Natural regeneration of senescent even-aged beech (*Fagus sylvatica* L.) stands under the conditions of Central Bohemia

L. Bílek, J. Remeš, D. Zahradník

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Prague, Czech Republic

ABSTRACT: The natural regeneration of beech (*Fagus sylvatica* L.) was studied under various shelterwood densities and silvicultural treatments in senescent beech stands in Central Bohemia. Four permanent research plots differed in shelterwood density, crown cover and average relative light intensities. Between 2003 and 2007, seed production, seedling emergence and survival were followed. The mean density of beech seeds (full and empty) per 1 m^2 was estimated in another forest stand. In the autumn of 2003 the values were distinctly higher than those indicated for full mast years of beech. Despite high losses during the wintering of seeds, relatively low germination and high first-season mortality, the high density of 1-year-old beech seedlings indicates that these elements are not the factors which hinder natural regeneration. The thickness of the humus horizons influenced the density of young beech seedlings during all the three years. Ground vegetation was more frequent outside the crown projections of parent trees and increased with distance from the nearest tree. A reduction of crown cover to the level of 80% was an appropriate measure that assured the high survival of beech regeneration during the observed four-year period. Border cutting with the outer face oriented towards the east has to be considered as less suitable for beech regeneration than shelterwood systems and group selection harvesting.

Keywords: *Fagus sylvatica* L.; natural regeneration; stand density; seedling survival; mortality; Voděrady Beechwoods

European beech was widely exploited for various purposes, later it was considered not to be a commercially interesting species in the last two centuries and then it was re-discovered by the ecologically oriented forestry of the last decades. As a result nowadays, we see a rapidly changing position in the status of beech, with an increasing demand for knowledge of its ecology.

We can expect that European beech, due to its favourable conditions, will gain more importance in the future Czech forests. It is resistant to biotic and abiotic stresses (insect plagues, fungal attacks, wind, storm and pollution), it helps to increase the biological diversity of forests (species, age, pattern, structure and ecosystem processes) and it improves water and soil protection, which in turn increases the production of high-quality timber.

Due to its broad ecological amplitude and management flexibility, European beech is a suitable tree species to be used to solve some very topical contemporary problems of Czech and European forestry and nature conservation. Secondary coniferous stands proved to be sensitive to abiotic and biotic stress factors and beech is the most important broadleaved tree species in the conversion of these plantations into mixed stands. Biodiversity and quality timber production as well as sustainability of forests will benefit from its substantially higher representation

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in forests. In the case of beech as a stabilizing element of forest stands, a greater emphasis should be laid on the preservation of its adaptability and ecological stability through the gene-pool conservation of the existing indigenous populations (Gömöry et al. 1998).

Beech is a shade-tolerant tree species producing a huge number of seeds in recurring mast years. Strong seed production in one year negatively affects seed production in the next one. Late frosts are the main limiting factor of seed production in the north of the area, whereas dry summers take negative effect in the south (Peters 1997). In the eastern part of its distribution beech flowers more often than e.g. in Western Europe, but this phenomenon does not lead to more frequent seed production (Standovár, Kenderes 2003). Seed production and survival may also be affected by insects, fungi and birds. Seed fall starts in September and reaches its maximum in the second half of October. Empty seeds and seeds affected by parasites may fall sooner (Šindelář 1993). The phaenology of individual trees (early or late flowering), social position (height class of Kraft) and position within the stand also affect seed production, thus the number of produced seeds can show high spatial variability within a single stand (Standovár, Kenderes 2003).

It is generally stated that the germination and survival of beech seedlings are problematic. Since beech has no apparent chemical defences against browsing and because it has a poor capability to recuperate, it depends on high seedling densities to avoid predation. During full mast the percentage of empty seeds and seeds affected by parasites is lower than that of the low masts (Šindelář 1993). The quantity and quality of light, the humus form and cover are important factors (e.g. Emborg 1998; Topoliantz, Ponge 2000). Beechnuts usually germinate in April or May depending on snow cover (Standovár, Kenderes 2003). Like the wintering beechnuts, the sprouting seedlings are vulnerable to climatic and soil chemical conditions, attacks by several insects and mammals. Čermák and Ježek (2005) stated that rodent populations responded to the poor crop of beechnuts and acorns by a decline in numbers and to the good seed crop by an increase (*Apodemus* spp.). In most cases beechnuts have better conditions for wintering in a mineral soil seedbed than in a mixed one. One of the underlying assumptions is that the rodents prefer to seek for beech nuts in the mixed soil seedbed, since it is easier for them to find cover there than in the mineral soil seedbed (Madsen 1995b). On the contrary, Ammer et al. (2002) proved that the coverage of seeds with leaf litter resulted in a distinct increase in the seedling number. It is likely that the most important effect of the coverage was a reduction in evaporation and increase in soil moisture. This underlines the necessity of sufficient soil moisture for satisfactory seed germination. Canopy trees increase both the interception and the root competition for water and so negatively influence the conditions for germination. Dead wood can provide an appropriate establishment site for tree species in certain forest types (Standovár, Kenderes 2003). The fungal pathogen activity can cause high rates of first-season beech seedling mortality. A common cause of seedling mortality is damage caused by aphids. Short warm and dry periods in winter may dry out seedlings resulting in a loss of viability. Once the radicle has emerged from the seed, it may be killed off by a late spring frost.

In the process of natural regeneration of beech forests, the formation of seedling bank may play a very important role (Swagrzyk et al. 2001). Yet, the occurrence of numerous seedlings on the forest floor is very often only an ephemeral impulse of regeneration with virtually no chance of ever attaining the sapling size. Beech seedlings can survive the light conditions that barely permit any growth for some time at least. Experiments under controlled conditions show that the minimum light intensity required for young beech seedlings to survive is around 1% of total radiation (Madsen 1995a; Collet et al. 2001). According to Peters (1997) beech establishment is optimal under a 50% crown canopy cover. Seedlings will reduce height growth above 75% of canopy cover, but may survive for substantial periods in the dark. In shade conditions beech will adapt itself by reduced growth and leaf morphology. This leaf adaptation consists in a strong reduction in mesophyll thickness, but a weak reduction in epidermis thickness. Collet et al. (2001) showed that 12-year-old seedlings were still able to resume active growth after canopy opening. An important fact is that the growth and morphology of seedlings may be influenced not only by current-year light conditions but also by previous-year light (Welander, Ottosson 1997).

The aim of the study was to investigate the density and mortality of beech regeneration after the heavy mast year 2003 in relation to density of the parent stand, seedbed type and weed competition.

MATERIALS AND METHODS

Study area

The National Nature Reserve Voděradské bučiny (Beechwoods of Voděrady) – (49°58'N, 14°48'E) is

Table 1. Overview of research plots and basic characteristics of forest stands included in the study

Research plots	Forest stand	Group of forest types	Age years	Elevation (m a.s.l.)	Exposure slope (%)
S1	434A17	4K3	166	455	N – 15
S2	417D16	4S7	154	455	E – 15
PRP 01	436C17	4B1	179	440	E – 15
PRP 03	434B17	4S4	189	450	N – 20
PRP 04	434E17	4S4	184	460	E – 17
PRP 05	436D17	4K3	169	440	E – 15

situated in the Mnichovská pahorkatina Hills. The parent rock is formed by granite of different texture. Predominantly Cambisols with low humus content are developed within forest stands (AOPK 2000). The mean annual temperature is 7.8°C and the mean annual precipitation is 623 mm; during the period from April to September the mean temperature is 14.0°C and the precipitation amounts to the total of 415 mm. The duration of the vegetation period is approximately 158 days. Due to intensive use and changed tree species composition in the last three centuries, European beech is the main tree species which often forms almost pure stands. Under given conditions beech regenerated successfully under the parent stand and was rarely regenerated artificially. It is highly probable that stands of beech older than 110 years are of the local origin (Čvančara, Samek 1959). All research plots are located in even-aged forest stands within the borders of the National Nature Reserve.

Data collection and statistical analyses

To quantify the seed production of beech during the heavy mast year 2003, in the forest stand 434A17 sampling plots were established in the regular matrix 20 m × 10 m (research plot S1). Six lines at distances of 20 m intersect the forest stand in parallel to its opened E edge. In each line at 10 m distances we recorded the number of beech seeds within a steel frame 25 × 25 cm. We noted the number of full and empty seeds. In the adjacent forest stand 417D16 we conducted the same study in a fenced plot (research plot S2), where the parent stand was already removed before the mast year. In total 74 sample plots were situated in the first stand, 27 sample plots in the second stand. During the vegetation period 2004 (4. 2004; 7. 2004; 9. 2004; 11. 2004) we repeatedly counted the number of seedlings within S1 (we used the same grid as for seed quantification using a frame 1 × 1 m).

For the research on the stand structure, in 1980 a series of permanent research plots (PRP) were established, each 100 × 100 m (1 ha) in size, representing even-aged almost pure beech forest stands. Four out of these PRP (01, 03, 04 and 05) were later used for the research of beech regeneration. In each plot we mapped all woody stems ≥ 3 cm dbh using Field-Map (IFER – Monitoring and Mapping Solutions, Ltd.). For each stem, we measured the dbh (double measurement in NS and EW), height, crown height and recorded the species, status (living, dying

Table 2. Stand characteristics and average illumination within 1 ha PRP

PRP	V_{total} (m^3/ha)	G (m^2/ha)	N (ha)	ρ	$d_{1.3}$ mean (cm)	h mean (m)	Crown cover (%)	RLI (%)
01	597.48	27.23	93	0.60	59.57	40.89	78.2	13
03	863.72	40.26	126	0.90	62.46	39.95	107.7	11
04	704.04	32.89	110	0.75	60.49	39.99	81.8	28
05	583.20	28.00	113	0.65	55.18	39.47	77.0	15

V_{total} – stand volume of all living trees, G – stand basal area, N – number of trees, ρ – stand density, RLI – relative light intensity or dead) and social status (dominant, codominant, subdominant and less than 20 m). We also mapped the crown projection of each live stem by measuring a minimum of five cardinal crown radii per tree. The mean diameter, mean stand height, dominant stand height (characterized as an average height of the 100 highest trees per 1 ha), stand density, volume and stand basal area were calculated by regular dendrometric methods using the volume tables and equations (Petráš, Pajtík 1991).

The illumination values for each plot were measured on 17 November 2008 between 10 a.m. and 14 a.m. using the same regular design in four PRP. We measured in constant steps along both diagonals intersecting the 1 ha plot. Another two lines normal to the side of the permanent research plot and going through the middle of the plot were used for the same processing. On both diagonals we measured at 15 standpoints, on both vertical lines at 11 standpoints. At all standpoints ($N = 52$ per plot) we carried out threefold measurements ($n = 166$ per plot). The values were recorded with the FX 101 luxmeter at the height of 1 m above the ground. During the day we repeatedly measured the illumination in the open space. The median of these measurements was used as 100% illumination. An overview of the research plots and basic characteristics of forest stands are given in Table 1 and values of relative light intensity (RLI) in Table 2.

To quantify the establishment and survival of regeneration we established sample plots (SP) in the regular matrix 20 m × 10 m spacing over the area of 1 ha in each of four PRPs. Sample plots were in the form of a square (1 m^2). On each plot we recorded the number of seedlings and species, the proportional cover of woody regeneration, herb vegetation, dead wood, stones, mineral soil, soil covered with litter fall, roots, roads and mosses. For each plot we measured the total thickness of holorganic and Ah horizons (double measurement in the opposite corners of the plot). The number of surviving seedlings was repeatedly recorded at the end of vegetation period in 2004, 2005 and 2007. The woody regeneration was counted according to species and in the case of beech also according to the developmental stage: 1-year-old seedlings (originating from the mast year 2003), older seedlings (originating mostly from the mast year 1995). In 2007 a new generation of beech seedlings after the moderate mast year 2006 occurred. For each sample plot we recorded the distance to the nearest tree of the parent stand.

The data was not distributed normally (for testing normality we used the Shapiro-Wilkes test). The Kruskal-Wallis test was used searching for differences among data sets. For pairwise comparison between PRPs we used the Kruskal-Wallis Z test. To determine the correlation, the Spearman nonparametric correlation coefficient was used. For pairwise comparison of mortality we used the χ^2 test for k independent samples, for multiple comparison see Hayter (1984). The analyses were done in software Statistica 8 and S-Plus. For all analyses, results were considered significant when $P \leq 0.05$.

RESULTS

Stand structure, management and illumination values

Important factors influencing the establishment and development of natural regeneration might be silvicultural treatments. On all PRPs predominantly

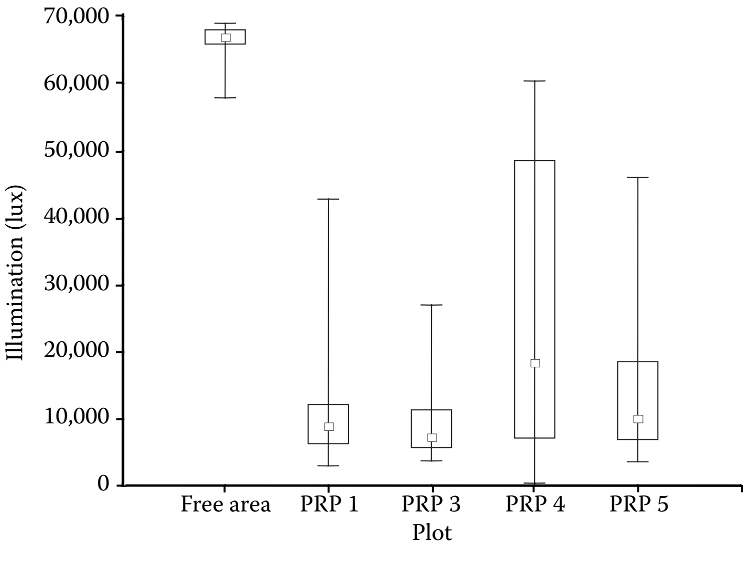

Fig. 1. Distribution of illumination according to PRPs

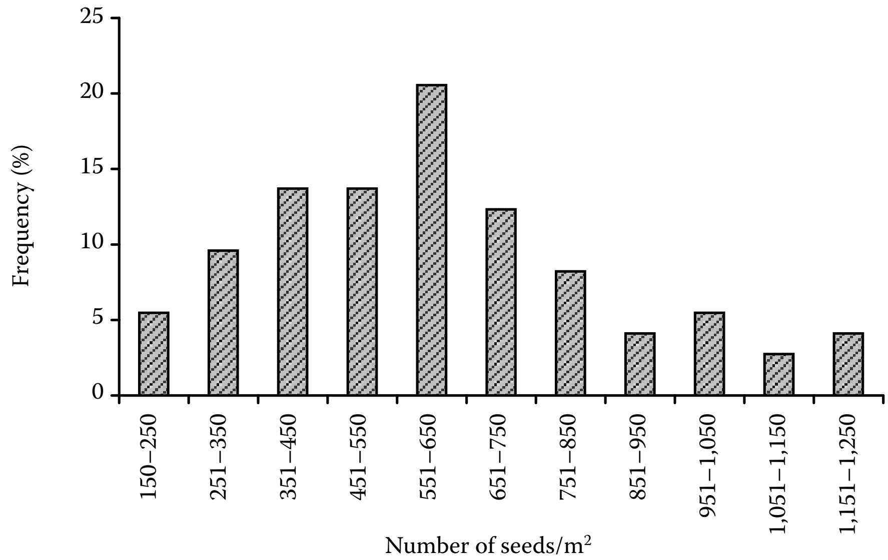

Fig. 2. Distribution of seed densities (per 1 m^2) under parent stand 434A17

group shelterwood felling is performed; on PRPs 03 and 04 in combination with the border cutting system. Basic stand characteristics for 2004 are given in Table 2. Preparatory felling carried out in 2002 and salvage cutting in previous years reduced the basal area (volume) on PRP 01 and 05 (reduction of stocking to 0.6 and 0.65, respectively). On PRP 04 the lower basal area (but still far above the values of previous plots, stocking 0.75) results from ongoing border cutting in east-west direction. The inner stand except for one gap (originating from salvage cutting) remains quite untouched, which is exactly the case of entire PRP 03.

Significant differences in illumination values among four PRPs and open space (100% illumination) were observed (Kruskal-Wallis test: d.f. = 4, $H = 89.99$, $P = 0.000$). The lowest ratio of illumination was found on PRP 03 with the highest growing stock, basal area, number of trees and crown cover. Obviously, ongoing border felling (north-east border) did not influence the illumination like in the case of PRP 04. Here, border felling already reached the limits of PRP (east border) and created light conditions on a part of the plot closer to those of open space, which explains high values of measured radiation and their heterogeneity (Fig. 1).

Seed production and seedling emergence

The mean density of beech seeds (full and empty) per 1 m^2 estimated in forest stand 434A17 (research plot S1 – under the canopy of parent stand) was

Table 3. Regeneration density (thousands/ha) according to tree species and developmental stages in the autumns of 2004, 2005 and 2007 (values in the parenthesis are given in percentage)

	Beech	Spruce	Fir	Pine	Larch	Maples	Hornbeam	Birch	Rowan	Total (%)
Autumn 2004										
1-year-old seedlings	206.9 (93.8)									
Seedlings	10.7 (4.9)	0.3 (0.1)	0.2 (0.1)	0.3 (0.1)	0.2 (0.1)	1.1 (0.5)	0.2 (0.1)	0.4 (0.2)	0.2 (0.1)	100
Autumn 2005										
2-year-old seedlings	119.4 (93.1)									
Seedlings	7.5 (5.8)	0.2 (0.2)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	1.1 (0.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	100
Autumn 2007										
1-year-old seedlings	44.4 (29.9)									
4-year-old seedlings	94.6 (63.7)									
Seedlings	7.3 (4.9)	0.6 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.2 (0.8)	0.2 (0.1)	0.2 (0.1)	0.0 (0.0)	100

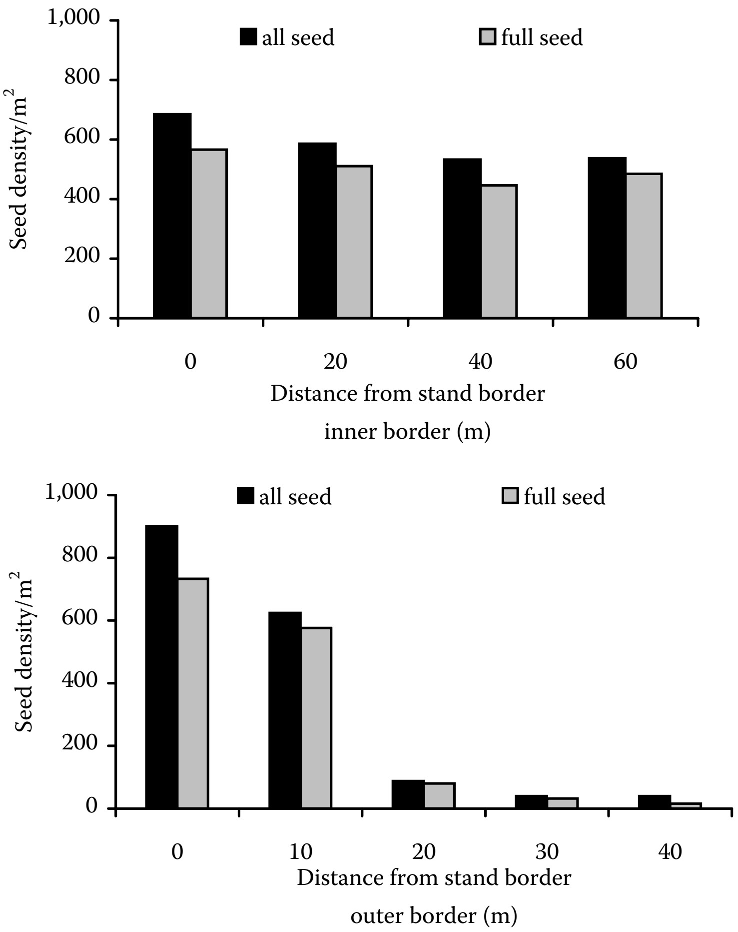

Fig. 3. Number of seeds under the inner and outer border of beech stand

624 (S = 275.7). Fig. 2 shows the relative frequency of seed numbers. In forest stand 417D16 (research plot S2 – in the open space) under parent beech trees standing in the proximity of a clear-cut area the average density of beech seeds reached the value 901 per m^2 (n = 6, S = 258.1). With increasing distance from the stand border the densities of seeds decreased, yet at a 10 m distance (in the open space) they outreached the value of 600 seeds per m^2. The highest seed fall was found in the proximity of stand border (east border). The capacity of heavy beech seeds to disperse is limited, nevertheless seeds were found at the distance of 40 m from parent trees. Numbers of seeds also decreased from the edge to the inner stand (Figs. 3a,b); yet there was no statistical difference in seed densities among data sets (Kruskal-Wallis test: d.f. = 5, H = 5.01, P = 0.414).

The ratio of empty seeds on research plots was 17% and 18.8% (S1 and S2). The germination of beech seeds in forest stand 434A17 was relatively low (6.8%). At almost one half of all sample plots (49.3%) only from 0 to 2.5% of the initial seed fall developed into seedlings. The average first-season survival of beech seedlings estimated from April to November 2004 was 44.0%. By the end of the growing season 2.36% of the fall of full seeds developed into seedlings. The rate of germinated seeds was much higher in controlled conditions without losses during the wintering of beech seeds and other negative biotic and abiotic factors. In 2003 we collected a small sample of beech seeds in forest stand 434A17. In the following year we tested the germination of five hundred full seeds in a nursery. From 12. 5. 2004 to 23. 6. 2004 (in the following two weeks we did not observe germination any more) 24.4% of full seeds germinated. Even by relatively low rates of germination (and high losses of wintering seeds) the seed production has to be regarded as sufficient and capable to provide successful natural regeneration of beech in the given conditions. The values observed on both research plots far overreached the values indicated for full mast years of beech. This result was not expected since both stands are far behind the usual rotation period of managed beech stands (Table 1). Beechnuts usually germinate from April or May and the sprouting seedlings are vulnerable to attacks by several insects. The first measurement was conducted on 23rd April and we observed damage caused by aphids very soon.

Woody regeneration dynamics

In total 9 tree species were found in the seedling bank in the studied stands (beech, Norway spruce, silver fir, maple, hornbeam, pine, rowan, birch, larch). Nevertheless, beech dominated the 2003 cohort and only single individuals of other woody species could be found (Table 3). This was anticipated because of a heavy mast year. The high density of 1-year-old beech seedlings indicates that the amount of seeds and their germination are not the elements which hinder natural regeneration. The densities of coniferous and other broadleaf species were quite low primarily because of their absence in the overstorey. The density of Norway spruce increased in 2007 due to the moderate seed year in 2006 (as well as in the case of beech). After three vegetation periods – in autumn 2007 – 45.7% of the initial density of 1-year-old beech seedlings was still present on the plot. The density of older seedlings (1995 cohort) decreased to 68.2%. After the seed year 2006 we observed the establishment of new 1-year-old seedlings that corresponded to 21.5% of the density in 2004. The seedling density was variable in the tree species (hornbeam, birch, rowan) which bear seeds amply and frequently. Yet, maples (sycamore and Norway maple) with a low increase in their density remained the most common species among other broadleaf ones (except beech). We presume that light-demanding species like pine and larch disappear from the regeneration due to low light environment and high competition from shade-tolerant beech.

Ground vegetation cover, seedbed type, regeneration survival

Significant differences in ground vegetation cover among four PRPs were observed (Kruskal-Wallis test: d.f. = 3, H = 10.52, P = 0.015), with mean values 23.02%, 19.91%, 13.81% and 34.91%. Similar results were recorded for regeneration cover (d.f. = 3, H = 10.45, P = 0.015), with mean values 12.05%, 6.45%, 11.42% and 7.24%. On the contrary, no differences were recorded in the thickness of humus layer among PRPs (d.f. = 3, H = 2.365, P = 0.500) – (Table 4). There is no significant correlation between the cover of ground vegetation and cover of regeneration. We found only a weak negative correlation between the thickness of humus horizons and regeneration cover (R = –0.1548, P = 0.0370) and a positive correlation between the distance from the nearest tree and cover of ground vegetation (R = 0.3078, P = 0.000). The thickness of humus horizons influenced the density of young beech seedlings in all three years (2004: R = –0.2945, 2005: R = –0.2832, 2007: R = –0.2173, $P \leq 0.0033$). In the

Table 4. Mean beech regeneration density (thousands/ha)

Variable	PRP 01	PRP 03	PRP 04	PRP 05	Kruskal-Wallis test: H	P-value
1ys – 2004	279.8a	92.7abc	274.7b	183.5c	14.96	0.002
s – 2004	10.6a	6.2b	25.2abc	4.4c	26.70	0.000
2ys – 2005	201.4ab	42.0ac	93.4b	126.4c	21.40	0.000
s – 2005	5.9a	5.7b	18.6abc	3.2c	12.58	0.006
4ys – 2007	168.1ab	19.8ac	58.9bd	96.6cd	19.03	0.000
s – 2007	5.4a	5.2b	18.2abc	1.6c	24.57	0.000
1ys – 2007	76.3ab	70.7cd	8.2ace	20.6bde	58.76	0.000
GVC (%)	23.02	19.91	13.81a	34.91a	10.52	0.015
RC (%)	12.05a	6.45	11.42b	7.24ab	10.45	0.015
LFHA (mm)	4.34	4.00	4.47	4.08	2.365	0.500

1ys – one-year-old seedlings; 2ys – two-year-old seedlings; 4ys – four-year-old seedlings; s – older seedlings; GVC – ground vegetation cover; RC – cover of regeneration; LFHA – thickness of humus horizons and results from the Kruskal-Wallis test (the same indexes show means with significant difference) case of older seedlings no correlation was found. On the contrary, we found a weak negative correlation between the ground vegetation cover and density of older beech seedlings (2004: $R = -0.2794$, 2005: $R = -0.2296$, 2007: $R = -0.1896$, $P \leq 0.0106$), which was not the case of young seedlings. The density of young seedlings was negatively influenced in 2005 by the presence of older seedlings, which was most evident on PRP 04 with the highest number of older seedlings ($R = -0.3016$, $P = 0.0466$). Further we divided all SPs into three groups according to their position under the canopy of parent trees (0 – SP under opened canopy, 1 – SP under canopy, 2 – SP at border position). We found significant differences in the ground vegetation cover among these groups (d.f. = 2, $H = 12.29$, $P = 0.002$; 0 – 39.94%, 1 – 17.79%, 2 – 29.56%). Similarly, but without significance, the regeneration cover was higher under opened canopy (13.51%) and lower under crowns (8.06%, 11.69% at border position). Both older seedlings and young seedlings were more frequent under closed canopy and were less frequent under micro-gaps between the crown projections of parent trees.

The relationship between the average second-year survival (2004–2005) and three-year survival (2004–2007) of the 2003 cohort was statistically significant ($R = 0.7301$, $P = 0.000$). Further we divided SPs according to their initial number of seedlings in autumn 2004. The highest second-year survival and three-year survival was on SPs with the lowest seedling densities (1–10 seedlings; 73.86% and 54.59%, respectively), the lowest survival on SPs with moderate seedling occurrence (11–40 seedlings; 52.37% and 39.65%, respectively), on SPs with high seedling occurrence (more than 40, maximum value 174 ind.) we recorded the average survival of 59.07% and 47.00%, respectively. The difference among data sets was statistically significant (Kruskal-Wallis test: d.f. = 2, $H = 8.34$, $P = 0.015$). The second-year survival of one-year-old seedlings and older seedlings on four PRPs (01, 03, 04, and 05) was as follows: 71.08%, 45.93%, 35.29% and 68.14%; 54.41%, 92.31%, 84.40% and 72.41% respectively. In the case of the 2003 cohort differences were statistically significant except for PRP 01 and 05; on the contrary, for older seedlings we recorded statistically significant differences only between PRPs 01–03 and PRPs 01–04. We have no explanation for the low survival of older seedlings on PRP 01 or for more than 50% mortality of older beech seedlings on PRP 05 between 2005 and 2007. On the other three plots during this period the survival of older seedlings always exceeded 90%. During this period the 2003 cohort performed higher survival on all plots than in the previous year (83.19%, 60.00%, 71.05% and 80.26%). Differences between PRP 01–05 and 03–04 were not statistically significant. In order to compare the survival of beech regeneration within and out of crown projections we divided all SPs into two groups (0 – SP under opened canopy, 1 – SP under canopy and 2 – SP at border position formed the second group). The survival was significantly different only during the first year of observation for the 2003 cohort (out of crown projection – 67.09%, within crown projection – 58.24%). It seems that seedlings have more difficulties to establish under micro-gaps, but once they emerged, the survival rates are higher there than in the proximity of parent trees. With a few exceptions mentioned above, survival rates also increased with the age of beech individuals.

DISCUSSION

Besides necessary assumptions of beech regeneration like fructification and seed dispersion, silvicultural treatments altering the density of parent stand, possible soil preparation and fencing are the most crucial human induced changes inside the forest stand that finally decide on the success or failure of natural regeneration. By changing the shelterwood density the light climate is greatly influenced, which may affect the performance of the seedlings and the outcome of the regeneration. The optimal shelterwood should be a compromise between a dense shelterwood for protection against frost and competition from ground vegetation and a sparse shelterwood for maximum seedling growth (Agestam et al. 2003). Yet, no general thresholds for stocking reduction, number of felling operations, size and duration of cutting operations can be given without precise analysis of local conditions.

A chance for the survival of older beech regeneration increased outside the crown projection of parent trees, where beech was able to overgrow the competing vegetation. Nevertheless, this is not the case in the proximity and under opened east edges of forest stands, where higher direct radiation and higher evaporation in early hours favour vital herbal vegetation to the detriment of beech regeneration (Vanselow 1949). On the contrary, young seedlings found more favourable conditions for establishment under crowns probably due to limited vegetation. Poor occurrence of young seedlings outside the crown projection could be related to the increase of ground vegetation, which may allow small rodents to find suitable habitats (Madsen 1995b). According to Szwagrzyk et al. (2001) the first-season survival depends on the numbers of germinants. In years with very large numbers (1996 and 1993) of germinants average survival amounted to 59 and 58%, respectively, in our case we observed a bit lower survival amounting to 44% (2003), which rather corresponds with results obtained by EMBORG (1998). Another important factor lowering the seedling occurrence may be the rodent consumption of beechnuts. OLESEN and MADSEN (2008) estimated that potentially 15 beechnuts/m^2 were consumed by rodents over winter. In the same study only 1% of the initial seed fall (44–54% viable beechnuts) developed into seedlings in unprepared soil indicating that the rates of surviving beechnuts are in general very low (in our case 2.36% of full seeds). Although we did not record the proximate causes of the first-season mortality, aphids can play an important role. Herbivory did not seem to be a significant factor in seedling mortality, although older seedlings of rowan were heavily browsed by deer in the locality. In all respects the first-season survival is not a good estimator of the likely formation of a seedling bank (SZWAGRZYK et al. 2001). We found the highest survival on SPs with the lowest seedling numbers; similarly the same author observed the highest survival in years when the numbers of germinants were very small, nevertheless permanent seedling banks formed only in plots with relative light intensities higher than 9%.

In given conditions the reduction of crown cover to 80% one year before the seed fall seems to be an appropriate measure (preparatory felling). We do not see the necessity to carry out regeneration felling in the winter following the mast year. With regard to the weakly developed root system of one-year-old seedlings, relatively thick humus horizons and usually poor snow cover, this operation has to be regarded as too risky. The results showed that the beech regeneration developed successfully on PRP 01 and 05 (crown cover 80%) during the next four years. Even in a strongly shade-tolerant species like beech adequate canopy openings are necessary for the long-term development of regeneration. After this time the canopy is usually further opened so that the regeneration has enough light for growth (forming the upright terminal), yet retaining enough shelter to protect them. Final cutting sees the removal of the remaining canopy trees and takes place once the young trees have reached 2–4 m and require any protection no longer. This model may coincide with the big scale shelterwood system used around 1830 in the area (so called "Dreischlag"), which in present days with respect to multipurpose forest management has to be regarded as insufficient and which would result in even-aged pure beech stands again. On PRP 03 the absence of preparatory felling and the highest crown cover with the lowest RLI values resulted in the lowest numbers of seedlings and higher mortality. PRP 04 showed the highest numbers of older seedlings whose emergence has to be related to accidental tree breaks followed by salvage cutting which resulted in successful dense gap regeneration of the 1995 cohort. This special event negatively influenced the establishment and development of the 2003 cohort again with lower survival rates than on PRP 01 and 05.

The regular, even-aged structure as observed in present-day managed stands is not natural for this ecosystem and is responsible for a loss of biodiversity (SCHNITZLER, BORLEA 1998). One approach to increase the habitat diversity in the interventional part of the reserve could be to develop management systems that mimic the natural patterns and processes related to the mosaic cycle. Management practices, mimicking the natural structural development driven by small-scale disturbances, should generally protect the authentic forest-related biodiversity more efficiently than management systems based upon periodical large-scale process disruptions (EMBORG et al. 2000). Nevertheless, we see the main limitation of such an approach in the age of existing forest stands (the life span of beeches in managed forests may be shorter than in virgin forests driven by natural development cycles; in general the life span of beech is shorter than that of silver fir or spruce known from natural forests of Central Europe) and in the homogeneity of tree species composition. Despite the fact that our data proved the existence of heavy mast year and higher survival on SPs with lower seedling emergence, the occurrence of only moderate seed falls in the future can be a crucial moment. The long regeneration period reckoning with regeneration from more mast years does not necessarily guarantee success in this case. One solution could be the maximum use of actual seed falls with variability in the shelterwood density inducing differentiation in the growth of regeneration and active approach in regeneration of silver fir that had formed an important part of the tree species composition in the area and that almost disappeared from the stands due to human activity (BÍLEK, REMEŠ 2006). Traditional regeneration practices that include soil preparation, planting and direct seeding may still be needed to support rehabilitation during the transition to nature-based forestry (OLESEN, MADSEN 2008). At the landscape level topographical irregularities of the landform and natural disturbances should replace uniform shelterwood cutting.

CONCLUSIONS

The shelterwood is necessary for natural regeneration of beech in given conditions; nevertheless the density of parent stand is not critical for seedling survival within a wide range of shelter densities.

(1) At present in Voděrady Beechwoods ageing beech stands far behind the common rotation period are also able to produce enough seeds with good distribution.

(2) The main factor affecting the seedling survival in the first vegetation period seems to be biotic damage caused by aphids and small mammals.

(3) Thick humus horizons are unfavourable for germination.

(4) Both ground vegetation and competition from the parent stand are an important hindrance for natural regeneration. Dense regeneration from the preceding mast year negatively influences the establishment of regeneration from the following mast year.

(5) The survival of three-year seedlings is closely correlated with the second-season seedling survival and initial number of seedlings.

(6) Reduction of crown cover of the parent stand to 80% assured successful four-year development of beech regeneration.

(7) Border cutting with the outer face oriented towards the east is less suitable for beech regeneration than shelterwood systems and group selection harvesting.

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Přirozená obnova stárnoucích stejnověkých bukových porostů v podmínkách středních Čech

ABSTRAKT: Studie se zabývá přirozenou obnovou buku (*Fagus sylvatica* L.) pod vlivem různého zakmenění porostů a různých obnovních postupů ve stárnoucích bukových porostech středních Čech. Čtyři trvalé výzkumné plochy se lišily zakmeněním, korunovým zápojem a relativním ozářením. Mezi lety 2003 a 2007 byla sledována semenná produkce, vzcházení semenáčků a jejich přežívání. V dalším porostu byla sledována hustota opadu semene (všech a plných semen). Na základě zjištěných údajů byl semenný rok 2003 nadprůměrně bohatý, několikanásobně převyšující hodnoty pro plné semenné roky, popisované v literatuře. Vysoké ztráty přezimujících semen, malý počet vyklíčených semen a vysoká mortalita během prvního vegetačního období nebyly faktory se zásadním vlivem na úspěch přirozené obnovy. Mocnost nadložních humusových horizontů ovlivňovala hustotu semenáčků během všech tří následujících let. Pokryvnost přízemní vegetace byla větší mimo korunové projekce mateřského porostu a vzrůstala se vzdáleností od nejbližšího stromu. Redukce korunového zápoje na 80 % zajistila vysokou míru přežívání semenáčků během sledovaného čtyřletého období. Okrajová seč s východní orientací je méně vhodná pro obnovu buku v daných podmínkách než clonné seče se skupinovitým výběrem.

Klíčová slova: *Fagus sylvatica* L.; přirozená obnova; hustota porostu; přežívání semenáčků; mortalita; Voděradské bučiny

Corresponding author:

Ing. Lukáš Bílek, Česká zemědělská univerzita v Praze, Fakulta lesnická a dřevařská, 165 21 Praha 6-Suchdol, Česká republika
tel.: + 420 224 383 795, fax: + 420 321 610 349, e-mail: bilek@fld.czu.cz