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Ecosystem carbon storage two decades after afforestation in Norway spruce and silver birch monocultures and mixtures on abandoned agricultural land in hemiboreal Estonia

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ABSTRACT

In silviculture, tree species mixing is seen as a potential measure to increase ecosystem carbon (C) sequestration due to higher resulting productivity compared to monocultures. Currently, there is a lack of studies on how monocultures and mixtures of the two main boreal tree species, Norway spruce and silver birch, compare regarding C sequestration and storage in planted stands. We evaluated ecosystem C stocks, stand productivity and soil nutritional status in spruce and birch monocultures as well as mixed stands with 50/50 mixing proportion two decades after afforestation of abandoned agricultural lands with homogeneous soil fertility. We found that Norway spruce monocultures had the highest mean annual increment (MAI), highest ecosystem C stock, and the highest periodic annual increment (PAI). In silver birch stands, C was mostly stored in the stems of the trees, whereas Norway spruce monocultures had a significantly higher share of C stored in the canopy. While the growth of individual silver birches was not influenced by the stand type, Norway spruce was suppressed by the inter-specific competition in the mixtures, where the average tree stem MAI was 56 % lower than in the monocultures. In general, the SOC and soil nutrient concentrations were similar in the mixed-species stands and monocultures. Spruce monocultures had a higher SOC stock in the forest floor. In conclusion, we did not confirm a higher productivity of mixed stands compared to monocultures, but different patterns of C allocations indicate the need for longer observations to identify the silvicultural system with the best climate benefit.

1. Introduction

Mixed species forests have gained more attention recently due to the adverse effects of climate change on monocultures. One of the main advantages of species diversity over single species forests is considered to be their resilience to disturbances resulting from climate change, such as storms, drought, diseases, and pests (Jactel et al., 2017; Pardos et al., 2021). Additionally, mixed forests provide a broader range of ecosystem services and support biodiversity (Gamfeldt et al., 2013; Felton et al., 2016). Another advantage of mixed forests is their potentially higher biomass production, allowing higher CO_2 fixation in tree biomass and soil (Liang et al., 2016; Lutter et al., 2019), thus providing a greater climate change mitigation effect.

One theory describes the higher productivity as the direct effect of biodiversity where higher species richness enhances ecosystem productivity (Liang et al., 2016). Another theory prioritizes the presence, availability, and uptake efficiency of resources as determinants of ecosystem productivity, where greater resource availability enables a higher number of species to coexist (Forrester and Bauhus, 2016; Högberg et al., 2017). Accordingly, there has been a long-term systematization of soil or site indexes in Nordic countries, which links higher ecosystem productivity and diversity with soil fertility (Cajander, 1926; Hägglund and Lundmark, 1977; Lõhmus, 1974). It is probable that the two theories complement each other as higher tree species diversity provides more efficient resource utilization due to reduced intra-specific competition (Pretzsch et al., 2010; Forrester et al., 2013; Forrester and Bauhus, 2016). The complementarity effect of accompanying tree species in a mixture can be described by niche differentiation, which allows more efficient access and utilization of different pools of below- and aboveground resources (Craine and Dybzinski, 2013). Whereas, individuals in the single-species ecosystem are competing for the same resources. Such structural diversification and more efficient resource

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usage can result in higher yields of mixed stands compared to monocultures, which is also reflected in higher accumulation of carbon (C) in the aboveground pool (Warner et al., 2023). However, the presence and extent of productivity gain and C uptake capacity of mixed forests is still unclear for boreal and hemi-boreal forest ecosystems (Huuskonen et al., 2021; Ruíz-Peinado et al., 2021). The broad generalization of higher productivity in mixed forests originates from studies of temperate forest ecosystems (Lu et al., 2016; Pretzsch and Schütze, 2021) or global generalizations (Liang et al., 2016; Warner et al., 2023), where Northern Europe is poorly covered.

The formation of tree species mixtures in managed forests in the boreal biome has primarily occurred through the combination of natural and artificial regeneration, where the shade intolerant pioneer tree species such as Scots pine (*Pinus sylvestris* L.) or silver birch (*Betula pendula* Roth) are often accompanied by the shade-tolerant Norway spruce (*Picea abies* [L.] H.Karst.) (Huuskonen et al., 2021). Spontaneous formation of mixtures results in stands comprising differently aged spruces and accompanying pioneer species, thus reflecting an unequal starting point, which complicates the interpretation of their potentially higher growth gain and the direct effect of tree diversity on the productivity gain. Typically, spruce-pine mixtures grow on low-fertility mineral soils and spruce-birch mixtures on more fertile sites (Felton et al., 2016; Huuskonen et al., 2021). In both types of mixed stands, late-successional Norway spruce grows beneath the dominant tree species, often resulting in a slower above-ground growth at the individual tree level for spruce compared to monocultures (Holmström et al., 2018; Huuskonen et al., 2021). The inter-specific competition in spruce-pine mixed stands results in a different below- and aboveground C allocation for spruce in comparison to a monoculture (Lutter et al., 2021a), which ultimately does not support the general expectation of higher productivity or C accumulation in mixed stands compared to monocultures (Holmström et al., 2018; Blaško et al., 2020). The reduced mixture effect on productivity in Northern Europe could be related to poor soil fertility (Högberg et al., 2017), where both tree species compete for the same soil resources (Lutter et al., 2021a). The available nutrient concentrations are low in deeper soil layers, and consequently, the fine roots are mainly allocated within the upper 30 cm layer in boreal soils (Kalliokoski et al., 2010), which means that the roots are allocated in the same niche in both monocultures and mixed stands (Lutter et al., 2021a). The potential for higher productivity and C accumulation compared to monocultures should be more eminent in spruce-birch mixed forests as the higher resource supply could reduce inter-specific competition, i.e., general diversity of vascular plants and productivity increases under higher site indexes (Cajander, 1926; Hägglund and Lundmark, 1977; Lõhmus, 1974). Given the historically lower economic value of birch in Northern Europe, the productivity and C sequestration capacity of spruce-birch mixed stands have been poorly studied at the ecosystem level in comparison to the monocultures of both tree species.

Tree species mixing is also advantageous for the soil quality, especially when the mixture comprises both broadleaf and conifer species. Rapidly decomposing deciduous tree leaf litter releases nutrients for accompanying conifers, whereas the slow decomposition of conifer litter supports soil organic carbon (SOC) accumulation. However, it remains unclear whether mixed stands support higher SOC stocks (Augusto et al., 2015; Gahagan et al., 2015) and opposite findings of higher SOC in pure conifer stands have also been reported (Berger et al., 2002). A number of studies have found higher SOC stocks in temperate old-growth mixed forests, possibly caused by root litter from more deeply rooted tree species (Schleuß et al., 2014; Dawud et al., 2016).

Tree species identity can influence soil formation, SOC accumulation, and stability due to litter quality, microorganism communities, and vertical root allocation (Augusto et al., 2002, 2015), but there is no clear understanding of the potential advantages of tree species mixing on SOC stocks in comparison to monocultures in Northern Europe. As a broad generalization, a study from hemiboreal Estonia reported that an increased share of broadleaved trees in premature and mature coniferous stands increases SOC stocks (Lutter et al., 2019). Additionally, Blaško et al. (2020) evaluated the effects of species mixing on SOC stocks in the boreal region with equal pre-study soil conditions and stand density, and found higher SOC stocks in the upper 20 cm soil layer of mixed stands and pine monocultures compared to spruce monocultures in 60-year-old stands.

Mixed stands of spruce and birch in managed forests usually develop as a combination of artificial and natural regeneration (Huuskonen et al., 2021). Planting of both species during regeneration can be considered an untraditional silvicultural practice. However, there is a shift in silviculture towards replace monocultures with mixtures by planting two or more species to improve forest resistance to climate change. Deliberately planted spruce-birch mixed forests that have reached canopy closure are very rare in Northern Europe. To the best of our knowledge, there have been no studies comparing the productivity or SOC stocks of artificially established spruce-birch mixed stands and monocultures of both species.

Our aim was to test the effect of tree species mixing on ecosystem carbon stocks (above- and belowground biomass, litter, and soil) two decades after afforestation in planted spruce-birch mixed forests as well as monocultures of both species in former agricultural lands. In addition, we compared the periodic annual increment (PAI) of stem volume based on measurements from 2020 to 2023. The design of the study was based on the equal starting point principle, i.e., the mixture had a 50/50 proportion of the two tree species during afforestation and all stands were growing on the same soil type. We raised the following hypotheses: i) spruce-birch mixture has higher productivity than the monocultures of both species; ii) SOC stock is higher in the mixture than in the monocultures; and iii) the overall ecosystem C stock is higher in the mixture than in monocultures.

2. Materials and methods

2.1. Study site

This study was conducted in commercial plantations in south-eastern Estonia, including monocultures of Norway spruce and silver birch as well as 50/50 mixture of both species. The spruce monoculture and spruce-birch mixture stands were located on the same estate in Tagaküla village (57.91 N, 26.89E, 97 m above sea level) and the birch monoculture stands were located within 10 km in Suurküla village (57.95 N, 27.03E, 90 m above sea level).

According to the data from the nearest weather station the long-term mean annual temperature from 1991 to 2020 was 6.5 °C and the annual precipitation 658 mm (The Estonian Environment Agency: https://www.ilmateenistus.ee/). The mean annual temperatures and precipitations over the study period are presented in Table 1.

The plantations were established on former arable lands of the same mineral soil type – *Retisol* according to the WRB classification (IUSS et al., 2022), which corresponds to the *Oxalis* site type according to the Estonian forest site type classification (Lõhmus, 1974). All sites were prepared before planting by using whole area ploughing and tillage. The density of the planted stands was 2500 stems ha^{-1} for all sites. Bare-rooted seedlings of spruce and birch were used in both spruce monocultures and mixed stands. Containerized seedlings were used in birch monocultures. The mixed stands and spruce monocultures were

Table 1
Mean annual temperatures and annual precipitations from the closest weather station to the study sites (The Estonian Environment Agency).

	Average temperature, °C	Annual precipitation, mm
2021	6.5	606
2022	7.0	563
2023	7.4	673

planted in the spring of 2004 and the birch monocultures in 2005, making the stands 20 and 19 years old by the end of the vegetation period of 2023, respectively. In the beginning of 2021, a total of 10 circular sample plots with a radius of 10 m were established in each stand type with the aim to study the effect of tree species mixing on productivity, competition, and nutrient acquisition in hemiboreal Estonia.

In the spruce monocultures and mixed stands, the first commercial thinning was carried out during the winter of 2020/21 just before the establishment of sample plots. After thinning, the stand densities (number of trees per ha) of the three different stand types were not significantly different from each other ($p = 0.207$). Due to increasing self-thinning in the birch monoculture, the stand densities had become significantly different ($p = 0.017$) by the end of the vegetation period of 2023.

2.2. *Growth sampling*

Diameter at breast height (DBH, cm) for every single tree was cross-calipered at 1.3 m using a standard forest caliper with a 0.1 cm scale. The height (m) of every third tree was measured with Vertex IV (Haglöf Sweden AB). The heights of the remaining trees were estimated as a function of DBH using R-package “lmfor” (Mehtatalo and Kansanen, 2022). The height model with the lowest average standard deviation of the residuals was used for each stand type. First DBH and height measurements were carried out after the vegetation period of 2020. Since then, the trees were re-measured at the end of every vegetation period (Table 3).

The total living standing stem volumes were calculated each year using Eqs. 1 and 2 from Appendix 11 of the Estonian forest survey guideline (Metsa korraldamise juhend, 2009). Values for the theoretical mixture of the two tree species were calculated so that the theoretical mixture equals the sum of half of the stand density values in monocultures of silver birch and Norway spruce.

$$M = G \times H \times F \tag{1}$$

where M is the total stem volume ($m^3\ ha^{-1}$), G is the stand basal area ($m^2\ ha^{-1}$), H is the average height (m), and F is the stand form factor (Eq. 2).

$$F = a + \frac{b}{H} + c \times \sqrt{H} + d \times \ln(H) \tag{2}$$

where a, b, c, d are parameters per tree species (Table 2), H is the average height, and ln(H) is natural logarithm of the average height.

Table 2
Parameters for Eq. 2 (Metsa korraldamise juhend, 2009).

Tree species	a	b	c	d
Birch	−1.6715	7.5641	−0.3429	1.1006
Spruce	0.9672	0.4713	0.0992	−0.3109

In order to account for the one-year age gap and differences in stand densities when comparing the yield of different stand types (Table 3), the mean annual increment of individual trees (MAI_{Ind}) was calculated (Eq. 3).

$$MAI_{Ind} = \frac{MAI}{N} \tag{3}$$

where MAI is the mean annual increment ($m^3\ ha^{-1}\ yr^{-1}$) of the stand and N is stand density (stems ha^{-1}). For MAI in Eq. 3, both the standing volume and volume of self-thinning or artificial thinning was accounted for.

2.3. *Biomass sampling*

Destructive model tree sampling was used to estimate the aboveground biomass (AGB). Silver birch biomass sampling with leaves was carried out in August 2023. Seven model trees were selected from each monoculture and mixed stand according to the DBH range. From each DBH-class, a representative model tree with average characteristics was chosen. For Norway spruce, the biomass sampling was carried out in September 2023 using the same method. The model trees were chosen inside the stand to avoid the edge effect. The model trees were felled at the root collar using a chainsaw Stihl MS 261 C-M.

The stem of each model tree was subsequently divided into subsections. The first section reached from the root collar to 1.3 m and the following sections starting from the height of 1.3 m were cut to 2 m length until the beginning of the living crown. The beginning of living crown was identified based on the attachment point of the lowest living branch. In instances where the distance to the next living branch was over 2 m, the lowest living branch was not considered as the starting point of the living crown. All stem sections were weighted in the forest to determine the fresh biomass weight. To estimate the share of stem bark and stem wood, a cross-sectional sample disc was cut from the balance point of each stem section.

The living crown was divided into three equal-length sections and all branches were pruned and weighed in the forest. Two representative model branches were taken from each crown section of each sample tree to be further analyzed in the laboratory. The model branches were fractionated in order to estimate the relative proportions of different sub-fractions of the entire crown section. The fractions used were as followed: current-year shoots; current-year needles or leaves; older branches; dead branches; and older needles for spruce.

All model tree fractions were weighed while fresh, dried to a constant weight at 60° C, and re-weighed to 0.01 g to estimate the dry mass share and calculate the dry-mass content of the entire tree.

The average stemwood density ($kg\ m^{-3}$) of the model trees was also evaluated by using cross-sectional sample discs. The circumference (converted to radius for calculations) of the fresh wood disc was measured using a tape measurer with a 0.1 cm scale. The thickness of the disc was measured using a caliper with a 0.01 mm scale at the widest and narrowest spot from which the average thickness was calculated.

Table 3
Characteristics of the studied monocultures and mixed stands. Values are represented as arithmetic means of 10 sample plots with standard errors.

Stand characteristic	Birch monoculture	Spruce monoculture	Mixture		
			Birch	Spruce	Total
Age (years)	19	20	20	20	
QMD (cm)	13.6 ± 0.26	15.4 ± 0.19	14.3 ± 0.25	11.1 ± 0.2	
Mean height (m)	16.7 ± 0.12	12.4 ± 0.13	18.4 ± 0.1	9.2 ± 0.18	
Top height (m)	17.8 ± 0.2	13.8 ± 0.14	19.5 ± 0.17	11.6 ± 0.08	
Stand density (trees ha^{-1})	1487 ± 69	1703 ± 58	812 ± 77	999 ± 46	1811 ± 116
Basal area ($m^2\ ha^{-1}$)	21.3 ± 0.62	31.6 ± 0.8	12.7 ± 0.75	9.7 ± 0.35	22.4 ± 0.86
Volume ($m^3\ ha^{-1}$)	170 ± 5.48	224 ± 6.76	111 ± 6.29	56 ± 2.33	167 ± 6.59
Harvested /self-thinned volume ($m^3\ ha^{-1}$)	1 ± 0.37	10 ± 2.62	21.5 ± 3.58	4.3 ± 1.28	25.8 ± 3.97

QMD - Quadratic mean diameter.

The circumference and the average thickness of the discs were used to calculate the volume of the fresh wooden disc. Subsequently, the discs were dried to a constant weight at 60° C and reweighed to obtain the dry weight. The dry weight (kg) was divided by the fresh volume (m^3) to obtain the density values of the discs. The weighted mean wood density per sample tree was calculated using dry weight of the wood in corresponding stem section as weight. The arithmetic mean wood density per tree species and stand type was calculated based on the weighted mean densities per sample tree.

2.3.1. Determination of stand total biomass and C pools

Allometric equation (Eq. 4) was parameterized based on the model tree data for each aboveground biomass fraction.

$$y = ax^b \tag{4}$$

where y is the absolute value (kg) or relative share of a biomass fraction, x is the diameter (cm) at breast height (1.3 m) measured over bark, and a and b are parameters of the equation. The dead branches of silver birch were not significantly associated with DBH. Therefore, the relative share of dead branches out of the total living crown (sum of current-year shoots, leaves, and branches) was estimated for silver birch which gave a statistically significant association (Table 4). The absolute value of dead branches per each single birch tree was obtained by multiplying the model estimated relative share by the absolute dry mass of the living crown.

The parametrized power equation was used to calculate the corresponding biomass fraction for each single tree located on the sample plots. The dry biomass values were summed per plot and then extrapolated to per hectare values.

Belowground biomass (BGB) for silver birch were estimated using Eq. 5 from a study conducted in Estonia by Buht et al. (2023). BGB for Norway spruce was estimated using Eq. 6 from a Latvian study by Liepiņš et al. (2018).

$$BGB = 0.0637 \times DBH^{2.1986} \tag{5}$$

$$BGB = 0.0224 \times DBH^{1.6300} \times H^{0.9420} \tag{6}$$

where BGB is the total belowground biomass in kg, DBH is the diameter at breast height (1.3 m) in centimeters, and H is the tree height in meters.

Tree biomass was converted to C values using a concentration of 0.5 for all biomass fractions of silver birch (Uri et al., 2012) and a concentration of 0.4952 for Norway spruce (Mensah and Petersson, 2024).

2.3.2. Estimation of harvested timber volume and the dry biomass of harvested timber and dead trees

Based on the model trees, the allometric equation (Eq. 3) was parametrized in order to estimate single tree stem volume based on the circumference of the stump and DBH of the trees (Fig. 1). The circumferences of the stumps of all the harvested trees from the commercial thinning were measured. To harmonize the methodology, stump circumferences were also measured for all trees that had died as a result of natural self-thinning. The stem volume for each dead or harvested tree was estimated, summed per plot, and extrapolated to per hectare values.

To be able to estimate the carbon sequestered in harvested and dead trees since the age of first commercial thinning, DBH was also estimated for all harvested trees (Fig. 1) by parametrizing a linear equation (Eq. 7).

$$DBH = a + bx \tag{7}$$

where DBH is the diameter at breast height (cm), a and b are parameters shown in Fig. 1, and x is the tree stump circumference (cm).

For dead trees, we used the DBH from the last vegetation period, when the tree was still described as alive. DBH and parametrized allometric equations (Table 4) were used to estimate the dry biomass of dead trees.

2.4. Soil sampling

Soil sampling was conducted in the spring of 2023. An approximately 0.75 m deep soil pit was dug 2 m away from the center of each sample plot. Soil sampling followed the previous published protocols of sampling former agricultural soil, where previous agricultural fertilization, ploughing, and tilling had homogenized soil nutritional variation (Lutter et al., 2016, 2023). The mineral soil profile (without litter layer) was divided into vertical sublayers for sampling: the upper 30 cm layer of mineral soil (humus, i.e. A-horizon) was divided to 0–10 cm, 10–20 cm, and 20–30 cm layers. Mineral subsoil (Elg- and B-horizon) was sampled

Table 4
Parameter estimates of Eq. 4 for predicting the different aboveground biomass fractions of the studied mixed stands and monocultures. N is the number of model trees, a and b are the equation parameter estimates, R^2 is the coefficient of determination, and p-value shows the significance of the model.

Tree species	Biomass fraction	Stand type	N	a	b	R^2	p-value
Silver birch	Total AGB*	Mix	7	0.1287	2.4348	0.992	< 0.001
		Mono	7	0.0812	2.5517	0.987	< 0.001
	Stemwood*	Mix	7	0.1310	2.3119	0.988	< 0.001
		Mono	7	0.0532	2.5914	0.983	< 0.001
	Stembark	Both	14	0.0147	2.3549	0.984	< 0.001
	Current-year shoots	Both	14	1.4×10^{-6}	4.7560	0.823	< 0.001
	Leaves	Both	14	6.6×10^{-4}	3.1647	0.946	< 0.001
	Branches	Both	14	1.97×10^{-3}	3.1409	0.961	< 0.001
	Relative share of dead branches from living canopy	Both	14	85.8881	−2.8989	0.659	< 0.001
Norway spruce	Total AGB	Both	14	0.1938	2.1706	0.975	< 0.001
	Stemwood*	Mix	7	0.0385	2.4453	0.993	< 0.001
		Mono	7	0.0853	2.2037	0.985	< 0.001
	Stembark	Both	14	0.0163	2.0859	0.956	< 0.001
	Current-year shoots*	Mix	7	0.0037	1.9641	0.875	0.0012
		Mono	7	2.2×10^{-4}	2.9377	0.908	< 0.001
	Current-year needles*	Mix	7	0.0085	2.0825	0.846	0.002
		Mono	7	7.9×10^{-4}	2.8588	0.908	< 0.001
	Branches*	Mix	7	0.0631	2.1329	0.875	0.0012
		Mono	7	0.0086	2.6358	0.938	< 0.001
	Older needles*	Mix	7	0.0444	2.1040	0.927	< 0.001
		Mono	7	0.0109	2.4385	0.933	< 0.001
	Dead branches*	Mix	7	0.0148	1.9156	0.515	0.042
		Mono	7	0.1938	1.2848	0.797	0.004

* Denotes a significant difference in the biomass fraction between stand types.

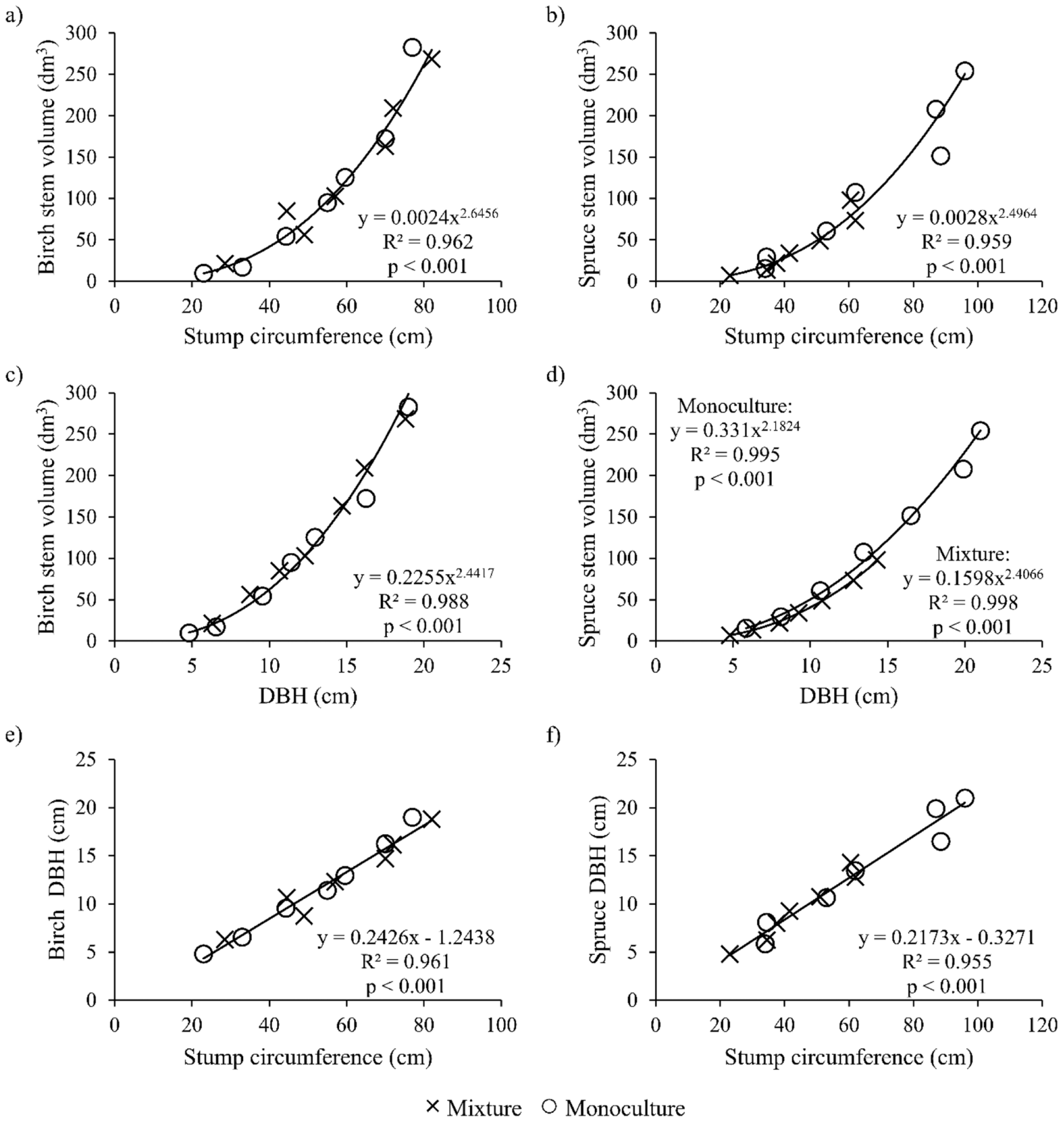

Fig. 1. Allometric equations for estimating stem volume (over bark) and DBH for birch (a, c, e) and spruce (b, d, f). a) and b) stem volume (dm^3) by stump circumference (cm), c) and d) stem volume (dm^3) by DBH (cm), and e) and f) DBH (cm) by stump circumference (cm).

as a mix of the 30–50 cm layer as they were overlapped in the vertical profile. One composite sample was collected from each vertical layer for determining soil acidity, SOC, and nutrients. The composite sample was obtained by combining three subsamples collected from different points of the soil pit. The collected mineral soil samples were dried at room temperature before laboratory analyses. Sampling of the forest floor (O-horizon) of every sample plot was done with a 0.2 × 0.2 m metal frame next to the soil pit. The litter biomass was cleaned from inorganic material and non-tree organic material at the laboratory. The forest floor samples were dried to constant weight at 60° C in the oven.

Soil acidity (pH_{KCl}) was determined from a 1 M KCl suspension according to the ISO 10390 standard. The concentration of plant-available phosphorous (P, mg kg^{-1}) and potassium (K, mg kg^{-1}) were determined according to the Mehlich III method (Mehlich, 1984). The concentration of total nitrogen (N_{tot}, %) and soil organic carbon (SOC, %) were determined using varioMAX CNS (Elementar Analysensysteme GmbH, Germany). For forest floor, only SOC and N_{tot} were measured. Soil chemical analyses were performed at the Laboratory of Agrochemistry of the Chair of Soil Sciences at the Estonian University of Life Sciences.

Soil bulk density (BD, g cm^{-3}) was measured for each vertical mineral soil layer in three replications per layer. BD samples were taken with a 43 cm^3-sized steel cylinder and oven-dried at 105° C to a constant weight.

SOC stock (Mg ha^{-1}) was calculated for each vertical soil layer by multiplying the given horizon volume, BD, and SOC concentration. Forest floor SOC stock was calculated by multiplying the mass of organic material inside the 0.04 m^2 metal frame with the SOC concentration. Both mineral and forest floor SOC stocks were converted to the hectare scale.

2.5. Statistical analysis

All statistical analyses were carried out using the R statistical software package in RStudio integrated development environment (IDE) (R Studio Team, 2020; R Core Team, 2023). The effect of stand type on growth characteristics, C stocks, and soil properties were tested with a linear model (lm). As a posthoc test, the statistical differences between forest types were evaluated with the Tukey's HSD test using the emmeans package (Lenth, 2023). The 95 % confidence intervals were calculated with Sidak-correction. The Shapiro-Wilk test was used to test the normality of the model residuals. The Kruskal-Wallis test was used when the data did not follow a normal distribution, followed by Dunn's test (Ogle et al., 2023) with the Bonferroni correction as a post hoc test to identify the differences between forest types. A significance threshold of $\alpha = 0.05$ was used. The in-text means are presented with ± SE, if not stated otherwise.

3. Results

3.1. Stem volume increment and wood density

Two decades after afforestation, the mean annual increment (MAI) of stem volume (includes self-thinning and artificial thinning) was significantly higher in the spruce monocultures (11.7 ± 0.35 m^3 ha^{-1} yr^{-1}) than in the mixed stands (9.7 ± 0.21 m^3 ha^{-1} yr^{-1}) and birch monocultures (9.0 ± 0.30 m^3 ha^{-1} yr^{-1}) ($p < 0.001$ and $p < 0.001$, respectively) (Fig. 2). The difference in MAI between the mixed stands and birch monocultures was insignificant ($p = 0.377$). The MAI of the theoretical mixtures (10.4 ± 0.25 m^3 ha^{-1} yr^{-1}) did not differ significantly from the actual mixtures ($p = 0.301$), but was lower than that of spruce monocultures ($p = 0.009$) and higher compared to birch monocultures ($p = 0.009$).

Similarly to MAI, the spruce monocultures had a significantly higher periodic annual stem volume increment (PAI) (23.3 ± 0.46 m^3 ha^{-1} yr^{-1}) than the mixed stands (19.2 ± 0.53 m^3 ha^{-1} yr^{-1}) and birch monocultures (16.4 ± 0.45 m^3 ha^{-1} yr^{-1}) ($p < 0.001$ and $p < 0.001$, respectively). The PAI of the mixed stands was significantly higher than the PAI of the birch monocultures ($p < 0.001$). The PAI of the theoretical mixtures (19.8 ± 0.26 m^3 ha^{-1} yr^{-1}) did not differ from the actual mixtures ($p = 0.702$), but was significantly lower compared to spruce monocultures ($p < 0.001$) and higher than birch monocultures ($p < 0.001$) (Fig. 3).

At the individual tree level, Norway spruce was disadvantaged from growing in the mixture as the average tree stem MAI_{Ind} of Norway spruce was 56 % lower in mixed stands than monocultures ($p < 0.001$). Silver birch MAI_{Ind} showed no significant difference between the mixed stands and monocultures ($p = 0.226$) (Fig. 4).

The stemwood density of Norway spruce was 329 ± 6.5 kg m^{-3} in the mixed stands and 331 ± 8.6 kg m^{-3} in the monocultures ($p = 0.868$). Silver birch stemwood density was significantly lower in the monocultures (429 ± 7.5 kg m^{-3}) than in the mixed stands (465 ± 6.9 kg m^{-3}) ($p = 0.004$).

3.2. Soil analyses

The bulk density up to a depth of 10 cm was significantly higher in birch monocultures compared to spruce monocultures ($p < 0.001$) and mixed stands ($p < 0.001$). In the 10–20 cm soil layer, the bulk density was similar between monocultures ($p = 0.271$) and between spruce monocultures and mixed stands ($p = 0.375$), whereas birch monocultures had significantly higher bulk density than mixtures ($p = 0.018$). In the deeper soil layers, there were no differences between the bulk densities of different stand types (Table 5).

Birch monocultures had a higher pH than spruce monocultures and mixed stands ($p < 0.001$ and $p < 0.001$, respectively) in the 0–10 cm soil layer. In the 10–20 cm soil layer, there was no difference in pH-values between birch and spruce monocultures ($p = 0.288$) as well as spruce monocultures and mixed stands ($p = 0.522$), whereas mixtures had lower pH-values than birch monocultures ($p = 0.007$). The posthoc test revealed no difference in pH-values in the 20–30 cm soil depth layer. In the 30–50 cm soil depth layer, the spruce monocultures had the highest pH-values and there was no difference between birch monocultures and mixed stands (Table 5).

No statistically significant differences were found for SOC and N_{tot} concentrations, except for N_{tot} in the 20–30 cm layer, where birch monocultures had higher concentrations than spruce monocultures ($p = 0.038$). In the 30–50 cm soil layer, there was more P in spruce monocultures than birch monocultures ($p = 0.001$). No other differences in P concentrations were identified between the soil layers of the three stand types. Consistently higher K concentrations were found in the birch monocultures compared to the spruce monocultures in all soil layers and the 0–30 cm soil layers of the mixed stands. In the deepest 30–50 cm layer there was no difference in K concentrations between the birch monocultures and mixed stands ($p = 0.099$) (Table 5).

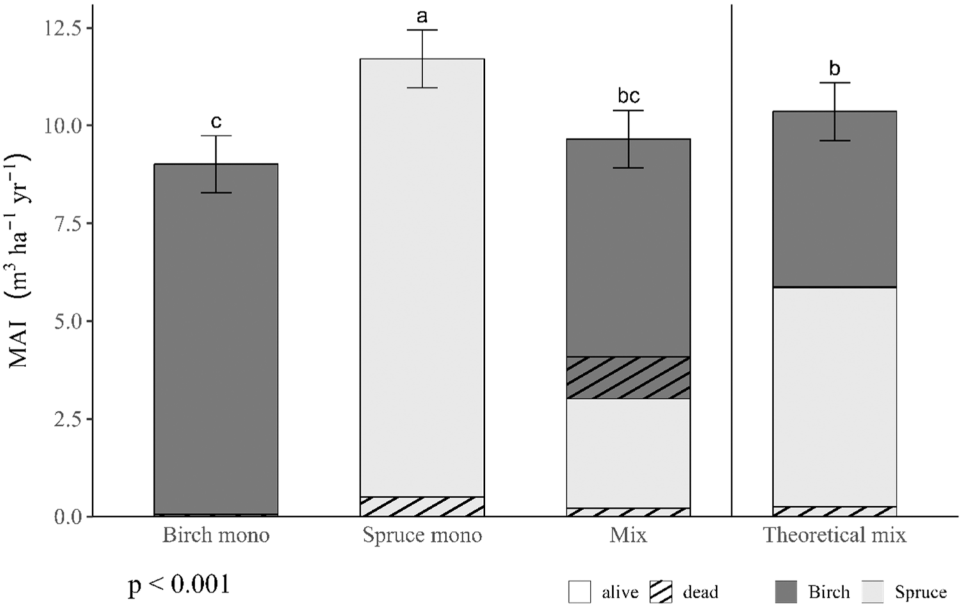

Fig. 2. The mean annual increment (MAI) of the studied stand types and the theoretical mixtures (sum of half of the MAI of silver birch and Norway spruce monocultures). Error bars show 95 % confidence intervals. P-value shows the significance of the main effect of stand type on MAI. Significant differences between stand types are shown with lowercase letters.

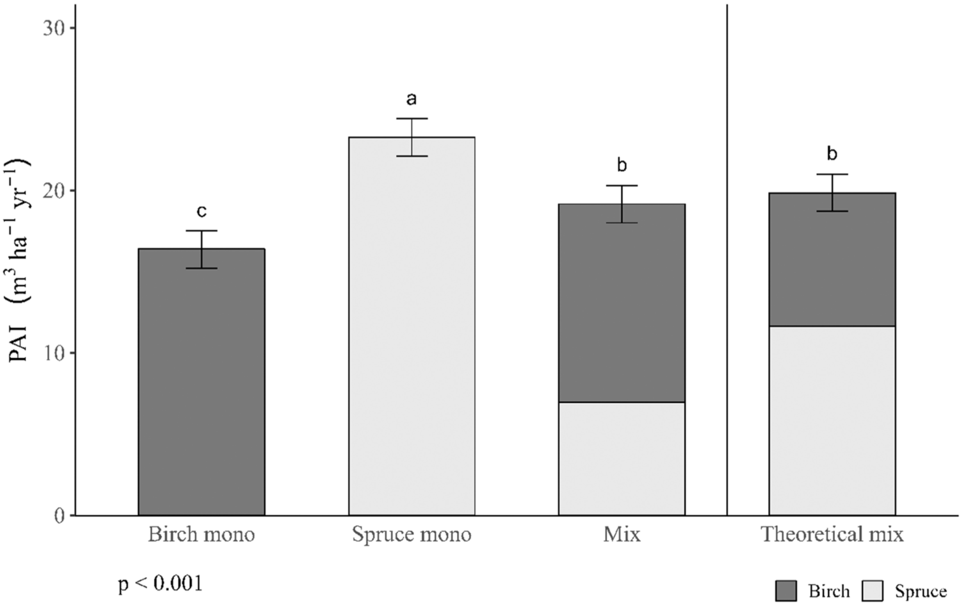

Fig. 3. The periodic annual increment (PAI) of the studied stand types and theoretical mixtures (sum of one half of the volume growth values in silver birch and Norway spruce monocultures) from 2020 to 2023. Error bars show 95 % confidence intervals. P-value shows the significance of the main effect of stand type on PAI. Significant differences between stand types are shown with lowercase letters.

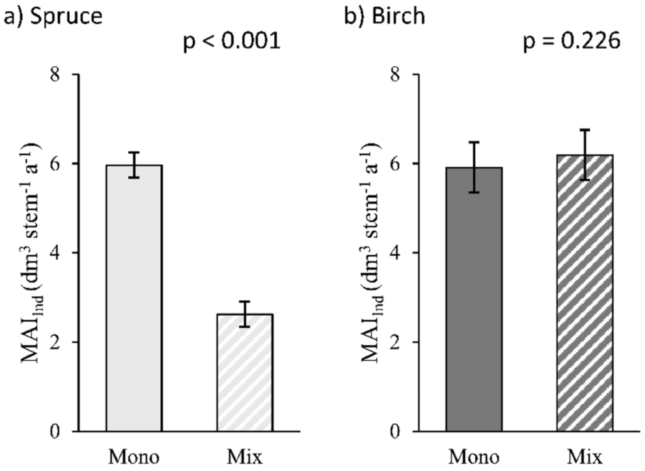

Fig. 4. Individual tree stem mean annual increment (MAI$_{Ind}$) of spruce (a) and birch (b) in monocultures and mixed stands. Error bars show 95 % confidence intervals.

3.3. *Ecosystem C stocks and allocation*

Ecosystem C stock was 12.3 % higher in the spruce monocultures (138.0 ± 7.16 Mg C ha^{-1}) than in the birch monocultures ($p = 0.028$) and 11.6 % higher than in the mixed stands ($p = 0.039$). Ecosystem C stock was similar between birch monocultures and the mixed stands ($p = 0.989$) (Table 6). Differences were also found in C stock allocation between the studied stand types. Stemwood and stembark C stock was significantly higher in birch monocultures than in spruce monocultures ($p = 0.018$ and $p < 0.001$, respectively). Stemwood C stock was similar among birch monocultures and mixed stands ($p = 0.081$), whereas birch monocultures had higher stembark C stocks than the mixed stands ($p = 0.001$). We found that spruce monocultures had significantly higher C stocks in the branches (leaf, current-year, older and dead branches) and roots than birch monocultures and mixed stands. Those C stocks compensated for the lower stemwood C stocks in the spruce monocultures and consequently the whole tree C stocks were significantly higher in spruce monocultures than in birch monocultures ($p < 0.001$) and mixtures ($p = 0.001$).

Soil analyses indicated that there was no difference in SOC stocks up to 50 cm depth between the different stand types ($p = 0.86$) (Table 6). However, O-horizon SOC stocks of the spruce monocultures were significantly higher than in the birch monocultures ($p = 0.008$). SOC stocks of the 0–10 cm layer were significantly higher in the birch monocultures than in the mixed stands ($p = 0.033$), while there was no effect of stand type on the SOC stocks of deeper soil layers (>10 cm).

4. Discussion

4.1. *Stem volume productivity*

Approximately two decades after afforestation of former agricultural lands with two commercially important tree species (Norway spruce and silver birch) in both monocultures and mixed stands of both species, we did not find higher stem volume productivity in the mixed stands based on MAI and PAI. The highest PAI and MAI values were found in the spruce monocultures and therefore, we can reject our first hypothesis. The growth and yield of Norway spruce and silver birch monocultures in comparison to a mixture of the two species has not yet been studied to our knowledge as a planted stand in Northern Europe (Huuskonen et al., 2021). Few existing modelling studies involving a comparison of spruce and birch mixtures with spruce monocultures have evaluated mixtures formed as a result of natural regeneration. Tham (1994) found that the mixing effect increases overall yield if the stand density of birch is lowered to 600–1200 stems ha^{-1} during pre-commercial thinning (PCT) and the birches are removed completely between 20 and 30 years of age. Mielikäinen (1985) reported a small increase in volume production (3–5 %) during the long rotation of 80–90 years when the proportion of silver birch was kept below 25 %. Overall, studies using forest growth simulations have reported similar or even lower productivity of equal spruce-birch mixtures compared to spruce monocultures (Fahlvik et al., 2015; Huuskonen et al., 2021; Dosumu et al., 2024). However, natural regeneration is uneven in terms of spatial location and the age of trees, which could make interpretation of higher productivity in the mixture difficult.

We found the lowest stand volume in birch monocultures, which was

Table 5

The effect of stand type on soil bulk density, acidity (pH), and the concentrations of soil organic carbon (SOC), total nitrogen (N_{tot}), phosphorous (P), and potassium (K) in different vertical soil layers. Mean values with standard errors are presented. Significant differences between the stand types within the same layer are indicated by lowercase letters.

Soil characteristic	Soil depth layer, cm	Birch monoculture	Spruce monoculture	Mixture	p-value
Bulk density, g cm^{-3}	0–10	1.24 ± 0.025^{a}	0.96 ± 0.025^{b}	0.99 ± 0.026^{b}	**< 0.001**
	10–20	1.3 ± 0.031^{a}	1.25 ± 0.013^{ab}	1.2 ± 0.030^{b}	**0.023**
	20–30	1.36 ± 0.029	1.39 ± 0.024	1.34 ± 0.016	0.437
	30–50	1.51 ± 0.027	1.45 ± 0.050	1.46 ± 0.048	0.548
pH_{KCl}	0–10[*]	4.9 ± 0.05^{a}	3.8 ± 0.07^{b}	3.8 ± 0.05^{b}	**< 0.001**
	10–20[*]	4.8 ± 0.06^{a}	4.8 ± 0.26^{ab}	4.3 ± 0.05^{b}	**0.010**
	20–30[*]	4.9 ± 0.07	5.3 ± 0.26	4.6 ± 0.09	**0.026**
	30–50	4.6 ± 0.1^{b}	5.2 ± 0.2^{a}	4.5 ± 0.11^{b}	**0.006**
SOC, %	0–10	1.75 ± 0.064	1.96 ± 0.07	1.8 ± 0.11	0.204
	10–20	1.22 ± 0.067	1.22 ± 0.054	1.39 ± 0.078	0.137
	20–30	1.03 ± 0.079	0.83 ± 0.108	0.92 ± 0.116	0.408
	30–50[*]	0.18 ± 0.013	0.32 ± 0.053	0.26 ± 0.045	0.061
N_{tot}, %	0–10	0.144 ± 0.005	0.149 ± 0.005	0.135 ± 0.009	0.362
	10–20	0.104 ± 0.005	0.094 ± 0.005	0.104 ± 0.005	0.266
	20–30	0.089 ± 0.007^{a}	0.06 ± 0.008^{b}	0.071 ± 0.009^{ab}	**0.046**
	30–50	0.016 ± 0.001	0.022 ± 0.003	0.018 ± 0.003	0.244
P, mg kg^{-1}	0–10[*]	59.4 ± 4.7	68.1 ± 13.52	90.5 ± 7.94	**0.040**
	10–20[*]	45.2 ± 5.36	43.2 ± 8.18	56.1 ± 7.93	0.268
	20–30[*]	46.3 ± 6.43	46.4 ± 11.05	42.8 ± 6.04	0.480
	30–50[*]	19.2 ± 4.09^{b}	59.5 ± 12.06^{a}	30.2 ± 4.8^{ab}	**0.002**
K, mg kg^{-1}	0–10	199.9 ± 11.3^{a}	59.8 ± 6.75^{b}	85.2 ± 4.78^{b}	**< 0.001**
	10–20[*]	134.9 ± 7.77^{a}	31.8 ± 5.49^{b}	57.1 ± 2.86^{b}	**< 0.001**
	20–30[*]	96 ± 6.54^{a}	28 ± 6.89^{b}	44.2 ± 3.57^{b}	**< 0.001**
	30–50	63.7 ± 5.97^{a}	29.9 ± 6.03^{b}	44.6 ± 6.84^{ab}	**0.003**

[*] Indicates where the data did not follow normal distribution and Kruskal-Wallis test was used. When no lowercase letters are shown for significant p-values then the posthoc test revealed no significant difference between groups.

surprising considering the faster expected growth of juvenile birch (Hynynen et al., 2010; Lutter et al., 2015). Birch, being a light-demanding pioneer tree species (Hynynen et al., 2010; Huuskonen et al., 2021), does not tolerate the high initial stand density in our study for long, which resulted in self-thinning that had already lowered the stem number per hectare (Hynynen et al., 2010). Accordingly, some other studies from the region have found that a higher proportion of birch lowered the overall yield of the mixed birch-conifer stands during the entire rotation (Fahlvik et al., 2015; Dosumu et al., 2024).

Higher productivity of mixed forests under certain conditions has been proven in the temperate and tropical biomes where the niche differentiation appears for wider choice of shade-tolerant or deep-rooted tree species (Pretzsch et al., 2010; Forrester, 2014; Pretzsch and Schütze, 2021). At present, in Northern Europe, majority of studies have focused on comparing spruce and pine monocultures and mixed stands (Drössler et al., 2018; Holmström et al., 2018; Aldea et al., 2021; Ruíz-Peinado et al., 2021). Those studies have reported a rather weak or no effect of tree species mixing. Drössler et al. (2018) found that with increasing latitude the overyielding effect of mixtures decreases.

No effect of species mixing on productivity indicates inter-specific

Table 6

Carbon stocks (Mg C ha^{-1}) in different compartments of the studied stand types two decades after afforestation. Arithmetic means with standard errors are presented.

Ecosystem compartment	Birch monoculture		Spruce monoculture		Mixture	
	Mg ha^{-1}	%	Mg ha^{-1}	%	Mg ha^{-1}	%
Stemwood	34.5 ± 1.00^{a}	28.1	29.9 ± 0.76^{b}	21.7	31.5 ± 1.35^{ab}	25.5
Stembark	5.1 ± 0.15^{a}	4.1	4.1 ± 0.10^{b}	3.0	4.3 ± 0.17^{b}	3.5
Total leaf/needle mass	2.0 ± 0.06^{c}	1.6	9.1 ± 0.24^{a}	6.6	5.3 ± 0.17^{b}	4.3
Current-year shoots	0.3 ± 0.01^{c}	0.2	0.6 ± 0.02^{a}	0.4	0.4 ± 0.01^{b}	0.3
Older living branches	5.6 ± 0.17^{c}	4.6	10.1 ± 0.26^{a}	7.3	8.8 ± 0.25^{b}	7.1
Dead branches	0.3 ± 0.01^{c}	0.2	5.3 ± 0.14^{a}	3.8	0.9 ± 0.04^{b}	0.7
Roots	14.6 ± 0.42^{b}	11.9	17.6 ± 0.51^{a}	12.8	13.5 ± 0.53^{b}	10.9
Total AGB	47.8 ± 1.40^{b}	38.9	59.2 ± 1.52^{a}	42.9	51.2 ± 1.99^{b}	41.4
Whole tree	62.4 ± 1.82^{b}	50.8	76.8 ± 2.03^{a}	55.7	64.8 ± 2.52^{b}	52.4
O-horizon	3.9 ± 0.78^{b}	3.2	6.5 ± 0.77^{a}	4.7	4.6 ± 0.33^{ab}	3.7
Soil 0–10 cm	21.5 ± 0.55^{a}	17.5	18.8 ± 0.75^{ab}	13.6	18.0 ± 1.33^{b}	14.6
Soil 10–20 cm	15.8 ± 0.67	12.9	15.3 ± 0.74	11.1	16.6 ± 0.95	13.4
Soil 20–30 cm	13.8 ± 0.90	11.2	11.4 ± 1.39	8.3	12.3 ± 1.47	9.9
Soil 30–50 cm	5.5 ± 0.41	4.5	9.2 ± 1.48	6.7	7.4 ± 1.19	6.0
Soil total	60.5 ± 3.31	49.2	61.2 ± 5.13	44.3	58.9 ± 5.27	47.6
Ecosystem C stocks	122.9 ± 5.13^{b}	100	138.0 ± 7.16^{a}	100	123.7 ± 7.79^{b}	100
Harvested or self-thinned C[*]	0.2 ± 0.08^{b}		2.6 ± 0.63^{ab}		6.9 ± 1.05^{a}	

[*] C stored in leaves, needles, and roots is not included in the harvested or self-thinned C compartments.

competition where spruce is outcompeted by birch or pine (Huuskonen et al., 2021; Aldea et al., 2021). This effect was also evident in our study, where at the individual tree level birch grew similarly in both mixed stands and monocultures, whereas spruce showed lower mean stem volume production in the mixed stands. This contradicts previous reports from the region (Tham, 1994; Huuskonen et al., 2021, 2022), which have found that the negative effect of naturally regenerated sheltering birch on the growth of improved spruce seedlings is relatively low. A study based on a planted spruce-pine mixture (Holmström et al., 2018) reported findings similar to ours, where the initially faster growing pioneer tree species benefits from growing in a mixture, as it lowers the overall competition for the dominant tree species of the stand in comparison to a fully stocked monoculture of the same species. Late-successional spruce can tolerate shade, but recent findings in boreal forests have shown differences in belowground nutrient acquisition and rooting strategy in spruce-pine example (Lutter et al., 2021a). The main pools of available nutrients are located in the upper soil layers and the fine root distribution of different species to explore vertical niches is poor (Kalliokoski et al., 2010). According to Lutter et al. (2021a), spruce has a proportionally wider lateral rooting area for nitrogen uptake than pine in a mixed stand, indicating below-ground inter-specific competition. Spruce-birch mixtures occupy more fertile soils than spruce-pine stands (Huuskonen et al., 2021), which might indicate below-ground competition for water, especially as a result of more frequent and longer drought periods during the summer. The results of PAI analysis indicated that spruce monocultures will even further surpass mixed stands and birch monocultures in stem volume. The higher PAI of mixed stands in comparison to birch monocultures will most likely cause the mixed stands to surpass birch monocultures in productivity in the near future.

It should be borne in mind that our study compared the productivity two decades after planting. The expected rotation cycle (based on financial maturity) for such birch monocultures is approximately 35–45 years (Tullus et al., 2012) and 50–55 years for Norway spruce (Korjus et al., 2011), which shows that this study reported the progress in productivity at the mid-term rotation phase.

4.2. Ecosystem C stocks and allocation

The highest ecosystem C stocks that include both above- and belowground C were found in spruce monocultures. Therefore, we can reject our third hypothesis that two decades after afforestation the mixtures of spruce and birch would show higher C stocks than the monocultures of both species. However, we found significant differences in C stock allocation between the studied stand types. The MAI and PAI of stem volume were higher in the spruce monocultures, whereas the C stocks of stemwood were highest in the birch monocultures. This can be explained by the 30 % higher wood density and lower share of branches in birch compared to spruce monocultures. A high share of C (18.1 %) from the ecosystem stock in spruce monocultures was allocated in the canopy. Two decades after afforestation, there was no effect of tree species mixing on SOC stocks up to the maximum evaluated depth of 50 cm, disproving the second hypothesis. Some studies report that time since afforestation, tree species identity, and former land-use type could be more important drivers for SOC stability than tree species diversity (Bárcena et al., 2014; Mayer et al., 2020). Hence, two decades might not be sufficient to influence mineral soil C levels on former agricultural lands (Bárcena et al., 2014). Forest floor (O-horizon) SOC stock was higher in the spruce monocultures than in the birch monocultures. The positive effect of conifers on forest floor SOC stocks have also been described in other studies (Mayer et al., 2020). This can be explained by the chemical characteristics and associated microbial communities of spruce litter, which takes longer to decompose than the litter of deciduous trees (Buresova et al., 2021). The first soil survey of the studied stands was carried out during the present study and therefore we are not able to describe pre-planting SOC stocks. Previous studies focusing on former agricultural land afforestation on similar soils indicate no major changes in SOC stocks in mineral soil layers during the first or second decade with deciduous species (Lutter et al., 2016, 2023). SOC gain in the forest floor seems to be the benefit of afforestation with spruce as it started to accumulate after planting, whereas mixed stands or birch monocultures do not support forest floor formation in the short-term perspective.

4.3. Management implications

Boreal forest management systems have so far focused on growing monocultural stands and there is limited information about the potential advantages of mixtures. In terms of climate mitigation through C fixation in the ecosystem, mixing spruces and birches does not provide additional climate benefits within two decades after afforestation of former agricultural lands. Mixed forests have also been shown to improve soil quality in comparison to conifer monocultures by raising soil pH and increasing soil microbial activity, which result in higher rates of C and N mineralization and increased SOC stocks (Smolander and Kitunen, 2011; Lutter et al., 2019).

Based on our results, we cannot conclude that mixed stands improved soil quality within 20-years after afforestation compared to spruce monocultures, although the potential difference could take more time to become evident (Huuskonen et al., 2021). Consistently higher soil K concentrations in the birch monocultures most likely indicate the legacy of different fertilization regimes of the agricultural lands in the past. K concentrations in spruce monocultures and mixed stands stayed in the range of afforested abandoned agricultural lands in the region (Lutter et al., 2023).

From the economic perspective, logging costs are expected to be higher in mixed stands, but the mixture may still be more profitable as flexible management of two species is less affected by the volatile timber prices of single tree species (Felton et al., 2016, Dosumu et al., 2024). C allocation analysis showed that a high share of C in the spruce monocultures was located in branches, which is later utilized for energy and has a weak impact on climate mitigation (Lutter et al., 2021b; Myllyviita et al., 2021). Birch allocated more C to stemwood, i.e., it had higher C stocks in merchantable timber, which supports C storage in long-lived wood products and provides additional climate benefits as a result of avoided CO_2 emissions (Lutter et al., 2021b).

The potential advantages of a spruce-birch mixture over monocultures cannot be assessed solely based on the present climate benefits and ecosystem C resistance to climate change should also be considered during species selection. Establishing a mixed forest can reduce the risk of disturbances in the forest, especially compared to a spruce monoculture. In the mixed stands, the spruces were shaded by the dominant birches, which should reduce water stress during dry summers and lower the intensity of bark beetle outbreaks (Jakuš et al., 2011). Additionally, the dimensions of spruces remained smaller in the mixed stands making them less attractive to bark beetles (Kärvemo et al., 2014).

5. Conclusions

We studied the effect of mixed spruce and birch stands on yield, carbon storage, and soil quality two decades after planting on former agricultural land in hemiboreal Estonia. We did not find advantages of species mixing over monocultures based on stem volume production or ecosystem C stocks. However, we found that aboveground C allocation was different in birches and spruces as in spruce monocultures a higher share of C was located in the branches. There was no effect of stand type on SOC stocks in the mineral soil, but spruce monocultures showed higher SOC stocks in the forest floor. At the individual tree level, spruces showed higher average growth rates in monocultures and were suppressed in mixed stands in terms of their stem volume mean annual increment.

In conclusion, two decades after afforestation, spruce monocultures provided higher climate benefits than spruce-birch mixed stands and birch monocultures at the ecosystem level. Longer observations spanning the entire rotation cycle are needed to assess C stock stability and avoided C emission levels resulting from the substitution effect of wood.

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CRediT authorship contribution statement

Kristjan Täll: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Arvo Tullus:** Writing – review & editing, Supervision, Resources, Methodology, Formal analysis. **Hardi Tullus:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Tea Tullus:** Writing – review & editing, Visualization. **Reimo Lutter:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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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Data Availability

Data will be made available on request.

References

Aldea, J., Ruiz-Peinado, R., del Río, M., Pretzsch, H., Heym, M., Brazaitis, G., Jansons, A., Metslaid, M., Barbeito, I., Bielak, K., Granhus, A., 2021. Species stratification and weather conditions drive tree growth in Scots pine and Norway spruce mixed stands along Europe. For. Ecol. Manag. 481, 118697. https://doi.org/10.1016/j.foreco.2020.118697.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., Ranger, J., 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. Biol. Rev. 90, 444–466. https://doi.org/10.1111/brv.12119.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59, 233–253. https://doi.org/10.1051/forest:2002020.

Bárcena, T.G., Kiær, L.P., Vesterdal, L., Stefánsdóttir, H.M., Gundersen, P., Sigurdsson, B. D., 2014. Soil carbon stock change following afforestation in Northern Europe: a meta-analysis. Glob. Change Biol. 20 (8), 2393–2405. https://doi.org/10.1111/gcb.12576.

Berger, T.W., Neubauer, C., Glatzel, G., 2002. Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (Picea abies) and mixed species stands in Austria. For. Ecol. Manag. 159 (1-2), 3–14. https://doi.org/10.1016/S0378-1127(01)00705-8.

Blaško, R., Forsmark, B., Gundale, M.J., Lundmark, T., Nordin, A., 2020. Impacts of tree species identity and species mixing on ecosystem carbon and nitrogen stocks in a boreal forest. For. Ecol. Manag. 458, 117783. https://doi.org/10.1016/j.foreco.2019.117783.

Buht, M., Padari, A., Aosaar, J., Varik, M., Aun, K., Uri, M., Becker, H., Kukumägi, M., Sepaste, A., Uri, V., 2023. Biomass allocation and equations for silver birch (Betula pendula) and downy birch (Betula pubescens) in Estonia. Scand. J. For. Res. 38 (7-8), 486–496. https://doi.org/10.1080/02827581.2023.2273250.

Buresova, A., Tejnecky, V., Kopecky, J., Drabek, O., Madrova, P., Rerichova, N., Omelka, M., Krizova, P., Nemecek, K., Parr, T.B., Ohno, T., Sagova-Mareckova, M., 2021. Litter chemical quality and bacterial community structure influenced decomposition in acidic forest soil. Eur. J. Soil Biol. 103, 103271. https://doi.org/10.1016/j.ejsobi.2020.103271.

Cajander, A.K., 1926. The theory of forest types. Acta For. Fenn. 29, 1–108.

Craine, J.M., Dybzinski, R., 2013. Mechanisms of plant competition for nutrients, water and light. Funct. Ecol. 27, 833–840. https://doi.org/10.1111/1365-2435.12081.

Dawud, S.M., Raulund-Rasmussen, K., Domisch, T., Finér, L., Jaroszewicz, B., Vesterdal, L., 2016. Is tree species diversity or species identity the more important driver of soil carbon stocks, C/N ratio, and pH? Ecosystems 19, 645–660. https://doi.org/10.1007/s10021-016-9958-1.

Dosumu, B., Aldea, J., Holmström, E., Nilsson, U., 2024. Thinning strategies impact the productivity, perpetuity and profitability of mixed stands. Scand. J. For. Res. 1–9. https://doi.org/10.1080/02827581.2024.2390901.

Drössler, L., Agestam, E., Bielak, K., Dudzinska, M., Koricheva, J., Liziniewicz, M., Löf, M., Mason, B., Pretzsch, H., Valkonen, S., Wellhausen, K., 2018. Over-and underyielding in time and space in experiments with mixed stands of scots pine and Norway spruce. Forests 9 (8), 495. https://doi.org/10.3390/f9080495.

Fahlvik, N., Ekö, P.M., Petersson, N., 2015. Effects of precommercial thinning strategies on stand structure and growth in a mixed even-aged stand of Scots pine, Norway spruce and birch in southern Sweden. Silva Fenn. 49 (3). https://doi.org/10.14214/sf.1302.

Felton, A., Nilsson, U., Sonesson, J., Felton, A.M., Roberge, J.M., Ranius, T., Ahlström, M., Bergh, J., Björkman, C., Boberg, J., Drössler, L., Fahlvik, N., Gong, P., Holmström, E., Keskitalo, E.C.H., Klapwijk, M.J., Laudon, H., Lundmark, T., Niklasson, M., Nordin, A., Pettersson, M., Stenlid, J., Sténs, A., Wallertz, K., 2016. Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest alternatives in Sweden. Ambio 45, 124–139. https://doi.org/10.1007/s13280-015-0749-2.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For. Ecol. Manag. 312, 282–292. https://doi.org/10.1016/j.foreco.2013.10.003.

Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity–Productivity Relationships in Forests. Ecol. Funct. 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Forrester, D.I., Kohnle, U., Albrecht, A.T., Bauhus, J., 2013. Complementarity in mixed-species stands of Abies alba and Picea abies varies with climate, site quality and stand density. For. Ecol. Manag. 304, 233–242. https://doi.org/10.1016/j.foreco.2013.04.038.

Gahagan, A., Giardina, C.P., King, J.S., Binkley, D., Pregitzer, K.S., Burton, A.J., 2015. Carbon fluxes, storage and harvest removals through 60 years of stand development in red pine plantations and mixed hardwood stands in Northern Michigan, USA. For. Ecol. Manag. 337, 88–97. https://doi.org/10.1016/j.foreco.2014.10.037.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4 (1), 1340. https://doi.org/10.1038/ncomms2328.

Hägglund, B., Lundmark, J.E., 1977. Site index estimations by means of site properties. Scots pine Nor. spruce Swed. Stud. For. Suec. 103, 5–38.

Högberg, P., Näsholm, T., Franklin, O., Högberg, M.N., 2017. Tamm review: on the nature of the nitrogen limitation to plant growth in Fennoscandian boreal forests. For. Ecol. Manag. 403, 161–185. https://doi.org/10.1016/j.foreco.2017.04.045.

Holmström, E., Goude, M., Nilsson, O., Nordin, A., Lundmark, T., 2018. Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. For. Ecol. Manag. 429, 287–293. https://doi.org/10.1016/j.foreco.2018.07.008.

Huuskonen, S., Domisch, T., Finér, L., Hantula, J., Hynynen, J., Matala, J., Miina, J., Neuvonen, S., Nevalainen, S., Niemistö, P., Nikula, A., Piri, T., Siitonen, J., Smolander, A., Tonteri, T., Uotila, K., Viiri, H., 2021. What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? For. Ecol. Manag. 479, 118558. https://doi.org/10.1016/j.foreco.2020.118558.

Huuskonen, S., Lahtinen, T., Miina, J., Uotila, K., Bianchi, S., Niemistö, P., 2022. Growth dynamics of young mixed Norway spruce and birch stands in Finland. Forests 14 (1), 56. https://doi.org/10.3390/f14010056.

Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., Velling, P., 2010. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. Forestry 83 (1), 103–119. https://doi.org/10.1093/forestry/cpp035.

IUSS Working Group WRB, 2022. World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps., 4th edition. International Union of Soil Sciences (IUSS), Vienna, Austria.

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree diversity drives forest stand resistance to natural disturbances. Curr. For. Rep. 3, 223–243. https://doi.org/10.1007/s40725-017-0064-1.

Jakuš, R., Edwards-Jonášová, M., Cudlín, P., Blaženec, M., Ježík, M., Havlíček, F., Moravec, I., 2011. Characteristics of Norway spruce trees (Picea abies) surviving a spruce bark beetle (Ips typographus L.) outbreak. Trees 25, 965–973. https://doi.org/10.1007/s00468-011-0571-9.

Kalliokoski, T., Pennanen, T., Nygren, P., Sievänen, R., Helmisaari, H.S., 2010. Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. Plant Soil 330, 73–89. https://doi.org/10.1007/s11104-009-0177-9.

Kärvemo, S., Rogell, B., Schroeder, M., 2014. Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance. For. Ecol. Manag. 334, 232–240. https://doi.org/10.1016/j.foreco.2014.09.011.

Korjus, H., Põllumäe, P., Rool, S., 2011. Männi-, kuuse-ja kasepuistute majandamise tasuvus lühikese raieringi korral/Profitability analysis of short rotations in Scots pine, Norway spruce and silver birch stands. For. Stud. 54 (1), 28–36. https://doi.org/10.2478/v10132-011-0093-7.

Lenth R., 2023. Emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.8.6. ⟨https://CRAN.R-project.org/package=emmeans⟩.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., et al., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354. https://doi.org/10.1126/science.aaf8957.

Liepiņš, J., Lazdiņš, A., Liepiņš, K., 2018. Equations for estimating above-and belowground biomass of Norway spruce, Scots pine, birch spp. and European aspen in Latvia. Scand. J. For. Res. 33 (1), 58–70. https://doi.org/10.1080/02827581.2017.1337923.

Lõhmus, E., 1974. Eesti metsade ordineerimisest ja klassifitseerimisest. [Ordination and classification of Estonian forests. Metsanduslikud Uurim. [For. Stud. 11, 162–194 (In Estonian).

Lu, H., Mohren, G.M.J., den Ouden, J., Goudiaby, V., Streck, F.J., 2016. Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in the Netherlands. For. Ecol. Manag. 376, 321–332. https://doi.org/10.1016/j.foreco.2016.06.032.

Lutter, R., Henriksson, N., Lim, H., Blaško, R., Magh, R.K., Näsholm, T., Nordin, A., Lundmark, T., Marshall, J.D., 2021a. Belowground resource utilization in monocultures and mixtures of Scots pine and Norway spruce. For. Ecol. Manag. 500, 119647. https://doi.org/10.1016/j.foreco.2021.119647.

Lutter, R., Kõlli, R., Tullus, A., Tullus, H., 2019. Ecosystem carbon stocks of Estonian premature and mature managed forests: effects of site conditions and overstorey tree species. Eur. J. For. Res. 138, 125–142. https://doi.org/10.1007/s10342-018-1158-4.

Lutter, R., Stål, G., Arnesson Ceder, L., Lim, H., Padari, A., Tullus, H., Nordin, A., Lundmark, T., 2021b. Climate benefit of different tree species on former agricultural land in northern Europe. Forests 12 (12), 1810. https://doi.org/10.3390/f12121810.

Lutter, R., Tullus, A., Kanal, A., Tullus, T., Vares, A., Tullus, H., 2015. Growth development and plant–soil relations in midterm silver birch (Betula pendula Roth) plantations on previous agricultural lands in hemiboreal Estonia. Eur. J. For. Res. 134, 653–667. https://doi.org/10.1007/s10342-015-0879-x.

Lutter, R., Tullus, A., Kanal, A., Tullus, T., Tullus, H., 2016. The impact of former land-use type to above-and below-ground C and N pools in short-rotation hybrid aspen (Populus tremula L.× P. tremuloides Michx.) plantations in hemiboreal conditions. For. Ecol. Manag. 378, 79–90. https://doi.org/10.1016/j.foreco.2016.07.021.

Lutter, R., Tullus, A., Vares, A., Sopp, R., Tullus, T., Kaivapalu, M., Ots, K., Kharel, B., Lundmark, T., Tullus, H., 2023. Twenty years of afforestation of former agricultural lands with silver birch plantations affects vertical distribution of SOC and macronutrients in the topsoil layer. Plant Soil 482 (1), 385–400. https://doi.org/10.1007/s11104-022-05695-9.

Mayer, M., Prescott, C.E., Abaker, W.E., Augusto, L., Cécillon, L., Ferreira, G.W., James, J., Jandl, R., Katzensteiner, K., Laclau, J.P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J.A., Vanguelova, E.I., Vesterdal, L., 2020. Tamm Review: Influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. For. Ecol. Manag. 466, 118127. https://doi.org/10.1016/j.foreco.2020.118127.

Mehlich, A., 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun. Soil Sci. Plant Anal. 15 (12), 1409–1416. https://doi.org/10.1080/00103628409367568.

Mehtatalo L., Kansanen K., 2022. _lmfor: Functions for Forest Biometrics_. R package version 1.6. ⟨https://CRAN.R-project.org/package=lmfor⟩.

Mensah, A.A., Petersson, H., 2024. Carbon concentration of living tree biomass of Pinus sylvestris, Picea abies, Betula pendula and Betula pubescens in Sweden. Scand. J. For. Res. 1–11. https://doi.org/10.1080/02827581.2024.2332439.

Metsa korraldamise juhend [Estonian forest inventory guideline], 2009. Keskkonnaministri määrus nr 2. Vastu võetud 16.01.2009. Hetkel kehtiv redaktsioon 16.07.2023. (In Estonian).

Mielikäinen, K., 1985. Koivusekoituksen vaikutus kuusikon rakenteeseen ja kehitykseen. Summary effects of an admixture of birch on the structure and development of Norway spruce stands. Commun. Inst. For. Fenn. 133, 1–79.

Myllyviita, T., Soimakallio, S., Judl, J., Seppälä, J., 2021. Wood substitution potential in greenhouse gas emission reduction–review on current state and application of displacement factors. For. Ecosyst. 8, 1–18. https://doi.org/10.1186/s40663-021-00326-8.

Ogle D.H., Doll J.C., Wheeler A.P., Dinno A., 2023. FSA: Simple Fisheries Stock Assessment Methods_. R package version 0.9.5. ⟨https://CRAN.R-project.org/package=FSA⟩.

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

Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., Zingg, A., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67, 712. https://doi.org/10.1051/forest/2010037.

Pretzsch, H., Schütze, G., 2021. Tree species mixing can increase stand productivity, density and growth efficiency and attenuate the trade-off between density and growth throughout the whole rotation. Ann. Bot. 128, 767–786. https://doi.org/10.1093/aob/mcab077.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.

R Studio Team, 2020. R Studio: Integrated Development for R. R Studio, PBC, Boston, MA. ⟨http://www.rstudio.com/⟩.

Ruíz-Peinado, R., Pretzsch, H., Löf, M., Heym, M., Bielak, K., Aldea, J., Barbeito, I., Brazaitis, G., Drössler, L., Godvod, K., Granhus, A., Holm, S.-O., Jansons, A., Makrickiene, E., Metslaid, M., Metslaid, S., Nothdurft, A., Reventlow, D.O.J., Sitko, R., Stankevičienė, G., del Rio, M., 2021. Mixing effects on Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies (L.) Karst.) productivity along a climatic gradient across Europe. For. Ecol. Manag. 482, 118834. https://doi.org/10.1016/j.foreco.2020.118834.

Schleuß, P.M., Heitkamp, F., Leuschner, C., Fender, A.C., Jungkunst, H.F., 2014. Higher subsoil carbon storage in species-rich than species-poor temperate forests. Environ. Res. Lett. 9 (1), 014007. https://doi.org/10.1088/1748-9326/9/1/014007.

Smolander, A., Kitunen, V., 2011. Comparison of tree species effects on microbial C and N transformations and dissolved organic matter properties in the organic layer of boreal forests. Appl. Soil Ecol. 49, 224–233. https://doi.org/10.1016/j.apsoil.2011.05.002.

Tham, Å., 1994. Crop plans and yield predictions for Norway spruce (Picea abies (L.) Karst.) and birch (Betula pendula Roth & Betula pubescens Ehrh.) mixtures (No. Stud. For. Suec. 195 (195).

Tullus, A., Lukason, O., Vares, A., Padari, A., Lutter, R., Tullus, T., Karoles, K., Tullus, H., 2012. Economics of hybrid aspen (Populus tremula L.× P. tremuloides Michx.) and silver birch (Betula pendula Roth.) plantations on abandoned agricultural lands in Estonia. Balt. For. 18 (2), 288–298.

Uri, V., Varik, M., Aosaar, J., Kanal, A., Kukumägi, M., Lõhmus, K., 2012. Biomass production and carbon sequestration in a fertile silver birch (Betula pendula Roth) forest chronosequence. For. Ecol. Manag. 267, 117–126. https://doi.org/10.1016/j.foreco.2011.11.033.

Warner, E., Cook-Patton, S.C., Lewis, O.T., Brown, N., Koricheva, J., Eisenhauer, N., Ferlian, O., Gravel, D., Hall, J.S., Jactel, H., Mayoral, C., Meredieu, C., Messier, C., Paquette, A., Parker, W.C., Potvin, C., Reich, P.B., Hector, A., 2023. Young mixed planted forests store more carbon than monocultures—a meta-analysis. Front. For. Glob. Change 6, 1226514. https://doi.org/10.3389/ffgc.2023.1226514.