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Density and spatial distribution of beech (*Fagus sylvatica* L.) regeneration in Norway spruce (*Picea abies* (L.) Karsten) stands in the central part of the Czech Republic

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The conversion of Norway spruce monocultures to mixed forest is a long-term and costly process, and little information is available on the silvicultural use of spontaneous regeneration of native tree species to such purposes. In this context, we focused on the natural expansion of European beech in pure Norway spruce stands currently occurring in central Europe. The study was conducted in three secondary spruce stands with single adult (seed) beech trees growing on acidic sites of the fir-beech vegetation zone in the Bohemian-Moravian Highlands (Czech Republic). The regeneration strategy of beech and spruce (in terms of density and height increment) was studied under different light regimes (expressed using the indirect site factor - ISF) on the forest edge (9.7-41.2% ISF) and within gaps in the forest interior (10.7-20.8% ISF). Beech showed a broad light adaptability, being present under the spruce canopy with high density, depending on the distance from beech seed trees. Sparse beech saplings were found at a distance of more than 100 m from adult beech trees; however, abundant beech regeneration was found up to a distance of 25 m. Contrastingly, the density and growth in height of the spruce regeneration was strongly affected by light conditions. Spruce reached a density higher than beech in the understory where ISF > 17% (*i.e.*, up to a distance of 45 m from the stand edge or within gaps no smaller than 400 m^2), and competed with beech in terms of height growth where ISF > 20% (*i.e.*, at the very stand edges). Knowledge of the spatial pattern and the light strategy of both species provided useful information to support the conversion of spruce monocultural stands to mixed spruce-beech forests.

Keywords: Natural Regeneration, Beech, Spruce Monoculture, Competition, Conversion, Mixed Forest

Introduction

Utilization of natural processes in forest management is one of the major challenges for ecologically-based forestry today. The central European model of cultivating broadleaves for converting unstable, often pure coniferous stands, to close-to-nature mixed forests is known and relatively well-documented (Spiecker et al. 2004, Fritz 2006). Few data exist, however, on the use of forest succession elements for management purposes. Remnants of adult individuals and groups of native species, primarily broadleaves (*e.g.*, oak, beech and maple) and/or conifers (such as fir), admixed in pure secondary coniferous stands, can be found both in Europe (Karlsson 2001, Ganz 2004, Kunstler et al. 2004, Stimm & Knoke 2004, Dobrovolný & Tesar 2010a, 2010b) and in other parts of the world (Hewitt & Kellman 2002a, 2002b). Their potential for spontaneous reproduction differs depending on climatic, site and stand conditions, as well as the silvicultural strategy. While Küßner (1997) in the eastern part of the Ore Mts. (Germany) and Diaci (2002) in the Slovenian Alps reported a slow succession of climax woody plants in spruce plantations due to the low number of fruiting individuals within populations, Dobrovolný & Tesar (2010a, 2010b) recorded an expansion of beech under the shelter of spruce stands in the Czech Republic and in the central Saxon part of the Ore Mts. (Germany). Today, in central Europe the percentage of beech is increasing spontaneously to the detriment of conifers both in managed forests (Sterba & Eckmüllner 2008) and in old-growth (Keren et al. 2014).

The spontaneous penetration of oak into pine stands due to a process referred to as "jay (*Garrulus glandarius*) seeding" is well documented (Mosandl & Kleinert 1998, Stimm & Knoke 2004). Oak saplings can be found up to several kilometers from the seed tree (Bossema 1979, Kollmann & Schill 1996, Gomez 2003). Similarly, spontaneous spreading of beech occurs in spruce stands of central Europe, though it has not been sufficiently documented yet. Beech seeds can be transported to a distance of several dozen meters by rodents (Jensen 1985) and even to longer distances by jays (Johnson & Adkisson 1985, Kunstler et al. 2004, Wagner et al. 2010). Although the dissemination distance may exceed 100 m (Ganz

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Tab. 1 - Characheristics of the studied stands.

RP	Stand	Floristic association/ type of site	Altitude (m a.s.l.)	Area (ha)	Age (years)	Volume (m^3 ha^{-1})	Species composition	Location
A	957F11	Acidic beech-silver fir forest	560	6.60	109	577	spruce 99%, oak 1%	49°17′ 34″ N 15°42′ 53″ E
B	829E 12	Acidic beech-silver fir forest	640	6.49	112	672	spruce 93%, beech 4%, Scots pine 1%, larch 1%, Douglas-fir 1%	49°23′ 14″ N 15°42′ 43″ E
C	33a10	Acidic beech-silver fir forest	640	5.52	102	563	spruce 95%, Douglas-fir 5%	49°24′ 47″ N 15°19′ 16″ E

2004, Irmscher 2009) or even several kilometers (Johnson & Adkisson 1985, Kunstler et al. 2004), the largest amount of beech seeds is frequently found up to 20 m from the seed tree (Unkrig 1997, Kutter & Gratzer 2006, Sagnard et al. 2007, Wagner et al. 2010).

The successful expansion of beech in the past 20-30 years has been partly attributed to more frequent and abundant masting, occurring at 2 to 5-year intervals (Gruber 2003, Övergaard et al. 2007, Schmidt 2006). During mast years, the abundance of beech seeds can be as high as 300-1000 seeds m^{-2} (Röhrig & Bartsch 2006). Even old or suppressed beech trees produce seeds in such periods (Borrmann 1993, Pettermann 2000, Dobrovolný & Tesar 2010a).

Besides seed production and ecology, natural regeneration of beech and its competitive ability are influenced by many biotic and abiotic factors such as animals, mildew, stand conditions, climatic factors, soil moisture and supply of nutrients, root competition, ground vegetation, etc. (Madsen & Larsen 1997, Barna 2008). Nevertheless, light obviously plays the key role in the natural regeneration of this species (Pacala et al. 1994, Wagner et al. 2010). Shade tolerance gives beech a competitive advantage over other species (Pacala et al. 1994, Madsen & Larsen 1997, Barna 2008, Wagner et al. 2010). Indeed, beech can survive under extremely low radiation (3-5%) for several years, with slow growth rate but a very fast response to release (Collet et al. 2001, Wagner et al. 2010). Height and diameter increments are highest at relative light intensity (RLI) of 100%, with only a slight decrease occurring at 30%<RLI<50% (Wagner et al. 2010). In general, the relative radiation should not fall below 5-10 % in order to maintain beech height growth and stem quality (Gralla et al. 1997, Leitgeb & Gärtner 2005, Diaci & Kozjek 2005). It has been reported that beech maintains its advantage over spruce when the relative diffuse radiation (RDR) is below 15% (corresponding approximately to a stand basal area of 30-35 m^2), while at values higher than 20%, spruce becomes dominant in terms of height growth (Leder & Wagner 1996, Unkrig 1997, Lüpke & Spellmann 1997, Kühne & Bartsch 2003, Stancioiu & O'Hara 2006).

The main goal of this study was to better understand the natural regeneration process of beech as compared with spruce in a Norway spruce monoculture which is being converted to a mixed forest. Specific goals were (i) to quantify the occurrence and density of beech regeneration in relation to the distance from seed trees; and (ii) to determine the dependence of the occurrence and height growth of beech and spruce regeneration on light conditions. Finally, the results should be used for silvicultural recommendations.

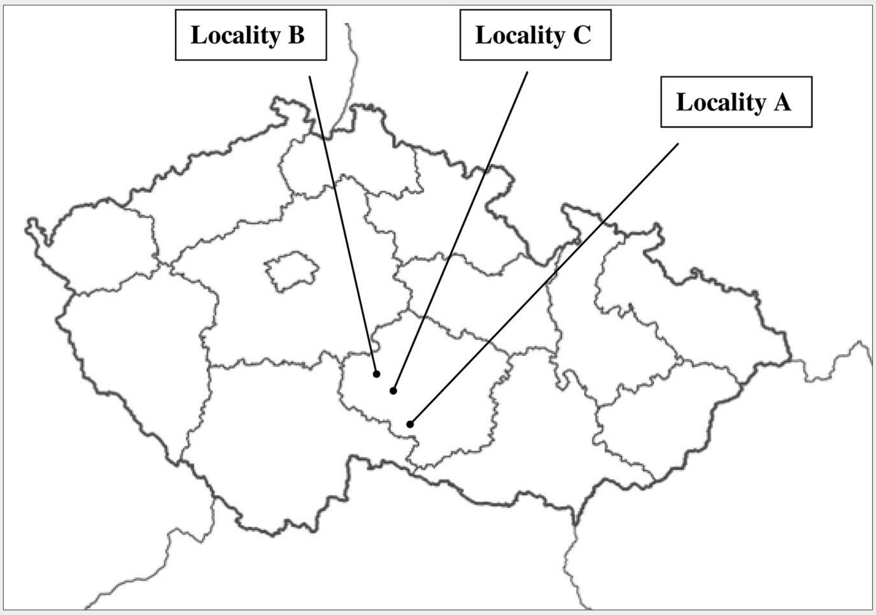

Fig. 1 - Location of the three study areas.

Material and methods

The research was carried out in the Bohemian-Moravian Highlands, the largest region of beech and fir-beech vegetation of the central part of Czech Republic. The region is currently covered by spruce plantations (about 70 % of the forest area) growing on acidic soil (Cambisols) at middle elevations, with an average total precipitation of 700 mm and a mean annual temperature of about 6 °C.

Three managed forest stands (A, B, C) characterized by adult spruce monocultures with irregular admixture of single adult beech trees were selected in the study area (Tab. 1, Fig. 1). The stocking density was around 80 % of the standard volume, due to salvage felling as a result of occasional damage by icing and bark beetles.

For each stand, the spatial pattern of distribution of beech regeneration up to 2 m in height was recorded, as well as the density and the height growth of seedlings and saplings of beech and spruce in different light environments (Fig. 2). Measurements were conducted in the summer of 2013 along two transects, the first staked between two adult beech trees (A: 52 m; B: 72 m; C; 54 m), while the second was starting at an adult beech tree and directed toward the homogeneous, pure spruce stand with no adult beech trees, up to a distance of 150 m (Fig. 2). Both transects were divided into sections of 2 m in length and the density of beech regeneration was determined in circular 1-m^2 subplots centered in the middle of each section. The total number of subplots was 101 at the site A, 111 at the site B, and 102 at the site C.

Measurements were conducted in two distinct areas with different light conditions: (i) in the 65 m-wide outermost zone of the forest (EDGE); (ii) in the inner part of the stands (INTERIOR). To this purpose, measurements were carried out along three transects set at a distance of 50 m each other (Fig. 2). The transects were staked perpendicular to the forest edge and directed towards the interior of the stand, their total length being 200 m (variant EDGE up to 65 m and variant INSIDE the next 135 m). Each variant was divided into sections of 5 m in length and a circular 5-m^2 subplot was established in the middle of each section. The total number of subplots established in each stand was 39 for the variant EDGE and 81 for the variant INSIDE. For each subplot, the following attributes of the regeneration of beach and spruce were measured: (i) density (n ha^{-1}); (ii) height of the apical bud above the ground (in cm); (iii) annual height increment of the leading shoot from the previous year (in cm). In the variant INTERIOR, the spatial positions of the canopy gaps above these transects were measured using the Field-Map technology (Institute of Forest Ecosystem Research, Ltd., Czech Republic). Canopy gaps were classified in the following classes: 25, 50, 100, 400 m^2. Hemispherical photographs were also taken in the middle of each section (of both variants) using a digital Nikon Coolpix 4500® camera with the FC-E8 fisheye converter. The indirect site factor ISF (*i.e.*, the intensity of relative diffuse radiation) was evaluated using the software WinsCanopy® 2008a (Regent Instruments Inc., Canada). In the case of variant EDGE, the ISF values ranged from 9.7 to 41.2%, while for the variant INTERIOR ISF ranged from 10.7 to 20.8 %.

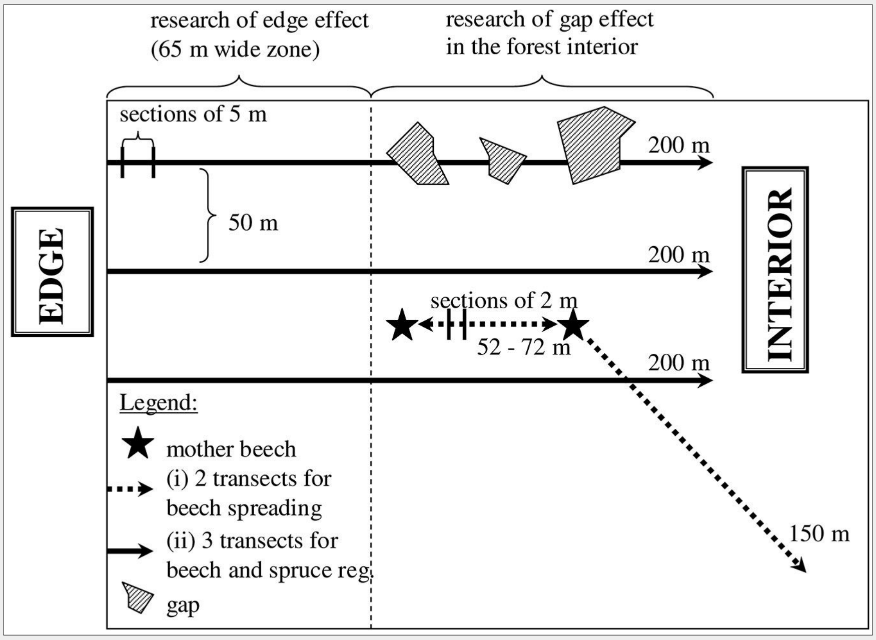

Fig. 2 – Graphical representation of the experimental design adopted in this study.

Statistical analyses were carried out using the software package STATISTICA® ver. 10 (StatSoft Inc., Tulsa, OK, USA). The Kruskal-Wallis one-way analysis of variance was used to test for differences in the regeneration variables between sites and variants. Binary logistic regression procedures were used to verify the relationship between selected factors (*i.e.*, distance from the adult beech tree, ISF and distance from the edge) and the occurrence of beech and spruce regeneration. Binary logistic regression estimates the probability (0-1) of occurrence of a selected characteristic (*e.g.*, the probability of "success"). For this analysis, the presence of saplings was used as a dependent variable. All the plots were classified according to the occurrence of beech or spruce regeneration, where 0 means no regeneration and 1 means one or more saplings per m^2. where. The general form of the model function used in this analysis was as follows (eqn. 1):

$$\pi = Pr(Y_i = 1 | X_i = x_i) = \frac{\exp(\beta_0 + \beta_1 x_i)}{1 + \exp(\beta_0 + \beta_1 x_i)}$$

where β_0 is the intercept and β_1 x_i is the regression coefficient multiplied by the predictor.

Results

In general, the average density of beech regeneration in the forest interior was greater than that of spruce, though significant differences were detected only for the variant "$A_{INTERIOR}$" (Tab. 2). As expected, there were significantly more favorable light conditions for spruce regeneration on the forest edge, and its density was significantly greater than for beech in all the studied stands. Beech regeneration showed higher values of height growth as compared to spruce in both variants EDGE and INTERIOR: significant differences were found among all variants except "C_{EDGE}". The forest edge was characterized by the highest and the more heterogeneous values of radiation compared with the forest interior. Obviously, the amount of light near the forest edge was varying based on the distance from the edge, while in the forest interior, it was affected by the sizes of the gaps (Tab. 2).

The percentage and average density of beech regeneration showed a steeply decreasing trend up to 25 m from the seed

Tab. 2 - Statistics of beech and spruce regeneration at the study sites. Mean ± 95% interval values are reported according to the stand studied (A, B, C) and the variant analyzed (EDGE and INTERIOR).

Stand	ISF (%)	Density of Beech (N ha^{-1})	Density of Spruce (N ha^{-1})	Height of Beech (cm)	Height of Spruce (cm)	Height increment of Beech (cm)	Height increment of Spruce (cm)
$A_{INTERIOR}$	13.4	35881	1973	36.9	24.6	9.6	2.81
±95%	0.1	6303	919	3.9	6.5	1.6	1.6
A_{EDGE}	16.4	10800	18263	64.0	34.8	15.9	6.0
±95%	0.3	3098	3409	10.5	3.2	4.9	0.5
$B_{INTERIOR}$	19.7	50556	126111	31.4	9.0	5.4	1.9
±95%	0.2	40586	40901	7.1	1.6	1.6	0.3
B_{EDGE}	24.2	42222	141944	50.1	18.0	9.5	4.2
±95%	2.3	21900	40277	12.0	3.8	2.0	0.8
$C_{INTERIOR}$	15.9	16200	8700	60.4	27.8	15.3	2.8
±95%	0.2	4980	5729	5.6	2.9	1.7	0.8
C_{EDGE}	25.9	9167	65556	39.3	23.0	7.5	3.8
±95%	1.3	4154	19182	8.7	8.4	2.0	1.0
$All_{INTERIOR}$	14.6	32254	14924	40.9	19.4	11.3	2.3
±95%	0.2	5659	5204	3.3	3.4	1.2	0.4
All_{EDGE}	18.0	17035	34809	55.3	31.6	12.5	5.5
±95%	0.5	5211	6279	6.8	2.8	2.7	0.4

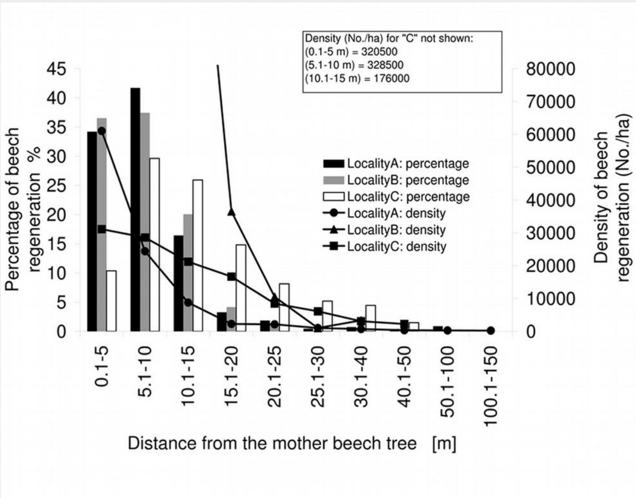

Fig. 3 - Average density of beech regeneration and percentage of the total number of individuals according to the distance from the seed tree. The highest density of regeneration was found at a distance of 0.1-5 m from seed trees, while the highest percentage of all individuals was recorded at a distance of 5-10 m.

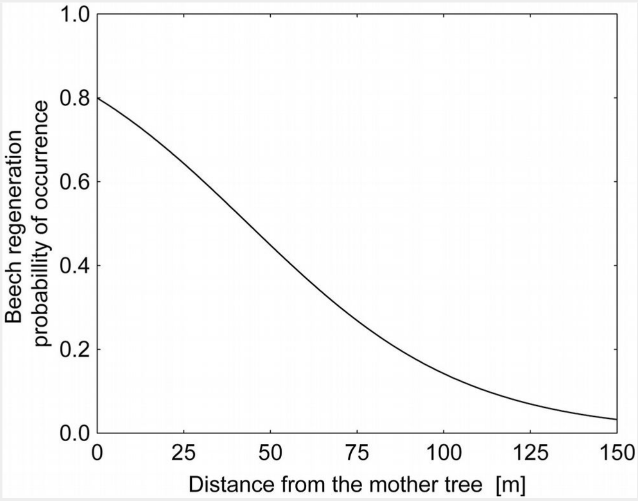

Fig. 4 - Logistic regression of beech saplings distribution. The probability of the occurrence of beech regeneration (present = 1, no regeneration = 0) as a function of the distance from the seed tree. At distances exceeding 50 m, the density of beech saplings is low and the probability of occurrence of beech regeneration falls below 0.5.

Tab. 3 - Statistics of the logistic regression.

Statistics	Param	Beech	Spruce
Distribution (Fig. 4)	B_0	1.386	-
	b	-0.032	-
	p	0.000	-
ISF (Fig. 5)	B_0	2.165	-7.270
	b	8.714	0.445
	p	0.000	0.000
Edge (Fig. 6)	B_0	-3.967	3.271
	b	0.084	-0.080
	p	0.000	0.000

tree in all the three stands investigated (Fig. 3). The highest density of beech saplings was found directly below the crown of the seed trees (within a radius of 0.1-5 m), while the highest percentage of all saplings was recorded in the surrounding area, at a distance of 5-10 m. At larger distances (>50 m) from seed trees the sapling density was low, though single individuals were found at distances exceeding 100 m. Pooling the data from all the three stands, we constructed a general model using the significant parameters for the abundance of beech saplings as a function of distance from seed trees (Fig. 4, Tab. 3). The curve confirmed a low probability of occurrence of saplings at distances exceeding 50 m from the seed tree.

Using the logistic regression on the data pooled over the three studied stands, we calculated the approximate value of ISF (value of diffuse radiation) at which beech and spruce showed similar regeneration abundance, *i.e.*, the competitive point for spruce and beech in terms of ISF (Fig. 5). Beech regeneration was more frequent below 17% ISF, while spruce exhibited a competitive advantage over beech above

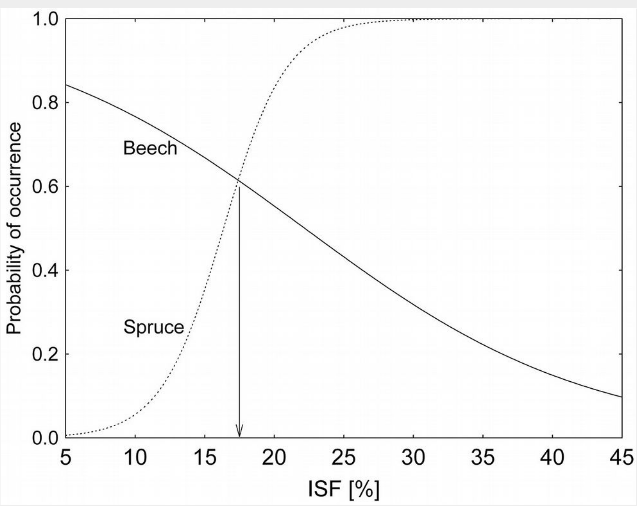

Fig. 5 - Probability of occurrence of beech and spruce regeneration (present = 1, no regeneration = 0) as a function of the diffuse radiation (ISF). As compared with spruce, the probability of occurrence of the beech regeneration resulted higher at lower diffusion radiation values in all the plots. The threshold of competitive advantage between the two species was about 17% ISF.

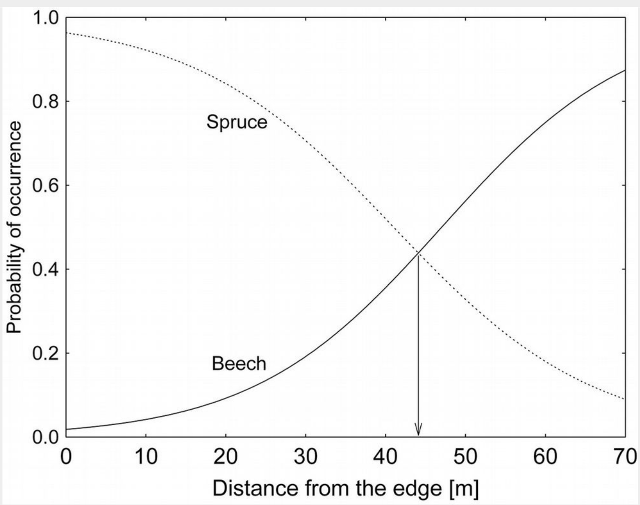

Fig. 6 - Probability of occurrence of beech and spruce regeneration (present = 1, no regeneration = 0) as a function of distance from the forest edge. The logistic regression model applied on the pooled dataset revealed that the probability of occurrence of spruce regeneration is higher than that of beech up to 45 m from the edge.

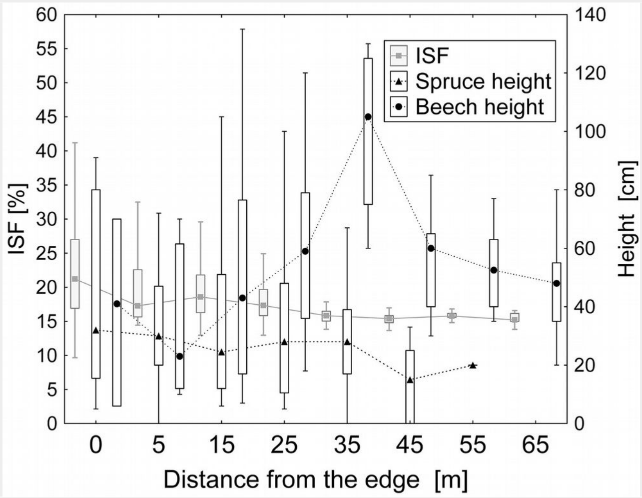

Fig. 7 - Diffusion radiation (ISF %) and height growth of beech and spruce regeneration at different distances from the forest edge. In terms of growth, beech outperformed spruce over the whole range of distances. Spruce showed a competitive advantage only at the very edges of the forest (ISF > 20%).

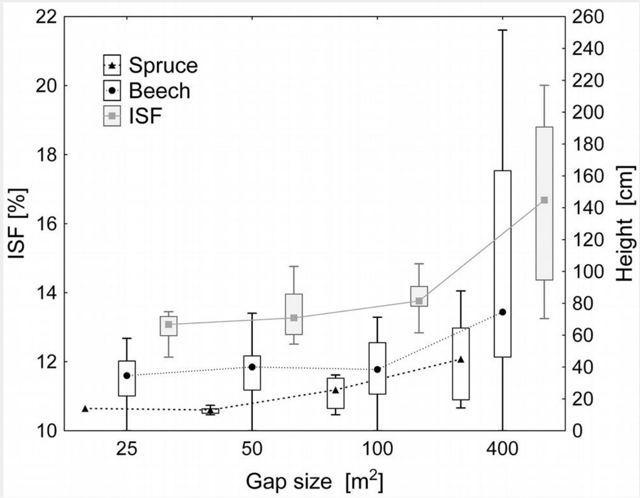

Fig. 8 - Diffusion radiation (ISF %) and height growth of beech and spruce regeneration according to the size of gaps. In terms of height growth, beech outperformed spruce over the whole range of the gap sizes. Spruce showed a significant height growth only in the largest gaps of 400 m^2.

such value. As a consequence, spruce regeneration overtakes beech regeneration up to 45 m from the forest edge, as displayed in Fig. 6.

In terms of height growth, spruce competed with beech only at the very edges of the forest with ISF above 20%, otherwise beech dominated (Fig. 7). As for the forest interior, spruce was outperformed by beech in the whole range of the gap sizes (Fig. 8). Spruce regeneration started to grow only in the largest gaps of approximately 400 m^2.

Discussion

Natural regeneration is a complex process affected by many biotic and abiotic factors. It was observed that in spruce monocultures with occasional presence of single adult beech trees, abundant regeneration of beech is expected to occur up to a distance of approx. 25 m from seed trees (Fig. 3). Similar distances from seed trees were also reported by other studies (Karlsson 2001, Kutter & Gratzer 2006, Ganz 2004, Wagner et al. 2010, Unkrig 1997). Beech regeneration, however, may occasionally occur at much greater distances (up to 100 m and possibly farther) from the seed tree (Fig. 3, Fig. 4). Indeed, Irmscher (2009) reported beech regeneration as far as 254 m from seed trees. All these observations clearly demonstrate the key role of animals in the dispersion of beech seeds, as already described by other studies (Turček 1961, Kunstler et al. 2004, Ganz 2004, Kutter & Gratzer 2006). From the silvicultural point of view, Dobrovolný & Tesar (2010b) consider the threshold of 20 m as the maximum distance between seed trees in order to achieve an adequate density of beech saplings (*i.e.*, a minimum of 10 000 saplings ha^{-1}), which is also the standard prescribed by the Czech thinning guideline (Slodičák & Novák 2007). Thus, approximately 2-3 seed trees ha^{-1} in a spruce stand may provide for up to 30% share of beech regeneration in the subsequent stand generation. Nevertheless, the minimum management objective can be achieved even with a lower density of beech saplings, from which new seed trees will originate.

Furthermore, our research confirmed a different regeneration strategy of beech and spruce. Beech saplings with their broad light adaptability occurred in various light conditions and their density was influenced mainly by their distance from seed trees. The low correlation between light conditions and the density of beech saplings in the initial regeneration phase are pointed out in numerous works (Madsen & Larsen 1997, Unkrig 1997, Szwagrzyk et al. 2001, Kühne & Bartsch 2003, Paluch 2007, Drössler & Lüpke 2007, Petritan et al. 2007, Petritan et al. 2009, Barna 2008); however, the correlation was stronger with increasing age (Szwagrzyk et al. 2001). Unlike beech, spruce requires more than 17% ISF (*i.e.*, a 45m-wide edge zone or gaps of at least 400 m^2 in the forest interior) to colonize the higher density spots and more than 20% of ISF (*i.e.*, at the very edges) to compete with beech in height growth. The competitive threshold of approximately 20% of the diffuse radiation is confirmed by many other authors (Leder & Wagner 1996, Kühne & Bartsch 2003). Lüpke & Spellmann (1997) observed a competitive advantage of beech over spruce with ISF 12.7 % (10-20%) and the exact opposite with 30.1 % (20-40%). Spruce found suitable conditions only inside the gaps (15-25 m in diameter) or in more opened parts, where the basal area decreased to approx. 60%. In an adult mixed stand Kühne & Bartsch (2003) observed only beech regeneration with a PAR site factor of 12.5% and only spruce regeneration with a mean PAR site factor of 21.2%. Within the range 0.2-28.9% of ISF, Unkrig (1997) reports pure beech regeneration where ISF < 12 % (mean = 7.1%), pure spruce regeneration between 8.6 and 19% (mean = 15.1%) and a mixture of the two species with ISF between 4 and 20% (mean = 10.9 %).

From a practical point of view, we found that beech has no problems in regenerating after low intensity felling as compared with spruce. This is in agreement with the evidence reported by Kühne & Bartsch (2003) on the natural regeneration of mixed stands in the submontane vegetation zone.

Conclusions

Under the natural and stand conditions explored in this study (Czech Republic – fir-beech vegetation zone – acidic site), beech showed a broad light adaptability and successfully colonized the space under the shelter of spruce canopy, depending upon the locations of adult beech trees. Despite the long distance of beech saplings from single seed trees (more than 100 m), abundant regeneration is expected to occur to a distance of 25 m. Thus, approximately 2-3 seed trees ha^{-1} may provide for an up to 30% share of beech saplings in the subsequent stand generation. As compared with beech, spruce showed a higher sensitivity to light, showing a higher probability of occurrence at the edge of the forest (in the 45 m-wide zone) or in the largest gaps (400 m^2) of the forest interior. In terms of height growth, spruce competes with beech only at the very edges. Knowledge of the spatial pattern and the light strategy of both species allows to control the natural regeneration and help in the conversion of spruce monocultures. Indeed, the conversion to a mixed spruce-beech forest requires a combination of various silvicultural practices focused to the light ecology of shade-tolerant beech and semi-shade-tolerant spruce. Beech can regenerate quite easily under a forest canopy (*e.g.*, using a shelterwood system or group selection), whereas for triggering spruce regeneration and its successful growth, a higher light intensity has to be ensured, *e.g.*, by regeneration in the forest edges no deeper than 45 m into the forest or by group felling in areas exceeding 0.04 ha.

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References

Barna M (2008). The effects of cutting regimes on natural regeneration in submountain beech forests: species diversity and abundance. Journal of Forest Science 54: 533-544. [online] URL: http://www.agriculturejournals.cz/publicFiles/02855.pdf

Borrmann K (1993). Zur Fuktifikation sehr alter Rotbuchen im Naturwaldreservat Heilige Hallen [Fructification of old European beech trees in the forest reserve Heilige Hallen]. Forst und Holz 48: 700-701. [in German]

Bossema I (1979). Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70: 1-117. - doi: 10.1163/156853979X00016

Collet C, Lanter O, Pardos M (2001). Effect of canopy opening on the height and diameter growth in naturally regenerated beech seedlings. Annals of Forest Science 58: 127-134. - doi: 10.1051/forest:2001112

Diaci J (2002). Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian Alps. Forest Ecology and Management 161: 27-38. - doi: 10.1016/S0378-1127(01)00492-3

Diaci J, Kozjek L (2005). Beech sapling architecture following small and medium gap disturbances in silver fir-beech old-growth forests in Slovenia. Schweizerische Zeitschrift für Forstwesen 156: 481-486. - doi: 10.3188/szf.2005.0481

Dobrovolný L, Tesar V (2010a). Growth and characteristics of old beech (*Fagus sylvatica* L.) trees individually dispersed in spruce monocultures. Journal of Forest Science 56: 406-416. [online] URL: http://www.agriculturejournals.cz/publicFiles/27551.pdf

Dobrovolný L, Tesar V (2010b). Extent and distribution of beech (*Fagus sylvatica* L.) regeneration by adult trees individually dispersed over a spruce monoculture. Journal of Forest Science 56: 589-599. [online] URL: http://www.agriculturejournals.cz/publicFiles/44722.pdf

Drössler L, Lüpke BV (2007). Stand structure, regeneration and site conditions in two virgin beech forest reserves in Slovakia. Allgemeine Forst- und Jagdzeitung 178: 121-135.

Fritz P (2006). Ökologischer Waldumbau in Deutschland: Fragen, Antworten, Perspektiven [Ecological conversion of forest in Germany: questions, answers, perspectives]. Oekom, München, Germany, pp. 351. [in German]

Ganz M (2004). Entwicklung von Baumartenzusammensetzung und Struktur der Wälder vom Schwarzwald bis auf die Schwäbische Alb - mit besonderer Berücksichtigung der Buche [Dynamic of tree specie composition and structure forests from Schwarzwald to Schwäbische Alb in regard to European beech]. Ph.D. Dissertation, University in Freiburg, Freiburg, Germany, pp. 183. [in German]

Gomez JM (2003). Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573-584. - doi: 10.1034/j.1600-0587.2003.03586.x

Gralla T, Müller-Using B, Unden T, Wagner S (1997). Über die Lichtbedürfnisse von Buchenvoranbauten in Fichtenbaumhölzern des Westharzes [Light demands of under-planted beech in spruce stands in Westharzes]. Forstarchiv 68: 51-58. [in German]

Gruber VF (2003). Steuerung und Vorhersage der Fruchtbildung bei der Rotbuche (*Fagus sylvatica* L.) durch die Witterung [Influencing and prediction of European beech fructification during the winter]. J. D. Sauerländer's Verlag, Frankfurt am Main, Germany, pp. 141. [in German]

Hewitt N, Kellman M (2002a). Tree seed dispersal among forest fragments: I. Conifer plantations as seed traps. Journal of Biogeography 29: 337-349. - doi: 10.1046/j.1365-2699.2002.00678.x

Hewitt N, Kellman M (2002b). Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls. Journal of Biogeography 29: 351-363. - doi: 10.1046/j.1365-2699.2002.00679.x

Irmscher T (2009). Zoochores Ausbreitungspotenzial der Rotbuche (*Fagus sylvatica* L.) mit Blick auf die Minimierung der Eingriffsintensität beim Waldumbau in Wäldern mit Naturschutzstatus [Zoochory distribution of European beech in regard to conversion of forests in protected area]. Forstarchiv 80 (1): 29-32. [in German]

Jensen TS (1985). Seed-seed predator interactions of European beech, *Fagus silvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. Oikos 44: 149-156. - doi: 10.2307/3544056

Johnson VC, Adkisson CS (1985). Dispersal of beech seeds by blue jays in fragmented landscapes. American Midland Naturalist 113: 319-324. - doi: 10.2307/2425577

Karlsson M (2001). Natural regeneration of broadleaved tree species in southern Sweden. Acta Universitatis agriculturae Sueciae 196, Alnarp, Sweden, pp. 44. [online] URL: http://pub.epsilon.slu.se/42/

Keren S, Motta R, Govedar Z, Lucic R, Medarevic M, Diaci J (2014). Comparative structural dynamics of the janj mixed old-growth mountain forest in Bosnia and Herzegovina: are conifers in a long-term decline? Forests 5: 1243-1266. - doi: 10.3390/f5061243

Kollmann J, Schill HP (1996). Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio 125: 193-205. - doi: 10.1007/BF00044651

Kühne C, Bartsch N (2003). Zur Naturverjüngung von Fichten-Buchen-Mischbetänden im Solling [Natural regeneration of spruce-beech mixed forests in Solling]. Forst und Holz 58: 3-7. [in German]

Kunstler G, Curt T, Jacques L (2004). Spatial pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus pubescens* Mill.) seedlings in natural pine (*Pinus sylvestris* L.) woodlands. European Journal of Forest Research 123: 331-337. - doi: 10.1007/s10342-004-0048-0

Küßner R (1997). Sukzessionale Prozesse in Fichtenbeständen (*Picea abies*) des Osterzgebirges - Möglichkeiten ihrer waldbaulichen Beeinflussung und ihre Bedeutung für einen ökologisch begründeten Waldumbau [Successional processes in spruce stands in the Ore Mts. in regard to ecological conversion]. Forstwesen 116: 359-369. [in German]

Kutter M, Gratzer G (2006). Current methods for estimation of seed dispersal trees - an example of seed dispersal of *Picea abies*, *Abies alba* and *Fagus sylvatica*. Austrian Journal of Forest Science 123: 103-120.

Leder B, Wagner S (1996). Bucheckern/Streu-Voraussaat als Alternative beim Umbau von Nadelholzreinbeständen in Mischbestande [Seedling of beech nuts as an alternative by conversion of coniferous monoculture]. Forstarchiv 67: 7-13. [in German]

Leitgeb E, Gärtner U (2005). Ökologische und waldbauliche Grundlagen für Buchenvoranbau unter Fichtenschirm [Silvicultural guidelines of planting of beech under spruce canopy - Results from the SUSTMAN Project EU Framework 5, QLK5-CT-2002-00851]. Bearbeitung, Bundesforschungs- und Ausbildungszentrum für Wald, Naturgefahren und Landschaft (BFW), Wien, Austria, pp. 10. [in German]

Lüpke B, Spellmann H (1997). Aspekte der Stabilität und des Wachstums von Mischbeständen aus Fichte und Buche als Grundlage für waldbauliche Entscheidungen [Aspects of stability and growth of beech – spruce mixed stands as the basis for silvicultural decisions]. Forstarchiv 68: 167-179. [in German]

Madsen P, Larsen J (1997). Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. Forest Ecology and Management 97: 95-105. - doi: 10.1016/S0378-1127(97)00091-1

Mosandl R, Kleinert A (1998). Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris* L.) stands. Forest Ecology and Management 106: 35-44. - doi: 10.1016/S0378-1127(97)00237-5

Övergaard R, Gemmel P, Karlsson M (2007). Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. Forestry 80: 555-565. - doi: 10.1093/forestry/cpm020

Pacala SW, Canham CD, Silander JA, Kobe RK (1994). Sapling growth as a function of resources in a north temperate forest. Canadian Journal of Forest Research 24: 2172-2183. - doi: 10.1139/x94-280

Paluch JG (2007). The spatial pattern of natural European beech (*Fagus sylvatica* L.) - silver fir (*Abies alba* Mill.) forest: a patch-mosaic perspective. Forest Ecology and Mangement 253: 161-170. - doi: 10.1016/j.foreco.2007.07.013

Petritan AM, Lüpke B, Petritan IC (2007). Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. Forestry 80: 397-412. - doi: 10.1093/forestry/cpm030

Petritan AM, Lüpke B, Petritan IC (2009). Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. European Journal of Forest Research 128: 61-74. - doi: 10.1007/s10342-008-0239-1

Pettermann L (2000). Zustand und waldbauliche Bewertung von Altbuchensolitären im Nordostteil des Tharandter Reviers [Silvicultural evaluation of old beech trees in north-eastern part of Tharandt forest]. Mgr Thesis, TU Dresden, Tharandt, Germany, pp. 112. [in German]

Röhrig E, Bartsch N (2006). Waldbau auf ökologischer Grundlage [Silviculture on ecological basis]. Eugen Ulmer, Stuttgart, Germany, pp. 479. [in German]

Sagnard F, Pichot C, Dreyfus P (2007). Modelling seed dispersal to predict seedlings recruitment: recolonization dynamics in a plantation forest. Ecological modelling 203: 464-474. - doi: 10.1016/j.ecolmodel.2006.12.008

Schmidt W (2006). Zeitliche Veränderung der Fruktifikation bei der Rotbuche (*Fagus sylvatica* L.) in einem Kalkbuchenwald [Temporal dynamics of seed production of beech in a limestone beech forest]. Allgemeine Forst- und Jagdzeitung 177: 9-19. [in German]

Slodičák M, Novák J (2007). Thinning of forest stands of the main forest tree species. VÚLHM, Strnady, Czech Republic, pp. 46.

Spiecker H, Hansen J, Klimo E (2004). Norway spruce conversion options and consequens. Brill-Leiden, Boston, MA, USA, pp. 269.

Stancioiu PT, O'Hara KL (2006). Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. European Journal of Forest Research 125: 151-162. - doi: 10.1007/s10342-005-0069-3

Sterba H, Eckmüllner O (2008). Invasion of beech (*Fagus silvatica* L.) in conifer forests - five case studies in Austria. Austrian Journal of Forest Science 125: 89-102.

Stimm B, Knoke T (2004). Hähersaaten: Ein Literaturüberblick zu waldbaulichen und ökonomischen Aspekten [Jay seeding: review of silvicultural and economical aspects]. Forst und Holz 59: 531-534. [in German]

Szwagrzyk J, Szewczyk J, Bodziarczyk J (2001). Dynamics of seedling banks in beech forest: result of a 10-year study on germination, growth and survival. Forest Ecology and Management 141: 237-250. - doi: 10.1016/S0378-1127(00)00332-7

Turček J (1961). Ökologische Beziehungen der Vögel und Gehölze [Ecological relationships between birds and trees]. Slowakischen Akademie der Wissenschaften, Bratislava, Slovakia, pp. 329. [in German]

Unkrig V (1997). Zur Verjüngung von Buche und Fichte im Naturwald Sonnenkopf [Regeneration of beech under spruce stands in the forest reserve Sonnenkopf]. Forst und Holz 52: 538-543. [in German]

Wagner S, Collet C, Madsen P, Nakashizuka T, Nyland R, Sagheb-Talebi K (2010). Beech regeneration research: From ecological to silvicultural aspects. Forest Ecology and Management 259: 2171-2182. - doi: 10.1016/j.foreco.2010.02.029