positive RHI (Fig. 3 A), supporting its growth potential. Furthermore, in the second growing season, competition suffered by beech was lower (Fig. S2 C), indicating legacy effect of its early growth (Brown et al., 2015; van Couwenberghe et al., 2013) and suggesting stability of its establishment (niche) also northwards from its range (Matisons et al., 2017). Red oak, which has similar seeding strategy to beech and is considered potentially invasive in the Baltics (Riepšas and Straygyte, 2008), however, did not show explicit invasive properties during the first two years after establishment.

Considering that explicit competition among trees reduces productivity of a stand (Forrester and Bauhus, 2016; Ratcliffe et al., 2015),
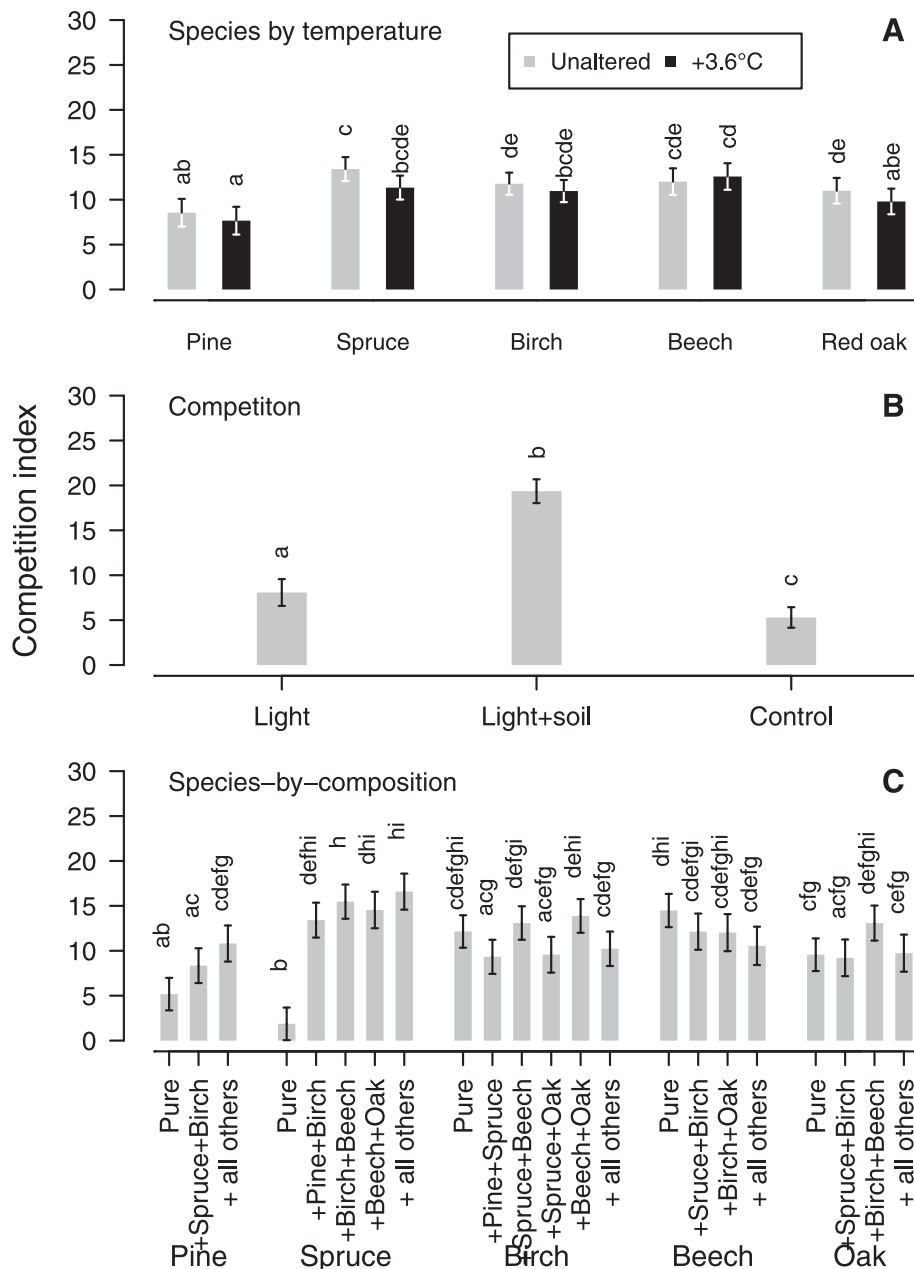
Fig. 4. Estimated marginal means and their 95% confidence intervals (whiskers) of the competition indices of trees after the first growing season according to species and temperature (A), type of competition (B), and species- by-composition (C). Similar letters above the bars indicate lack of significant differences between the groups as determined by Tukey's HSD test (in C, for lettering α set to 0.1 for clarity).

compositions resulting in lowest and most balanced competition among the species appear advantageous for sustainability of forest (Condés et al., 2013). Although competition within a stand is a temporary shifting process (Kalliokoski et al., 2010; Fynn et al., 2005), among the studied, pure stands of oak and pine, as well as combinations of oak, pine and birch appeared to meet such criteria (Fig. 4 C, S2 C), suggesting balanced early development of the mixture. The RHI of birch and oak tended to be higher when growing in mixture with other species, indicating some facilitating diversity-productivity relationships (Forrester and Bauhus, 2016). In contrast, beech outcompeted others, thus favouring formation of pure stands (Ratcliffe et al., 2015; Bolte and Villanueva, 2006) also under harsher climate outside its range, which corresponds with the predicted changes in species distribution (Buras and Menzel, 2019). This also suggests that less involvement might be needed for the establishment of stands with such target species, thus aiding for the sustainability of management system (Koivula et al.,

2014).

5. Conclusions

Early height growth and competitiveness of the studied species indicated increased growth potential of deciduous trees already at the early stages of stand development irrespectively of reproductive (seed size), origin, and life strategies at older age. Nevertheless, the differences in competitiveness implied varying compatibility of species, resulting in uneven development, highlighting legacy effects of the initial composition. The hypothesis of the study was confirmed partially, as the increase of temperature had a minimal effect on the trade-offs in competitiveness among the species (beech vs. others) particularly in the year of establishment. Nevertheless, already at the current conditions, beech showed the fastest height growth and highest competitiveness irrespectively of cold damage, indicating growing commercial potential

of the species in the eastern Baltic region (Baltics) and supporting its range expansion. High competitiveness of beech also suggested some invasive properties and formation of monospecific stands. Still, among the studied conifers, Norway spruce suffered increased competition when occurring in a mixture with other species, supporting the predicted shifts in forest composition in the eastern Baltic Region. However, the compositions of red oak, silver birch, and Scots pine resulted in the most equivalent inter-specific competition, suggesting balanced establishment and early development, aiding to sustainability of respective stands. Although chamber experiment neglects many environmental factors, which might modulate the observed inter-species relationships, the results indicate that initial species combination can affect sustainability of regenerating stand.

CRediT authorship contribution statement

Roberts Matisons: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, Supervision. **Annija Kārkliņa:** Conceptualization, Visualization, Data curration. **Oskars Krišāns:** Conceptualization, Visualization, Data curration. **Didzis Elferts:** Methodology, Supervision, Software. **Āris Jansons:** Conceptualization, Writing - review & editing, Supervision.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118499.

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