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# Production and soil restoration effect of pioneer tree species in a region of allochthonous Norway spruce dieback

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**Abstract**

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The paper analyses the growth, structure, production and soil chemistry of different tree species stands 20 years after allochthonous spruce dieback. The experiment was carried out at lower altitudes (300 m a.s.l.) at rich sites of the Central Europe region. Norway spruce (*Picea abies* Linnaeus) and beech (*Fagus sylvatica* Linnaeus) stands established by artificial regeneration were compared with silver birch (*Betula pendula* Roth), aspen (*Populus tremula* Linnaeus) and birch-aspen stands, which were regenerated naturally. Spruce stands showed a decrease of site index (site index 3), compared with the previous generation (site index 2). This leads to an expected lower production at the age of 100 years, compared to mature beech stands, which showed a site index of 1. The highest production (tree overbark volume) was found out in the aspen stand – 294 $m^3 \cdot ha^{-1}$. The production (tree overbark volume) of other monoculture stands was comparable and reached 201–222 $m^3 \cdot ha^{-1}$. Most of the soil chemical characteristics under the compared stands (Ca and Mg content, Al content and active and potential soil reaction) were significantly better under aspen and decreased in the following trend: birch – beech – spruce.

**Keywords**: forest transformation; regeneration methods; birch; aspen; wood production; soil chemistry

Pioneer tree species which are creating the preparatory stands (i.e. the initial stage of stand development) are an important part of forest dynamics after disturbances (Oliver, Larson 1990; Brzeziecki, Kienast 1994). The role of these species in forest management of Central and Western Europe was influenced by the traditional "German forest school" (Fanta 1997; Sands 2005). Pioneer species were systematically eliminated in forest stands because they were considered competitors of spruce and pine trees till the end of the 20th century (Kenk, Guehne 2001; Spiecker et al. 2004). It was only after great disasters that the interest in these species increased (Pommering, Murphy 2004; Schelhaas 2008; Tesař et al. 2011). Tree species like birch (*Betula pendula* Roth, *Betula pubescens* Ehrhart) or rowan (*Sorbus aucuparia* Linnaeus) are recommended for their non-produc-

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tion function in the region of Central Europe (Podrázský 1995; Fanta 1997; Kula 2011).

The dieback of allochthonous Norway spruce (*Picea abies* Linnaeus) stands has continued in many regions of lower altitudes of Central and Western Europe until today (Schmidt-Vogt 1989; Schulze 1989; Holuša 2004; Spiecker et al. 2004). Many reasons for this dieback have been discussed, such as drought, nutrient availability, fungi, bark beetle and also emissions (Cape et al. 1990; Oszlanyi 1997; Grabařová, Martinková 2001; Jankovský 2003; Hlásny, Sitková 2010). One of the most affected regions in the Czech Republic is the Sudetes Mountains and North Moravia (Holuša, Liška 2002; Main-Knorn et al. 2009; Šrámek et al. 2015).

There is an interest in the economic and ecologic qualification of regeneration methods and selection of the species composition after the dieback of these allochthonous spruce stands (Kulla, Šebeň 2012). Succession and pioneer species provided many possibilities to establish a new forest (Fischer et al. 2002; Jonášová, Prach 2004; Huth, Wagner 2006; Bose et al. 2014). In addition, pioneer species enhance species richness, increase forest resistance and provide a suitable environment for the preservation of sites (Fanta 1997; Čermák, Holuša 2011).

In the boreal region of Europe the pioneer species are also interesting for the forest economics (Valkonen, Valsta 2001; Repola 2008; Hynynen et al. 2010), while in the region of Central and Western Europe, their production and economic evaluation is taken into account only scarcely (Jirgle, Tichý 1981; Slodičák et al. 2008; Stark et al. 2015). However, the use of pioneer tree species as nurse crops, short rotation coppice for biomass production (Vande Walle et al. 2007; Stark et al. 2013) and the selection of trees providing a high quality of timber are discussed (Buriánek 1993; Kula 2011).

One of the most important aspects of forest yield sustainability is preservation of soil fertility and favourable site conditions (Assmann 1970; Šály 1978; Poleno, Vacek 2006). Species composition should influence soil acidification and nutrient availability (Alban 1982; Augusto et al. 1998; Podrázský, Remeš 2010). For example, spruce cultivation at the lower altitudes of beech zones increases acidification (Kulhavý, Klimo 1997; Tesař et al. 2004), while the presence of broadleaf species should reduce acidification and increase nutrient availability in sites of allochthonous spruce stands (Lesná, Kulhavý 2003).

Objectives of this study were the following: (*i*) to compare the growth, structure, and production of stands, differing in the species composition, established and regenerated after the spruce stand dieback 20 years ago, (*ii*) to compare the soil chemical properties of the same forest stands, (*iii*) to define an optimal time scale of pioneer successions as the first step towards natural forest regeneration under the evaluated conditions.

## MATERIAL AND METHODS

**Site description**. The experimental area located in North Moravia, the northeastern part of the Czech Republic (GPS 9°51'N, 18°5'E; 300 to 350 m a.s.l.), belongs to the lower part of the Sudetes Mts. The 25-year (1990–2015) average temperature was 9.3°C and the annual precipitation was 713 mm. The potential vegetation there is lime-rich oak-hornbeam woodland (Neuhäuslová et al. 1998). Norway spruce was a dominant commercial species in this region throughout the 20th century. The second- or third-generation allochthonous spruce stands showed massive dieback at the end of the last century (Holuša 2004; Main-Knorn et al. 2009).

The experiment was carried out in a stand established in a 50–70-year-old 4 ha prevailing spruce monoculture which declined after 1994 and was regenerated at the same time.

**Experimental design**. Five forest stands, differing in tree species composition, were the subject of our research:

(*i*) spruce monoculture established by planting with 1.3 × 1.4 m spacing;

(*ii*) beech monoculture established by planting with 1.0 × 1.0 m spacing;

(*iii*) birch dominated stands that originated from succession;

(*iv*) aspen dominated stands that originated from succession;

(*v*) mixed stands composed of birch and aspen established by succession.

The area of each forest stand was approximately 0.20 ha and was of rectangular shape. The average age of all stands throughout the measurement period performed in 2014 was 20 years.

**Growth, structure and production**. In order to find the stand variability and reduce the edge effect, three circular sample plots of 0.01 ha in size were established in the middle of each stand. DBH was measured on all trees higher than 2 m ($h >$ 2 m). Tree basal area was calculated from DBH.

Stand basal area per hectare was calculated as a sum of basal areas of all trees. Within each stand, the heights of 15 trees at least were measured with a Haglöf Electronic Clinometer (Haglöf Sweden AB, Sweden) to get a representative dominant tree height and to model the height-diameter relationship according to the model defined by Michailoff (1943), as Eq. 1:

$$\hat{h}_i = 1.3 + a \times \exp^{\left(\frac{b}{\mathrm{DBH}_i}\right)} \qquad (1)$$

where:

$\hat{h}_i$ – fitted height of a tree $i$,

$a$, $b$ – model parameters,

$\mathrm{DBH}_i$ – diameter at breast height of a tree $i$.

For each stand the tree species composition was calculated according to the stem number, stand basal area and volume of large wood. The canopy was estimated for each stand. Tree density was calculated for all trees and for living trees respectively. Tree density was also calculated separately for trees with DBH larger than 7 cm (Table 1).

**Soil chemical characteristics**. For each of the three 0.01 ha stand plots, soil samples of organic (O) and organomineral horizon (A) were collected. Samples were analysed for chemical and physicochemical characteristics. The humus form and layer thicknesses were also recorded.

All samples were analysed for active and potential soil reaction (pH/$H_2O$ and pH/KCl respectively), exchangeable nutrients: K, Mg, Na, Fe and Al according to Gillman (ISO 11260, solution in $BaCl_2$); K and Na were determined by atomic emission spectrometry; Ca, Mg, Al, Fe and Mn by atomic absorption spectrometry. $H^+$ was assessed by dual pH measurement according to Adams and Evans (1990). Values of cation exchange capacity (CEC) were estimated by the summation method of particular elements (Eq. 2):

$$\mathrm{CEC} = \mathrm{ExchAc} + \mathrm{BC} \qquad (2)$$

where:

ExchAc – exchangeable acidity (Al + Fe + Mn + $H^+$),

BC – sum of base cations (Ca, Mg, Na, K).

Base saturation (BS) was calculated according to Eq. 3:

$$\mathrm{BS} = \frac{\mathrm{BC}}{\mathrm{CEC}} \times 100 \qquad (3)$$

Total nitrogen ($N_{tot}$) was determined by titration after distillation (wet mineralization using $H_2SO_4{\cdot}H_2O_2$) (Zbíral et al. 2011). Oxidizable carbon (Cox) was determined by the photometrical approach after oxidation, using a chromosulphuric mixture (Zbíral et al. 2011).

**Data analysis**. The tree overbark volume (volume of whole tree) and the volume of large wood (> 7 cm diameter overbark) were assessed according to the volume equations defined by Petráš and Pajtík (1991). The minimal DBH which was used for the volume equation was 5 cm. The mean diameter was calculated from the mean tree volume. The mean height of the tree was calculated using the height-diameter model of each stand. The prediction of the development of stand volume ($m^3{\cdot}ha^{-1}$) and mean volume increment ($m^3{\cdot}ha^{-1}{\cdot}yr^{-1}$) of different stands (species) was assessed according to Černý et al. (1996) and Černý and Pařez (1998).

Compared were the mean values of the volume of large wood and the tree overbark volume between stands using the Kruskal-Wallis test.

The same type of test was used for the comparison of the mean values of the soil parameters [i.e. Ca, Mg, K, Na, Fe, Al, pH (KCl), pH ($H_2O$), CEC, Cox, $N_{tot}$, C/N ratio and BS]. The significance level of analyses of all data was $\alpha = 0.05$. Statistically homogeneous groups of stands are designated by the same letter (as superscript) in the result tables.

## RESULTS

### Growth, structure and production

The tree composition of spruce monocultures was strongly influenced by succession, as new trees regenerated in gaps after spruce dieback (Table 2). Most of the naturally regenerated species outgrew spruce in height, DBH and tree volume. The height structure of spruce is highly variable; the maximum height of spruce was 14 m, however the mean height was only 10 m (Fig. 1). The site index (mean height at the age of 100 years) (Černý et al. 1996) of this species is 30 m. Spruce monocultures showed the highest stand basal area per hectare (Table 3). The tree overbark volume and volume of large wood were similar to those of beech and birch monocultures (Table 3). Spruce production was influenced by the admixture of other species (Table 2).

Only beech monoculture was pure without the natural regeneration of other species (Table 2), as a result of intensive past forest management (which was also the only one protected against browsing by fencing), and good growth of beech. The mean height of beech was approximately 12 m and the highest trees reached 14 m (Fig. 1). The site index of beech on comparable sites reaches 34 m,

Table 1. Tree density (trees with $h > 2$ m) at a stand age of 20 years (mean ± standard error)

| Stand | Total No. of trees per hectare | No. of living trees per hectare | Total No. of trees with DBH > 7 cm per hectare | No. of living trees with DBH > 7 cm per hectare |
|---|---|---|---|---|
| Spruce | 8,133 ± 803 | 5,567 ± 331 | 3,433 ± 136 | 3,133 ± 144 |
| Beech | 5,500 ± 47 | 5,233 ± 72 | 3,667 ± 136 | 3,667 ± 136 |
| Birch | 4,500 ± 499 | 4,200 ± 125 | 2,200 ± 125 | 2,167 ± 98 |
| Aspen | 10,533 ± 1,114 | 7,767 ± 1,344 | 2,533 ± 775 | 1,933 ± 334 |
| Mixture | 6,400 ± 772 | 5,300 ± 634 | 2,200 ± 189 | 1,900 ± 249 |

DBH – diameter at breast height

although the high initial tree density exhibits the lowest stand basal area per hectare compared to other stands (Table 3). The beech stand shows the lowest volume of large wood (125.50 m$^3$).

The birch monoculture exhibited the lowest total ($h > 2$ m) tree density, although the number of trees (DBH > 7 cm) was similar to stands established by natural regeneration (Table 1). A lower tree density and open canopy were probably the result of weak natural regeneration, consequent bigger mean diameter, and a reduction in the stand basal area per hectare (Table 3). The maximum height of 16.5 m and the mean height of 14 m indicated a site index of 28 m. The volume of the birch stand exceeds that in the yield tables according to Černý and Pařez (1998).

The highest total tree density of individuals was found in the aspen dominated stand (Table 1) with a high share of dead trees and trees with smaller diameter than 7 cm (Table 1). Although the number of alder, rowan, hornbeam, oak, birch and other trees was high, their share of the stand basal area per hectare and volume was only 12 and 1%, respectively (Table 2). The height of dominant aspens reached 22 m and the mean height 20 m (Fig. 1). The site index was 30 m (Černý, Pařez 1998). The stand basal area per hectare was comparable to that of spruce (Table 3). The tree overbark volume and volume of large wood were about 100 m$^3$ higher than in spruce (Table 3).

The total tree density of mixture was different between that of birch and aspen (Table 3) but the density of the trees (DBH > 7 cm) was (like in aspen) very low (Table 1). The dominant heights of aspen and birch were comparable, and were 20 m (Fig. 1). The mean height of aspen was 1.5 m lower than in birch and the mean height of birch was 0.5 m higher than in the birch monoculture. The share of birch and aspen in terms of volume was 53.5 and

Table 2. Tree species composition of analysed stands according to stem number (a), stand basal area (b), and volume of large wood (c)

| Stand | Criterion | Tree species composition (% ± SE) | | | | | |
|---|---|---|---|---|---|---|---|
| | | spruce | beech | birch | aspen | other conifers (larch, pine) | other broadleaves (rowan, alder, shrubs, hornbeam, willow, oak) |
| Spruce | a | 68.8 ± 1.8 | – | 12.7 ± 0.6 | 3.1 ± 1.6 | 9.5 ± 1.6 | 5.9 ± 2.4 |
| | b | 56.2 ± 5.8 | – | 18.6 ± 6.2 | 8.9 ± 3.7 | 14.0 ± 3.0 | 2.2 ± 0.3 |
| | c | 42.1 ± 7.2 | – | 23.6 ± 10.4 | 17.7 ± 6.8 | 15.1 ± 3.7 | 4.5 ± 0.7 |
| Beech | a | – | 100 | – | – | – | – |
| | b | – | 100 | – | – | – | – |
| | c | – | 100 | – | – | – | – |
| Birch | a | 3.7 ± 2.3 | – | 79.8 ± 3.1 | – | – | 16.8 ± 0.9 |
| | b | 0.7 ± 0.6 | – | 93.1 ± 0.5 | – | – | 6.1 ± 0.8 |
| | c | 0.3 ± 0.3 | – | 98.8 ± 0.5 | – | – | 0.8 ± 0.3 |
| Aspen | a | 1.5 ± 1.3 | – | 6.1 ± 0.9 | 31.3 ± 7.7 | 0.3 ± 0.2 | 60.8 ± 8.4 |
| | b | 0.2 ± 0.1 | – | 2.9 ± 1.0 | 88.2 ± 2.5 | – | 8.8 ± 2.0 |
| | c | – | – | 1.0 ± 0.5 | 98.9 ± 0.6 | – | 0.1 ± 0.1 |
| Mixture | a | 3.0 ± 2.4 | – | 53.1 ± 8.9 | 9.7 ± 1.3 | – | 34.2 ± 8.5 |
| | b | 0.7 ± 0.6 | – | 55.1 ± 8.5 | 35.8 ± 7.0 | – | 8.4 ± 2.1 |
| | c | – | – | 53.5 ± 8.9 | 46.5 ± 8.8 | – | – |

SE – standard error, rowan – *Sorbus aucuparia* Linnaeus, alder – *Alnus glutinosa* (Linnaeus) Gaertner, hornbeam – *Carpinus betulus* Linnaeus, willow – *Salix* spp., oak – *Quercus petraea* (von Mattuschka) Lieblein

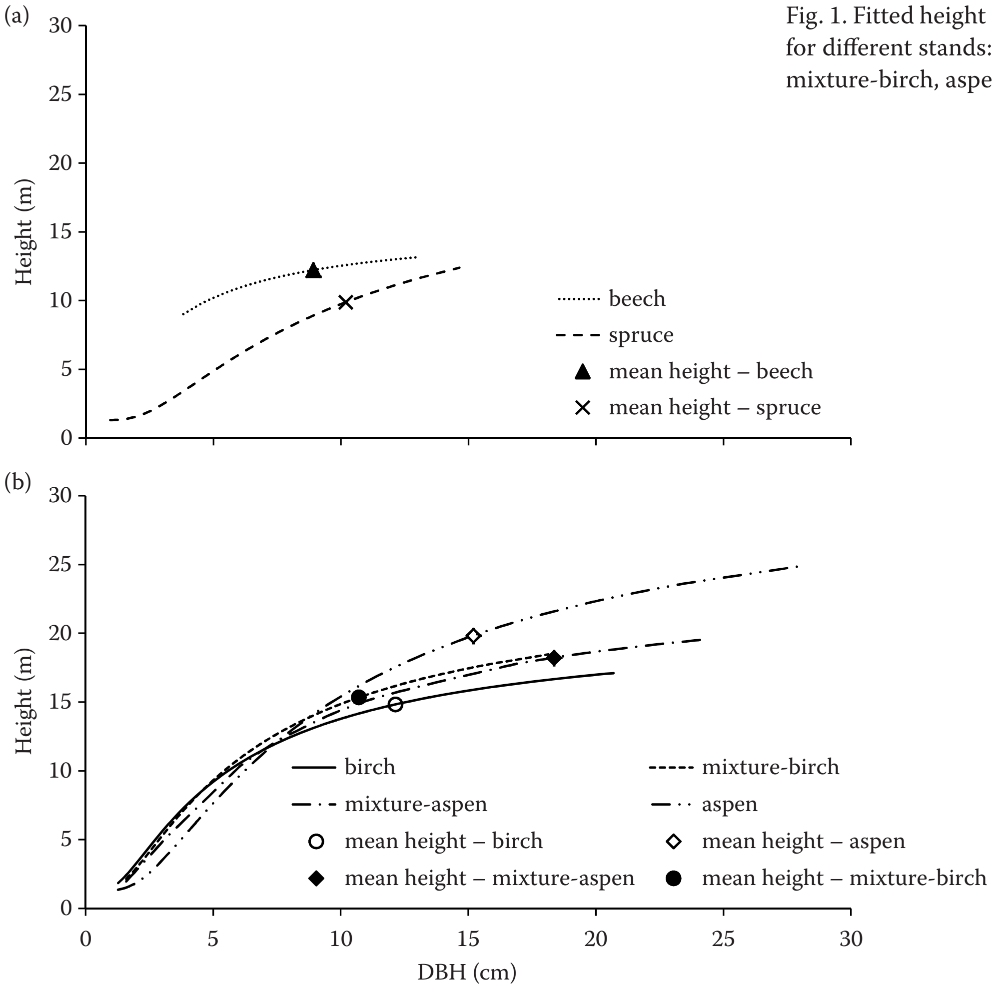

Fig. 1. Fitted height curves and mean heights for different stands: beech, spruce (a), birch, mixture-birch, aspen, mixture-aspen (b)

Table 3. Mean tree species characteristics (with standard errors) for different stands for all species (a) and dominant species (b)

| Stand | Criterion | DBH (cm) | 10 trees with the highest DBH (cm) | Stand basal area ($m^2 \cdot ha^{-1}$) | Canopy | Volume of large wood ($m^3 \cdot ha^{-1}$) | Tree overbark volume ($m^3 \cdot ha^{-1}$) |
|---|---|---|---|---|---|---|---|
| Spruce | a | 7.29 ± 2.33 | 16.39 ± 0.68 | 36.62 ± 1.39 | 0.9 | $140.17^{a}$ ± 8.28 | $201.67^{a}$ ± 0.08 |
|  | b | 7.29 ± 1.77 (spruce) | 12.38 ± 0.54 (spruce) |  |  |  |  |
| Beech | a | 7.92 ± 1.11 | 12.43 ± 0.27 | 27.82 ± 0.91 | 0.9 | $125.50^{a}$ ± 8.63 | $222.00^{a}$ ± 0.07 |
|  | b | 7.92 ± 1.11 (beech) | 12.43 ± 0.27 (beech) |  |  |  |  |
| Birch | a | 7.90 ± 2.68 | 16.78 ± 1.14 | 28.09 ± 1.06 | 0.7 | $137.47^{a}$ ± 12.38 | $215.33^{a}$ ± 0.11 |
|  | b | 8.79 ± 2.70 (birch) | 16.93 ± 1.00 (birch) |  |  |  |  |
| Aspen | a | 4.83 ± 3.13 | 22.09 ± 1.36 | 34.68 ± 2.07 | 1.0 | $246.03^{b}$ ± 14.34 | $294.67^{b}$ ± 0.18 |
|  | b | 12.68 ± 3.45 (aspen) | 22.09 ± 1.36 (aspen) |  |  |  |  |
| Mixture | a | 6.71 ± 2.78 | 19.89 ± 1.44 | 32.32 ± 0.71 | 1.0 | $176.87^{a}$ ± 8.54 | $253.33^{a}$ ± 0.03 |
|  | b | 7.78 ± 2.14 (birch) | 14.58 ± 0.44 (birch) |  |  |  |  |
|  | a | 15.33 ± 4.29 (aspen) | 18.40 ± 2.83 (aspen) |  |  |  |  |
|  | b | 8.79 ± 2.90 (birch + aspen) | 19.89 ± 1.44 (birch + aspen) |  |  |  |  |

DBH – diameter at breast height, the same letters (a, b as superscripts) indicate statistically homogeneous groups

Table 4. Parameters of height-diameter models

| Stand | Model parameter | Estimate | Standard error | *T*-value | *P*-value |
|---|---|---|---|---|---|
| Spruce | a<br>b | 19.9304<br>–8.5866 | 3.2677<br>1.6897 | 6.0992<br>–5.0815 | < 0.0000<br>0.0003 |
| Beech | a<br>b | 14.1739<br>–2.2364 | 0.6979<br>0.3889 | 20.3069<br>–2.9811 | < 0.0000<br>< 0.0000 |
| Birch | a<br>b | 19.9086<br>–4.6299 | 1.3820<br>0.5851 | 14.4048<br>–7.9119 | < 0.0000<br>< 0.0000 |
| Aspen | a<br>b | 32.0004<br>–8.1759 | 1.1402<br>0.4375 | 28.0641<br>–18.6866 | < 0.0000<br>< 0.0000 |
| Mixture-aspen | a<br>b | 23.0414<br>–5.6594 | 1.0119<br>0.6291 | 22.7699<br>–8.9958 | < 0.0000<br>< 0.0000 |
| Mixture-birch | a<br>b | 22.9296<br>–5.2547 | 1.9411<br>0.8392 | 11.8126<br>–6.2611 | < 0.0000<br>< 0.0000 |

46.5%, respectively (Table 2). The DBH of both species was lower than in the non-mixed stands (Table 3). The tree overbark volume and volume of large wood of this stand were between those of aspen and other stands.

All parameters of height-diameter models were statistically significant. The fitted parameters of these models are shown in Table 4.

### Soil chemical characteristics

The analyses show significantly higher values of both active and potential soil reaction in aspen and mixed stands compared to all other stands in humus layers (O). In the case of organomineral A-horizons the statistically significant differences were confirmed only in aspen stands (Table 5, Fig. 2). The same pattern (like the soil reaction in A-horizon) was indicated by base elements (Ca, Mg, K – Table 5) and by the sum of base cations, which is in accordance with the CEC dynamics (Table 5) and base saturation (significantly higher for aspen forest stands) (Table 5, Fig. 3). In O-horizon were significantly higher values of base saturation in aspen, birch and mixed forest stands (Table 5, Fig. 3).

One could find the highest values of Al and Fe in litter under spruce. The second highest content of aluminium was found in humus under beech, with all other contents significantly lower. Cox had similar values in humus layers in all tree species stands, while in spruce the content was insignificantly higher. In A-horizons, Cox predominated in aspen. C/N ratios were the same in aspen, beech, birch and mixed forest stands, but higher in spruce. Such differentiation was even more apparent in the epipedon (A-horizons).

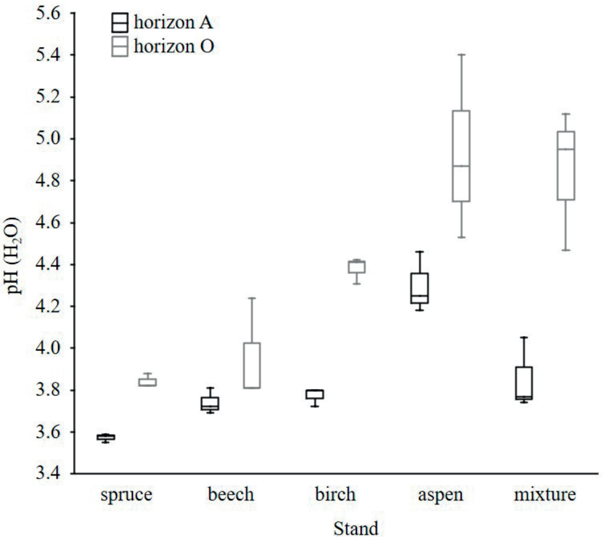

Fig. 2. Box plots of actual soil reaction for different stands horizon, A – organomineral, horizon O – organic (humus layers)

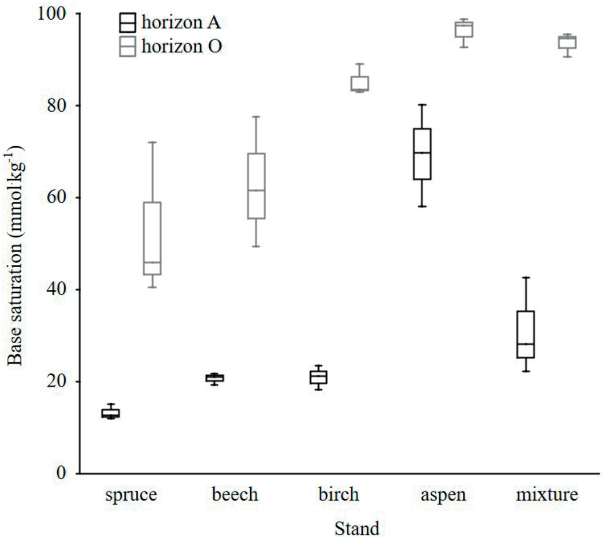

Fig. 3. Box plots of base saturation for different stands horizon, A – organomineral, horizon O – organic (humus layers)

Table 5. Mean values of soil chemical parameters in forest stands

| Soil chemical parameter | Horizon | *P*-value | Stand | | | | |
|---|---|---|---|---|---|---|---|
| | | | spruce | beech | birch | aspen | mixture |
| Ca ($mg\cdot kg^{-1}$) | O | 0.0252 | 1,544$^{a}$ | 1,840$^{a}$ | 2,686$^{a}$ | 4,767$^{b}$ | 3,956$^{b}$ |
| | A | < 0.0000 | 210$^{a}$ | 310$^{a}$ | 330$^{a}$ | 1,569$^{b}$ | 497$^{a}$ |
| Mg ($mg\cdot kg^{-1}$) | O | 0.0044 | 262$^{a}$ | 259$^{a}$ | 399$^{a}$ | 782$^{b}$ | 601$^{b}$ |
| | A | < 0.0000 | 43$^{a}$ | 55$^{a}$ | 55$^{a}$ | 299$^{b}$ | 80$^{a}$ |
| K ($mg\cdot kg^{-1}$) | O | 0.3300 | 254$^{a}$ | 221$^{a}$ | 340$^{a}$ | 288$^{a}$ | 348$^{a}$ |
| | A | 0.0004 | 43$^{a}$ | 56$^{a}$ | 55$^{a}$ | 139$^{b}$ | 67$^{a}$ |
| Na ($mg\cdot kg^{-1}$) | O | 0.0557 | 17$^{a}$ | 11$^{a}$ | 14$^{a}$ | 19$^{a}$ | 14$^{a}$ |
| | A | 0.0502 | 8$^{a}$ | 4$^{a}$ | 5$^{a}$ | 11$^{a}$ | 7$^{a}$ |
| Fe ($mg\cdot kg^{-1}$) | O | 0.0118 | 77$^{a}$ | 42$^{a}$ | 5$^{b}$ | 7$^{b}$ | 3$^{b}$ |
| | A | 0.0758 | 110$^{a}$ | 64$^{a}$ | 92$^{a}$ | 47$^{a}$ | 59$^{a}$ |
| Al ($mg\cdot kg^{-1}$) | O | 0.0003 | 445$^{a}$ | 390$^{a}$ | 103$^{b}$ | 40$^{b}$ | 47$^{b}$ |
| | A | 0.0002 | 581$^{a}$ | 547$^{a}$ | 491$^{a}$ | 274$^{b}$ | 477$^{a}$ |
| pH ($H_2O$) | O | 0.0016 | 3.84$^{a}$ | 3.95$^{a}$ | 4.38$^{a}$ | 4.93$^{b}$ | 4.84$^{b}$ |
| | A | 0.0001 | 3.57$^{a}$ | 3.74$^{a}$ | 3.77$^{a}$ | 4.29$^{b}$ | 3.85$^{a}$ |
| pH (KCl) | O | 0.0015 | 3.15$^{a}$ | 3.42$^{a}$ | 3.75$^{a}$ | 4.36$^{b}$ | 4.27$^{b}$ |
| | A | 0.0003 | 3.00$^{a}$ | 3.14$^{a}$ | 3.10$^{a}$ | 3.58$^{b}$ | 3.17$^{a}$ |
| CEC ($mmol\cdot kg^{-1}$) | O | 0.1160 | 197$^{a}$ | 186$^{a}$ | 206$^{a}$ | 320$^{a}$ | 273$^{a}$ |
| | A | 0.0025 | 117$^{a}$ | 104$^{a}$ | 108$^{a}$ | 152$^{b}$ | 109$^{a}$ |
| Cox (%) | O | 0.7386 | 28.8$^{a}$ | 23.2$^{a}$ | 26.4$^{a}$ | 24.9$^{a}$ | 26.8$^{a}$ |
| | A | 0.0014 | 6.4$^{a}$ | 6.2$^{a}$ | 6.8$^{a}$ | 12.2$^{b}$ | 7.3$^{a}$ |
| N (%) | O | 0.8747 | 1.25$^{a}$ | 1.25$^{a}$ | 1.41$^{a}$ | 1.36$^{a}$ | 1.32$^{a}$ |
| | A | < 0.0000 | 0.23$^{a}$ | 0.27$^{a}$ | 0.30$^{a}$ | 0.79$^{b}$ | 0.36$^{a}$ |
| C/N | O | 0.0012 | 23.0$^{a}$ | 18.7$^{b}$ | 18.7$^{b}$ | 18.3$^{b}$ | 20.3$^{b}$ |
| | A | 0.0303 | 28.3$^{a}$ | 22.7$^{b}$ | 22.3$^{b}$ | 15.3$^{b}$ | 20.3$^{b}$ |
| BS (%) | O | 0.0011 | 52.9$^{a}$ | 62.9$^{a}$ | 85.2$^{b}$ | 96.3$^{b}$ | 93.6$^{b}$ |
| | A | < 0.0000 | 13.3$^{a}$ | 20.7$^{a}$ | 20.9$^{a}$ | 69.4$^{b}$ | 30.9$^{a}$ |

CEC – cation exchange capacity, Cox – oxidizable carbon, BS – base saturation, O – organic horizon (humus layers), A – organomineral horizon, the same letters (a, b as superscripts) indicate statistically homogeneous groups

## DISCUSSION

Allochthonous spruce has been cultivated all over Europe for more than the last 150 years as a main commercial species (Fanta 1997; Spiecker et al. 2004). The new young generation shows a worse site index (site index 3), compared to that of beech, birch and aspen (site index 1) (Černý, Pařez 1998). For the present generation, we could also predict a lower stand volume of spruce compared to that of beech (Fig. 4).

Spruce stands of the previous generation showed a better site index (site index 2) in the same region (according to forest management plan), which is in contradiction with results of Pretzsch et al. (2014). The authors present the faster growth of new spruce and beech generations in Central Europe due to an increase in temperature and longer growing seasons. The available climatic data show an increase in the average temperature (1990–2014) by up to 1°C compared to 1960–1975 and 0.9°C compared to 1975–1990, the average value in the region of our experiment. This trend is similar to the one presented by Pretzsch et al. (2014) for Germany. Unlike there, the annual precipitation did not increase in our region (approximately 700 mm).

A decrease in spruce vitality in our experiment is most probably the result of the synergies of negative factors affecting the decline of spruce (Cape et al. 1990; Holuša 2004; Main-Knorn et al. 2009; Čermák, Holuša 2011). The occurrence of *Armillaria* spp. was observed which reduce spruce vitality and lead to increasing mortality of young trees (Kaliszewski et al. 2007; Šrámek et al. 2015). Fast-growing spruce of the previous generation had also negatively influenced the soil fertility (Augusto et al. 1998), which is considered the main factor for the preservation of long-term stand productivity (Sands 2005; Poleno, Vacek 2006). The analysis of the soil under spruce confirms soil acidification and a decrease in the availability of Ca and Mg, the most important chemical elements

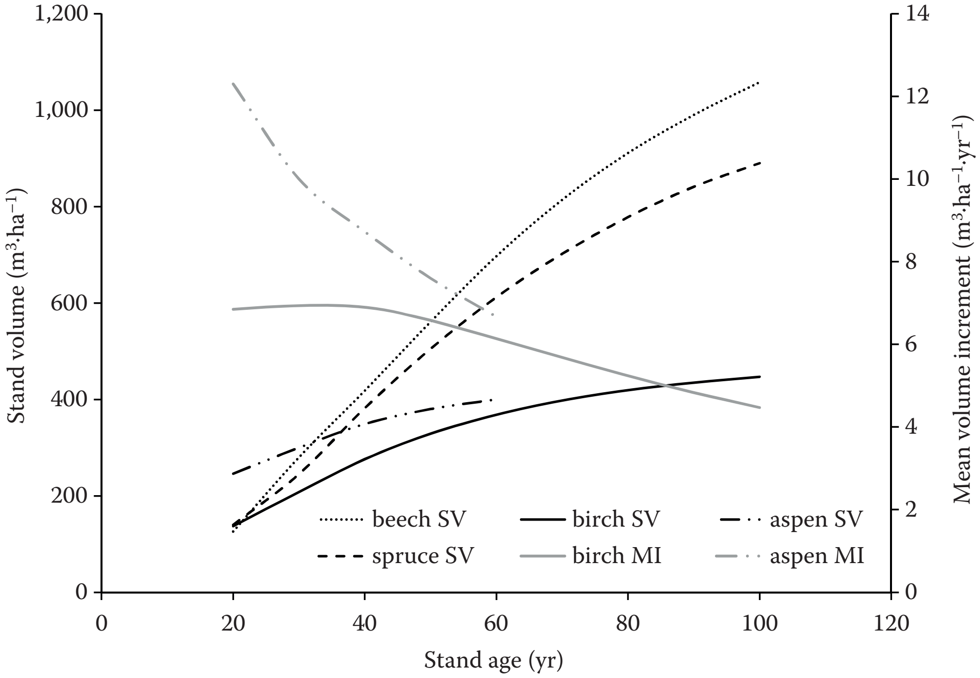

Fig. 4. Prediction of the development of stand volume (SV) and mean volume increment (MI) in different stands

necessary for soil to be fertile (Kulhavý, Klimo 1997; Augusto et al. 2002; Tesař et al. 2004; Šrámek et al. 2015). Also, the presence of birch and most broadleaf species in spruce (conifer) stands improves the soil and raises the ecological stability of these stands (Larsen 1995; Podrázský 1995). It is possible that there will be a more dramatic increase in acidification and nutrient availability under pure spruce without the presence of birch and/or aspen – both analysed pioneer species show better soil chemical properties compared to those of spruce. The birch and aspen also help to maintain a high production in spruce stands (Table 2). Although the presence of birch in spruce stands often negatively influences production (Frivold, Groven 1996), in our case, due to the dieback of young spruce and regeneration of birch and other species, it is exactly the opposite. Similarly, the proportion of admixed species (birch, pine) in order to maintain productivity, it is recommended as an adaptive management measure to mitigate negative consequences of climatic extremes in pure spruce stands in Northern Europe (Ge et al. 2011).

The production of birch was comparable to spruce and much higher than in aspen at the age of approximately 20 years (Table 3, Fig. 4). The expected (modelled) decrease in the production of these pioneer species, compared to that of spruce and beech (Fig. 4), may be connected with the life strategy of these early succession species and their position in forest ecosystem cycles after disturbances (Korpeľ 1989; Oliver, Larson 1990).

A decrease in the mean annual increment of birch and aspen (Fig. 4) and the production potential of these species (Table 3), together with a high number of additional seedlings of climax species under pioneer species indicate that approximately the 20–40 year period could represent an optimal rotation period for these species in these specific conditions. At this age, some gradual improvement in the soil chemistry properties induced by the pioneer broadleaf species could also be expected (Table 5, Figs 2 and 3).

Richter and Saniga (2006) found that in the case of a virgin beech dominated forest and under similar conditions in Slovakia, the intermediate forest (i.e. understory reinitiation) stage begins after a period of twenty years. The analysis of younger and older pioneer stands could confirm this finding. Finally, the additional regeneration of climax species under pioneer trees also provides possibilities for conversion towards continuous cover forestry (Pommerening, Murphy 2004; O'Hara 2014).

Successful growth of planted beech on a clear-cut is often limited by browsing, drought or weed attack (Gemmel et al. 1996). Good growth of the beech was probably the result of intensive former forest management (fencing, weed control) and the position of this stand within the experimental area (close to the edges of old stands). Despite the better characteristics in the soil of beech stands, compared to spruce, such conditions suit pioneer species far better than the beech (Table 5, Figs 2 and 3). A higher production of aspen (or a comparable production of birch), lower regeneration costs of succession variants, expected lower quality of beech wood grown in a clear-cut (Leonhardt, Wagner 2006; Wagner et al. 2010) and the risk of drought effect on beech vitality (Mátyás et al. 2008; Čermák, Holuša 2011) are all advantages of the use of pioneer species as the first step of a regeneration process after disturbances.

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