

Dynamics of natural regeneration of even-aged beech (*Fagus sylvatica* L.) stands at different shelterwood densities

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ABSTRACT: The article presents results of research focused on the development of natural regeneration of beech stands in the National Natural Reserve Voděradské bučiny, based on information acquired in regeneration plots established in 2004 and 2009. After five years of the study, 5 different generations of beech, representing 97.4% of the whole woody regeneration, were registered. In the second year of life, the two oldest generations of seedlings had the highest mortality registered so far. The last year survival of seedlings was not influenced by increased canopy openings as a result of harvest or mortality. The data from a new plot with higher stand density confirmed the negative effect of high parent stand density on the formation of new regeneration. An elevated proportion of litter in the ground cover was found to be negatively related to the establishment and survival of beech seedlings.

Keywords: European beech; *Fagus sylvatica* L.; natural regeneration; natural reserve; stand density

Beech forests of the Czech Republic are mostly located in protected areas; beech can be considered as the most important commercial broadleaved tree species, playing an important role in the conversion of extensive spruce monocultures (JURÁSEK 2000). The species is traditionally reproduced by natural regeneration based on the frequency of mast years, which occur every 4 to 6 years on average, and such a frequency is said to be encouraged by a temperature higher than 30 °C from July to September of the prior year, although site index and high deposition of atmospheric nitrogen can also affect this frequency positively (ÖVERGAARD et al. 2007). Flowering and seed production of European beech begin at about 40–50 years of age (WAGNER et al. 2010), and its pollen effectively disperses to less than 250 m within forests (WANG 2001). Beechnuts commonly disperse by barochory usually to around 20 m (WAGNER et al. 2010), but can reach up to 125 m by zoochorous dispersal even introducing beech into stands of other species (KRAMER 2004). According to SKRZISZOWSKI and KUPKA (2008), the quite

strong growth rate of fine roots in beech seedlings during the first 4 years makes it appropriate for plantations. Additionally, for successful development, young plants need protection from parent trees against late frost, drought and high temperatures (HUSS 2004). The local high density of beech seedlings has a strong negative influence on their diameter growth and a smaller influence on height growth (COLLET, CHÉNOST 2006). According to WELANDER and OTTOSSON (1998), beech seedlings preserve a higher portion of biomass in the shoot than in the root during the first year of life, which favours photosynthesis and supports a good adaptation to low light conditions, making the species suitable for regeneration under shelterwood. MADSEN and LARSEN (1997) stated that larger canopy openings show higher variance in height growth and higher sapling density of beech seedlings. The same authors also affirmed that higher soil water content increases the regeneration growth while an increase in soil carbon content has the opposite effect, possibly due to the accumulation of raw humus, which

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results in poor nutrient supply. Similarly, under appropriate supply of water in the soil and sufficient fertilization, a relatively open canopy can generate convenient conditions for a large increase of beech seedling growth (MADSEN 1995). There is also a relation between different provenances of beech in Europe and their response to soil water content, so that provenances from lower altitudes show higher increments in growth under conditions of high soil water content as a sign of adaptation to longer vegetation period and higher precipitation amount (NIELSEN, JØRGENSEN 2003). Different studies showed that although beech possesses mechanisms for responding to water deficits, it is not a drought-tolerant species (FOTELLI et al. 2009). When competition is strong, beech trees show a high sensitivity to water balance whereas, at a low competition level, trees react positively to high temperatures (CESCATTI, PIUTTI 1998). Seedling growth has also been related to light availability and root density of old beech (WAGNER 1999).

The aim of the study was to investigate the long-term development of seedling banks under different stand conditions after heavy mast year and following secondary beech fructifications in the locality of the Voděradské bučiny National Nature Reserve (NNR).

MATERIALS AND METHODS

The Voděradské bučiny National Nature Reserve was established in 1955 within an area of 658 ha. Most of the forest stands originated in the period 1820–1850 as a result of a very intense three-phase shelterwood system with the very short regeneration period lasting approximately over 15 years, which, in consequence, formed even-aged stands

with the relatively simple vertical and horizontal structure that prevail on the major part of the reserve. Only a few patches of several hectares of old-growth forests were left unmanaged since 1955 on the area, and they exhibit relatively heterogeneous stand structures (BÍLEK et al. 2009).

In 1980, five 1 ha permanent research plots (PRP) were established in even-aged beech forest stands of the NNR in order to analyze their stand structure. In 2004, four of these plots (plots 1, 3, 4 and 5) were used again for a broader evaluation of their structure (Table 1) involving the measurement of dbh (diameter at breast height), total height, crown height, species, social status (dominant, codominant, subdominant and less than 20 m) and horizontal distribution using the Fieldmap equipment (IFER Monitoring and Mapping Solutions Ltd., Jílové u Prahy, Czech Republic). The evaluation of horizontal distribution included a description of the crown projection of each live stem by measuring a minimum of five cardinal crown radii per tree. For the study of the natural regeneration, a regular matrix of 20 × 10 m was set throughout the extent of each 1 ha PRP. Each intersection of the matrix (marked with a wooden stake) indicates the corner of a 1 m² square subplot, in which the quantification of seedlings and survival according to cohorts (generations) was registered repeatedly at the end of the vegetation period in 2004, 2005, 2007, 2008 and 2009. Each cohort found in this study is defined by the year of the seed production, which is one year before the germination of seedlings. In the first year of the study we distinguished only between 1-year-old seedlings and older ones (originating mostly from the mast year in 1995). In the same year, we registered the description of the ground cover by determining the percentages of woody regeneration, herb vegetation, dead wood, stones, mineral soil, soil covered with litter fall, roots, roads and moss, as well as the total thickness

Table 1. Stand characteristics of permanent research plots included in the study, after evaluation in 2009

PRP	Forest stand	V	G	N	ρ	D mean	H mean	Crown cover (%)	Forest type	Age (years)	Elevation (m.a.s.l.)	Exposure slope (%)
1	436C17	477.5	21.6	65	0.47	63.5	40.9	60.6	4B1	180	440	E – 15
2	32D15z	623.0	42.5	304	1.21	40.9	28.3	100.4	4K3	165	490	Plain
3	434B17	800.6	37.7	117	0.82	62.8	40.0	97.6	4S4	190	450	N – 20
4	434E17	606.6	28.3	90	0.62	62.0	40.0	69.3	4S4	185	460	E – 17
5	436D17	576.0	27.8	110	0.63	55.7	39.3	75.1	4K3	170	440	E – 15

PRP – permanent research plot, V – volume (calculated for timber above 7 cm of diameter over bark (m³·ha⁻¹)), G – basal area (m²·ha⁻¹), N – number of trees (individuals·ha⁻¹), ρ – stand density, D mean – mean dbh (cm), H mean – mean total height (m)

of holorganic and Ah horizons (double measurement in the opposite corners of the plot) and distance to the nearest tree. In 2009, the fifth of the PRP's initially established in 1980 (PRP 2) was also included in our research for the study of stand structure and natural regeneration (Table 1), and therefore, for this plot, we registered two cohorts only (cohort 2008 and older than 2008). The silvicultural system applied in the area is shelterwood, although on two PRP (3 and 4), a combination of shelterwood and border cutting is carried out. Due to the lack of normality in the data distribution, it was necessary to include in the calculations the Kruskal-Wallis non-parametric method to determine the degree of statistical difference among samples, and the Spearman correlation coefficient to verify correlations between variables. The Statgraphics Centurion XV software was employed for the calculations of statistical values.

RESULTS

Considering PRP's 1, 3, 4, 5, besides beech other 10 species were present in the woody regenera-

tion: Norway spruce (*Picea abies* [L.] Karst.), sycamore maple (*Acer pseudoplatanus* L.), hornbeam (*Carpinus betulus* L.), silver birch (*Betula pendula* Roth.), larch (*Larix decidua* Mill.), rowan (*Sorbus aucuparia* L.), willow (*Salix caprea* L.), silver fir (*Abies alba* Mill.), Scotch pine (*Pinus sylvestris* L.), and poplar (*Populus tremula* L.), which account for 1.24, 0.56, 0.34, 0.28, 0.28, 0.17, 0.17, 0.17, 0.11 and 0.11 thousand individuals per hectare on average, respectively. Most of them were registered after 2007 and emerged at the border of the stands. In 2009, these species represented 2.6% of the total woody regeneration in the four PRP's. This concurs with the proportion of species in the canopy, since beech represents 99.2% of the canopy individuals in the plots of the study, regardless of the existence of patches of other species in the surroundings of the area.

The total number of beech seedlings registered for plots 1, 3, 4 and 5 till 2009 (Table 2) shows the highest density of the regeneration of cohort 2003 in plot 1, with almost 300 thousand seedlings per ha during the first year (Fig. 1). After five years of study, the number of seedlings remaining from

Table 2. Average density of beech seedlings on four permanent research plots (thousands per hectare) and values for the Kruskal Wallis test

Year of evaluation	Cohort	PRP 1	PRP 3	PRP 4	PRP 5	Kruskal-Wallis test <i>H</i>	<i>P</i> -value
2004	older than 2003	13.8 ^a	6.7 ^b	30.3 ^{abc}	5.5 ^c	23.64	0.000
	2003	298.8 ^a	78.1 ^{ab}	197.0	167.9 ^b	8.84	0.031
2005	olther than 2003	11.8 ^a	6.3 ^b	24.2 ^{abc}	4.2 ^c	13.74	0.003
	2003	218.2 ^{ab}	36.9 ^{ac}	68.8 ^{bd}	114.3 ^{cd}	14.85	0.002
2007	older than 2003	10.9 ^a	6.1 ^b	23.7 ^{abc}	3.1 ^c	18.43	0.000
	2003	202.6 ^{ab}	24.4 ^{ac}	50.3 ^{bd}	94.9 ^{cd}	18.23	0.000
	2006	64.8 ^{ab}	75.4 ^{cd}	9.0 ^{ac}	22.7 ^{bd}	47.12	0.000
2008	older than 2003	10.0 ^a	5.8 ^b	21.8 ^{abc}	3.0 ^c	16.46	0.001
	2003	201.4 ^{ab}	24.2 ^{ac}	42.8 ^{bd}	94.3 ^{cd}	20.96	0.000
	2006	47.7 ^{ab}	40.6 ^c	4.4 ^{acd}	18.4 ^{bd}	38.37	0.000
	2007	5.2 ^{ab}	0.6 ^a	0.0 ^{bc}	2.8 ^c	12.18	0.007
2009	older than 2003	10.0 ^a	5.8 ^b	21.5 ^{abc}	2.8 ^c	15.86	0.001
	2003	191.4 ^{ab}	21.7 ^{ac}	39.0 ^{bd}	89.4 ^{cd}	22.66	0.000
	2006	42.8 ^{ab}	30.3 ^{cd}	2.8 ^{ace}	12.6 ^{bde}	44.68	0.000
	2007	3.7 ^{ab}	0.3 ^a	0.0 ^{bc}	1.2 ^c	9.69	0.021
	2008	16.9 ^{abc}	3.8 ^a	6.6 ^b	4.5 ^c	15.61	0.001
total (2009)		264.7	61.9	69.9	110.6	–	–

P-value – probability for the Kruskal Wallis test; values marked with the same latter (a, b, c, d, e) indicate statistical difference between plots

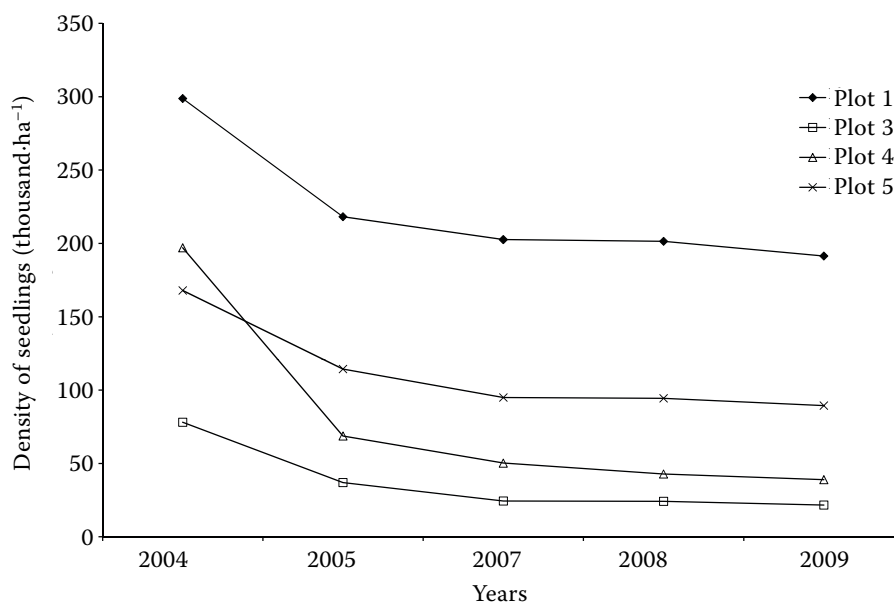


Fig. 1. Average density of beech regeneration (cohort 2003) in four PRP's

those 300 thousand·ha⁻¹ equals the initial number of seedlings of the same cohort in plot 4 (almost 200 thousand·ha⁻¹), which is the second highest density among the four plots in 2004. The plots show a similar tendency of decrease for this cohort during the years, except for plot 4, which presents a higher decrease during the second year, placing it as the third highest density among the plots. These results do not concur with the number of seedlings older than 2003 (Fig. 2), given that in the last case the highest density is reached by plot 4, and plot 1 takes the second place. As stated by BÍLEK et al. (2009), the density of young seedlings is negatively influenced by the presence of older cohorts.

In 2009, a recount of the stock of research plots registered a reduction in the number of parent

trees present in plots 1, 3, 4 and 5 due to harvesting or mortality; such reductions were equal to 30, 7, 18, and 6%, respectively. To evaluate the possible effect that removed trees could have on the survival of seedlings, we separated all subplots in two groups (one group of subplots for which the nearest tree was still the same, and one group for which the nearest tree changed). The first group averaged 90% of survival for the cohort 2003 during the last year and the other group averaged 87%, which led to an $H = 0.22$ and $P = 0.64$ in the Kruskal-Wallis test, showing insignificant difference. Only 17 of the 196 subplots on 4 permanent research plots were included in the group of changed nearest tree subplots and the small number of individuals in them made it possible to compare only cohorts

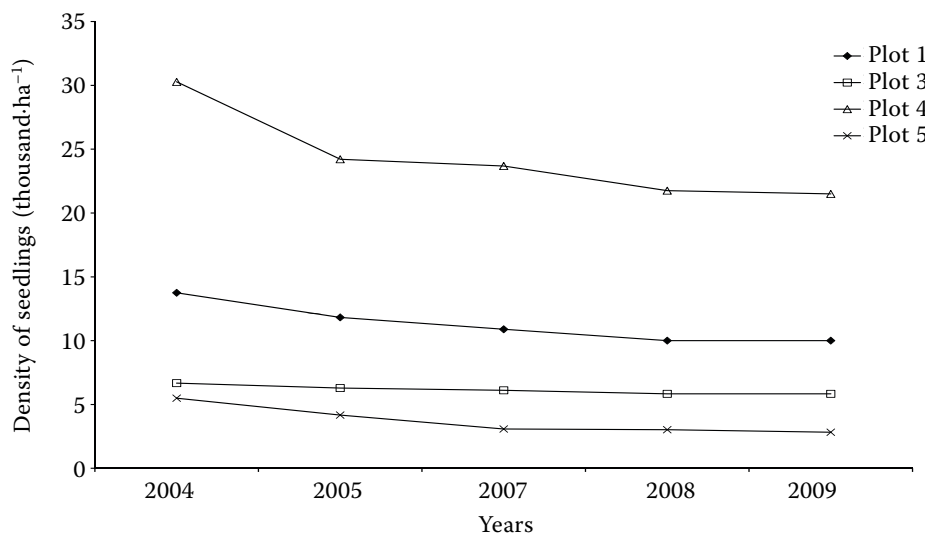


Fig. 2. Average density of beech regeneration (seedlings older than cohort 2003) in four PRP's

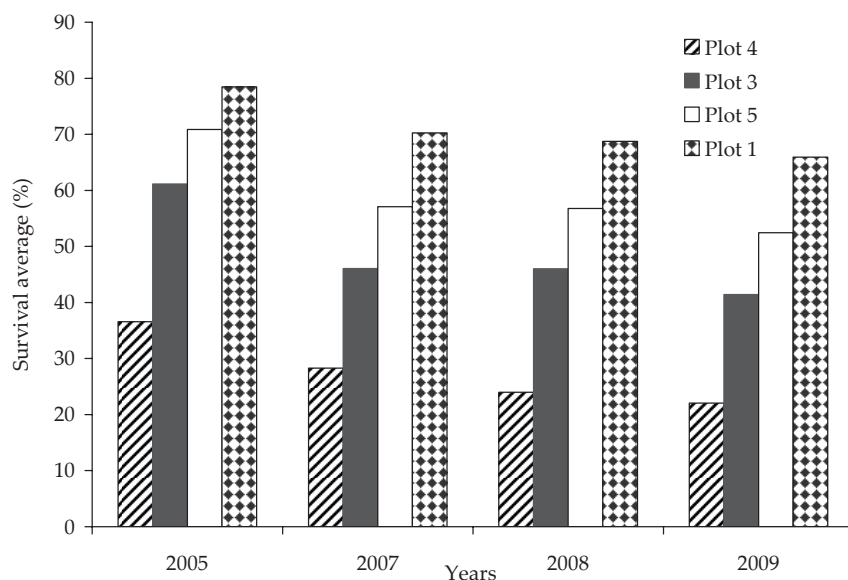


Fig. 3. Average survival of beech regeneration (cohort 2003) in four PRP's

2003 and 2007. For the latter one, we did not register a significant difference between both groups either ($H = 0.59$, $P = 0.44$).

The density of the two latest generations in their first year, cohorts 2007 and 2008, ranged between 0 and 5.2 thousand·ha⁻¹ for the first one and 3.8 and 16.9 for the second one, which is even less than in cohort 2006 with 9.0–75.4 thousand·ha⁻¹. All these three generations originate from intermediate seed falls that did not reach the initial number of seedlings like in the full mast year 2003, which ranged between 78.1 and 298.8 thousand·ha⁻¹ for the research plots (Table 2).

The different generations of seedlings were analyzed separately. Cohort 2003 showed a high mor-

tality rate between 2004 and 2005 (Figs. 1 and 3) especially in plots 3 and 4, where border cutting was performed (63 and 39%, respectively), but since 2007 the mortality ranged from 1% to 15% on a very constant average year by year in all four plots. Only in plots 3 and 5 a small change was observed – almost no mortality by the year 2008, which resumes the following year. The group of seedlings older than cohort 2003 also showed higher mortality in 2005 than in the subsequent years (Fig. 4), but in this case the highest mortality rates were recorded in plots 5 and 4 (25 and 33%, respectively). The plots experienced unequal but very constant mortality during the years, with values from 0% to 7% yearly, although plot 5 had a very high mortality

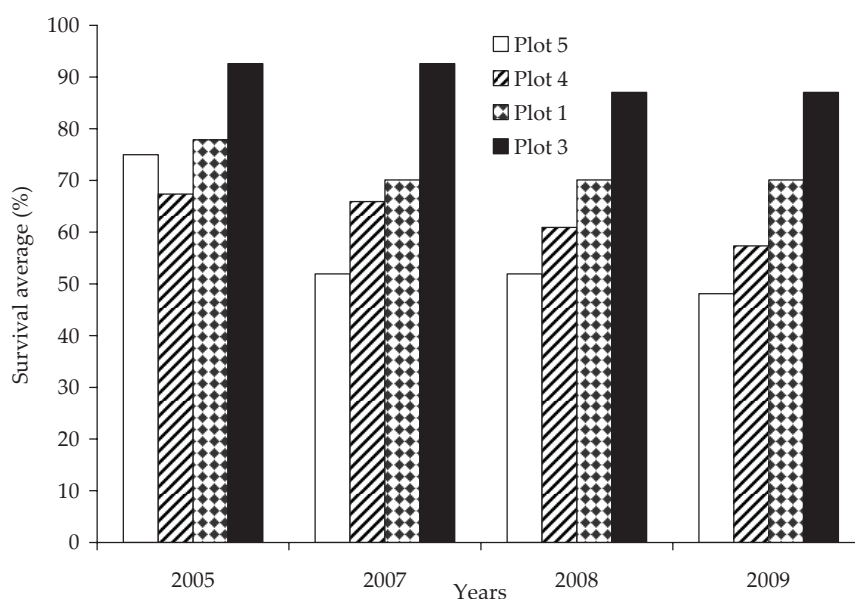


Fig. 4. Average survival of beech regeneration (seedlings older than cohort 2003) in four PRP's

rate from 2005 to 2007 (23%), reaching 11.5% a year (Fig. 4). The values of mortality for cohort 2006 in the year 2008 were very similar to those in cohort 2003, where plots 3 and 4 also had the lowest survival, but in this case the mortality was still considerably low for the year 2009 (39% to 48% in the four plots), except for plot 1 with 11% mortality in 2009. Cohort 2007 also had elevated mortality for 2009 with 29, 50 and 50% in plots 1, 3, and 5 (plot 4 did not register any seedlings from that generation in 2008).

We also organized the subplots of the four old plots according to the initial number of seedlings from cohort 2003 and divided them into three groups (1 to 10, 11 to 40, and more than 40 seedlings) in order to evaluate the relation between the initial number of seedlings and survival (Fig. 5). The results show that in the second year of life (2005) the highest mortality over the years of the study was confirmed for each group; the highest survival rate occurred in subplots with the lowest initial number of seedlings, the lowest survival occurred in subplots with medium number of initial seedlings, and the medium survival was in subplots with the highest initial number of seedlings. In the fourth year of life (2007), the mortality rate was 17% as an average of the three groups, in the next year it was 3% on average, and a slightly higher mortality of 6% was observed in the year 2009.

The analysis of Spearman correlation between ground cover attributes and survivals showed the following results: for seedlings older than 2003, the survivals showed a negative correlation with the percentage of litter in 2005 ($R = -0.2911$, $P = 0.0208$) and 2009 ($R = -0.2955$, $P = 0.0406$), and with the percentage of roots only in 2007

($R = -0.3289$, $P = 0.0156$); for cohort 2003, the survivals proved a negative correlation with the percentage of litter in 2005 ($R = -0.1686$, $P = 0.0438$) and 2007 ($R = -0.2563$, $P = 0.0031$); for cohort 2006, the percentage of stones and deadwood showed a negative correlation with the survivals only in 2008 ($R = -0.1855$, $P = 0.0430$ and $R = -0.2032$, $P = 0.0267$, respectively); lastly, for cohort 2007, the ground vegetation showed a negative correlation with the survivals in 2009 ($R = -0.4789$, $P = 0.0282$).

The density of seedlings in plot 2 represents a remarkable difference compared to the other four plots, since the values for new beech seedlings (cohort 2008) and older ones are 0.8 and 2.1 thousands·ha⁻¹, respectively (in 2009 the density of plots 1, 3, 4, 5 was 3.8–16.9 and 58.1–247.8 thousand·ha⁻¹ for one-year-old seedlings and older ones, respectively – Table 2). However, apart from the large differences in the main tree stock (Table 1), the soil cover of plot 2 was found to be statistically different from the rest of the plots (Table 3), specifically considering humus thickness, percentage of litter and percentage of deadwood. In those three cases the comparison of old plots (1, 3, 4 and 5) showed no significant difference, but the inclusion of plot 2 in the process changed the result and revealed a significant difference. Moreover, the pairwise comparison of plot 2 with each of the other plots confirmed significant differences. The reason is that the cover of humus and deadwood (8 and 4% in plot 2) doubled the average in the rest of the plots, while the percentage of litter amounted to 93% in plot 2 and averaged 62 on the other plots. On the other hand, the evaluation of the other soil cover attributes produced diverse results; the percentages of mineral soil, stones and

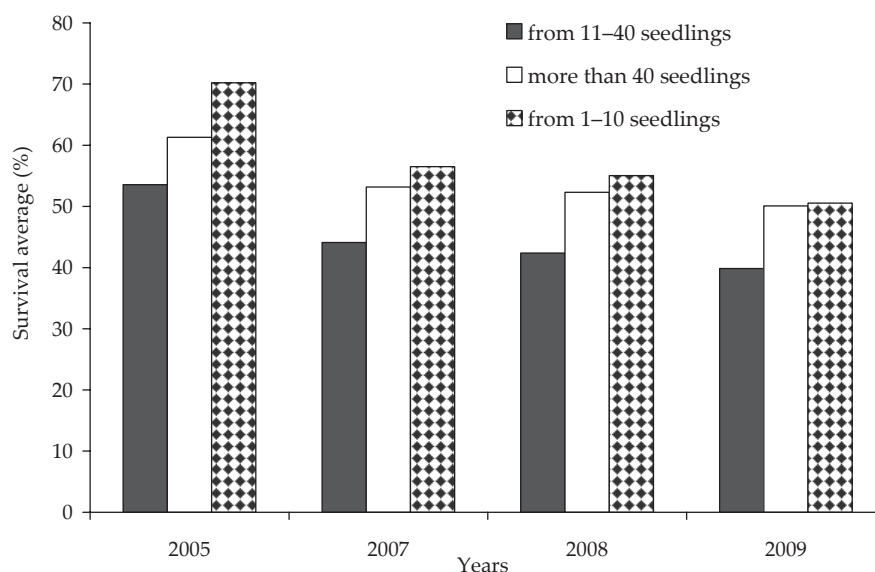


Fig. 5. Average survival of beech regeneration (cohort 2003) in four PRP's after the classification of subplots according to the initial number of seedlings

Table 3. Average values of ground cover attributes for the five PRP's

PRP	Thickness of Ah (cm)	Regeneration (%)	Litter (%)	Herbs (%)	Dead-wood (%)	Min. soil (%)	Stones (%)	Roots (%)	Moss (%)	D (m)
1	4.3	12.00	60.4	23.0	1.7	1.5	0.2	0.3	0.57	4.3
2	8.0	0.14	92.8	0.3	4.1	0.1	0.8	0.5	1.27	2.0
3	4.0	6.50	64.8	19.9	1.5	0.4	6.7	0.1	0.22	5.3
4	4.5	11.40	70.3	13.8	4.0	0.2	0.5	0.2	0.02	4.1
5	4.1	7.20	54.2	34.9	1.3	0.2	0.3	0.8	0.65	3.8
Kruskal Wallis <i>H</i>	88.88	76.30	40.78	64.30	75.07	20.48	37.50	3.33	17.73	58.66
<i>P</i> -value	0.0	0.000	0.000	0.000	0.000	0.000	0.000	0.505	0.001	0.000

Thickness of Ah (cm) – thickness of holorganic and Ah horizons, Min. soil – mineral soil, *D* – distance to the nearest tree, *P*-value – probability for the Kruskal Wallis test

vegetation showed significant differences including plot 2 in the process and without it, but the percentage of roots did not denote any such differences among or between any plots. The case of the ground vegetation cover has a particularity, since the value for plot 2 averaged 0.3% compared with the values 13.8–34.9% of the rest of the plots, which is still a significant difference regardless of the variability within the whole group of plots. The indicator – distance to the nearest tree – in plot 2 (2 m on average) reached approximately only 50% of the values observed in the other plots. The differences were statistically significant both for the group of five plots and for most of the combinations in the pairwise evaluation.

Among the different factors of soil cover registered for plot 2, the only ones that represented a significant correlation with the cover of regeneration were litter ($R = -0.4187$, $P = 0.0028$) and vegetation ($R = 0.4875$, $P = 0.0005$). Comparing the same soil cover factors with the absolute values of regeneration of young and old beech seedlings the ground vegetation cover maintained a positive correlation with the old seedlings ($R = 0.5459$, $P = 0.0001$), while the young ones showed only a weak correlation with the presence of roots ($R = 0.2999$, $P = 0.0322$).

DISCUSSION

The highest mortality of cohort 2003 was registered in the second year of life. In 2005, the registered mortality could indicate a strong struggle for adaptation to climatic conditions, possibly worsened by severe damage caused by aphids; besides, the sharing of space between two different large groups of seedlings (cohort 2003 and older ones) would definitely favour the older ones by virtue of better adaptation and vigour. The preservation of a

low and very constant rate of mortality after the second year of life, regardless of the degree of mortality at the beginning, supports the theory that after the second year of life the seedlings have overcome quite a difficult stage, after which the level of adaptation reduces the mortality rate independently of the treatment or structure of the main stand. Even when comparing groups of subplots with different initial number of seedlings, it is possible to notice a clear difference between the second year survival and the subsequent years. The highest mortality registered in plot 4 by the second year of life may be related to the very abundant advanced regeneration present there (possibly as a result of openings in the canopy of the parent stand) that can represent a restraint for new seedlings in their competition for resources. We have no exact explanation for high mortality suffered by seedlings older than cohort 2003 by the year 2005, but it is likely to be related to the damage caused by small herbivores. The persistent correlation found between the percentage of litter and the survivals of cohort 2003 and older seedlings is an indication of how locations with inadequate fertility, soil moisture and/or illumination can restrict the development of regeneration and ground vegetation, which leaves space mainly for slowly decomposing layers of litter.

The dynamics of the regeneration in plot 2 is a clear evidence of the great effect of parent stand density on the establishment and development of seedlings under the canopy. Almost total absence of individuals of regeneration of any tree species within this plot (few seedlings registered in the plot germinated at the border of the stand) confirmed increased competition for resources (light, water, nutrients) as a result of high stand density with entirely closed canopy. Although a negative significant regression between canopy openness and mean density of beech seedlings has been described in other sites (MODRÝ

et al. 2004), a range from 10 to 40% of relative light intensity is considered to be optimal conditions for a sufficient number and satisfactory morphology of beech seedlings (NICOLINI et al. 2001, WAGNER et al. 2010). The depth of humus in plot 2 is quite superior to the other plots perhaps because of the lack of slope and the high intensity of leaf fall coming from the canopy that, giving the deficit of light, has a low decomposition rate. It is understandable that the high stand density not only greatly affects the amount of light reaching the ground but also additionally reduces the area of land available to the seedlings, which can result in an increase in competition for soil water from the neighbouring trees. Nevertheless, it would be very interesting to define the exact difference between the soil water content available in plot 2 and that existing in one of the other plots, since the existence of seedlings around the borders, where light is higher but density is not different, could indicate that the availability of light is a greater limitation for seedlings than the supply of water.

The number and distribution of seedlings in research plots 1, 3, 4 and 5 are sufficient to assure the natural regeneration of the stands. Nevertheless, in spite of the fact that even after a long period of suppression the height growth of beech seedlings increases following each canopy disturbance (COLLET, CHÉNOST 2006), the seedling banks formed under given conditions are not stable and require additional improvement of microsites. The key to the regeneration improvement lies mainly in the type of management and density of the stand. The explanation why in plot 4 a large proportion of seedlings older than cohort 2003 reached more than 2 m in height is still unclear. Even though the large gap at one side of the plot is greater than any other gap in the research plots, plots 1 and 5 also have similar canopy cover, though more disperse. For the rest, the density of stems and crown cover proved to be a constraint for regeneration when it assumes high values.

CONCLUSIONS

After five years of the study, our research supports the following conclusions: a small density of seedlings (less than 10 per m²) established in the first year favours their long-term survival; none of the soil cover attributes shows a clear effect on the survival of seedlings; regeneration under the shelter of parent stand reduces the competition of herbal vegetation and other than shade-tolerant tree spe-

cies; full stand density prevents the establishment of any kind of regeneration. Although the highest mortality rates were observed only in the first 3 years of life of the regeneration, even after 5 years the stand cannot be considered as fully established.

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