

ECOLOGY OF BEECH REGENERATION IN THE ALLOCHTHONOUS SPRUCE STANDS – A CASE STUDY

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Abstract

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We study the successional process of beech in a allochthonous spruce monocultures. In the natural regeneration of the predominately spruce stand (area: 14.28 ha, age: 110 years) with single mother beech trees admixture the spruce regeneration occupies the most part of the study area. However, about one quarter of area is occupied relatively regular by beech regeneration. The spruce density was at all times higher than that of beech while the spruce height grow was by contrast at all times lower than that of beech. Mean distance of beech seedlings dispersion is 12.7; at a distance greater than 40m, the density already neared zero. Density of spruce increases with increasing light intensity, the density of beech decreases – the competition point was found about 19% of diffuse radiation or about 14% of canopy openness. The both species respond to increase of light intensity with increase of height grow (by beech only weekly) – the spruce starts to dominate the beech at about 32% of diffuse radiation or about 22% of canopy openness. The silvicultural goal in the next stand generation – converting of spruce forest into mixed forest, i.e. achievement of the legal proportion of beech as a soil-improving and reinforcing tree species (proportion about 30% and more) in the spruce stand can be reliably realized by natural way only using a combination of more intensive shelterwood or border felling with group selection system.

natural regeneration, spruce, beech, species conversion

Concept of close-to-nature silviculture searches for possibilities how to implement the natural processes into forestry management. At our department we study in the long-term the successional process of beech, fir and oak in a allochthonous spruce or pine monocultures. Here we get next case study from the ecology of beech regeneration in the predominantly spruce stand. Two key factors of the research of beech regeneration process in the dominant spruce stand are important for our aim of our previous research (Dobrovolný and Tesař, 2010a,b) and in this study – i) spreading of beech – the mean and silviculturally useable distance of beech seedlings from the mother beech trees and ii) competition of beech and spruce regeneration for light.

More abundant mast years of beech (periodicity 2–3 years) in the last 20–30 years were mentioned by many authors (e.g. Övergaard *et al.*, 2007). Predominant way of beech spreading strategy is barochory, i.e. seed fall directly under the crown of mother trees or surroundings. Beech nuts can be also transported by animals (zoochory) to a distance of several tens of metres by rodents (Jensen, 1985) and by jays even to large distances (Johnson and Adkinsson, 1985; Kunstler *et al.*, 2004; Wagner *et al.*, 2010). However, the most often mentioned highest amount of beech nuts is reported at a distance of up to 20m from the mother tree (Unkrig, 1997; Kutter and Gratzer, 2006; Wagner *et al.*, 2010; Dobrovolný and Tesař, 2010a,b). Beech can survive up to several years at extremely low radiation values 3–5%; however, its growth would be very slow and

the growth response to release very instant (e.g. Collet *et al.*, 2001; Wagner *et al.*, 2010). Assessing the competitive relations of beech and spruce regeneration in relation to light and/or other stand characteristics, a majority of works arrive at a similar value of relative radiation (ca. 15%) or basal area (ca. 30–35 m²) as a certain threshold of the two species. Below this limit, beech would maintain its advantage and above this limit, the height growth of spruce would begin to catch up with the beech. Above 20%, beech would lose the advantage and would be surmounted by spruce as to height growth (e.g. Unkrig, 1997; Kühne and Bartsch, 2003; Stancioiu and O'Hara, 2006).

METHODOLOGY

The mother beech trees in our case mostly originate from the previous stand generation where they grew suppressed under first generation of spruce and after spruce felling they were kept into present (second) spruce generation. In present time these trees are source of beech nuts. The research object "Markvarec" is situated in the Bohemian-Moravian Upland near the town Pelhřimov on the czech typological unit 531 – spruce management on the acidic sites of higher elevations. Altitude is about 640 m a.s.l., in flat lands where the mean annual precipitation amount is about 700 mm and the mean annual temperature is ca. 6 °C. Two experimental predominantly spruce stands (Tab. I) are in the direct neighborhood and in the both cases shelterwood silvicultural system and border felling as regeneration methods are used.

The data were collected according to different purpose in this way:

- A. Situation of mother beech trees and regeneration of spruce and beech: area-wide mapping of beech trees position (by aerial photos) and locating and classifying of regeneration in polygons, where we evaluate the type of mixture, density and mean height of seedlings on tree small research plots at each polygon.
- B. The distance of beech regeneration from the mother trees was investigated on two parallel transects between 2 mother trees (distance about 70 m) at the small plots 1 × 1 m, where the density of seedlings was counted. Relationship between distance of mother trees and density of seedlings was calculated using the Waldstat software (TU Dresden). The result is log-normal model of beech dispersion (Wagner, 1999). The significance or strength of this relationship was

tested by correlation of measured and model values.

- C. The shade-tolerance and competition of beech and spruce regeneration was investigated on 3 research plots – RP 30 × 30 m in different light conditions – 2 plots were established at north (RP1) and south (RP2) part of stand edge and 1 plot inside the stand (RP3). These plots were divided into small sections 5 × 5 m. On each section in the centre of the small plot 1 × 1 m² were measured species, number of seedlings, total height and height increment of each seedling and were taken the hemispherical photographs using Nikon Coolpix 4500 and fisheye convertor FC-E8, assessed by WinsCanopy 2008a software for diffuse (DSF %) and direct (ISF %) site factor estimation. The Kruskal-Wallis test and linear regression procedure were used to estimation of the dissimilarity and relations of the regeneration.

RESULTS

A. Stand situation

A total number of 95 mother beech trees (7 trees.ha⁻¹) were mapped on 14.28 ha of mainly spruce stand (Fig. 1). Their mean diameter was 54 cm (min. 31 – max. 77 cm). Furthermore, 154 polygons of regeneration were mapped. The regeneration occurred on 97% of the total area, where a species dominant was spruce (64%), most often without or with a small admixture of beech (Tab. II). Beech was dominant on 35% of the area with varying spruce admixtures. The regeneration of other tree species was pure (Douglas fir 2%, European larch 0.4%, pine 0.1% and fir 0.1%). The regenerating beech was relatively evenly distributed across the plot (Fig. 1) with the highest density in the vicinity of clumped mother trees. In these stand conditions the average density of the beech regeneration was significantly lower than that of spruce while the mean height of beech was significantly greater (Tab. III).

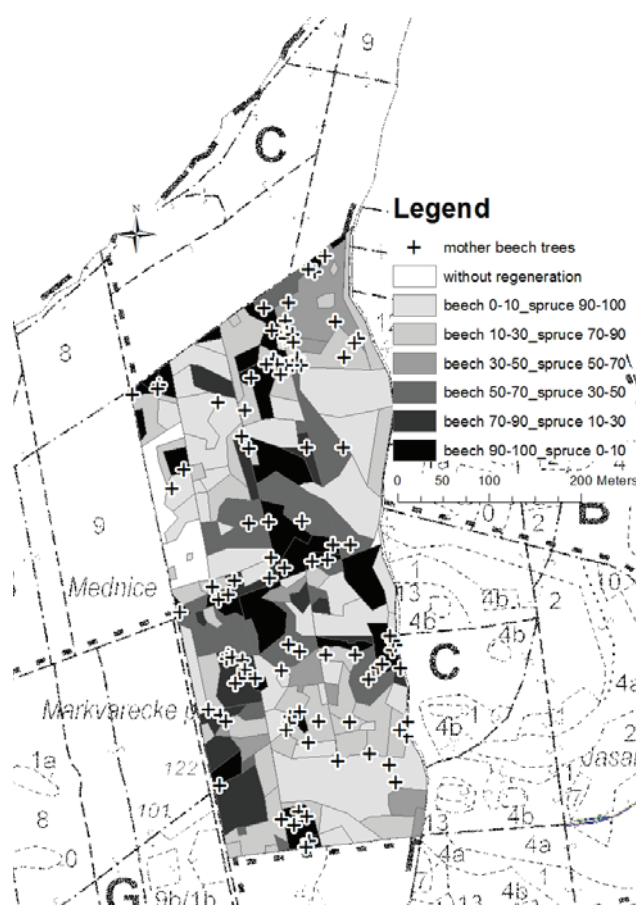
B. Beech seedlings dispersion from the mother tree

Results from the Waldstat software (Tab. IV) are number of seedlings of one mother of beech trees (M), the mean distance of seedlings dispersion (D), parameters of log-normal function (μ , σ).

The high value of correlation coefficient (R) (Tab. IV) indicates a significant relation between the density of the beech regeneration and the distance from the mother tree (Fig. 2), where the maximum

I: Research object data

Stand	Area ha	Age years	Stock density	Volume m ³ .ha ⁻¹	Admixture	Location
829D11	14.28	106	0.9	641	90% spruce, 6% beech, 3% scots pine, 1% larch	49°23'14.392"N
829E 12		112	0.9	672	93% spruce, 4% beech, 1% scots pine, 1% larch, 1% Douglas-fir	15°4'43.539"E



1: Spatial distribution of mother trees and polygons with type of regeneration mixture

II: Proportion of types of mixture in the polygons of regeneration

Types of mixture (%)	Number of polygons	Area (ha)	Area (%)
beech 0–10, spruce 90–100	63	8.31	58
beech 10–30, spruce 70–90	16	0.61	4
beech 30–50, spruce 50–70	9	0.23	2
beech 50–70, spruce 30–50	22	1.49	10
beech 70–90, spruce 10–30	16	1.63	11
beech 90–100, spruce 0–10	28	2.01	14
suma	154	14.28	100

III: General statistics of regeneration in the polygons

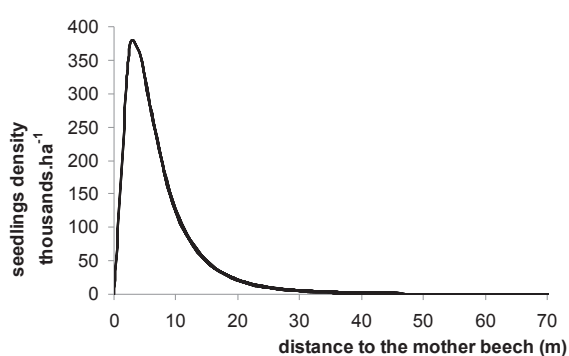
		average	median	std. dev.	min.	max.
spruce	density (thousand.ha ⁻¹)	70.26*	40.00	81.73	0.00	430.00
	height (cm)	66.93*	30.00	94.36	10.00	500.00
beech	density (thousand.ha ⁻¹)	36.95*	20.00	56.80	0.00	460.00
	height (cm)	90.46*	80.00	59.34	10.00	300.00

(* significant diferencies)

IV: The parameters of seedlings dispersion

M	D (m)	μ	σ	R
15424	12.72	2.32	0.67	0.85

density was reached at ca. 5 m from the mother tree, i.e. on the crown perimeter; at a distance greater than 40 m, the density of the beech seedlings already neared zero.



2: Model curve of beech seedling dispersion

V: Differences of canopy and radiation parameters on the research plots (RP)

							significance between RP1-3	
	RP	average	std.dev.	median	min.	max.	RP1	RP2
openness %	1	17.84	3.84	16.20	13.80	27.32	*	no
	2	18.25	2.74	18.12	13.81	23.07	no	*
	3	11.55	0.47	11.64	10.77	12.42	*	*
direct site factor %	1	9.37	2.54	9.05	4.13	14.81	*	*
	2	35.33	15.12	31.34	16.81	65.97	*	*
	3	18.70	2.33	18.73	14.11	23.45	*	*
indirect site factor %	1	24.15	6.68	21.00	17.35	41.18	*	no
	2	25.85	3.99	24.97	20.02	33.83	no	*
	3	19.68	0.59	19.71	18.51	20.83	*	*

(* significant differences)

VI: Differences of parameters of regeneration on the research plots (RP)

							significance between RP1-3	
	RP	average	std.dev.	median	min.	max.	RP 1	RP 2
density of spruce (thousand.ha ⁻¹)	1	141.94	120.00	119.03	0	520.00	*	*
	2	65.55	56.69	50.00	0	240.00	*	*
	3	126.11	120.88	90.00	0	430.00	no	*
density of beech (thousand.ha ⁻¹)	1	42.22	64.72	20.00	0	270.00	*	*
	2	9.16	12.27	5.00	0	40.00	*	*
	3	50.55	119.95	0	0	480.00	*	*
height of spruce (cm)	1	18.03	10.42	14.50	5.00	50.00	*	no
	2	22.95	22.89	14.50	6.00	105.00	no	*
	3	9.01	4.75	8.00	2.50	25.00	*	*
height of beech (cm)	1	50.15	28.49	57.00	6.00	92.50	*	*
	2	39.25	17.40	38.75	12.00	70.00	*	*
	3	31.44	13.36	36.25	11.50	54.00	*	*
height increment of spruce (cm)	1	4.23	2.14	4.00	1.00	9.00	*	no
	2	3.84	2.69	3.00	1.00	11.00	no	*
	3	1.87	0.90	2.00	1.00	4.00	*	*
height increment of beech (cm)	1	9.46	4.67	10.75	2.00	19.00	*	no
	2	7.47	3.98	8.00	2.00	14.00	no	*
	3	5.38	2.99	4.50	1.50	11.00	*	no

(* significant differences)

C. Competition for light between spruce and beech

The mean values of canopy openness (11–18%) and direct (9–35%) and diffuse (19–26%) radiation are on the each research plots (RP1-3) significantly different (Tab. V).

Parameters of the regeneration of the both species were significantly differed in the individual variants (plots) (Tab. VI). The density of the spruce regeneration separately was significantly highest at the northern stand edge (RP1) and lowest at the southern edge (RP 2). The density significantly correlates with the values of diffuse radiation and direct radiation, namely inside the stand (RP3) (Tab. VII, Fig. 3). No significant relationship was found on the northern stand edge (RP1); interesting are values of negative correlation on the southern stand edge (RP2) (Tab. VII). The height and height increment were at all times the lowest inside the stand (RP3). On all the plots, the height of spruce show the best and very strong correlation (positive) with the diffuse radiation (Tab. VII, Fig. 4).

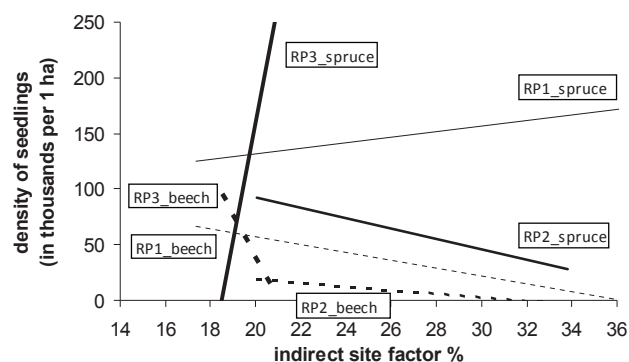
The density of the beech regeneration separately was the highest inside the stand; the height was the greatest at the northern stand edge and the lowest inside the stand while the increment was the highest at both stand edges and the lowest inside the stand. On all the plots, the density of beech regeneration significantly and negatively correlates with the value of diffuse radiation and on the southern stand edge (RP2) also with the value of direct radiation and canopy openness (Tab. VII, Fig. 3). The beech responds to changed light conditions by height growth only weakly or not at all (Tab. VII, Fig. 4).

Comparing spruce and beech on the same variants (plots), the spruce density was at all times higher than that of beech while the spruce height was by contrast at all times lower than that of beech (confirmation of the results from polygons). Comparing different variants (plots) we found out that the increment of spruce at both stand edges (RP1 and 2) equalled the increment of beech inside the stand (plot 3). An intersection or a competitive point about 19% diffuse radiation of density of both species can be found inside the stand (RP3) (Fig. 3),

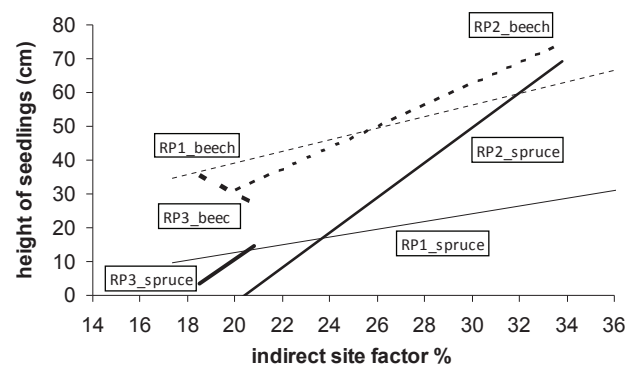
VII: Correlation and regression parameters of relationships between factors and regeneration on the research plots (RP)

	RP	openness		direct site factor %					indirect site factor %				
		R	R	b0	b1	R ² %	p		R	b0	b1	R ² %	p
density of spruce	1	0.11	0.16						0.06				
	2	-0.38*	-0.37*	116.33	-1.44	12	.02		-0.29				
	3	0.25	0.45*	-251.43	20.19	13	.02		0.58*	-2005.48	108.33	26	.00
density of beech	1	-0.42*	-0.04						-0.50*	127.01	-3.51	11	.03
	2	-0.52*	-0.54*	22.31	-0.37	19	.00		-0.60*	50.86	-1.61	25	.00
	3	0.11	0.06						-0.40*	817.78	-38.99	1	.26
height of spruce	1	0.69*	-0.25						0.55*	-8.98	1.14	54	.00
	2	0.68*	0.76*	-18.89	1.22	63	.00		0.79*	-90.76	4.44	57	.00
	3	0.22	0.13						0.52*	-65.62	3.79	21	.00
height of beech	1	0.30	-0.54*	105.24	-5.88	24	.01		0.12				
	2	-0.05	-0.11						0.10				
	3	0.42	0.22						0.43				

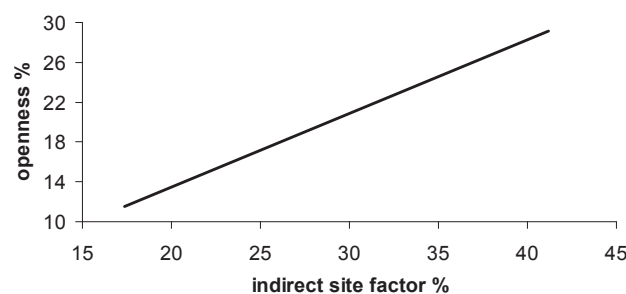
(* significant correlations)



3: Relationships between indirect site factor and density of spruce and beech regeneration



4: Relationships between indirect site factor and height of spruce and beech regeneration



5: Relationship between indirect site factor and canopy openness

at which the density of spruce regeneration becomes higher than the density of beech. The stand edge are at all times dominated by spruce. The height growth of beech generally dominates the spruce with the exception of RP2 (southern stand edge) where the spruce starts to dominate the beech at about 32% of diffuse radiation (linear trend of beech being however insignificant) (Fig. 4).

DISCUSSION AND CONCLUSIONS

From our work these essential results are conducted:

1. In the natural regeneration of the predominately spruce stand (area: 14.28 ha, age: 110 years) with the single beech trees admixture (about 5% = 7 individuals.ha⁻¹) on the acidic sites the spruce regeneration occupies the most part of the study area. However, about one quarter of area is occupied relatively regular by beech regeneration. The spruce density was at all times higher than that of beech while the spruce height grow was by contrast at all times lower than that of beech. However, the increment of spruce at both stand edges equalled the increment of beech inside the stand.
2. Maximal model density of beech seedlings (about 380 000 seedlings.ha⁻¹) was reached about 5 m from the mother tree (perimeter of crown). Mean distance of seedlings dispersion is 12.7 m. The legal number of beech seedling per 1 ha in the czech low (8000 plants per 1 ha) is reached at the distance 1–26 m from the mother tree. These results confirm other studies (see Unkrig, 1997; Kutter and Gratzner, 2006; Wagner *et al.*, 2010; Dobrovolný and Tesař, 2010b).
3. Light conditions influence significantly density and height grow by both species. Density of spruce increases with increasing light intensity, the density of beech decreases. Competition point of density of both species inside the stand is about 19% of diffuse radiation (about 14% of canopy openness – Fig. 5). The both species respond to increase of light conditions with increase of height grow. However, the beech responds to changed light conditions by height growth only weakly or not at all. The beech generally dominates the spruce with the exception of Plot 2 (southern stand edge) where the spruce starts to dominate the beech at about 32% of diffuse radiation (about 22% canopy openness – Fig. 5).
4. The silvicultural goal in the next stand generation – converting spruce forest into mixed forest, i.e. achievement of the legal proportion of beech as a soil-improving and reinforcing tree species (proportion about 30% and more) in the spruce stand can be reliably realized by natural way only on the given site and under the given stand conditions by natural way only. This would entail a combination of more intensive shelterwood or group (border) felling for the achievement of regeneration of spruce with a group shelterwood and selection (mild canopy reduction about 15–20%) around the mother beech trees (radius ca. 20–30 m from the tree) for the initiation of

beech regeneration. However, the research results indicate that the reproduction potential of mother beech trees is much higher. The model distance of silvicultural usable density of beech regeneration (about 8000 plants per hectare) up to about 25 m from one mother tree could mean up to 100% of area coverage by beech regeneration at the given density of ca. 7 mother trees per hectare in theoretically regular distribution and under low light conditions, for example if a application of selection silvicultural system only. These conclusions confirm the results of the previous studies from allochthonous spruce stands conducted mainly in Germany (Ganz,

2004; Irmscher, 2009) or in the Czech Republic (Dobrovolný and Tesař, 2010 b; Dobrovolný *et al.*, 2012). The rate and distance at which the beech occupies the area within a pure stand of another tree species is admirable. The invasion and expansion of beech as a phenomenon of central Europe are mentioned from Sterba and Eckmüller, 2008.

5. At that, the beech makes use of its ecological advantages: 1) rich and frequent mast years in the last two decades, 2) long-distance seed dispersion, 3) tolerance to shade, 4) decline of mature spruce.

SUMMARY

In the natural regeneration of the predominately spruce stand (area: 14.28 ha, age: 110 years, see Tab. I) with single beech trees admixture (about 5% = 7 individuals.ha⁻¹) on the acidic sites the spruce regeneration predominates (Tab. II). However, about one quarter of area is occupied relatively regular by beech regeneration. The spruce density was at all times higher than that of beech while the spruce height grow was by contrast at all times lower than that of beech (Tabs. III and VI). Maximal model density of beech seedlings was reached about 5 m from the mother tree (perimeter of crown). Mean distance of seedlings dispersion is 12.7; at a distance greater than 40 m, the density of the beech seedlings already neared zero (Fig. 2). Light conditions influence significantly the density and height grow of both species (Tab. VII, Fig. 3 and 4). Density of spruce increases with increasing light intensity, the density of beech decreases. Competition point of density of both species inside the stand is about 19% of diffuse radiation (about 14% of canopy openness – Fig. 5). The both species respond to increase of light conditions with increase of height grow. However, the beech responds by height growth only weakly or not at all (Tab. VII, Fig. 3 and 4). The beech generally dominates the spruce with the exception of southern stand edge where the spruce starts to dominate the beech at about 32% of diffuse radiation (about 22% openness – Fig. 5). The silvicultural goal in the next stand generation – converting spruce forest into mixed forest, i.e. achievement of the legal proportion of beech as a soil-improving and reinforcing tree species (proportion about 30% and more) in the spruce stand can be reliably realized by natural way only using a combination of more intensive shelterwood felling with group selection system. At that, the beech makes use of its ecological advantages: 1) rich and frequent mast years in the last two decades, 2) long-distance seed dispersion, 3) tolerance to shade, 4) decline of mature spruce.

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