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Comparison of growth, structure and production in stands of naturally regenerated *Betula pendula* and *Populus tremula*

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Abstract: In Central Europe, the most important pioneer species are silver birch and European aspen. Changes in disturbance regime and an economic interest for this species have led to studies on this species and stands. Two naturally regenerated dense stands of birch (*Betula pendula* Roth – silver birch monoculture) and aspen (*Populus tremula* L. – European aspen monoculture) were selected from a *Querceto – Fagetum mesotrophicum* site to observe responses under the same conditions in Central Europe. Both stands regenerated after the allochthonous Norway spruce stands dieback at the site in 1999. Within a 10 m × 25 m transect established in both stands, the diameter at breast height (*DBH*) of all the trees was measured between 2015 and 2020. In addition, the height and position were recorded for all trees, and sample trees of both species were felled for biomass measurement. A higher volume production of aspen at the beginning (107.48/96.80 m^3) and at the end of the experiment (178.32/143.08 m^3) was accompanied with a lower above-ground wood biomass (*WAB*). The *WAB* of birch increased from 81.9 $t \cdot ha^{-1}$ to 103.3 $t \cdot ha^{-1}$ and aspen allocated 79.5 $t \cdot ha^{-1}$ to 94.8 $t \cdot ha^{-1}$ of biomass. The current annual increment of biomass for these stands was 4.3 $t \cdot ha^{-1}$ and 3.1 $t \cdot ha^{-1}$ in the age range of 17 to 22 years. The culmination of the volume increment has not yet occurred in any of the stands, but the mean annual increment of wood biomass has already been reached for both stands. Furthermore, the aspen stand tended to be more dynamic in terms of biomass allocation and mortality. Also, the lower self-tolerance of aspen confirmed our hypothesis: the two native pioneer species differ in their social behaviour within monospecific stands.

Keywords: above-ground wood biomass; aspen; birch; pioneer stands; self-thinning

Spontaneous processes are often recommended for the purpose of forest regeneration after disturbance events (Pommerening, Murphy 2004; O'Hara, Ramage 2013; Brang et al. 2014). That often means the utilisation of pioneer species in the case of large, disturbed areas as the first step towards the estab-

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lishment of a new forest (Unseld, Bauhus 2012; Martiník et al. 2014; Stark et al. 2015; Konôpka et al. 2021). These strategies become more significant as a form of recovery of forest ecosystems in regions with long-term cultivation of allochthonous spruce in disturbed soil (Fanta 1997; Šrámek et al. 2015). There seems to be a growing interest in pioneer species (stands) due to the occurrence of unpredictable disturbance events. The current interest began about ten years ago after the last Norway spruce dieback in Central Europe (Holuša, Liška 2002; Krejza et al. 2021). In the region of Central Europe, silver birch (*Betula pendula* Roth) and European aspen (*Populus tremula* L.) are considered the most suitable recovering (nurse) tree species (Zakopal 1958; Stark et al. 2015; Martiník et al. 2016).

In natural forests, these pioneer species dominate in the early forest initiation stage and create preparatory (pioneer) stands (Korpeľ 1989; Oliver, Larson 1990; Fischer, Fischer 2012). The structure of pioneer stands tends to be very simple because these species are shade intolerant (Brzeziecki, Kienast 1994). On the other hand, the structure of these pioneer stands depends on the disturbance regime (Oliver, Larson 1990; Brzeziecki, Kienast 1994) and environmental conditions (Špulák et al. 2014; Martiník, Adamec 2016). From the ecophysiological point of view, pioneer species are well adapted to large, cleared areas – they demand light, grow very fast when they are young, and have a relatively short life cycle (Grime 1977; Brzeziecki, Kienast 1994).

In Europe, naturally regenerated stands of silver birch are more dominant compared to European aspen, which occurred mostly as an admixture tree (Huth, Wagner 2006; Myking et al. 2011; Fischer, Fischer 2012; Martiník et al. 2016). The growth and vitality of birch trees in these cases depend on canopy opening, soil conditions, and density of young stands (Suchockas 2002; Huth, Wagner 2006; Martiník, Adamec 2016). The density of younger, naturally regenerated birch stands can exceed 100 thousand trees per ha and decreases progressively with stand age due to self-thinning and management (Hynynen 1993; Niemistö 1995; Uri et al. 2012). The total volume yield of mature birch stands can often reach 500 m^3 per ha in the age range of 40 to 80 years (Cameron 1996; Hynynen et al. 2010). It is advised to introduce a shorter rotation period for the energetic utilisation of birch stands. The productivity of these optimally stocked stands can be more than 5 tons of dry wood biomass per ha each year, depending on site conditions and management (Ferm 1993; Johansson 1999; Uri et al. 2012; Aun et al. 2021).

Compared to the information available on silver birch, there are only a few scientific works and silvicultural recommendations for European aspen. In general, aspen production is comparable to or higher than birch in nutrient-rich soil with a good supply of water (Worrell 1995b). A greater demand for nutrients and particular regeneration strategies prevent aspen from being a more common species (Svoboda 1957; Ellenberg 2009; Myking et al. 2011). Seeds of aspen are more sensitive to environmental conditions and lose their ability to germinate very fast; artificial regeneration is expensive, and this leads to lower composition of aspen in Europe (Worrell 1995a; Tiebel et al. 2018). From a silviculture point of view, aspen is considered a less sensitive species when it comes to stand damage as a result of delayed thinning (Worrell 1995b; Rytter, Werner 2007).

A detailed comparison of the growth and structure of birch and aspen stands can aid in understanding these species, and a deeper knowledge of these tree species can facilitate silvicultural treatment towards economic goals (i.e. the choice of species in the process of reforestation or afforestation, thinning regime etc.). Many research plots were established, and experiments have been conducted in the Czech Republic ever since in order to gain a deeper understanding of the natural processes within these pioneer stands and to be able to manage them properly (Dobrovolný et al. 2011; Martiník et al. 2018). This paper deals with two of these plots, in the same site conditions, with the stands of similar age but different in species composition.

The main objective of this study was to analyse differences in the dynamics of forest structure and production of birch and aspen stands growing in the same natural conditions and with the same age (ranging from 17 to 22 years) over five years. We hypothesised that two different native pioneer species growing in monospecific stands of similar site conditions exhibit different behaviour.

MATERIAL AND METHODS

Experimental stands. For the purpose of this study, two naturally regenerated stands were selected in the same environmental conditions of Central Europe. One stand (49°88'N, 18°10'E) is composed mainly

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of silver birch (*Betula pendula* Roth) – hereafter referred to as 'birch'; the second one (49°88'N, 18°12'E) by European aspen (*Populus tremula* L.) – hereafter referred to as 'aspen'. The distance between these stands is approximately 1 km. Both stands regenerated naturally after the allochthonous spruce stands dieback at the site in 1999. These stands cover an area of 0.30 ha (birch) and 0.50 ha (aspen).

The stands are located in the north-eastern part of the Czech Republic at altitudes of 300 m a.s.l. (aspen) and 320 m a.s.l. (birch) in rich soil. Both stands are located on a plain with a slope of up to 5%. The geology is the same at both sites – clay shale bedrock and the stagnic luvisol soil (IUSS 2022). The region is characterised by an annual average temperature ranging from 8.1 °C to 9.0 °C and by an average annual sum of precipitation between 701–800 mm. According to forest type classification (Viewegh et al. 2003), both sites belong to *Querceto-Fagetum mesotrophicum* (nutrient-rich oak-beech). These sites belong to one of the most common central European forest categories – beech forest (EEA 2006). Specifically in the Czech Republic, this forest type covers more than 20% of the total forested area (Poleno et al. 2007). This site is considered the optimum for both the analysed trees in the forests of Central Europe (Martiník, Souček 2022). In natural climax forests, these sites are both primarily occupied with European beech, with an admixture of broadleaf (e.g. oak, maple) or silver fir (Ellenberg 2009).

Data collection. The following characteristics were the main objects of interest: mortality, tree height development, diameter structure, volume yield production, above-ground wood biomass (*WAB*), volume and above-ground biomass increments, and spatial tree distribution. All measurements were carried out within 10 m × 25 m research plots established in both stands. The research plots were located in the middle of each stand to avoid any edge effect. In the location of these stands, there was a high tree density and closed canopy. Both plots were divided into 10 sub-plots of 5 m × 5 m. Trees taller than 2 m were marked. The admixed subdominant trees (two birch in aspen; oak and pine in birch) and advanced regeneration level (tree species lower than 2 m) composed of fir, beech, lime and oak were omitted.

The positions of all live trees were determined by Field-Map technology (IFER, Czech Republic) at the beginning of the experiment. The diameter at breast height 1.3 m (*DBH*) of all marked trees was calculated from the tree circumference, which was measured by circumference tape at the end of the vegetation season every year from 2015 to 2020.

For modelling the height-*DBH* relationship (*H-DBH*), fifteen trees of each species (birch and aspen) were randomly selected within the plots and their heights were measured at the beginning (2015) and the end (2020) of the experiment using a hypsometer Nikon Forestry Pro (Nikon, Japan). Final *H-DBH* models were fitted by the Michailoff function (Michailoff 1943), see Equation (1):

$$H = 1.3 + ae^{\frac{b}{DBH}} \qquad (1)$$

where:
H – total tree height;
a, b – model parameters;
DBH – diameter at breast height of a tree.

The *H-DBH* models were fitted by nonlinear regression.

The estimation of above-ground wood biomass (*WAB*) was based on site- and species-specific allometric equations. Sample birch and aspen trees were used for destructive analyses in order to develop above-ground biomass allometric equations and on the consecutive application of these equations to the stand level (Johansson 1999). Sample trees were selected for each stand (species) to represent the diameter distribution using the technique of quantiles of the total (Čermák et al. 2004) within stands (outside the research plots) in 2015 and 2017. In total, 17 (8 in 2015 and 9 in 2017) sample birch trees were harvested in birch and 16 (8 + 8) aspen trees in aspen plots. Sample trees were harvested during the winter (leafless) period so that birch biomass represented only *WAB* (biomass of stem wood plus biomass of branches wood, but not the biomass of leaves). The stems were divided into three parts and fresh weights of the stem parts were determined. The stem disc samples were taken from the middle of each section. These discs were weighed and dried at 80 °C until they reached a constant weight so it would be possible to obtain the conversion factor for dry weight of the stem. After a fresh weighing of all branches, a representative branch from each third of the crown was selected and followed a similar process as with the stems. Each tree component was weighed to within an accuracy of 10 g.

To estimate the age of trees (stands), a disc was taken from the bottom of sample trees. The number of rings (age) was measured using

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a VIAS TimeTable measuring system (©SCIEM; VIAS Dendrolab, Austria).

Data analyses. The five-year development of both stands was described in these characteristics: number of trees (pcs·ha^{-1}), tree mortality (%), tree mortality within diameter classes (2: 1.0–2.9 cm; 4: 3.0–4.9 cm; ...), five-year diameter increment of each surviving tree (cm), basal area (*BA*; m^2), and net annual basal area increment converted to one tree (*BA*-net increment). The relationship between the five-year diameter increment of each surviving tree and its diameter at breast height was modelled by ordinary linear regression. We used the Chow test for the comparison of final models for both species to each other. This test compares if the model parameters (intercept *a* and slope *b*) are statistically equal in two tested linear models used on different datasets. The level of significance alpha was set to value 0.05.

Both stands were monospecific and even-aged with complete closure in the crown canopy. The model of relationships between stem number (*N*) and tree size (quadratic mean diameter – D_q) was used for the comparison of self-tolerance within birch and aspen. The Reineke (1933) power function was used, see Equation (2):

$$\ln N = k - a \times \ln D_q \quad (2)$$

where:

N – stem number;

k – intercept parameter;

a – slope exponent, considered constant and equal to −1.605 for all the species, was revaluated by real data;

D_q – quadratic mean diameter.

For modelling of the relationship between stem number and tree size we used ordinary linear regression. We compared the final Reineke's models for both species to each other using the Chow test.

The individual tree volume of birch and aspen was calculated by volume equations (Petráš, Pajtík 1991). These equations are not developed directly for aspen, so we used the equation for the poplar species (*Populus* sp.). The total tree height and diameter at breast height of a tree are used in these equations as independent variables. From these tree values, the stand growing stock and mean annual increment were calculated for 2015 and 2020. The current increment and total current increment were also calculated for the entire monitoring period.

The allometric equations between *DBH* and dry above-ground biomass components (stem biomass – *SB*, branch biomass – *BB*, and *WAB*) were established based on the sampled trees. The nlstools (Version 1.0-2, 2015) function (nonlinear least-squares method) in the R software (Version 4.2.2, 2022) was used to fit the allometric relationship. Allometric equations consistently fit (Table 1) with *DBH* as an independent variable (R^2 ranging from 0.76 to 0.99). We used these *DBH*-biomass relationships to estimate biomass at the stand level. The mean annual increment of *WAB* was calculated for 2015 (i.e. 17 years old) and 2020 (i.e. 22 years old). The current annual increment of *WAB* was calculated for the period between 2015 and 2020. Trends in gross and net annual increment of *WAB* were calculated. Net annual increment was calculated as the biomass increment of living trees, whereas gross annual increment was calculated as the difference between the current and previous biomass stocks (taking into account tree mortality).

Table 1. Allometric relationship between diameter at breast height (*DBH*) and biomass of individual tree components for birch and aspen

Species	Biomass component	Equation	Coefficient		Statistics		
			a	*b*	R^2	*AIC*	*MEP*
Birch	*SB*	$y = a \times DBH^b$	0.18042	2.16244	0.992	27.75	5.83
	BB	$y = ae^{(b \times DBH)}$	0.13077	0.31816	0.991	−20.10	0.40
	WAB	$y = a \times DBH^b$	0.12419	2.37944	0.993	32.06	6.44
Aspen	*SB*	$y = a \times DBH^b$	0.13984	2.23859	0.959	37.42	19.15
	BB	$y = a \times DBH + b \times DBH^2$	0.03123	0.03531	0.768	6.66	2.32
	WAB	$y = a \times DBH^b$	0.18703	2.17732	0.946	46.12	33.51

BB – branch biomass; *SB* – stem biomass; *WAB* – above-ground woody biomass; *a*, *b* – estimated parameter of biomass equations; R^2 – coefficient of determination; *MEP* – mean quadratic error of prediction; *AIC* – Akaike information criterion

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The aggregation index R (Clark, Evans 1954) was used for the description of horizontal distribution trees within the forest stands. The index is defined by the Equation (3):

$$R = \frac{\overline{r}_A}{0.5 \times \sqrt{\frac{A}{N}}} \quad (3)$$

where:

R – aggregation index;

$\overline{r}_A$ – average distance from randomly selected trees to their nearest neighbour;

A – area of the forest stand;

N – number of trees on the sampled plot.

The interpretation of the aggregation index R values is as follows: $R > 1$ if the pattern has a tendency toward regularity, $R = 1$ if it is completely random, and $R < 1$ if there is clustering in the pattern (Pommerening 2002). The aggregation index R was calculated at a scale of the whole 250 m^2 research plot for both species.

Weighted Voronoi polygons were used for the evaluation of the growth reaction of individual trees to available growing space (Krejza et al. 2015). The outcome of the analysis involves dividing the forest stand into non-overlapping distinct polygons that represent the growth spaces for individual trees (see Krejza et al. 2015 for details). Basal area of individual trees was used as weights. The calculations and projections were performed in the plugin software ET Surface (Version 5.0, 2013) for the ArcGIS (Version 10.2, 2013). The relationship between tree Voronoi polygons (weighted by particular basal area) and tree biomass allocation to above-ground wood components was fitted by ordinary linear regression. We used the Chow test for the comparison of final models for both species to each other.

RESULTS

Ring analyses confirmed the same age for both birch and aspen. The age of the tree samples ranged from 16 to 18 years. The mean age, at the beginning of the experiment in 2015, was therefore estimated as 17 years (Table 2).

The initial number of trees was higher for birch; aspen showed a higher mortality. During the five-year period, the survival rate for birch was 64%, and only 50% of aspen trees survived (Figure 1; Table 2). This indicates a greater self-thinning in aspen, compared to that in birch. The relationship between the number of trees N and the quadratic diameter D_q modelled by Reineke's function confirms this tendency (Figure 2). A slightly higher value of the slope parameter $a = -1.600$ (i.e. steeper line) was detected in aspen, compared to that in birch where $a = -1.483$. The differences between these two models were statistically significant (Chow test – P-value = 0.0026).

There was also a difference in the mortality between aspen and birch in the diameter classes; it was higher in middle classes of aspen (Figure 3A). For example, more than 80% of the trees died in the 6 cm diameter class and only 25% of the birch trees died during the period of observation. None of the aspen and birch trees that were thicker than 11 cm *DBH* died.

On the other hand, aspen trees grew faster in *DBH* compared to birch trees and these differences increased with diameter (Figure 3B). On average over the five study years, the thickest trees

Table 2. Basic characteristics (mean value ± standard deviation) of analysed birch and aspen in 2015 and 2020

Parameters	Birch		Aspen	
	2015	2020	2015	2020
Age	17 ± 1	22 ± 1	17 ± 1	22 ± 1
N ($pcs \cdot ha^{-1}$)	4 720 ± 1 395	3 000 ± 651	3 920 ± 926	1 960 ± 631
DBH (cm)	7.0 ± 3.2	9.8 ± 3.4	7.9 ± 2.9	12.0 ± 3.7
BA ($m^2 \cdot ha^{-1}$)	22.1 ± 3.8	25.6 ± 5.5	21.8 ± 5.9	24.3 ± 7.4
Net basal area increment of one tree (cm^2)	3.95 ± 1.72	5.03 ± 2.56	5.36 ± 1.79	8.55 ± 4.26
R aggregation	1.07	1.15	1.19	1.08

N – number of trees; *DBH* – diameter at breast height; *BA* – basal area

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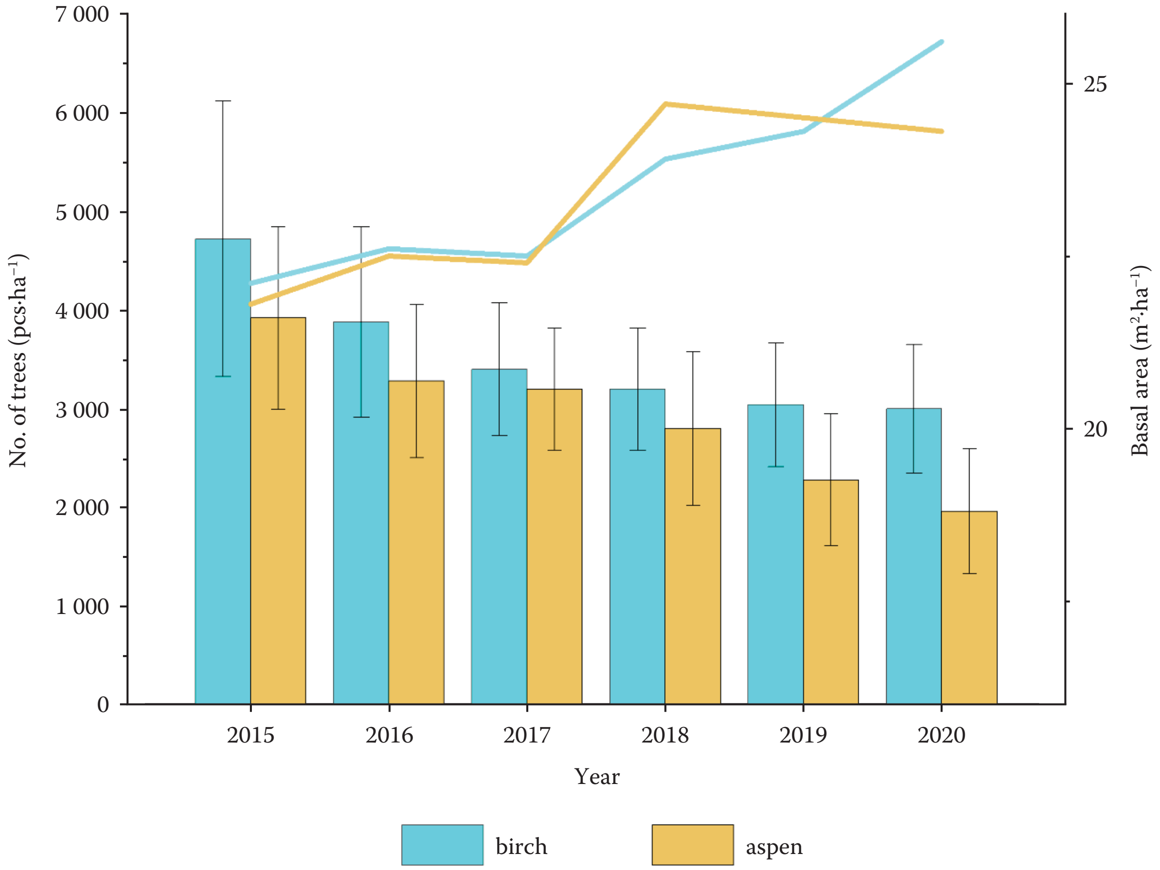

Figure 1. Development of the number of trees and basal area in the analysed birch and aspen stands between 2015 and 2020
Columns and whiskers represent the mean values and standard deviations

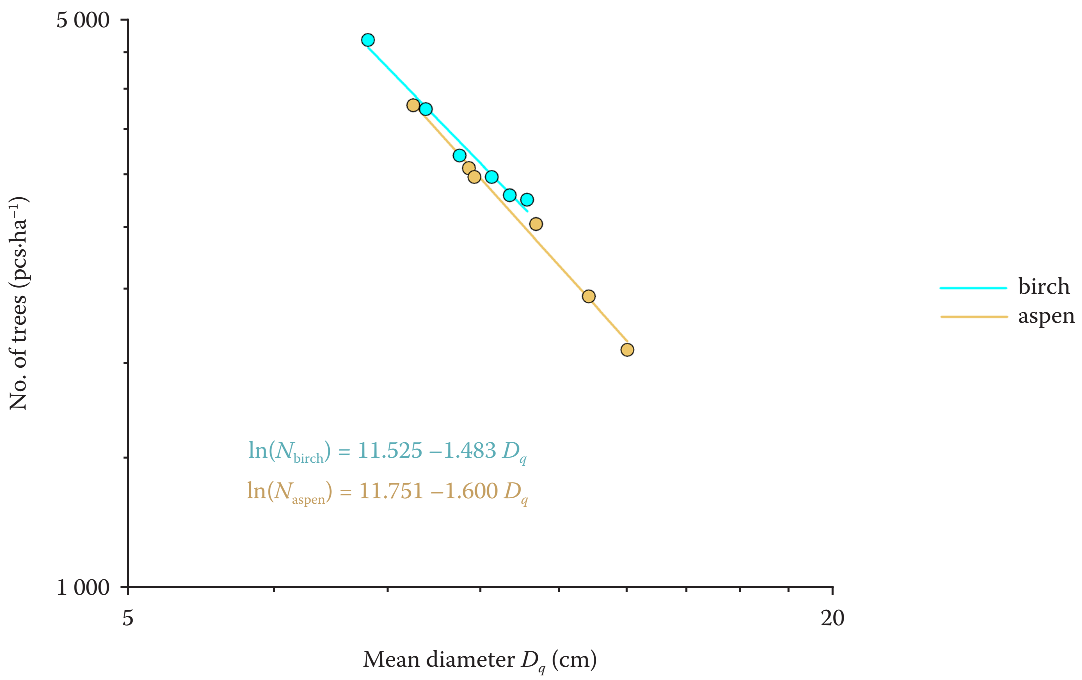

Figure 2. Relationship between the logarithm of the number of trees per ha (N) and the logarithm of quadratic mean diameter (D_q) for birch and aspen between the ages of 17 and 22 years

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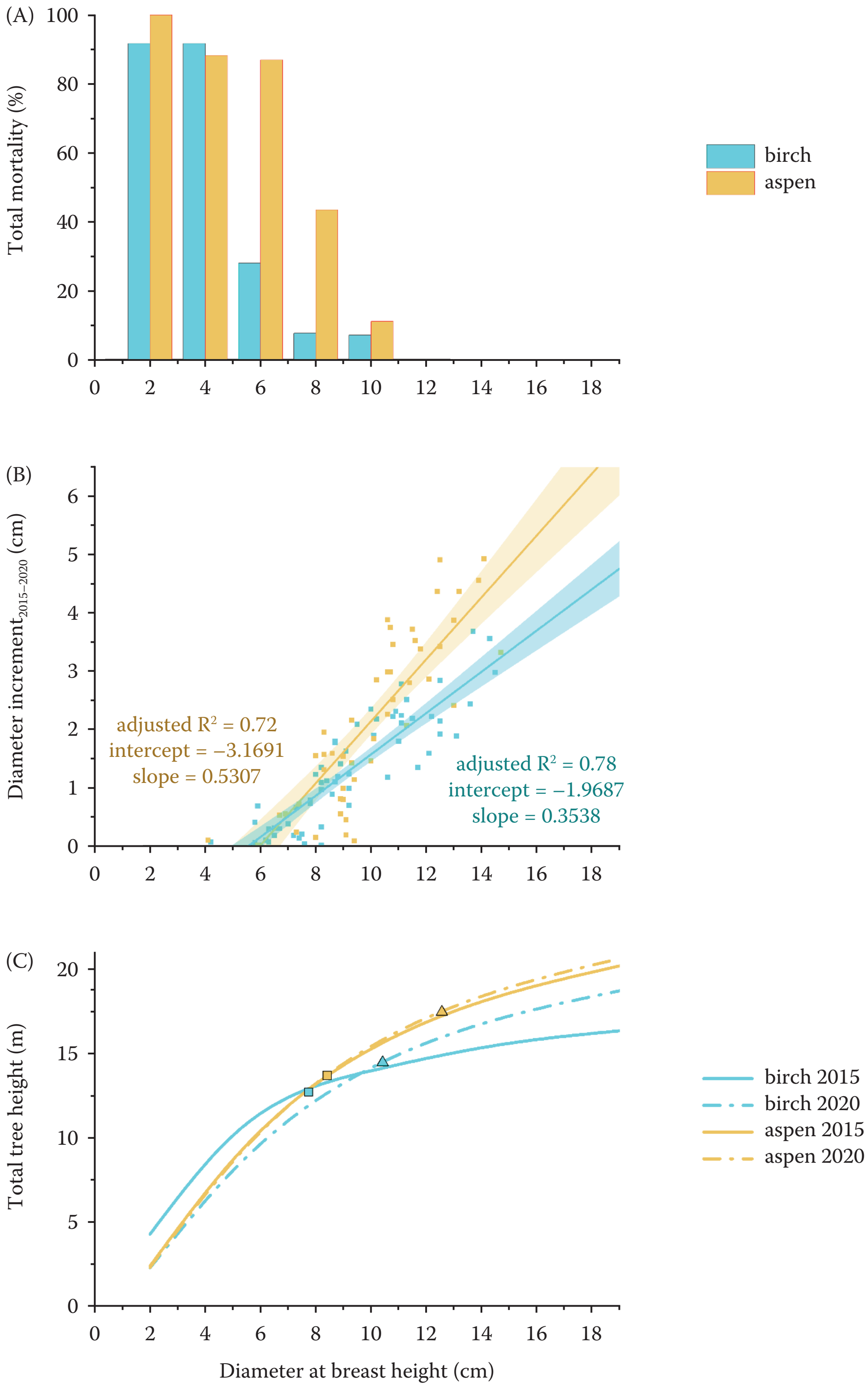

Figure 3. (A) Relative total mortality (%) in diameter classes for birch and aspen between the ages of 17 and 22 years; (B) diameter increment of birch and aspen trees in birch and aspen from 2015 to 2020; the coloured areas represent 95% confidence band; (C) fitted values of height-diameter models (blue and brown lines) and mean tree heights (based on quadratic mean diameter) of analysed species in 2015 and 2020

Blue square and triangle – mean heights of birch in year 2015 and 2020; brown square and triangle – mean heights of aspen in year 2015 and 2020, respectively

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Table 3. Estimated parameters of height-diameter Michailoff models for birch and aspen in 2015 and 2020

Parameters	Birch		Aspen	
	2015	2020	2015	2020
Parameter *a*	18.201	24.460	26.435	27.410
Parameter *b*	–3.619	–6.446	–6.381	–6.633
R^2	0.841	0.898	0.958	0.742

a, *b* – estimated parameters of height-diameter equations; R^2 – coefficient of determination

(i.e. trees with *DBH* around 14 cm) increased in diameter by 3 cm for birch and 4 cm for aspen. A higher value of the slope parameter (slope = 0.53; i.e. steeper line) was detected in aspen, compared to that in birch where slope 0.35. This statistically significant difference between diameter increment models of the tested species was confirmed by the Chow test (*P*-value < 0.0001).

The value of *BA* fluctuated during the period of observation due to self-thinning and the increment of individual trees. The slightly higher value of *BA* for birch, at the beginning and the end of the experiment, was confirmed by a greater relative increment of *BA*. The increase in the *BA* in birch was 15%, whereas the increase in aspen was only 11%. On the other hand, the lower number of aspen trees means a higher increment of *BA* per individual tree (Table 2).

The five-year self-thinning process also affected the horizontal distribution of trees within the analysed stands. The value of the aggregation index *R* in birch changed from 1.07 to 1.15 (i.e. more regularities); in aspen, the value of *R* changed from 1.19 to 1.08 (i.e. less regularities, towards a random distribution).

Aspen trees were taller than birch trees with the same *DBH* (Figure 3C; Table 3), although the difference decreased during the period of observation. More thick trees and a greater height with the same *DBH* of aspen led to a higher volume of wood (growing stock) in this stand. The differences were 47% (i.e. 10 m^3) at the beginning of the experiment and 66% (i.e. 25 $m^3\cdot ha^{-1}$) at the end of the experiment (Table 4). A higher total volume of the aspen stand was projected in the values of the current annual increment and the mean annual increment. The mean annual increment yielded by the aspen stand was 6.3 $m^3\cdot ha^{-1}$ and 8.11 $m^3\cdot ha^{-1}$, respectively, whereas the mean annual increment yielded by the birch stand was 5.7 $m^3\cdot ha^{-1}$ and 6.5 $m^3\cdot ha^{-1}$, respectively (Table 4). As the value of the current annual increment shows, the aspen stand yielded about 5 m^3 annually more than the birch stand (Table 4). A comparison of the current annual increment and the mean annual increment also shows that the culmination of the volume increment has not yet occurred in any of the stands.

The total *WAB* of birch ranged from 81.94 $t\cdot ha^{-1}$ (± 16.61 $t\cdot ha^{-1}$) to 103.30 $t\cdot ha^{-1}$ (± 26.65 $t\cdot ha^{-1}$). At the same time, *WAB* of aspen increased from 79.47 $t\cdot ha^{-1}$ (± 20.07 $t\cdot ha^{-1}$) to 94.82 $t\cdot ha^{-1}$ (± 27.32 $t\cdot ha^{-1}$) (Table 4). Figure 4 shows the differences in the year-to-year development of the wood biomass increment (allocation) within the analysed stands. Aspen

Table 4. Production parameters of birch and aspen stands in 2015 and 2020 (mean value ± standard deviation)

Parameters	Birch		Aspen	
	2015	2020	2015	2020
Growing stock ($m^3\cdot ha^{-1}$)	96.80 ± 27.23	143.08 ± 46.48	107.48 ± 42.94	178.32 ± 64.84
Mean annual increment ($m^3\cdot ha^{-1}\cdot y^{-1}$)	5.69 ± 1.60	6.50 ± 2.11	6.32 ± 2.53	8.11 ± 2.95
Current increment ($m^3\cdot ha^{-1}\cdot y^{-1}$)	9.26 ± 4.20		14.17 ± 6.92	
Total current increment ($m^3\cdot ha^{-1}\cdot y^{-1}$)	9.79 ± 3.94		16.95 ± 6.52	
WAB ($t\cdot ha^{-1}$)	81.94 ± 16.61	103.30 ± 26.65	79.47 ± 20.07	94.82 ± 27.32
Mean annual increment of *WAB* ($t\cdot ha^{-1}\cdot y^{-1}$)	4.82 ± 0.98	4.70 ± 1.21	4.67 ± 1.18	4.31 ± 1.24
Current annual increment of *WAB* 2015–2020 ($t\cdot ha^{-1}\cdot y^{-1}$)	4.27 ± 2.68		3.06 ± 3.86	

WAB – above-ground wood biomass

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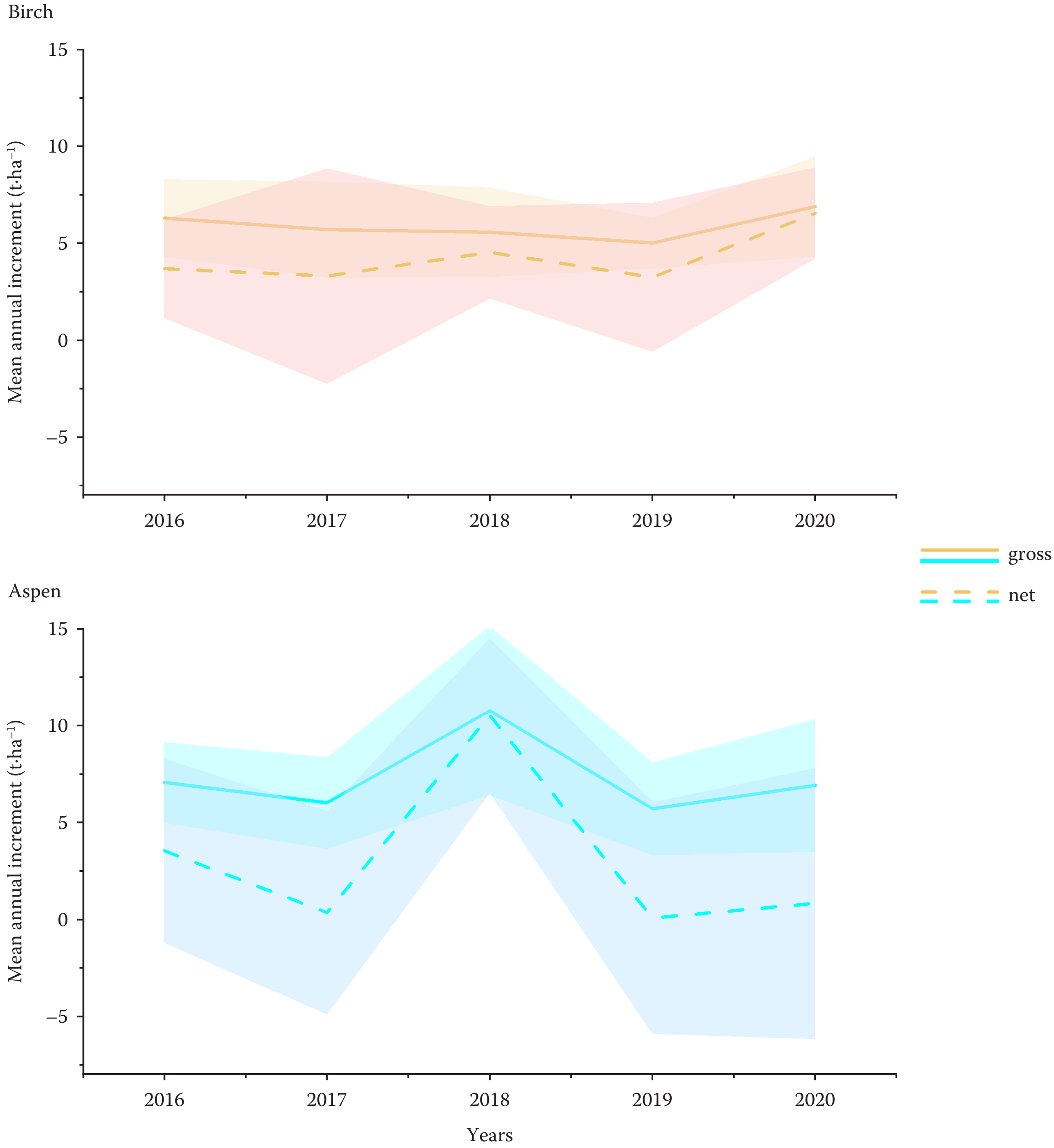

Figure 4. Development of gross and net mean annual increment of above-ground wood biomass (with confidence intervals) within birch and aspen during the period of 2015 to 2020

The coloured areas represent standard deviations

showed greater variability and a higher gross increment. On the other hand, lower mortality in birch led to a higher net biomass increment. Thus, during the five-year period, birch produced 4.3 t·ha^{-1} yearly, and aspen only 3.1 t·ha^{-1} (Table 4). The value of the mean annual increment of the *WAB* of birch and aspen decreased from 4.82 t·ha^{-1} to 4.70 t·ha^{-1}, and from 4.67 t·ha^{-1} to 4.31 t·ha^{-1}, respectively (Table 4). A smaller current increment of biomass, compared to the mean increment, also suggests that the peak of biomass allocation had already been reached.

Different behaviour of aspen and birch trees in monoculture confirmed analyses of Voronoi polygons (Figure 5). There is a trend that with the in-

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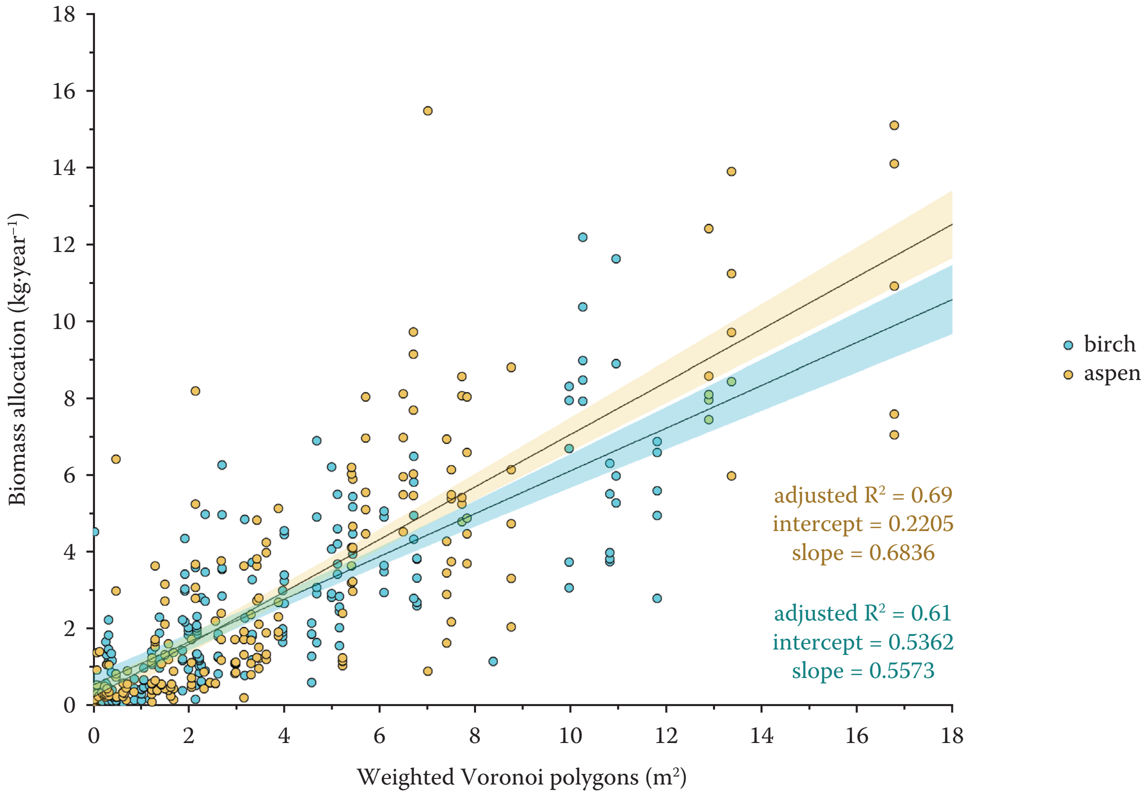

Figure 5. The relationship between tree Voronoi polygons weighted by particular basal area and the corresponding tree biomass allocation to above-ground wood components for 2015–2020

The coloured areas represent 95% confidence band

crease of polygons area aspen trees allocated more biomass than birch trees (slope = 0.68 and 0.55). This difference between biomass allocation models of the tested species was confirmed by the Chow test (P-value < 0.0001).

DISCUSSION

When considering bionomic strategy and ecological requirements of plant species, pioneer tree species tend to create even-aged monospecific stands. Both of the analysed birch and aspen emerged after moderate disturbance of allochthonous Norway spruce stands and they can presently be considered as monospecific and even-aged.

The basic parameters of the analysed 17- to 22-year-old birch stand were: N = 4 720–3 000 trees per ha, BA = 22.2–25.6 m^2 per ha and average DBH = 7–9.8 cm. The values recorded are in accordance with the results from naturally regenerated, unmanaged birch stands growing in Central and North Europe (Johansson 1999; Uri et al. 2012, Zasada et al. 2014). For example, Uri et al. (2012) analysed an 18-year-old birch stand growing on a fertile site in Estonia and documented these stand parameters: N = 3 630 trees per ha, BA = 21.9 m^2 per ha, and average DBH = 8 cm.

The very little data that is available on aspen stands was published by Johansson (1996). The author found out that a 23-year-old aspen stand growing in Sweden had a tree density of 1 480 per ha and an average DBH of 10.4 cm. This is comparable to aspen from our study, which had an age ranging from 17 to 22 years, a decreased density ranging from 3 290 down to 1 960 trees per ha, and an average DBH ranging from 7.9 up to 12 cm.

The relationship between the number of tress (N) and the mean quadratic diameter (D_q; size-density allometry) provides information that is relevant to ecophysiology and production economy (Pretzsch 2009). The stand density rule: $N = b \times D_q^{-1.605}$ for monospecific even-aged stands was defined by Reineke (1933). According to Zeide (1985, 2004) and Pretzsch (2009), the allometric exponent of this rule is species-specific and demonstrates species self-tolerance. The results of our experiment show a higher value of this

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exponent for aspen (–1.600), which demonstrates a higher self-thinning or lower self-tolerance compared to birch (–1.483). The value of the exponent found for aspen is slightly lower than the value published by Perala and Alm (1990). Depending on the data set, the authors state the value –1.61 or –1.91 for European aspen, which was more than for trembling aspen (*Populus tremuloides*). On the other hand, the allometric exponent that we found was far from the value published by Hynynen (1993). For birch stands growing in North-East Europe, he calculated the value –2.3. This difference may be due to the different conditions, species, and ages of the analysed stands. Hynynen (1993) analysed stands of both *Betula* species *(B. pendula* and *B. pubescens)* with an age of 23 to 78 years and, as stated by Zeide (1985), the slope of the self-thinning line changes according to the stage of development.

Our observations support the earlier findings and established knowledge (Svoboda 1957; Worrell 1995a, b; Martiník et al. 2016) that aspen trees grow faster than birch. The tallest aspen tree was close to 20 m and the tallest birch was more than 15 m. Regarding the site classes concept, our study area represents one of the best sites for both species (Lockow 1997; Černý, Pařez 1998; Dubois et al. 2020; Martiník, Souček 2022).

The greater height of the aspen trees also led to the difference in volume production. The total volume production, namely growing stock, of aspen was 11 m^3 and 35 m^3 greater than that of birch at the age of 17 and 22 years, respectively. This corresponds to previous knowledge about the production capacity of naturally regenerated aspen and birch stands growing in Central Europe (Martiník et al. 2016). The increase in the difference was also noted for the values of the mean annual increment, which varied from 0.6 $m^3 \cdot ha^{-1}$ (5.7/6.3 $m^3 \cdot ha^{-1}$) at the beginning to 1.6 $m^3 \cdot ha^{-1}$ (6.5/8.1 $m^3 \cdot ha^{-1}$) at the end of the experiment. The value of mean annual increment that we found corresponds to those in the studies that had been published on the productivity of aspen and birch stands (Svoboda 1957; Cameron 1996; Dubois et al. 2020). The value of the current annual increment for birch during the five-year period (9.3 $m^3 \cdot ha^{-1}$ from 17 to 22 years) is in accordance with that published by Ferm (1993), who presents the range from 8 to 15 $m^3 \cdot ha^{-1}$ in the culmination stage (i.e. from 15 to 30 years old). We have not yet managed to discover any detailed data for European aspen current annual increment culmination, but according to Rytter and Stener (2005), the culmination of hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) does not begin until the age of 14 years, where the value of the current annual increment varies from 15 $m^3 \cdot ha^{-1}$ to > 50 $m^3 \cdot ha^{-1}$. The lower value of the mean annual increment, compared to the current annual increment, also suggests that the culmination of volume production within these stands has not yet been reached.

Besides height, growth and the trend of the *DBH* increment of mainly the biggest birch and aspen trees affect the difference in the volume production of the analysed stands (see Figure 3B). Most of the aspen trees with a diameter greater than 10 cm increased their *DBH* from 3 to 5 cm during a period of 5 years, whereas birch trees only increased *DBH* from 2 to 3 cm. The values of *DBH* and the trend of the increment within both stands indicated that the biggest aspen and birch trees can reach 30 cm at the age of 35 or 45, respectively. The value of 30 cm or 40 cm is considered a target diameter for high-value timber production of both species and this value should be reached between 30–55 years of age, depending on the site and silvicultural system (Worrell 1995b; Cameron 1996; Hein et al. 2009; Hynynen et al. 2010). It is clear that silvicultural intervention in the analysed stand (clearing and thinning) would increase the diameter growth of the released trees. However, not all of the biggest trees are of the best quality and would, therefore, not be released during further forest growth.

Currently, pioneer species are not only considered for the production of high-quality timber in a rotation period of about 50 years but also for biomass for energy production (Hynynen et al. 2010; Uri et al. 2012; Stark et al. 2015). The rotation period for this approach varies from 10 to 25 years at the time of the culmination of the mean annual increment (Ferm 1993; Johansson 1999; Martiník et al. 2018). Within both the analysed stands, we found a decrease in mean annual increment, which is higher than that of the current annual increment. This suggests that the culmination of the mean annual increment has already been reached (Pretzsch 2009). Therefore, if the analysed stands are to be managed for biomass production, they are at the right age to be harvested. The value of mean annual increment of *WAB* (around 5; Hein et al. 2009 $t \cdot ha^{-1}$) of birch corresponded to those gained on better sites with naturally regenerated birch stands of the same age, growing in Central and Northern Europe (Johans-

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son 1999; Uri et al. 2012; Martiník et al. 2018; Aun et al. 2021). Available data for biomass production of naturally regenerated aspen stands are rare, but they indicate that similar productivity can be expected from this species (Stark et al. 2015; Špulák et al. 2016). On the other hand, poplar stands intensively managed on agricultural land often provide more wood biomass than naturally regenerated birch, or aspen stands growing on forest lands (Liesebach et al. 1999; Nielsen et al. 2014).

As our experiment revealed, aspen grows faster and produces more growing stock than birch. On the other hand, aspen *WAB* production and productivity were lower than birch. This is most likely due to the lower wood densities of aspen trees (Pretzsch 2009). Depending on wood density estimation, the values for aspen are 20 to 30% lower than for birch (Worrell 1995b; Martiník et al. 2017). Furthermore, as is shown in Figure 3, aspen is very dynamic in terms of increment but also mortality. Strong biomass allocations show the dominance of bigger aspen trees and, in comparison with birch, it is possible to say that the self-tolerance of aspen is lower (Zeide 1985).

Differences between the stands are confirmed by changes in the aggregation index (Table 2); aspen tends towards random distribution, birch towards regular. Usually, naturally regenerated stands tend towards regularity. The pattern observed in aspen (shifting from more regularity towards randomness) may be only a temporary stage resulting from stronger self-thinning (Pommerening 2002; Pretzsch 2009). According to Pretzsch (2009), regular tree distribution leads to maximum basal area increment. Relative increment of *BA* was higher in the birch stand (regularity) than in aspen (random). More about the dependence of spatial arrangement and tree growth is provided in Figure 5. Weighted Voronoi polygons are based on tree distribution and basal area (Pretzsch 2009; Krejza et al. 2015). Also, growing space, as represented by the Voronoi polygon, shows that bigger aspen trees are more effective in terms of biomass allocation (Figure 5).

Finally, a longer monitoring period and a greater number of plots are needed to confirm the results of this experiment. These results showed that the successful, naturally regenerated young birch stand produced more *WAB* biomass than the aspen stand growing in similar conditions. On the other hand, as was published by Stark et al. (2015), artificially regenerated aspen stands with wide spacing (nurse crop methods) can be more productive than birch stands with the same design. This corresponds with the results of this study – *WAB* and cubic volume mass are concentrated in dominant trees. Thus, naturally regenerated dense aspen stands seem to be more suitable for the production of wood than biomass. From the silvicultural point of view, our results confirm that aspen seems to be more tolerant of late thinning than birch (Worell 1995b).

It should also be added that the presented results are based on an environment strongly influenced by ongoing climate change.

CONCLUSION

In Central Europe, early successional stands are composed mainly of silver birch or a mixture with this species; European aspen pure stands are rare. However, changes in disturbance regime in this region and an economic interest in pioneer species have led to studies on this species and stands.

Different behaviour in monoculture stands was found for birch and aspen growing in the same region and site. The naturally regenerated aspen grew faster than birch in terms of height, diameter, and wood volume. Also, the dynamics of *WAB* in the aspen were stronger than in birch. On the other hand, net biomass allocation was higher in birch. In terms of silvicultural recommendations, aspen stands tend to be more suitable for wood production and birch stands for biomass utilisation. Furthermore, the behaviour of promoting individual trees detected in aspen indicates that this species can prospect well in mixture stands.

The results of the study confirmed our hypothesis; the two native pioneer species differ in their social behaviour within monospecific stands.

To confirm this statement, more naturally regenerated stands of these species in different environmental conditions should be studied.

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