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Young Silver Birch Grows Faster and Allocates Higher Portion of Biomass into Stem Than Norway Spruce, a Case Study from a Post-Disturbance Forest

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Abstract: The aim of the paper was to compare young silver birch (*Betula pendula* Roth.) and Norway spruce (*Picea abies* L. Karst) growing at the identical site, from the point of contribution of tree components to their aboveground biomass stock, their wood density, radial increment and aboveground biomass production. Our research activities were performed in the High Tatra Mts., which belong to the Tatra National Park (TANAP), Northern Slovakia. Currently, the substantial part of the TANAP territory is covered by post-disturbance young forests which have been growing there since the large-scale windstorm episode in November 2004. Our study combined non-destructive repeated tree measurements performed at two transects in 2016–2020, with destructive tree sampling of twenty 14-year-old individuals for each species. From the gathered data, we derived models estimating standing stock and annual production of aboveground biomass in individual tree components (foliage, branches, stem bark and stem wood), using diameter at breast height (DBH) as a predictor. The results showed contrasting contributions of tree compartments to aboveground biomass stock between birch and spruce. While spruce trees had four times higher contribution of foliage than birches, the reverse situation (1.5-fold difference) was observed for stem over bark biomass. At the same time, birch trees had a 40% greater diameter increment and a 30% denser stem wood than spruce. As for aboveground biomass production, the contribution of the stem as an economically important component was greater in birch than spruce. The results suggest that, in the young growth stage, birch may be advantageous over spruce in both ecological and production properties. Therefore, we believe that strengthening research activities focused on birch ecology and production issues would bring practical recommendations for better utilization of this tree species in forestry and wood-processing industry sectors

Keywords: *Betula pendula*; *Picea abies*; aboveground tree components; diameter increment; stem volume; wood density; biomass production

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1. Introduction

Windstorms cause serious damages to forests in most European countries, especially in Western, Central and Northern Europe [1]. Its impact is evident also in the Western Carpathians (mostly situated in Slovakia), where the area of damaged forests by windstorms accompanied by bark beetle outbreaks has a gradually increasing tendency especially since the beginning of the new millennium [2]. Generally, increasing frequency of strong winds and their growing impacts on forests in these European regions are mostly interpreted as an inherent phenomenon of climate change [3] and accumulating amount of aboveground tree biomass [4], which can together with some other aspects worsen forest stability [5]. The main consequence of recent windstorm disturbances is the increasing windthrown area, later covered by young forests. This is the principal reason why current scientific attention should focus on post-disturbance areas and forest development to a larger extent than in the past.

Under the conditions of boreal and temperate Europe, Norway spruce (*Picea abies* L. Karst) is considered the tree species most prone to wind damage [6]. At the same time, the species has long been economically extremely important [7]. Since the regeneration potential of this species is usually high (thanks to seed-producing survivors after disturbance and well-dispersing and germinating seeds), spruce trees often dominate in species composition of young post-disturbance forests [8]. At the same time, in disturbed forest areas, seeds of different species—especially light-demanding, are granted an opportunity to germinate and cover the open soil surface [9]. In the case of large-scale disturbances, "pioneer tree species" play an important role in forest regeneration, which are in Slovakia especially silver birch (*Betula pendula* Roth.), goat willow (*Salix caprea* L.) and common rowan (*Sorbus aucuparia* L.; see for instance Konôpka et al. [10]).

On the Slovak forests, the largest windstorm disaster occurred on 19 November 2004 [11]. The negative feature of the episode was that the epicentre of wind destruction was located in the Tatra National Park (TANAP), which is the oldest and most famous national park in Slovakia. At that time, wind damaged nearly 130 km^2 of forests dominated by Norway spruce [12]. Our previous work [13] indicated that Norway spruce and birches (*Betula* sp.), especially silver birch (*B. pendula* Roth.), were most frequent and most contributing tree species to forest biomass stock in the post-disturbance area of TANAP. These two species have very contrasting qualities, out of which some are well-known, such as foliage traits (leaves vs. needles, deciduous vs. evergreen), lifespan, ecological demands (e.g., drought and light tolerance). Due to the above-mentioned differences, we assume that the species differ also in biomass production and allocation, which have not been examined in the form of an inter-specific comparative study yet.

We investigated these two tree species under post-disturbance conditions because both prominently contribute to forest regeneration [13] and thanks to their contrasting properties they may complement each other at the mutual site. For instance, since in initial developmental stages birch grows faster and tolerates extreme climatic conditions better than spruce [14], birch trees often create a "shelter" and make favorable conditions for spruce growth [15]. Although unlike in Northern Europe birch species are not important for commercial purposes in Slovakia, their ecological advantages, as well as their production potential, can be exploited in the context of disturbances and global warming environment (e.g., see Reference [7]). Previous works showed that in early developmental stages birches are usually more productive than most other forest tree species on post-disturbance [13] or former agricultural lands [16,17]. Wood of birches, but also of other pioneer tree species regenerated on disturbed areas, will very probably become a source of supply for production of renewable energy [18]. This may reduce demands for wood of "traditional" commercial tree species, such as Norway spruce.

Thanks to fast growth, birches can play an important role in carbon sequestration at sites where other tree species hardly survive. Experience from Scandinavian and Baltic countries [19,20] suggests that birches can be economically relevant species with a variety of utilization possibilities. According to Tiebel et al. [21], renewed interest in silver birch has been recently raised with regard to forest management at higher altitudes. The main reason for it is the ability of birch to promptly and extensively re-colonize post-disturbance areas (mostly after windfalls and bark beetle outbreaks), which is an extremely important quality in the context of the increased risk of catastrophic events in European spruce-dominant forests. At the same time, such a development creates conditions for mixed forests stands with higher species richness. Likely, Norway spruce might be then preferred exclusively only on autochthonous sites, i.e., at high altitudes with mostly sufficiency of precipitation. That is besides other ecological aspects important in terms of the ongoing climate change [22].

The aim of the paper was to compare contribution of tree components to aboveground biomass between silver birch and Norway spruce growing at the identical site, specifically in the post-disturbance area of TANAP. Further, we focused on the inter-specific comparisons from the point of their wood density, diameter increment and aboveground biomass production. The main mission of our study was to widen the knowledge base related to the potential (especially in wood production and carbon sequestration) of silver birch as an alternative or additive species to Norway spruce in young forest growth stages.

2. Materials and Methods

2.1. Research Site and Transects

Our field activities were performed in the High Tatra Mts., which are a part of TANAP, Northern Slovakia. The bedrock of the High Tatra Mts. is predominantly represented by granodiorites sediments. The soils in the mountains are mostly lithic leptosols, cambisoils and podzols. The climate is typically cold with annual mean temperature around 5.0 °C, annual precipitation totals over 1000 mm, and snow cover of nearly 120 days.

Currently, the main part of the TANAP territory is covered by post-disturbance forests which have been growing there since the large-scale windstorm episode on 19 November 2004. On that day, the wind destroyed spruce-dominated forests at elevations from 700 to 1400 m a.s.l. The destroyed forests occurred within 3–5 km wide and nearly 35 km long belt [13]. The forest stands inside the windstorm epicenter were almost completely destroyed (more often uprooted than stem-broken) except for a few forest clusters dominated by European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.).

Post-disturbance management was differentiated based on the degree of nature protection: from salvaging all amount of merchantable wood in the parts with the lower degree of nature protection, through partial processing of calamity wood, up to complete exclusion of salvage harvesting with exclusive natural succession in the parts under the higher degree of nature protection. The substantial amount of the calamity wood was logged during the years 2005–2006. Similarly, various approaches were implemented for reforestation respecting the degree of nature protection. While natural regeneration was generally preferred, combined natural and artificial reforestation occurred at some sites, and in a few exceptional cases forests were reforested exclusively by tree planting.

Our research started in 2016 (i.e., twelve years after the wind disturbance), when the area was prevailingly covered by young forests that originated from both natural regeneration and planting. Open areas that occurred within the young forest stands were overgrown by other plant species adapted to forest clearings, particularly by grasses, herbs, and shrubs. To acquire the information on tree characteristics, two research transects—one near the site called "Danielov dom" (hereinafter as DD transect) and another one close to the village of Horný Smokovec (HS transect) were established. The forests at these localities are managed by the State Forests of the Tatra National Park. Both sites belong to the territory with the lowest degree of nature protection. Hence, the post-disturbance management at these sites was performed as full-area processing of calamity wood and combined (tree planting and natural regeneration) reforestation. Actually, the entire forest management, i.e., from forest regeneration to harvest, in this area is very close to "ordinary" forestry approaches in Slovakia promoting both wood production and other ecosystem services. On the other hand, forest management is limited or fully excluded only in the core area of the Tatra National Park (not our case), specifically at high altitudes typical with alpine vegetation, and in deep valleys with old-growth forests.

Both transects are located in the central part of the wind-disturbed belt. Their orientations are from Northwest to Southeast. The altitudes of the DD and HS transects varied from 970 to 1000 m a.s.l and between 920 and 950 m a.s.l., respectively. The transects are 4 m wide and 300 m long. Detailed data from both transects have already been analyzed in our previous works, which thoroughly describe their stand properties [13,23].

For our current study we used only data covering tree heights and stem breast diameters (diameter at breast height (DBH)) of Norway spruce and silver birch trees with

DBH ≥ 7.0 cm. The minimum DBH of 7 cm was chosen since in Slovak forestry this dimension is a standard threshold used in forestry evidence to calculate stand stock of merchantable wood and other related forest characteristics. Tree heights were measured with a hypsometer TruPulse 360°R with a precision of ±0.1 m, and DBH with a digital caliper Masser BT, precision ± 0.1 mm. The data on tree heights and DBHs of spruce and birch trees measured in the years 2016, 2017, 2018, 2019 and 2020 were utilized for further calculation and modeling. Since additional trees reached the DBH limit of 7 cm in consecutive years, the set of measured trees inter-annually increased (Table 1). While in 2016, 114 birches and 42 spruces were measured, in 2020 we measured 153 birch and 227 spruce trees. Here we would like to point out that both measured and sampled trees (described in the following chapter) represented the upper tree layer of stands. At the same time, it is necessary to note that trees did not create a closed canopy, but rather sparse forests with mild crown competition.

Table 1. Basic tree characteristics of silver birch and Norway spruce trees measured in the years 2016–2020. Standard deviations are shown in parentheses.

Tree Species	Year	Number of Trees	Mean DBH * (cm)	Mean Height (m)
Silver birch	2016	114	12.28 (3.04)	8.24 (1.31)
	2017	129	13.03 (3.64)	8.99 (1.54)
	2018	138	14.28 (4.14)	9.47 (1.63)
	2019	147	15.03 (4.71)	10.12 (1.81)
	2020	153	16.00 (5.05)	10.90 (1.91)
Norway spruce	2016	42	8.75 (2.06)	6.02 (0.83)
	2017	84	8.80 (1.89)	6.22 (1.07)
	2018	115	9.17 (2.05)	6.49 (1.11)
	2019	172	9.25 (2.16)	6.80 (1.13)
	2020	227	9.66 (2.35)	7.14 (1.29)

* DBH, diameter at breast height.

2.2. Aboveground Tree Biomass Sampling

At the end of 2019 growing season, i.e., nearly 15 years after the wind disturbance, destructive collection of aboveground tree biomass was performed. We selected 20 spruce and 20 birch trees with predominant, dominant or co-dominant social position (Kraft classes [24]) growing in the surrounding of the DD transect. Each selected tree was cut with a chain saw at the ground level. Tree age was determined as number of annual tree rings visible on the cross section of the stem base. Tree height and DBH were measured with metal measuring roller (precision of ±1 mm) and a digital caliper Masser BT (precision of ±0.01 mm). Then, branches with foliage were cut off from the stem and the stem was divided into 100 cm–long sections. These components were packed separately to labeled paper bags and transported to laboratory.

In laboratory, diameters of stem sections were measured with a digital caliper (precision of ±0.01 mm) at both ends in two perpendicular directions. Bark was peeled off from stems with a knife, and diameters of stem wood were measured in the same way as before debarking. Stem wood and stem bark of individual trees were packed in labeled paper bags and dried in a large-capacity drying oven, Komeg KOV-1500L, to reach the constant weight (under a temperature of 95 °C for 120 h). Dry material of stem wood and bark was weighed by using a digital scale, Radwag, WLT 3/6/X (precision of ±0.1 g). Branches with foliage were left in a well-ventilated room for a couple of weeks. Then, foliage was manually separated from branches (nearly all spruce needles and a part of birch leaves shed from branches themselves). Foliage and branches were dried in the drying machine, to reach the constant weight (under a temperature of 95 °C for 96 and 72 h for foliage and branches, respectively) and weighed.

2.3. Calculations, Modeling and Statistical Approach

Stem volumes under and over bark (V_{SUB}, V_{SOB}) were calculated for each sampled tree as a sum of volumes of all 100 cm–long stem sections. Volume of one stem section was calculated by using Newton's formula:

$$V_{ij} = \frac{L\ (A_b + 4A_m + A_s)}{6}$$

where V_{ij} is volume of stem section i of tree j (cm^3), L is a length of stem section (cm), A_b is a cross-sectional area at the bottom end of the section (cm^2), A_m is a cross-sectional area in the middle of the section (cm^2) and A_s is a cross-sectional area at the top end of the section (cm^2).

Bark volume was calculated as a difference of stem volume over bark and stem volume under bark.

Stem wood density and stem bark density were calculated as ratios between the respective biomass weight (of wood or bark) and the corresponding volume. Under the term "wood density" we understand here basic wood density, ρ, calculated as a ratio of oven-dry wood mass, m_0, to its green volume, V_{max}:

$$\rho = \frac{m_0}{V_{max}} 1000$$

where ρ is basic wood or bark density (kg m^{-3}), m_0 is oven-dry wood or bark mass (g), V_{max} is green wood or bark volume with wood moisture above the hygroscopicity threshold (m^3).

Further, we constructed allometric relations for stem volume and biomass of separate tree components (foliage, branches, stem bark and stem wood), as well as aboveground tree biomass using DBH and a combination of DBH and tree height as predictors. We applied a basic ($Y = a\ X^b$), as well as an expanded version of an allometric equation as follows:

$$Y = b_0\ X_1^{b_1}\ X_2^{b_2} \theta$$

where Y is the dependent variable, i.e., either stem volume under or over bark (V_{SUB}, V_{SOB} in m^3), or biomass (B in kg) of a particular tree component as defined above; X_1 and X_2 are independent variables, i.e., breast height diameter (DBH in cm) and tree height (h in m); b_0, b_1, and b_2 are model regression coefficients; and θ is a multiplicative error term.

The relationship between tree height h and DBH was described with the following equation:

$$h = \frac{DBH^2}{c_0 + c_1\ DBH + c_2\ DBH^2}$$

where h is tree height (m); DBH is tree diameter at breast height, i.e., at a height of 1.3 m (cm); c_0, c_1 and c_2 are regression coefficients.

Tree annual production of aboveground biomass, of stem biomass over bark, and of stem volume over bark was calculated as an inter-annual change of the respective variable, using the formula:

$$\Delta Y = b_0 DBH_2^{b1} - b_0 DBH_1^{b1}$$

where ΔY is the tree annual production of a particular biomass, i.e., its annual increment (kg); DBH_1 is the actual diameter at breast height in the first year (cm); DBH_2 is the diameter at breast height in the second year (cm) estimated as the actual diameter at breast height increased by species-specific mean annual diameter increment, i.e., $DBH_2 = DBH_1 + \Delta DBH$; b_0 and b_1 are regression coefficients of a particular equation.

Mean annual diameter increment ΔDBH was calculated separately for each tree species from repeated measurements of trees monitored at transects. By accounting for all years of measurements, we obtained mean annual increment of spruce and birch equal to 1.0 and 1.4 cm, respectively.

Species-specific annual production of foliage was derived by using biomass equations as follows:

$$\Delta Y foliage = b_0 \cdot DBH_2^{b1} \text{ for birch,}$$

$$\Delta Y foliage = \frac{b_0 \cdot DBH_2^{b1}}{3} \text{ for spruce.}$$

The formula for the calculation of spruce annual production of foliage is based on the previous experience and knowledge obtained from a similar experiment [25] that annual foliage production of spruce is approximately one third of the total foliage biomass at the end of the growing season.

To test significant differences between the tree species we used two-way ANOVA followed by Fisher's Least Significant Difference (LSD) test and *t*-test (with $p < 0.05$).

3. Results

Based on the number of annual tree rings at a stem base of the sampled trees we found that in the year 2019 trees were 14 (±1) years old. Hence, they were born in the growing season of 2005 or 2006. Our set of sampled trees indicated that birch trees had greater dimensions than spruce trees (Table 2). Specifically, in the sample of trees taken for biomass analysis, birches were thicker and higher than spruce trees (mean DBH = 14.98 cm versus 8.9 m, and mean height = 9.80 versus 6.4 m), and rather interestingly the difference in mean aboveground tree biomass between the species was threefold (biomass of a birch and a spruce tree was 72.86 and 24.08 kg, respectively).

Table 2. Basic characteristics of 14-year-old sampled trees—average numbers derived from twenty individuals of silver birch and twenty Norway spruce trees. Standard deviations are shown in parentheses.

Mean Tree Characteristics	Silver Birch	Norway Spruce
DBH (cm)	14.98 (5.61) *	8.88 (3.13)
Height (m)	9.80 (1.73) *	6.41 (1.58)
Foliage biomass (kg)	5.01 (3.29)	7.04 (5.07)
Branch biomass (kg)	23.25 (19.51) *	6.70 (4.97)
Stem wood biomass (kg)	34.27 (25.15) *	8.07 (5.73)
Stem bark biomass (kg)	10.33 (6.18) *	1.91 (1.21)
Aboveground biomass (kg)	72.86 (53.09) *	24.08 (16.75)

* Asterisk indicates statistically significant differences in tree characteristics between tree species (*t*-test; $p < 0.05$).

Derived allometric relationships for aboveground tree components of birch (Table 3) and spruce (Table 4) showed that DBH was a good predictor of their biomass since R^2 values of derived relationships fluctuated between 0.923 and 0.972 for birch and between 0.914 and 0.980 for spruce. Adding tree height to the model improved the model explanatory power only slightly, specifically R^2 values of these relationships were between 0.940 and 0.977 for birch and between 0.917 and 0.992 for spruce depending on the tree component (Tables 3 and 4).

Table 3. Models for biomass quantities of tree components derived from the information on twenty sampled individuals of silver birch, using DBH and DBH plus tree height as predictors. Specific abbreviations indicate as follows: b_0, b_1 and b_2 are regression coefficients with their standard errors (SEs); p is the respective p-value; R^2 is coefficient of determination; and MSE is mean standard error.

Predictor (Equation)	Component	b_0 (SE) p	b_1 (SE) p	b_2 (SE) p	R^2	MSE
Diameter at breast height (*DBH*) ($B_{tc} = b_0 DBH^{b_1}$ where B_{tc} is tree component expressed in kg)	Stem over bark	0.186 (0.080) 0.032	1.982 (0.143) < 0.001	-	0.957	44.09
	Stem under bark	0.106 (0.055) 0.071	2.087 (0.173) < 0.001	-	0.946	35.87
	Foliage	0.036 (0.018) 0.063	1.792 (0.169) < 0.001	-	0.923	0.87
	Branches	0.014 (0.012) 0.237	2.633 (0.269) < 0.001	-	0.931	27.65
	Stem Bark	0.118 (0.049) 0.027	1.629 (0.140) < 0.001	-	0.930	2.81
	Aboveground biomass	0.186 (0.072) 0.018	2.149 (0.127) < 0.001	-	0.972	83.4
Diameter at breast height (*DBH*) together with tree height (*h*) ($B_{tc} = b_0 DBH^{b_1} h^{b_2}$ where B_{tc} is tree component expressed in kg)	Stem over bark	0.04093 (0.020) 0.060	1.730 (0.121) < 0.001	0.946 (0.234) < 0.001	0.979	22.32
	Stem under bark	0.01694 (0.010) 0.118	1.818 (0.147) < 0.001	1.101 (0.277) < 0.001	0.974	18.4
	Foliage	0.00992 (0.008) 0.209	1.605 (0.190) < 0.001	0.773 (0.375) 0.055	0.940	0.72
	Branches	0.03274 (0.036) 0.372	2.697 (0.272) < 0.001	−0.424 (0.418) 0.324	0.935	27.7
	Stem Bark	0.05527 (0.036) 0.146	1.452 (0.167) < 0.001	0.538 (0.339) 0.131	0.940	2.56
	Aboveground biomass	0.08695 (0.048) 0.085	2.041 (0.135) < 0.001	0.454 (0.242) 0.078	0.977	72.43

Table 4. Models for biomass quantities for tree components derived from the information on twenty sampled individuals of Norway spruce, using DBH and DBH plus tree height as predictors. Specific abbreviations indicate as follows: b_0, b_1 and b_2 are regression coefficients with their standard errors (SEs); p is p-value; R^2 is coefficient of determination; and MSE is mean standard error.

Predictor (Equation)	Component	b_0 (SE) p	b_1 (SE) p	b_2 (SE) p	R^2	MSE
Diameter at breast height (*DBH*) ($B_{tc} = b_0 DBH^{b_1}$ where B_{tc} is tree component expressed in kg)	Stem over bark	0.088 (0.019) < 0.001	2.110 (0.088) < 0.001	-	0.980	0.997
	Stem under bark	0.066 (0.016) < 0.001	2.142 (0.096) < 0.001	-	0.976	0.778
	Foliage	0.064 (0.029) 0.042	2.111 (0.183) < 0.001	-	0.914	2.316
	Branches	0.035 (0.017) 0.056	2.327 (0.195) < 0.001	-	0.922	2.045
	Stem Bark	0.024 (0.006) < 0.001	1.961 (0.097) < 0.001	-	0.971	0.046
	Aboveground biomass	0.183 (0.052) 0.002	2.167 (0.114) < 0.001	-	0.968	9.467
Diameter at breast height (*DBH*) together with tree height (*h*) ($B_{tc} = b_0 DBH^{b_1} h^{b_2}$ where B_{tc} is tree component expressed in kg)	Stem over bark	0.035 (0.008) < 0.001	1.610 (0.111) <0.001	1.048 (0.200) < 0.001	0.992	0.411
	Stem under bark	0.023 (0.005) < 0.001	1.578 (0.110) < 0.001	1.193 (0.200) < 0.001	0.993	0.269
	Foliage	0.095 (0.067) 0.171	2.350 (0.377) < 0.001	−0.485 (0.664) 0.475	0.917	2.378
	Branches	0.074 (0.054) 0.186	2.738 (0.374) < 0.001	−0.869 (0.672) 0.213	0.929	1.971
	Stem Bark	0.017 (0.006) 0.017	1.766 (0.201) < 0.001	0.395 (0.350) 0.275	0.973	0.045
	Aboveground biomass	0.176 (0.081) 0.044	2.145 (0.232) < 0.001	0.045 (0.415) 0.914	0.968	10.017

The models showed that birch and spruce trees with identical DBH had nearly the same amounts of aboveground biomass (Figure 1a). For instance, the aboveground tree biomass of an individual tree with DBH of 15 cm was about 70 kg irrespective of tree species. The derived models showed also very similar branch biomass of both species (Figure 1c), moderate differences in stem bark biomass (Figure 1d), as well as in stem biomass under bark (Figure 1e) and over bark (Figure 1f), but very contrasting amounts in foliage (Figure 1b). For instance, a spruce tree with DBH equal to 15 cm had as much as 20 kg of foliage biomass, while the foliage amount of the birch tree with the same DBH was only 5 kg. As for stem volume, the two species had very similar relationships between DBH and stem volume under bark (Figure 2a) or over bark (Figure 2b). Derived models for stem volume prediction using DBH as an explanatory variable were significant and explained more than 90% of volume variability for both birch (Table 5) and spruce (Table 6). The models clearly showed that for the specific DBH the compared tree species were characterized by almost identical values of stem volume, both under and over bark.

Table 5. Models for volume of stem over and under bark made from twenty sampled individuals of silver birch, using DBH and DBH plus tree height as predictors. Specific abbreviations indicate as follows: b_0, b_1 and b_2 are regression coefficients with their standard errors (SEs); p is p-value; R^2 is coefficient of determination; and MSE is mean standard error.

Component	Predictor (Equation)	b_0 (SE) p	b_1 (SE) p	b_2 (SE) p	R^2	MSE
Stem over bark volume (m^3)	*DBH* ($V_{sob} = b_0 DBH^{b_1}$)	0.0003631 (0.000137) 0.016	2.005 (0.125) < 0.001	-	0.968	1.5×10^{-4}
	DBH and *h* ($V_{sob} = b_0 DBH^{b_1} h^{b_2}$)	0.0001110 (0.000051) 0.045	1.810 (0.114) < 0.001	0.739 (0.215) 0.003	0.982	8.7×10^{-5}
Stem under bark volume (m^3)	DBH ($V_{sub} = b_0 DBH^{b_1}$)	0.0002629 (0.000114) 0.033	2.048 (0.144) < 0.001	-	0.960	1.3×10^{-4}
	DBH and *h* ($V_{sub} = b_0 DBH^{b_1} h^{b_2}$)	0.0000480 (0.000021) 0.034	1.792 (0.105) < 0.001	1.030 (0.199) < 0.001	0.986	4.7×10^{-5}

Table 6. Models for volume of stem over and under bark made from twenty sampled individuals of Norway spruce, using DBH and DBH plus tree height as predictors. Specific abbreviations indicate following characteristics: b_0, b_1 and b_2 are regression coefficients with their standard errors (SEs); p is p-value; R^2 is coefficient of determination; and MSE is mean standard error.

Component	Predictor (Equation)	b_0 (SE) p	b_1 (SE) p	b_2 (SE) p	R^2	MSE
Stem over bark volume (m^3)	*DBH* ($V_{sob} = b_0 DBH^{b_1}$)	0.0002349 (0.000053) < 0.001	2.136 (0.092) < 0.001	-	0.979	8.6×10^{-6}
	DBH and *h* ($V_{sob} = b_0 DBH^{b_1} h^{b_2}$)	0.0000946 (0.000024) < 0.001	1.628 (0.118) < 0.001	1.058 (0.214) < 0.001	0.992	3.8×10^{-6}
Stem under bark volume (m^3)	DBH ($V_{sub} = b_0 DBH^{b_1}$)	0.0001767 (0.000042) < 0.001	2.170 (0.095) < 0.001	-	0.979	6.1×10^{-6}
	DBH and *h* ($V_{sub} = b_0 DBH^{b_1} h^{b_2}$)	0.0000636 (0.000014) < 0.001	1.607 (0.103) < 0.001	1.180 (0.188) < 0.001	0.994	2.0×10^{-6}

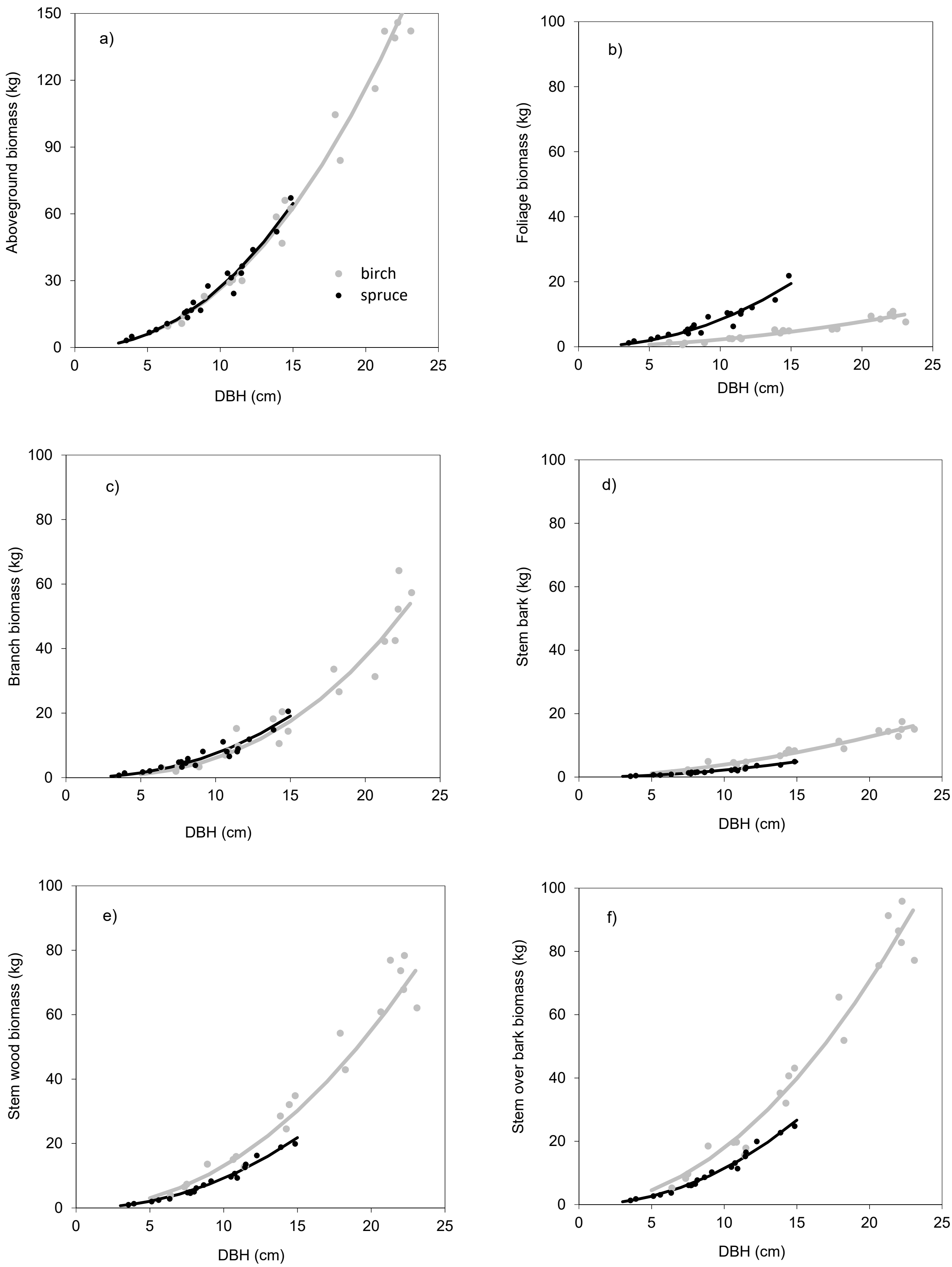
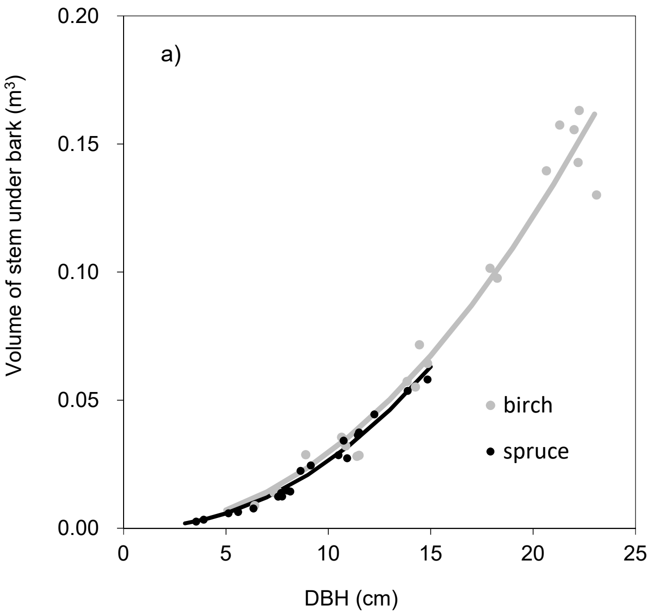


Figure 1. Relationships between DBH and biomass of tree components in silver birch and Norway spruce, specifically for aboveground biomass (**a**), foliage (**b**), branches (**c**), stem bark (**d**), stem under bark (**e**) and stem over bark (**f**). See also Tables 3 and 4 for more details on the models.



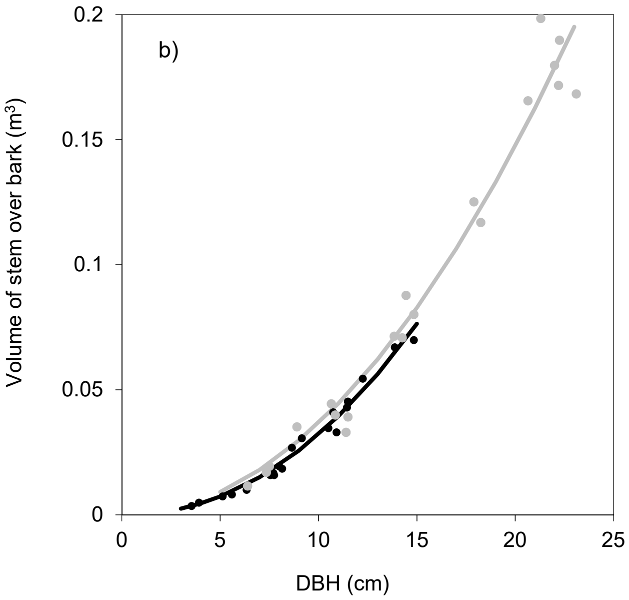


Figure 2. Relationship between DBH and stem volume under bark (**a**) and stem volume over bark (**b**) for silver birch and Norway spruce. See also Tables 5 and 6 for more details on the models.

Further, we used the data from the sampled trees to derive mean tree compartments contributions to aboveground tree biomass (Figure 3). The results showed that only mean contribution of branches to aboveground biomass was insignificantly different between both species (29.5% and 27.2% for birch and spruce, respectively). The difference in foliage contribution was fourfold (7.5% and 31.7% for birch and spruce, respectively), and nearly the double difference was revealed in stem bark (13.3% and 8.4% for birch and spruce, respectively). Stem wood contributed to aboveground biomass most regardless of species, but its contribution in birch was significantly higher (46.7%) than in spruce (32.7%).

As for density, significantly higher density values of both stem wood and stem bark were revealed for birch than spruce (Figure 4). While spruce wood and bark densities were similar (360 versus 370 kg m^{-3}), birch wood density was significantly lower than its bark density (470 versus 520 kg m^{-3}). Moreover, the results also revealed that the variability of birch bark density was greater than the variability of birch or spruce wood or bark density (Figure 4).

The relationships between measured tree heights and DBH of birch and spruce trees growing at transects showed differences between the two species (Figure 5). Specifically, birch trees were by about 1.0 m higher than spruce trees with the same DBH. Even greater differences occurred between highest birches (about 15 m) and highest spruces (approx. 10 m). The data also showed that, while DBH of the thickest birches was about 28 cm, the greatest measured DBH of spruce was only 23 cm.

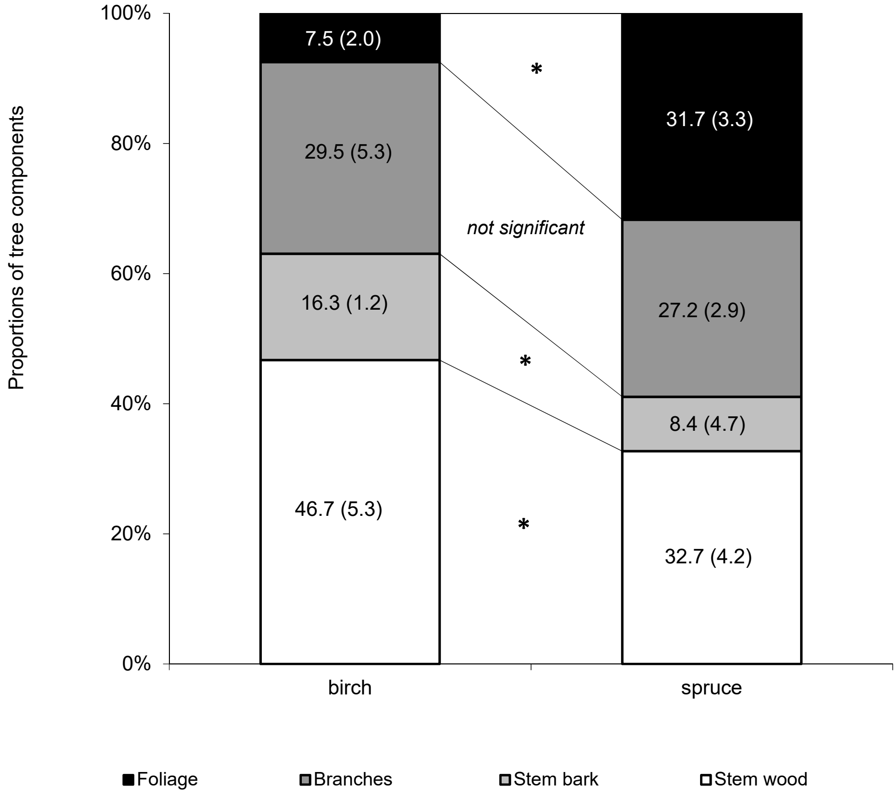


Figure 3. Comparison of mean biomass allocated in aboveground tree components between silver birch and Norway spruce (n = 20 for each species). Values for averages and standard deviations (in parentheses) are shown. Asterisk indicates significant differences between species in a specific component (Least Significant Difference (LSD) test, p < 0.05).

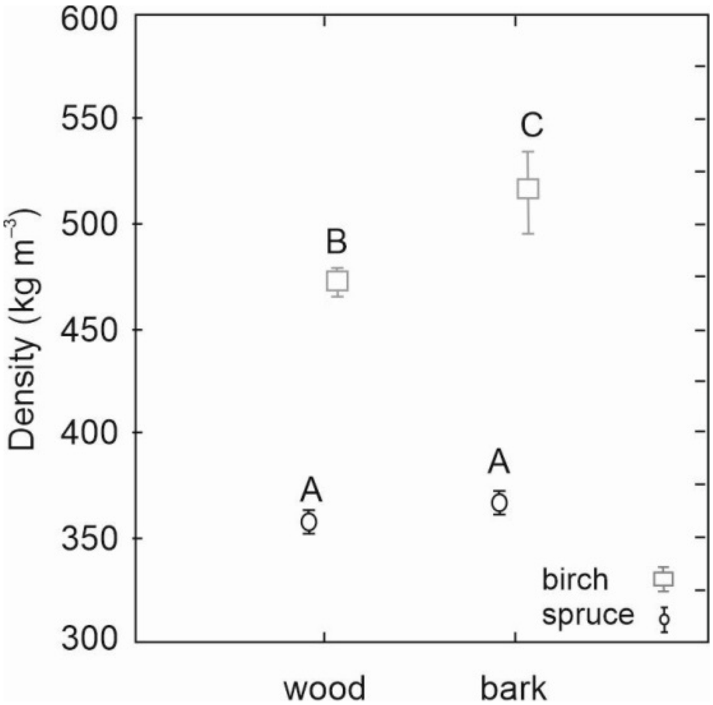
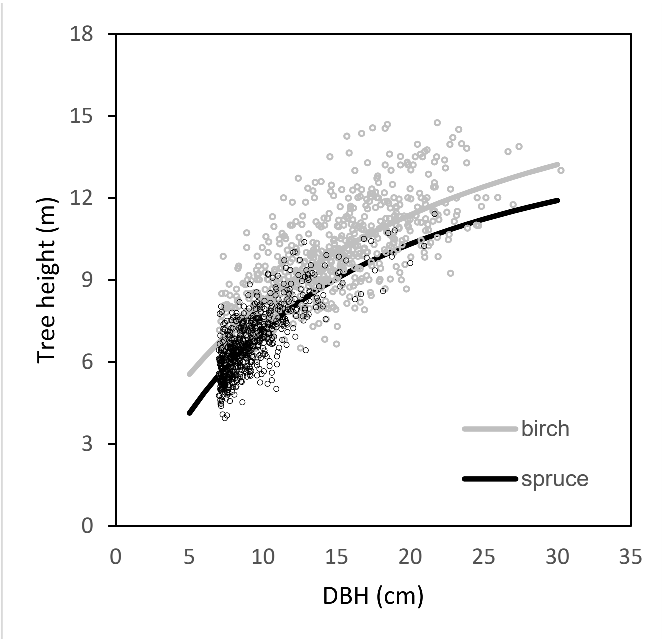


Figure 4. Stem wood density and stem bark density of silver birch and Norway spruce determined from sampled trees (n = 20 for each species). Error bars represent standard errors. Different letters indicate significant differences between the respective density values (LSD test, p < 0.05).



Birch

$$h = \frac{DBH^2}{-0.706 + 0.792DBH + 0.050DBH^2}$$

R^2=0.596

Spruce

$$h = \frac{DBH^2}{1.147 + 0.681DBH + 0.060DBH^2}$$

R^2=0.612

Figure 5. Relationship between DBH and tree height (*h*) for silver birch and Norway spruce derived from all tree measurements in the years 2016–2020.

The analysis of mean annual diameter increments derived from consecutive DBH measurements revealed significantly faster diameter growth of birch trees than spruce (Figure 6). The increments differed significantly not only between tree species but also between some years. While in the case of spruce, only one mean annual diameter increment in the year 2019 was significantly lower than in other years, the differences between the annual increments of birch were more pronounced, except for similar increments in the last two years (2019 and 2020).

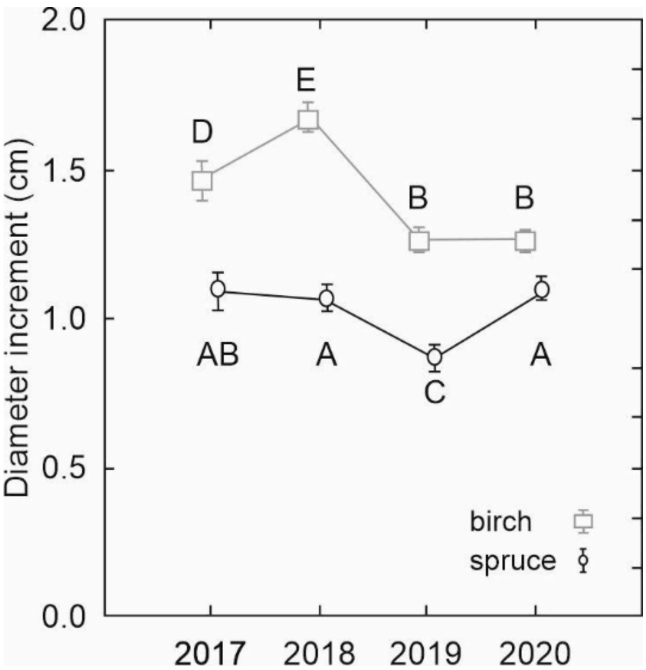


Figure 6. Comparison of mean annual diameter increments between silver birch and Norway spruce in the years 2017–2020. Error bars represent standard errors. Different letters indicate significant differences between the increments (LSD test, $p < 0.05$).

Moreover, inter-specific comparisons of annual production of aboveground biomass and of individual tree components were performed (Figure 7). The comparisons considered real mean values of diameter increment for each species derived as averages of four mean annual diameter increments, i.e., 1.4 cm and 1.0 for birch and spruce, respectively. The results indicated that 14-year-old birch trees produced annually slightly more aboveground biomass than the spruce trees of the same age with the same DBH (Figure 7a). The opposite situation was found for foliage production, especially for trees with greater DBH (Figure 7b). Birch produced annually more branch biomass than spruce (Figure 7c), as well as more stem bark (Figure 7d), stem wood (Figure 7e) and, hence, also more stem under bark biomass (Figure 7f). The interspecific differences in the production of tree component biomass increased with DBH (Figure 7).

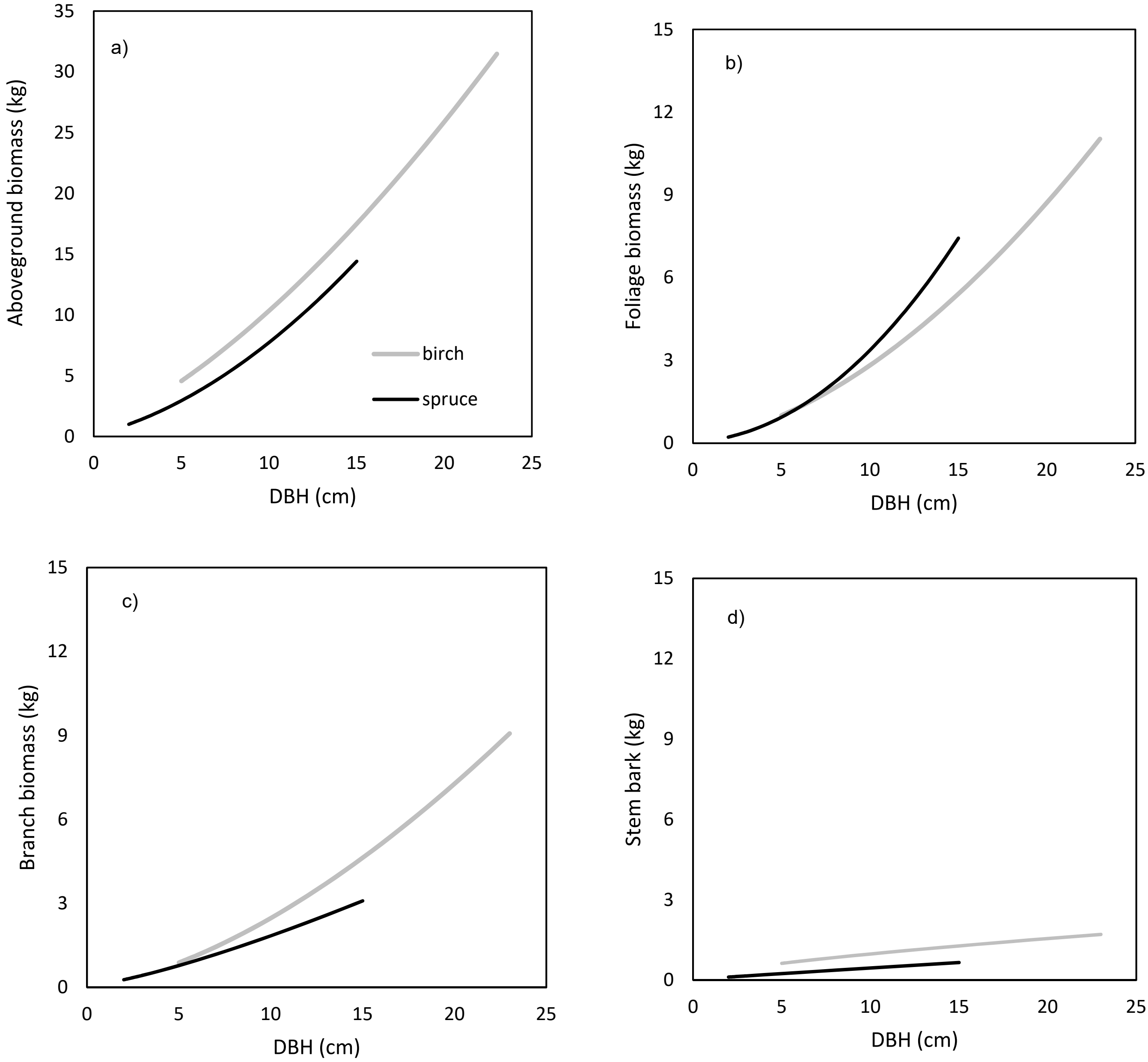


Figure 7. *Cont.*

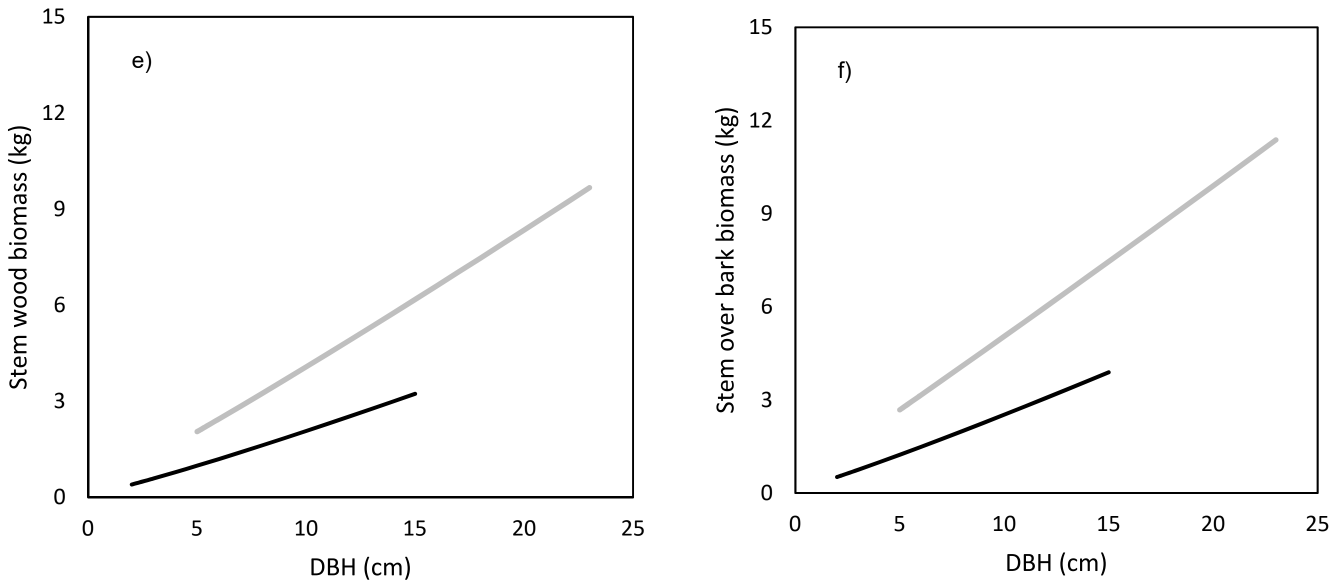


Figure 7. Comparison of modeled annual production of aboveground tree biomass (**a**), foliage biomass (**b**) branches (**c**), stem bark (**d**), stem wood (**e**) and stem over bark (**f**) between silver birch and Norway spruce. We considered real values of mean annual diameter increment for each species, i.e., 1.4 and 1.0 cm for birch and spruce, respectively.

To present an example of tree component biomass stock and production (Tables 7 and 8) we selected DBH approximately in the middle of the interval of sampled trees (i.e., 10 cm). Aboveground biomass stocks of both species in the current (x) year and the previous (x − 1) year were very similar. On the other hand, annual aboveground biomass production of birch was by 33.6% greater than of spruce. The greatest inter-species differences in production were found for foliage (in favor of spruce) and stem bark and wood (in favor of birch, see Tables 7 and 8). In addition, we also revealed the difference in the annual production of litter. While the annual foliage litter production of a birch tree was 2.23 kg year^{-1}, that of spruce was 1.53 kg year^{-1} (or 1.69 kg year^{-1} if applying the relationship derived by Pajtík et al. [26] and Konôpka [27]).

Table 7. Example of silver birch tree biomass stock and annual production by components in the case of DBH = 10 cm and radial increment = 1.4 cm.

Tree Component in Birch	Stock in Year x − 1	Stock in Year x	Production *	Mean Share in Stock	Share in Production	Foliage Litter
	(for DBH = 10.0 cm)	(for DBH = 11.4 cm)	$P_x = S_x - S_{x-1}$	$(S_{x-1} + S_x)/2$		$L_x = S_{x-1}$
	S_{x-1} (kg)	S_x (kg)	(kg year^{-1})	(%)	(%)	(kg year^{-1})
Foliage	2.23	2.82	2.82 *	8.66	27.26	2.23
Branches	6.01	8.49	2.48	24.88	23.95	negligible
Stem bark	3.89	4.87	0.97	15.03	9.42	negligible
Stem wood	12.96	17.02	4.07	51.43	39.37	negligible
Sum	25.09	33.20	10.34	100.00	100.00	—

* Foliage production in year x equals foliage stock in year x.

Table 8. Example of Norway spruce tree biomass stock and annual production by components in the case of DBH = 10 cm and radial increment = 1.0 cm.

Tree Component in Spruce	Stock in Year x − 1	Stock in Year x	Production *	Mean Share in Stock	Share in Production	Needle Litter **
	(for DBH = 10.0 cm)	(for DBH = 11.0 cm)	$P_x = S_x - S_{x-1}$	$(S_{x-1} + S_x)/2$		$L_x = (S_{x-1} + P) - S_x$
	S_{x-1} (kg)	S_x (kg)	(kg year^{-1})	(%)	(%)	(kg Year^{-1})
Needles	8.26	10.11	3.37	30.47	43.55	1.53
Branches	7.43	9.28	1.85	27.71	23.84	negligible
Stem bark	2.19	2.64	0.45	8.03	5.83	negligible
Stem wood	9.16	11.22	2.07	33.79	26.78	negligible
Sum	27.04	33.25	7.74	100.00	100.00	—

* To estimate annual needle production we used the relationship $P_x = S_x/3$ (according to Konôpka and Pajtík [25]. ** Another relationship may also be valid: $L_x = S_x/6$ (based on combined data from Pajtík et al. [26] and Konôpka [27]). Hence, the value in our case would be 1.69 kg year^{-1}.

Finally, we focused on modeling the contribution of stem (both over and under bark) biomass to aboveground biomass production (Figure 8) with respect to tree DBH. The results showed that the proportion of stem production on the annual aboveground biomass production had a decreasing trend with the increasing DBH. Moreover, birch trees invested a higher share of aboveground biomass production to stem than spruce ones.

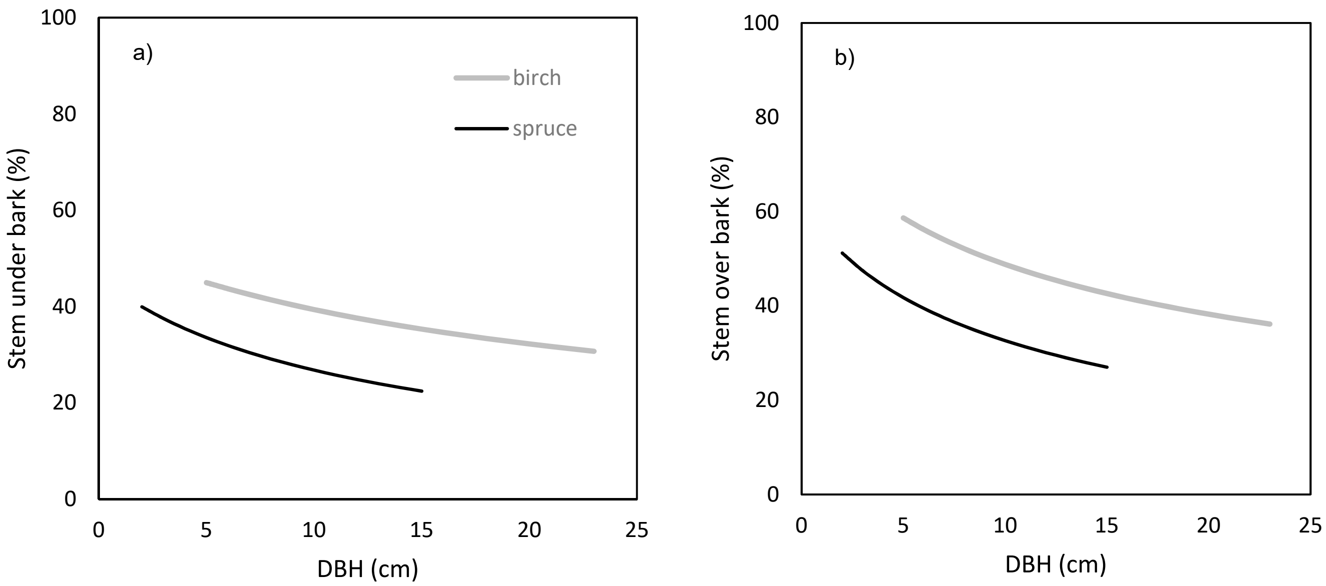


Figure 8. Contribution of stem over bark (**a**) and under bark (**b**) annual production to aboveground biomass production against diameter at breast height (DBH) for silver birch (considering radial increment = 1.4 cm) and Norway spruce (radial increment = 1.0 cm).

4. Discussion

4.1. Ecological Aspects

Our results showed that birch leaves contributed to aboveground biomass four times less than spruce needles (8% versus 32%). Rather surprisingly, contribution of spruce needles was nearly the same as that of stem wood (without bark). At the same time, birch produced about double the stem biomass (an example of DBH of 10 cm) than spruce. This suggests that stem wood production efficiency of birch leaves is much higher than that of spruce needles. In other words, much less birch foliage biomass is needed for the production of the same amount of stem wood biomass than in the case of spruce. This is probably related to different morphological features of foliage between the species (especially specific leaf area (SLA)) but also foliage age. As for SLA, our previous results in young stands showed that while birch SLA was about 180 cm^2 g^{-1} [28,29], SLA of spruce was three times lower [25,29]. While birch has only current-year leaves, spruce retains also older (2–5-year-old) needle sets besides current needles. Older needles are less efficient in photosynthesis and production of carbohydrates than current ones (e.g., see Reference [30]).

As for quantity of spruce foliage litter, our previous papers (combined data from References [26,27]) from the research site Vrchslatina in central Slovakia suggested that it was about 1/6 of total needle biomass. Since the altitude and tree age of our stands in this study were very similar to those at Vrchslatina, we may expect approximately similar ratios between needle litter and needle standing stock at the transects. At the same time, we found that the standing stock of spruce needles was about four times greater than birch foliage. Since all foliage of birch drops annually (foliage production ≈ foliage standing stock ≈ foliage litter), under the assumption of equal stem diameters (DBH = 10 cm) greater amount of birch foliage litter can be expected than spruce needle litter (by 67% more in birch than spruce). Moreover, quality of birch litter is higher than that of Norway spruce especially in terms of alkaline elements (calcium, magnesium and potassium) concentration [31] and nitrogen [32]. These two aspects, i.e., quantity and quality of foliage litter are more favorable for birch, which is commonly recognized as a soil improving species (e.g., see References [33,34]). In contrast, litter of Norway spruce needles accumulates because it decays more slowly than foliage litter of broadleaved tree species [26,35]. Berger and Berger [35] stated that lowered decomposition rate of spruce needles is mostly related to environmental conditions typically created under its monocultures. Therefore, mixed stands conditions would stimulate litter decomposition with consequent promotion of species diversity in the understory. In most cases, transformation of spruce stands into birch stands restored or improved soil fertility via limiting the loss of base cations and decreasing the nitrate percolation [36] and even reversing soil podsolization [37]. Silver birch foliage litter in contrast to Norway spruce needle litter, increases soil pH and decreases carbon to nitrogen ratio that, besides other consequences, has positive effects on humus quality (from mor to mull form [38]). Positive effects on soil properties can be expected not only in the case of complete stand transformation, i.e., from spruce to birch monoculture, but also via enhancing share of birch in coniferous, especially spruce-dominant, stands [14].

Silver birch and Norway spruce have very different ecological demands, morphological features and as for Slovakia also contrasting frequency in forests and contrasting economic importance. On the other hand, both species can often occur together especially in young growth stages on post-disturbance areas after destruction of spruce-dominant stands [13]. Silver birch is prospective in post-disturbance areas thanks to huge production of seeds (one tree can produce a few millions of seeds in a mast year) and their very large dispersal distance (e.g., see Reference [21]). Birch trees can provide a protective habitat for seedlings of other tree species, including those that are rather frost-sensitive, such as Norway spruce [39]. Birches growing in areas with high soil erosion rate can provide a particularly valuable service in watershed protection and soil stabilization [40]. From the point of keeping or supporting growth of silver birch in mixed stands, its great advantage is the fact that it is much less attractive for large herbivores than most other broadleaved species, especially the pioneer ones like aspen and willows [41]. This is thanks to terpenoides, especially betulin [42]. At the same time, birch is rather resistant to wind load and can be a stabilizing species even on water-logged sites [43]. On the other hand, birch is known to be very sensitive to snow and ice mechanical damage, especially in sparse forest stands that might be its disadvantage at some exposed sites [15]. Anyway, admixture of birch in Norway spruce plantations was pointed, especially in the newest works [44,45] as an efficient means to increase habitat and species diversity, including diversity of ground flora [46], invertebrates [47] or birds [48].

4.2. Wood Production Aspects

Our results obtained for post-disturbance conditions of Northern Slovakia showed that diameter increment of young silver birch trees was by about 40% greater than that of Norway spruce (Figure 6). Consequently, similar differences in favor of birch were recorded also for stem wood production—more in biomass than in volume expression (Figures 7 and 8), due to the greater density of birch wood (Figure 4). On the other hand, smaller inter-species differences were found for aboveground biomass production (Figure 7a). The phenomenon is related to rather contrasting biomass allocation of silver birch and Norway spruce, since birch invested a higher share of biomass to stem wood. In the examined early developmental stage, Norway spruce invested a higher proportion of biomass to the non-merchantable component, i.e., needles, than silver birch (Figure 7 and Tables 7 and 8).

At the same time, we estimated that density of birch stem wood was about 470 kg m^{-3} and its bark density was nearly 520 kg m^{-3}. Both values were significantly greater than for Norway spruce (Figure 4), which is in accordance with the results from Finland [49]. This wood quality of silver birch is advantageous not only in terms of production (quantitative) aspects, but it is also beneficial for further wood utilization as material with high mechanical resistance [14]. In Slovakia, stem wood density of birch can vary between 460 and 610 kg m^{-3} [50]. Works from Poland show silver birch wood densities between 400 and 652 kg m^{-3} [51–53], while the research from Latvia reported about 455 kg m^{-3} [54]. Some authors (e.g., see References [49,51]) commented that wood density is related to a variety of factors, especially tree age, habitat and geographic location.

Wood density determines its mechanical properties, namely the denser wood the better features might be expected. Reference [55] reported better mechanical properties of birch, specifically bending strength (modulus of rupture), stiffness (modulus of elasticity) and compressive strength parallel to grain, than of most common broadleaved species. Similarly, the newest review paper on silver birch [14] pointed out at very good mechanical properties of birch wood. They indicated that physical and mechanical properties of birch are similar to those of European beech. Moreover, due to the diffuse-porous structure of birch wood the quality of wood products is not affected by the ring width, and its processing and finishing is easy [14]. At the same time, silver birch has higher share of lignin in wood than Norway spruce [56]. Silver birch produces good quality hardwood pulp and veneer, and for these purposes it is used in Northern Europe and North America [19,57].

At our site, some of our 14-year-old birch trees reached a height of nearly 14 m, which means that their annual mean height increment was about 1 m. This value slightly exceeded heights of the same old trees shown in several birch tables from Northern Europe [58]. Eriksson et al. [59] pointed out that birch is typical with rapid early growth, and at best sites it can reach a height of up to 24–25 m within 30 years.

Results from Estonia [60] showed that maximum annual volume increment in silver birch was reached at the age of about 15 years. That is nearly the age of the birch trees included in our study, which may indicate that the volume increment may be reduced in next years. Although silver birch is typical with fast growth and great production potential (e.g., see Reference [61]), its vitality and vigorous growth is sustained only if it grows as dominant trees in a stand with a relatively wide spacing [19]. Therefore, silvicultural measures (thinning and tending) applied in mixed spruce–birch stands would be very probably based on maintaining rather low stand density. Older works from Scandinavia [62,63] manifested that the growth of spruce was simulated by increasing proportion of birch. Similarly, Mielikäinen [64] found that the yield obtained from mixed stands of Norway spruce and silver birch was greater than that from a pure spruce stand. Valkonen and Valsta [65] indicated that in Finnish economic and technical conditions it is profitable to grow a birch overstorey in a spruce plantation up to commercial volume. Their suggestions were based on economic analyses of the two-storied birch–spruce mixed stands.

Management of mixed birch–spruce stands should respect different rotation periods of the two species. While the rotation period of birch is usually about 40–50 years (e.g., see Reference [55]), the one of spruce is almost twice as long [66], although it might be shortened in the case of low initial tree density [67,68]. Liski et al. [69] manifested that shortening the rotation length of Norway spruce decreased the carbon stock of trees but increased the carbon stock of soil because of increased production of litter and harvest residues. They concluded that longer rotation periods at spruce sites would be favorable for carbon sequestration. On the other hand, increasing risk caused by inherent climate change phenomena (especially strong wind and drought stress) and consecutive secondary pests (mainly bark beetles) of spruce support shortening the rotation period (e.g., see Reference [6]). Under the conditions of Czechia, Martiník et al. [70] suggested birch as an alternative tree species to spruce and beech vegetation at middle altitudes of the north-eastern part of the country after the ongoing spruce decline. Similar situations concerning spruce forest decline exist also in neighboring countries of Czechia, especially in Germany and Slovakia. Therefore, we think that broad and intensive research of mixed birch–spruce stands with regard to their management is necessary. Research should not only focus on wood production, including its profitability, but also on carbon sequestration and forest adaption issues.

5. Conclusions

Our results proved that silver birch is a very fast-growing (40% greater diameter increment than in Norway spruce) tree species that is typical for young developmental stages of a forest. At the same time, it produced denser wood (by 30%) and allocated a higher share of biomass to stem wood (economically important tree fraction) than Norway spruce. However, birch silviculture, processing and market have not been thoroughly studied in Central and Western Europe. Due to this, the production potential of this species is not properly examined and utilized. Nevertheless, long-term experience from Scandinavia, Baltic countries and Russia showed that this genus, especially the species silver birch, can be efficiently used in forestry and forest-based industry. Another great advantage of silver birch is its high ecological adaptability, thanks to which it is a prospective species under the conditions of climate change. Moreover, birch presence may enrich tree species composition, and probably also diversity of flora and fauna in mixed forest stands in almost the entire Eurasian continent. Based on the results of our own study and findings from other works, we suggest strengthening research activities focused on birch ecology and production issues and subsequently bringing practical recommendations for better utilization of this tree species in forestry and wood-processing industry sectors.

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