Extent and distribution of beech (*Fagus sylvatica* L.) regeneration by adult trees individually dispersed over a spruce monoculture

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ABSTRACT: Recently individually dispersed adult beech trees have regenerated in spruce monocultures and this fact could be used to manage the transformation of stands into a mixed forest. Three such cases in the fir-beech and spruce-beech forest zones were analyzed. Beech regeneration is dispersed to distances of several hundred meters regardless of the configuration of the terrain. Using a model we describe this process by a dispersion curve that can be broken up into three sections: (1) directly under the crown as the result of barochory; (2) from 15 to 30 m from the trunk, where the barochoric and zoochoric dispersal of beech nuts intersects; (3) from the "breakpoint" to farther away as a result of zoochory. Regeneration is utilizable as an optimal or at least acceptable method for creating the next economically valuable stands only in sections 1 and 2. In section 3 individual trees may be the central points for the transformation of the second successive forest generation. With spontaneous development without protection from game the density is in the range of hundreds of individuals; in protected groups density can be in the range of tens of thousands of individuals per hectare.

Keywords: beech; dispersed trees; forest dynamics; regeneration; transformation of spruce monocultures

The successful regeneration of each tree species is dependent on many favourable circumstances and regeneration is not often successful, even when it is managed using the application of all available biological knowledge. Therefore, the high regeneration potential of beech, which has been recorded approximately over the last twenty years, is noteworthy. It is particularly surprising for the fact that beech advance regeneration that started with just a few isolated individuals has spontaneously penetrated deep into homogenous artificial spruce stands.

A similar phenomenon has already been observed and precisely studied in the temperate zone of Europe for oak (pedunculate and sessile oak), wherein they were dispersed to areas far from the regenerating trees. Either they contributed to forest recolonization on abandoned areas and on clearings caused by natural disasters or clear cutting, or they penetrated into forest stands, most frequently pine stands, and started off a spontaneous change in the tree species composition. Interest was above all in how acorns were dispersed. It was discovered that birds play a critical role, mostly jays (*Garrulus glandarius*) (Bossema 1979; Kollmann, Schill 1996; Mosandl, Kleinert 1998; Gomez 2003; Stimm, Knoke 2004). Small ground rodents are other main dispersal agents. Both groups of animals carry acorns to various distances and store them in different ways. A jay may carry acorns up to 4 km from the source (Turček 1961); for example Gomez (2003) noted an average distance of 250 m (max. 1,000 m) from the source. The maximum dispersal distance was about 10–20 m for mice and it was estimated several hundred meters for jays.

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Mice collected hoards of several seeds at about 2 cm depth in the soil, whereas jays stored single seeds (Kollmann, Schill 1996).

There are much fewer papers on the dispersal of beech nuts. Beech nuts are a part of the food chain for 26 bird species and 17 animal species according to Turček (1961). Amongst birds the greatest consumers are jays (*Garrulus glandarius*), spotted nutcrackers (*Nucifraga caryocatactes*), Eurasian nuthatches (*Sitta europea*), tits (*Parus* sp.), pigeons (*Collumba* sp.), and bramblings (*Fringilla montifringilla*). Jays are the greatest dispersers of beech nuts over long distances (Turček 1961; Johnson, Adkisson 1985; Ganz 2004; Kunstler et al. 2004). Turček (1961) discovered one case when a jay transported as many as 15 beech nuts at once. These were hidden in the forest floor in groups of two to eight, 100 to 200 m uphill on the transformational border between beech forest and spruce forest, or in spruce forests. Thus, birds, for example in the mountains, can maintain over the long-term or even push up the elevation of beech forests. According to Johnson and Adkisson (1985), jays can collect and transport 3–14 beech nuts at once (7 beech nuts on average) to a distance of up to 4 km from the source. Rodents (*Clethrionomys glareolus* and *Apodemus flavicollis*) stored beech nuts 1 to 13 m away from the tree (Jensen 1985). Normally this distance does not exceed 30 m (Nilsson 1985; Johnson, Thompson 1989 in Kunstler et al. 2004). During the analysis of the spatial pattern of beech and oak seedlings Kunstler et al. (2004) discovered a clustered arrangement.

We have registered several experiments that attempt to model the beech dispersion process, however not as the dispersion of beech nuts, but through the relation of seedling density to their distance from the regenerating tree. Two sources present results of studies of this process in stands with more than individual beeches being represented and that are limited to the area near the crown (approximately up to 20 m from the tree crown), thus showing mainly the effects of barochory. Kutter and Gratzer (2006) worked in spruce-fir-beech stands of the Rothwald old growth forest. With the aid of an empirical model (Ribbens et al. 1994) in Kutter and Gratzer (2006) they indicate an average dispersal distance of 6.1 m, $r = 0.65$ and with the aid of a mechanistic model (with "winddisper" software) 11.7 m, $r = 0.1$. Karlsson (2001) studied the problem in the south of Sweden on clearings in spruce stands surrounded by hardwood stands and described regeneration dispersal by an exponential function that expressed the great closeness of the relationship ($R^2 = 0.92$).

Two papers on beech dispersal from trees individually located in spruce stand are closer to our problem. Ganz (2004) reports beech regeneration in Schwarzwald and Schwäbische Alb at distances of up to 60 m (average distances of 13 to 19 m dependent on the configuration of the terrain) as a result of zoohoric beech nut dispersal. Regeneration density in relation to the distance from the regenerating tree was modelled by a polynomial of the second degree and at about 3 meters by the related exponential. In the Harz National Park Irmscher (2009) noted regeneration at distances up to 250 m, however closer studies of the area about 20 m around each tree were not dealt with in the study. Using the function according to Ribbense ("Waldstat" software) he derived a mean beech dispersal distance of 35.4 m.

The purpose of this paper is not to analyze beech fructification and the causes of its fluctuating frequency, but to show how to take advantage of the fact that beech has been recently spontaneously, and in places vehemently, regenerating. Therefore, the goal of this paper is to derive a mathematical model of the regeneration spatial pattern based on three different cases of beech regeneration from isolated individuals in spruce monocultures that can be used for decision-making on how to utilize this regeneration in silvicultural practice.

MATERIAL AND METHODS

The studied areas are located at higher elevations of the Hercynian on acidic to fresh sites between the fir-beech and spruce-beech forest vegetation zones, where the average precipitation accumulation ranges from 800 to 1,050 mm and the average annual temperature is between 4.5 and 6°C. In the spruce monocultures (age 60–100 years) there are different numbers of individually present regenerating beeches that are variously spatially arranged in them, which come from the preceding generation of spruce stands. The Kremesnik and Telc areas are in the Bohemian-Moravian Uplands (CZ) and the Ansprung area is in the central Saxon part of the Ore Mts. (D) (Table 1). Altogether four research plots (hereinafter referred to as RP) were measured (Table 1; Figs. 1–3), two in neighbouring stands on the "Kremesnik" site and by one on the other sites.

The intent of the study was to understand how regeneration was dispersed from specific isolated trees. Isolation is understood to mean a situation when the effects of "foreign" regenerating trees are eliminated to a distance of 500 m at least. Unfor-

Table 1. Description of stands and sample plots

Forest inventory					Research plot				
Locality	stand	age	density (%)	habitat type	Loc_N	Loc_E	elevation (m)	area (ha)	slope/ aspect
Kremesnik	42a10 42a6	101 62	80 90	beech-fir forest	49°24'46" 49°24'41"	15°19'37" 15°19'44"	650 670	0.85 1.07	gentle/ N-W
Telc	957F11	109	80	fir-beech forest	49°17'34"	15°42'53"	560	0.7	gentle/ S-E
Ansprung	89a2	67	95	spruce-beech forest	50°37'47"	13°16'7"	750	5.8	middle/N

tunately, we were unable to locate such a situation and certainly it does not even exist. Isolation distance conditions are met on the "Telc" site, on condition that there is another tree outside the RP at a distance of about 40 m, and on the "Ansprung" site, although there are 4 trees in the RP. "Kremesnik" presents a special case as multiple dispersed beech individuals have been regenerated in the stand.

Analysis of beech regeneration

In the RPs positions were measured with the parameters of regenerating trees (Table 2), including beech regeneration. In the "Telc" and "Ansprung" areas we were able to measure the position of each regenerated individual, but in the "Kremesnik" RP, due to its high density, we were able to measure only regeneration polygons, i.e. definable groups with relatively homogeneous densities. In the "Ansprung" RP we did not measure any regenerated individuals under the crowns of trees, our interest being to analyze the zoochoric dispersal primarily. All position measurements were conducted using the FieldMap tool.

In all RPs the parameters (diameter at breast height "dbh", tree height "*h*", crown base height "h_b" and crown projection "*P*") of old beech trees were collected. In two RPs we also determined the biometric parameters of regeneration. At "Kremesnik" these were average density values (individuals·m−2) from three representative areas of each polygon determined with a 1 × 1 m frame, the height of individuals in the main layer (they are not visibly dominant, nor are they suppressed) and finally the thickness of the root collar to the nearest 0.1 mm. In the case of "Telc" it was the height and thickness of the root collar of sample regenerated individuals selected from within the fencing and outside of it.

The basic spatial statistic of the point layer of regenerated individuals in "Telc" and "Ansprung" was calculated with the assistance of the ESRI "Nearest Neighbour Program (VBA Macro)" external script in ArcInfo 9.2. The algorithm according to Clark and Evans (1954) with Donnelly (1978) edge correction was used to calculate the aggregate index (NNIndex). The results are conclusive for the level of statistical significance of 0.01. The main result in all cases is a dispersion model by which the relationship between the density of individual regenerated beeches ("*individuals*", indicated in thousands per hectare), i.e. *a dependent variable*, and their distance to the closest tree ("*distance*"), i.e. *an explanatory variable*, is simulated. Variables

Table 2. Characteristics of beech rejuvenating trees

Locality	Rejuvenating beech	dbh (cm)	*h* (m)	h_b (m)	*P* (m^2)	Location in the stand
Kremesnik (average, σ)	1–22	69.70	31.10	8.50	122.50	inside
		12.40	2.60	2.90	40.90	
Telc	tree1	71.0	33.50	13.90	136.80	inside
	tree2	63.30	32.10	9.10	204.10	clearing
Ansprung	tree1	45.60	23.00	1.90	77.00	road edge
	tree2	37.30	22.00	2.20	191.80	road edge
	tree3	64.80	22.70	6.31	188.20	inside
	tree4	55.80	21.80	3.19	127.20	inside

dbh – diameter at breast height, *h* – tree height, h_b – crown base height, *P* – crown projection were acquired using the script Dobrovolny 1.2 (Dobrovolný 2008). The core of the method involves laying out 2 × 2 m square grids ("Kremesnik", "Telc") and a 10 × 10 m square grid ("Ansprung") over the experimental areas using ArcInfo 9.2. For each central point of the square, information was extracted about regeneration density from the regeneration polygon or outside of it ("Kremesnik"), or the number of regenerated individuals in the square was calculated ("Ansprung" and "Telc"), and furthermore the distance of this point to the nearest tree was calculated. Of course, the influence of other nearby regenerating trees cannot be completely eliminated in practice in this way (for example in the "Telc" RP the tree "tree2", and similarly in the "Ansprung" RP trees "tree1 and 2"). Because the distribution of the values was not normal, a generalized linear model was applied with Poisson distribution and a logarithmic link function that can generally be formulated as follows:

$$[\log(\mu_1) = \alpha + \beta_{dis}\tan e_i]$$

where:
$individuals_i \sim Poi(\mu_i)$.

During a further analysis, the necessity to "enrich" the model with polynomial elements was indicated. The model parameters were calculated and tested, and the percentage assignable variation, the so-called deviance (the equivalent of the coefficient of determination – R^2) was calculated using R 2.8.1 software. With the use of the same software lattice graphs of the relationship between the studied variables were created. For "Kremesnik" the model is derived from the entire area for all trees at once; for "Telc" from "tree1", separately for *fenced* and *unfenced* parts. The minimum distance of trees from the fence border is 10 m and the maximum is 25 m, therefore the model curve will start at about 10 m for the unfenced variant and the fenced variant will end at 25 m. For "Ansprung" the model is derived by relating regeneration to the trees "tree3" and "tree4". When leaving out regenerated individuals under the crown, the curve will start at the crown projection circumference approximately five meters from the tree.

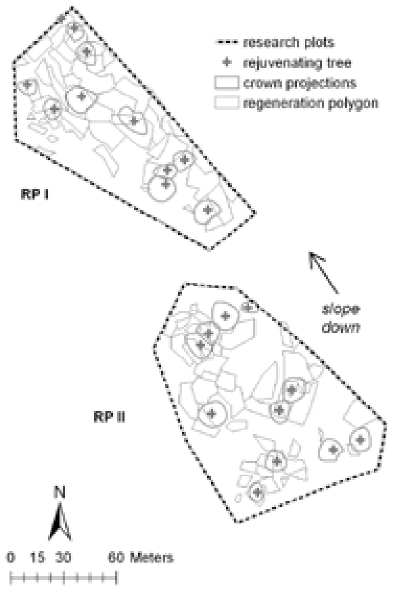

Fig. 1. Map of regenerated polygons and rejuvenating trees (Kremesnik)

RESULTS

On the two research plots of the "Kremesnik" site 85 regeneration polygons (0.001 to 0.03 ha) with a total area of 0.75 ha (Fig. 1) were mapped within the range of 22 individual beeches (their average spacing was about 16 m) on an area of 1.9 ha. Approximately 40% of the stand area is covered by regeneration; its density in the polygons is different. The highest values were in the range of 10,000 to 30,000 per hectare, and the average value was 22,500 individuals per hectare (Fig. 2) at an average distance of 14.4 m (1.7 to 42.4 m, i.e. to the border of the RP) from the tree. The average regeneration height is 29.8 cm (σ =16.3) and the thickness of the root collar is 5.9 mm (σ = 2.5).

On the 0.71ha "Telc" RP 1,710 regenerated individuals were recorded coming from one or two regenerating trees (Fig. 3). Class 6 is the largest class of regenerated individual abundance classes (i.e. when converted 4,000 to 8,000 individuals per hectare) (Fig. 4). The average regeneration density in the fenced area is 19,600 individuals per hectare at an average distance of 10.1 m (0.95 to 21.1 m) from the regenerating tree; in the unfenced area, there are 500 individuals per hectare at an average distance of 43.8 m (11.5 to 114.9 m) from the tree. The average height of regenerated individuals in the fenced area is 46.5 cm (σ = 29.7) and the thickness of the root collar is 9.8 mm (σ = 4.6); outside the fence the figures are 32 cm (σ = 12.9) and 10.2 mm (σ = 2.8).

On the 5.75ha "Ansprung" research plot 463 regenerated individuals were found, which came from four regenerating trees (Fig. 5). Regeneration achieved an average density of 95 individuals per hectare with the most frequent value being 100 individuals (Fig. 6). The average distance of indi-

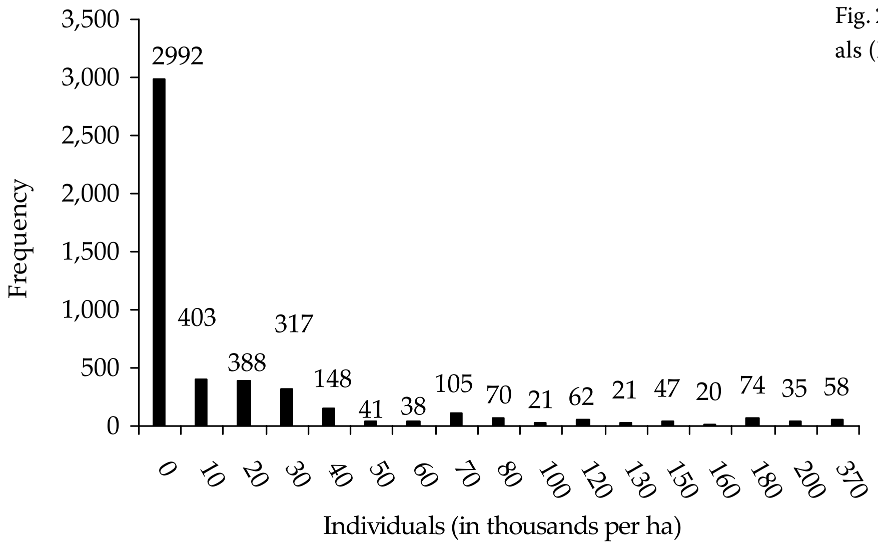

Fig. 2. Abundance of rejuvenated individuals (Kremesnik)

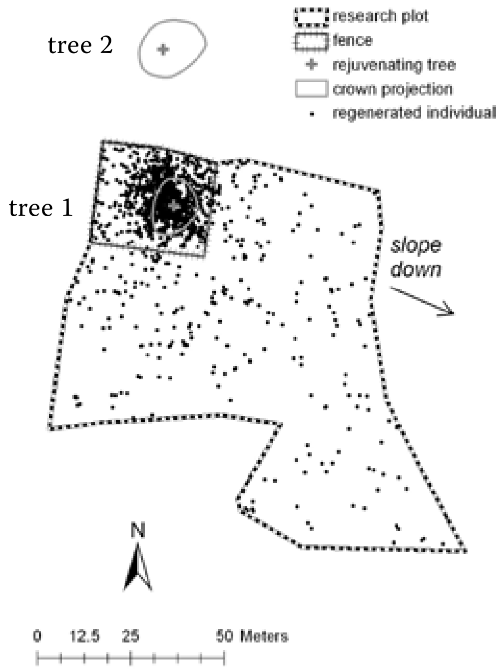

Fig. 3. Map of regenerated individuals and rejuvenating trees (Telc)

viduals from regenerating trees is 101.2 m (5.7 to 254.3 m).

With a simple glance at the sketch maps (Figs. 2 and 3) and the depiction of the relationship between the variables "*distance*" and "*individuals*" (Figs. 7 and 8) we can get the first impression of regeneration dispersal. In the "Telc" and "Ansprung" RPs, it is always concentrated under the crown of the beech or close to it. As the distance from the tree increases, density decreases, at first markedly and then from a certain distance only slightly or not at all. It is interesting to note a localized increase in regeneration density at all distances. For "Ansprung" there are even as many as 600 individuals per hectare at more than 200 m away from the tree uphill. The regenerated individuals pattern over the area is significantly non-random and clustered in

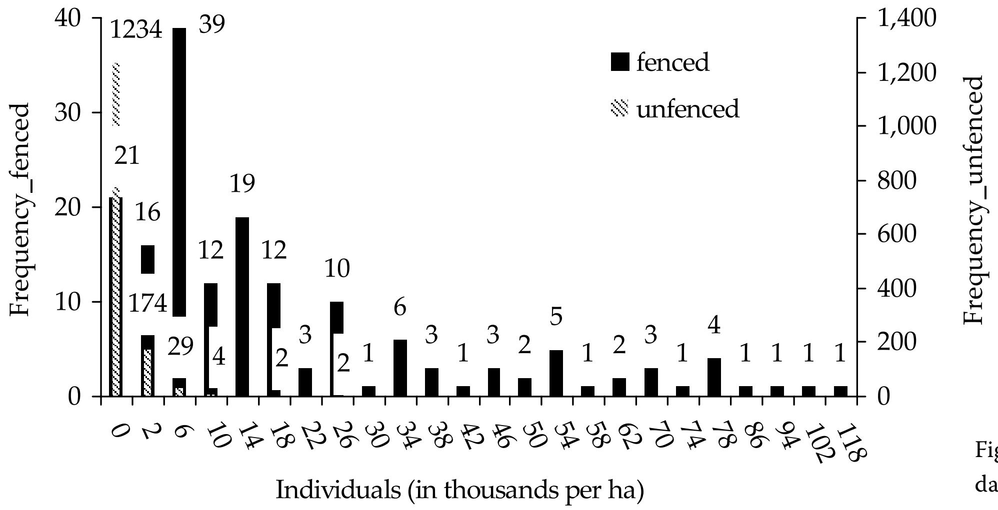

Fig. 4. Regeneration abundance classes (Telc)

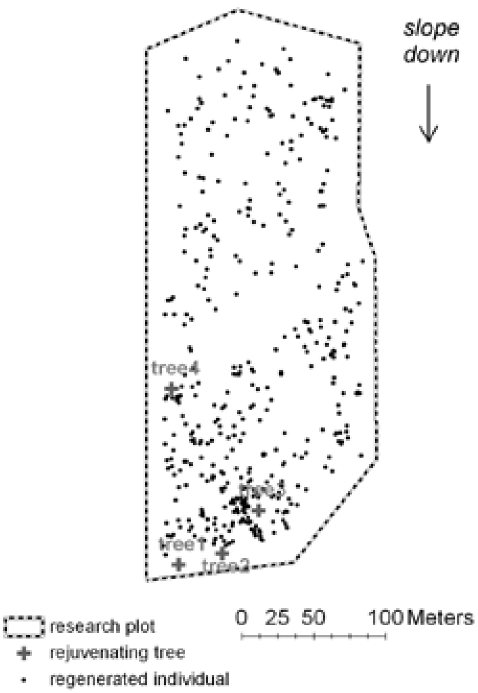

Fig. 5. Map of regenerated individuals and rejuvenating trees (Ansprung)

both cases ("Telc": NNIndex = 0.51, Z = 37.6; "Ansprung": NNIndex = 0.67, Z = 12.9). The spacing between each regenerated individual in the case of "Telc" is 0.27 m in the fenced area and 1.69 m in the unfenced area, and 3.8 m in the other case.

In the case of "Kremesnik" (Fig. 9) a polynomial shape of the distribution curve of regeneration is visible with a maximum regeneration density of approximately 38,000 individuals per hectare at approximately 11 m from the tree, thus outside of the crown projection. Nine of twenty-two trees do not show any signs of regeneration under their crowns. For other trees, regeneration covers on average 48% (14 to 93%) of the area under the crown. From approximately 11 to 30 m from the trees, there is a marked decrease in regeneration density in the range of the tens of thousands. The model with significant parameters explains 13% of total variability (Table 3).

In the case of "Telc" (Fig. 10), the greatest regeneration density is reached under the crown of the tree in the fenced part. From the foot of the trunk there is a markedly exponential decrease in density in the range of tens of thousands of individuals per hectare (from approximately 90,000 to 1,000) over a relatively short distance of 25 m from the tree. Approximately from this distance the decrease in the unfenced part is slight and is in the range of hundreds of individuals per hectare at a distance of approximately 100 m. In the unfenced area beeches took hold only sporadically with very low density and the model illustrates only 5% of total variability in this case. In the fenced area the model illustrated 63% of total variability (Table 3).

Table 3. Estimates of model parameters

	Kremesnik together	Telc fenced	Telc unfenced	Ansprung tree3	Ansprung tree4
Intercept	1.89	4.741	0.367	0.356	–1.585
x	0.33	–0.200	–0.022	–0.051	0.022
x^2	–0.02	–	–	$-1.6e^{-03}$	$1.42e^{-04}$
x^3	–	–	–	$3.4e^{-05}$	$-3.12e^{-07}$
x^4	–	–	–	$-1.6e^{-07}$	–
Deviance explained (%)	13.08	63.37	5.36	43.24	3.35

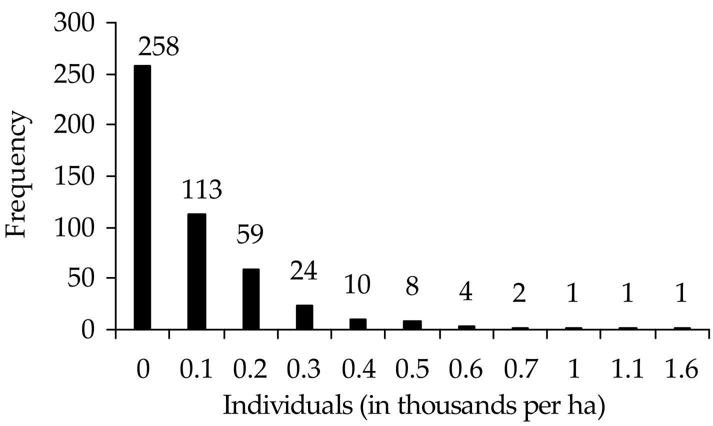

Fig. 6. Abundance of rejuvenated individuals (Ansprung)

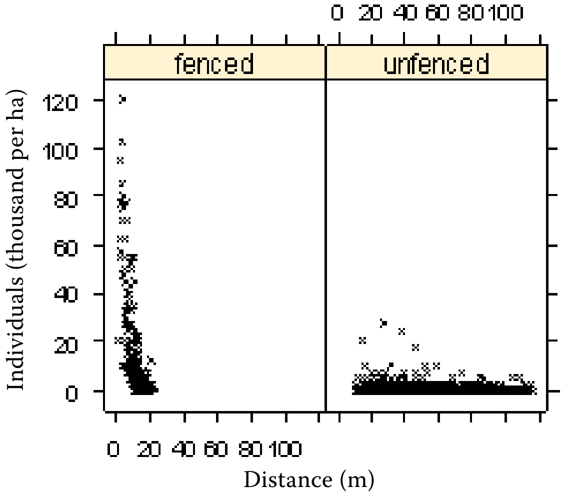

Fig. 7. Relation between regeneration density and distance (Telc)

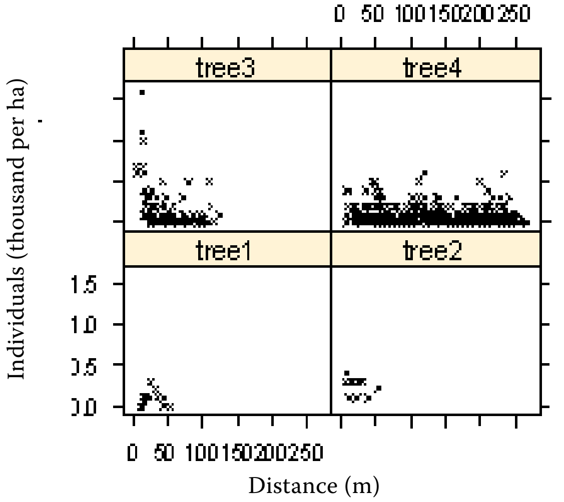

Fig. 8. Relation between regeneration density and distance (Ansprung)

In the case of "Ansprung" (Fig. 11) the greatest regeneration densities were reached surrounding the crowns of regenerating trees; with increasing distance the density decreases from each tree differently. For "tree3" the decrease for distances up to about 30 m was marked, although only in the range of hundreds of individuals per hectare (from approximately 1,000 to 50 individuals per hectare), farther the decrease levelled off and at approximately 70 m the density even grew with the pinnacle being at approximately 110 m (density of approximately 150 individuals). For "tree4" the decrease in density (with a lower starting density of approximately 200 individuals) at approximately 100 m is slight and in the range of tens of individuals per hectare, and farther at the limit of occurrence of approximately 254 m it is not visible. The relationship of the studied variables was best illustrated by "tree3", where the percentage of explanatory variability was approximately 53.0%; in contrast, for "tree4" it was only 3.4% (Table 3).

DISCUSSION

The existence of beech regeneration spontaneously starting from a few isolated individuals and penetrating deep into a homogeneous artificial spruce stand is a phenomenon that when understood properly can be used as a means for "biological rationalization" during the transformation of a spruce monoculture into a forest with more natural composition and greater ecological stability. Mosandl and Kleinert (1998) pointed out this possibility for the penetration of oak into pine monocultures, and for beech, this was done mainly by Petermann (2000), Ganz (2004), Hartig (2008) and Irmscher (2009).

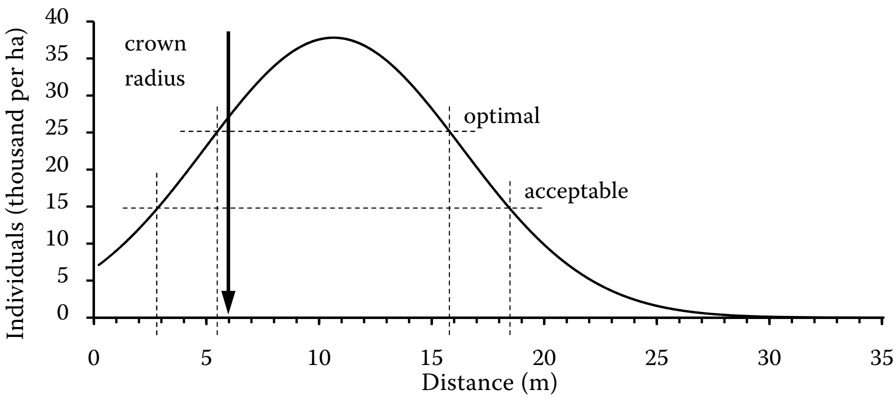

Fig. 9. Regenerated individual dispersion model (Kremesnik)

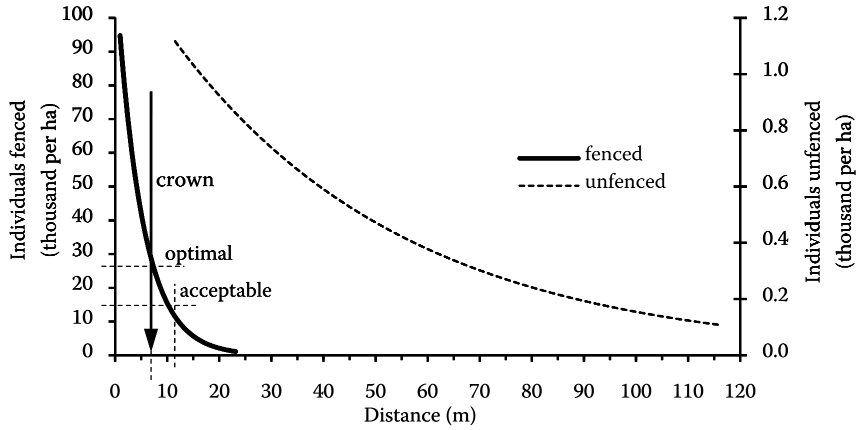

Fig. 10. Regenerated individual dispersion model ("Telc")

The maximum model distances for beech dispersal (theoretical density of 1 individual per hectare) estimated for the "Telc" site ("unfenced" variant) and "Ansprung" ("tree4" variant) are respectively 350 and 400 m, with a maximum actual distance of 115 m and 254 m. Ganz (2004) found out an actual value of approximately 60 m with an average distance of 13 to 19 m depending on the terrain, whereas Irmscher (2009) reported 254 m with an average distance of 35 m. The regenerated individuals pattern over the area is significantly clustered in all of our cases. It was not rare to observe regeneration in tight bunches that contained even more than ten individuals. All these facts unambiguously prove the important role of animals in the process of beech regeneration. Other studies also confirmed this finding (Turček 1961; Petermann 2000; Kunstler et al. 2004; Ganz 2004; Kutter, Gratzer 2006; Irmscher 2009).

The analysis of all three cases of regeneration dispersal allows for a generalization of the dispersion curve (Figs. 9–11; Table 4). Three sections can be determined:

(1) directly under the crown of the regenerating tree, where regeneration is almost exclusively the result of beech nut fall (the effect of barochory),
(2) around the crown from about 15 to 30 m from the trunk, where beech nut fall and carrying occur to a different extent, the combined effects of barochory and the zoochoric activities of mice and birds, and finally
(3) farther into space toward the edge where beech nuts get only by being carried by birds.

In sections 1 and 2 we find the greatest regeneration density and at the same time its most steep exponential decrease at a relatively short distance from the tree. Section 1 is determined by the width of the crown, section 2 by the span of the distance from the trunk circumference to the breakpoint of the curve. From this point in section 3 the curve trend continuously changes to become slightly decreasing or constant or it even grows locally to distances over 100 m ("Telc") or above 250 m ("Ansprung"). With this, the distance factor loses significance or other unexplained factors are at

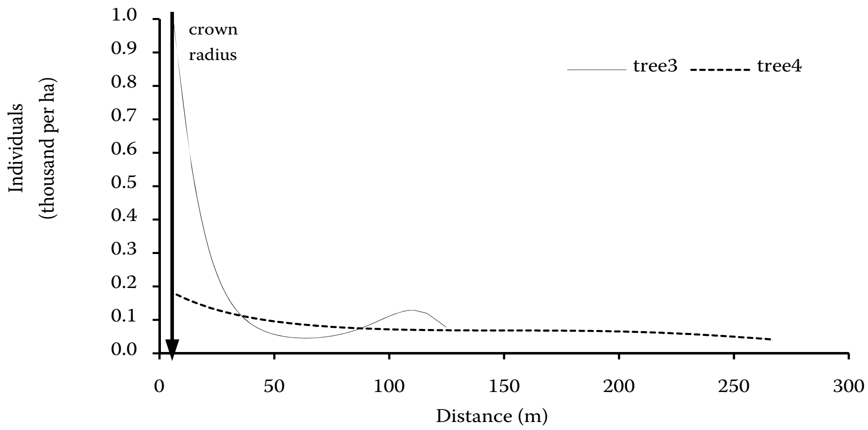

Fig. 11. Regeneration individual dispersion model (Ansprung)

Table 4. Correlation (Spearman) of density and distance by segments

Example/ Segment	Kremesnik	Telc fenced	Telc unfenced	Ansprung tree3	Ansprung tree4
1	0.02	–0.54	–	–	–
2	0.25	–0.48	–	–0.67	–0.48
3	–0.04	–0.18	–0.18	–0.04	–0.13

work, as we can assume the effects of animals. This is very visible during the observation of the correlation of variable values, i.e. distance and density, separated into corresponding sections (Table 5). We estimated the location of the breakpoint from the dispersion curve of the individual cases ("Kremesnik" – approximately 25 m, "Telc" – approximately 15 m, "Ansprung" – approximately 30 m). The differing positions in each specific case are certainly determined by local variations, for example by the configuration of the terrain, by the size of the diaspore carrier populations, etc.

The exponential course of the dispersion curve that we determined for "Telc" and "Ansprung" is general knowledge in the ecology of beech dispersal (Karlsson 2001; Ganz 2004; Kutter, Gratzer 2006; Irmscher 2009). Only Ganz (2004) reported a low regeneration density in the close proximity of the trunk (approximately to 3 m) of the regenerating tree; we made a similar finding for "Kremesník". The author expressed this fact using a 2nd degree polynomial. She did not however study the causes of this phenomenon in greater detail; she indicated only a possible complex of factors and pointed out unfavourable radiation and moisture conditions. We can assume that one of the main causes is the amount of solar radiation or side light available under the crown of the tree. To support this idea we note that the tree in "Telc" with maximum regeneration density directly under the crown is located in the stand, but it is about 15 m from the edge of an expansive open area. Also near the tree in "Kremesnik" where there was regeneration under the crown, there was always a large gap in the crown canopy.

The generalized course of the dispersion curve is interesting from the aspect of the ecology of beech regeneration. Each regenerated beech in a spruce monoculture does not have an immediate management value guaranteeing reliable regeneration results or stand transformation. Most of all it must achieve a certain density and be vital. We empirically established an optimal density as the value exceeding 25,000 individuals per hectare. Taking into consideration the growth conditions of beech in the fir-beech to spruce-beech forest vegetation zones and the natural growth dynamics of beech, an economically valuable stand is created from this type of regeneration. We consider a density above 15,000 to be even more acceptable, and for which cultivating these groups sufficient essential quality intensive care is needed. According to these criteria we ascertained (Fig. 9–11; Table 4) that such results in sections 1 and 2 can be achieved only with individually isolated trees where regeneration is protected from game (see "Telc_fenced") or with the effect of regeneration from multiple regenerating trees (see "Kremesnik") in areas with overall higher percentages of beech, meaning that game animals are distributed over a larger area. In the first case regeneration distances of approximately 10 m can be utilized and in the second case this distance is approximately 19 m from the tree. During spontaneous development without focused management measures (see "Telc_unfenced" and "Ansprung") only a few hundred individuals per hectare can be expected.

This corresponds to the findings of the above-mentioned authors (Petermann 2000; Ganz 2004; Hartig; Irmscher 2009), who in agreement recommend the utilization of the reproductive potential of dispersed regenerating beech individuals for the transformation of spruce stands. However, some authors simultaneously stated that the avail-

Table 5. Model values of regenerated individuals (in thousand) at a fixed adjustment of distance

Distance (m)	2	5	10	15	20	25	30	50	100	150	200	250
Kremesnik	11.989	23.172	37.571	28.243	9.843	1.590	–	–	–	–	–	–
Telc fenced	76.801	42.119	15.476	5.687	2.090	–	–	–	–	–	–	–
Telc unfenced	–	–	1.155	1.033	0.924	0.826	0.739	0.472	0.155	0.051	0.017	0.005
Ansprung tree3	–	1.069	0.757	0.518	0.350	0.238	0.164	0.057	0.111	0.001	–	–
Ansprung tree4	–	0.185	0.168	0.153	0.141	0.130	0.121	0.096	0.072	0.068	0.065	0.050

able number of individuals in advance regeneration does not have to meet the requirements of silvicultural practice and to achieve an economically optimal mixed stand it is necessary to complement the advance regeneration with plantings. While Ganz (2004) and Irmscher (2009) reported densities in the range of hundreds of individuals per hectare, Petermann (2000) reported a density in the range of hundreds of thousands in fenced groups of regenerated individuals. Taking into account local experience, the latter author derived a distance of 20 m from the regenerating tree as the upper limit for the meaningful economic utilization of regeneration.

In management planning it will be necessary to incorporate regeneration into the transformation system and to respect marked temporal and spatial arrangements. Because regeneration has a certain model distribution from the regenerating tree, the basis for planning transformation shall be the position and arrangement of trees.

CONCLUSIONS

The validity of the findings about how adult beech trees individually dispersed in a spruce monoculture regenerate can be generalized for ecological conditions of the fir-beech and spruce beech forest zones in which we analyzed three cases.

Depending upon the local situation offspring can be found at distances greater than 200 m from a specific tree. We can generalize the spatial regeneration distribution by a dispersion model – by a curve that describes how regeneration density changes in relation to a distance from the tree. Three sections can be determined: the highest regeneration density with a sufficient amount of light can be expected in the first section under the crown of the tree or in its proximity where most beech nuts fall. Regeneration from regenerating trees decreases exponentially to the breakpoint of the curve, which ranges in individual cases at the distance of 15–30 m from the tree. From this point on in the third section reaching the limit of occurrence the relation between regeneration density and distance from the tree is not significant/free; farther density slightly decreases and in certain places it can be constant or it even increases.

This model spatial arrangement may be an orientation aid for making decisions on the silvicultural use of regeneration for management purposes. It can be derived from the analyzed stands that the presence of two to three productive trees per hectare of stand area should be sufficient to ensure 30% beech coverage in the next stand generation. Regeneration in a radius of approximately 20 m from the tree is such a reliable starting point for firmly setting beech in the new spruce stand generation that it guarantees the creation of an economically valuable part of the stand as the highest possible management goal.

With the low-density regeneration it is possible to achieve the minimum management goal, as from this generation beech will regenerate in the next regeneration cycle. The significance of this focus is otherwise clear from this study; several individual beeches in a foreign stand are capable of covering a relatively large area with their offspring.

Beech regeneration is in no case spared hoofed game browsing. Whereas in fenced areas its density is in the range of tens of thousands of individuals per hectare, in unfenced areas at comparable distances from the tree the numbers are in hundreds. If regeneration is to be utilized as much as possible, then its protection from game is an essential management measure.

There are several aberrances from the conclusive main trend of decreasing regeneration density with increasing distance from the tree. Besides the influence of game, the presence of regeneration is undoubtedly influenced by many other positive and negative factors which are impossible to identify without further deeper studies of individual phenomena. The question is what to focus on. Is it enough to understand the characteristics of the stand climate and the surface soil horizons or will it be necessary to combine them with an ecophysiological study of regeneration itself during the entire process of its creation, i.e. from its advance until it is firmly in place. If we recall that in the last two or three decades of the 20th century the mast years of beech in large areas of Europe have been rather rare, then we can acknowledge that the rich regeneration of beech that has been recorded recently and that is almost invasive, is an episodic phenomenon. Therefore, research should be aimed at determining the effects of the main phenomena so that they can be managed by silvicultural measures. This is also for maintaining or intensifying the fructification capabilities of the tree as well as for creating the optimal stand microclimate for regeneration.

References

Bossema I. (1979): Jays and oaks: An eco-ethological study of a symbiosis. Behaviour, ***70***: 1–117.

CLARK P.J., EVANS F.C. (1954): Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, ***35***: 445–453.

DOBROVOLNÝ L. (2008): Spatial pattern application by evaluation of spontaneous beech (*Fagus sylvatica* L.) regeneration. In PRKNOVÁ H. (ed.): Pěstování lesů na počátku 21. století. Praha, ČZU: 1–9. (in Czech)

DONNELLY K. (1978): Simulations to determine the variance and edge-effect of total nearest neighbor distance. In: HODDER I. (ed.). Simulation Studies in Archaeology. New York, Cambridge University Press: 139.

GANZ M. (2004): Entwicklung von Baumartenzusammensetzung und Struktur der Wälder vom Schwarzwald bis auf die Schwäbische Alb – mit besonderer Berücksichtigung der Buche. [Ph.D. Thesis.] Freiburg, Univeristy of Freiburg: 183.

GOMEZ J.M. (2003): Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography ***26***: 573–584.

HARTIG M. (2008): Die sächsischen Walder auf dem Weg zu nachhaltiger Bewirtschaftung. Der Sächsische Waldbesitzer, ***3***: 10–13.

IRMSCHER T. (2009): Zoochores Ausbreitungspotenzial der Rotbuche (*Fagus sylvatica* L.) mit Blick auf die Minimierung der Eingriffsintensität beim Waldumbau in Wäldern mit Naturschutzstatus. Forstarchiv, ***80***: 29–32.

JENSEN T.S. (1985): Seed-seed predator interactions of European beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. Oikos, ***44***: 149–156.

JOHNSON V.C., ADKISSON C.S. (1985): Dispersal of beech nuts by blue jays in fragmented landscapes. American Midland Naturalist, ***113***: 319–324.

KARLSSON M. (2001): Seed dispersal from broadleaved stands and effects of scarification on seedling emergence. [Ph.D. Thesis.] Alnarp, Acta Universitatis Agriculturae Sueciae: 44.

KOLLMANN J., SCHILL H.P. (1996): Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio, ***125***: 193–205.

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.

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.

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.

PETTERMANN L. (2000): Zustand und waldbauliche Bewertung von Altbuchensolitären im Nordostteil des Tharandter Reviers.[Master Thesis.] Tharandt, TU Dresden: 112.

STIMM B., KNOKE T. (2004): Hähersaaten: Ein Literaturüberblick zu waldbaulichen und ökonomischen Aspekten. Forst und Holz, ***59***: 531–534.

TURČEK F.J. (1961): Ökologische Beziehungen der Vögel und Gehölze. Bratislava, SAV: 329.

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