ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE
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DISERTAČNÍ PRÁCE

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Struktura a obnova porostů s odlišným způsobem managementu v podmínkách NPR Voděradské bučiny

vypracoval samostatně pod vedením prof. Ing. Iva Kupky, CSc. s využitím citované literatury na Katedře pěstování lesů, Fakulty lesnické a dřevařské, České zemědělské univerzity v Praze. Souhlasím s případným zapůjčením práce pro studijní a vědecké účely.

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Structure and regeneration of forest stands with different management in the conditions of the National Nature Reserve Voděradské bučiny

Struktura a obnova porostů s odlišným způsobem managementu v podmínkách NPR Voděradské bučiny

Disertační práce

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1. INTRODUCTION

Central Europe is an area of very divergent forest conditions and a very long forestry tradition intensively influencing species composition and structure of forests over last 300 years. Once the most widespread tree species in original forests, European beech was widely exploited for various purposes, degraded to a commercially not interesting species in the last two centuries and re-discovered by the ecologically oriented forestry of the last decades. As a result nowadays, we see a rapidly changing position and the status of beech and beech forests, with an increasing demand for knowledge about its ecology and possibilities of near to natural forest management.

In the past European beech covered almost 40% of the total forest area of the Czech Republic, but nowadays its representation is less than 6%. Nevertheless beech forests still cover a large part of the European landscape and are a major resource for timber production, biodiversity conservation, amenity and watershed protection. We can expect that European beech due to its favourable conditions, will gain more importance in the future Czech forests. It is resistant to biotical and abiotical stresses (insect plagues, fungal attacks, wind, storm, pollution), it helps to increase the biological diversity of forests (species, age, pattern, structure, ecosystem processes) and it improves water and soil protection (unstable soils in flysh areas), 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. Both biodiversity and quality timber production as well as sustainability of forests will benefit of its substantially higher representation in forests. This literature research covers the region of European beech forests (*Fagus sylvatica* L. without *subsp. orientalis*), with special focus on the conditions in the Central European uplands.

2. LITERATURE RESEARCH

2.1. History and Management of Beech in the Central European Uplands

2.1.1. Pre-industrial period (From the Neolithic period to 1700)

Beech (*Fagus sylvatica* L.) survived the Quarternary cold periods in the Balkans and the Apennine peninsula. Its post-glacial migration to the North from the latter area had been blocked by the geographical barriere of the Alps. As a consequence, the whole present European area of beech had been colonized from the refugia in the Balkans (Demesure et al. 1996; Taberlet et al. 1998). During its post-glacial migration, beech colonized a broad area of Europe in both lowlands, colline-submontane, montane-altimontane and subalpine zones and became the most widespread tree species of Central Europe (Ellenberg 1996).

From the Neolithic times onwards (in Central Europe from ca. 5500 BC) the colonization of Central Europe by man had changed landscape patterns – first in the fertile and warm lowlands; then extending gradually to the beech-dominated submontane and montane zones. Deforestation and fragmentation of forest cover continued with varying intensity in parts of Central Europe until the Middle Ages. The abandonment of migratory life, population growth, change in the social structure of the population, technical progress and organized land colonization in the early Middle Ages enabled further and more intensive use of landscape, which resulted in ongoing deforestation and forest fragmentation. At the end of the Middle Ages the forested land in Central Europe was reduced to its minimum extent.

2.1.2. Beech Forests in the Industrial Period (1700 – 1980)

The beginning of the 18th century is marked by the first attempts and efforts to get the acute shortage of timber and wood under control. It is also the very beginning of organized forestry as a rational commercial activity aiming at wood production. Basic ideas were logged by H.C. von Carlowitz in his work *Sylvicultura Oeconomica* from 1713. Further steps in the development of the Central European forestry were made during the second half of the 1700s and in the beginning of the 1800s (Hartig 1791, 1808; Hundeshagen 1828). Forestry academies of Tharandt and Eberswalde, Germany (H. Cotta, M.R. Pressler), undertook this development, which, since the end of the 1800s, became known as the German forestry school based on the soil rent theory. Its main goal was to maximize production of timber, the sustainable yield and financial profit for the forest owner, realized in man-made forests. During this "forest restoration period" (Waldaufbauphase) from 1700 to 1980 (Teuffel, Krebs 1999), hundreds of thousands of hectares of "overexploited and degraded" forests were restored, new forests planted on derelict agricultural land in order to produce timber and wood. In this system, where clearcut was a usual and economically effective method of harvesting timber for common beech, only a modest role was reserved locally. On the other hand, since the 18th century, mixed broad-leaved forests, especially those of the middle-forest type, were converted into pure beech forests because regeneration practices favoured beech.

In the 18th century, the fuelwood shortage and rising prices made beech silviculture economically feasible (Peters 1997). Probably the first attempt to organize the beech forest management in Central Europe was the Hanau-Muenzenbergische Forstordnung by Moser from 1737 (Moser 1757). Moser laid down the principles of the 3-phases shelter wood management system, which has been applied to beech forests until the present days.

Under the influence of the soil rent theory, the representation of beech in some Central European countries diminished drastically. This development dominated during the 1800 and in the first half of the 1900s. It has especially affected countries with a long forestry tradition – Saxony, Bavaria, Bohemia, Moravia, Austria. In the present Czech Republic, e.g., the representation of beech has been reduced from more than 40% of the (reconstructed) natural representation to less than 6% today, while the share of Norway spruce increased from some 11 to 55% (Vašíček 1997). The paradigm of the Central European forestry of the 19th and the first half of the 20th century was based on the intensive treatment of forest stands organized in the age-classes system. To keep this timber production system under control in a closed management system, natural processes in forests have been largely ruled out. The attempts to develop another model of forestry, e.g. the Dauerwald (Möller 1922) and Naturgemaesse Waldwirtschaft – close-to-nature forestry (Krutsch, Weck 1935) have had some influence locally but were not broadly accepted at that time. The very last remnants of primeval forests have been spared in South Bohemia and became the first European nature reserves. Until 1950 the main function of forests, including beech woodlands, was timber and wood production. Devastating effects on forests of the World War II gave rise to a revival of nature protection movements in particular countries and attempts to development of a different forest management model, based on increasing ecological insight (Fanta 1999). Since the 1960s Central European forests have been heavily affected by the acid deposition in particular countries. Instability of coniferous plantations reached disastrous dimensions. Forests have repeatedly suffered from storms, snow and insect plagues with following unacceptably high financial losses and ecological setbacks. In the former Czechoslovakia, e.g., the salvage cut amounted to more than 60% in the period 1980-1990, with a maximum 85% in 1984 (Moldan 1990; Vašíček 1997). In 2005 the salvage cut represented 29.3% of total cut, in 2006 it amounted to 45.0% (mainly abiotic damages) – (MZe 2006).

2.1.3. Beech Forests in the Modern Period (since 1980)

Whereas low tree species diversity in natural European beech forests may be the result of millennia of human forest-use, most pure beech forests are the result of intensive management during the past three centuries. Therefore it is not clear, in which direction the European beech forest will develop spontaneously. Forests and forestry are expected to meet ecological and economical functions, which will be fully anchored in the principle of sustainability. This orientation follows the resolutions of the UN Conference in Rio de Janeiro 1992 and the following forestry conferences in Helsinki, Montreal, Lisbon and Vienna. After the political break in 1989 Czech forestry, nature conservation and management have had to face a new situation in changing economical and social conditions. This period is marked by ongoing discussion about the role of multifunctional management system and about non-production forest function in general.

2.2. Beech Forests in Czech Republic

2.2.1. General description and historical background

The total forest land of the Czech Republic is 2 649 147 ha. This represents 33.7% of the area of the country (MZe 2006). During the medieval forest exploitation and following 300 years of commercial forestry activities, the original tree species composition of forests has been strongly changed in favour of conifers, esp. Norway spruce and/or Scotch pine on less favourable sites. Since its very beginning, forestry was not concerned with beech at all; under the strong influence of the German forestry school (Hartig 1791) beech forests had been managed in a regular large-scale shelter wood system applying the 3, 4 or 5 phases procedure. An acute shortage of wood in the 1800s was the main reason to introduce, on large scale, monocultures of coniferous tree species. In the 1930s Czech forestry achieved several important impulses. New ecological ideas and their application to forestry were introduced by Konšel (1931). As a reaction to the growing disastrous impact of insects (*Lymantria monacha* L., *Ips typographus* L.) in the 1950s, the Czech forestry sector developed a strategy of conversion of coniferous monocultures into mixed forests, principally based on a small-scale shelter wood system (Polanský 1956). In this concept beech should play an ecologically stabilizing element, but unfavourable political situation turned the Czech forestry back to coniferous monocultures with preferential use of clear-cuts. Increasing environmental pollution and inappropriate forestry management on endangered areas resulted in partial destabilization of forests in these parts of Czech Republic (an extremely high casual felling and an extensive forest dieback of mountain forests) - (Kubíková 1991). Nowadays we see a return to the approach developed in the 1950s, where beech again will gain more importance.

2.2.2. Concepts of management and conservation

With the exception of protected forests, most beech forests have a production function or have been managed as multifunctional forests with a preference for timber production (Lesprojekt 1983). Beech forests on extreme sites (e.g. dry calcareous, steep slopes, high mountainous) have been proclaimed nature reserves with a nature and/or soil protection function, or made part of national parks and/or protected landscape areas. From the total area of 153.000 ha of beech forests in the country more than 115 000 ha fall under one or another category of conservation or protection.

The practice of forest management follows in general, the directives and recommendations linked up with forest typology (Ministerstvo zemědělství 1997). Within this approach, clear cuts up to 1 ha, large and small-scale shelter wood and selection practices are allowed to achieve the management target types expressed in % of the tree species representation in particular situations. Intensive tending of young stands aims at achieving quality, by removing "forerunners" and trees with a fork or broom stem form. Also the desired admixed tree species can be best supported in this development stage (Indruch 1985). The target of thinning is to achieve the highest possible stem quality of all trees in the upper level of stands, both beech and admixed species. On mesic sites in the age range 60-70 years the number of trees in the upper canopy can be as high as 400 ind. per ha, grown in closed canopy and with an understorey without openings. Further tending to matured stands aims at regular development of the crowns of the best trees, and stimulation of the dbh increment to achieve the desired dimensions. Within this approach, natural regeneration can be taken for granted, especially when the large-scale shelter wood system has been applied (Indruch 1985). By applying a small-scale approach, however, the desired representation of valuable admixed broadleaves (oaks, ash, linden, elms, sycamore maple, wild cherry etc.) can be better on protected during the natural regeneration. Also the risk of failure of natural regeneration is limited and control over development, can be better realized in a small-scale shelter wood system (Polanský 1956).

Today, forests in nature reserves, national parks and protected landscape areas comprise approximately 25% of forest cover of the country. Due to the fact that these protected areas are mostly situated in hilly and mountainous areas, beech forests there play an extraordinary important role, supported by the Nature and Landscape Protection Act (1992). As mentioned earlier, 75% of all beech forests lie in these protected areas. This fact results in the necessity of multifunctional conception of beech forests. The ecological, protective and social functions attain more emphasis than timber production. Nature reserves are also an important reference object for managed production forests and a true playground for evaluating new methods for near natural silviculture based on principles of sustainability (Průša 1985).

Since the 1970s the remnants of natural (beech) forests in nature reserves have been subjected to research and monitoring to reveal scientific information about the natural dynamics of these forests (Míchal 1983; Vrška et al. 2001). Within this research program, valuable information has been gathered which, among others, can be applied in both regular and restoration forest management. Management principles of protected beech forests based on the biodiversity concept, natural ecosystem dynamics and maximum use of natural processes have been formulated by Moravec, Míchal (1999).

2.2.3. History of Forest Management in the study area Voděradské bučiny

In the historical period before the first settlement the human impact on the area was very sparse. In the year 1088 we find the first allusion to the existence of the village Voděrady (similarly in 1318 Mukařov, 1320 Střimelice, 1321 Zvánovice). The study area was always part of the manor of Černý Kostelec, whichrom 1558 to 1621 belonged to the descendents Smiřičtí (Šrámek 1983). At that time the forest was appreciated rather for its richness of game than for its wood producing function. We have no precise information about the form of management, but we assume the existence of high grading followed by natural forest regeneration (Rakušan, not published). The impact of the Thirty Years' War was devastating for the area. Sixteen villages totally disappeared. With the decrease in human population also, the forest management became less intensive. Due to abandonment of agricultural land the total forest area increased. In 1655 the manor devolved to the Liechtenstein family that remained owner till 1933. With the help of the oldest forest management plans we are able to restore the progress of forest management over the following centuries. Since 1740 the principle method is the shelterwood felling, often with retaining of standard trees. In the Dominican land register from 1775 we find information about the disconsolate forest conditions in the area. In the forest district Voděrady, 2/3rds of the whole area are covered by coppice forest or by forests without any portion of old growth wood. Large diameter wood namely softwood occurs in only 1/3rd of the district (Pokorný 1962; Šrámek 1983).

The year 1780 represents the beginning of artificial regeneration that at first increased the representation of conifers, especially of Norway spruce and Scotch pine. Between 1790 – 1800 local foresters start sowing acorns, pine and birch. Before 1800 the main conifer used in the plantation was pine, after 1805 spruce. Until 1850 only seed of local origin was used for the forest establishment. Purchase and import of allochthonous planting stock was more common after 1860 (Pokorný 1958). In 1802 the first forest nursery for European larch was established (Rakušan). The main method of regeneration is still shelterwood felling with reserving of seed trees - 42 trees per hectare. After 1838 in accordance with the new forest instruction the three-phase shelterwood felling was implemented. The whole parent stand being removed within 12 – 15 years. Release felling was followed by secondary felling and after next 4 or 5 years the whole process was finished by final cutting (Šrámek 1983). This very short regeneration period results in almost pure and even-aged beech stands (Pokorný 1963). The first half of the 19th

century is the period with the highest harvesting rates in the area. Large scale reforestation of felled forests took place. From 1810 to 1850 almost 500 ha of the area (i.e. 76% of the surface of Voděradské bučiny) was felled and again regenerated.

The year 1848 represents an important turning point in the history of local forests. The new forestry instruction implements large area management with consecutive reforestation of spruce. In 1865 the first stand conversions from coppice-with-standards to high forest took place but most of them were realized from 1900 to 1910. After the assignation of the forests to the Czech Agricultural University clear felling was totally abandoned, the reforestation is almost entirely realized in the natural way using border felling combined with shelterwood felling. Until now, a very fine shelterwood system with dominant natural regeneration is practiced in the protected area.

Human activities from the very beginning of the colonization until now have had very strong impact on the stand structure of the forests and also tree species composition has changed dramatically (Table 1.).

Table 1. Development of tree species composition in the forest stands of Voděradské bučiny.

Year	Norway spruce	Silver fir	Scotch pine	Silver oak	European beech	Hornbeam	Other
1650	6%	44%	2%	6%	33%	4%	5%
1735-1780	6%	33%	5%	6%	39%	9%	2%
1859	13.5%	4.5%	0.3%	3%	46.1%	26.3%	6.3%
1936	33.8%	1.6%	3%	9.2%	35.5%	7.3%	9.6%
1961	30.9%	1.8%	2.5%	10.5%	38.3%	6.6%	9.4%
1991	34%	0.9%	2.2%	8.6%	42.4%	4.3%	7.6%

Among others the table shows that Norway spruce and Scotch pine are an autochthonous species in Černokostelecko. Nevertheless they never formed pure stands and expanded first after the forest devastation. The middle of the 17th century was the time the first historical report was compiled about forest conditions, the main tree species being the silver fir. Its dramatic decrease reflects the increasing impact of humans during the centuries. The decline has four main reasons. For its slower growth and sensitivity the silver fir was removed from plantations sooner than Norway spruce. Similarly in the old growth stand during the regeneration felling the silver fir was removed on behalf of the beech (Pokorný 1963). Silver fir also suffered from the conversion to low forest, where only broadleaved species were cultivated. Finally strong wind disturbances from 1735 – 1737 could have had an influence on the tree species composition (Pokorný 1958). The main tree species is the European beech, which often forms almost pure stands. As a shade tolerant tree species it regenerated successfully under the parent stand and was only rarely artificially regenerated (Čvančara, Samek 1959). Until the end of the 19th century only autochthonous seed was used for forest establishment. The purchase and import of allochthonous planting stock (mostly from Jeseniky Mts. and Českomoravská vysočina) is more common after 1900 (Pokorný 1958; Šrámek 1983). It is highly probable that stands of beech older than 110 years are of the local origin. The National nature reserve Voděradské bučiny has been established in 1955 (issue MKŠ n.13600/55) on the total area of 658 ha with the object to protect large old beechwoods with near to natural stand structure and natural species composition. In the same year the reserve was divided into two parts, one with total protection (only damaged or uprooted trees and snags could be removed) and the other with forest management aimed at the enhancement of forest structure. In the year 1971 this arrangement was cancelled. Recently it was decided to create 60 ha of (core) zone without any forest management.

2.3. The Environment of Beech

2.3.1. Temperature, Water and Soil

Temperature is an important climatic factor that affects the range limits of beech. Temperature not only determines its presence or absence, but also affects tree vitality and success of flowering. Under favourable moisture conditions, the length of the growing season increases with an increase of temperature (beech flushes earlier, but the leaf fall remains about the same time). In European lowlands, the length of the growing season increases towards the south. For example from south Sweden to north Germany the growing season increases from 140 to 170 days (Peters 1997). On the other hand the length of the growing season doesn't seem to be limiting the range of the beech. At the upper altitudinal limit of *Fagus sylvatica* L. in Bosnia (altitude 1800 m) the growing season is only 100 days. Beech can survive extreme minimum winter temperatures of – 35 °C, but a late spring frost may restrict beech in areas with sufficiently high summer temperatures and humidity (young leaves freeze at – 2.0 to – 2.5 °C, seedlings die back, failure in seed production) - (Peters 1997).

Beech is absent where rain is insufficient, or where the soil is too dry (Ellenberg 1996). In Southern Europe beech occurs only on mountains with low possibilities of drought and with frequent fogs. In the Apennines beech does not occur lower than 1000 m asl. and in Greece not lower than 1300 m asl. (Svoboda 1955). In the southwestern limit of the beech range moist Atlantic winds are of great importance. Moisture deficit is responsible for the lower altitudinal limit of beech (Peters 1997).

Beech occurs over a wide range of mesic soils, with pH ranging from 3,5 to over 7, and humus form mull to mor (Le Tacon 1981). In central Europe, beech dominates the major and central part of the moisture and nutrient range of forests (Ellenberg 1996). Soil textures range from clay-loam to loamy sand. Water availability is important, especially if the summer precipitation is irregular or insufficient. Beech is neither found on soils with pseudogley, nor when reducing conditions are found within 20 cm from the soil surface (Otto 1994; Le Tacon 1981). Among broadleaved trees in Europe, beech and oak leaves are slowest to decompose, it takes about 3 years (Ellenberg 1996; Albers et al. 2004). Beech can have acidifying and podzolization effect on soil with strong humus accumulation (Peters 1997). The European beech trees mostly grow on cambisols, luvisols, podzols and leptosols (FAO 1988). See chapter 3.3.3. concerning forest typology.

2.3.2. Beech Range in Europe

The European beech (included subsp. *orientalis*) covers large temperature and moisture ranges. In the system of zonobiomes, beech forests cover the typical temperate (with short period of frost) and the warm temperate (maritime, humid) zonobiomes and the temperate and Mediterranean orobiomes in mountainous environments. Almost pure beech forest occurs in the lowland/colline zone of western and central Europe and the montane zone of southern Europe. In the montane/subalpine zone of central and southeastern Europe the conifers *Abies alba* and *Picea abies* are often dominant tree species (Peters 1997). These coniferous species have lower temperature optima for photosynthesis than beech, which gives them a relative advantage in cool summers (Ellenberg 1996). Many European beech forests may experience some water stress during the growing season, which limits the net photosynthesis. Coniferous may also dispose of higher nutrient use efficiency. The dominance of broadleaved deciduous trees in the European beech zone may be the result of the extinction of many conifer taxa during the Pleistocene and the short time during the last glaciation (Peters 1997).

Fig. 1 shows the main environmental factors influencing the nature range of *Fagus sylvatica* L. (note: without vertical distrubution; *Fagus sylvatica subsp. orientalis* not included). A: Atlantic border: partly pure land/sea border; partly wind and soil border (swamps, inundated soils). B: Boreal border: temperature and frost border in combination with short vegetation period. C: Continental Border: drought, late frosts, heat border. D: South Mediterranean border: drought and heat border (after Otto 1994).

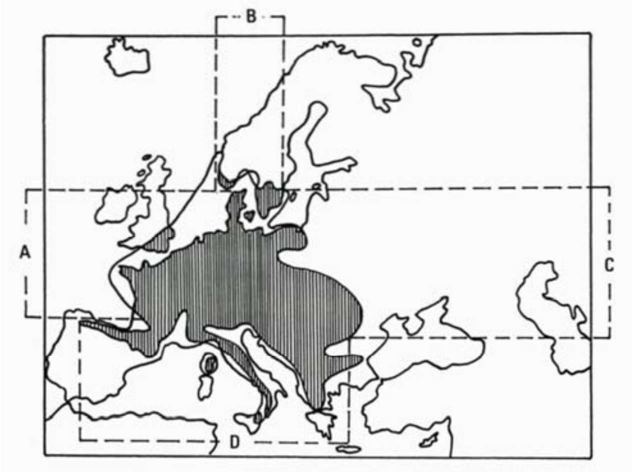


Fig.1. Definition of the natural range of beech in Europe (after Otto 1994).

Some authors describe the climate of Central Europe as a beech forest climate (Ellenberg 1996; Mayer 1984). For characterizing the limit of beech growth, Ellenberg (1996) developed an index, the so-called Ellenberg quotient (Q) for Central Europe:

$$Q = \frac{Mean\ July\ temperature\ (°C)}{Annual\ precipitation\ (mm)} \times 1000$$

Values below 20 indicate pure beech climate, between 20 and 30 its competitive vigour decreases, and above 30 oak becomes more competitive than beech.

Beech occurs from the colline sub-montane lowlands to the sub-alpine level. Summers are relatively warm and frost free, with cold winters. Summer temperatures rarely exceed 30 °C and winter temperatures rarely fall below - 20 °C. Its natural range clearly shows that beech is species of oceanic and sub-oceanic climate. In Apennines, Vosges, Schwarzwald, Pyrénées, on the Balkans, but also in Carpathian Mountains beech forms the treeline. In central Europe beech reaches its optimum by precipitations over 1000 mm and mean annual temperature about 10 °C (Otto 1994; Svoboda 1955). Wide ecological amplitude is expressed in wide range of forest types, where beech is dominant. In Czech republic beech forests occur from 350 to 1100 m asl., with mean annual temperatures from 4 °C to 8 °C and precipitation 600 to 1200 mm (Rejšek 1996).

2.3.3. Forest Typology in the Czech Republic

In the conditions of the Czech Republic, beech occured originally in the submontane, montane and subalpine zones from 300 m asl. to 1300 m asl. According to the map of the potential natural vegetation, we can identify three great groups of forest beech communities based on soil and topography (Neuhauslová et al. 1998).

- Eu-Fagenion: rich beech woodlands on mesotrophic sites in submontane and montane zones (the most important community is *Dentario-eneaphylli-Fagetum*). These also called mull beech forests grow on rendzic leptosol, eutric cambisol and luvisols, which are richer in nutrients and have a higher pH.
- Cephalantero-Fagenion: calcicole beech woodlands on eutrophic, bases-rich sites, esp. in the submontane zone (eutric cambisols located on steep slopes)

- Luzulo-Fagion: acidophilous beech and silver fir woodlands on acidic, mineral poor soils in the submontane and montane zones (most often occuring community Luzulo-Fagetum). Also called moder beech forests (common soil units are: Dystric cambisol, luvisols, umbric leptosol and cambric podzol with a low pH).

The Czech system of forest typology (Plíva 1991) incorporatesa range of forest types containing beech:

- forests with beech as the dominant species on optimal sites in the lower montane zone
- beech forests with admixed oaks on submontane sites
- mixed beech-Norway spruce forests in the higher montane zone
- mixed beech-silver fir forests (forest type unit with a very small representation in the reality)

2.4. Natural Regeneration of Beech Forests in Europe

2.4.1. Seed production, germination, establishment and survival

Beech generally regenerates by seeds. Seed production of beech can start very early at an age of 40 to 60 years (sooner by open canopy growing trees). It produces seeds in mast years. A frequency of every 5 – 10 years is reported (Svoboda 1955). Although this is variable and seed production in between these mast years is not uncommon. 1 kg of seed contains 3500 – 4500 beechnuts, 1000 beechnuts weigh 210 – 420 (280) g (Svoboda 1955). Seed production is influenced by summer conditions the year before seed fall. High temperatures (June and July temperatures at least 1.5 ^{o}C above long term average), sunny conditions with low precipitation, have a positive effect, whilst rain and night frost during flowering and seed set negatively affect seed production. Mast years do not occur after years with high precipitation and low temperatures in the summer months. The high precipitation in April of the current year has a negative influence on the seed production, while high precipitation and low temperatures during summer of the current year affect the production positively (Peters 1997). In the eastern part of its distribution beech flowers more often than in e.g. West Europe, but this phenomenon does not lead to more frequent seed production (Standovár, Kenderes 2003). The occurrence of mast years is lower in regions with frequent late frosts and on stands, where beech by reason of drought or low temperatures nears its natural range. 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). Table 2 shows seed production of beech forests in northwest Europe in relation with a terrestrial latitude.

Table 2. Seed production of beech forests in northwest Europe (Peters 1997).

Location	Latitude	Period	n*	No mast	Low mast	Average mast	Full mast
				(%)			
south Sweden	57	1971-1983	13	31	31	15	23
Denmark	55	1846-1955	110	47	13	25	15
England	52	1921-1950	30	33	30	10	27
Germany (Worbis)	51	1839-1873	35	66	22	9	3
Germany (Baden-Würt.)	49	1886-1909	24	42	29	21	8
Grmany (Bavaria)	49	1850-1963	114	71		18	11

*n: number of observations

A strong seed production in one year negatively affects the seed production in the next. Seed production and survival may be also 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). Phaenology of individual trees (early or late flowering), social position (height class of Kraft) and position within the stand (numbers and the proportion of vital seeds decreased from the edge to the inner stand) also affect seed production, thus the number of seeds produced can shows high spatial variability within a single stand (Standovár, Kenderes 2003).

It is generally stated that the germination of beech is problematic. Since beech has no apparent chemical defences against browsing and a poor capability to recuperate, it depends on high seedling densities to avoid predation. By full mast the percentage of empty seeds and seeds affected by parasites is lower than by low masts (Šindelář 1993). In addition to these aspects, 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 and attacks from several insects and mammals. Čermák, 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 in numbers (*Apodemus* spp.). Another response was the prolongation of reproduction period. In most cases beechnuts have better conditions for wintering in a mineral soil seedbed than in one of mixed soil. One of the underlying assumptions is that the rodents prefer to seek beech nuts in a mixed soil seedbed, since it is easier for them to find cover there than in a 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 seedling number. It is likely that the most important effect of the coverage was the reduction in evaporation and increase of soil moisture. This underlines the necessity of sufficient soil moisture for satisfactory seed germination. Canopy trees increase both interception and root competition for water and so negatively influence the conditions for germination. Dead wood can provide appropriate establishment site for tree species in certain forest types. In mixed or deciduous forest this role of logs has received less attention, although the presence of characteristic stilt roots has been observed in several Central European natural forests (Standovár, Kenderes 2003).

Beech seedlings are able to respond strongly to primary growth factors such as soil water content, nutrient supply and light intensity. Madsen (1995a) studied the interaction of these growth factors and their impact on natural regeneration of beech. Under the open canopy (13% of full light) the seedling growth increased three to four times on plots with sufficient water and nutrient supply. Often, even under the closed canopy a high coverage of germinated beech seedlings occurs. These very low relative light intensities (below 1% of full sunlight) permit first season survival of seedlings of large seeded species like beech and oak (Welander, Ottosson 1998). Without adequate light intensity increase they may all die during the next season. Fungal pathogen activity can cause high rates in first-season beech seedling mortality. Common cause of seedling mortality is damage caused by aphids. Short warm and dry periods in winter may dry out seedlings resulting in loss of viability. Once the radical has emerged from the seed, it may be killed off by late spring frost.

In the process of natural regeneration of beech forests, the formation of a seedling bank may play very important role (Swagrzyk et al. 2001). The occurrence of numerous seedlings on the forest floor is very often only an ephemeral pulse of regeneration with virtually no chance of ever attaining the sapling stage. The shade-tolerance of seedlings is not a guarantee of their success in tree stands dominated by shade-tolerant tree species (Emborg 1998) and permanent seedling banks are formed only in proximity of canopy openings. The first-season survival is not a good estimator of the likely formation of a seedling bank (Swagrzyk et al. 2001).

In European forests browsing is an important factor that often decides the success or failure of natural regeneration. Roe deer (*Capreolus capreolus*) seems to be the most important factor for the reduction in the number of seedlings. Except for deer the seedlings might be browsed by hares, mice or voles that can locally cause by gnawing on the stems of young plants high damages on beech stands. Other common browsers are red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*).

2.4.2. Growth: shade tolerance

Shade tolerance of beech is important for the understanding of its growth strategy. Shade tolerance is especially important during juvenile stages, because juveniles in the understorey are likely to be subject to shade suppression. Beech seedlings at least for some time can survive light conditions that barely permit any growth, however they become more vulnerable to attacks from pests or other damaging factors (Madsen 1995a; Collet et al., 2001).

In Denmark, Emborg (1998) found that only few beeches survived the light levels of 2% RLI (relative light intensity). Above this limit the numbers and sizes of seedlings increased with increasing light levels. Successful development of beech was ensured at RLI above 3%. Experiments under controlled conditions show that the minimum light intensity required for young beech seedlings to survive is around 1% of total radiation. Nevertheless, it may be very difficult to give the exact general thresholds under field conditions, where beech seedlings respond strongly to primary growth factors such as soil water content and nutrient supply (Madsen 1995a; Collet 2001). Even at 5% RLI Madsen (1995a) found that light was the main limiting growth factor. The optimal light levels for seedling growth are much higher. 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 by reduced growth and leaf morphology. This leaf adaptation consists of strong reduction in mesophyl thickness, but little reduction in epidermis thickness. Numerous studies have shown that beech seedlings growing under low light availability exhibit low diameter–height, root–shoot, and branch–stem ratios (e.g. Minotta, Pinzauti 1996; Welander, Ottosson 1998; Topoliantz, Ponge 2000). Under closed canopy, Collet et al. (2002) observed a reduction of secondary growth, with a progressive disappearance of latewood, a reduction in vessel diameter and a loss of the diffuse-porous organization of the wood. Important fact is that growth and morphology of the seedlings may be influenced not only by current-year light conditions but also by previous-year light (Welander, Ottosson, 1997).

In beech the proportion of dry mass allocated to the shoot is larger than to the root, whereas in the oak allocation is mostly larger to the root (Welander, Ottosson, 1998). This shift in partitioning, which may be also influenced by light intensity, differs between species and is considered indicative for a difference in shade tolerance (Van Hees, Clerkx 2003). This should imply that beech is better adapted to low light levels during the first year (the light capturing part is more favoured). However during the year of seedling emergence the oak seems to benefit from seed reserves and is also able to survive in heavily shaded conditions (Welander, Ottosson, 1998). Modrý et al. (2004) examined the effect of light and soil on basal diameter and height of nine naturally regenerated tree species. Light climate had a significant effect only on the height of beech and diameter of the beech and Norway maple. Also Madsen (1997) stated that increased canopy opening increased the potential of height growth.

Generally, the seedlings of shade tolerant European tree species utilize light dispersed under the forest canopy and do not profit strongly from direct light imput. Increased direct irradiation may lead to higher cover of herbal vegetation and increased competition for resources (Modrý et al. 2004). Light conditions may also influence the growth response of a beech seedling on soil fertility. In low light environments this response is reduced, whereas in non-limiting light conditions seedling growth is markedly influenced by nutrient availability (Minotta, Pinzauti 1996). Collet et al. (2001) indicate annual seedling height and diameter increment of 1.2 cm and 0.17 mm as threshold values for seedling growth that are necessary for survival in shade conditions. The growth rate of such seedlings is close to the growth rate observed on branches of senescent beech trees or on deep-shaded branches of adult beech trees. After canopy opening, diameter growth increased the first year and showed no clear increasing trend in the following three years. Conversely, height growth did not increase immediately after canopy opening and increased regularly in the following three years. Fig. 2. shows relationship between average seedling annual height increment and relative light intensity in gaps or under canopy (after Collet et al. 2001).

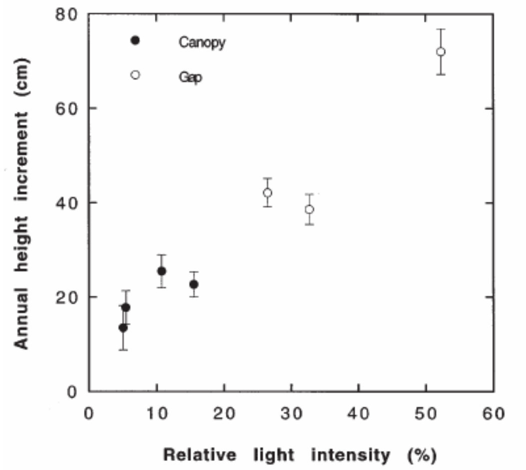


Fig. 2. Relationship between average seedling annual height increment and relative light intensity in gaps or under canopy (after Collet et al. 2001).

In shade, seedlings occur in low densities in Fontainebleau in France. In these conditions they cannot form several layers of leaves and invest in shoots. Higher mortality rates occur in these conditions, than in gaps (Topoliantz, Ponge 2000, Pontallier et al. 1997). Also Szwagrzyk et al. (2001) stated that, in places with no large openings in the canopy, there is little chance of germinants attaining sapling size irrespective of how many seedlings exist on the forest floor and how many survive the first growing season. Peltier et al. (1997) found most young seedlings under mature trees in (half) shade. Older seedlings (>3yrs) were encountered more in gaps, indicating that for germination light is less important than for development (Peltier et al. 1997).

In relation to shade tolerance the architectural flexibility of beech is important. In shade beech saplings follow one of two strategies. Either they perform (pseudo)sympodial branching, with long shoot and absence of a top-shoot, or they develop a monopodial top-shoot consisting of short shoots (Peters 1997). When released from suppression, the monopodial top-shoot can easily form long-shoots and increase a height-grow rate, but the sympodial type can not easily resume vertical growth. In shade, beech saplings form smaller crowns with fewer and smaller branches and a lower height to diameter ratio (Assmann 1968).

The relative shade tolerance of beech compared to other overstorey tree species indicates what kind of canopy cover and dynamics are necessary to maintain beech dominance. In the case that beech is the most shade tolerant overstorey species, then a high canopy cover will be enough to ensure dominance of beech regeneration at the forest floor. If beech is less tolerant than some other overstorey species, then the canopy cover necessary for its dominance depends on the relative growth rates of beech and the other overstorey species (silver fir, Norway spruce, oaks, maples etc.) - (Peters 1997). Where several shade-tolerant tree species share space in a given forest type, dominance can easily change from one species to another between two consecutive generations (Swagrzyk et al. 2001; Reininger 2000). However, the mechanisms behind that phenomenon are still unclear. Also the way shade tolerance is determined is important. For distinction between the different species it is important the time span such low light intensities can be survived. As mentioned earlier one-year-old oak and beech seedlings are equally adapted to low light conditions, but with developmental stage oak seedling become less tolerant (Welander, Ottosson 1998). Collet et al. (2001) showed that 12-year-old seedlings were still able to regain active growth after canopy opening. Otto (1994) indicates that the highest shade tolerance (5 from five-place scale) is for silver fir, Norway spruce, small-leaved and large-leaved linden. Sycamore maple and Norway maple perform only average shade tolerance (3 points) and pedunculate and sessile oak the lowest shade tolerance of 1 point. The ash stands between the maples and oaks.

2.4.3. Gap-phase regeneration in natural forests

As mentioned above, in natural forest dominated by shade tolerant tree species, regeneration depends on several factors such as seed production and seed dispersal (Wagner 1999), germination and survival (Szwagrzyk et al. 2001), site factors (Madsen 1995a; Madsen, Larsen 1997), canopy openings (Emborg 1998), the competition of understorey herbal vegetation (Dolling 1996), browsing and individual species performance (Modrý et al. 2003). In general, tree seedlings react positively to increased light level (e.g. Minotta, Pinzauti 1996; Szwagrzyk et al. 2001) often initiated by tree fall gaps. Since the light is a key growth factor in combination with water and nutrients (Madsen 1995a), the regeneration success in (near) natural forests is often related to structure dynamics and gap-formation (Emborg 1998).

Important tool in understanding forest dynamics is the concept of forest cycle with forest development stages (Korpel' 1995; Leibundgut 1982) - (these systems developed by different authors are not completely compatible and the recognition of stages is to a certain extent observer-dependent) - (Standovár, Kenderes 2003). Nevertheless, the concept of the forest cycle as a model of the forest dynamics in tempereate deciduous forest can be described as a continuous shift between a sequential series of upgrading and downgrading development phases: innovation, aggredation, early biostatic, late biostatic and degradetion phases, which builds a asynchronny mosaic shifting over time and place (Emborg 1998; Emborg et al. 2000). Fig. 3 shows Korpel's model of beech forest cycle on rich stands (Standovár, Kenderes 2003).

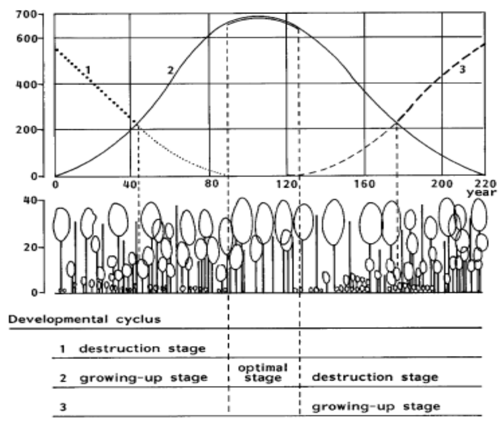


Fig. 3. Korpel's model of beech forest cycle, simplified (in Standovár, Kenderes 2003).

The gap triggers regeneration and initiates a new turn of the cycle. The mosaic mapped in 10.65 ha plot in near-natural forest Suserup Skov had an avarage path size of 839 m^2, ranging from 100 to 12 730 m^2. Rademacher et al. (2004) give average area of mosaic pattern that are at different developmental stages around 0.3 ha. Even very small natural beech forests could exhibit very high temporal and structural diversity that may not qualitatively or quantitatively differ from spatiotemporal dynamics typical from larger forests (Rademacher et al. 2004, Emborg et al. 2000).

In general, two types of forest cycles can be discerned; the internal or autogenic forest cycle and the external or exogenic forest cycle (Peltier et al. 1997). The internal cycle is related to the life span of the dominant trees, surviving up to 200 - 300 years, with a decline over a period of 60 years, creating small gaps and increased light environments (Peltier et al. 1997; Emborg 1998). Seedlings and saplings occur also in shady conditions, but may die when reaching the lower branches of mature trees (Peltier et al. 1997). The external cycle is dominated by storms. Under prevailing climatic conditions of East and Central Europe wind, ice and snow are the major abiotic disturbance factors in the beech forests of the region (Standovár, Kenderes 2003). Beech is, thanks to its root system, in general considered to be a wind-resistant woody plant species. Nevertheless, the root system shape, growth and development are mostly influenced by soil conditions and groundwater level (Kodrík, Kodrík 2002). Beech appears to be more sensitive than oak to soil constraints. The greater the constraint, the more superficial the soil-root complex appears to be (Lebourgeois, Jabiol 2002). Beech is particularly sensitive to storm since the taproot disappears and has thus a superficial root system (Pontallier et al. 1997). Wind was reported for several „virgin forest" as important disturbance agent. Badin Virgin Forest in Slovakia suffered from serious wind damage in 1947 (Korpel‘ 1995). A heavy gale impacted the surroundings of the Boubin Virgin Forest in Czech Republic on 26 October 1870, which caused extensive - though not quantified - wind breakages (Průša 1985). In central Europe, with the exception of extraordinary storms in 1990 and 1999, storm that cause large-scale catastrophic blowdowns are infrequent, but strong winds with local thunderstorms are more common. Nagel et al. (2006) suggest that infrequent, intermediate windstorm disturbances play an important role in the structure and dynamics of central European forests creating more coarse-garined forest structures than in stands regulated by smaller-scale gap processes.

In gaps a higher insolation may result in higher mineralisation and nitrification, there is a lower beech litter production and higher herbal litter production with a better C/N ratio and higher nutriet availability, increasing species diversity (Muys et al. 1988, Pontallier et al. 1997). Similar results showed Podrázský, Remeš (2006) in their study in near natural forest Voděradské bučiny. The amount of dry matter decreased by ca. 25% several years after canopy opening, especially in the H horizon, the pH, base content and base saturation increased, as well as the content of macronutrients (with the exception of total calcium). The results proved considerable changes in the humus forms during the natural and semi-natural forest cycles connected with the stand regeneration. The chemical shifts were comparable also to the changes during natural development cycles in other semi-natural forests (Podrázský, Viewegh 2005).

Furthermore, uprooted trees may create favourable germination sites, through an absence of a thick holorganic layer (difficult to penetrate and higher fungal infestation), absence of herbal competition, crumbled compacted loamy soil, and decreased soil acidity. Muys et al. (1988) found in Belgium higher seedling densities and seedling height (for both beech and other species) in uprooted zones. The closure of gaps is rapid, due to lateral expansion of existing tree crowns. Koop (1987) found in France that trees neighboring the gaps are more subject to decline and tree fall than other trees, presumably due to increased insolation and asymmetric crowns, thus enlarging gap area. Large number of dead trees, which expand gaps further, supports the theory of shifting mosaics (Drößler, von Lüpke 2005). Following Runkle's (1992) recommendations, same authors estimated that a large portion of the single-tree gaps did not increase in size, but at the same time 1/5 of the trees initiated gaps by their death, while 4/5 of the trees extended gaps. Often, new populations are related to gaps, but there may be a delay of 1 to 20 years in establishment (Pontallier et al. 1997). Beech seedlings occur less in larger gaps due to an ineffective dispersal, creating opportunities for other species (Peltier et al. 1997). Ash is predominantly found in half shade of beech trees, possibly due to poorer soil conditions in gaps (Peltier et al. 1997). In the young phase, seedlings suffer high mortality rates, due to fierce competition for water, nutrients and light and high litter production with above grown saplings (Topoliantz, Ponge 2000). Most seedlings are suppressed, waiting for favourable conditions to develop (Topoliantz, Ponge 2000). Due to sensitivity of beech to drought, wind, high insolation, insect and fungal attacks, and poor recuperation, opportunities arise for more shade intolerant species to establish and mature. In larger gaps, other species regenerate, such as Scotch pine, larch, sessile oak, common birch, common ash and maple (Pontallier et al. 1997).

2.4.4. Natural beech regeneration in managed forests

An appreciation of the natural processes in forests is essential in order to propose rules for sustainable management (Schnitzler 1998). In the case of beech we see that this approach is not totally new. Beech is the species most suited to natural regeneration that was, and continues to be, fundamental to the management of beech forests. In central Europe, silvicultural systems for beech have been developed since the 18th century. These systems were based on considerable knowledge of the ecology of the different tree species. Shade tolerance of the different tree species was well understood (Burschel, Huss 1997). The shelterwood system was developed in uplands with a dominance of beech. As mentioned before, its first extensive description is to be found in Hanau-Muenzenbergische Forstordnung by Moser from 1737 (Moser 1757). Later Hartig (1791) published "Generalregeln des Schirmschlagbetriebes" with three to four uniform cuttings, that had to ensure successful beech regeneration.

- i) A preparatory felling occurs a few years prior to the desired regeneration (release of the crowns and promotion of seed formation in mature, but rarely thinned stands, and promotion of soil activity)
- ii) Seeding felling or regeneration felling is carried out in the winter following a mast year. The canopy is further opened so that the emergent seedlings have enough light to survive and grow, yet retaining enough shelter to protect them (from late frost, too high light intensities leading to overheating and drying out)
- iii) Secondary felling usually take place once the young trees have reached heights of 0,5 m
- iv) Final cutting sees the removal of the remaining canopy trees and takes place once the young trees have reached 2 - 4 m, and no longer require any protection

Twenty to thirty years after the preparatory felling, the regeneration process is completed. The effect of the presence of an overhead canopy over this time period on light demanding admixed species is to restrict their quick initial growth. This, in combination with very light thinning, has resulted in large areas of pure beech stands. Hartig's shelterwood system was widespread in the 18th and mainly in the first half of the 19th century (Burschel, Huss 1997). As a reaction to the large-scale uniform shelterwood system, Gayer in 1886, formulated the concept of a small scale shelterwood system in German called Femelschlagbetrieb. During this time, both systems developed in many forms and variations corresponding to changing natural conditions and different silvicultural tradition. All these silvicultural systems are based on knowledge of the ecology of beech, which includes shade tolerance, a strong growth response of beech (crown) and natural regeneration (Peters 1997). Because of the possibility of the development of red heartwood, which severely reduces the marketable value of timber (e.g. Knoke 2002), the aim of current management regimes is to achieve greater dbhs over a relatively short time. In the 1960s, Assmann (1968) formulated a system of management (open stand system) with trees ultimately harvested on the basis of a target diameter. The dense stand phase (qualification phase) is followed by phase of selection and promotion of potential final crop trees (dimensioning phase). Unlike the shelterwood system this form of continuous cover management is not primarily aimed at the ecological requirements of the young growth. However, because of the permanent regeneration capability of the stands, no provisions for the establishment and development of young trees are necessary. Canopy trees are only removed, when they have reached their target diameter. In general, the gradual felling of mature trees in shelterwood system creates favourable conditions for regeneration and its subsequent development with the retained forest stand components still fulfilling the commercial and non-commercial forest functions (Souček 2007).

As has been mentioned, beech is the single most important Central European species in terms of natural regeneration. This does not means that the natural regeneration of beech is without any problems. Essential ingredients for successful natural regeneration of beech in managed woodland may be (1) abundant mast with good seed distribution, (2) low deer and rodent populations or adequate protection from them, (3) limited influence of other unfavourable biotic conditions (4) suitable soils that will conceal seeds and provide adequate moisture and nutrients, (5) limited ground vegetation, (6) protection from frost, (7) adequate light, (8) limited root competition, and (9) lack of damage during tree felling. Among others Agestam et al. (2003) showed that conditions for seedling establishment are less favourable in the clear-cut than in the shelterwood. More frequent events of frost and browsing were common causes of higher mortality, distribution of seedlings was uneven. The main effects of the shelterwood are reduced competition from ground vegetation and reduced frost damages.

2.5. The Occurence of Dead Wood and its Role in Beech Forests

The amount of dead wood is still one of the major topics in the discussion on sustainable forest management and nature-based silviculture. In the process of developing Pan-European indicators for sustainable forest management (MCPFE meetings) dead wood is included as indicator 4.5 *'Volume of standing deadwood and of lying deadwood on forest and other wooded land classified by forest type'* (MCPFE 2002). In natural forests deadwood provides a wildlife habitat and plays an important part in ecological and geomorphological processes (Samuelsson et al. 1994). Dead wood is regarded as an important aspect of forest biodiversity forming key habitats for many species. For example invertebrates, fungi, bryophytes, lichens, birds and mammals depend on or utilize dead wood as a source of food or shelter (Otto 1994). It is expected that a forest, which has remained unmanaged, would contain dead wood in all decay phases (due to a biological decomposition of the dead wood). In most cases the amount of dead wood present is a combination of former forest management, stand development stage, and the pattern caused by irregular, natural disturbances. In managed forests, dead wood occurs mainly as logging waste and stumps, whereas large logs and snags are rare. The average dead wood volume in present day production forests is less than 10 $m^3.ha^{-1}$ (UNECE/FAO, 2000; Green, Peterken 1997). It is reported that the amount of dead wood is in the order 10-20 times higher in unmanaged than in intensively managed production forests (Christensen et al. 2005). In managed forests deadwood volumes are reduced by harvesting and sanitation felling. Indeed in mature stands, that had not been managed for a century, the volume and size class distribution can reach the same values as in natural or near natural stands (Green, Peterken 1997). Unfortunately there is less information about the natural amount of dead wood in Central European uplands, in which the *Fagus sylvatica* L. (beech) is a dominant or co-dominant tree. Only very few sites have been strictly protected and have had any influence of forestry management (Diaci 1999, Průša 2001). In contrast, in the mountains of Central and East Europe there are several surviving “virgin” reserves and strict forest reserves with a long protection history, and less influenced by human activity before designation (Korpel’1995; Průša 1985).

The levels of total dead wood volume in the beech forest reserves reported from different countries vary considerably. It was found that the mean volume is 130 $m^3.ha^{-1}$ and the variation among reserves was high, ranging from almost 0 to 550 $m^3.ha^{-1}$. More dead wood was found in montane (rather than lowland/submontane) reserves, longer-established reserves (time since designation) and reserves with higher volumes of living wood. The percentage of dead wood that was standing was almost twice as high in montane than in lowland/submontane forest reserves (45% versus 25%) - (Christensen et al. 2005).

Table 3. CWD (Coarse woody debris) volume in Beech forest reserves in Czech Rep. and Slovakia (after Christensen et al. 2005).

Forest reserve	Area in ha	Reserve establishment	Year recorded	Snag volume ($m^3.ha^{-1}$)	Log volume ($m^3.ha^{-1}$)	Total CWD volume (m3.ha^{-1})	CWD/ living wood ratio (%)	References
Boubín	47	1858	1996	74	185	258	30	Vrška et al. (2001c)
Milesice	10	1948	1996	52	101	153	24	Vrška et al. (2001b)
Mionsí	171	1933	1994	63	108	172	26	Vrška et al. (2000b)
Polom	19	1955	1995	49	104	152	23	Vrška et al. (2000a)
Razula	24	1933	1995	89	199	287	35	Vrška et al. (2001a)
Salajka	22	1956	1994	89	159	248	47	Vrška (1998)
Stozec	53	1989	1974			63	9	Průša (1982, 1985)
V Klučí	25	1953	2000	54	169	223	30	Odehnalová (2001)
Žákova hora	38	1933	1995	33	114	147	23	Vrška et al. (1999)
Žofín	98	1838	1975	54	87	141	19	Průša (1982, 1985)
Badín	31	1913	1997	42	228	271	46	Saniga (1999) Saniga and Schütz (2001b)
Dobroc	102	1913	1998	66	190	256	41	Saniga and Schütz (2001b)
Havesova	171	1964	1999	32	70	103	17	Saniga and Schütz (2001a)
Kyjov	53	1974	1993	47	115	162	42	Korpel' (1995), Saniga and Schütz (2001a)
Rastun	18		1983	28	31	58	13	Korpel' (1992, 1997)
Rozok	67	1964	1999	28	96	124	18	Saniga and Schütz (2001a)
Sitno	45	1951		24	62	86	17	Korpel' (1997)
Stuzica	218	1965	1991	51	40	91	19	Korpel' (1997)

Former research demonstrates that there is no one level of natural dead wood, rather that level differs greatly from site to site. This is related to the general cycle of dead wood levels in natural stands. As a stand progresses into maturity the volume of dead wood tends to increase; it then peaks during and immediately after the break-up of the old-growth stand; and then falls to a minimum during the stem exclusion stage as the replacement stands develops towards maturity. Dead wood dynamics are typically related to disturbance types, where each disturbance type has its own characteristics regarding frequency and intensity, providing large differences in the spatial and temporal distribution of dead wood relating the distribution of dead wood to different developmental phases. Within the natural distribution range of beech in Europe, the disturbance regime is characterised by a combination of frequent small-scale disturbance events (gap-dynamics) and occasional large-scale disturbances, mainly caused by wind/ice/snow-storms and drought (Leibundgut 1982, Emborg et al. 2000, Nagel et al. 2006). Disturbance regimes may differ within Europe. Natural disturbance patterns are probably larger in NW Europe than elsewhere on the continent, because severe windstorms are more common here (e.g. Peterken 1996, Koop, Hilgen 1987). In Central and East Europe, stand dynamics are typically small-scale, but even here quite large-scale disturbances can occur occasionally. However no one single factor causes the death of individual tree (except uprooting, stembreak etc.). Typically, fungi enter trees through wounds in the stem or where branches have broken off. The fungi cause the tree to rot and may eventually kill the tree, or make it more susceptible to wind (Leibundgut 1982, Korpel' 1992, Korpel' 1997).

3. STARTING POINTS

3.1. The aim of the study

As mentioned before, the National nature reserve Voděradské bučiny has been established in 1955 (issue MKŠ n.13600/55) on the total area of 658 ha in former managed forest, including both homogenous even-aged forests stands and stands with (near) natural forest structure. Recently it was decided to create a non-interventional (core)zone on the area of 60 ha (approximately 1/10 of the total area of the nature reserve). The biological value of this part can be increased by management interventions before the part of reserve is to be considered completely non-intervention forest. Felling groups of trees could dissolve the homogeneity by establishing mosaic structure and initiating gap-phase dynamics, while leaving felled trees behind at the forest floor could increase the amount of dead wood. Group selection harvesting and systems based on the principle of nature-automation might contribute to higher resistance in managed stands. In order to develop such management system the understanding of the natural processes in the particular region is necessary. With this intention we divided this dissertation into three main research areas:

- *Natural regeneration of homogenous senescent even-aged beech stands*
- *Natural regeneration of near natural forest stands*
- *Structure of beech forest stands with different management history*

In each part we formulated the research aims:

- *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.*
- *Investigate the effects of the parent stand on the growth and survival of beech regeneration in relation to light intensity, seedbed type and weed competition.*
- *Investigate the influence of management interventions on forest structure and forest dynamics.*

Research questions are formulated as follows:

- Are the senescent beech stands able to produce enough seed with good distribution?
- What are the main factors influencing the establishment of forest regeneration?
- Does the stand density influence the regeneration establishment during first vegetation periods?
- How is the natural beech regeneration related to the gap formation within natural forest dynamics?
- What is the role of main growth factors and weed competition in this process?
- How does the “authentic” or “natural” forest structure in given condition looks like?
- Is the role of browsing in given conditions important for the process of natural regeneration of beech?

Based on the obtained results, in general conclusions we will try to formulate management recommendations for given natural conditions and propose management guidelines for both managed and protected forest stands.

3.2. Natural Conditions of the Study Area Voděradské bučiny

The National nature reserve Voděradské bučiny (49˚58′N, 14˚48′ E) is situated in Mnichovská pahorkatina (Natural forest area 10: Středočeská pahorkatina). The lowest point is 345 m asl. (Jevanský potok) the highest point is the top of the hill Kobyla in 501 m asl. (AOPK 2000). The parent rock is granite of different texture. Predominantly cambisols with low humus content and different depth are developed within forest stands. The soil reaction pH_{KCL} in holorganic horizons reached values from 3.2 to 4.7. The values of base saturation in holorganic horizons reached values from 22.1% to 63.3% In uppermost humus enriched horizon from 10.1% to 22.7% of base saturation (for detailed soil description see also Appendix – Soil analysis). In pure beech stands accumulation of holorganic horizons with anaerobic decomposition (due to initial stand structure and relatively dry climate) is not exception (Šrámek 1983). The nearest climate and precipitation station is located in Říčany (401 m asl.). Mean annaual tempreture is 7.8 ºC, annual precipitation is 623 mm; in the period from April to September mean temperatrure is 14.0 ºC and precipitation in these month reches the total of 415 mm. The duration of vegetation period with mean temperature above 10 ºC is more than 158 days. Macroclimatic conditions are strongly modified by relief resulting in a strong mesoclimatic divergence. Under given conditions beech regenerated successfully under the parent stand and was rarely artificially regenerated. 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 forest stands within the borders of the National nature reserve. Table 4 gives general overview of plots included in the study. According to Macháček (1996) the most important agent influencing the health status of old beech stands in the NNR are wood decaying fungi (in total 39 species observed in NNR). In the locality the most destructive to beech are *Fomes fomentarius* (L. ex Fr.) Kick. and *Hypoxylon deustum* (Hoffm. et Fr.) Grev.

Table 4. Overview of research plots and forest stands included in the study.

Research plot	**Area code**	**Area (ha)**	**Forest stand**	**Forest type**	**Age* (years)**	**Genetic class.***	**Elevation m asl.**	**Exposure Slope**
S1	-	-	434A17	4K3	166	A	455	N – 15%
S2	-	-	417D16	4S7	154	C	455	E – 15%
01	296E79	1	436C17	4B1	179	C	440	E – 15%
03	298E79	1	434B17	4S4	189	A	450	N – 20%
04	299E79	1	434E17	4S4	184	A	460	E – 17%
05	300E79	1	436D17	4K3	169	B	440	E – 15%
06	-	1	417A16a/8a	4B1	155/80	C	470	N – 10%
07	-	1	417A16a/8a	4B1	155/80	C	470	N – 10%

* According to forest management plan (stand 2001)

3.3. Materials and methods

Within the frame of all three research areas we examined: the seed production, seedling emergence and survival, regeneration patterns, light and soil conditions under the forest stands, forest structure and occurrence of deadwood. For detailed description of each methodological approach see the corresponding case study (**chapters 4.1.2., 4.2.2. and 4.3.2.**).

As additional research we conduced soil analysis on selected research plots. Soil samples were taken on September 25 and October 1, 2005 on research plots PRP 01, 03, 04, 05, 06 and S1. Samples were taken for holorganic, as well as for mineral horizons. Individual analyses of particular samples were carried out. The following chemical analyses were performed:

- total humus content was determined by Springer-Klee method, total nitrogen content by standard Kjeldahl method and Cox,
- soil reaction (in water and in 1N KCl solutions) was determined potentiometrically,
- soil adsorption complex characteristics were determined by Kappen method: S – base content, T-S (H) – hydrolytical acidity, T (S + H) – cation exchange acidity and V – base saturation,
- plant available nutrients were determined in a 1% solution of citric acid – this method is old, not used in the world literature any more, but it is used in the Czech forestry and it enables to make comparisons with older results. The nutrient contents are given in oxide forms. Phosphorus was determined in the solution spectrophotochemically, potassium colorimetrically and calcium and magnesium by AAS (atomic absorption spectrophotometry),
- parameters of exchange acidity were determined in a KCl solution,
- total nutrient content after mineralization of holorganic horizons using the mixture of sulphuric acid and selenium,
- total nutrient content in mineral and holorganic horizons was determined by Mehlich III method
- textural mineral soil analysis determined by pipette method.

The analyses were performed by the commercial laboratory Tomáš in Opočno. Overview tables are given in Appendix.

In order to estimate the growth dynamics of present beech stands, on January 11, 2004 in forest stand 434A17 we cutted down co-dominant beech tree ($h = 34.5$ m, $h_{crown} = 19$ m, $d_{1.3} = 49.35$ cm) and analysed the diameter structure in section of 0.1h (in total 12 profiles in distance $d = 3.45$ m). Sample tree analyses are given in Appendix.

4. Case studies

4.1. Natural regeneration of homogenous senescent even-aged beech stands

4.1.1. Introduction

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 its substantially higher representation in forests. In the case of beech as a stabilizing element of forest stands, much more emphasis should be given to the preservation of its adaptedness and ecological stability through the gene-pool conservation of the existing indigenous populations (Gömöry et al. 1998).

Beech is shade tolerant tree species producing huge number of seed in recurring masting years. A strong seed production in one year negatively affects the seed production in the next. 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 in e.g. West Europe, but this phenomenon does not lead to more frequent seed production (Standovár, Kenderes 2003). Seed production and survival may be also 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 seeds produced can shows high spatial variability within a single stand (Standovár, Kenderes 2003).

The germination and survival of beech seedlings is problematic. Since beech has no apparent chemical defenses against browsing and 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 from several insects and mammals. Čermák, 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 here 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 seedling number. It is likely that the most important effect of the coverage was the reduction in evaporation and increase of soil moisture. This underlines the necessity of sufficient soil moisture for satisfactory seed germination. Canopy trees increase both the interception and root competition for water and so negatively influence the conditions for germination. Dead wood can provide appropriate establishment site for tree species in certain forest types (Standovár, Kenderes 2003). Fungal pathogen activity can cause high rates in 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 loss of viability. Once the radical 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 a seedling bank may play very important role (Swagrzyk et al. 2001). Yet, the occurrence of numerous seedlings on the forest floor is very often only an ephemeral pulse of regeneration with virtually no chance of ever attaining the sapling size. Beech seedlings at least for some time can survive light conditions that barely permit any growth. 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 by reduced growth and leaf morphology. This leaf adaptation consists of strong reduction in mesophyl thickness, but little reduction in epidermis thickness. Collet et al. (2001) showed that 12- year-old seedlings were still able to regain active growth after canopy opening. An important fact is that growth and morphology of the 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.

4.1.2. Materials and methods

Data collection and statistical analyses

To quantify the seed production of beech during the heavy masting year 2003, in the forest stand 434A17, sampling plots were established in the regular matrix 20 m x 10 m (research plot S1). 6 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 the fenced plot (research plot S2), where the parent stand was already removed before the masting year. In total 74 sample plots were situated in the first stand, 27 sample plots in the second stand (number of sample plots per stand correspond to the area where the study was conduced). During the vegetation period 2004 (April 2004; July 2004; September 2004; November 2004) we repeatedly counted the number of seedlings within S1 (we used the same grid as for seed quantification using frame 1 x 1 m).

For the research on the stand structure, in 1979 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 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), the height, the crown height and recorded the species, status (living, dying or dead), and social status (dominant, codominant, subdominant, less than 20 m, broken or dead tree). 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, stand density, volume and stand basal area were calculated by regular dendrometric methods using the volume tables and equations (Petráš, Pajtík 1991). For more information see the chapter 4.3.2.

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 on 11 standpoints. On all standpoints (N = 52 per plot) we carried out threefold measurement (n = 166 per plot). The values were recorded with the luxmeter FX 101 at the height of 1 m above the ground. During the day we repeatedly measured the illumination on the free area. The median of these measurements was used as a 100% illumination. An overview of the research plots and basic characteristics of forest stands are given in Table 5 and values of relative light intensity (RLI) in Table 6.

To quantify the establishment and survival of regeneration we established sample plots (SP) in the regular matrix 20 m x 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 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 to the developmental stage: 1-year-old seedlings (originating from the masting year 2003), older seedlings (originating mostly from masting year 1995). In 2007 a new generation of beech seedlings after the moderate masting year 2006 occurred. For each sample plot we recorded the distance to the nearest tree of the parent stand.

The data was not normally distributed (for testing normality we used the Shapiro-Wilkes test). The Kruskal-Wallis test was used searching for differences among data sets. For pair wise comparison between PRPs we used the Kruskal-Wallis Z test. To determine the correlation, the Spearman non parametric correlation coefficient was used. For pair wise 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 analysis, results were considered significant when $p \leq 0.05$.

Table 5. Research plots and basic characteristics of forest stands included in the study.

Research plots	Forest stand	Group of forest types	Age* (years)	Elevation m asl.	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%

* According to forest management plan (stand 2001)

4.1.3. Results

Stand structure, management and illumination values

Important factors influencing the establishment and development of natural regeneration might be the silvicultural treatment. On all PRPs predominantly group shelterwood felling is performed; on PRPs 03 and 04 in combination with border cutting system. Basic stand characteristics for 2005 are given in Table 6. 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 lower basal area (but still far above values of previous plots, stocking 0.75) results from ongoing border cutting direction east-west. The inner stand except for one gap (originating from salvage cutting) remains rather untouched which is exactly the case of entire PRP 03.

Table 6. Stand characteristics and average illumination within 1 ha PRP.

PRP	V total ($m^3.ha^{-1}$)	G ($m^2.ha^{-1}$)	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.

Significant differences in illumination values among four PRP and free area (100% illumination) were observed (Kruskal-Wallis test: d.f. = 4, H = 89.99, P = 0.000). Lowest ratio of illumination was found on PRP 03 with highest growing stock, basal area, number of trees and mean stand height. Obviously, ongoing border felling (north-east border) did not influenced the illumination like in the case of PRP 04. Here, border felling already reached the limits of PRP (east border) and created on part of the plot light conditions closer to that of free area, which explains high values of measured radiation and their heterogeneity (Fig. 4).

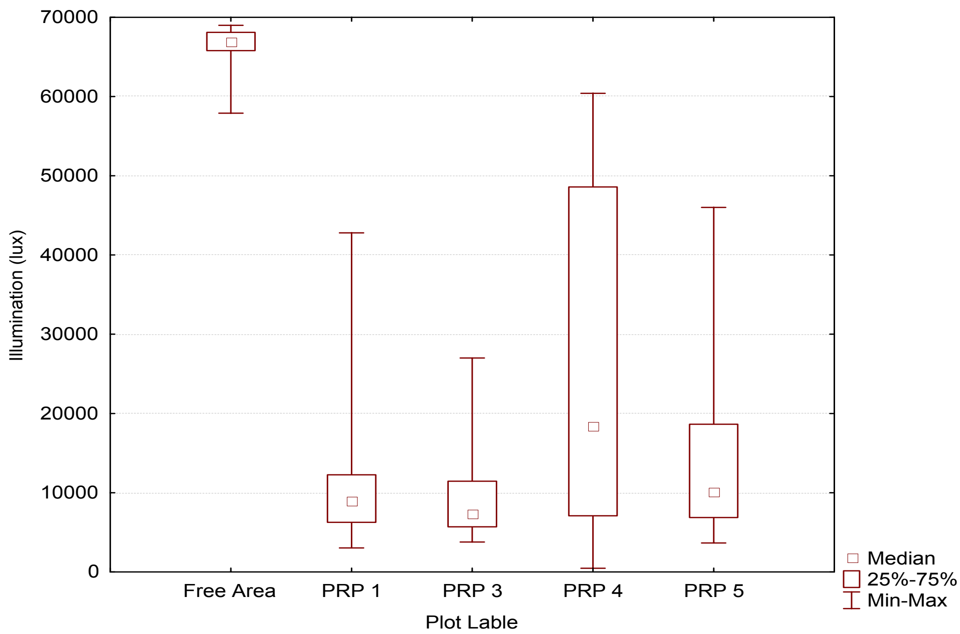


Fig. 4. Distribution of illumination according to PRPs.

Seed production and seedling emergence

The mean density of beech seeds (full and empty) per 1 m^2 estimated in the forest stand 434A17 (research plot S1 - under the canopy of parent stand) was 624 (S = 275.7). Fig. 5 shows relative frequency of seed numbers. In forest stand 417D16 (research plot S2 – on free area) under parent beech trees standing in the proximity of clear cut area the average density of beech seeds reached the value 901 per square meter (n = 6, S = 258,1). With increasing distance from the stand border the densities of seed decreased, yet at 10 m distance (on free area) outreached the value of 600 seeds per square meter. Highest seed fall was found in the proximity of stand border (east border). The capacity of heavy beech seed to disperse is limited, nevertheless seed was found at the distance of 40 m from parent trees. Numbers of seeds also decreased from the edge to the inner stand (Fig. 6a and 6b); yet there was no statistical difference between seed densities among data sets (Kruskal-Wallis test: d.f. = 5, H = 5.01, P = 0.414).

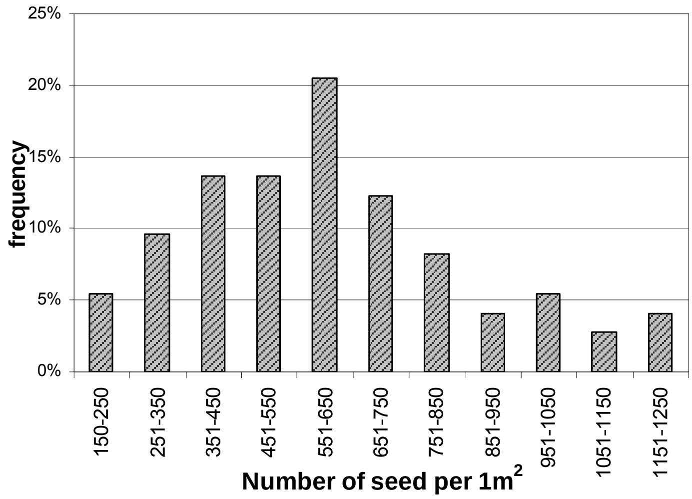


Fig. 5. Distribution of seed density (per 1 m^2) under the parent stand 434A17.

The ratio of empty seed on research plots was 17% and 18.8% (S1 and S2). The germination of beech seed in the 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 seed developed into seedlings. The rate of germinated seeds was much higher in controlled conditions without losses during wintering of beech seeds and other negative biotic and abiotic factors. In 2003 we collected in the forest stand 434A17 small sample of beech seeds. Following year we tested the germination of five hundred full seeds in nursery. From 12 of May 2004 to 23 of June 2004 (following two weeks we did not observed more germination) 24.4% of full seeds germinated. Even by relatively low rates of germination (and high losses of wintering seeds) seed production has to be regarded as sufficient and capable to provide successful natural regeneration of beech in given conditions. The values observed on both research plots far overreached values indicated for full masting years of beech. This result was not expected since both stands are far behind usual rotation period of managed beech stands (Table 1). Beechnuts usually germinate from April or May and the sprouting seedlings are vulnerable to attack from several insects. First measurement was conduced on April 23 and we very soon regarded damages caused by aphids.

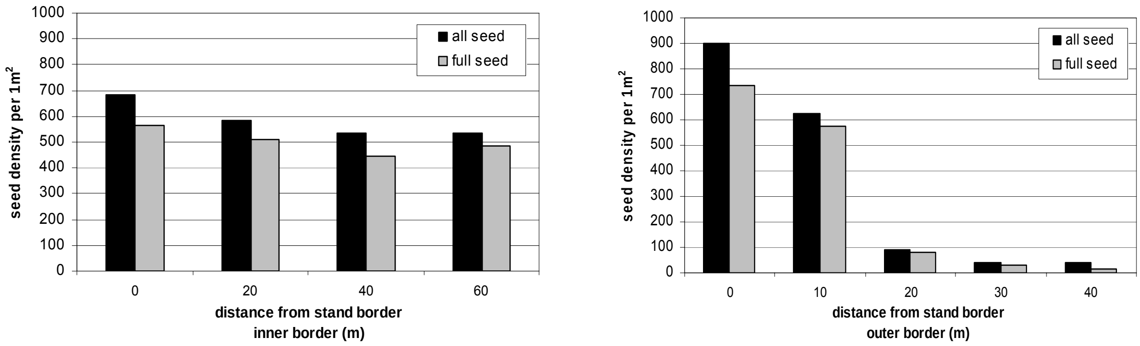


Fig 6a, 6b. Number of seeds under the inner and outer border of beech stand.

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 cohort 2003 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 beech 1-year-old-seedlings indicates that the amount of seeds and their germination are not the elements which hinder natural regeneration. Low densities of coniferous and other broadleaf were quite low primarily because of their absence in the overstorey. The density of Norway spruce increased in 2007 due to 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 beech 1-year-old seedlings was still present on the plot. The density of older seedlings (cohort 1995) decreased to 68.2%. After seed year 2006 we observed new 1-year-old seedlings establishment that corresponded to 21.5% of the density in 2004. The seedlings density was variable for tree species (hornbeam, birch, rowan), which bear seeds amply and frequently. Yet, the most common species among other broadleaf (except beech) remained maples (sycamore and Norway maple) with low increase in its density. 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.

Table 7. Regeneration density (in thousands per hectare) 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	Hornb.	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

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 there were no differences in the thickness of humus layer among PRPs recorded (d.f. = 3, $H = 2.365$, $P = 0.500$) – (Table 4). There is no significant correlation between cover of ground vegetation and cover of regeneration. We found only weak negative correlation between thickness of humus horizons and regeneration cover ($R = -0.1548$, $P = 0.0370$) and positive correlation between 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 case of older seedlings no correlation was found. On the contrary we found weak negative correlation between 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 in 2005 negatively influenced by the presence of older seedlings, which was most evident on PRP 04 with highest number of older seedlings (R = - 0.3016, P = 0.0466). Further we divided all SPs in three groups according to their position under the canopy of parent trees (0 – SP under opened canopy, 1 – SP under canopy, 2 – SP in border position). Among these groups we found significant differences in ground vegetation cover (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% in border position). Both older seedlings and young seedlings were more frequent under closed canopy and were less frequent under micro-gaps between crown projections of parent trees.

Table 8. Mean beech regeneration density (in thousands per hectare): 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 Kruskal-Wallis test (same indexes shows means with significant difference).

Variable					Kruskal-Wallis test: H	P – value
	PRP 01	PRP 03	PRP 04	PRP 05		
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	5.7 b	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	5.2 b	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 (%)	4.34	4.00	4.47	4.08	2.365	0.500

The relationship between 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. Highest second-year survival and three-year survival was on SPs with lowest seedlings densities (1 – 10 seedlings; 73.86%, 54.59% respectively), lowest survival on SPs with moderate seedlings occurrence (11 – 40 seedlings; 52.37%, 39.65% respectively), on SPs with high seedlings occurrence (more than 40, maximal value 174 ind.) we recorded average survival 59.07%, 47.00% respectively. The difference among data sets was statistically significant (Kruskal-Wallis test: d.f. = 2, H = 8.34, P = 0.015). Second year survival of one- year-old seedlings and older seedlings on four PRPs (01, 03, 04, and 05) was following: 71.08%, 45.93%, 35.29% and 68.14%; 54.41%, 92.31%, 84.40% and 72.41% respectively. In the case of cohort 2003 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. For low survival of older seedlings on PRP 01 we have no explanation as well for more than 50 % mortality of older beech seedlings on PRP 05 between 2005 and 2007. On other three plots during this period the survival of older seedlings always succeeded 90%. Cohort 2003 during this period performed on all plots higher survival than in 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 survival of beech regeneration within and out of crown projections we divided all SPs in two groups (0 – SP under opened canopy, 1 – SP under canopy and 2 – SP in border position formed the second group). The survival was significantly different only during the first year of observation for the cohort 2003 (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 here than in the proximity of parent trees. With few exceptions mentioned above, survival rates also increased with the age of beech individuals.

4.1.4. Discussion

Beside 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 about the success or failure of natural regeneration. By changing the shelter-wood density the light climate is greatly influenced, which may affect the performance of the seedlings and the outcome of the regeneration. The optimal shelter-wood should be a compromise between a dense shelter-wood for protection against frost and competition from ground vegetation and a sparse shelter-wood for maximal 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.

The chance for survival of older beech regeneration increased outside the crown projection of parent trees, where beech was able to overgrowth 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 favor 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) first-season survival depends on the numbers of germinants. In years with very large numbers (1996 and 1993) of germinants average survival amounted 59 and 58%, respectively, in our case we observed a bit lower survival amounting 44% (2003), which rather corresponds with results obtained by Emborg (1998). Another important factor lowering the seedlings occurrence may be the rodent consumption of beechnuts. Olesen, 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 seedling in unprepared soil indicating that the rates of surviving beechnuts are in general very low (in our case 2.36% of full seed). Although we did not record the proximate causes of 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 highest survival on SPs with lowest seedling numbers; similarly the same author observed the highest survival in years when numbers of germinants were very small, nevertheless permanent seedlings banks formed only in plots with relative light intensities higher than 9%. On PRP 03 the absence of preparatory felling and highest crown cover with lowest RLI values resulted in lowest numbers of seedlings and higher mortality. PRP 04 showed highest numbers of older seedlings whose emergence has to be related to accidental tree break followed by salvage cutting which resulted in successful dense gap regeneration of the cohort 1995. This special event negatively influenced the establishment and development of the cohort 2003 again with lower survival rates than on PRP 01 and 05. The beech regeneration developed successfully on PRP 01 and 05 (crown cover reduction to 80%) during the next four years.

4.1.5. Conclusions

Shelter-wood 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) In Beechwood of Voděrady also ageing beech stands far behind common rotation period are at present able to produce enough seeds with good distribution. (2) The main factor affecting the seedling survival in the first vegetation period seems to be biotical damages caused by aphids and small mammals. (3) Thick humus horizons are unfavourable for the germination. (4) Both ground vegetation and competition from parent stand are an important hindrance for natural regeneration. Dense regeneration from preceding mast year negatively influences establishment of regeneration from following mast year. (5) Three-year seedlings survival is closely correlated with the second-season seedlings survival and initial number of seedlings. (6) Reduction of crown cover of parent stand to 80% assured successful four-year development of beech regeneration. (7) Border cutting with outer face oriented towards east is less suitable for beech regeneration than shelter-wood systems and group selection harvesting.

4.2. Natural regeneration of near natural forest stands

4.2.1. Introduction

Today, forests in nature reserves, national parks and protected landscape areas comprise approximately 25% of forest cover of the country. In the Czech Republic 75% of all beech forests lie in these protected areas. This fact results in the necessity of multifunctional management of beech forests. Beech woods are one of the most important types of forest not only in the Czech Republic, but also in Europe. Past management of these forests has led to diverse situations ranging from natural to intensively managed beech forests prevailing throughout most of Europe (Merino 2007). Whereas low tree species diversity in natural European beech forests may be the result of long-lasting human forest-use, most pure beech forests are the result of intensive management during the past three centuries. Nevertheless, many of these forests are are included in protected areas. Therefore it is not totally clear, in which direction the European beech forest will develop spontaneously. With the exception of protected forests, most beech forests in the Czech republic have a production function or have been managed as multifunctional forests with a preference for timber production (Lesprojekt 1983). Since the 1970s the remnants of natural (beech) forests in nature reserves have been subjected to research and monitoring to reveal scientific information about the natural dynamics of these forests (Míchal 1983; Vrška et al. 2001). In this study valuable information has been gathered which can be applied in both regular and restoration forest management. Management principles of protected beech forests based on the biodiversity concept, natural ecosystem dynamics and maximum use of natural processes have been formulated by Moravec, Míchal (1999).

In natural forest dominated by shade tolerant tree species, regeneration depends on several factors such as seed production and dispersal (Wagner 1999), germination and survival (Szwagrzyk et al. 2001), site factors (Madsen 1995a; Madsen, Larsen 1997), canopy openings (Emborg 1998), the competition of understorey herbal vegetation (Dolling 1996), browsing and individual species performance (Modrý et al. 2003). In European beech forests windstorms often create canopy gaps and change the level of incident light, soil moisture and nutrient availability on the forest floor (Gálhidy et al. 2006). In general, tree seedlings react positively to increased light level (Minotta, Pinzauti 1996; Szwagrzyk et al. 2001) often initiated by tree fall gaps. Since the light is a key growth factor in combination with water and nutrients (Madsen 1995a), the regeneration success in (near) natural forests is often related to structure dynamics and gap-formation (Emborg 1998). Furthermore, uprooted trees may create favourable germination sites, through an absence of a thick holorganic layer (difficult to penetrate and higher fungal infestation), absence of herbal competition, crumbled compacted loamy soil, and decreased soil acidity. Muys et al. (1988) found in Belgium higher seedling densities and seedling height (for both beech and other species) in uprooted zones. The closure of gaps is rapid, due to lateral expansion of existing tree crowns. Koop, Hilgen (1987) found in France that trees neighboring the gaps are more subject to decline and tree fall than other trees, presumably due to increased insolation and asymmetric crowns, thus enlarging gap area. Large number of dead trees, which expand gaps further, supports the theory of shifting mosaics (Drößler, von Lüpke 2005). Gálhidy et al. (2006) proved that gap size had a profound effect on the environmental variables like light intensity and soil moisture and the herbaceous vegetation. Since different mixtures of herbaceous species and their patches affect tree seedlings differently, this mechanism could also contribute to maintaining tree species richness. Changes in abiotic and biotic conditions depend both on gap size and within-gap position. The gap triggers regeneration and initiates a new turn of the cycle. The mosaic mapped in 10.65 ha plot in near-natural forest Suserup Skov had an average path size of 839 m^2, ranging from 100 to

12 730 m^2. Rademacher et al. (2004) give average area of mosaic pattern that are at different developmental stages around 0.3 ha. Even very small natural beech forests could exhibit very high temporal and structural diversity that may not qualitatively or quantitatively differ from spatiotemporal dynamics typical from larger forests (Rademacher et al. 2004; Emborg et al. 2000).

The aim of the study is to investigate the effects of the parent stand on the growth and survival of beech regeneration in relation to light intensity, seedbed type and weed competition. An improved understanding of the effect of these factors and their interactions in local conditions may contribute to better silvicultural treatment both in terms of production and protection.

4.2.2. Materials and methods

Data collection and statistical analyses

Two permanent research plots (PRP "Virgin forest" 06 and 07) were established in 2005 for the research on the stand and regeneration structure, both 100 × 100 m (1 ha) in size, representing the most differentiated stands with minimal management interventions in the area (forest stand 417A16a/8a, forest type 4B1, forest age 155/80 (upper layer and understorey), elevation 470 m asl., exposure – slope N 10%). 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), the height, the crown height and recorded the species, status (living, dying or dead), and social status (dominant, codominant, subdominant, less than 20 m, broken or dead tree). 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 (SBA) were calculated by regular dendrometric methods using the volume tables and equations (Petráš, Pajtík 1991). For detailed description see the chapter 4.3.2. Normal distribution of the data was tested using Shapiro-Wilkes test. The data distribution was not normal. Kruskal–Wallis test was used to search for statistical differences between different site conditions. To determine the correlation Spearman non parametric correlation coefficient was used. The analyses were done in software Statistica 8 and S-Plus. For all analysis, results were considered significant when $p \leq 0.05$.

Table 9. Basic characteristics of stands.

PRP	Percentage in V					V total (m^3.ha^{-1})
	Beech %	Larch %	Hornbeam %	Spruce %	Others %	
06	96.0	2.6	1.0	0.3	0.1	707.21
07	69.4	12.1	8.3	9.5	0.7	505.60
PRP	G (m^2/ha)	N (ha)	ρ	$d_{1.3}$ mean (cm)	h mean (m)	h_{100} (m)
06	35.56	203	0.71	31.9	17.8	28.33
07	30.77	272	0.72	29.6	20.2	33.69

V – volume (d ≥ 7 cm o.b.), G – stand basal area, N – number of trees ($d_{1.3}$ above 3.0 cm), ρ – stand density, $d_{1.3}$ – diameter at breast height, h – height, h_{100} – height of the 100 highest trees per ha.

Within permanent research plot (PRP) 06 smaller research plots (RP) were selected (inside small gap, under canopy and inside big gap – the age of gaps was estimated on more than 40 years), within PRP 07 another two research plots (RP) were selected (under small and under big gap). In each partial RP in the regular grid of 5 x 5 m sampling plots 1.5 x 1.5 m (SP) were established. SPs were situated in order to cover all the area of the gaps.

Table 10. Basic data for research plots (RP) within PRP 06 and 07.

RP	Forest stand	PRP	Location	Nr. of SP	Area (ha)	Exposure
A	417A16a/8a	06	Small gap	23	0.04	N
C	417A16a/8a	06	Canopy	34	0.06	N
D	417A16a/8a	06	Big gap	44	0.07	N
E	417A16a/8a	07	Big gap	30	0.05	N
F	417A16a/8a	07	Small gap	20	0.03	N

In particular SP following field data were recorded:

- light conditions (on 54 sampling plots within PRP 06)
- presence of dead wood (coarse woody debris CWD)
- cover in percent was visually estimated from above for tree regeneration, herbal ground vegetation, CWD, litter, bare soil and surface rocks. Layering was ignored and the interval for the total cover estimation was 1-100%.
- in addition cover was estimated separately for each species (tree, shrub and herbal) in the ground layer
- number and height of seedlings
- game damages of tree regeneration recorded in 3rd quadrant of SP (minor damage = less than 10% of the plant defoliated, terminal shoot not damaged; middle damage = 10 – 50% of the plant defoliated; serious damage = more than 50% of the plant defoliated)

Dead wood was classified as branches of diameter ≤ 10 cm or branches and stems of diameter ≥ 10 cm (diameter classes I and II). In the second class more detailed decay classes were recorded (1 = hard, branches present, bark present on more than 50% of the surface, section oval; 2 = hard, branches present, bark present on less than 50% of the surface, section oval, 3 = soft, cut in 1-5 cm of depth, section oval; 4 = soft, small parts missing, section elliptical; 5 = soft, contour deformed, section elliptical; 6 = soft, reduced, no contours, CWD cowered with soil). Within each sampling plot the number of seedlings in 8 height classes was counted (one-year seedlings, seedlings ≤ 20 cm, 21 cm – 50 cm, 51 – 90 cm, 91 – 130 cm, 131 – 200 cm, 201 – 300 cm, ≥ 300 cm). Damage by browsing, structure and vitality characteristics of five dominant beeches were recorded (total length of the stem, last year growth, diameter of root collar in mm; form of terminal shoot: direct, twin stem – acute angel, twin stem – obtuse angel, multiple branching; growth characteristics: upright, knee-shaped, bow-shaped, sabre-shaped, plagiotropic growth) - (Fig. 7).

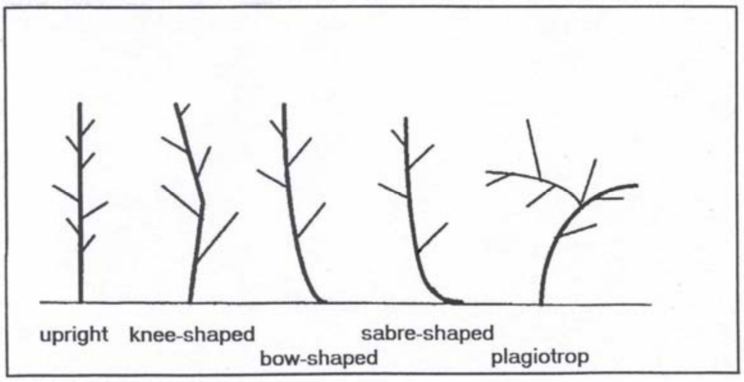


Fig. 7. Characteristics of dominant trees of beech regeneration.

Film hemispherical photographs were taken with a Nikon F50 camera body and a Sigma 8 mm, f/4 fisheye lens. The fisheye lens was calibrated to establish the lens distortion (Diaci, Kolar 2000). Light measurements were preformed at breast height in completely overcast sky conditions to avoid direct radiation. Photographs were taken with the top of the camera oriented north. Film was scanned and images were processed on a computer with Corel PHOTO-PAINT 9 software to acquire quadratic binary images in GIF format. After that they were analysed by hemIMAGE software (Bruner 2002) – (research conduced by Slovenian colleagues).

4.2.3. Results

Light conditions

Values of direct and diffused solar radiation are expressed as per cent ratio from light input on open area (Table 11). There is a significant difference between research plots. Big gap (D) clearly shows the highest light input, light conditions under the closed canopy (C) and small gap (A) are more similar to each other with higher heterogeneity in the latter case. It is surprising that the values of direct light under small gap (RP A) are lower than under the canopy (RP C). There is a positive correlation (R = 0.431, P = 0.002) between both light components diffused and direct solar radiation. Diffused light in small gap reached 65% of the values in big gap. Direct light reached only 23%.

Table 11. Values of direct and diffused light under small gap (A), canopy (C) and big gap (D).

RP	N	Average	Median	Variation	Q25	Q75	standard deviation	Min	Max
	Direct solar radiation %								
A	20	3.57	2.28	10.45	1.05	6.15	3.23	0.42	9.76
C	11	4.98	5.44	5.11	3.12	6.46	2.26	1.32	8.54
D	23	15.48	16.91	71.30	5.84	23.28	8.44	2.37	28
	Diffused solar radiation %								
A	20	10.51	10.58	5.5492	8.52	11.69	2.36	6.74	16.2
C	11	5.61	5.82	1.3029	4.464	6.31	1.14	4.07	7.88
D	23	16.06	15.30	18.943	12.45	20.27	4.35	9.35	24.1

Presence of dead wood

PRP 06

Coarse woody debris (CWD) of the diameter class I (d ≤ 10 cm) was present on the whole area of RPs, nevertheless its distribution was rather irregular. Highest differences in this diameter class were recorded between RP C (under canopy) and RP A and D (under gaps). Under the canopy CWD (d ≤ 10 cm) was recorded on 97% of all SP, average cover was 4.25%. Average cover on RP A and D was 1.27% and 0.52% (CWD was present on 61% resp. 41% of SPs). Diameter class II was present only on RP C and D (1.43% and 0.5%, CWD was present on 9.1% resp. 11.8% of all SP). Under the canopy only decay classes 2, 3 and 4 were present. Under the gap the majority of CWD was in decay class 5.

PRP 07

On RP E the high cover of CWD in both diameter classes was caused by fallen trees, thus forming the gap (cover 5.45% in diameter class I, 6.21% in diameter class II, present on 100% resp. 16.6% of SPs). On RP F similar values as in the case of RP C were recorded (cover 3.07% in diameter class I, 1.28% in diameter class II, present on 95% resp. 15% of SPs). On both RP only decay classes 5 and 6 were present. It can be stated that generally under the canopy smaller branches and branches of lower decay classes are present. Under the gaps the amount of thicker branches in higher decay classes increases, which is connected with the time of the gap formation. Within and near the gaps the probability that the falling tree or thicker branch hits the area increases.

Total cover
PRPs 06 and 07
Values of regeneration cover differ significantly between RPs. Highest cover was found on RPs A and F (small gap). On contrary lowest values shows RP C (under canopy). RPs E and D (big gap) lies between these values.

Table 12. Avarage and median cover on SPs.

	Nr. of SP	%	Regeneration	Vegetation	CWD	Soil	Litter	Stones	Roots	Other
A	23	average	43.96	11.96	1.25	0	41.75	0.26	0.17	0.65
		median	40	8	0.5	0	40	0	0	0
C	33	average	2.5	6.32	4.92	0.39	84.74	0.03	0.03	1.06
		median	0	2	4	0	89	0	0	0
D	44	average	17.85	23.57	2	0	52.95	0.23	0.5	2.9
		median	10	20	0.1	0	51.95	0	0	0
E	29	average	18.91	6.11	11.66	0.86	55.56	1.93	3	1.97
		median	10	2	5	0	51	0	0	0
F	20	average	26.35	1.58	4.35	1	62.04	2.78	1.15	0.75
		median	20	1	3	0	71	0	0	0

Vegetation cover
PRP 06
On the PRP 01 in total 30 plant species were found (5 tree species: beech, hornbeam, sycamore maple, spruce, larch; 1 shrub, 3 ferns, 11 grasses, 1 moss, 9 herbs). More plant species were present under gaps (RP A – 21 sp. RP D – 23 sp.) than under closed canopy (RP C - 17 sp.). There is statistical difference (Kruskal-Wallis test: $P < 0.001$) both in total vegetation cover and cover of beech regeneration on RPs. Total vegetation cover was higher under gaps (RP A – 64.7%, RP D – 48.3%) than under the canopy (RP C – 9.3%). RP A (small gap) and D (big gap) were dominated by beech (46.4%, resp. 17.5%), under the big gap the hornbeam was an important contribution to the tree regeneration (3.0%). Important was also the per cent ratio of grass species on RP D (big gap) – 21.9% (compared to 4.4% on RP C and 4.2% on RP A). RP A had the richest tree species composition in the regeneration cover. Only here sycamore maple was present, also few individuals of larch occurred in the regeneration; both species with average cover less than 1%. Spruce was present on two thirds of all SPs, hornbeam on one third, their average per cent ratio did not exceed 2%. On individual SP the cover of hornbeam reached the values from 5 to 15%. Under the canopy the beech reached the average cover only 2.6%. The per cent ratio of spruce was negligible. The regeneration was clearly dominated by beech that presented 75.8% of all individuals. Hornbeam was the second species presenting 15.5% of all individuals. Table 5 shows data for individual RPs.

PRP 07
The average total vegetation cover on RP E was 26.1% (17 plant species: 1 tree species, 5 herbs, 8 grasses, 2 ferns, 1 moss), on RP F 28.8% (14 plant species: 1 tree species, 5 herbs, 6

grasses, 1 fern, 1 moss). Beech was the only tree species dominating the tree regeneration (average cover RP E - 18.9%, RP F – 26.4%; present on 86% resp. 90% of SPs).

Table 13. Density of regeneration per ha.

Species	RP A		RP C		RP D		RP E		RP F	
	N	%	N	%	N	%		%		%
Fagus sylvatica	71305	78.68	9020	95.85	51414	69.25	54713	100	75778	100
Carpinus betulus	5411	5.97	130	1.38	21515	28.98	0	0	0	0
Picea abies	8117	8.96	261	2.77	909	1.22	0	0	0	0
Larix decidua	773	0.85	0	0	404	0.54	0	0	0	0
Acer pseudoplatanus	5024	5.54	0	0	0	0	0	0	0	0
Total	90630		9411		74242		54713		75778	

Number and height classes of beech regeneration, game damage

Not only the tree species composition, but also the age structure differs between RPs under gaps and RP C under the closed canopy. Highest density of beech regeneration was found under small gaps (RP A and RP F); with highest tree density in 3rd height class. Similar height development with lower densities was recorded for RPs under big gaps (RP D and RP E). Lowest density of beech regeneration was under closed canopy where limiting conditions resulted also in lower heights (the majority in 2nd height class) - (Fig. 8). On RP D, RP A and RP E important per cent ratio of beech regeneration reached the 4th height class. Plants higher than 50 cm can be regarded as successful regeneration with high probability of further development without negative influence of competing weed plants. On RP F considerable number of plants in 7th an 8th height class per ha was found (667 resp. 222 individuals; not included in the figure).

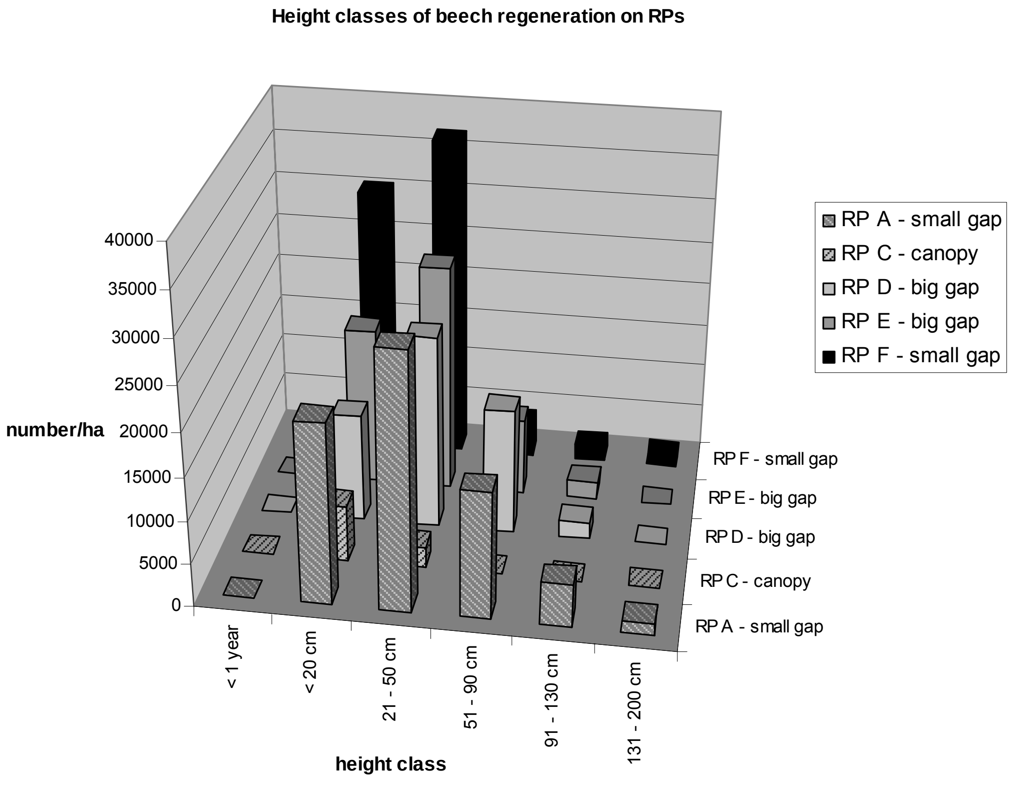


Fig. 8. Height classes of beech regeneration on RPs.

Damage caused by game browsing was recorded in 3rd quadrant of each SP (25% of the area). The analysis covered 23.6% (PRP 06) and 23.7% (PRP 07) of all individuals of the tree regeneration. Two measurements were performed, first one in June, second one in September. In general the damage caused by browsing increased during the vegetation period (following data shows the state of the 2nd measurement). Higher damage on beeches was found on RP A and D; 13.3% resp. 21.0% of individuals with middle damage by browsing. Only on RP F beeches with serious damage were recorded (4.1%). Other 20.6% showed middle damage, 75.3% of trees showed minor damage. On RP E 81.7% of beeches were not browsed or were browsed slightly, 18.3% showed middle damage. On RP C (under canopy) only 7.7% plants showed middle damage. On contrary on other RPs hornbeam was heavily browsed (7.1% serious damage, 28.6% middle damage). Almost no browsing was recorded on coniferous species.

Characteristics of dominant trees of beech regeneration
PRPs 06 and 07
Height
There is a significant difference between the heights of dominant beech individuals. Greatest differences are between RPs under gaps and RP C under the canopy. There is a positive correlation ($R = 0.213$, $P = 0.002$) between the values of diffused solar radiation and the height of the beech regeneration. There is no correlation between the values of direct light input and the height of the beech regeneration.

Table 14. Heights of dominant trees of beech regeneration.

RP	N	Average (cm)	Median (cm)	Variation	standard deviation	Min	Max
A	106	72.13	70	1719	41.46	12	180
C	39	21.84	20	136.82	11.69	8	85
D	176	53.97	48.5	756.42	27.50	12	140
E	103	60.94	57	1012	31.81	18	174
F	81	68.51	50	2789	52.81	14	247

Last year growth
Similar results show the analysis of the last year increment of dominant beeches. There is significant difference between RPs; with lowest values for RP C under the canopy. No correlation between the values of height increment and direct or diffused light could be found.

Table 15. Last year growth of dominant trees of beech regeneration.

RP	N	Average (cm)	Median (cm)	Variation	standard deviation	Min	Max
A	106	19.81	20	73,58	8.57	3	38
C	39	6.96	6	17,18	4.14	0.5	23
D	176	14.59	15	51,84	7.20	0	32
E	103	16.34	17	68	8.26	0	36
F	81	15.02	12	159	12.60	0	53

Diameter of root collar
There is significant difference between the diameters of root collars on RPs. Highest values are again on RP A (small gap), lowest values under the canopy (RP C).

Table 16. Diameter of root collar of dominant trees of beech regeneration.

RP	N	Average (mm)	Median (cm)	Variation	standard deviation	Min	Max
A	106	10.12	10	21.34	4.62	2	25
C	39	4.89	5	5.67	2.38	1	15
D	176	8.74	8	19.68	4.40	0.5	25
E	103	8.69	8	18.82	4.33	2.7	24.1
F	81	9.36	8	24.91	4.99	2.1	24.6

Form of terminal shoot and growth characteristics

On PRP 01 - 45% of all dominant beech individuals had direct terminal shoot, 11% of individuals showed multiple branching. Upright growth showed 38%; 16% of individuals did perform plagiotropic growth. There is no difference between RPs in number of plants with direct shoot. Lowest portion of multiple branched individuals was recorded under the canopy (RP C), where also game browsing was relatively lower than on other plots. On contrary high game browsing and occurrence of multiple branching was highest on RP D. Minor quality of beech regeneration was recorded under the canopy (RP C): absence of upright individuals, majority of individuals with knee-shaped growth. We were surprised to find important number of plagiotropic individuals on the RP A (small gap). On PRP 02 again high portion of multiple branched beeches was found. There is probably connection between heavy browsing on RP F and high number of individuals carrying this damage (due to mechanical injury).

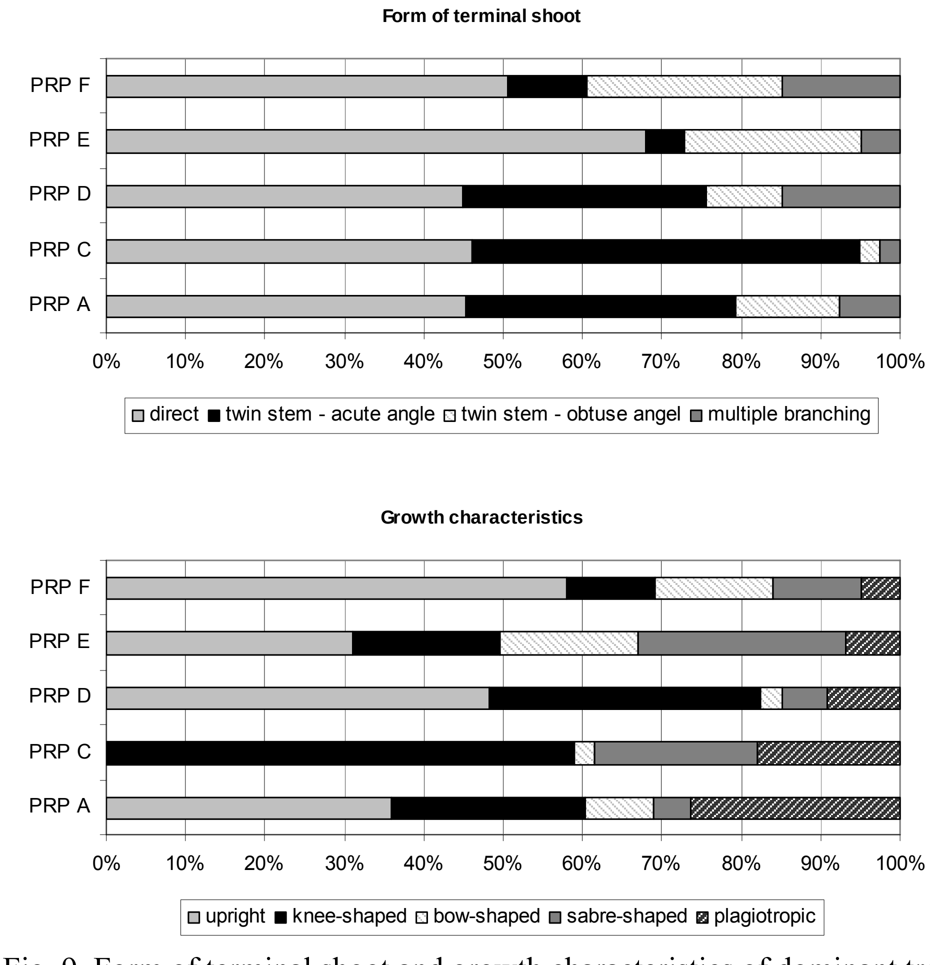


Fig. 9. Form of terminal shoot and growth characteristics of dominant trees of beech regeneration.

4.2.4. Discussion

Beech seedlings are able to respond strongly to primary growth factors such as soil water content, nutrient supply and light intensity. In the forest environment these changes are normally induced by gap formation during the forest cycle with forest development stages (Pontallier et al. 1997). In gaps a higher insolation may result in higher mineralization and nitrification, there is a lower beech litter production and higher herbal litter production with a better C/N ratio and higher nutrient availability, increasing species diversity (Muys et al. 1988; Pontallier et al. 1997). Gap microclimates may enhance seed germination and increase growth rates of herbs and woody species in comparison with rates in the forest understorey where the herb layer in closed beech forests is rather poor. Light environment induce changes in soil conditions and the absence of parent trees may increases soil moisture (Gálhidy et al. 2005). In their study in near natural forest Voděradské bučiny conduced on PRP 01 Podrázský, Remeš (2006, 2007) showed that the amount of dry matter decreased by ca. 25% several years after canopy opening, especially in the H horizon, the pH, base content and base saturation increased, as well as the content of macronutrients (with the exception of total calcium). The results proved considerable changes in the humus forms during the natural and semi-natural forest cycles connected with the stand regeneration. The chemical shifts were comparable also to the changes during natural development cycles in other semi-natural forests (Podrázský, Viewegh 2005). For the establishment and development of beech regeneration nutrient, water and light supply are of crucial importance. Under small gaps the combination of higher values of diffused light and relatively lower levels of direct light input may create favourable conditions for the establishment and growth of forest regeneration. Small gaps (RPs A and F) showed both highest cover of forest regeneration and highest density of individuals per ha. Gálhidy et al. (2006) proved that relative light intensity values in small gaps could not reach those in large gaps, maxima of soil moisture was the same in small gaps and large gaps. The pattern of soil moisture is generally more spatially variable than light. Madsen (1995a) showed that under the open canopy (13% of full light) the seedling growth increased three to four times on plots with sufficient water and nutrient supply. Nevertheless, even under the closed canopy a high coverage of germinated beech seedlings occurs. These very low relative light intensities (below 1% of full sunlight) permit first season survival of seedlings of large seeded species like beech and oak (Welander, Ottosson 1998), but seedlings are suppressed, waiting for favourable conditions to develop (Topoliantz, Ponge 2000). Peltier et al. (1997) found most young seedlings under mature trees in (half) shade. Older seedlings (>3yrs) were encountered more in gaps, indicating that for germination light is less important than for development. Even at 5% relative light intensity (RLI) Madsen (1995a) found that light was the main limiting growth factor. In Denmark, Emborg (1998) found that only few beeches survived the light levels of 2% RLI. Above this limit the numbers and sizes of seedlings increased with increasing light levels. Successful development of beech was ensured at RLI above 3%. In our study by these light conditions (RP C, Table 11) the beech reduced its height growth two to three times (compared to RPs under gaps), nevertheless the density of beech regeneration was still higher than the recommended afforestation rate for this commercial species (5 000 – 10 000 ind.ha^{-1} according to Burschel, Huss 1997). According to Madsen (1995a) and Collet et al. (2001) beech seedlings at least for some time can survive light conditions that barely permit any growth; however they become more vulnerable to attacks from pests or other damaging factors. In our case on the contrary higher browsing by game was recorded under gaps with higher densities of beech seedlings. Lower plant densities and the absence of other tree species made the RP C under canopy less attractive to game browsing. Roe deer (*Capreolus capreolus* L.) seems to be the most important factor for the reduction in the number of seedlings. The roe-deer densities vary during the year, nevertheless the density normally do not exceed 40 ind. per 1000 ha (on average 35 ind. per 1000 ha). Except for deer the seedlings might be browsed by hares, mice or voles that can locally cause by gnawing on the stems of young plants high damages on beech stands. Other common browser in the area is wild boar (*Sus scrofa* L.*)* with similar density as roe-deer.

Madsen, Larsen (1997) stated that increased canopy opening increased the potential of height growth. Generally, the seedlings of shade tolerant European tree species utilize light dispersed under the forest canopy and do not profit strongly from direct light input. In our study increased direct irradiation under gaps had lead to higher cover of herbal vegetation thus increasing competition for resources (Modrý et al. 2004). Under the big gap (RP D) higher cover of herbal vegetation and important portion of hornbeam in the natural regeneration as reaction to higher direct light input was observed. Light conditions may also influence the growth response of a beech seedling on soil fertility. In low light environments this response is reduced, whereas in non-limiting light conditions seedling growth is markedly influenced by nutrient availability (Minotta, Pinzauti 1996). Collet et al. (2001) indicate annual seedling height increment of 1.2 cm as threshold values for seedling growth that are necessary for survival in shade conditions. The growth rate of such seedlings is close to the growth rate observed on branches of senescent beech trees or on deep-shaded branches of adult beech trees. Even in poorest light conditions within our research plots the average height increment of beeches dominating the regeneration reached the value 6.96 $cm.r^{-1}$. Better light conditions resulted in higher values of total height and diameter of root collar of beech individuals growing under opened canopy. Nevertheless, there is a positive correlation only between the values of diffused light and the height of the beech regeneration. There is also significant shift in distribution of height classes of beech regeneration (under the canopy the majority of beech individuals were in 2^{nd} height class, on all other plats in 3^{rd} height class).

In relation to shade tolerance the architectural flexibility of beech is important. In shade beech saplings follow one of two strategies. Either they perform (pseudo)sympodial branching, with long shoot and absence of a top-shoot, or they develop a monopodial top-shoot consisting of short shoots (Peters 1997). When released from suppression, the monopodial top-shoot can easily form long-shoots and increase a height-grow rate, but the (pseudo)sympodial type can not easily resume vertical growth. Under the closed canopy the absence of upright individuals and the majority of knee-shaped individuals with tendency to twin stem underline the importance of light environment for the form and quality of beech regeneration, in the most part relevant for commercial forests. Difference in allocation of photosynthate lead in differences in tree architecture. Beech has decurrent growth and its growing space has a strong influence on the form of the leader. Most stem forking and leaning stems occurred where percent of above canopy light was below 20 (Stancioiu, O'Hara 2006).

In given condition the relative shade tolerance of beech will ensure the dominance of beech also in the future forest generation. Where several shade-tolerant tree species share space in a given forest type, dominance can easily change from one species to another between two consecutive generations (Swagrzyk et al. 2001; Reininger 2000). In Voděradské bučiny in the middle of the 17^{th} century, the silver fir was the main tree species. Nevertheless its dramatic decrease reflects rather the increasing impact of humans during the centuries (Pokorný 1963) than natural shift between dominating tree species. It is likely that in given conditions further break down of the existing canopy and the formation of larger gaps will contribute to higher portion of hornbeam in the tree species composition.

4.2.5. Conclusions

This study has revealed the influence of light on natural regeneration community and development. The performance of tree seedlings is influenced by different light levels as a result of gap formation described in the model of forest cycle. Light has direct and indirect influence on the establishment and growth of tree regeneration via changes in water and nutrient availability. Light has direct influence on the form and growth of beech individuals. Higher vegetation cover, especially of herbal vegetation, is connected with higher intensity of direct light, also hornbeam profit from establishment of larger openings in the canopy, which perhaps improves its competing ability due to better temperature conditions. Browsing by deer does not play important role determining natural regeneration development. The old-growth has reached degrading phase induced by small scale tree fall with regeneration phase in the following generation of the forest (under the gaps and in its proximity). It seems that very important might be also changes of soil moisture connected to gap formation. This aspect should be included in the future study.

4.3. Structure of beech forest stands with different management history

4.3.1. Introduction

Forests in the Czech Republic were during last thousand years increasingly influenced by human activities. Currently in Central Europe there are no forest ecosystems that would be excluded from human impact. Old-growth deciduous forests in western and central Europe, for the most part, consist of small tracks that often may be atypical due to human disturbance, poor soil productivity or inaccessibility. In addition, very little information on tree age distribution, structural heterogeneity and tree spatial patterns appears to be available for these forests (Rozas 2006). The knowledge of structure and development of our forests is a valuable guideline for management in protected areas, where the non-wood-producing functions should be of the greatest importance. In this field the comparison of adjacent forest stands with different management history during the last 50 years in similar natural conditions may be an interesting source of knowledge.

A general definition of old-growth for temperate forests includes a relatively high degree of patchiness and heterogeneity, dead trees and logs, relatively old age, reverse-J shaped size distribution and multicohort age distribution, but not necessarily without any evidence of human activity (Foster et al. 1996). It is commonly accepted that old-growth temperate forests are largely structured by disturbances, where major disturbances can initiate new forest stands, but only small-scale disturbances are evident in near-steady state (e.g., Leibundgut 1982; Nagel et al. 2006; Standovár, Kenderes 2003). The smaller the scale and higher the frequency of disturbances, the more diversified the horizontal and vertical forest structure should be. The patches forming the mosaic are distinguishable on the basis of stand volume accumulation, age and size structure, canopy openness, occurrence of regeneration, and/or eventually, species composition (Korpel' 1995). Nevertheless Paluch (2007) stated that occurrence of diversified vertical structures should not be related to lower levels of basal area. In his study the structural diversity of individual patches may depend more on the resistance to disturbance of large canopy trees than on competitive stress to which the sub-canopy tree and under-canopy tree are subjected. Thus the study results are incompatible with models that anticipate a stage of beech forest development characterized by high biomass accumulation and a more or less homogenous vertical structure. According to this author the natural beech stands may exhibit more or less diversified vertical structure and spatial texture depending upon site- and location-specific disturbance regime. The ecological features of beech alone should not preclude the shaping of stand of a given structure type.

Moreover, as almost all forest in Europe has been managed, forest restoration has always to deal with stands with a composition, structure and function developed through a history of repeated, intense anthropogenic disturbances (Wolf 2005). Any wood, which is to be treated as a natural reserve and restored, will inherit a structure created by past management that should be preserved as a starting point for the future forest structure.

Foresters have traditionally used old-growth studies to develop a natural or ecological system of forest management in which management of forest is guided by natural ecosystem dynamics. The maintenance of many natural ecosystems requires the protection not only of current old-growth areas, but also of naturally disturbed forests that represent future old-growth (Foster et al. 1996). According to Schnitzler, Borlea (1998) the sustainable forest management depends on two complementary actions: (i) protection of remnant areas of high degree of naturalness and/or their extension to areas compatible with the viability of all populations of both plants and animals (ii) definition of criteria for management which would be as close as possible to natural models of forest dynamics. The whole natural pattern of eco-units and mosaics promoted by natural disturbances must be respected.

The aim of the study is to investigate the influence of management interventions, respectively the absence of forest management on forest structure and forest dynamics. An appreciation of natural processes in forests is essential in order to propose rules both for conservation and sustainable management. The study analyses a concrete case in an intensively managed landscape, structure of semi-natural forests is described from small unmanaged stands (with no management intervention since 50 years). Despite it is impossible to exclude indirect human impact on forest stands and consequently it is hard to make precise characteristics of forest naturalness (according to forest structure), yet we suppose that the forest structure changes surprisingly fast and give us important guidelines about future development of these plots. Another question is how these changes within limited areas of research plots could be interpreted on the level of whole forest stands and forest areas.

4.3.2. Materials and methods

In the summer of 2004 we took over four (PRP 01, 03, 04, 05) 1-ha (100 m x 100 m) permanent research plots established by department of forest management of CULS in part of the even-aged beech old-growth forest. All plots have similar stand structures and are all managed in the same way: through shelterwood cutting. They slightly vary in canopy closure with respect to different intensity of cutting. The rotation period is 130 years, with a regeneration interval of 40 years (according to LHP). Plots were established in 1979 with aim to describe growth and development of mensurational indices in ageing parent stands. Thus, we have exact data about the forest structure from the 1980 and 1997. To determine the difference between stands structures in managed forests and in semi-natural beech stand in the National Nature Reserve we set up in 2005 another two 1-ha (100 m x 100 m) permanent plots in non-interventional stand in so-called locality “Virgin forest” (PRP 06 and 07). PRP 01 and 05 will be part of the non-interventional zone of the reserve. PRP 03 and 04 will stay management forest.

In each PRP 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), the height, the crown height (hypsometer Verte, accuracy 0.1 m) and recorded the species, health status (living, dying or dead), and social status (dominant, codominant, subdominant, less than 20 m, broken or dead tree). We also mapped the crown projection of each live stem by measuring a minimum of five cardinal crown radii per tree. The volume of dead wood ≥ 10 cm (log volume - dead fallen trees and stumps; snag volume - dead standing trees) was estimated by complete enumerations within permanent plots. For logs we measured the length and diameter on the butt and on the small end. Deadwood was classified according to decay classes (for detailed description see the methodology in chapter 4.2.2). All trees within the research plots are enumerated. We regard the documentation of the coordinates of all measured entities for the reasons of long-term studies in the area.

The volume of deadwood was estimated separately for logs and snags. For logs we used the formula after Smalin:

$$V = (g_o + g_n)L/2 \qquad (1)$$

g_o, g_n ...basal areas on both ends
L ... lenght

The volume of snags was estimated after Denzin:

$$V = d^2_{1,3}\,(cm)\,/1000 \qquad (2)$$

This equation is valid for standing trees of height around 25 m. Therefore we made volume reduction of 3% for each meter of difference.

The quantification of growth, production and structural characteristics is made by standard dendrometrical methods (Korf 1972, Šmelko 2000):

Diameter structure
Tree number distribution (n_j) in diameter classes is characterized as:

$$\bar{d} = \frac{\sum_{j=1}^{k} n_j d_j}{n} \qquad (3)$$

For particular permanent research plots and if necessary also for particular tree species mean diameters $d_{1.3}$ are given. According to Šmelko (2000) the most important statistical characteristics of diameter distribution are: arithmetic mean, standard deviation and coefficient of variance. Diameter of mean stem (counted from basal area) as basic characteristic for research plots and if necessary for tree species is given.

Height structure
Height curves for particular permanent research plots, mean heights, dominant heights $h_{10\%}$ and h_{100} are given (height of 10 % and 100 highest trees on research plot).

$$h = f(d_{1,3}) \qquad (4)$$

Basic stand characteristics
Stand density, volume and stand basal area were calculated by regular dendrometric methods using the volume tables and equations (Petráš, Pajtík 1991). Same methods were used for older measurements in order to allow comparison with new results. Volume and basal area on particular PRPs were calculated as the total of volumes of all trees (in this study we calculated volume of timber to the top of 7 cm over bark):

$$Vt = \sum v_i \qquad (5)$$

$$Gt = \sum g_i \qquad (6)$$

Tree species composition
Tree species composition is given as portion of particular tree species (N_j) on total number of trees (N), as portion of volume of particular tree species (V_j) on total volume of PRP (V) and as portion of basal area of particular tree species (G_j) on total basal area of PRP (G).

Basal area
Basal area is calculated from measured values of $d_{1.3}$:

$$g = \frac{\pi}{4} \cdot d_{1,3}{}^{2} \qquad (7)$$

Stand density
Stand density is defined as proportion of observed value (number of trees N_{SK}, basal area G_{SK}, volume V_{SK}) to standard value per 1 ha (N_{RT}, G_{RT}, V_{RT}). For higher precision of stand density we used two decimal places:

$$\rho = \frac{V(G)_{SK}}{V(G)_{RT}} \qquad (8)$$

Standard values were taken from mensurational tables ÚHÚL – Brandýs nad Labem and VÚLHM Zbraslav Strnady, valid from 1. 1. 1990.

Increment
For all PRP were repeated inventarisations were conduced we calculated the values of volume increment. Volume increment i_v is the result of growth of all basic characteristics taking part on the growth of tree (diameter, basal area, height). Current volume increment between t_{n-1} and t_n is equal to the difference in volumes at the beginning and at the end of the period:

$$i_v = v_t - v_{t-n} \qquad (9)$$

$$CPB = Z_2 - Z_1 + T - D \qquad (10)$$

CPB = Total current increment; Z_1 = Volume at the beginning of given period; Z_2 = Volume at the end of given period; *T* = Harvest; *D* = Ingrowth.

Dividing the value of current volume increment i_v through number of years *n* of given period we obtain the annual current volume increment ($m^3.a^{-1}$).

Diameter increment
Current diameter increment i_d for given period is calculated as:

$$i_d = d_t - d_{t-n} \qquad (11)$$

Dividing the value of current diameter increment i_d through number of years *n* of given period we obtain the annual current diameter increment ($cm.a^{-1}$).

Basal area increment
Analogous to diameter increment we calculate the basal area increment as:

$$i_g = g_t - g_{t-n} \qquad (12)$$

Dividing the value of current basal area increment i_g through number of years *n* of given period we obtain the annual current basal area increment ($m^2.a^{-1}$).

h/d ratio (slenderness ratio)
h/d ratio (K) is calculated as:

$$K = h/d_{1.3} \qquad (13)$$

Indices of forest structure and spatial patterns are given in this order:

Hopkins-Skellam aggregation index (Hopkins, Skellam 1954). It is defined by the equation

$$A = \frac{\sum_{i=1}^{N} \omega_i'}{\sum_{i=1}^{N} \omega_i' + \sum_{i=1}^{N} \omega_i}, \qquad (14)$$

Pileou-Mountford aggregation index (Pielou 1959 and Mountford 1961). It is defined by the equation

$$\alpha = \frac{1}{N}\pi\left(\frac{N}{P}\right)\sum_{i=1}^{N} \omega_i'. \qquad (15)$$

Clark-Evansův aggregation index (Clark, Evans 1954). It is defined as a ratio of average distance between the nearest neighbors $\bar{r} = \sum_{i=1}^{N} r_i$ to expected distance r_E in the case of so called Poisson forest, i. e. the forest with randomly distributed trees. This distance equals

$$r_E = \frac{1}{2\sqrt{\lambda}}. \quad \text{Then} \quad R = \frac{\bar{r}}{r_E} = 2\bar{r}\sqrt{\lambda} \qquad (16)$$

The spatial structure of forest stands was also tested using the **Ripley's *K* – function** (Penttinen et al. 1992; Ohser 1983):

$$K(r) = \sum_{0<\|x_i - x_j\|\le r} \frac{1}{\lambda^2 s(\|x_i - x_j\|)}, \qquad (17)$$

r … sociability
λ …average tree number per plot,
$s(r) = \frac{ab - r(2a + 2b - r)}{\pi}$ correction for edge effect,
a, b … dimension of plot
$\|x_i - x_j\|$ … distance between i-th and j-th tree. A distance of 25 m was assumed as a maximal distance of analysis.

Table 17. Overview of the aggregation indices included in the study.

Index	Mean value	Aggregation	Regularity
Hopkins-Skellam	$A = 0.5$	$A > 0.5$	$A < 0.5$
Pielou-Mountford	$a = 1$	$a > 1$	$a < 1$
Clark-Evans	$R = 1$	$R < 1$	$R > 1$

All mentioned indices belong to so-called distance dependent indices, for their assessment the coordinates of trees on PRP are used. For the calculation we used the software PointPro 2.1 developed at the Department of forest management at CULS Prague (Zahradník). *Monte Carlo* methods simulate randomly generated plots of the same dimensions to compare the value of the function *K(t)* with that expected from a randomly distributed group of points and to assess its significance. The edge effect of PRP was involved in the study. In the case of near-natural forest stands (PRP 06 and 07) we investigated the spatial pattern of the whole plot and in particular layers (trees lower than 10 m, trees from 10 to 20 m and trees higher than 20 m). In managed stands (PRP 01, 03, 04, 05) we compared the spatial pattern in 1980 and 2005.

4.3.3. Results

Tree species composition

On both PRP beech was a dominant tree species. On PRP 06 beech was representated by 93%, on PRP 07 by 66.8% (based on basal area). Based on tree numbers its representation was 90.6% and 71.7% respectively. On PRP 06 other tree species are (compositon: basal area – tree mumbers): hornbeam (2.9% - 5.9%), spruce (0.6% - 1.0%), and birch (0.4% - 0.5%). On PRP 07 other tree species are: hornbeam (13.7% - 15.8%), larch (10.6% - 5.5%), birch (0.4% - 0.4%) and sycamore maple (0.7% - 0.4%). PRP 01 is almost pure beech stand with only one full-canopy larch tree (2.0% - 1.1%). PRP 03 and 04 are pure beech stands with no admixed species. On PRP 05 two oaks are present (1.2% - 1.8%).

The occurrence of dead wood

The amount of log volume in research plot 06 was 21.52 $m^3.ha^{-1}$ (20.04 m^3 beech, 1.1 m^3 birch and 0.37 m^3 birch). The second decay class was represented by 67%. In general only lower decay classes were present. In the 4th decay class only 0.17 % of CWD was present. The snag volume was 18.70 $m^3.ha^{-1}$ (three beech individuals). The total amount of dead wood was 40.22 $m^3.ha^{-1}$. On PRP 07 the volume of snags amounted only 4.23 m^3 (one standing death beech). On the contrary the volume of logs was higher than on PRP 06. In total 46.27 $m^3.ha^{-1}$(beech 42.69 m^3, birch 2.33 m^3, hornbeam 1.01 m^3 and larch 0.24 m^3). The 2nd, 3rd and 4th decay classes were mostly represented (32%, 28 % and 24% of total CWD volume). Total volume of deadwood (CWD) on PRP 07 amounted 50.50 $m^3.ha^{-1}$. On PRP 01, 03, 04 and 05 the occurrence of dead wood was restricted to felling debris of diameter less than 10 cm. There were no logs recorded. On PRP 01 we recorded volume of snags 3.34 $m^3.ha^{-1}$, on PRP 03 - 4.83 $m^3.ha^{-1}$, on PRP 04 - 1.26 $m^3.ha^{-1}$ and on PRP 05 – 6.11 $m^3.ha^{-1}$.

Diameter structure, basal area

From the diameter distribution on PRP 06 is evident the presence of upper layer and understorey in the stand (two peaks in the frequency of tree diameter classes). Mean diameter of beech was 48.09 cm. Top diameter (represented by 10 thickest trees) was 103.9 cm. The total basal area of the stand was 35.562 $m^2.ha^{-1}$, the beech amounted 33.427 $m^2.ha^{-1}$, larch 1.225 $m^2.ha^{-1}$, hornbeam 0.603 $m^2.ha^{-1}$, spruce 0.199 $m^2.ha$ and birch 0.108 $m^2.ha^{-1}$.

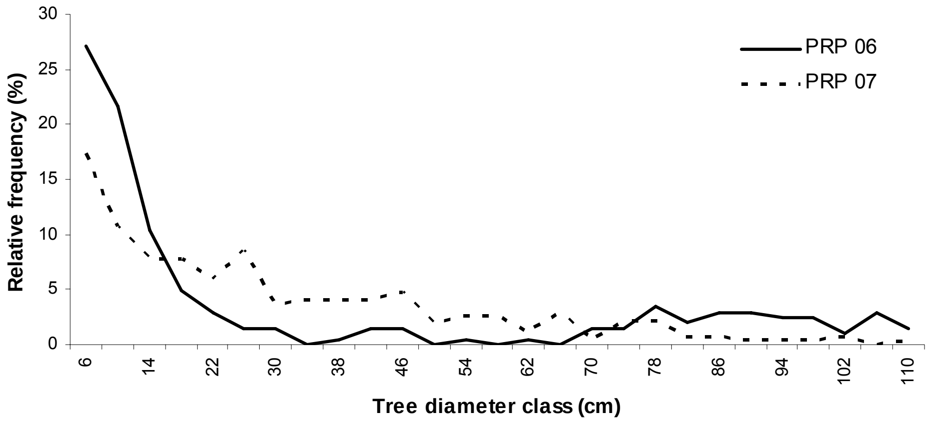


Fig. 10. Diameter structure on PRP 06 and 07.

The mean diameter of beech on PRP 07 was 35.92 cm, top diameter was 84.75 cm. Both values are lower than on PRP 06 with considerable number of full-size canopy trees in upper layer. On PRP 07 the number of these trees is much lower, on the contrary middle layer formed by beech and other tree species is present. On both plots many small recruits in understorey are waiting for release from suppression. The total basal area of the stand was 30.775 $m^2.ha^{-1}$, the beech amounted 19.758 $m^2.ha^{-1}$, larch 4.178 $m^2.ha^{-1}$, hornbeam 3.248 $m^2.ha^{-1}$, spruce 3.304 m^2.ha, birch 0.112 $m^2.ha^{-1}$ and sycamore maple 0.176 $m^2.ha^{-1}$.

Table. 18. Statistic characteristics of diameter distribution in partial plots.

	Permanent research plot /Year													
Characteristics	06	07	01			03			04			05		
	2005	2005	1980	1997	2005	1980	1997	2005	1980	1997	2005	1980	1997	2005
Mean value (cm)	31.88	29.62	51.33	55.16	59.57	55.42	60.11	62.46	53.20	57.76	60.49	44.56	49.05	55.18
Count	203	272	170	149	93	149	138	126	139	127	110	221	194	113
Stand. dev. (cm)	34.93	23.78	12.49	13.70	13.43	11.74	12.60	12.98	10.66	11.72	12.25	11.31	11.92	10.55
C. of variation (%)	109.57	80.28	24.33	24.84	23.94	21.18	20.96	20.78	20.04	20.29	20.25	25.38	24.30	19.12
Standard error	2.45	1.44	0.96	1.12	1.39	0.96	1.07	1.16	0.90	1.04	1.17	0.76	0.86	0.99
Minimum (cm)	3.6	3.1	24.5	25.6	28.75	26.6	32.3	33	27.6	28.6	31.5	18.85	21.95	35.15
Maximum (cm)	110.2	108.2	93	91.8	95.6	81	87.35	95	87.2	91.65	102.1	72.15	78.7	83.15
Range (cm)	106.2	105.1	68.5	66.2	66.85	54.4	55.05	62	59.6	63.05	70.6	53.3	56.75	48.35
Curtoses	2.50	3.42	2.99	2.62	2.83	2.56	2.37	2.54	3.00	2.78	3.34	2.36	2.35	2.43
Skewness	1.10	1.06	0.19	0.15	0.06	-0.23	-0.20	-0.17	0.13	-0.01	0.17	0.13	0.16	0.20

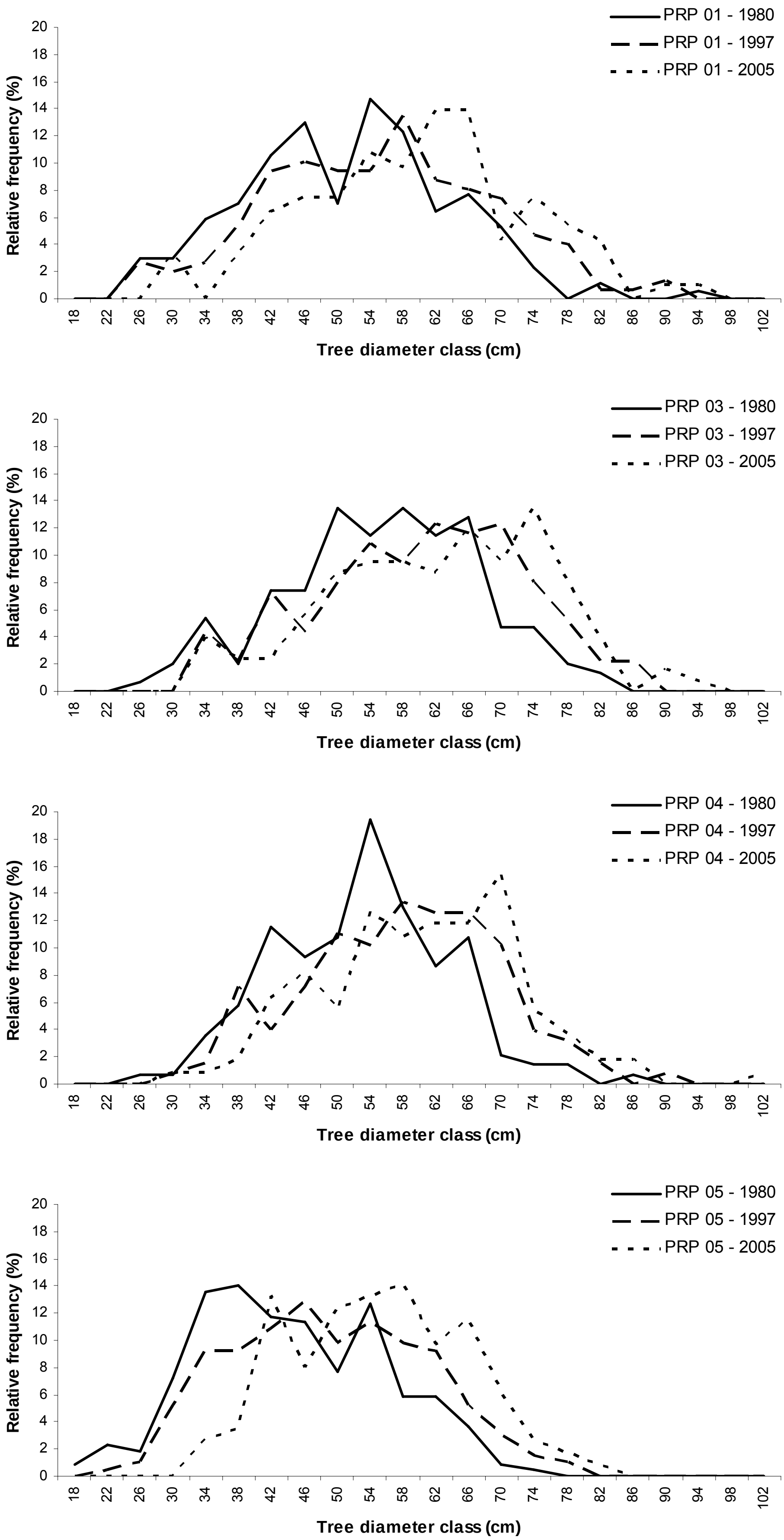


Fig. 11. Diameter distribution on particular plots in managed stands and its evolution in time.

The coefficient of variation (%) is the relative rate of the diameter variability. It expresses the standard deviation in percentages from arithmetic mean and in this way it allows a mutual comparison of the diameter diversity also for such stands, which have different average diameter (Barna, Marušák 2003). We see from Table 18 that the coefficient of variation reaches the highest value on PRP 06 and 07 (with high diameter differentiation due to high number of trees in undergrowth) and lowest on PRP 05. Other managed plots show very similar values to that of PRP 05 with slightly higher value on PRP 01. From the viewpoint of time a decline of the values of coefficient of variation occurred only on the PRP 05. The time dependency was not found on other plots. According to (Barna, Marušák 2003) the dynamic changes are quicker the more intensive cutting was applied and the coefficient of variation goes drops with increasing cutting intensity. This is exactly the case of PRP 05 where intensive cutting from 1997 to 2005 resulted in decrease of the coefficient of variance (see also Table 21). The biggest shift of the frequency curve on the axis *x* to the right was recorded on this PRP by two diameter classes. A similar development was also recorded on other plots but in a smaller extent.

Stand density, crown cover

Stand density was calculated from the basal area. Table 19 gives overview of stand density for particular tree species and in three stand layers on PRP 06 and 07. Understorey was defined as diameter classes 2 – 14 (≤ 16 cm), middle layer as diameter classes 18 – 58 (≤ 60 cm), upper layer as diameter classes 62 – 110 (≤ 112 cm). The crown cover was estimated separately for trees higher than 30 m and trees lower than 30 m. On PRP 06 the crown cover was 109.1% and 37.0 % respectively. On PRP 07 the crown cover was 67.4 % and 65.4 % respectively. Crown cover on PRP 01, 02, 03 and 05 ranged from 77.0% to 107.7%. The stand density ranged from 0.6 to 0.9. For exact characteristics see also Table 6 and 9. For crown cover see also Appendix – Horizontal structure of PRPs.

Table 19. Total density of stand, density for particular tree species and density for particular stand layers.

PRP 06				PRP 07		
species	diameter cl.	density		species	diameter cl.	density
beech	62 - 110	0.585		beech	62 - 110	0.271
	18 - 58	0.028			18 - 58	0.177
	2 - 14	0.044			2 - 14	0.032
	total	0.657			total	0.480
hornbeam		0.021		hornbeam		0.098
larch		0.022		larch		0.076
spruce		0.004		spruce		0.057
birch		0.003		birch		0.003
maple		-		maple		0.005
Density - total		0.707		Density - total		0.719

Height structure, h/d ratio, crown length, crown projection

According to height distribution the stand on PRP 06 can be divided into two vertical layers (undercanopy and overcanopy). The frequency curve on Fig. 12 has two peaks reflecting the dbh distribution. The middle layer was almost missing with only few individuals firstly of admixed tree species (not displayed), whereas the ovorstorey and understorey were dominated by beech (see also centotic position). The highest tree on the plot amounted 43.1 m (beech). PRP 07 similar to dbh distribution showed the presence of abundant middle layer (again formed mainly by admixed tree species). The highest tree on the plot amounted 41.4 m (beech). On managed plots with the exception of PRP 03 the heights were normally distributed (Fig. 13).

On all plots the dominant height (10% highest trees) was close to 45 m, on PRP 01 the dominant height overreached 46 m (for exact values see Table 20).

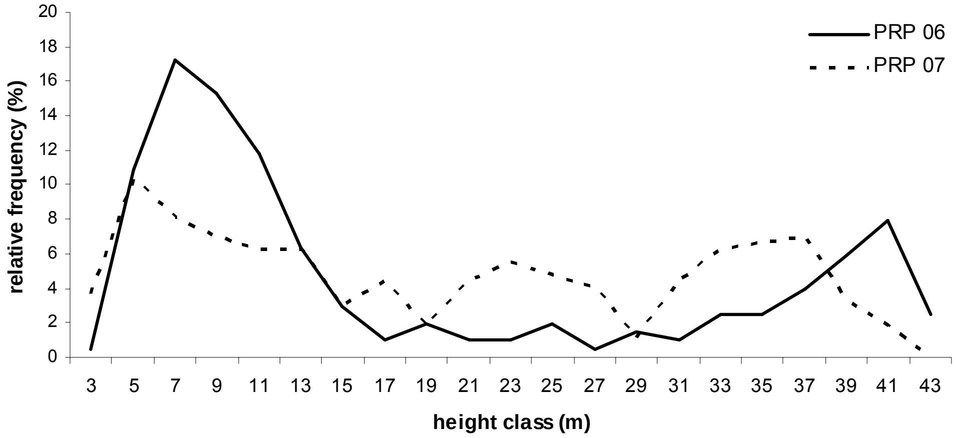


Fig 12. Height distribution on PRP 06 and 07 – unmanaged stands.

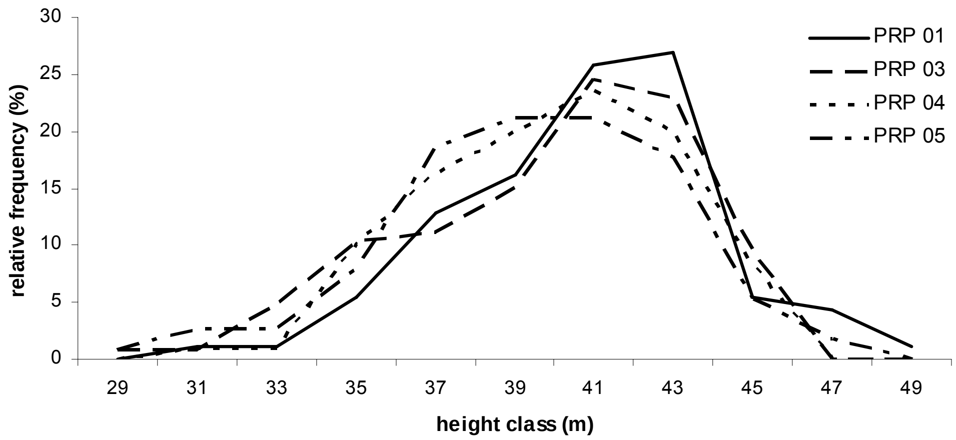
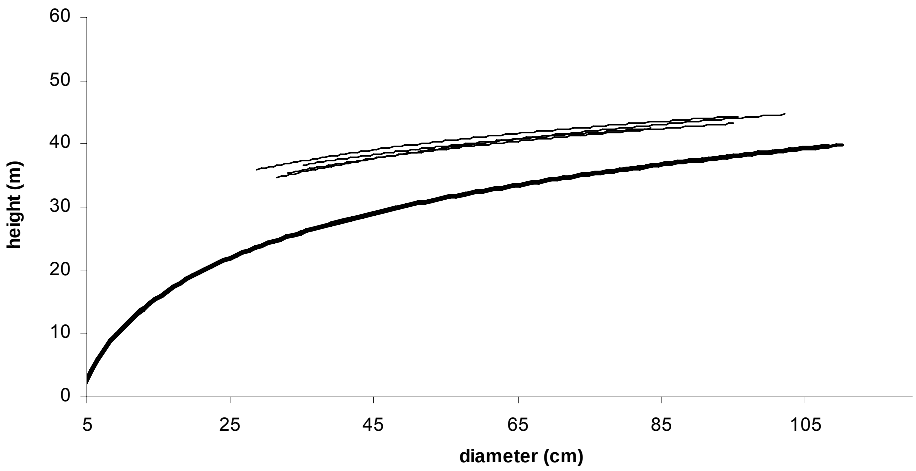


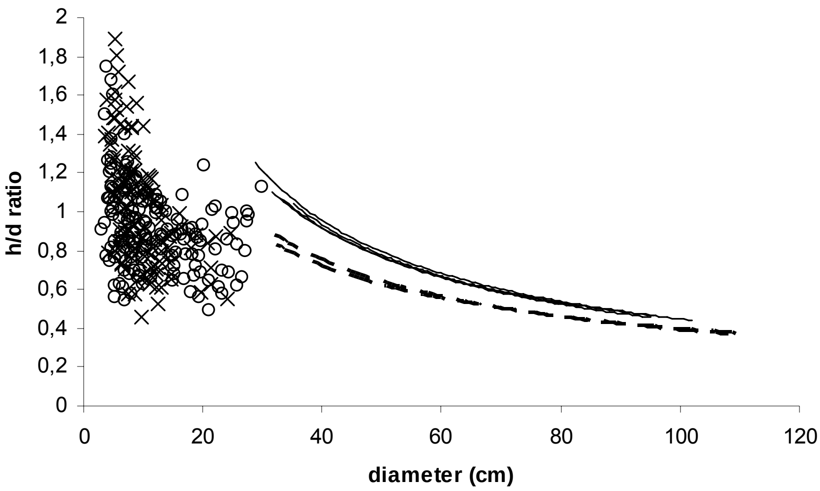
Fig 13. Height distribution on PRP 01, 03, 04 and 05 – managed stands (period 2005).



(thin line – managed stands, bold line – identical height curve for PRP 06 and 07)

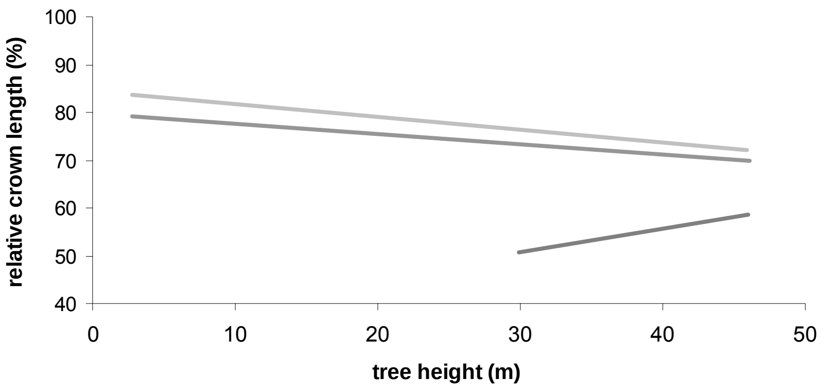
Fig. 14. Height curves of beech on particular research plots (period: 2005).

For the adjustment of stadial height curves we used the equation y = A.Ln(x) – B. There is no difference between height curves of PRP 06 and 07. Height curves in managed stands are moved upwards probably due to felling of thinner trees and absence of management interventions in unmanaged stands where subcanopy trees remain in the stand, thus lowering the arithmetical mean of tree height for the whole stand and in particular diameter classes. Nevertheless we were surprised to see so pronounced difference in height curves for managed and unmanaged plots (Fig. 14). Critical value of h/d ratio for beech is given in the range 1.8 – 2.2 (Korpel' et al. 1991). On PRP 06 the values ranged from 0.28 to 1.89. Only two individuals overreached the critical value. On PRP 07 the h/d ratio ranged between 0.35 – 1.75, the critical value was not reached in any case. All beeches with higher h/d ratio were of lower dimensions forming the understorey of unmanaged stand with different architecture than the overstorey. In order to compare managed and unmanaged plots, we divided the woody compartment on PRP 06 and 07 into two groups of diameter lower and higher than 30 cm. From Fig. 15 is evident that in managed stands trees with same dbh had higher values of h/d ratio than beech trees in unmanaged stand, but still with similar development. On the contrary extreme values were reached in the dimensions of pole timber making the understorey more susceptible to abiotic agents (especially snowbreak) known from young managed stands. According to stability, the stand can be divided into two groups: the overstorey with h/d ratio as stability indicator lower than in managed stands and the understorey with values significantly higher, thus indicating higher risk of abiotic damages. For the adjustment of curves in Fig. 15 we used function $y = A.x^b$ ($R^2 \geq 0.741$ for unmanaged plot and $R^2 \geq 0.811$ for managed plots).



(dotted line – unmanaged stands, solid line – managed stands, cross – PRP 06, circle – PRP 07)
Fig. 15. Relation between diameter and h/d ratio of beech.

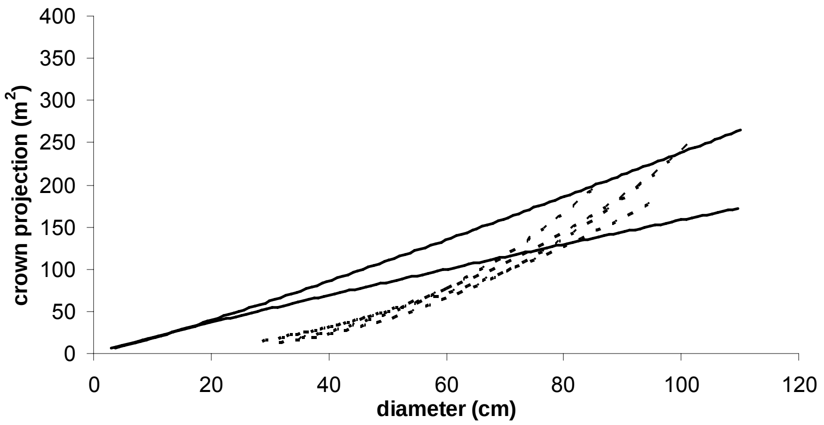
For the estimation of relation between tree height and the relative crown length of beech (as main tree species) we used linear regression. Fig. 16 shows that in managed stands (with low range of tree heights) the trend was slightly increasing. On the contrary on plots leaved for spontaneous development the relative crown length was rather negatively correlated with total tree height. Thus, understorey trees and trees of middle layer established crowns lower than main canopy trees. Trees of same height formed larger crowns in unmanaged stands than in managed.



(upper line – PRP 07, middle line – PRP 06, lower line – managed stands)

Fig. 16. Relation between tree height and relative crown length of beech.

The relation between dbh and relative crown length showed identical results (not displayed). In unmanaged stands in lower dbh classes the relative crown length amounted in average 80% of the tree height, in higher dbh classes still considerable ratio of 70% of tree height was reached. In managed stands the relative crown length in average ranged from 50% to 60%. The crown length may be influenced by two different mechanisms: in managed stands qualitatively less valuable individuals are removed from stand thus arithmetically increasing the mean height of clear stem of remaining trees, secondly remaining trees in the proximity of gaps have more space to develop bigger crowns (beech reacts very positively to increased light input and is a very good "gap-filler"). Wide crowns of dominant beeches on PRP 06 would than also indicate longer continued period with lower stand density related to gap formation with enough time to develop such extensive crowns (in chapter 4.2. we estimated the age of gaps on PRP 06 with natural regeneration on the forest floor on more than 40 years) – (Fig. 17).



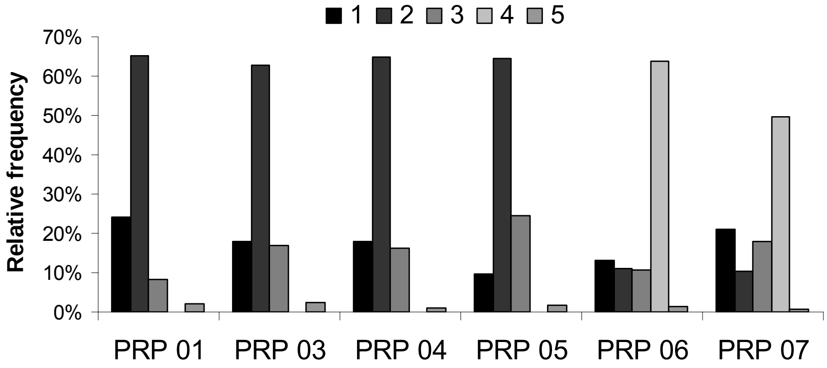
(upper full line - PRP 06, lower full line – PRP 07, dotted lines – managed stands)

Fig. 17. Relation between diameter and crown projection of beech on managed and unmanaged plots.

In general, in all managed plots the size (width) of crowns in relation to dbh was very similar. The mean value of crown projection area reached from 70.0 m^2 to 85.4 m^2. On PRP 06 the size of crowns (mean 73.9 m^2) for given dbh overreached values of managed plots, but also that of PRP 07 (mean 49.1 m^2), indicating that main canopy trees did have enough space and time to develop bigger crowns. On PRP 07 high number of undercanopy trees with small crowns lowered the average value, which is not exactly the case of PRP 06 with mean value comparable with that of managed plots. Nevertheless from dbh 70 cm trees (mainly dominant trees) in homogenous stands are able to develop crowns of similar or higher projection areas than in stands with spontaneous development (Fig. 17). For the adjustment of curves in Fig. 17 we used function $y = A.x^b$ ($R^2 \geq 0.782$ for unmanaged plot and $R^2 \geq 0.624$ for managed plots).

Cenotic position

On all managed plots we see absence of trees lower than 20 m. Few broken individuals (largely dead) form the 5th cenotic position. Most represented (63% - 65% of all trees) are codominant individuals forming homogenous vertical structure with few dominant or subdominant individuals. On PRP 06 and 07 tree species composition in particular cenotic classes is important. Whereas on PRP 06 the main canopy and undergrowth are for the most part formed by beech individuals (1 – 96.3%, 2 – 91.3%, 4 – 98.5%) the middle layer (subdominant trees) is formed by admixed tree species (beech – 48.8%, hornbeam - 38.1%, spruce – 9.5%, larch – 4.8% and birch - 4.8%). Nevertheless this layer on PRP 06 was less represented with only 21 individuals.



(1 – dominant tree, 2 – codominant tree, 3 – subdominant tree, 4 – height less than 20 m, 5 – broken tree).

Fig. 18. Cenotic position of trees on particular plots

On PRP 07 dominant trees were formed by beech (59.4%) larch (22.8%) and spruce (17.5%). Codominant trees were represented by all tree species present on the plot (beech – 42.9%, hornbeam – 32.1%, spruce - 14.3%, larch, birch and maple were represented by one individual – 3.6% each). Similarly to PRP 06 the middle layer (subdominant trees) is mainly formed by admixed tree species (beech – 40.8%, hornbeam - 55.1%, spruce – 2.0%, larch). On both plots the 5th cenotic position was formed for the most part by beech.

Growing stock and increment

Table 20. Basic stand characteristics (2005).

PRP	N (ha)	G m²/ha	ρ	Crown cover	V $m^3.ha^{-1}$	Vcwd $m^3.ha^{-1}$	V/Vcwd (%)	$d_{1.3}$ mean (cm)	$d_{1.3}$ mean stem (cm)	h mean (m)	h mean stem (m)	h_{100} (m)	$h_{10\%}$ (m)
01	93	27.23	0.60	78.2	597.48	3.34	0.6	59.57	61.06	40.89	41.21	-	46.11
03	126	40.26	0.90	107.7	863.72	4.83	0.6	62.46	63.79	39.95	40.28	-	44.97
04	110	32.89	0.75	81.8	704.04	1.26	0.2	60.49	61.70	39.99	40.35	-	44.91
05	113	28.00	0.65	77.0	583.20	6.11	1.0	55.18	56.17	39.47	39.80	-	44.72
06	203	35.56	0.71	146.1	707.21	40.22	5.7	31.9	48.09	17.8	30.5	28.33	39.98
07	272	30.77	0.72	132.8	505.60	50.50	10.0	29.6	35.92*	20.2	26.4*	33.69	36.8

*due to high stand diversification and species richness value only for beech (hornbeam /$d_{1.3}$ and h of mean stem/: 31.01 cm – 24.2 m, larch: 59.55 cm – 36.9 m, spruce: 49,74 cm – 33.9 m).

For growing stock on PRP 06 and 07 see Table 9 in chapter 4.2.2. PRP 06 is almost pure beech stand (according to % of total volume for particular tree species). On PRP 07 important part of stand volume is formed by larch – 12.1%, spruce – 9.5% and hornbeam – 8.3%. Managed stands are almost pure beech stands (see Tree species composition in this chapter).

Table 21. Stand characteristics of managed stands in 1980, 1997 and 2005.

PRP	Year	Age (Years)*	*N* (ha)	$d_{1.3}$ mean (cm)	*h* mean (m)	$h_{10\%}$ (m)	*V* ($m^3.ha^{-1}$)	Harvest ($m^3.ha^{-1}$)	Annual current volume increment ($m^3.ha^{-1}.a^{-1}$)
PRP 01	1980	158	170	51.33	38.24	43.71	757.99	-	
	1997	175	149	55.16	40.70	44.10	816.23	78.14	8.02
	2005	183	93	59.57	40.89	46.11	597.48	291.77	9.13
PRP 03	1980	168	149	55.42	37.41	42.57	745.31	-	
	1997	185	138	60.11	39.50	41.54	859.29	36.26	8.84
	2005	193	126	62.46	39.95	44.97	863.72	67.91	9.04
PRP 04	1980	163	139	53.20	38.76	43.04	659.23	-	
	1997	180	127	57.76	40.07	43.50	737.06	54.22	7.77
	2005	188	110	60.49	39.99	44.91	704.04	104.04	8.88
PRP 05	1980	148	220	44.55	35.67	41.55	691.72	-	
	1997	165	194	49.05	38.76	42.05	790.56	33.03	7.76
	2005	173	113	55.18	39.47	44.72	583.20	287.13	9.97

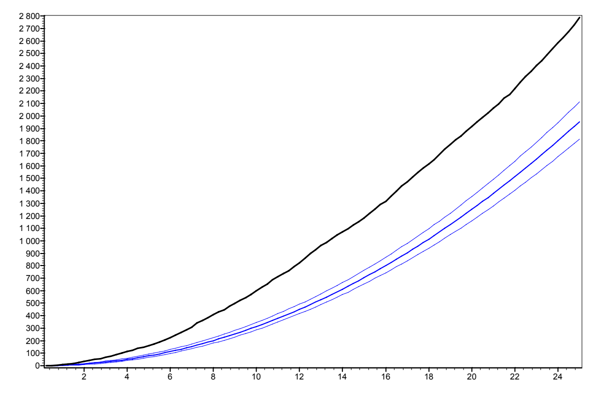
*Age given for actual year

N - number of trees per ha, $d_{1.3}$ – mean diameter, *h* mean – mean stand height, $h_{10\%}$ - dominant height of 10% highest trees, *V* – total volume (d ≥ 7 cm o.b.).

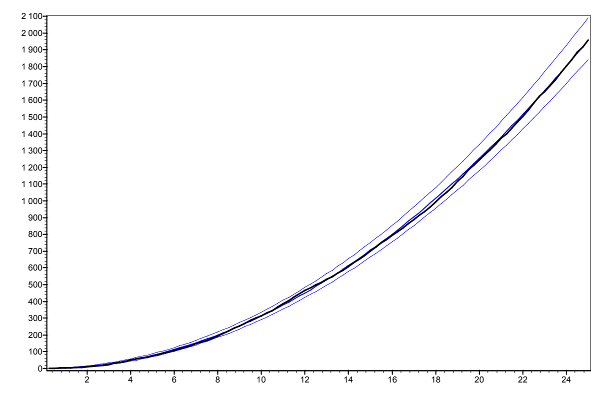
In managed beech stands the intention was mainly to remove dying, ill and low-quality trees. Nevertheless relative high amount of salvage cutting during the last decades (according to forest management plan) caused that the harvest was carried out in all diameter classes. In general we see high values of total current year increment on all plots in both periods of observation. Quite surprising is the highest volume increment on PRP 05 (forest type 4K3) probably reflecting quite good growth conditions and also high amount of harvest that induced light increment. However on PRP 01 (4B1) with very similar amount of felling we observed a bit lover current increment (height distribution on Fig. 13 and height curve /Fig. 14/ actually indicate better growth conditions). Large increase of dominant height during the last period is probably caused by different measurement techniques and is not a real increment of tree height. On the contrary the mean stand height in effect did not change during the last eight years.

Forest structure - spatial patterns

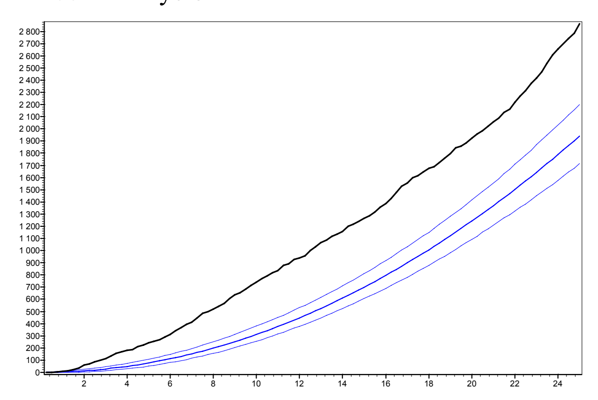
PRP 06, 07 – locality "Virgin forest"



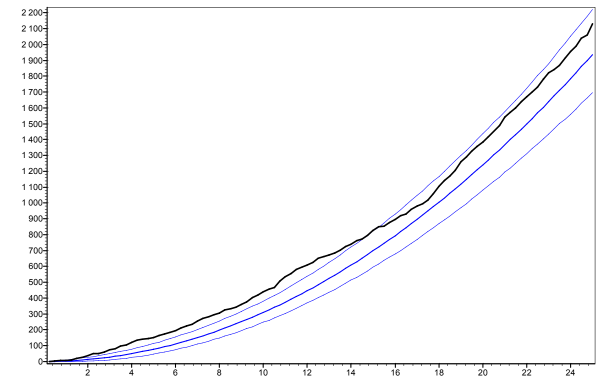
PRP 06 – all layers



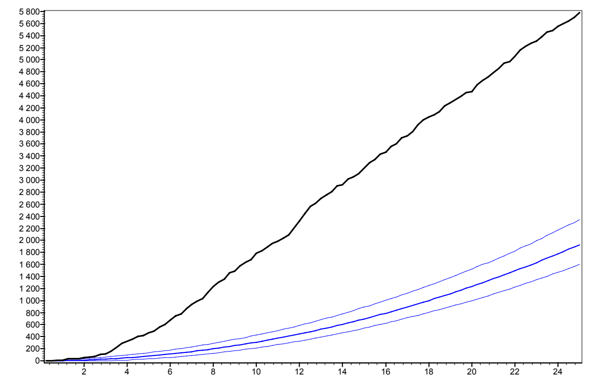
PRP 07 – all layers



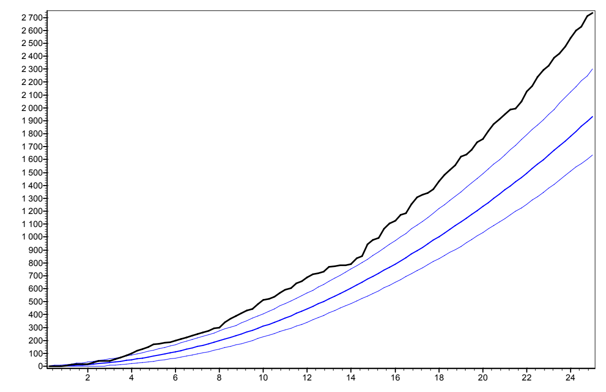
PRP 06 – trees lower than 10 m



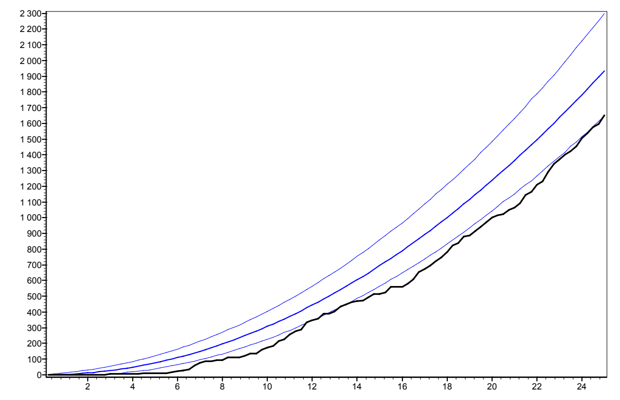
PRP 07 - trees lower than 10 m



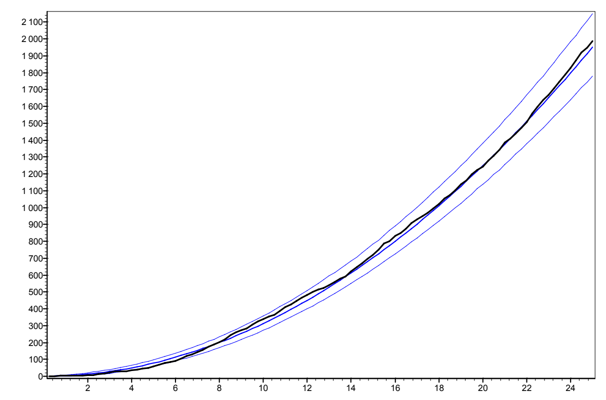
PRP 06 – trees from 10 to 20 m



PRP 07 – trees from 10 to 20 m



PRP 06 – trees higher than 20 m



PRP 07 – trees higher than 20 m

Fig. 19. Ripley's *K*-function - locality "Virgin forest": PRP 06 and 07.

Table 22. Indices of spatial patterns - PRP 06.

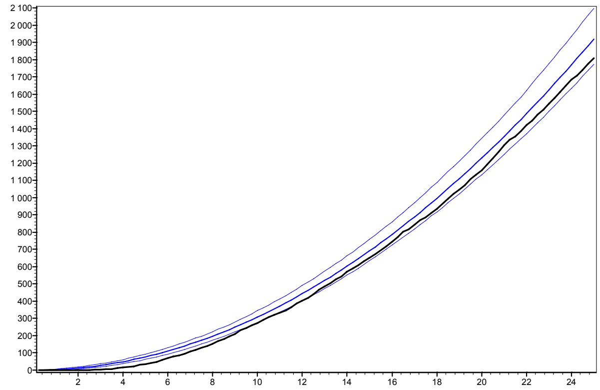
Index	Observed value	Expected value	Lower bound	Upper bound
all layers				
Hopkins-Skellam	0.545	0.499	0.433	0.571
Pielou-Mountford	1.478	1.076	0.890	1.317
Clark-Evans	0.965	1.031	0.951	1.110
trees lower than 10 m				
Hopkins-Skellam	0.714	0.499	0.403	0.610
Pielou-Mountford	2.759	1.116	0.837	1.515
Clark-Evans	0.778	1.047	0.923	1.168
trees from 10 to 20 m				
Hopkins-Skellam	0.736	0.497	0.370	0.643
Pielou-Mountford	3.745	1.145	0.783	1.715
Clark-Evans	0.910	1.065	0.902	1.233
trees higher than 20 m				
Hopkins-Skellam	0.381	0.497	0.381	0.633
Pielou-Mountford	0.918	1.130	0.796	1.653
Clark-Evans	1.321	1.057	0.911	1.203

Table 23. Indices of spatial patterns - PRP 07.

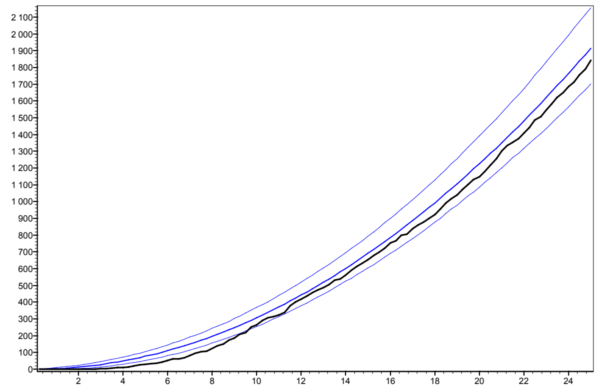
Index	Observed value	Expected value	Lower bound	Upper bound
all layers				
Hopkins-Skellam	0.494	0.499	0.445	0.560
Pielou-Mountford	1.120	1.065	0.909	1.259
Clark-Evans	1.079	1.026	0.959	1.094
trees lower than 10 m				
Hopkins-Skellam	0.701	0.498	0.398	0.612
Pielou-Mountford	1.909	1.118	0.822	1.536
Clark-Evans	0.818	1.051	0.923	1.178
trees from 10 to 20 m				
Hopkins-Skellam	0.574	0.499	0.381	0.631
Pielou-Mountford	1.524	1.139	0.796	1.664
Clark-Evans	0.939	1.057	0.910	1.208
trees higher than 20 m				
Hopkins-Skellam	0.477	0.499	0.421	0.584
Pielou-Mountford	1.147	1.092	0.865	1.390
Clark-Evans	1.141	1.037	0.940	1.134

All three indices on PRP 06 and 07 show for trees of understorey and middle layer clumped to random patterns. Trees higher than 20 m have random to regular distribution over the area. All layers as whole on PRP 06 incline to clumped structure, on PRP 07 to random distribution. Similar results gives the Ripley's *K*-function with pronounced tendency to aggregation of trees between 10 to 20 m of height on both plots. Nevertheless on PRP 07 the tree layer to 10 m of height shows tendency to rather random distribution. In general, understorey and middle layer on PRP 07 show less-clumped spatial distribution indicating slower disruption process of the main tree layer on this plot. For horizontal structure of the stands see also Appendix – Horizontal structure of PRPs.

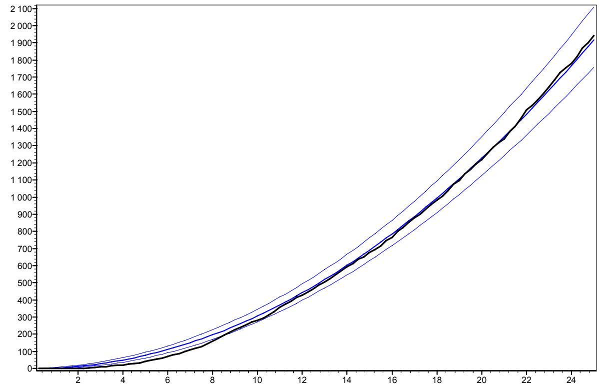
Managed stands – PRP 01, 03, 04, 05



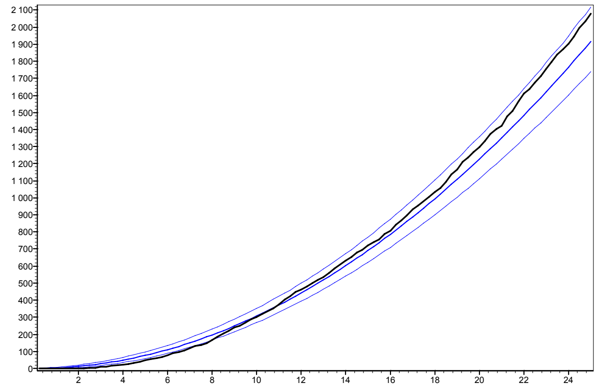
PRP 01 – stand 1980



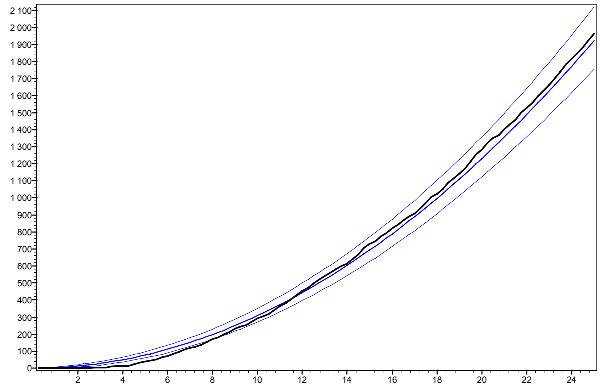
PRP 01 – stand 2005



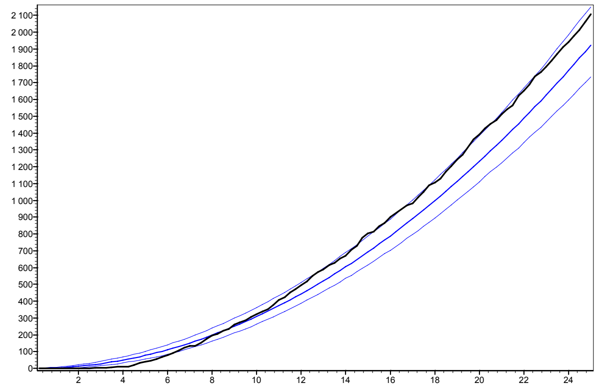
PRP 03 – stand 1980



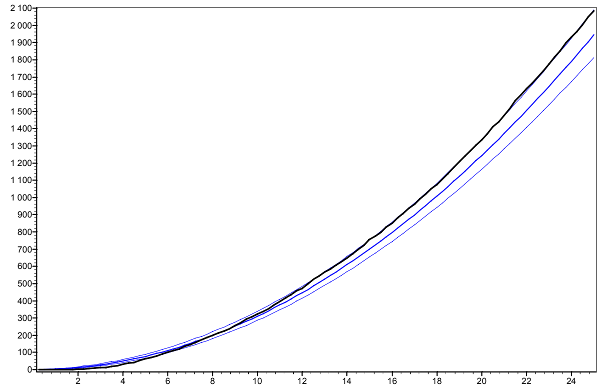
PRP 03 – stand 2005



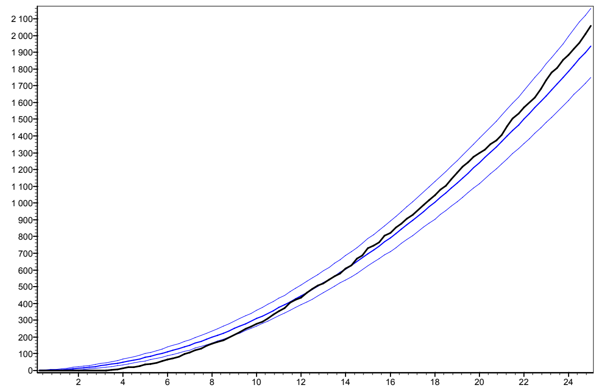
PRP 04 – stand 1980



PRP 04 – stand 2005



PRP 05 – stand 1980



PRP 05 – stand 2005

Fig. 20. Ripley's *K*-function - managed forest stands: PRP 01, 03, 04, 05.

Table 24. Indices of spatial patterns – Managed stands (period 1980).

Index	Observed value	Expected value	Lower bound	Upper bound
PRP 01				
Hopkins-Skellam	0.368	0.499	0.429	0.579
Pielou-Mountford	0.884	1.083	0.879	1.350
Clark-Evans	1.341	1.033	0.947	1.120
PRP 03				
Hopkins-Skellam	0.370	0.499	0.422	0.581
Pielou-Mountford	0.875	1.087	0.874	1.363
Clark-Evans	1.294	1.036	0.944	1.129
PRP 04				
Hopkins-Skellam	0.426	0.498	0.421	0.585
Pielou-Mountford	1.063	1.088	0.866	1.380
Clark-Evans	1.308	1.037	0.938	1.133
PRP 05				
Hopkins-Skellam	0.433	0.499	0.439	0.566
Pielou-Mountford	1.001	1.075	0.900	1.301
Clark-Evans	1.227	1.031	0.958	1.105

Table 25. Indices of spatial patterns – Managed stands (period 2005).

Index	Observed value	Expected value	Lower bound	Upper bound
PRP 01				
Hopkins-Skellam	0.336	0.500	0.406	0.606
Pielou-Mountford	0.764	1.113	0.836	1.499
Clark-Evans	1.328	1.044	0.923	1.159
PRP 03				
Hopkins-Skellam	0.405	0.498	0.417	0.586
Pielou-Mountford	0.886	1.093	0.863	1.405
Clark-Evans	1.208	1.039	0.944	1.137
PRP 04				
Hopkins-Skellam	0.484	0.499	0.411	0.597
Pielou-Mountford	1.235	1.103	0.850	1.445
Clark-Evans	1.249	1.042	0.934	1.149
PRP 05				
Hopkins-Skellam	0.374	0.498	0.415	0.595
Pielou-Mountford	0.845	1.101	0.860	1.459
Clark-Evans	1.294	1.043	0.939	1.146

Hopkins-Skellam index shows the regular structure of the managed stands on all PRPs. No significant changes are apparent during evolution in time. Yet on PRP 01 and 05 we see decrease in the value, which means shift to more regularity. On the contrary PRP 03 and 04 showed slight increase in the value of the index, which can be interpreted as shift to random distribution. This can be explained by the effect of ongoing border-cut that already reached the border of PRPs 03 and 04. Pielou-Mountford index shows random to regular distribution of the forest stands, with the exception of PRP 04 in 2005 with clumbed spatial pattern. Clark-Evans index in all cases shows regularity in the forest structure. Similar results shows the Ripley's *K*-function with slight aggregation on PRP 03 and 04 in 2005. For horizontal structure of the stands see also Appendix – Horizontal structure of PRPs.

4.3.4. Discussion

According to other authors the average dead wood volume in present day production forests is less than 10 $m^3.ha^{-1}$ (UNECE/FAO 2000; Green, Peterken 1997). In contrast, it is shown that in mature stands, which had not been managed for a half of century, the volume of dead wood is increasing rapidly and can approach the values as in natural stands. Christensen et al. (2005) reported the mean volume of total dead wood in the beech forest reserves 130 $m^3.ha^{-1}$. The variation among reserves was high, ranging from almost 0 to 550 $m^3.ha^{-1}$. Nevertheless, not only the total volume of dead wood is important for the maintenance of biodiversity and natural cycles, but also its quality, that is dead wood of different types (tree species, decay classes), dimensions and its long-term continuity in forest stands. Dead wood is not only regarded as an important aspect of forest biodiversity forming key habitats for many species, but may also provide a refuge from deer browsing, which could play an crucial role in the case of silver fir.

Overstorey trees have random (PRP 07) to regular (PRP 06) spatial patterns caused by loss of trees in the old-growth stage with more pronounced effects of winds, pathogens and other biotical and abiotical agents. The spatial patterns of beech understorey trees on both PRPs 06 and 07 (locality "Virgin forest") is rather clumped, which corresponds with observations from Nagel et al. (2006) made in old-growth *Fagus sylvatica-Abies alba* forest in southeastern Slovenia. PRP 06 is marked by faster break-up of the upper layer of dominant beeches creating larger gaps and high number of trees in understorey. Comparing both plots, due to slower degradation of the parent stand on PRP 07 (with less pronounced gap formation), the spatial patterns of understorey and middle storey are not as clumped as on PRP 06. DBH distribution shows absence of middle layer on PRP 06. On PRP 07 the dbh distribution is closer to that of selection forests showing typical reverse-J shaped size distribution. In the absence of significant exogenous disturbance ingrowth of new trees of shade-tolerant species can cause this type of diameter distribution and less-clumped spatial patterns than more strongly clumped distribution and strongly limited middle layer related to creation of larger gaps. A bimodal pattern as on PRP 06 was observed for some near-natural forests in Central Europe, with a second maximum ranging from 100 to 180 years (Emborg et al. 2000). The author suggests that the bell-shaped section of the diameter distribution at these ages reflects large-scale beech regeneration due to a natural phase of decline and regeneration or after cattle grazing ceased. In general, it seems that younger trees in forests driven by spontaneous development start off clumped and populations become more uniform as the forest ages. According to Wolf (2005) two contrasting sets of processes affect the spatial structure of natural forest stands. Direct density-dependent competition between neighboring individuals in a clumped stand should progressively lead to a more regular pattern. Opposed to this are processes that tend to create mosaics and clumped distribution. These processes might be influenced by microsites mosaics, canopy gaps and history. In general, regular pattern gives evidence for competition playing the major role, whereas clumping suggests that gap dynamics and favourable microsites are more important. In managed stands optimal growth for all trees is obtained by equal spacing. Our results showed that during the regeneration period the parent stand could become more clumped (due to creation of gaps and/or stand edges). Wolf (2005) stated that when management ceased, recruitment changed the pattern towards more randomness with the gap regeneration being the main driving force behind the changes. The same author stated that monitoring the changes in spatial pattern is a comparatively fast indicator for following up the achievements of conservation, which aims to bring back forest into natural state. Although it seems that in temperate deciduous forest on mesotropic sites the gap formation and gap regeneration plays very important role in spatial patterns of forests, no general thresholds of "randomness" or "regularness" of near-natural forest stands can be given. In forests leaved for spontaneous development the initial structure of the stands might be of great importance.

Studies that investigate natural stand dynamics in central Europe are hampered by the lack of large tracts of old-growth forests, making it particularly difficult to understand spatial and temporal variation in disturbance regimes at landscape scale (Nagel et al. 2006), consequently the specification of "natural" or "authentic" forest structure on the landscape level may be loaded by high uncertainty. Nevertheless obtained results reflects the structural development of former managed stands, now about half century without direct interventions, driven by tree falls, small-scale gap formation, growth differentiation and natural regeneration. In the stand 417A16a/8a we observe ongoing formation of small gaps (gap-dynamics) with increased light environment. Heterogeneous microclimatic conditions within the stand gave probably more room to other tree species to establish in the subcanopy (hornbeam, spruce, birch). Larch is in given conditions mainly full-canopy tree of higher dimensions. Typical for the small-scale disturbances is also the diameter distribution of beech, with many small recruits and also a considerable number of full-size canopy trees. However, it seems that the presence of sub-canopy trees on PRP 07 decreased the number of trees in lover diameter classes. This observation may be in agreement with results of Paluch (2007), who stated that basal area of the under-canopy trees is more crucial for the presence of beech regeneration bank than the basal area of the surrounding stand and the closure of canopy trees. Locally, this factor has a greater influence on light conditions on the forest floor than tree fall of a canopy tree in patch with sub-canopy trees. This event may not improve conditions for regeneration emergence and its subsequent recruitment in long term. Interesting fact is also higher presence of hornbeam in the middle layer of PRP 07 (mainly in diameter class 22 – 38 cm). In this stand we do not see expressed gap formation as on adjacent plot, where higher rate of hornbeam in forest regeneration was connected to occurrence of larger gaps. One explication could be the absence of beech mast years during longer periods of decades (personal communication). In managed plots we see size-class distribution typical for homogenous even-aged beech forest stands mainly with normal distribution of diameter classes. With relatively closed canopy during the evolution of managed stands and due to high competition between trees the diameter distribution is generally symmetrical, yet with large diameter range (high plasticity of beech as shade-loving species: from 28.75 cm to 102.10 cm in 2005) and with typical flat diameter curve (visible on all managed research plots).

4.3.5. Conclusions

The distribution of the number of trees at diameter classes changes in the course of the stand life. The changes in managed stands are of two kinds: mechanical – they are caused by thinning and shelterwood cutting and dynamics – caused by the diameter increase in consequence of the tree growth. The obtained results show ongoing structural differentiation on unmanaged PRP 06 and 07, yet with differences in structural characteristics within the same forest stand depending on the initial structure and disruption dynamics of old-growths. We already see differences between fine-scale tree falls (PRP 07) and more expressed gap formation on PRP 06 influencing both diameter distribution and spatial patterns. Individuals of mature trees in main canopy layer show random to regular distribution, middle layer and understorey more or less clumped distribution. The presence of spruce and larch indicates human induced changes in tree species composition.

5. General Conclusions

Based on obtained results, answers on research questions formulated in chapter *3.1. Aim of the study* are following:

- *Are the senescent beech stands able to produce enough seed with good distribution?*

In Beechwood of Voděrady also ageing beech stands far behind common rotation period are at present able to produce enough seeds with good distribution. Even by relatively low rates of germination (and high losses of wintering seeds) seed production has to be regarded as sufficient and capable to provide successful natural regeneration of beech in given conditions. The values observed after seed year 2003 on research plots far overreached values indicated for full masting years of beech. In 2006 another moderate masting year occurred.

- *What are the main factors influencing the establishment of forest regeneration?*

In managed stands the main factor affecting the seedling survival in the first vegetation period seems to be biotical damages caused by aphids and small mammals. Thick humus horizons, ground vegetation and competition from parent stand are an important hindrance for natural regeneration. Dense regeneration from preceding mast year negatively influences establishment of regeneration from following mast year. Three-year seedlings survival is closely correlated with the second-season seedlings survival and initial number of seedlings.

- *Does the stand density influence the regeneration establishment during the first vegetation periods?*

Reduction of crown cover of parent stand to 80 % assured successful four-year development of beech regeneration. After this period even for strong shade-tolerant species like beech adequate canopy openings are necessary for long term development of regeneration.

- *How is the natural beech regeneration related to the gap formation within natural forest dynamics?*

The density and performance of tree seedlings is influenced by different light levels as a result of gap formation described in the model of forest cycle. The old-growth has reached degrading phase induced by small scale tree falls with regeneration phase in the following generation of the forest (under the gaps and in its proximity). The size of gaps has influence on tree species composition and future stand structures.

- *What is the role of main growth factors and weed competition in this process?*

Light has direct and indirect influence on the establishment and growth of tree regeneration via changes in water and nutrient availability. Light has direct influence on the form and growth of beech individuals. Higher vegetation cover, especially of herbal vegetation, is connected with higher intensity of direct light. Nevertheless, we did not find correlation between cover of ground vegetation and cover of regeneration in managed stands, older seedlings were able to overgrowth the ground vegetation.

- *How does the "authentic" or "natural" forest structure in given condition looks like?*

The obtained results show ongoing structural differentiation in unmanaged stand, yet with differences in structural characteristics within the same forest stand depending on the initial structure and disruption dynamics of old-growths. After 50 years of spontaneous development on PRP 07 we see reverse-J shaped diameter distribution, on other PRP 06 bimodal distribution with two local maxima connected to more expressed gap formation. Increasing amount of dead wood and changes in spatial patterns are one of main indicators for "naturalness" of forest stands. However, in general no exact thresholds can be given.

- *Is the role of browsing in given conditions important for the process of natural regeneration of beech?*

Herbivory did not seem to be a significant factor in seedling mortality, although in managed stands older seedlings of rowan were heavily browsed by deer. In general the damage caused by browsing increased during the vegetation period. Where high seedling densities are present, browsing by deer increases, but does not play important role determining survival of natural regeneration. Negative impact on the form of terminal shoot was observed. Lower plant densities and the absence of other tree species made areas under canopy less attractive to game browsing.

The main structure of managed beech stands is regular, with wide stands uniform in size and age. According to management plan the rotation of beech is 130 years (without difference among forest types), nevertheless most beech stands in the area are far behind this rotation period (nevertheless selected co-dominant tree – in age of 173 years - still did not reached the culmination of average volume increment; see Appendix – Sample tree analysis). Even these stands are at present able to produce enough seeds with good distribution. In given conditions the reduction of crown cover to 80% one year before the seed fall seems to be appropriate measure (preparatory felling) for successful regeneration establishment. According to forest regeneration we do not see the necessity to carry out regeneration felling in the winter following the mast year. With regard to 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. Even in a strongly shade-tolerant species like beech adequate canopy openings are necessary for long term development of regeneration. After this time the canopy is usually further opened so that the regeneration has enough light to growth (forming 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 no longer require any protection. Nevertheless it should be mentioned that in this phase considerable damages in regeneration caused by felling of trees with largely developed crowns are hard to prevent, especially when big scale shelter wood felling is used. This model may coincide with the big scale shelter-wood 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 again result in even-aged pure beech stands. Regular, even-aged structure as observed in present-day managed stands is not natural for this ecosystem. In managed stands we also observed general lack of woody debris. They have also a general high degree of artificiality for species composition in trees (lack of silver fir and presence of non-native species or species not appropriate for given forest types: larch, red oak, *Thuja plicata*, spruce). 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 periodically large-scale process disruptions (Emborg et al. 2000). Nevertheless, we see main limitation of such an approach in the age of existing forest stands (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 the homogeneity of tree species composition. Despite the fact that our data proved the existence of heavy masting year and higher survival on SPs with lower seedling emergence, crucial moment can be the occurrence even only of moderate seed falls in the future. Long regeneration period reckoning with regeneration from more mast years in this case does not necessarily guarantee success (in the past there were recorded longer periods without beech regeneration during decades). One solution could be the maximal use of actual seed falls with variability in the shelter-wood density inducing differentiation in the growth of regeneration and active approach in regeneration of silver fir that had formed important part of tree species composition in the area and that due to human activity almost disappeared from the stands (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). An effort should be also aimed at the maintenance and creation of as diverse as possible uneven-aged and spatial structures of forest stands. More complicated stand structure could be created by early and intensive tending at the young stand age, also increasing the static stability (Štefančík 2006). According to Merino et al. (2007) protective measures undertaken in old managed stands should enhance biodiversity and the role of both soil and tree components as long-term C sinks. The potential C storage in these systems is very high, especially in the unmanaged forests, which include large, old live trees.

For managed stands in the NNR Voděradské bučiny we propose: The natural regeneration of beech should be the rule (by the maximal use of present seed years), artificial regeneration of silver fir to suitable forest sites, if accompanied with decrease in browsing pressure by the wild game, could help to dissolve the homogeneity of managed beech stands and approximate the stands to natural tree species composition. Regeneration of non-native tree species should be avoided. Even in managed stands we propose creation of small unmanaged patches within larger woods. It also means avoidance of regular structures. At the landscape level topographical irregularities of the landform and natural disturbances should replace uniform shelter-wood cutting. Border-cutting oriented towards east has to be regarded as not appropriate for beech regeneration in given conditions. Some trees (3-5 per ha) should be left to senescence and natural death. Beside these measures restoring more naturalness in NNR, it is necessary to leave some larger areas unmanaged in order to cover the whole range of stand types (in given conditions at least 60 ha). These stands should be selected according to their ongoing differentiation in forest structure with the probability of future natural development. In reality only few forest stands fulfill this criteria (localtity “Virgin forest” and few small patches around the area). Forest stands without autoregulation processes should not be included in these zones. Consequently we see the necessity to define borders of forest stands around these “corezones”, where the management will be oriented strictly on enhancement of tree species composition and forest structure, before these transition areas are left totally unmanaged. The new zonation has to respect the presence and intensity of autoregulation processes and minimal area of given ecosystem type.

Actual stand of most forests in NNR Voděradské bučiny does not fulfill the criteria of protected areas. According to regulation nr. 60/2008 Coll. in appendix 2 - Assesment of naturalness of forest stands (Mžp 2008), only few small patches in the reserve correspond to degree of naturalness *close-to-nature*, the majority of forests has to be judged as *cultural*. One possible way in the future development of the reserve would be the creation of smaller non-interventional core zone (but still respecting the minimal area) with spontaneous development as mentioned above and diversified forest management in 2nd zones. One part of 2nd zone could be prepared to future integration with 1st zone, simultaneously selected area of present beech woods would serve as reference object for close-to-nature silvicultural methods and their comparison with spontaneously developing unmanaged stands. Such silvicultural object as total would integrate both the conservation approach and evaluation of silvicultural methods derived from direct researches and observations. The comparison of these stands from diverse point of view would be certainly a valuable source of knowledge not only for silviculturalists but also for forest managers, policy makers and economists.

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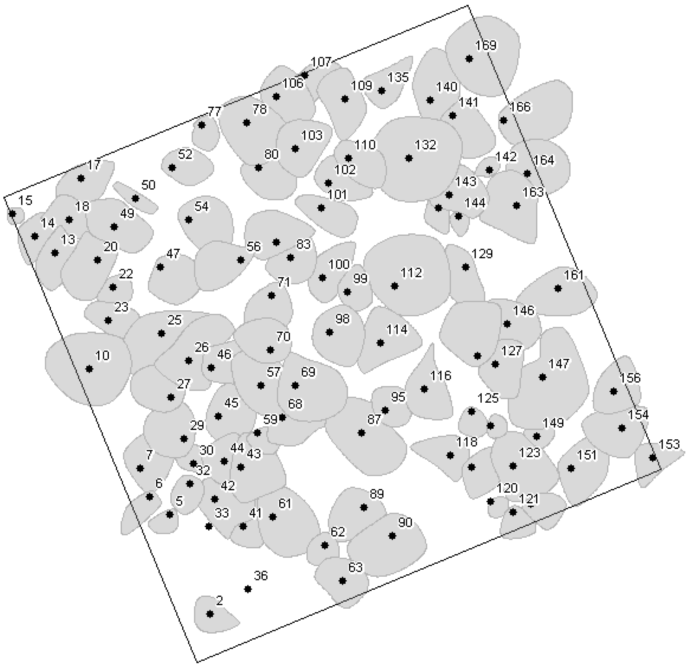
7. APPENDIX

Horizontal structure of PRPs

PRP 01



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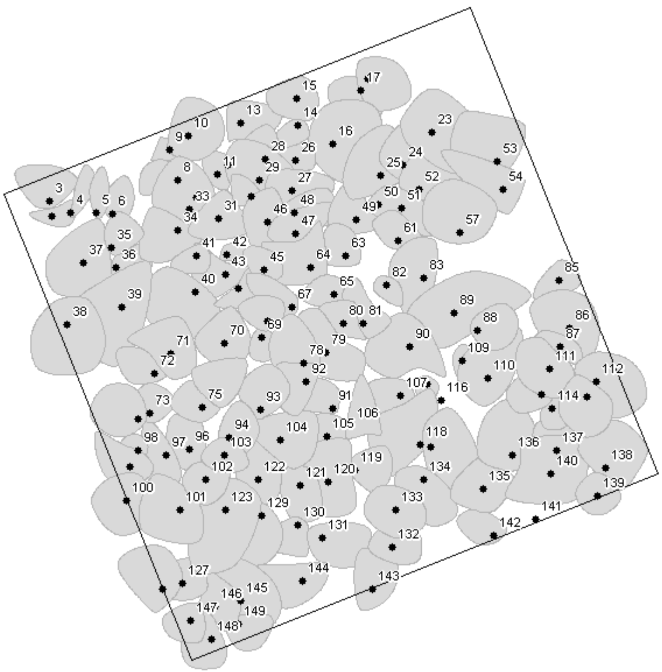
PRP 03



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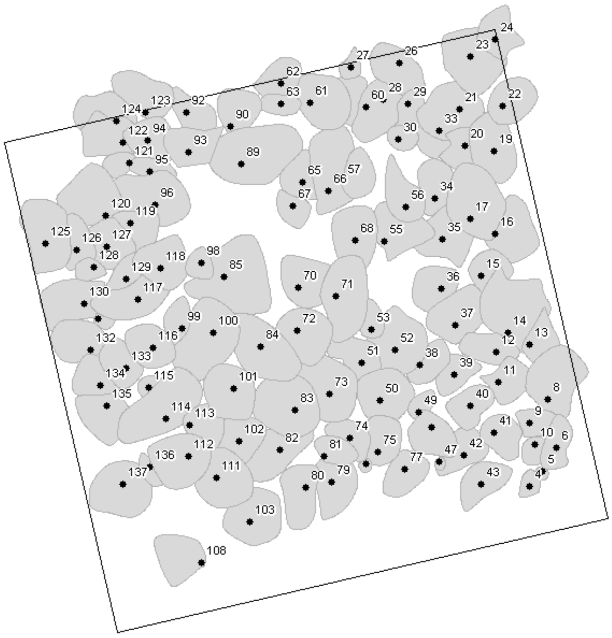
PRP 04



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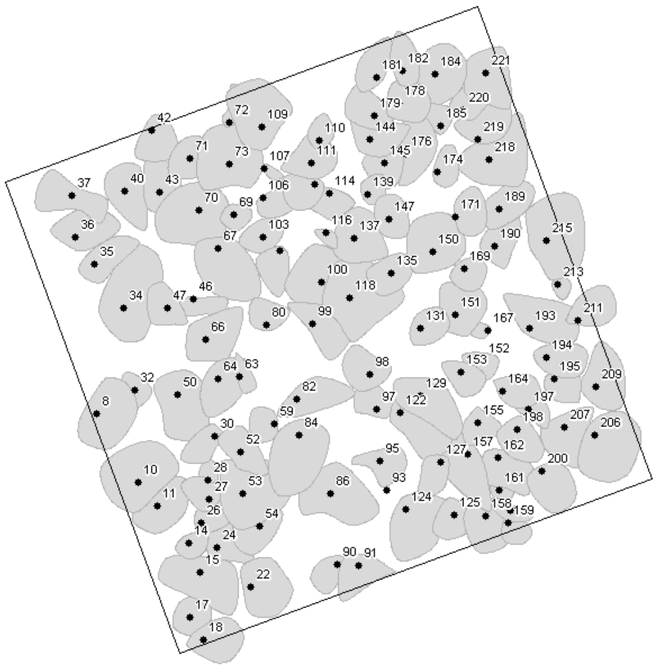
PRP 05



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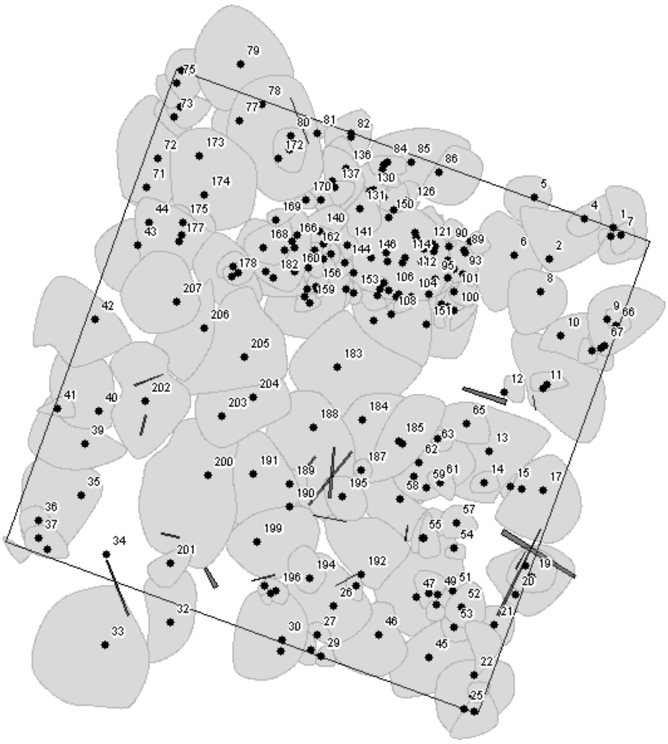
PRP 06



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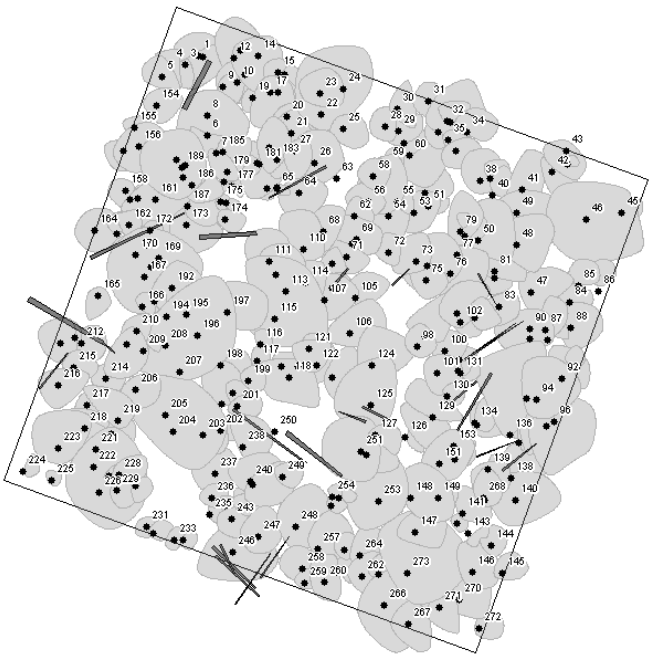
PRP 07



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Soil analysis

Table 1. Exchange titration acidity characteristics				
horizon	thickness (cm)	Exchange titration acidity (mval/kg)	Exchangeable H^+ (mval/kg)	Exchangeable Al^{3+} (mval/kg)
PRP 1	**436C17**			
L	0-1	40.2	24.4	15.8
F	1-2	33.7	9.0	24.7
H	2-2.5	56.0	3.1	52.9
Ah1	2.5-8	63.6	2.5	61.1
Ah2/B	8-15	62.6	0.7	61.9
B	15-45	58.8	0.0	58.7
stone	45-60			
C	60-80	33.8	0.0	33.7
PRP 3	**434B17**			
L	0-2	18.7	9.9	8.8
F	2-4	20.7	7.7	13.0
H	4-5	44.7	5.2	39.5
Ah	5-12	60.9	0.7	60.2
B1	12-40	44.1	0.5	43.6
B2	40-60	36.3	0.6	35.6
B/Cn	60+	37.4	0.2	37.2
PRP 4	**434E17**			
L	0-0.5	30.5	18.3	12.2
F	0.5-1	30.0	17.7	12.3
H	1-1.5	36.8	9.8	27.0
Ah	1.5-7	83.3	4.3	79.0
B	7-30	57.5	0.5	57.0
B/C	30-45	47.0	0.0	47.0
C	45-90	39.5	0.2	39.3
PRP 5	**436D17**			
L	0-1	28.5	22.2	6.3
F	1-2	23.5	15.7	7.8
H	2-2.5	62.8	11.1	51.7
Ah	2.5-4	61.1	2.1	59.0
B1	4-30	48.9	0.6	48.3
B2	30-50	41.2	0.0	41.2
B/C	50-70	35.5	0.0	35.4
C	70-100	32.0	0.0	32.0

Table 1. Exchange titration acidity characteristics				
horizon	thickness (cm)	Exchange titration acidity (mval/kg)	Exchangeable H^+ (mval/kg)	Exchangeable Al^{3+} (mval/kg)
PRP 6	**417A16a/8a**			
L	0-2	19.2	13.2	6.0
F	2-3	33.7	20.3	13.4
H	3-4	24.0	10.4	13.6
Ah	4-10	44.3	1.0	43.3
B	10-45	40.1	0.4	39.7
B/C	45-60	32.1	0.2	31.9
Cn	60+	36.0	0.2	35.7
S1	**434A17**			
L*		23.0	7.1	15.9
F	0-2	41.5	7.9	33.6
H	2-4	49.7	13.5	36.2
Ah	4-7	60.1	0.8	59.3
B1cambic	7-30	44.3	0.6	43.8
B2 luvic	30-50	46.1	0.2	45.9
Br	50+	75.1	0.3	74.8
LGW**	70			

Table 2. Soil texture						
horizon	thickness (cm)	2-0.25 mm (%)	0.25-0.05 mm (%)	0.05-0.01 mm (%)	0.01-0.001 mm (%)	< 0.001 mm (%)
PRP 1	**436C17**					
Ah1	2.5-8	37.64	4.44	33.03	13.32	11.57
Ah2/B	8-15	27.57	8.83	34.95	18.53	10.11
B	15-45	27.29	9.75	33.14	17.45	12.37
stone	45-60					
C	60-80	71.87	7.18	11.11	3.05	6.79
PRP 3	**434B17**					
Ah	5-12	21.82	16.19	40.43	17.20	4.36
B1	12-40	30.72	14.08	31.22	17.23	6.75
B2	40-60	26.04	14.35	36.18	16.71	6.72
B/Cn	60+	1.86	54.58	26.00	10.20	7.36
PRP 4	**434E17**					
Ah	1.5-7	46.47	9.81	30.87	7.44	5.42
B	7-30	15.48	18.82	39.07	19.19	7.44
B/C	30-45	26.66	17.09	36.84	17.00	2.41
C	45-90	61.19	18.72	11.34	6.43	2.32
PRP 5	**436D17**					
Ah	2.5-4	13.95	19.95	47.24	15.20	3.66
B1	4-30	14.85	15.53	44.14	19.16	6.32
B2	30-50	18.99	15.10	40.55	18.63	6.72
B/C	50-70	53.40	23.19	12.97	6.29	4.14
C	70-100	51.31	24.66	14.33	6.55	3.14
PRP 6	**417A16a/8a**					
Ah	4-10	25.60	9.00	38.19	16.97	10.24
B	10-45	23.89	9.67	38.45	18.86	9.12
B/C	45-60	32.57	7.94	36.98	16.38	6.13
Cn	60+	35.14	8.30	32.11	15.15	9.30
S1	**434A17**					
Ah	4-7	17.29	6.54	44.67	20.48	11.01
B1cambic	7-30	17.99	8.72	42.18	20.38	10.73
B2 luvic	30-50	12.17	5.99	49.49	19.81	12.54
Br	50+	14.48	13.78	41.90	17.47	12.37

Table 3. Total nutrient content (Melich III)					
horizon	thickness (cm)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)
PRP 1	**436C17**				
L	0-1	54	864	3294	358
F	1-2	60	534	2790	294
H	2-2.5	42	318	1260	146
Ah1	2.5-8	38	83	354	56
Ah2/B	8-15	38	53	188	29
B	15-45	99	38	182	25
C	60-80	66	19	171	24
PRP 3	**434B17**				
L	0-2	64	780	3786	580
F	2-4	68	484	3128	478
H	4-5	36	308	1914	240
Ah	5-12	5	68	331	58
B1	12-40	4	45	229	45
B2	40-60	13	39	248	45
B/Cn	60+	52	71	293	50
PRP 4	**434E17**				
L	0-0.5	46	878	3568	398
F	0.5-1	70	904	3848	394
H	1-1.5	54	580	1976	196
Ah	1.5-7	40	119	422	64
B	7-30	161	21	173	24
B/C	30-45	106	17	200	27
C	45-90	57	23	207	27
PRP 5	**436D17**				
L	0-1	36	872	3626	392
F	1-2	50	800	3968	452
H	2-2.5	30	670	1506	182
Ah	2.5-4	7	99	236	42
B1	4-30	2	36	195	27
B2	30-50	9	30	182	24
B/C	50-70	67	49	214	26
C	70-100	29	50	215	27
PRP 6	**417A16a/8a**				
L	0-2	112	1790	4064	674
F	2-3	136	1624	4724	710
H	3-4	72	800	2518	276
Ah	4-10	17	105	323	57
B	10-45	37	39	204	41
B/C	45-60	43	62	193	40
Cn	60+	31	52	199	41
S1	**434A17**				
L*		34	1840	1472	260
F	0-2	46	826	1996	358
H	2-4	48	924	1920	356
Ah	4-7	1	126	208	56
B1cambic	7-30	1	65	182	43
B2 luvic	30-50	1	62	180	43
Br	50+	1	119	223	110

Table 4. Total humus Cox and N content (%)				
horizon	thickness (cm)	Humus (Springel-Klee)	Cox	Nitrogen (Kjeldahl)
PRP 1	**436C17**			
L	0-1	62.5	36.3	1.58
F	1-2	43.9	25.4	1.36
H	2-2.5	35.4	20.5	1.25
Ah1	2.5-8	13.6	7.9	0.48
Ah2/B	8-15	3.0	1.7	0.11
B	15-45	1.8	1.0	0.08
C	60-80	0.6	0.3	0.02
PRP 3	**434B17**			
L	0-2	55.3	32.1	1.44
F	2-4	43.4	25.2	1.41
H	4-5	33.6	19.5	1.00
Ah	5-12	7.7	4.5	0.20
B1	12-40	1.9	1.1	0.06
B2	40-60	1.2	0.7	0.04
B/Cn	60+	0.4	0.2	0.01
PRP 4	**434 E 17**			
L	0-0.5	58.3	33.8	1.22
F	0.5-1	65.0	37.7	1.61
H	1-1.5	45.4	26.3	1.57
Ah	1.5-7	13.4	7.8	0.47
B	7-30	1.9	1.1	0.08
B/C	30-45	1.0	0.6	0.05
C	45-90	0.3	0.2	0.02
PRP 5	**436D17**			
L	0-1	54.1	31.4	1.36
F	1-2	55.3	32.1	1.86
H	2-2.5	56.4	32.7	1.83
Ah	2.5-4	11.5	6.6	0.33
B1	4-30	1.9	1.1	0.08
B2	30-50	0.9	0.5	0.04
B/C	50-70	0.3	0.2	0.02
C	70-100	0.3	0.2	0.02
PRP 6	**417A16a/8a**			
L	0-2	61.5	35.7	1.32
F	2-3	66.6	38.6	1.81
H	3-4	47.8	27.8	1.45
Ah	4-10	6.9	4.0	0.26
B	10-45	1.2	0.7	0.04
B/C	45-60	0.4	0.2	0.02
Cn	60+	0.4	0.2	0.02
S1	**434A17**			
L*		55.2	32.0	1.04
F	0-2	58.8	34.1	1.11
H	2-4	57.1	33.1	1.46
Ah	4-7	6.9	4.0	0.15
B1cambic	7-30	1.9	1.1	0.06
B2 luvic	30-50	0.5	0.3	0.02
Br	50+	0.3	0.2	0.02

Table 5. Soil reaction and adsorbtion comlex characteristics							
horizon	thickness (cm)	pH/H2O	pH/KCl	S (mval//100g)	T-S (mval//100g)	T (mval//100g)	V (%)
PRP 1	**436C17**						
L	0-1	4.6	4.2	36.2	29.7	65.9	55.0
F	1-2	4.3	4.0	26.9	34.1	61.0	44.2
H	2-2.5	4.1	3.2	10.5	34.9	45.4	23.1
Ah1	2.5-8	3.8	3.1	3.2	18.3	21.5	15.0
Ah2/B	8-15	4.5	3.5	0.5	8.8	9.3	5.1
B	15-45	4.5	3.9	0.2	6.7	6.8	2.3
stone	45-60						
C	60-80	4.5	4.2	0.2	3.1	3.2	4.7
PRP 3	**434B17**						
L	0-2	4.9	4.5	36.3	25.8	62.1	58.5
F	2-4	4.7	4.1	27.1	28.7	55.7	48.6
H	4-5	4.1	3.7	17.0	30.0	47.0	36.2
Ah	5-12	4.1	3.2	2.5	13.5	16.0	15.5
B1	12-40	4.6	4.0	0.5	5.4	6.0	8.8
B2	40-60	4.8	4.2	0.5	4.2	4.7	9.9
B/Cn	60+	5.0	4.5	1.2	3.8	5.0	24.0
PRP 4	**434E17**						
L	0-0.5	4.7	4.5	36.5	22.6	59.1	61.8
F	0.5-1	4.4	4.3	36.3	33.2	69.5	52.2
H	1-1.5	4.0	3.5	18.0	39.6	57.5	31.2
Ah	1.5-7	3.8	3.2	3.7	17.6	21.3	17.3
B	7-30	4.1	3.9	0.2	6.2	6.4	3.8
B/C	30-45	4.4	4.0	1.4	4.2	5.6	24.8
C	45-90	4.6	4.2	1.6	3.2	4.8	34.0
PRP 5	**436D17**						
L	0-1	4.8	4.5	32.8	23.7	56.5	58.0
F	1-2	4.5	4.3	40.2	31.5	71.7	56.1
H	2-2.5	4.0	3.1	15.9	55.9	71.7	22.1
Ah	2.5-4	4.0	3.2	1.4	12.5	14.0	10.1
B1	4-30	4.6	3.8	0.2	5.2	5.5	4.1
B2	30-50	4.7	4.0	0.2	4.4	4.6	4.5
B/C	50-70	4.3	4.0	1.7	3.3	5.0	34.5
C	70-100	4.3	4.0	1.9	2.8	4.7	41.3

Table 5. Soil reaction and adsorbtion comlex characteristics							
horizon	thickness (cm)	pH/H2O	pH/KCl	S (mval//100g)	T-S (mval//100g)	T (mval//100g)	V (%)
PRP 6	**417A16a/8a**						
L	0-2	5.2	4.7	44.9	26.1	71.0	63.3
F	2-3	4.5	4.5	53.8	28.6	82.4	65.3
H	3-4	4.5	4.0	28.9	30.9	59.8	48.4
Ah	4-10	4.5	3.8	2.7	9.1	11.8	22.7
B	10-45	4.5	3.8	0.2	5.1	5.4	4.5
B/C	45-60	4.9	4.1	0.2	3.9	4.1	4.9
Cn	60+	4.6	4.0	0.5	4.0	4.4	10.1
S1	**434A17**						
L*		4.9	4.4	20.7	18.8	39.4	52.4
F	0-2	4.6	4.2	22.1	13.1	35.1	62.8
H	2-4	4.1	3.2	17.9	49.8	67.7	26.5
Ah	4-7	4.1	3.4	1.3	9.5	10.8	12.2
B1cambic	7-30	4.6	4.1	1.0	5.6	6.6	14.8
B2 luvic	30-50	4.6	3.9	0.8	4.9	5.7	14.2
Br	50+	4.6	3.8	2.1	6.8	8.9	23.6

Table 6. Plant available nutrient content						
horizon	thickness (cm)	P_2O_5 (mg/kg)	K_2O (mg/kg)	CaO (mg/kg)	MgO (mg/kg)	Fe_2O_3 (mg/kg)
PRP 1	**436C17**					
L	0-1	767	840	5307	688	81
F	1-2	494	288	3133	477	377
H	2-2.5	236	164	1267	185	797
Ah1	2.5-8	208	75	240	65	835
Ah2/B	8-15	194	54	100	44	1075
B	15-45	266	36	87	25	937
stone	45-60					
C	60-80	478	38	373	31	288
PRP 3	**434B17**					
L	0-2	685	883	7680	1008	173
F	2-4	849	387	3347	523	445
H	4-5	327	172	1947	280	665
Ah	5-12	90	89	220	47	1426
B1	12-40	35	49	60	18	585
B2	40-60	42	37	73	17	552
B/Cn	60+	239	91	307	83	363
PRP 4	**434E17**					
L	0-0.5	1032	1035	7627	1008	96
F	0.5-1	852	940	6080	792	115
H	1-1.5	400	400	2240	309	361
Ah	1.5-7	263	123	327	102	952
B	7-30	396	30	87	19	754
B/C	30-45	285	20	107	19	523
C	45-90	664	34	613	23	249
PRP 5	**436D17**					
L	0-1	1027	357	7947	912	56
F	1-2	569	500	5627	733	99
H	2-2.5	285	500	1387	213	244
Ah	2.5-4	106	134	120	45	852
B1	4-30	57	40	67	21	955
B2	30-50	57	23	67	21	800
B/C	50-70	616	78	567	42	361
C	70-100	564	51	580	28	210

Table 6. Plant availible nutrient content						
horizon	thickness (cm)	P_2O_5 (mg/kg)	K_2O (mg/kg)	CaO (mg/kg)	MgO (mg/kg)	Fe_2O_3 (mg/kg)
PRP 6	**417A16a/8a**					
L	0-2	1013	1040	7307	1104	112
F	2-3	944	773	7627	1045	208
H	3-4	683	460	2853	337	635
Ah	4-10	216	105	260	65	1206
B	10-45	87	29	73	23	660
B/C	45-60	105	30	127	19	402
Cn	60+	103	74	140	27	362
S1	**434A17**					
L*		973	5093	3787	709	147
F	0-2	512	1013	3253	581	180
H	2-4	426	693	1787	388	276
Ah	4-7	105	66	73	39	1585
B1cambic	7-30	50	48	67	19	1010
B2 luvic	30-50	4	68	67	23	683
Br	50+	3	79	87	97	560

Table 7. Total nutrient content of holorganic horizons						
horizon	thickness (cm)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
PRP 1	**436C17**					
L	0-1	1.52	0.11	0.14	0.78	0.064
F	1-2	1.59	0.11	0.16	0.28	0.046
H	2-2.5	1.29	0.10	0.36	0.12	0.008
PRP 3	**434B17**					
L	0-2	1.39	0.11	0.12	0.90	0.072
F	2-4	1.22	0.12	0.16	0.94	0.038
H	4-5	1.17	0.12	0.36	0.18	0.012
PRP 4	**434 E 17**					
L	0-0.5	1.18	0.10	0.12	0.82	0.070
F	0.5-1	1.64	0.11	0.12	0.46	0.071
H	1-1.5	1.53	0.11	0.18	0.18	0.028
PRP 5	**436D17**					
L	0-1	1.44	0.10	0.14	0.94	0.070
F	1-2	2.00	0.11	0.16	0.42	0.084
H	2-2.5	2.03	0.13	0.14	0.10	0.018
PRP 6	**417A16a/8a**					
L	0-2	1.50	0.14	0.20	1.24	0.092
F	2-3	1.90	0.15	0.20	0.82	0.090
H	3-4	1.68	0.17	0.28	0.12	0.052
S1	**434A17**					
L*		1.08	0.09	0.32	0.52	0.062
F	0-2	1.18	0.11	0.18	0.38	0.042
H	2-4	1.49	0.14	0.20	0.08	0.048

*Only partial occurence
**Level of ground water

Sample tree analysis

Fig. 1. Sample tree analysis (each 5th growth layer is displayed).

Fig. 2. Growth curve of co-dominant beech tree (forest stand 434A17).

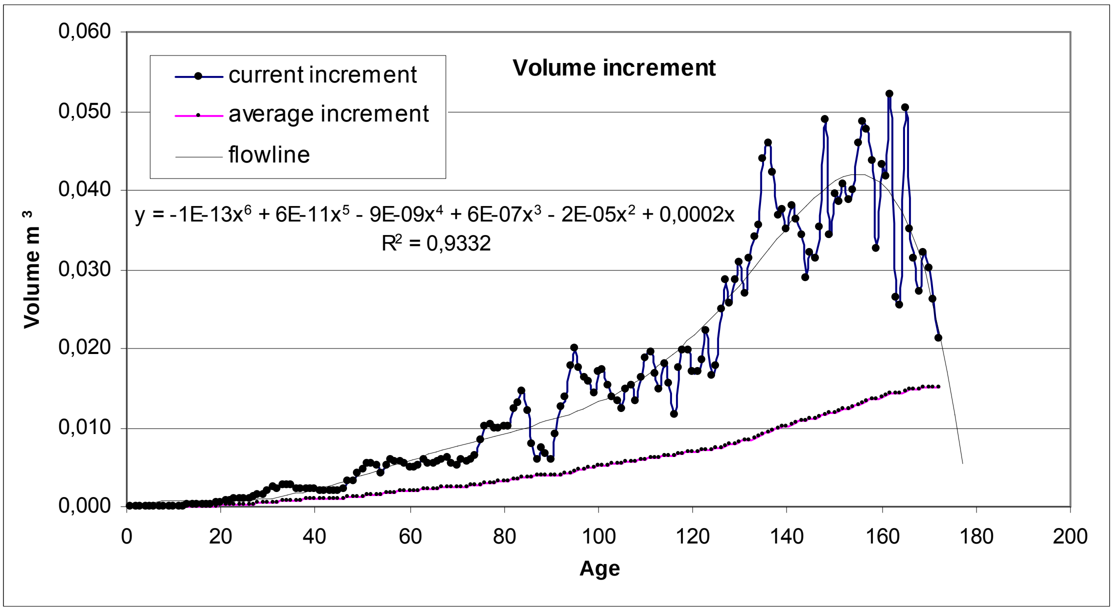

Fig. 3. Volume increment of co-dominant beech tree (forest stand 434A17).

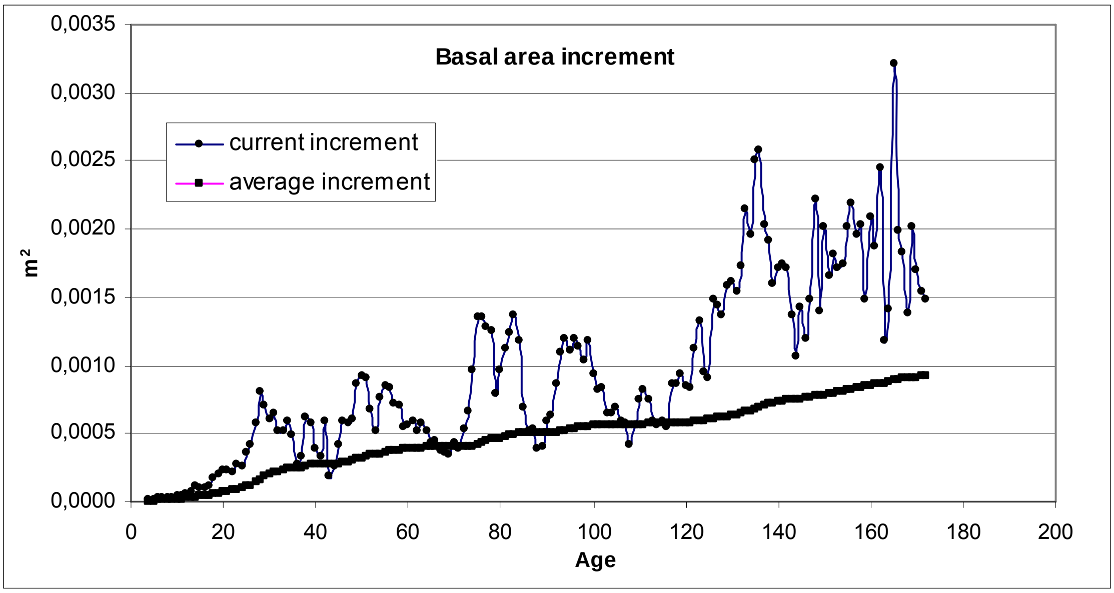

Fig. 4. Basal area increment of co-dominant beech tree (forest stand 434A17).

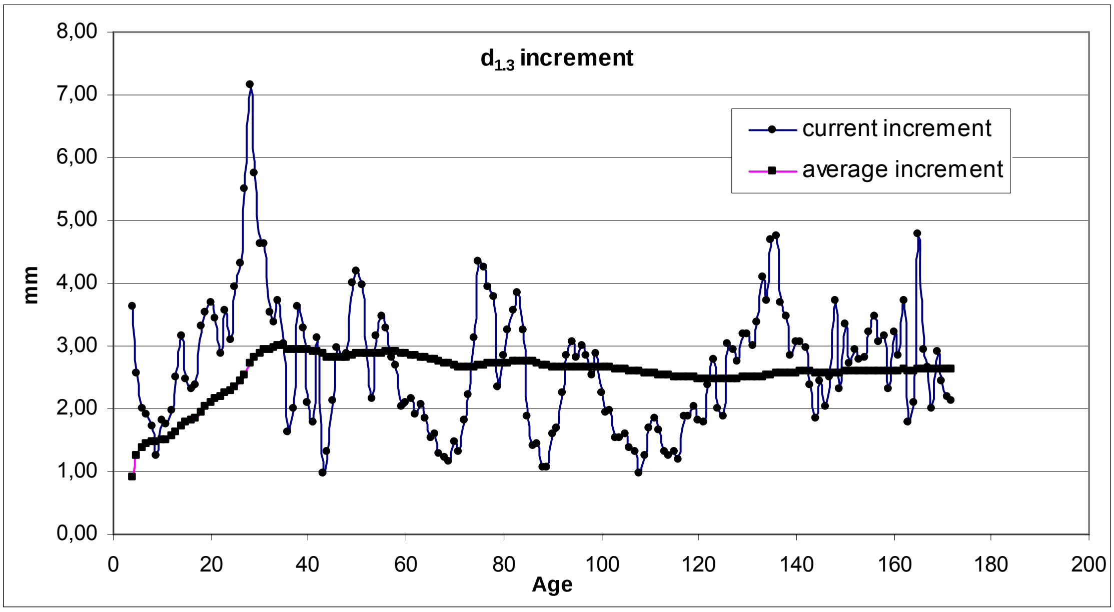

Fig. 5. Diameter $d_{1.3}$ increment of co-dominant beech tree (forest stand 434A17).

Fig. 6. Area of interest (1:50 000).

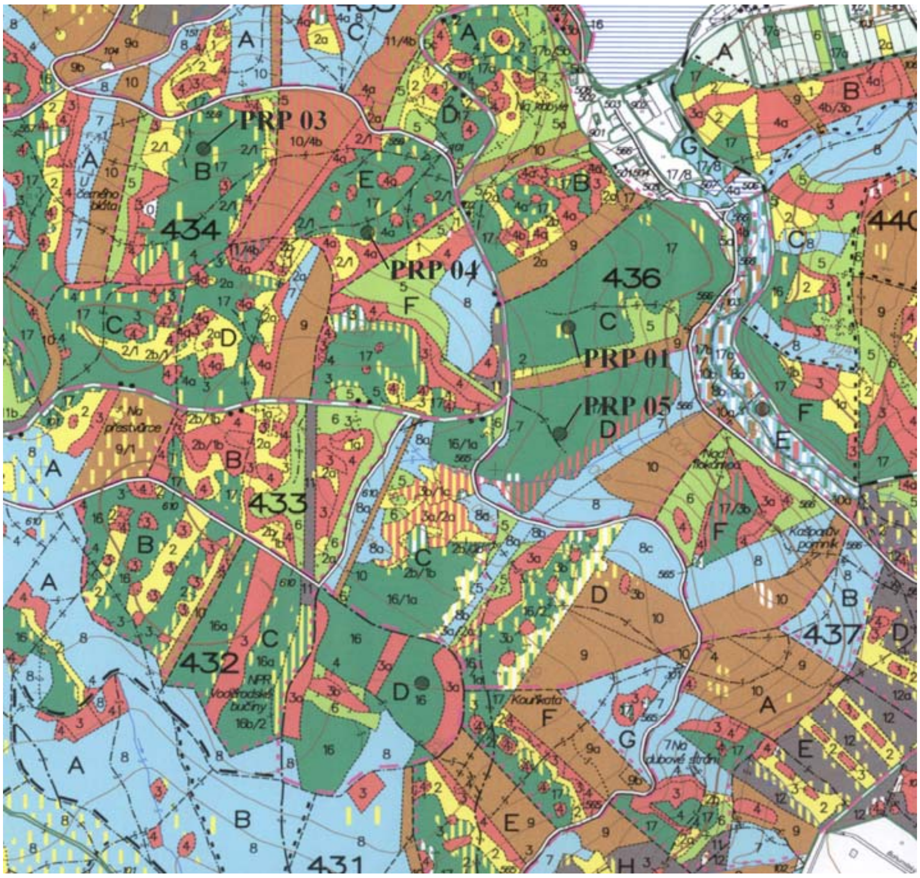

Fig. 7. Localization of PRP 01, 03, 04 and 05 in the area.

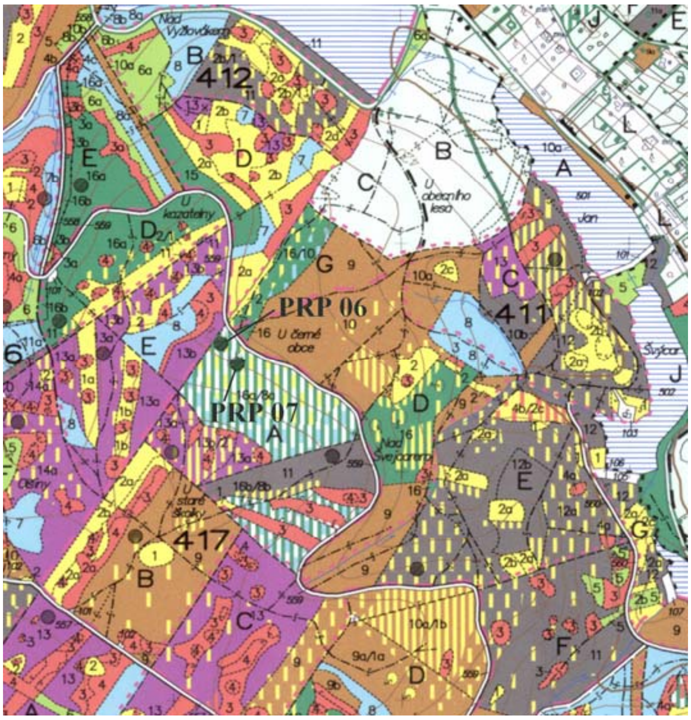

Fig. 8. Localization of PRP 06 and 07 in the area.

Fig. 9. Homogenous even-aged beech forest stand (PRP 05).

Fig. 10. Gap formation on PRP “Virgin Forest“ 06.

Fig. 11. East oriented stand edge with unfavourable conditions for forest regeneration (PRP 04).

Fig. 12. Soil pit on PRP “Virgin Forest“ 06.