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**Structural and Regeneration Development of Near-Nature and Even-Aged Beech Stands in the Voděradské Bučiny National Natural Reserve**

**Dissertation thesis**

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**ABSTRACT**

An ongoing analysis to the four plots of 1 ha established in 2004 found two additional generations of seedlings of minimal presence in the plots after two years. The survival of the generation 2003 and older ones showed a constant reduction for two following years, and the second year survival remained as the lowest registered so far. The evaluation of survival considering in the last year did not show evidence of being affected by the new spaces in the canopy created by missing trees. The inclusion of a new plot with higher stand density in the study verified the negative effect that this factor applies on the formation of new regeneration. An analysis of the position of subplots inside the stand did not show a relation between the existence of crown cover directly over the subplots, or the absence of it, and the survival of seedlings of the generation 2003. Seedlings under different levels of soil water availability and variations during the growing season can manifest different levels of survival and germination. The level of canopy cover of a particular spot can show relation to seed density. Spots under canopy but with advantageous closeness to a gap may offer better conditions for seedling establishment. The recount of two regeneration plots in non interventional stands showed a reduction in the abundance of species different to beech under every kind of canopy covering. The species diversity of a big gap after its creation and with minimal levels of woody debris was notably affected by the species diversity of grown trees around the gap. The structural evaluation of stands of different management history showed that even aged stands under shelterwood treatment keep a regular or random dispersion, and harvest in random pattern can preserve well regular dispersions of stands during consecutive periods. Aggregated ingrowth and small mortality do not change patterns of the stand in a short period of years. Periodical ingrowth mostly emerges attached to established clusters of young saplings. Size spatial dispersion of managed stands displays regular to random pattern, and the mixture of sizes do not appear to be notably affected by harvesting patterns. High tree densities appear to be an impediment for height development of matured tree cohorts both in manage and unmanaged stands. Differences among the sizes of neighboring trees have a direct correlation with diametric increment, and high tree densities combined with low harvest can have a positive affect on relative volume production.

Prohlašuji, že jsem disertační práci na téma:

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# 1. INTRODUCTION

A growing international concern in the preservation of natural ecosystems that has led to the increase in the number and size of nature reserves and the enhancement of more nature friendly forest practices has included the most important broadleaved tree species of Central Europe (beech, *Fagus sylvatica* L.) in a series of dynamic interdisciplinary investigations aiming to describe its entire set of ecological connections. The quest for knowledge tries to identify the perfect blend between production and protection as a way to give forest management the orientation that could define it as a true natural resources management discipline.

Decades of research and documentation of the forest management in the Czech Republic have determined the reasons of ecological transformation that has taken originally dominant tree species to almost rare species, and has converted a diversity of forest habitats in uniform and structurally simple environments incapable of performing the basic inherent processes that assure the subsistence of an additional number organisms. Moreover, the lack of complexity of these ecosystems diminishes drastically the capacity of resilience, causing a high dependence on anthropological control and foreseeable devastating effects after the occurrence of disturbances of variable intensities.

This study uses long-term evaluation of common dasometric variables and regeneration sampling to compare beech stands under different historical management and opposite ecological characteristics in order to understand the differences in autonomous and conducted development, their present weakness and strengths as well as future tendency. Additionally, in an effort to perform a more integral environmental analysis, localized measurement of soil water in relation to variable canopy cover attempts to establish its connection with regeneration progress.

## 2. LITERATURE RESEARCH

### 2.1. Czech Forests

Despite the fact that the Czech Republic belongs to the European countries with a smaller area (80,000 km$^2$), it has a great variety of natural richness, forests undoubtedly being one of the most valuable. Significant diversity of sites together with the geographical position of the country, which is situated on the cross roads of several phytogeographical areas, resulted in the creation of a wide range of plant associations including naturally predominant forests. A great variety of forest types determined in a relatively small area of the present Czech Republic is influenced by the vertical structure of the territory, by the geological and pedological conditions and presence or better accessibility of water in the landscape (Vančura et al. 2007).

- **Natural (ontogenetic) forest develoment**

During the Early Atlantic period (5500-4000 BC), pine and other tree species of Boreal period gave way to mixed oak forests, spruce and beech. Spruce and beech spread even more in the Late Atlantic period (4000-2500 BC). The beginning stump extraction and grazing within colonization result in lower density of forests. During the Sub-Boreal period between the years 2500-500 BC, spruce and mixed oak forests started to retreat giving way to beech and fir. Spruce is predominant in Šumava, but in Jizerské hory with the altitude of 750 m it represents only a third of all growing species. Natural forests used to grow in the territory of the Czech countries approximately until the 4th century BC and the actual vegetation zones settled down approximately at the beginning of the Christian era. Oak forests with a mix of lime and hornbeams were predominant in lowlands, fir and beech forests at mid-altitudes with oak or spruce in colder areas. Mountain forests were composed of spruce with beech, fir and sycamore. Uplands of the Older Atlantic period (500 BC - 1300 AD) were represented by forests mixed of beech and fir, spruce was still predominant in higher altitudes (Vančura et al. 2007).

- **Human impact on forests**

The undisturbed evolution of forests in the Central Europe came to its end around the 7th century AD, although deforestation around Celtic settlements already occurred in the territory between the 5th and 2nd century BC. For the construction of their oppida the Celts needed a significant volume of timber. Moreover they used to remove the forest stands obstructing their guards' views. The decrease in the forest area was related to the need of agricultural land, need of timber and firewood mainly in the later period in connection with the production of charcoal for potters, metallurgists, smiths and glass workers. Activities related to the construction of castles, cloisters and towns also had a natural impact on forest conditions. Volumes of timber were also used for timbering shafts within extraction of precious metals. Even in the 11th century, forests covered approximately 80 % of the area of Bohemia. Forest vegetation zones were moving along with the development of settlement and the way of livelihood. We can talk about natural forests in the beginning of Slavic settlement period (6th century AD) only in the area of the frontier mountains and Českomoravská vrchovina. At present, the places undisturbed by man can be found only close to inaccessible peatlands and at the tops of some mountains (Vančura et al. 2007).

- **Forest land area, tree species composition and ownership structure**

The critical lack of timber in the 18th century caused the replacement of many broadleaved and mixed forests by coniferous monocultures. In the last 50 years, however, the share of broadleaved species has gradually increased, from 12.9% in 1950 to 22.3% in 2000. Broadleaved trees made up 65.3% of the original forest composition. The Norway spruce *(Picea abies*) made up 11.2% of the natural composition of Czech forests; the Scots pine *(Pinus sylvestris)*, originally comprised 3.4%. The share of the European beech *(Fagus sylvatica)*, on the other hand, has dropped dramatically from an initial 40.2%. The result of these long-term changes is a *low biodiversity and ecological stability* of present forest stands, which leads to widespread exposure of forests by factors both biotic (especially bark beetles) and abiotic (especially wind, air pollution and drought) (Organisation for Economic Co-Operation and Development 2005). Total acreage of forest land area in the Czech Republic currently amounts to approximately 2.6 million hectares and is slightly increasing. Nearly 59.9% of the forest area is in state possessions, about 23.4 % of total forest lands are in private ownership, 15.7% belongs to municipal forests and a 1% to forest cooperatives. Most of the forest lands (three quarters) are covered by conifer trees, namely by spruce. Broadleaved species constitute only one fourth. Nonetheless, their share keeps growing also due to the tireless effort of foresters aimed at the enhancement of tree species diversity in the forests. In a more detailed description, spruce accounts today for 52.2% of the forests individuals, fir has 1.0%, pine has 16.9%, larch has 3.9%, oak has 6.8%, beech has 7.2%, birch has 2.8%, and other species represent the remaining 9.0% (Ministry of Agriculture 2009)

In the Czech Republic, forest vegetation zones are determined by mesoclimate, plant society and site quality. The natural ecosystem of these zones is dominantly influenced by one or two tree species, which are used for the labeling of the zones (Kupka et al. 2002). Current characteristics of these zones in the country are listed in Table 1.

Table 1. Forest vegetation zones and their share in the Czech forests (Forest Management Institute 2008)

| code | prevailing species | % | Elevation above sea level m | Average annual temperature °C | Annual precipitation mm | Growing season days |
|---|---|---|---|---|---|---|
| 1 | oak | 4.48 | <350 | >8.0 | <600 | >165 |
| 2 | oak with beech | 10.48 | 350-400 | 7.5-8.0 | 600-650 | 160-165 |
| 3 | beech with oak | 25.23 | 400-550 | 6.5-7.5 | 650-700 | 150-160 |
| 4 | beech | 17.72 | 550-600 | 6.0-6.5 | 700-800 | 140-150 |
| 5 | beech with fir | 23.52 | 600-700 | 5.5-6.0 | 800-900 | 130-140 |
| 6 | beech with spruce | 12.72 | 700-900 | 4.5-5.5 | 900-1050 | 115-130 |
| 7 | spruce with beech | 4.39 | 900-1050 | 4.0-4.5 | 1050-1200 | 100-115 |
| 8 | spruce | 1.25 | 1050-1350 | 2.5-4.0 | 1200-1500 | 60-100 |
| 9 | dwarf pine | 0.21 | >1350 | <2.5 | >1500 | <60 |

## 2.2. Beech Characteristics and Environment

### 2.2.1. Beech Forests

Beech forests of the Czech Republic are mostly located in protected areas, though European beech can be considered the most important commercial broadleaved tree species of the area, playing an important role in the conversion of extensive spruce monocultures (Dušek et al. 1985; Mauer 1997). A structural characterization of large areas of beech forest in the Czech Republic reveals decreasing local relative variability of major stand structural features with increasing plot size, though even one hectare values is highly variable, with a volume stock of living trees ranging from 474 to 1049 $m^3$/ha within one site (Král et al. 2010). The high shade tolerance of beech is related to leaf phenological differentiation. Microclimate influences the characteristics of sun and shade leaves of young beech trees regenerated naturally after clear-cut. Stomata closure in young sun leaves occur at higher leaf relative water content than in young shade leaves. Summer and autumn leaves do not show that behavior clearly. In ecosystems with higher difference between sun and shade light conditions, shade leaf water content is higher, coinciding with high soil moisture. Similarly, stomata density is higher in sun than shade leaves regardless of tree age and phenology. The content of non-structural carbohydrates is always higher in sun than in shade leaves (Closa et al. 2010). Current regional ecological alterations in beech forests have been reported by Durak (2010) registering similar direction in vegetation changes within both managed and unmanaged beech forests of the Eastern Carpathian, verifying the existence of a regional pattern of changes in beech forests involving a decrease in the shares of arborescent species within the shrub layer, disturbance of the canopy layer, acidification of the top layer of the soil, change of light conditions, increase in shares of generalist species and decrease in shares of specialist species. The decrease in anthropogenic pressure, aging of forest stands, functioning of large, dense forest areas and sustainable forest management strategies mimicking natural deciduous forest disturbance regime constitute factors shaping the regional changes of the forest vegetation, which can lead to biotic and spatial homogenization of the forests. One of the problems associated to the production of beech forest is the presence of red heartwood, which seems to be frequent in trees reaching older ages, while in trees up to an age of 80 to 90 years old without fork formations in their stems and injures in the bark do not bear much risk of presence of red heartwood (Knoke 2003). Additionally, aging of beech trees affects growth increment since carbon allocation to storage and reproductive functions in beech stands increases with age to the detriment of carbon allocation to growth functions (Genet 2010).

## 2.2.2. Beech and Environmental change
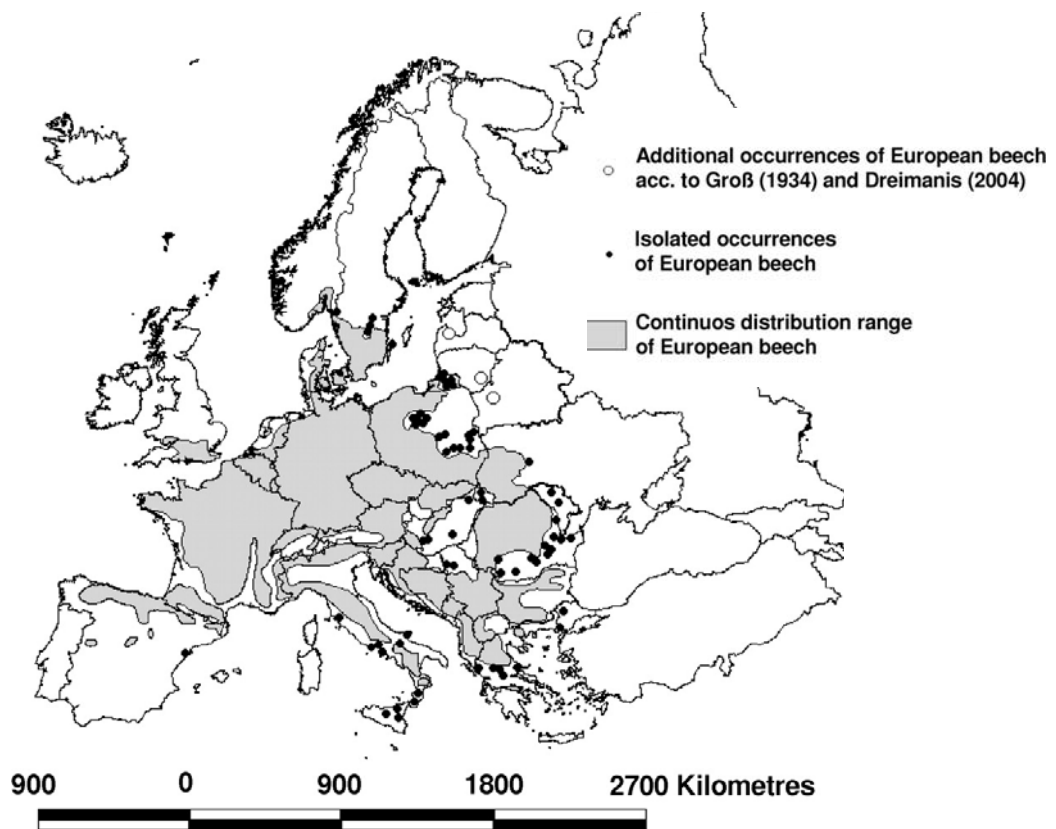


Fig. 1. Presence of beech in Europe (Bolte et al. 2007)

Beech presence through the European continent is well extended (Fig.1), and the northern and eastern Poland are defined as distributional margins of the species in the southern regions of the Baltic States (Bolte et al. 2007). The natural distribution of beech has been subject of concern facing global climate changes, and studies have established possible future scenarios and current distribution variations. An evaluation of possible climate change models in the future distribution of beech showed that the species has the potential to expand its northern edge and loose habitat at the southern edge (Kramer, et al. 2010). On the other hand, the expansion of beech in Slovenia was found more pronounced in lower altitudes, on sites with steep topography, and on sites with a higher proportion of beech in potential natural vegetation. Moreover, the increment of the distance to the nearest compartments of forests with beech affected negatively the probability of expansion (Poljanec, 2010). In terms of production, an analysis of provenance and macroclimatic adaptedness of beech in Hungary considered that foreseeable climatic warming in the central-northern part of the range may lead to production increase, but growth depression and vitality loss are predicted under stressful and uncertain conditions at the lower (xeric) limit of the species (Mátyás et al. 2009). Environmental changes may as well create competitivity disadvantages for the species. A study of height growth potential in France, using May, July and January temperatures as variables, plus December precipitation, and soil factors like pH and C/N, found that the height growth potential in the north-west region of the country is not linked to limit

in the species distribution. Instead, environmental factors affecting reproduction and mortality, or relative environmental advantages of competitors seem to be responsible of the discrepancy (Seynave et al. 2008).

Extreme weather conditions in particular years can bring about noticeable reactions of the species. Fotelli et al. (2009b), proved how a warmer and drier climate in 2003 affected the N balance of beech in north-west Greece. The lower N availability caused the remobilization of N-storage compounds to satisfy normal N demands. Moreover, Jung (2009) reported that from 2003 to 2007 an infestation of *Phytophthora* species in Bavarian beech forests, in addition to an attack of bark and wood boring insects, provoked bark and wood decay and subsequent scattered or clustered mortality. The study indicated an involvement of Phytophthora species in the complex "Beech Bark Disease" and its relation with excessive rainfalls and droughts. However, the reaction of the species is not evenly perceived. Fotelli et al. (2009a) analyzed the physiological effect of Greek climatic conditions in 2003. Though that year was more xeric than 2004 and 2005, it was in the local range of precipitation, and physiological factors like leaf water potential, effective quantum yield and plant carbon isotopic composition were not indicative of draught stress. There is, in fact, a relation between different provenances of beech in Europe and their response to soil water content, so that provenances from lower latitudes show higher increment in growth under high soil water content conditions, as an adaptation to a longer vegetation period and higher precipitation (Nielsen & Jørgensen 2003).

The timberline of beech have been described by Pezzi et al. (2008) in the northern Apennines (Italy), where an upper limit of beech woods corresponded to a border with mean annual temperature of 4.5°C, coldest month mean temperature of −2.3°C, summer mean of 11.5°C, warmest month mean temperature of 13°C, and 139 days with maximum temperatures of 10°C or higher, reaching to 1825 m a.s.l. Yet, altitudinal distribution alterations have been described by Peñuelas et al. (2007) for beech trees in Catalonia (Spain) in its low and high altitudinal limits plus the central area, as a result of climate warming. In the low limit, the species is being replaced by holm oak (*Quercus ilex*) in the last decades, due to the better recruitment rates of the last one. The presence of young beech individuals in the low limit is then reduced to the half of the density reached in the high limit, which rises to 13 individuals in 100m of tree line. These trees are mostly younger than 35 years old and about 36m of altitude above the timberline (1600 to 1700 m a.s.l)

Lendzion and Leuschner (2008), alternatively, give importance to atmospheric water vapor pressure deficit in beech forest during possible climate change, demonstrating that low air humidity conditions lead to drought stress of saplings even under ample soil moisture supply, which in the end affects biomass growth. All in all, European beech seems to have an underestimated phenotypic plasticity and evolutionary adaptability that could counteract distribution contraction due to a climate change (Bolte et al. 2007).

Atmospheric contamination, another kind of environmental alteration, has also been a subject of silvicultural research of the species. The effect of root pathogen *Phytophthora citricola* on beech regeneration may vary under different conditions. According to Winkler et al. (2009) a number of three years old beech saplings growing under high concentrations of $O_3$ and in the presence of *Phytophthora citricola* had significantly

reduced aboveground plant growth by elevated ozone but not affected by *P. citricola*, though biomass partitioning between fine and coarse roots as well as vertical root distribution showed to be significantly affected by both factors. Also, when comparing the susceptibility changes of beech seedlings to *Phytophthora citricola* under different conditions of $CO_2$ and soil nitrogen, an elevated $CO_2$ and low nitrogen supply caused and enhancement of the seedling susceptibility to the pathogen (Fleischmann et al. 2010).

### 2.2.3. Beech Regeneration

### 2.2.3.1. Fructification and Dispersal
Beech is traditionally reproduced by natural regeneration, which typically begins when the trees reach 40-50 years of age and flowering and seed production start to take place (Wagner et al. 2010). The Natural regeneration process is based on the frequency of mast years, which occur every 4 to 6 years in average. Such frequency is said to be encouraged by dry periods from July to September in the prior year and with a temperature higher than 30 °C, although site index and high deposition of atmospheric nitrogen can also affect positively such frequency (Övergaard et al. 2007; Salisbury 1942). A limited negative effect of masting on diameter growth in the following years is short term and typically occurs in the year of actual masting (Drobyshev et al. 2010). Packham et al. (2008) reported 11 good mastings between 1980 and 2006 in England, the best one in 1990. Each masting followed by a very poor seeding year.

Beech pollen effectively disperses less than 250 m within forests (Wang 2001). Chybicki et al. (2009) found, in two populations in Central Europe, clustering of beech individuals up to 40m (following a so called isolation by distance), and a seed dispersal 10-100 times more restricted than pollen flow, with a significant portion of short-distance pollinations responsible for biparental inbreeding. Beechnuts commonly disperse by barochory, usually around 20 m (Wagner et al. 2010), but can reach up to 125 m by zoochorous dispersal even introducing beech into stands of other species (Kramer 2004). Local high density of beech seedlings has a strong negative influence on their diameter growth and a smaller influence on height growth (Collet & Chenost 2006). What is more, there has been established a good level of predictability of mortality based on a negative correlation with annual diameter increment of beech seedlings in natural regeneration of a mature beech forest. Similarly, competition index and initial height also have showed good level of likelihood in relation to mortality (Collet & Le Moguedec 2007).

### 2.2.3.2. Soil Requirements
Beech grows well on a wide range of sites with a preference for base-rich soils, though the occurrence of windthrow is done mainly on gley and pseudogley soils (Savill et al., 1997). Additional factors interact with seedling establishment. Widdicombe (1999), for example, found a mayor importance of vegetation cover than presence of seed trees in the establishment of beech seedlings in combination with *Quercus spp.* increasing establishment success on soils with litter cover but also on exposure of mineral soil. Beech roots do not show conspecific competition (Lang et al. 2010), and their growth was characterized by an increment of live and total fine root biomass from May to July

during a particular growing season, followed by a decrement in both factors, in forests of Mediterranean ecosystems in Greece (Zerva et al. 2008).

- **Soil Water Relation**

Beech water requirements are marked by the fact that although beech possesses mechanisms for responding to water deficits, it is not a drought-tolerant species (Fotelli et al. 2009a). When competition is strong, beech trees show a high sensitivity to water balance whereas, at low competition level, trees react positively to high temperatures (Cescatti & Piutti 1998). A reduction of forest productivity was noticed by Piovesan et al. (2008), after comparing water availability in beech forests of the central Apennines and their basal area increment, which was due to drought stress persistence after a reduction in the availability of water from 1970. Similarly, Charru et al. (2010) exposed an analysis of production of even-aged pure beech forest in France, that confirmed the hypothesis of a recent decline in common beech vitality in its temperate range, connected to severe drought events (1976 and 2003), pointing out the predominant role of water availability in the changes observed. Drought constraints for beech can be identified in ecophysiological terms by the critical limit for xylem cavitation and loss of hydraulic conductivity, reached at a shoot water potential of -1.9 MPa, and a reduction in gross primary production and total ecosystem respiration when relative extractable soil water reaches 40 and 20 per cent, respectively (Bolte et al. 2007). Spatial and temporal variability in soil moisture content of homogeneous beech sites, as stated by Schwärzel et al. (2009), is due to soil properties and root intensity. Mund et al. (2010) details the complexity of the physiological effect inside an old-growth mixed-deciduous forest with a dominant part of *Fagus sylvatica* and codominant presence of *Fraxinus excelsior* and *Acer pseudoplatanus* during 5 years, where an annual stem growth of *Fagus* favored by warmer spring periods, *Fraxinus* by high precipitation in June, and no significant weather relations of stem growth were detected in *Acer*. When the relative plant-available water in soil dropped below a threshold of about 60% between May and July the intra-annual stem growth of all species was strongly reduced. The stem growth was generally not limited by insufficient carbon resources, and only indicated possible short-term carbon shortage occurring in spring during mast years. Alternatively, the comparison of four populations of beech with different precipitation regimes found a reduction on 30-40% in individual total root mass under drought conditions due to median fine root lifespan reduction in 50%, plus a decrease in fine root growth rate related to productivity per standing root biomass, though there was not a increment of root:shoot rate. The root biomass reduction in response to drought was not related to genotypes from the different precipitation regimes (Meier & Leuschner 2008). The behavior of C storage in beech stands with difference of annual precipitation showed a decrease of 25% of soil organic carbon from stands with more than 900mm/year to those with 600mm/year, with a slight increment in stem C storage. Fine root production increase with precipitation reduction, but a fine root biomass and soil organic C in organic layers decreased. A long-term deduction of the precipitation decrease envisages a reduction of soil organic C pools under substantial precipitation decrement due to high decomposition rates turning temperate beech forests into carbon sources instead of carbon sinks (Meier & Leuschner 2010).

Madsen and Larsen (1997) affirm that higher soil water content increases the regeneration growth while an increment of soil carbon content has the opposite effect, possibly due to an accumulation of raw humus, which results in poor nutrient supply. Similarly, under appropriate supply of water in the soil and sufficient fertilization, a

relatively open canopy can generate convenient conditions for a large increase of beech seedlings growth (Madsen 1995).

- **Ectomycorrhizas and Nutrient Balance**

Ectomycorrhizal presence has a special importance in beech soils. A comparison between gap and closed canopy environments in four locations in Europe showed higher ectomycorrhizal species richness in natural than in managed forests and a significant reduction of diversity indices, ectomycorrhizal and fine root dynamics in gaps of beech forests (except in gaps with pronounce abundance of regeneration) in comparison with closed canopy stands, The above indicates the high importance of maintaining and protecting natural forest areas for conservation of soil biodiversity and forest genetic resources. The litter and soil pH, number of beech seedlings, and presence of a gap had a pronounced effect on the ectomycorrhizal community (Grebenc et al. 2009). Stoelken et al. (2010), nonetheless, found that beech seedlings perform a higher uptake of organic N than inorganic N in non-mychorrhizal roots, which determines the importance of organic N in beech nutrition, and the inessential work of mychorrhizal presence in beech development. Beech management and N balance was linked by Dannenmann et al. (2006), when stating that the possible decrement of N soil retention after thinning was registered in beech managed forest, with variable resistance to the N balance disturbance depending on contents of C and C/N ratios of the ecosystems, which are also related to microclimate. Tree species can also affect each others N uptake, as the case of seedling competition between beech and sycamore maple (*Acer pseudoplatanus)*, where a negative influence in the uptake of inorganic and organic N by beech roots was found in the presence of the competing tree species, while the presence of beech stimulated inorganic N uptake by sycamore maple roots (Simon et al 2010).

In the same way, different associations of beech can affect C balance. A comparison between litter decomposition in beech, spruce and beech/spruce stands showed 60% of C loss after two years contrasted to 40% in spruce in the same period. Such higher rate of decay was not related to N content, but higher level of microbial biomass was found in beech leaves, indicating more presence of compounds suitable for microbes. The last mentioned factors were higher in 120 years old stands than in 30 years old ones. The same factors were intermediately ranked in mixed stands, indicating a counteract effect of the mixture in the conditions of decomposition. The lower values found in spruce needles are thought to be related to environmental constraints, like high presence of polyphenol, rather than to inherent resistance to decay (Albers et al. 2004). Litter decomposition rates may depend on their chemical properties and given tree species. Jacub et al. (2010) studied the litter decomposition of pure beech and non pure beech stands and found that decomposition rates were positively correlated with the initial N and Ca concentrations of the litter, and negatively with the initial C:N, C:P and lignin:N ratios, which supports the idea that the overall decomposition rates are mainly influenced by the chemical composition of the individual litter species. Biodiversity in ground vegetation is associated to soil properties. A comparison between soil characteristics and biodiversity under beech and hornbeam trees found lower species richness under beech trees associated to low pH, high mass of organic layer and low soil moisture. Litter decompositions were generally slower (Kooijman & Cammeraat 2010).

**2.2.3.3. Climate and Overstorey Dynamics Response**

In general, beech seedlings are susceptible to damage by late spring frosts, drought, high temperatures and competition from ground vegetation. It is, therefore, difficult to establish beech on open exposed sites without overhead shelter. In such open situations, other species must be planted as nurse trees (Savill et al. 1997; Huss 2004). Additionally, as stated by Birkedal et al. (2010), there is a correlation between the number of granivorous rodents in one of two following years and the proportion of lost seeds after direct seeding in clear-cut areas. The light requirements for the species detail a negative regression between canopy openness and mean density of beech seedling has been described (Modrý et al. 2004), and a range from 10-40% of relative light intensity is considered to be optimal for enough number and sufficient morphology of beech seedlings (Nicolini et al. 2001, Wagner at al. 2010). Beech seedlings low light adaptation is related to the bigger proportion of biomass in the shoot than in the root during the first year of life, which favors photosynthesis, which makes the species suitable for regeneration under shelterwood (Welander & Ottosson 1998), though, according to Skrziszowski and Kupka (2008), the quite strong growth rate of fine roots in beech seedlings during the first 4 years makes it appropriate for plantations. Seedling growth has also been related to light availability and root density of old beech (Wagner 1999).

Specific light requirements of beech link the species to ecological dynamics. It is known that beech seedlings have the capacity to increase height growth following a canopy disturbance even after a long period of suppression (Collet & Chénos 2006). According to Madsen and Larsen (1997) larger canopy openings show higher variance in height growth and higher sapling density of beech seedlings. However, after canopy opening, a larger vulnerability to cavitation during the first year could limit stomatal opening and therefore the ability of beech saplings to use the available light for photosynthesis and could therefore partly explain why the growth increase was delayed to the second growing season after canopy opening (Caquet et al. 2009). Gap characteristics and presence of beech under different gap sizes are explained by Gálhidy et al. (2006), with the analysis of two different sizes of gaps (35-40m and 10-15m in diameter) of beech forests in Hungary. It was found relative light intensity values lower in small gaps than in big ones, while the center of both kinds of gaps registered similar soil moisture levels. An increased number of herbaceous species in gaps was characterized by the presence and specific location of the species according to different requirements of light and soil moisture. A bigger density of beech seedlings in small gaps was explained by limited seed dispersal. Different gap sizes are exposed in beech forests of Slovenia and Croatia with 10 years old large gaps (700-2000m$^2$) and small ones (200-500m$^2$) in old-growth communities, that showed five times more total regeneration density (6.2 sedlings/m$^2$) and higher beech regeneration in the Slovenian site, but more ground vegetation density and density of silver fir (*Abies alba*). In every case, both species preferred under canopy or close to gap edges establishment, with lower radiation levels. Beech seedling densities did not have significant variation on microsites, but height growth was higher in presence of higher radiation. It was concluded that light conditions did not influence all tree regeneration and ground vegetation factors, but under similar stand site conditions a larger presence of herbivores could affect total vegetation densities (Dusan et al. 2007). Rodríguez-Calcerrada et al. (2010) explain an exponential leaf respiration increment with the diurnal increases in temperature for understorey and gap plants, irrespective of watering conditions and a lower respiration at 25 °C in the understorey than the gaps that was significantly lower in the unwatered than in the watered gap plants by the end

of summer. In the same way, Hank and Madsen (2008) show the response of canopy opening in nature-based managed beech stands, which registered higher seedling density in relation to higher soil moisture and opposite reaction with intensities of light. Fencing of regeneration area did not show significative effect on seedling growth or density. Three to four years was the time needed for the natural closure of the canopy gaps created by felling of three mature trees. After this period, new regeneration was not able to get successful establishment. For Umeki et al. (2010) beech saplings with slanting shoots and simultaneous foliar phenology are particularly successful in shaded environments, where beech often dominates, because they appear to maximize the annual carbon budget by avoiding self-shading and extending leaf lifespans. In the other hand, in the presence of vertical light gradients, which can occur in canopy gaps, saplings with upright shoots had larger annual photosynthetic gains than counterparts with slanting shoots. Also, humus properties in beech virgin forests are characterized by the heterogeneity in the stratification of humus through the extension of a canopy gap, mainly due to differences in the vegetation cover (Patzel & Ponge 2001).

### 2.2.3.4. Effect of Associated Species
The interaction of beech seedlings with other species has been studied under different conditions. The height growth of beech seedlings growing under *Picea abies* is more affected by belowground resource availability than for light availability in recently germinated seedlings, followed by a more important influence of light in following stages. In seedlings identical in initial size but differing in age, the increment in PAR causes a greater height growth in older seedlings than in younger seedlings. The ranking of seedling height by year shows that small differences in size at the end of the first growing season results in continuously increasing differences during the following years. The chances of a seedling surviving intraspecific competition were strongly determined by the ranking of its dominance within the first 5 years after establishment (Ammer et al. 2008). The influence of one year old seedlings of an early successional species like blackberry (*Rubus fruticosus*) in competition with beech in different air temperature and irradiance brings positive effect of high air temperature and low irradiance on biomass, root/shoot ratio and N uptake of beech competitive development. A combination of high air temperature and irradiance is negative for beech, and a low air temperature combined with full light or shade does not show important influence (Fotelli et al. 2005). An evaluation of the growth behavior of two years old beech seedlings in the presence of different densities of silver birch (*Betula pendula*) or Scots pine (*Pinus sylvestris*) in full light conditions during three years showed diameter reduction of beech in presence of the neighbors, especially of the extensive development of pine. Soil moisture was lower under pine and was correlated to beech diameter growth. Small increment in specific leaf area, height-to-diameter ratio and crown length-to-crown width ratio of beech was registered with competition from neighbours (Prévosto & Belandier 2007). A comparison between young beech growth under silver birch and scots pine stands registered a superior growth of beech under pine than under birch, though a slight higher light availability was present in the second case. Aging of beech and approach to the upper tree layer decreased this growth trend. A higher root biomass of competitor trees and ground vegetation under birch was considered the real limitation causing in beech growth differences between the two sites (Prévosto & Curt 2004). Lastly, an evaluation of shade influence in saplings (1-8m high) of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech under shelterwood canopy of different densities reported beech as the one with the least

mortality under low light, though it also gained the smaller growth rate under high light availability among the three species. Increasing light showed the fastest decline in beech, and a 15% of light availability approached the species to zero mortality. The higher soil moisture registered coincided with the best height growth in the three species only in combination with high light availability (Petritan et al. 2007).

## 2.7. Near Nature Management

There are no longer "virgin forests" in Central Europe but mostly forest with semi-natural species composition, and the establishment of nature reserves has aimed to improve the representativeness of forest reserves based on plant associations or on forest site type classifications (Diaci 1999). Following basic and logical mimic of nature, the establishment of a mosaic of areas of different ages facilitates the preservation of numerous forest habitats as a way to generate ecological sustainability (Bergeron et al. 2007). Natural-disturbance-based management can be a way to preserve ecological resilience when there is an acknowledgement of the importance of biodiversity and natural disturbances in the long-term ecosystem functioning, generation of structural and compositional heterogeneity at multiple scales and the decrease of likelihood of unexpected catastrophic changes. The purpose of the natural-disturbance-based management is then to foster the processes that retain desired structural states, while discouraging processes that lead to undesired states (Drever et al. 2006). This management principle can be used to achieve diversity of structure and composition at large scale forest landscapes, by applying simultaneous silvicultural treatments to specific forest zones. The method allows the practice of selective harvesting for encouragement of late successional species and clear-cutting for early successional species favoring, which in fact simulates the occurrence of severe fires (Harvey et al. 2002). According to Larsen and Nielsen (2007), the transformation of forest from age-class forests to nature-based ones requires the collaboration of professionals and scientist in the definition of long-term goals in terms of stand structure and dynamics, which often remains as an objective very difficult to clarify. One of the benefits of near nature forest structure is the presence of deadwood, which favors biodiversity conservation by providing food and shelter to endangered species, especially invertebrates (Mountford 2002). For Bergeron et al. (2006) natural disturbance based management can be used in fire dominated forests as a way to substitute fire by harvesting, to retain the natural forest spectrum of compositions and structures at different scales. The profitability of near-natural beech stand management is primarily achieved through the utilization of natural ecological processes, with the purpose of producing valuable timber at low establishment costs (Nord-Larsen 2003).

Kuuluvainen (2009) exposed the structural variation of natural boreal forests of northern Europe in comparison with clear-cut forests, which have been traditionally defined by others as very structurally similar to natural conditions. The author expressed concern for the unlikely biodiversity conservation and ecological sustainability of areas under similar management models. In practice, the application of forest vegetation management environmentally friendly in Europe during the present century displays limitations. That is the case of a persistent use of herbicides in some degree especially in the southern and central region, though other means of vegetation control like mechanical cut, overstorey manipulation for reduction of light in the understorey,

application of mulches and biological control are also applied, in some cases regardless of the higher costs (Mccarthy et al. 2011).

Schütz (1999) points out a natural simplification process of some forests that makes difficult their permanent adaptation to more complex ones in terms of structure and biodiversity. Mixtures of tree species complicate stand evolution, and mixed stands need more silvicultural interventions to ensure the survival of less competitive tree species. In fact, European "virgin" forests are mostly monospecific. Only where site and climatic conditions deteriorate do we find naturally mixed forests. With decreasing precipitation, for instance, oak successively replace beech. Beech-fir-spruce mixed forests appear with decreasing temperature, as for in the mountain elevation belt. Also, virgin forest generally show regular structures, at least during an essential part of their development, from the phase of "aggradation" to the end of the "optimal" phase, there is an homogenization process, altered only in a "regenerative" phase. The only silvicultural method known that has led to permanent irregular structures is the plentering method (or selection forest system), which is based on perfect vertical structuring and yield individualization achieved by and dependant on intensive and recurring interventions. Nevertheless, most attempts to apply this model in broadleaved stands have failed. The shade tolerance of beech is not free of disadvantages in an irregular structure, since a prolonged period of shade can lead to a plagiotropic growth that endangers its capacity to achieve vertical growth after release, and the rapid lateral expansion of the crown produced after release restricts an efficient use of the space. Alternative close to nature models dealing with beech disadvantages and other broadleaved species may give importance to small clustering of individuals that achieve individualization in the upper storey and the creation of small gaps gradually expanding or uniting (Schütz 2002).

Ecological benefits of the appropriate nature management of beech forests have been defined. According to Willner et al. (2009) there are 110 understorey species closely associated to European beech forests. The highest number of beech forest species is found in the Southern Alps and adjacent regions, and species numbers decrease with increasing distance from these regions. Considering only narrow-range species (species present in <10 regions) secondary maxima are found in Spain, the southern Apennines, the Carpathians, and Greece. Distance to the nearest potential refuge area is the strongest predictor of beech forest species richness. Rot holes in beech trees are important microhabitats for epiphytes to be preserved. Slow growing trees of different ages and sizes, under interaction of fungus *Psathyrella cernua* are found to be a key combination in the creation of this microhabitat (Fritz & Heilmann-Clausen 2010). Correspondingly, an important diversity of bryophyte species, some of them threatened, were reported in old-growth beech stands in the central Balkans in relation with the presence of deadwood of different stages of decay as habitat (Sabovljevic et al. 2010). Bark-strip from red deer *Cervus elaphus* does not appear to be driven by nutritional needs, but it may help deer in improving digestion efficiency by parasite protection due to its content of tannin (Saint-Andrieux et al.2009). These are few examples of how biological diversity inevitably interconnects species in the ecosystem and justifies its absolute conservation

## 2.8. Soil water

The content of water in the soil is the result of processes of water entering the forest ecosystem and losing it. Apart from the water balance in the ecosystem also the character of the soils of the localities is determinant. Soil water is the main and decisive source of water for the plants, including tree species. Its content and dynamics determine plant life directly as the source of water for transpiration and with it connected transport processes in the soil-plant system; also indirectly by way of mechanical, physical, chemical and soil-biological properties. The main source of water in the soil is precipitation. The amount is based on climate conditions and is modified by the aboveground components of the ecosystems (interception, transpiration). Another source is ground water supplied by natural filtration from the surroundings or by capillarity from the ground water level (Vančura et al. 2007). In agricultural systems, water is often the major factor limiting growth. When water availability is limited as a result of limited supply or high cost, its efficient use becomes critical to successful production systems (Trimble 2008). A particular indication of the importance of soil water for plants is its effect in root growth. For a given location, numerous publications have confirmed that relatively dry soil conditions can induce plants to develop a more extensive root system (Gregory 2006). *Fagus sylvatica*, in this case, even though it will grow on all slopes and aspects, plains and lowlands within its natural distribution area, and can thrive on a wide range of soil conditions, from acid to alkaline, nevertheless, does not tolerate waterlogging (Joyce et al. 1998).


## 2.8.1. Soil water content

Soil water content is an expression of the mass or the volume of the water in the soil. Different levels of water content can be distinguished by soil water potentials, which describe the energy status of the soil water and is an important parameter for water transport analysis (WMO 2008):

**Gravitational water.** Water freely draining from soil after water application ceases. Plants may absorb some of this water before it leaves the soil (Chesworth 2008).

**Field capacity.** It is the soil water content after the free drainage stops. It is considered the upper limit of a soil's capacity to store water for plant use and is approximated to 0.033 MPa of soil water potential (Chesworth 2008). Many factors influence water content at field capacity like previous soil water history, soil texture and structure, temperature, water table, depth of wetting, presence of impeding layers and evapotranspration (Kirkham 2005).

**Permanent wilting point.** Is the lower limit of *plant available water*, which is the largest soil water content at which indicator plants growing in a particular soil wilt and then fail to recover turgidity when placed in a humid chamber. It is approximated to 1.5 MPa of soil water potential (Chesworth 2008).

Unavailable water is held in soil by forces strong enough to prevent significant absorption by plant roots. This water is held in fine pores and as extremely thin layers on soil particles (Chesworth 2008).

## 2.8.2. Indirect soil water content measurement

Some of the different kinds of methods for soil moisture measurement described by IAEA (2008) are:

**Neutron moisture meter.** A radioactive source emits fast neutrons, which lose energy as they collide with other atoms, in particular hydrogen. The surrogate is the concentration of slow neutrons. Since the only rapidly changing source of hydrogen in the soil is water, soil water content can be calibrated vs. the count of slow neutrons.

**Thermal sensors.** A pulse of heat is generated and the subsequent rise or fall in temperature of adjacent soil is measured over time. Soil is a poor conductor of heat, and water a good one, so the amount of heat or rate of heat transmission is closely related to the soil water content.

**Time domain reflectometer (TDR).** A fast rise time electromagnetic pulse is injected into a waveguide inserted into or buried in the soil. The time required for the pulse to travel along the metal rods of the waveguide is determined by the bulk electrical permittivity of the soil. The soil water content is a major factor influencing the bulk permittivity. True TDR involves capture of a waveform and analysis to find the travel time of the highest frequency part of the pulse.

**Conductivity sensors (e.g., granular matrix sensors and gypsum blocks).** An alternating current voltage is placed on two electrodes in a porous material in contact with the soil, and the amount of current is a measure of the conductivity and amount of water in the porous material between the electrodes. These are used for estimation of soil water tension (suction), not water content.

**Tensiometers**. Capillary forces retaining water in the soil pores are connected through the soil water to water in a porous cup connected to a tube filled with water. This generates a negative pressure within the tube, which can be measured with a vacuum gauge. These are used for estimation of soil water tension (suction), not water content.

Gypsum block sensors are 32 mm long and 22 mm in diameter and cover the range -50 to -1500 kPa. Gypsum sensors have a limited lifetime because they slowly dissolve in the soil, and their calibration will consequently change with time (Bouyoucos 1953; Wellings et al. 1985). The life of gypsum sensors may be more than 10 years in dry soil but the useful life in very wet (or acid) may be no longer than 1 year (Bouyoucos 1953).

# 3. THE AIM OF THE STUDY

The study area Voděradské Bučiny National Natural Reserve conjugates a mixture of stands with different densities, ages and species proportions. The conditions of many of the over-matured beech stands bring questions about the inappropriate productive capacity, health and future trend. Furthermore, the upcoming change from managed to non-interventional treatment in some of the current stands evidences the need of a final fitting transformation to guarantee their autonomy and stability. Changes in total canopy cover, canopy opening creation, species proportion in understorey and overstorey, and additional protection and stimulation of seedlings are some of the proceedings that should take place in the given stands, but their approximate extent should be specified. The comparison between managed and non-interventional stands gives a real description of the effect of two different approaches of treatment, and their detailed characterization is the key for the determination of an intermediate phased conversion. Current changes in stand values due to growth, mortality and harvesting, plus the incorporation of new stands and environmental data in the study allow an additional assessment of the registered data. At this point, individual aims of the study are as follow:

- To evaluate the presence of natural regeneration at the permanent research plots and to characterize it according to year of fructification and emergence, and its relative progress in terms of mortality in order to establish the influence of particular management treatments.
- To evaluate the current conditions of the main stand structures and quantify the effect that particular management treatments have had in their growth parameters.
- To propose silvicultural strategies necessary for the successful transformation of even-aged managed forests to non-interventional and self- regulated near-nature ones

Particular research questions are meant to be answered:

- What is the importance of secondary fructification, different to mast seeding, in the regeneration process of beech forests?
- What is the influence of the appearance of new gaps in the overstorey on the nearby establishment of seedlings?
- What is the difference between the rate of diameter growth of managed stands and non interventional ones?
- What is the long-term development of even-aged beech forest like, in the absence of a regular intense intervention?
- What is the influence of soil moisture under different kinds of canopy cover on the development of the natural regeneration?
- What is the relation between age structure of the main stand and seedling development?

# 4. VODĚRADSKÉ BUČINY NATIONAL NATURE RESERVE (STUDY AREA)

The Voděradské bučiny (Voděrady Beechwoods) NNR was declared in 1955 on a territory of 658 ha and includes an extensive forested complex on the right bank of the Jevanský stream. The forests lie between the municipalities of Louňovice, Vyžlovka, Jevany, Černé Voděrady and Struhářov in the Středočeský kraj - Central Bohemian region about 30 km east of Prague. The lowest elevation is at 345 m by the Jevanský potok and the highest is Kobyla hill at 501 m. The majority of the territory has a geological basement of coarse-grained Říčany granite, within which we can find small bodies of feldspar (orthoclase) several centimetres in diameter, rather fine-grained aplitic granite and small areas of other minerals such as sandstone and shale (Nature Conservation and Landscape Protection in the Czech Republic 2008). Predominantly cambisols with low humus content and different depth are developed within forest stands. The soil reaction pH$_{KCL}$ in holorganic horizons reaches values from 3.2 to 4.7. The values of base saturation in holorganic horizons reaches values from 22.1% to 63.3% In uppermost humus enriched horizon from 10.1% to 22.7% of base saturation (Bílek 2009).

The main subject of the protection is the extensive complex of acidophilous and herb-rich beech forests with typical flora and fauna. The predominant forest community is acidophilous beech forest with wood-rush with several typical plant species − wavy hair-grass (*Avenella flexuosa*), white wood-rush (*Luzula luzuloides*) and few-leaved hawkweed (*Hieracium murorum*). Smaller areas are covered with herb-rich beech forest with a richer species diversity with nine-leaved toothwort (*Dentaria enneaphyllos*), coralroot (*Dentaria bulbifera*), woodruff (*Gallium odoratum*), dog's mercury (*Mercurialis perennis*), mezereon (*Daphne mezereum*), and others. The streams are fringed with stream alder communities and waterlogged localities are covered with alder stands with remote sedge (*Carex remota*). Steeper slopes are the home of ravine maple stands with goatsbeard (*Aruncus vulgaris*), the mustard garlic *Allinaria officinalis* and others. Natural spruce stands can be found in the valleys and occasionally with an mixture of fir, sycamore and Norway maple. Relict fauna species and significant species from a zoogeographical viewpoint have been recorded here. The species composition indicates that the Voděradské bučiny could be the most westerly element of the migration of beech forest from the Carpathians in the east (Nature Conservation and Landscape Protection in the Czech Republic 2008). Most of the forest stands in the area originated during the period of 1820-1850, as a result of a very intense three-phase shelterwood with very short regeneration period lasting approximately over 15 years. This, in consequence, formed even-aged stands with relatively simple vertical and horizontal structure that prevail on the major part of the reserve. Only few patches of several hectares of old-growth forest were left unmanaged since 1955 on the area, and exhibit relatively heterogeneous stand structures (Bílek et al. 2009). Climatic conditions for the area, according to the nearest meteorological station (Říčany at 401 masl.), register a mean annual temperature of 7.8 ºC, annual precipitation of 623 mm; a mean temperature of 14.0 ºC from April to September and precipitation of 415 mm during the same period (Čvančara & Samek 1959).

## 5. CASE STUDIES

## 5.1. Natural regeneration of even-aged beech stands at different shelterwood densities

### 5.1.1 Introduction

Most of the beech forests in the Czech Republic lie in protected areas, though; it is the most important commercial broadleaved tree species, playing an important role in conversion of extensive spruce monocultures (DUŠEK ET AL. 1985, cited by JURÁSEK 2000). The species is traditionally reproduced by natural regeneration based on the frequency of mast years, which occur every 4 to 6 years in average and such frequency is said to be encouraged by a temperature higher than 30 °C from July to September of the prior year, although site index and high deposition of atmospheric nitrogen can also affect positively such frequency (ÖVERGAARD ET AL. 2007). Flowering and seed production of European Beech begin at about age of 40-50 (Wagner et al. 2010), and its pollen effectively disperses less than 250 m within forests (WANG 2001). Beechnuts commonly disperse by barochory, usually around 20 m (WAGNER ET AL. 2010), but can reach up to 125 m by zoochorous dispersal even introducing beech into stands of other species (KRAMER 2004). According to SKRZISZOWSKI AND KUPKA (2008), the quite strong growth rate of fine roots in beech seedlings during the first 4 years makes it appropriate for plantations. Additionally, for successful development, young plants need protection from parent trees against late frost, drought and high temperatures (Burley et al. 2004). Local high density of beech seedlings has a strong negative influence in their diameter growth and a smaller influence in height growth (COLLET, CHÉNOST 2006). According to WELANDER AND OTTOSSON (1998), beech seedlings preserve a bigger proportion of biomass in the shoot than in the root during the first year of life, which favors photosynthesis and supports a good adaptation to low light conditions, making the species suitable for regeneration under shelterwood. MADSEN AND LARSEN (1997) stated that, an increase in the canopy opening increases the potential for a variance height growth and sapling density of beech seedlings, while higher soil water content increases the regeneration growth and an increment of soil carbon content reduces the regeneration growth, possibly due to an accumulation of raw humus, which results in poor nutrient supply. Similarly, under appropriate supply of water in the soil and sufficient fertilization, a relatively open canopy can generate convenient conditions for a large increase of beech seedlings growth (MADSEN 1995). There is also a relation between different provenances of beech in Europe and their response to soil water content, so that provenances from lower latitudes show higher increment in growth under high soil water content conditions, as an adaptation to a longer vegetation period and higher precipitation (NIELSEN, JORGENSEN 2003). Different studies showed that although beech possesses mechanisms for responding to water deficits, it is not a drought-tolerant species (FOTELLI ET AL. 2009). When competition is strong, beech trees show a high sensitivity to water balance whereas, at low competition level, trees react positively to high temperatures (CESCATTI, PIUTTI 1998). Seedling growth has also been related to light availability and root density of old beech (WAGNER 1999). One of the problems associated with the economic profitability of beech forests is the presence of red heartwood, regularly occurring in older stands, while in trees up to 80 to 90 years old (without fork formations and mechanical injuries) do not bear much risk of presence of red heartwood (KNOKE 2003).

The aim of this study was to evaluate the annual progress of established cohorts of natural regeneration in managed stands, verify the occurrence of annually established secondary cohorts, and to give an approach to the assessment of soil moisture and its influence on natural regeneration development.


## 5.1.2. Materials and methods

In 1980, five 1 ha permanent research plots (PRP) were established in stands of even-aged beech forest in the NNR, in order to analyze their stand structure and production. In 2004, four of these plots (plots 1, 3, 4 and 5) were used again for a broader evaluation of their structure (Table 2), involving the measurement of dbh (diameter at breast height), total height, crown height, species, social status (dominant, codominant, subdominant and less than 20 m) and horizontal distribution using the Fieldmap equipment (IFER Monitoring and Mapping Solutions Ltd.). The evaluation of horizontal distribution included the description of crown projection of each live stem by measuring a minimum of five cardinal crown radii per tree. For the study of the natural regeneration, a regular matrix of 20 x 10 m was set throughout the extent of each 1 ha PRP. Each intersection of the matrix (marked with a wooden stake) indicates the corner of a $1m^2$ square subplot, in which the quantification of seedlings and survival according to cohorts (generations) was registered repeatedly at the end of the vegetation period in 2004, 2005, 2007, 2008 and 2009. Each cohort found in this study is defined by the year of the seed production, which is one year before the germination of seedlings. In the first year of the study we distinguished only between 1-year-old seedlings and older ones (originated mostly from the mast year in 1995). The same year, we registered the description of the ground cover by determining the percentages of woody regeneration, herb vegetation, coarse woody debris, stones, mineral soil, soil covered with litter fall, roots, roads and moss, as well as the total thickness of holorganic and Ah horizons (double measurement in the opposite corners of the plot), and distance to the nearest tree. The coarse woody debris of more than 10 cm of diameter was classified according to the level of degradation in the following way:

 1) wood hard, branches present, rind on more than 50% of the surface, profile oval
 2)  wood hard, branches present, rind on less than 50% of the surface, profile oval
 3) soft, cut 1 - 5 cm, profile oval
 4) soft, small fragments missing, profile elliptic
 5) soft, contours deformed, profile elliptic
 6) soft, reduced, no contours, wood covered by soil


In 2009, the fifth of the PRPs, initially established in 1980 (PRP 02) was also included in our research for the study of stand structure and natural regeneration, and therefore, for this plot, we only registered two cohorts (cohort 2008 and older than 2008). The silvicultural system predominant in the area is shelterwood, although on two PRP (03 and 04), a combination of shelterwood and border cutting is carried out.

Due to the lack of normality in the distribution of the data, it is necessary to include in the calculations the Kruskal Wallis non-parametric method to determine the degree of statistical difference among samples, and the Spearman correlation coefficient to verify correlations between variables. The Statgraphics Centurion XV software was employed for the calculations of statistical values.


*Measurement of Soil Moisture*

In 2008, plot 04 was chosen for the measurement of soil moisture in selected subplots, with the intention to determine the existence of differences of soil moisture conditions under diverse canopy covers, taking into account the presence of a large gap in the canopy of this plot. The instrument used was the gypsum block sensor KS–D1 (Delmhorst Instrument Co.). Eight different regeneration subplots were chosen for the establishment of the gypsum blocks; three subplots under canopy, three subplots near the gap and two subplots in the border of the gap. The center of the gap was chosen as the ninth point for the establishment of the gypsum blocks, though it was not registered the woody regeneration in that point. The gypsum blocks were placed 20 cm under the soil, considering the depth at which young beech seedling roots can reach. The sensor readings were registered once a week, in the morning, from the beginning of April to the end of September of 2008, to complete a whole vegetation period.

The readings of the sensor normally range from 4 to 100 and can be converted to available soil moisture (%) using a figure provided by the manufacturer. For the conversion of all readings registered in the study area, it was necessary the construction of an equation that could give more precision to the obtained values. Using Microsoft Excel, an X-Y graph with specific values from the figure was created and a polynomial trend line, order 5, was added to the graph. The displayed equation for the trend line was used for the conversion of the readings.


### 5.1.3. Results

Considering the PRP's 01, 03, 04, 05, besides beech in the population of woody regeneration of the research plots, there are other 10 species with a minimum presence, which are: Spruce, Maple, Hornbeam, Birch, Larch, Rowan, Willow, Fir, Pine, and Poplar, that account for 1.24, 0.56, 0.34, 0.28, 0.28, 0.17, 0.17, 0.17, 0.11 and 0.11 thousands per hectare in average, respectively. Most of them were registered after 2007 and emerged at the border of the stand. In 2009, these species represented the 2.6% of the total woody regeneration in the four PRP's. This concurs with the proportion of species in the canopy, since beech represents the 99.2% of the canopy individuals in the plots of the study, regardless of the existence of patches of other species in the surroundings of the area.

Table 2. Stand characteristics of permanent research plots included in the study, after evaluation in 2009. Some of the data are taken from Korejtko (1997).

| PRP | Forest stand | V | G | N | ρ | D mean | H mean | Crown Cover (%) | Forest type | Age (years) | Elevation (m.a.s.l.) | Exposure slope (%) |
|-----|------|--------|-------|-----|------|------|------|-------|------|------|------|-------|
| 01 | 436C17 | 477.49 | 21.55 | 65 | 0.46 | 63.5 | 41.0 | 53.55 | 4B1 | 187 | 440 | E – 15 |
| 02 | 32D15z | 684.03 | 42.21 | 306 | 1.21 | 40.9 | 28.4 | 87.37 | 4K3 | 174 | 490 | Plain |
| 03 | 434B17 | 800.64 | 37.41 | 116 | 0.82 | 62.8 | 39.9 | 76.71 | 4S4 | 197 | 450 | N – 20 |
| 04 | 434E17 | 605.41 | 28.22 | 90 | 0.62 | 62.0 | 40.1 | 59.26 | 4S4 | 192 | 460 | E – 17 |
| 05 | 436D17 | 575.99 | 27.76 | 110 | 0.63 | 55.7 | 39.3 | 64.77 | 4K3 | 176 | 440 | E – 15 |

*V – volume (calculated for timber above 7 cm of diameter over bark ($m^3$/ ha)), G – basal area ($m^2$/ha), N – number of trees (ind./ha), ρ – stand density, D mean – mean dbh (cm), H mean – mean total height (m), m.a.s.l. – meters above sea level

The total number of beech seedlings registered for plots 01, 03, 04 and 05 till 2009 (Table 3), shows an outstanding behavior of the regeneration of cohort 2003 in plot 1, with almost 300 thousand seedlings per ha during the first year (Fig 2). After five years of the study, the number of seedlings remaining from those 300 thousand/ha equals the initial number of seedlings of the same cohort in plot 04 (almost 200 thousand/ha), which was the second highest density among the four plots in 2004. The plots show a similar tendency of decrease for this cohort during the years, except for plot 04, which presents a higher decrease during the second year, placing it as the third highest density among the plots. These results do not concur with the number of seedlings older than 2003 (Fig. 3), given that in the last case the highest density is reached by plot 04, and plot 01 achieves the second place. As stated BíLEK ET AL. (2009), the comparison of the densities of both cohorts, evidences the negative effect of the presence of the older seedlings on the establishment of the newer ones.

For the year 2009, a recount of the stock of the research plots registered a reduction in the number of trees present in plots 01, 03, 04 and 05 due to harvesting or mortality; such reductions were equal to 30, 7, 18, and 6% respectively.  To evaluate the possible effect that removed trees could have on the survival of seedlings, we separated all subplots in two groups (one group of subplots for which the nearest tree was still the same, and one group for which the nearest tree changed). The first group averaged 90% of survival for the cohort 2003 during the last year and the other group averaged 87%, which led to an H = 0.22 and P = 0.64 in the Kruskal Wallis test, showing not significant difference.  Only 17 of the 196 subplots on 4 permanent research plots were included in the group of changed nearest tree subplots, and the small number of individuals in them made possible only the comparison of cohorts 2003 and 2007. For the last one, we also did not register significant difference between both groups (H = 0.59, P = 0.44).

The density of the two latest generations in their first year, cohorts 2007 and 2008, ranked between 0 and 5.2 thousands/ha for the first one and 3.8 and 16.9 for the second one, which is even lower than cohort 2006 with 9.0 – 75.4 thousands/ha. All these three generations are intermediate seed falls that did not reach initial number of seedlings as

in the full mast year 2003, which ranked between 78.1 and 298.8 thousands/ha for the research plots (Table 3).
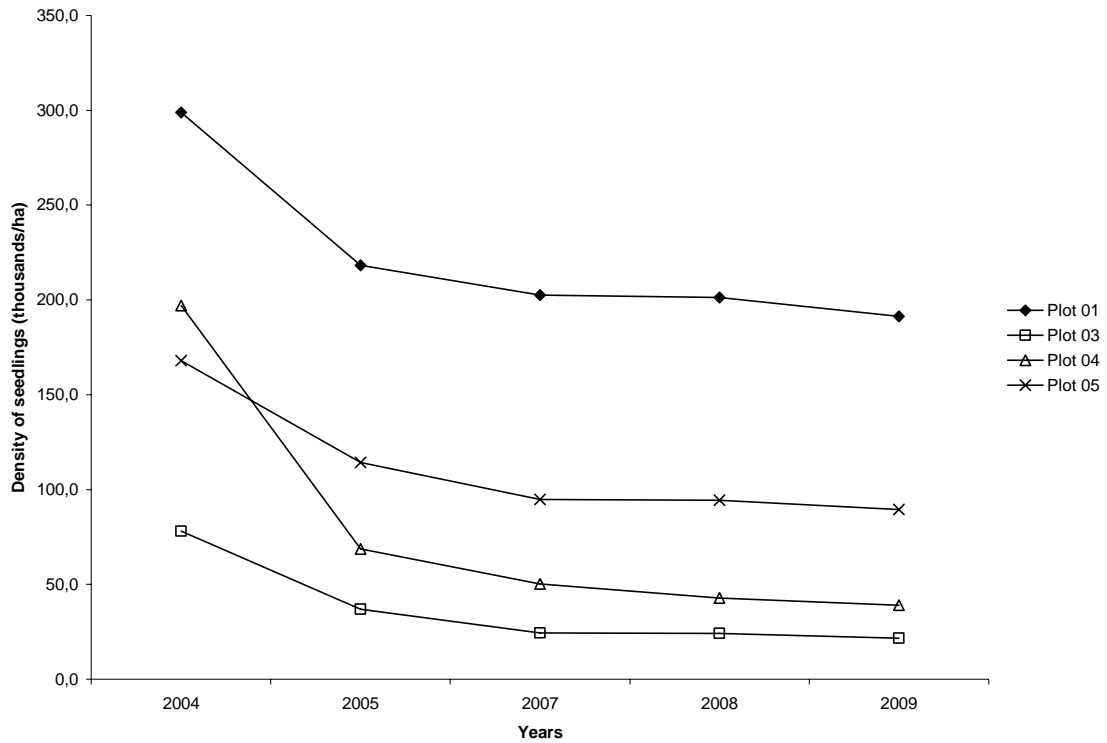


Fig. 2. Average density of beech regeneration (cohort 2003) in four
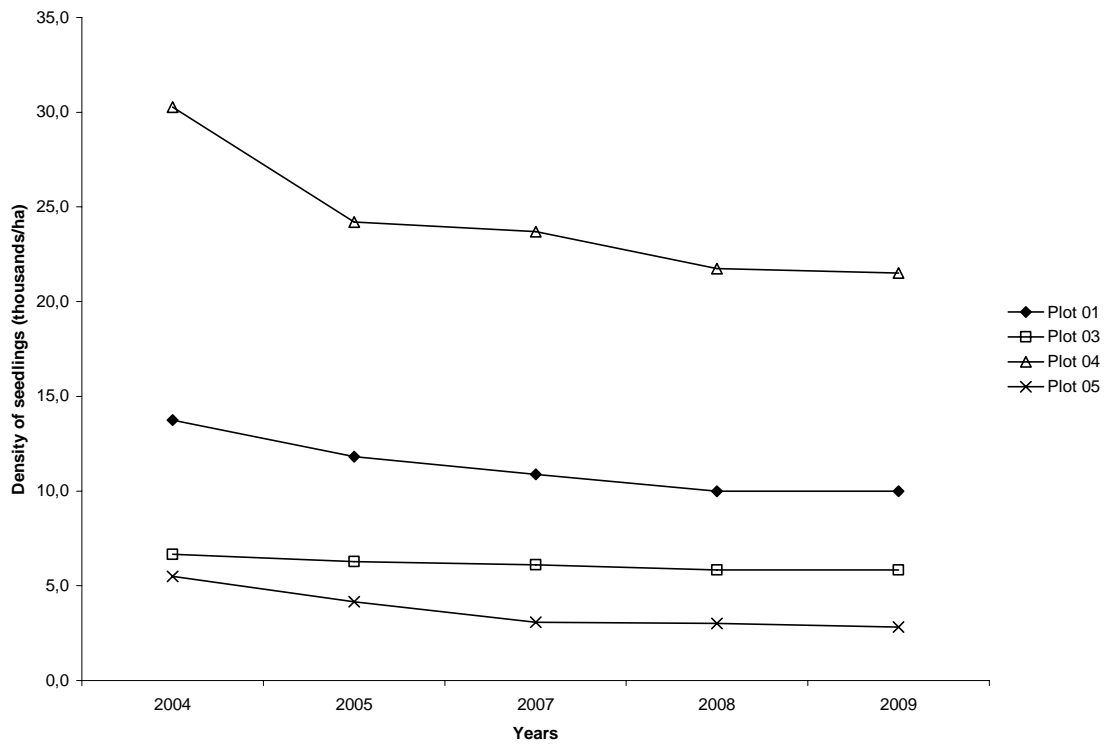


Fig. 3. Average density of beech regeneration (seedlings older than cohort 2003) in four PRP's

Table 3.  Average density of Beech seedlings in the managed plots (in thousands per hectare), and values for the Kruskal Wallis test.  The data showed till 2007 was calculated by Bílek (2009).

| Year of evaluation | Cohort | PRP 01 | PRP 03 | PRP 04 | PRP 05 | Kruskal-Wallis test: H | P-value |
|---|---|---|---|---|---|---|---|
| 2004 | Older than 2003 | 13.8a | 6.7b | 30.3abc | 5.5c | 26.70 | 0.000 |
| | 2003 | 298.8a | 78.1ab | 197.0 | 167.9b | 14.96 | 0.002 |
| 2005 | Olther than 2003 | 11.8a | 6.3b | 24.2abc | 4.2c | 12.58 | 0.006 |
| | 2003 | 218.2ab | 36.9ac | 68.8bd | 114.3cd | 21.40 | 0.000 |
| 2007 | Older than 2003 | 10.9a | 6.1b | 23.7abc | 3.1c | 24.57 | 0.000 |
| | 2003 | 202.6ab | 24.4ac | 50.3bd | 94.9cd | 19.03 | 0.000 |
| | 2006 | 64.8ab | 75.4cd | 9.0ac | 22.7bd | 58.76 | 0.000 |
| 2008 | Older than 2003 | 10.0a | 5.8b | 21.8abc | 3.0c | 17.93 | 0.000 |
| | 2003 | 201.4ab | 24.2ac | 42.8bd | 94.3cd | 22.04 | 0.000 |
| | 2006 | 47.7ab | 40.6c | 4.4acd | 18.4bd | 39.37 | 0.000 |
| | 2007 | 5.2ab | 0.6a | 0.0bc | 2.8c | 11.17 | 0.011 |
| 2009 | Older than 2003 | 10.0a | 5.8b | 21.5abc | 2.8c | 16.70 | 0.001 |
| | 2003 | 191.4ab | 21.7ac | 39.0bd | 89.4cd | 21.89 | 0.000 |
| | 2006 | 42.8ab | 30.3cd | 2.8ace | 12.6bde | 43.91 | 0.000 |
| | 2007 | 3.7ab | 0.3a | 0.0bc | 1.2c | 9.55 | 0.023 |
| | 2008 | 16.9abc | 3.8a | 6.6b | 4.5c | 15.48 | 0.001 |

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

The different generations of seedlings were analyzed separately.  The cohort 2003 registered a high mortality in 2005 (Fig. 4) especially in plots 03 and 04, where border cutting is performed (63 and 39% respectively), but from 2007, the mortality ranks from 1% to 15% in a very stable average year by year in all four plots. Only in plots 03 and 05, there is noticed a small change of almost no mortality by the year 2008, which resumes the following year.  The group of seedlings older than cohort 2003 also presents high mortality in 2005 (Fig. 4), but in this case the highest mortalities are in plots 05 and 04 (25 and 33% respectively). The plots experienced an unequal but very stable mortality during the years, with values from 0 to 7% yearly, although plot 5 had a very high mortality from 2005 to 2007 (30%), reaching 15% a year.  The values of mortality for cohort 2006 in the year 2008 were very similar to those ones in cohort 2003, where plots 03 and 04 also had the lowest survival, but in this case the mortality was still considerably low for the year 2009 (39 to 48% in the four plots), except for plot 01 with 11% of mortality in 2009.  The cohort 2007 also had elevated mortality for 2009 with 29, 50 and 50% in plots 01, 03, and 05 (plot 04 did not register any seedlings from that generation in 2008).
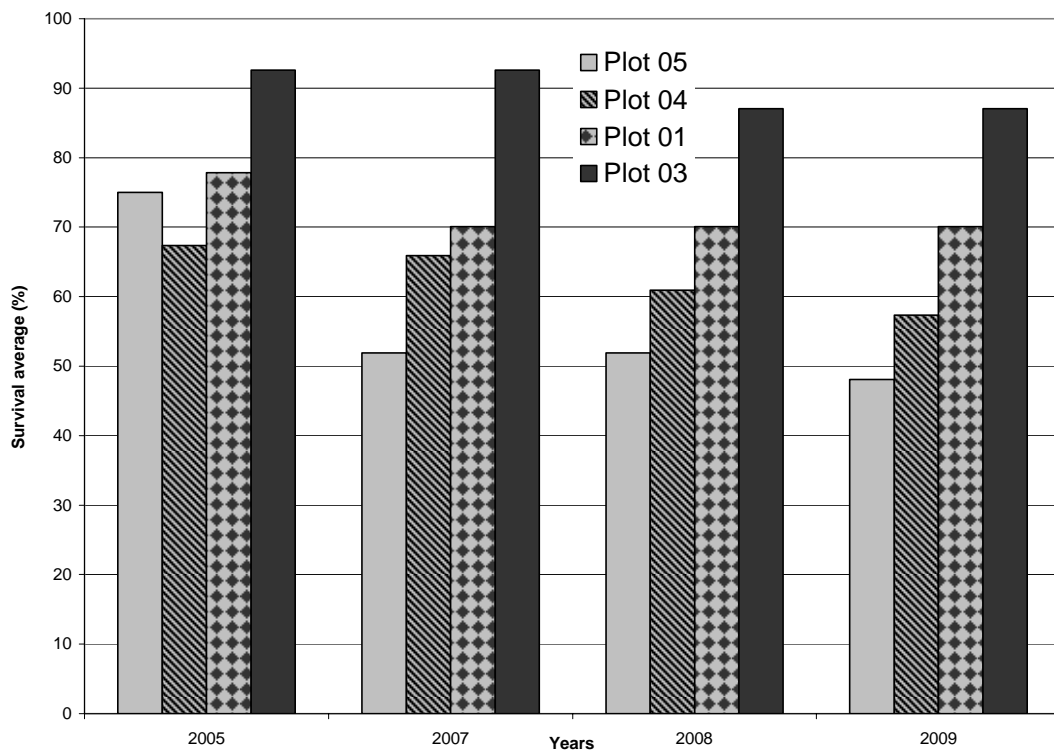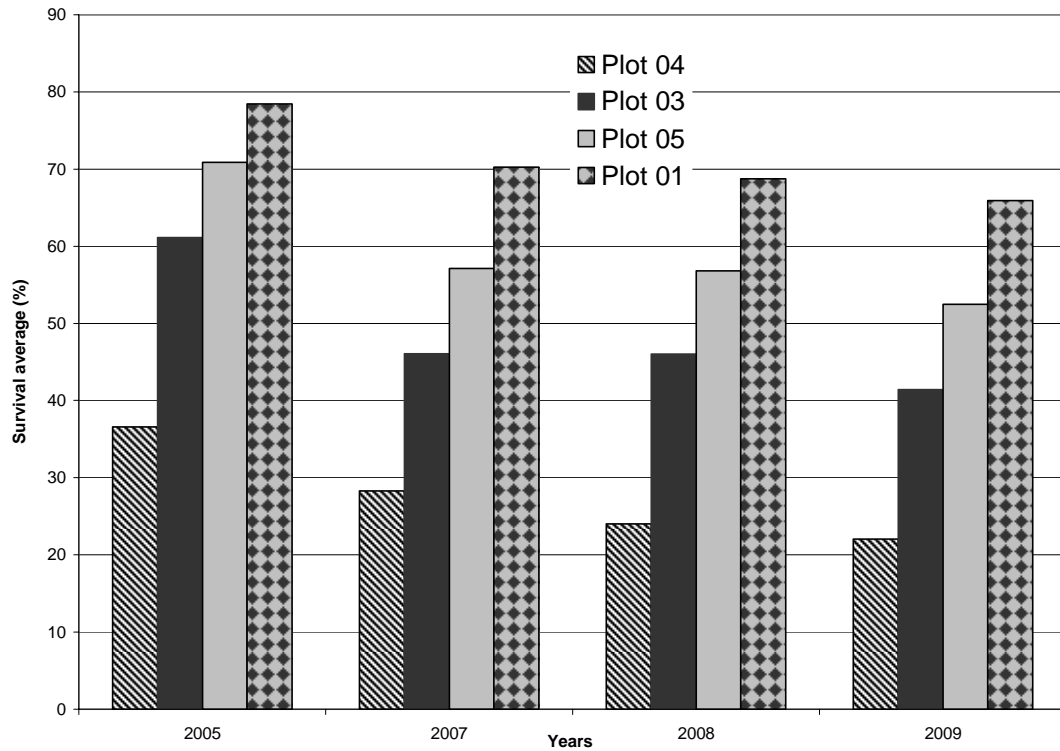
Fig. 4. Average survival of beech regeneration in cohort 2003 (up), and seedlings older than cohort 2003 (down) in four PRPs.
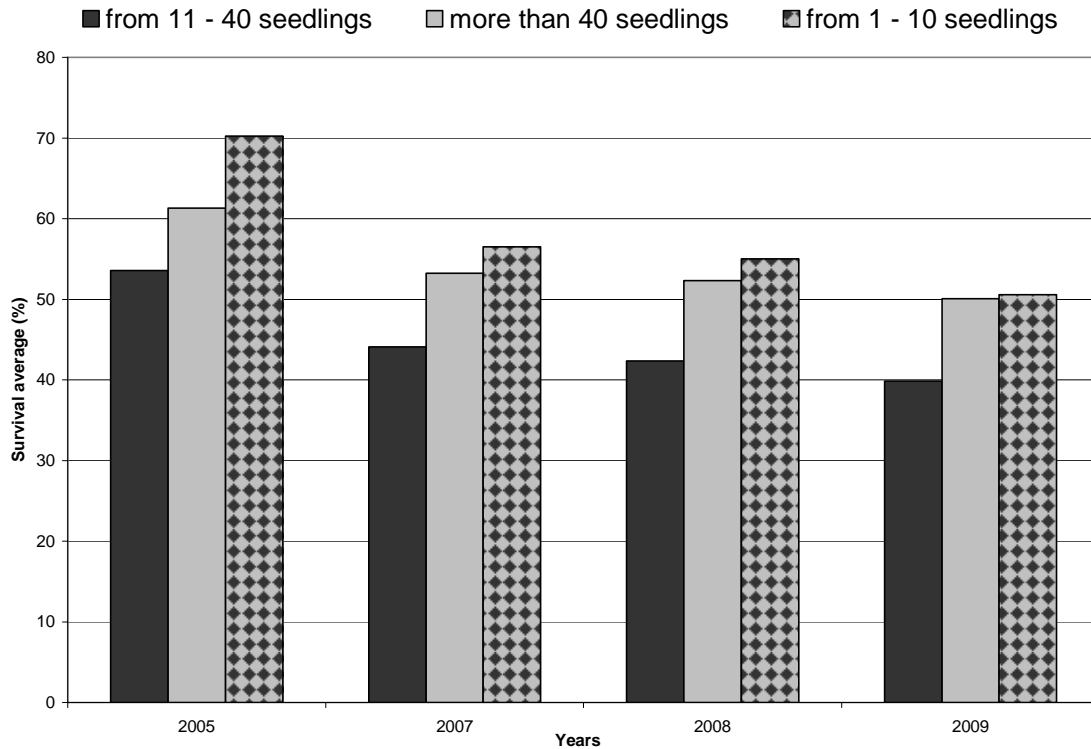
Fig. 5. Average survival of beech regeneration (cohort 2003) in four PRP's after the classification of subplots according to initial number of seedlings

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

An analysis of Spearman correlation among ground cover attributes and survivals showed the following results: for seedlings older than 2003, the survivals showed a negative correlation with the percentage of litter in years 2005 ($R = -0.2911$, $P = 0.0208$) and 2009 ($R = -0.2955$, $P = 0.0406$), and with the percentage of roots only in 2007 ($R = -0.3289$, $P = 0.0156$); for cohort 2003, the survivals proved negative correlation with the percentage of litter in years 2005 ($R = -0.1686$, $P = 0.0438$) and 2007 ($R = -0.2563$, $P = 0.0031$); for cohort 2006, the percentage of stones and deadwood showed negative correlation with the survivals only in year 2008 ($R = -0.1855$, $P = 0.0430$ and $R = -0.2032$, $P = 0.0267$ respectively); lastly, for cohort 2007, the ground vegetation showed negative correlation with the survivals in 2009 ($R = -0.4789$, $P = 0.0282$).

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Table 4. Average values of ground cover attributes for the managed plots.

| PRP | Thickness of Ah (cm) | Regeneration (%) | Litter (%) | Herbs (%) | Deadwood (%) | Min. Soil (%) | Stones (%) | Roots (%) | Moss (%) | D (m) |
|---|---|---|---|---|---|---|---|---|---|---|
| 01 | 4.3 | 12.00 | 60,4 | 23.0 | 1.7 | 1.5 | 0.2 | 0.3 | 0.57 | 4.3 |
| 02 | 8.0 | 0.14 | 92,8 | 0.3 | 4.1 | 0.1 | 0.8 | 0.5 | 1.27 | 2.0 |
| 03 | 4.0 | 6.50 | 64,8 | 19.9 | 1.5 | 0.4 | 6.7 | 0.1 | 0.22 | 5.3 |
| 04 | 4.5 | 11.40 | 70,3 | 13.8 | 4.0 | 0.2 | 0.5 | 0.2 | 0.02 | 4.1 |
| 05 | 4.1 | 7.20 | 54,2 | 34.9 | 1.3 | 0.2 | 0.3 | 0.8 | 0.65 | 3.8 |
| Kruskal Wallis H | 88.88 | 76.30 | 40.78 | 64.30 | 75.07 | 20.48 | 37.50 | 3.33 | 17.73 | 58.66 |
| P-value | 0.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.505 | 0.001 | 0.000 |

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

The density of seedlings in plot 02 represents a remarkable difference with the other four plots, since the values for new beech seedlings (cohort 2008) and older ones are 0.8 and 2.1 thousands per hectare respectively (in 2009 the density of plots 01, 03, 04, 05 was 3.8 – 16.9 and 58.1 – 247.8 thousands/ha for one year old seedlings and older ones respectively - Table 3). However, apart from the big differences in the main tree stock (Table 2), the soil cover of the plot 02 has proved to be statistically different from the rest of the plots (Table 4), specifically considering the humus thickness, percentage of litter and percentage of deadwood. In those three cases the comparison of old plots (01, 03, 04 and 05) showed no significant difference, while the inclusion of the plot 02 in the process changed the result and revealed significant difference; in fact, the pairwise comparison of plot 02 with each of the other plots maintained a significant difference. The reason is that the cover of humus and deadwood (8 and 4% in plot 2) doubled the average in the rest of the plots, while the percentage of litter reached 93% in plot 02 and the rest averaged 62. In the other hand, the evaluation of the other soil cover attributes had diverse results; the percentages of mineral soil, stones and vegetation showed significant differences including plot 02 in the process and without it, but the percentage of roots did not denote such differences among or between any plots. The case of the ground vegetation cover has a particularity, since the value for plot 02 averages 0.3% compared with values of 13.8 – 34.9% of the rest of the plots, which is still an important difference regardless of the variability among the whole group of plots. The distance to the nearest tree in plot 02 (2 m in average) was doubled by the other plots and the group of five plots showed statistical difference, though the pairwise test showed differences in most of the combinations.

Among the different factors of soil cover registered for the plot 02, the only ones that represented a significant correlation with the cover of regeneration were litter (R = - 0.4187, P = 0.0028) and vegetation (R = 0.4875, P = 0.0005). Comparing the same soil cover factors with the absolute values of regeneration of young and old beech seedlings the ground vegetation cover maintained a positive correlation with the old seedlings (R = 0.5459, P = 0.0001), while the young ones only showed weak correlation with the presence of roots (R = 0.2999, P = 0.0322).

Table 5. Summary of available soil moisture data registered in the specific subplots.

| Subplot reference | Location in plot | Maximum available soil moisture (%) | Minimum available soil moisture (%) | Average available soil moisture (%) |
|---|---|---|---|---|
| G5 | near gap | 88.75 | 11.46 | 64.64 |
| H5 | near gap | 88.20 | 0.69 | 64.82 |
| F4 | near gap | 89.03 | 43.09 | 84.21 |
| F5 | border gap | 89.03 | 27.66 | 79.02 |
| H4 | border gap | 88.47 | 0.34 | 64.89 |
| E3 | under canopy | 88.47 | 0.00 | 63.85 |
| F3 | under canopy | 89.59 | 36.47 | 77.31 |
| G3 | under canopy | 88.47 | 0.07 | 58.68 |
| X | center gap | 89.03 | 1.04 | 70.15 |
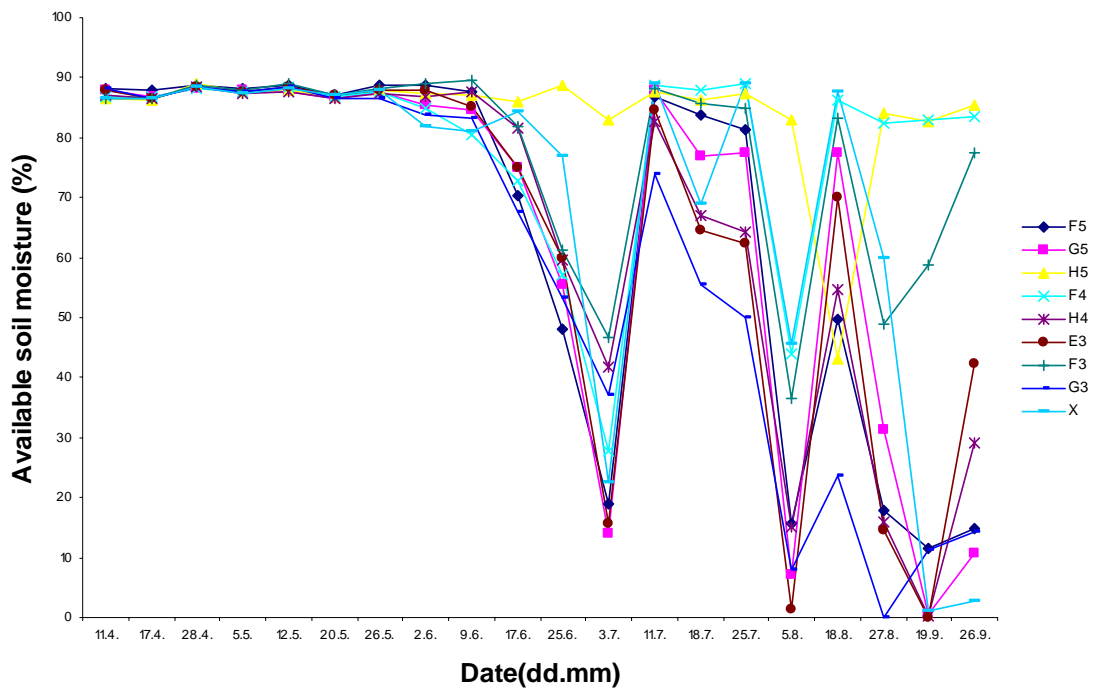


Fig. 6. Available soil moisture (%) in particular days of the year, and specific subplots (2008).

The polynomial trend line obtained from the figure of available soil moisture against the sensor readings had the following equation:

$$y = 5E\text{-}10x^6 - 1E\text{-}07x^5 + 1E\text{-}05x^4 - 0,0009x^3 + 0.03x^2 + 0.5982x - 0.5531$$

Where:

    x = Sensor readings
    y = Available soil moisture (%)

Soil moisture readings did not register changes among the subplots during April and May, where low temperature and precipitation kept soil moisture at the highest values. Increasing temperatures started to affect the soil moisture values only at the beginning of June. After one month, environmental conditions lead most of the subplots to reach 50 to 20% of soil water availability. Substantial levels of precipitation increased soil moisture to the highest levels in some of the subplots in the middle of July. Two additional minimums occurred at the beginning of August and middle of September. There is much perception of irregularity in the responses of the subplots to environmental changes. Plots with high soil moisture loss during a dry period may not lose proportional levels in the following ones, and vice versa.

The statistical evaluation of the obtained soil moisture data did not find important relationships. The group of nine points did not prove dissimilarities for the measurements during the year. From all the possible combinations in the pairwise evaluation, only three combinations proved significant differences. Likewise, after averaging the four groups of data according to the position of the measuring point inside the forest, none of the combinations was found significantly different. Similarly, a series of Spearman Rank correlation comparisons did not prove statistical correlation to the 95% of probability when comparing the averages, minimums and maximums of soil moisture availability in the measuring points with the survivals of the different cohorts from 2005. The comparison to the percentage of ground vegetation of the soil cover and depth of humus of the measuring points did not reveal correlation as well. The additional analysis of correlation between absolute values of beech seedlings of every cohort from 2004 and soil moisture values also fail to prove possible statistical correlation. Though it was not possible to verify similarities inside the groups of subplots statistically, the total count of seedlings by 2009 showed evident differences among groups. Under canopy spots had 8 seedlings in average, while near gap ones had 17 and border of gap 2 seedlings in average.


## 5.1.4. Discussion

The survival of seedlings in cohort 2003 during these five years shows a very important impact of the survival at the second year of life. In 2005, the registered mortality could indicate a strong struggle for adaptation to climatic conditions, possibly aggravated by an important damage caused by aphids; besides, the sharing of space between two big groups of seedlings (cohort 2003 and older ones) would definitely favor the older ones by virtue of a better adaptation and strength. The preservation of a low and very constant rate of mortality after the second year of life, regardless of a degree of mortality in the beginning, strengthens the theory that after the second year of life the seedlings have overcome a quite difficult stage, after which the level of adaptation reduces the mortality ratio independently of the treatment or structure of the main stand. Even when comparing groups of subplots with different initial number of seedlings, it is possible to notice a clear difference between the second year survival and the following years. The highest mortality registered in plot 04 by the second year of life may be related to the very abundant advance regeneration present there (possibly caused by the large size of gaps and micro gaps), that can represent a restraint for new seedlings in their search for resources. It is unclear the reason for the kind of mortality suffered by seedlings older than cohort 2003 by year 2005, but it is likely to be related to the damage caused by small herbivores. The persistent correlation found between the

percentage of litter and the survivals of cohort 2003 and older seedlings is an indication of how locations with inadequate fertility, soil moisture and/or illumination can restrict the development of regeneration and ground vegetation, which leaves space mainly for slowly decomposing layers of litter.

The behavior of the regeneration in plot 02 is a clear evidence of the great effect of density on the establishment and development of seedlings under closed canopy. The almost absence of individuals of regeneration of any species in an area with a stand density up to 2.5 times higher than the rest of the plots, where the canopy absorbs almost the whole amount of direct solar radiation during the growing season, and the average distance to the nearest tree doubles the values found in the other plots, is even more revealing if we realize that most of the very few seedlings registered in the plot germinated at the border of the stand, where the availability of light increases sharply. Although, a negative significant regression between canopy openness and mean density of beech seedling has been described from other sites (MODRÝ ET AL. 2004), a range from 10-40% of relative light intensity is considered to be optimal conditions for enough number and sufficient morphology of beech seedlings (NICOLINI ET AL. 2001, WAGNER AT AL. 2010). The depth of humus in plot 02 is quite superior to the other plots perhaps because of the lack of slope and the high intensity of leaf fall coming from the canopy that, giving the deficit of light, has a low decomposition rate. It is understandable that the high stand density affects greatly not only the amount of light reaching the ground, but simultaneously the area of land available for the seedlings, which can result in an increment of competition for soil water from the neighboring trees. Nevertheless, it would be very interesting to precise differences between soil water content availability in plot 02 and the other plots, since the existence of seedlings around the borders, where light is higher but the density is not different, could indicate that availability of light is a bigger limitation for seedlings that the supply of water.

The number and distribution of seedlings in the research plots 01, 03, 04 and 05 is sufficient to assure the natural regeneration of the stands. Nevertheless, in spite of the fact that even after a long period of suppression, height growth of beech seedlings increases following each canopy disturbance (COLLET, CHÉNOS 2006), seedling banks formed under given conditions are not stable and require additional improvement of microsites. The key to the regeneration improvement lies greatly in the kind of management and density of the stand. The explanation of why in plot 04 a large proportion of seedlings older than cohort 2003 get to heights bigger than 2 m, is still unclear. Even though, the large gap at one side of the plot is bigger than any other gap in the research plots, plots 01 and 05 also have similar canopy cover, though more disperse. For the rest, the density of stems and crown cover has at least proved to be a constraint for regeneration when it rises to high values.

Though water availability must have an important impact in the development and survival of the different cohorts, the low predictability of its manifestations displayed around the spots and through the period of measurements makes it very difficult to identify preferable conditions. However, regardless of the small size of the sample, there was clear indication that differences in location under the canopy cover per se can have an effect on the number of seedlings. The numbers would indicate that the more favorable protection of the canopy from total exposure could be specified to narrow strips next to the border of the gap. Nevertheless, the count of seedlings at the center could contradict this statement. Comparisons between the lowest soil water availability

that the spots reached during the period showed that subplots with the highest number of seedlings older than cohort 2003 could get close to the lowest registered value for the total of subplots (around 20%), but they also could get medium values in the first dry event and lower in the next one. Mixed results were found in the rest of the spots. There is then no indication that very low soil water content, independently of other factors can hinder appreciably the tree regeneration.

## 5.1.5. Conclusions

None of the soil cover attributes shows a clear effect on the survival of seedlings; regeneration under the shelter of parent stand reduces the competition of herbal vegetation and other than shade-tolerant tree species; full stand density prevents the establishment of any kind of regeneration. Although the highest mortality rates were observed only in the first 3 years of life of the regeneration, even after 5 years the stand cannot be considered as fully established. Seedlings under different levels of soil water availability and variations during the growing season can manifest different levels of survival and germination. The level of canopy cover of a particular spot can be perceived as an indicator of seedling density. Spots under canopy but with advantageous closeness to a gap may offer better conditions for seedling establishment.

## 5.2. Natural regeneration in unmanaged "near nature" forest stands

### 5.2.1. Introduction

The ecological benefits of the appropriate nature management of beech forests have been defined. According to Willner et al. (2009) there are 110 understorey species closely associated to European beech forests. The highest number of beech forest species is found in the Southern Alps and adjacent regions, and species numbers decrease with increasing distance from these regions. Considering only narrow-range species (species present in <10 regions) secondary maxima are found in Spain, the southern Apennines, the Carpathians, and Greece. Distance to the nearest potential refuge area is the strongest predictor of beech forest species richness. Rot holes in beech trees are important microhabitats for epiphytes to be preserved. Slow growing trees of different ages and sizes, under interaction of fungus *Psathyrella cernua* are found to be a key combination in the creation of this microhabitat (Fritz & Heilmann-Clausen 2010). Correspondingly, an important diversity of bryophyte species, some of them threatened, were reported in old-growth beech stands in the central Balkans in relation with the presence of deadwood of different stages of decay as habitat (Sabovljevic et al. 2010). Bark-strip from red deer *Cervus elaphus* does not appear to be driven by nutritional needs, but it may help deer in improving digestion efficiency by parasite protection due to its content of tannin (Saint-Andrieux et al.2009). These are few examples of how biological diversity inevitably interconnects species in the ecosystem and justifies its absolute conservation.

Specific light requirements of beech link the species to ecological dynamics. It is known that beech seedlings have the capacity to increase height growth following a canopy disturbance even after a long period of suppression (Collet & Chénos 2006). According to Madsen and Larsen (1997) larger canopy openings show higher variance in height growth and higher sapling density of beech seedlings. However, after canopy opening, a larger vulnerability to cavitation during the first year could limit stomatal opening and therefore the ability of beech saplings to use the available light for photosynthesis and could therefore partly explain why the growth increase was delayed to the second growing season after canopy opening (Caquet et al. 2009). Gap characteristics and presence of beech under different gap sizes are explained by Gálhidy et al. (2006), with the analysis of two different sizes of gaps (35-40m and 10-15m in diameter) of beech forests in Hungary. It was found relative light intensity values lower in small gaps than in big ones, while the center of both kinds of gaps registered similar soil moisture levels. An increased number of herbaceous species in gaps was characterized by the presence and specific location of the species according to different requirements of light and soil moisture. A bigger density of beech seedlings in small gaps was explained by limited seed dispersal. Different gap sizes are exposed in beech forests of Slovenia and Croatia with 10 years old large gaps (700-2000m$^2$) and small ones (200-500m$^2$) in old-growth communities, that showed five times more total regeneration density (6.2 sedlings/m$^2$) and higher beech regeneration in the Slovenian site, but more ground vegetation density and density of silver fir (*Abies alba*). In every case, both species preferred under canopy or close to gap edges establishment, with lower radiation levels. Beech seedling densities did not have significant variation on microsites, but height growth was higher in presence of higher radiation. It was concluded that light conditions did not influence all

tree regeneration and ground vegetation factors, but under similar stand site conditions a larger presence of herbivores could affect total vegetation densities (Dusan et al. 2007).

The aim of the study was to evaluate the differential development of seedling cohorts under unmanaged stands, and to broaden the spectrum of near nature stands by comparing prior results with the ones obtained from an additional plot of similar characteristics.


## 5.2.2. Materials and methods

The permanent research plots (PRP "Virgin forest" 06 and 07) were established in 2005 for the study of the stand and regeneration structure, both plots are 100 × 100 m (1 ha) of area, and represent 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). In 2007 a third PRP was established in the forest stand 436B17, forest type 4K3 and forest age 180. The topographical digitalization of the plots included the mapping of 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, tree status (living, dying or dead), and social status (dominant, codominant, subdominant, less than 20 m, and broken tree). We also mapped the crown projection of each live stem by measuring a minimum of five cardinal crown radii per tree. The data distribution was not normal.

Smaller research plots (RP) were selected within permanent research plot (PRP) 06 (inside small gap, under canopy and inside big gap), within PRP 07 another two research plots (RP) were selected (under small and under big gap). In PRP 08, RPs were established in similar locations to PRP 06 (inside small gap, under canopy and inside big gap). A regular grid of 5 x 5 m was set inside each RP. Sampling plots 1.5 x 1.5 m (SP) were established in each intersection of the grids.

The description of the ground cover was registered by determining the percentages of woody regeneration, herb vegetation, coarse woody debris, stones, mineral soil, soil covered with litter fall, roots, roads and moss, as well as the total thickness of holorganic and Ah horizons (double measurement in the opposite corners of the plot), and distance to the nearest tree. The coarse woody debris of more than 10 cm of diameter was classified according to the level of degradation in the following way:

1) wood hard, branches present, rind on more than 50% of the surface, profile oval
2) wood hard, branches present, rind on less than 50% of the surface, profile oval
3) soft, cut 1 - 5 cm, profile oval
4) soft, small fragments missing, profile elliptic
5) soft, contours deformed, profile elliptic
6) soft, reduced, no contours, wood covered by 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).

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. Statgraphics Centurion XV software was employed for the calculations of statistical values.. For all analysis, results were considered significant when $p ≤ 0.05$.

The data evaluate in this study corresponds to the first remeasurement of the regeneration plots in PRPs 06 and 07 in 2009, and the first measurement of the regeneration plots in PRP 08.

### 5.2.3. Results

Table 6. Characteristics of the research plots (RP) within PRP 06, 07 and 08.

| 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 | Under 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 |
| I | 436B17/4a | 08 | Big Gap | 20 | 0,03 | N |
| J | 436B17/4a | 08 | Under Canopy | 20 | 0,03 | N |
| K | 436B17/4a | 08 | Small Gap | 15 | 0,02 | N |

Table 7. Average and median ground cover (%) on SPs.

| RP | 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 |
| I | 20 | Average | 2.25 | 6.50 | 37.10 | 0.58 | 51.68 | 0.65 | 0.28 | 1,03 |
| | | Median | 1 | 4.50 | 43.75 | 0 | 42.75 | 0.25 | 0 | 0,25 |
| J | 20 | Average | 0.63 | 3 | 4.43 | 0.15 | 86.93 | 0.78 | 0.20 | 3,93 |
| | | Median | 0 | 2.50 | 3.75 | 0 | 88.75 | 0 | 0 | 2,50 |
| K | 15 | Average | 34.40 | 1.20 | 3.10 | 0.03 | 60 | 0.23 | 0.47 | 0,57 |
| | | Median | 15 | 1 | 2 | 0 | 78 | 0 | 0 | 0 |

Table 8. Density of regeneration per ha for 2009.

| Species | RP A | | RP C | | RP D | | RP E | | RP F | | RP I | | RP J | | RP K | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % | N | % | N | % | N | % | N | % |
| *Fagus sylvatica* | 67246.38 | 92.06 | 12026.14 | 98.92 | 67171.72 | 91.47 | 58666.67 | 100 | 44000 | 99 | 21111.11 | 64.19 | 10000 | 95.74 | 77925.93 | 98.50 |
| *Carpinus betulus* | 0 | 0 | 0 | 0 | 5656.57 | 7.70 | 0 | 0 | 444.44 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Picea abies* | 5797.10 | 7.94 | 130.72 | 1.08 | 606.06 | 0.83 | 0 | 0 | 0 | 0 | 222.22 | 0.68 | 0 | 0 | 888.89 | 1.12 |
| *Larix decidua* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3555.56 | 10.81 | 0 | 0 | 0 | 0 |
| *Acer pseudoplatanus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sorbus aucuparia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 444.44 | 4.26 | 0 | 0 |
| *Abies alba* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2666.67 | 8.11 | 0 | 0 | 0 | 0 |
| *Pinus sylvestris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 666.67 | 2.03 | 0 | 0 | 0 | 0 |
| *Betula pendula* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3333.33 | 10.14 | 0 | 0 | 0 | 0 |
| *Salix caprea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1333.33 | 4.05 | 0 | 0 | 0 | 0 |
| *Quercus robur* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 296.30 | 0.37 |
| Total | 73043.48 | 100 | 12156.86 | 100 | 73434.34 | 100 | 58666.67 | 100 | 44444.44 | 100 | 32888.89 | 100 | 10444.44 | 100 | 79111.11 | 100 |
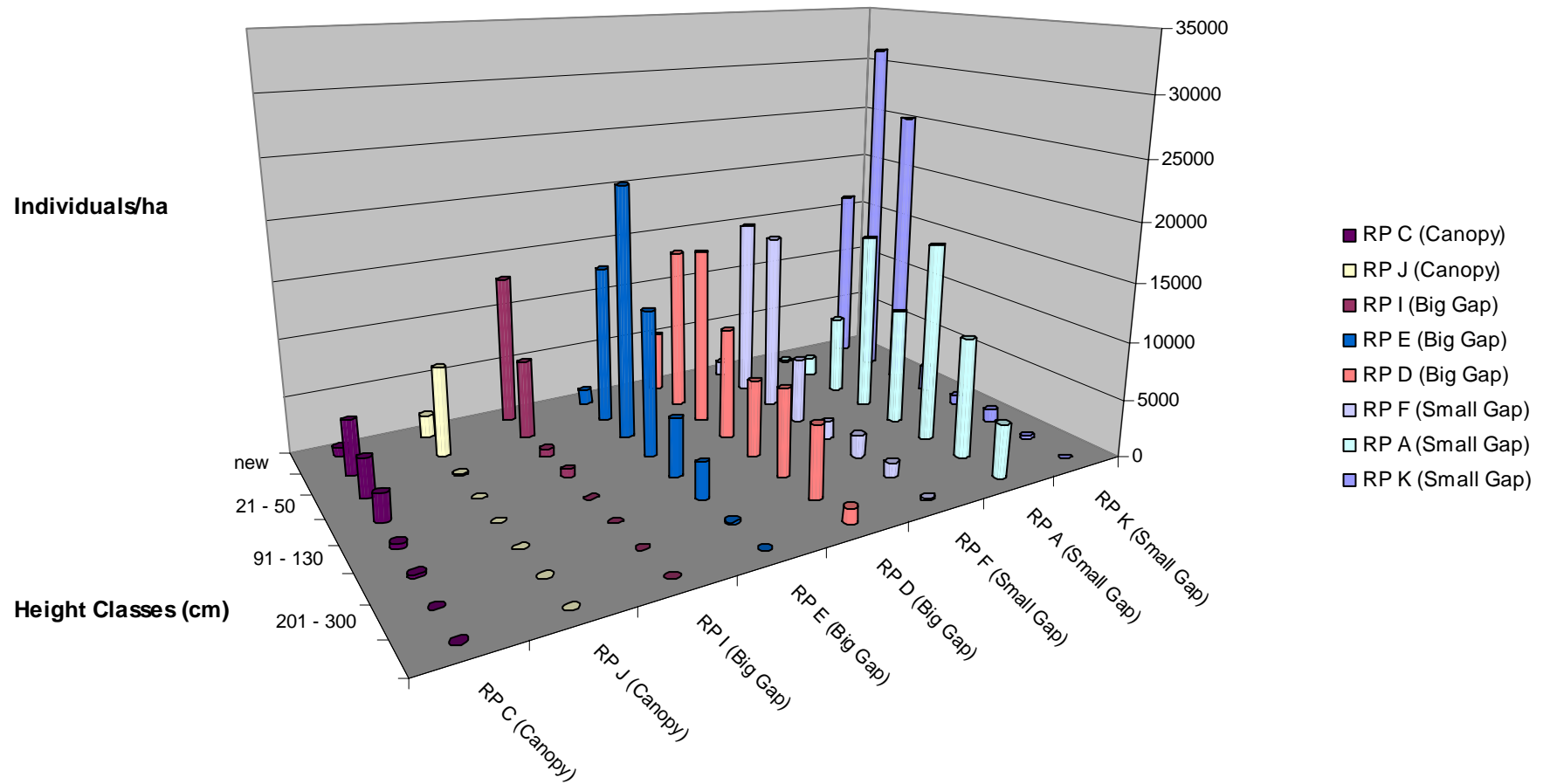
Fig. 7. Density of beech regeneration according to height class for 2009

RP I shows a notable difference in its CWD cover in comparison with the other RPs (Table 6). The 37.1%, of average in this RP comprises mostly diameter class 1, since diameter class 2 is present in only 15% of the SPs (mainly in decay classes 1 and 2). Only one of the twenty SPs in RP J registered the presence of woody debris in diameter class 2 (5% of cover), and two of the 15 SPs in RP K (1,5% and 8% of cover). Though the percentage of CWD is high in RP I and the size of the gap would suggest the presence of a bigger proportion of CWD in diameter class 2, this assumption does not occur. The origin of the gap is artificial and executed harvesting did not allow remaining of major quantities of larger woody debris.

As it could be expected, values of litter cover for all the RPs in PRP 08 remained high and very similar to the values recorded in RPs of equal classification according to canopy cover (Table 6). The development of the main stand trees and their constant production of litter cause the occupation of most of the free spaces left on the ground, even on slightly steep lands like this one. Where the percentage of regeneration and vegetation is low, the presence of litter represents the highest proportion. The Spearman correlation analysis for PRP 08 only noted significant negative correlation between regeneration and litter coverage in RP K

The regeneration cover had important values only in RP K (34.4%) (Table 7). Such value is comparable to the one in RP A, which is another small gap of the study. Nonetheless, individual values among the SPs in RP K ranged from 1.5% to 81.5% depending on the sizes of the seedlings or saplings. Its number of individuals ranged from 4 to 34, and an average of 18 individuals per SP, which is quite superior to the values of its neighbors (4.8 in RP I and 2.3 in RP J). The regeneration densities per ha for these three RPs increase almost exponentially in the order: under canopy, big gap, and small gap. This characteristic changes when observing the regeneration cover of the ground. Here, the superiority of RP K seems more decisive, since most of the seedlings in RPs I and J are too small to represent a larger proportion in the total ground cover. The total regeneration ground cover and total regeneration density of RP I do not evidence its greater species richness. With 7 species in total, of which 4 are not found in any other RP of the study, it is the highest species richness of the group. The variety of tree species in older stages growing next to the gap but outside of the PRP explains the great difference in the regeneration composition. The unusual species composition surrounding RP I reduces the proportion of dispersed and established beech regeneration, unlike its similar RPs D and E (Table 8). The unique appearances of rowan and oak in RPs J and K represent a small but valuable addition to the biodiversity of the area. After 4 years of development, beech total regeneration density in PRP 06 and 07 showed positive variation in big gaps and under canopy (3006.14, 15757 and 3953.67 individuals per ha of density increment in RP C, D and E resp.) and negative variation in small gaps (4058.62 and 31778 individuals per ha of density decrease in RP A and F respectively). In general, secondary species reduced their presence. Larch an Maple disappeared from the accounts, hornbeam decreased its density to almost the fourth of the values of 2005, and spruce suffered decrements ranging from 130 to 2300 individuals per ha.

Fig. 7 shows highest concentrations of beech regeneration in the lower height classes, especially in the classes 2, 3 and 4. The increment of individuals in the higher classes involves a more equal distribution among all the different classes or even a reduction in the lowest ones. A good example of that tendency is the comparison of RPs E, D and A.

These three cases, observed in that order, describe a positive development of the regeneration and a redistribution of proportions of individuals in the growth categories. The recruitment of new seedlings in RPs A to F only reached 1333 seedlings per ha (with the exception of RP D, with 5455 seedlings per ha). The values of recruitment in RPs I and K can be 10 to 12 times higher that those found in the other cases and, what is more important, the highest value (16296 individuals per ha) is found in a small gap (RP K). Though, the lowest regeneration concentration is found under canopy (RP C and J) there is a relevant difference in the dimensions of the existing regeneration. RP J concentrates almost all of its individuals in height class 2 and barely reaches class 3, while RP C even counts with presence in the class 6. RP I is the third lowest beech regeneration density (even though it is a big gap), and most of its seedlings are new recruitments. The high density found in RP K for height classes 1, 2 and 3 (by far the highest ones of the group), places it as the greatest beech density among all the RPs. This is more important if it is considered that the presence of regeneration individuals reaches even height class 7 on this same spot.

The comparison of soil cover properties between RP K and RPs A and F (RPs under small gap) by Kruskal-Wallis test proved dissimilarities only for K and A but not K and F, both for CWD and vegetation percentage. RPs C and J (under canopy) did not prove dissimilarities in any soil cover property. In the other hand, RP I (under big gap) proved statistically significant differences with D and E for regeneration and CWD percentage. Additionally, I and D proved differences in terms of mineral soil cover values.


## 5.2.4. Discussion

The very early development stage of RP I affects the influence of each of the soil cover elements evaluated on the regeneration. The sudden disappearance of the main stand structure and the liberation of space cause the immediate colonization of plant species that are able to establish their presence on the ground by any of their reproductive ways. Since most of the regeneration found in the place was new recruitments established after the origin of the gap, the most important factors affecting the presence of these seedlings are the availability of light and water and, evidently, the near presence of mature trees during the fructification stage or the activation of a dormant seed bank. The percentage of coverage of elements on the ground cannot be expected to play an important roll on the regeneration process at this stage, even when some of the values appear to be clearly dissimilar to the ones found in other spots, like an elevated percentage of the CWD cover. The density of trees in the main stand existing prior to the opening of the gap was similar to that found at RP J (under canopy). It is then understandable that the regeneration cover present on the first spot should be as low as the second one, and the establishment of new seedlings after the canopy opening did not find much competition from older individuals.

It is interesting to see that the density of new seedlings established under a small gap can be equal or higher than the one found under a big gap, as it is observed by comparing RPs I and K. The negligible level of recruitment found in the nearby RP J (under canopy) is substantially increased with the appearance of the small gap, but oddly, the recruitment density related to the canopy opening does not seem to increase with an additional availability of space. The difference of regeneration among these three RPs does not agree with what was found by Nagel et al. (2010), who described

similar levels of regeneration of beech and fir both under canopy and gap areas. The static observation of the current pattern described in RP K suggests the existence of optimal environmental conditions for the establishment and consolidation of beech seedlings till 50 cm height. After this point, the level of competition and demand of resources reduces sharply the number of remaining saplings that will occupy the limited space. Nonetheless, the great differences between RPs K and F (small gaps) do not allow the generalization of the first case. The differences in new recruitment population between RP K and the other two small gaps (A and F) were proved statistically significant by Kruskal Wallis. Even though, the lower levels of new recruitments in other gap spots can be related to a higher amount of individuals after height class 4, RP F does not keep such elevated densities in upper height classes and its total density is almost the lowest among gap spots. Its percentage of regeneration cover is also slightly lower than the one in RP K (26.35% against 34.4%). A correlation analysis between new recruitments and regeneration and vegetation soil cover in RP K did not show noticeable correlation. Under these circumstances, and assuming an equal distribution of beech seeds in all the study area, it is not clear the reason for the low recruitment of new seedlings in RP F, though a solar radiation measurement at the ground level could be the kind of description that would find real differences among small gaps related to the new recruitments.

The diversity of species found in RP I are known to have different ecological and silvicultural characteristics. Larch (L. decidua) is a pioneer species that can colonize after forest fires, wind storms and cattle grazing, and may form pure or mixed stands with Pinus cembra and Pinus uncinata, spruce, alder (Alnus viridis) or beech (Bachasson, 1982). It is a shade-intolerant tree that requires abundant light and space (Horsman, 1988). Since larch seedlings establish only on cleared sites, regeneration cuttings can favor natural regeneration for even-aged forests and selection forests. Plus, soil scarification is recommended to provide enough light to young seedlings. High transpiration rates of larch makes necessary to ensure sufficient availability of soil water (Fourchy, 1952). Though height growth of seedlings is fast, herb control is needed during the first 3 years of establishment (Cook, 1969). Larch seeds are viable for at least three years (Plants-Future, 2012). Spruce (P. abies) does not have a strong light demand or shade tolerance, though a common slow height growth in young stages is better under high light conditions (Siren, 1955; Dengler et al., 1982). Also, its seedlings can survive for decades under closed canopy, though when it grows in low light conditions it does not adapt well to an increment in light (Siren, 1955; Dengler et al., 1982). Svoboda et al. (2010) found 50 to 80% of spruce seedlings and saplings developed under coarse woody debris substrate that act as "nurse logs", and stated that extraction of dead wood to control bark beetle outbreaks can lead to low regeneration of spruce as it has been seen in close forest of the same region. Silver fir (A. alba) is believed to be susceptible to diseases and difficult for natural regeneration (forestry compendium, 2012). Understorey vegetation is an impediment for natural regeneration (Diaci, 1997), which is also considerably affected by high ungulate population, since fir advance growth is a preferred food for deer (Mayer, 1976). Scots pine (P. sylvestris) is a very shade-intolerant tree, able to colonize exposed sites by its far flying wing seeds (forestry compendium, 2012). Silver birch (B. pendula) is a fast-growing deciduous tree that rarely dominates in forest stands, though it can compete with beech and spruce. Birch is a light demanding species with adaptability to moist and dry sites, as well as low and high temperatures (forestry compendium, 2012), besides preferring larger canopy openings (> 50 m$^2$, but < 1000 m$^2$). Goat willow (S. caprea) is a very important

colonizing species in bare lands and forest gaps, that can improve soil by production of easily decomposed litter, and that is included in mixed plantings to encourage biodiversity. Though it appears sporadically, it is important as a soil protection agent (forestry compendium, 2012). It prefers full sun exposure, but tolerates partial shade (Smith, 2012).

Presence of understory herbaceous species, which can affect negatively certain tree seedlings, was reported by Van Couwenberghe et al. (2011) in soils with different levels of PH and canopy openness. Variation of both variables changed species diversity and relative abundances but did not eliminate herb presence. Nevertheless, Kelemen et al. (2012) suggest that creation of small gaps can decrease herb colonization chances. In this way, Huth & Wagner (2006) shows an important constraint of birch regeneration establishment by grass competition in gaps larger than 1000 m$^2$ in a spruce stand, though the seedlings established in the middle of grass cover show outstanding growth. The 6.5% of ground vegetation in RP I does not represent a limitation for the population of tree seedlings at this early stage, but the relative openness of the gap, due to a long shape and low heights at the border, it would not be unexpected to reach fast risky herb levels in the near future, considering that both regeneration and woody debris do not get to cover much of the ground.

Presence of this number and kind of species, naturally regenerated in the same site, has not been reported, and therefore it is not easy to compare these records with the ones found in other studies of the region. However, there are examples of some of the registered species coexisting in the same environment. Dekker et al. (2007), evaluating saplings till 13.7cm of DBH and 11.8m of height, found Scots pine and birch as two of the four tree species regenerating under Douglas fir (P. menziesii) monocultures. Birch was one of the two species with the best height growth rate. Birch was also described as having high slenderness and low leaf biomass, while pine had low slenderness and low leaf biomass. The failure of pine, in view of its poor height development and undergrowth, was considered an evidence of low competitiveness against other pioneers, which could be counteracted by liberation treatment or clump establishments of the same species. Paluch and Bartkowicz (2004) support the positive effect of old pines presence on the near abundance of pine seedlings, due to a lower sensitivity to the upper story and reduced ground competition. Van Couwenberghe (2010) included beech, birch and willow among eight broadleaved species in a study of gap partitioning, showing no indication of soil PH affecting the probability of presence of seedlings of the three species. Shade intolerant species, birch and willow, showed preference for the center of gaps, which also had higher probability for the presence of tall seedlings (height > 0.5m), while beech preferred gap edges. This can be related to the higher levels of light and soil moisture registered there (Gálhidy, 2006), affected by lower interception, higher precipitation and absence of living roots (Ritter & Vesterdal, 2006; Gray et al. 2002). Jonášová et al. (2006) described spruce, birch, fir and pine among nine species regenerating in coniferous plantations. Spruce discerned in its better abundance under canopy than in gap, unlike the other species, regardless of the best growth achieved by all species in gaps. The preference of Birch for large gaps was recognized. De Chantal et al. (2003) distinguished the slightly better aboveground biomass growth of pine in comparison to spruce as an early response to gap opening, which agrees with the light requirements recognized for the species. There is an obvious lack of comparable references to assert more certain possibilities for the future of the

gap. Nonetheless, the referred cases may strength or even broaden the already known characteristics of some of the species in question.

On the other hand, beech, as the dominant species, is a well known very shade-tolerant tree, normally benefited by partial overstory shade management techniques that reduce chances to regenerate more light-demanding associated species (Wagner et al., 2010). Szwagrzyk et al. (2001) highlighted the essential function of canopy openings for the regeneration of shade-tolerant species like beech, showing that permanent seedling banks formed only in plots where relative light intensities were between 9 and 15% due to the occurrence of canopy gaps in close proximity. In their study, only 2 out of 6000 seedlings reached more than 20cm height, which establishes an even much lower chance for sapling achievement. Nagel et al. (2010) found higher number of pole sized beech trees (> 5 cm dbh, < 20 m tall) in larger gaps of a beech-fir forest, which suggests more successful development of regeneration in larger gaps, though gap filling was due to advance regeneration and not from post-treefall establishment. The author states then that gap size didn't affect presence of both tolerant species because they were there already before gap formation. On the opposite side, fir appears to be more shade tolerant at pole size, capturing smaller gaps, due to an ability to survive longer periods of suppression than beech. It is then stated that more frequency and larger disturbances favor beech and other intolerants, but lower frequencies and smaller disturbances favor fir.

Herbivore presence can be an important hindrance to natural regeneration, especially affecting big gaps due to feeding preference (Kelemen et al., 2012). Herbivory browsing can reduce competition to herbs by tree regeneration consumption (Naaf & Wulf, 2007), which in turn can increase the regeneration constraint. Kenderes et al. (2008) found about 90% of the saplings (till 1m height) affected by browsing, due to an increment of moufl on (Ovis musimon), red deer ( Cervus elaphus), roe deer (Capreolus capreolus) and wild boar (Sus scrofa) population, in a beech forest reserve. The absence of 1m to 2m height saplings, and existence of 2m saplings in large gaps suggested that 2m saplings are outside reach of game. A 2-4 white-tailed deer (Odocoileus virginianus) popultion per $km^2$ was considered appropriate for the survival of red oak (Quercus rubra) regeneration above a browseline (137 cm seedling height) to keep its presence as a co-dominant species in a mixed forest. (Reo & Kart 2010).

The seedling densities found in RP I could be represented by a square with 6.7 m of side length, in which there is only 1 seedling of spruce, 3 of pine, 6 of willow, 12 of fir, 15 of birch, 16 of larch and 95 of beech. Under these competitive conditions, the few seedlings of spruce will react positively to the high intensity of light, but its growth rate will not be the best. Also, the very low amount of coarse woody debris on the ground will not help the seedling establishment. The slightly larger number of pine seedlings will react with better growth rate than spruce, also given the low density of total seedlings. Light conditions also favor willow's first establishment, and will probably enjoy full growth during the first years. The lower cover of understory vegetation will benefit fir seedlings, but their small density, shade-tolerance and general vulnerability in natural regeneration will reduce the expectative for further establishment. As a shade intolerant, birch does not show low seedling density (0.33 seedlings per $m^2$ is comparable to the 0.4 seedlings per $m^2$ that Huth and Wagner, (2006) referred to as a high density), though the size of the gap is at the limit of its requirements. Larch is another pioneer with acceptable seedling density. If herb cover does not hamper its

growth during the first three years it may progress satisfactorily. Beech, with the 64% of seedlings, is expected to reach a better development at the gap edges. Nevertheless, the persistence and growth at these edges will probably hinder the other species keeping and increasing the dominated territory. The size of the gap, absence of advance regeneration and reduced cover of woody debris may promote herb establishment, which would affect seedlings survival. This, added to game browsing and normal mortality would delay tree appropriation of the gap. In such case, it could be expected that the remaining established tree seedlings will gradually change the ground conditions, reducing the herb cover, giving way to new seedling generations and a slower recovery of the stand. A later tree count would prove a reduction in tree diversity and proportion of rare species, but the very interesting point will be to verify a possible movement of the line dividing the two forest types that allowed the seedling diversity present in the gap in the earliest stage.

## 5.2.5. Conclusions

The biological functionality that canopy gaps provide to old-growth forests like these ones increments its complexity and potential when a larger number of organisms are involved. Neighboring communities that seem permanently static evidence their constant competitive function when an addition of resources availability takes place. In this way, canopy gaps at the border of stand have a much higher possibility to modify their species composition than canopy gaps happening inside the stand. The lower the level of regeneration attained before the removal of canopy trees, the higher the potential that canopy gaps at the border of the stand have for species composition modification. Beech early seedling density does not seem to respond to differences in the size of the canopy opening. Repeated regeneration measurements have evidenced a reduction in the abundance of species different to beech under every kind of canopy covering, confirming its strong value as a dominance species.

**5.3. Stand structure evaluation of beech stands with different management history**

**5.3.1. Introduction**

Despite the fact that the Czech Republic belongs to the European countries with a smaller area (80,000 km$^2$), it has a great variety of natural richness, forests undoubtedly being one of the most valuable. A great variety of forest types determined in a relatively small area of the present Czech Republic is influenced by the vertical structure of the territory, by the geological and pedological conditions and presence or better accessibility of water in the landscape (Vančura et al. 2007).

There are no longer "virgin forests" in Central Europe but mostly forest with semi-natural species composition, and the establishment of nature reserves has aimed to improve the representativeness of forest reserves based on plant associations or on forest site type classifications (Diaci 1999). Following basic and logical mimic of nature, the establishment of a mosaic of areas of different ages facilitates the preservation of numerous forest habitats as a way to generate ecological sustainability (Bergeron et al. 2007). Natural-disturbance-based management can be a way to preserve ecological resilience when there is an acknowledgement of the importance of biodiversity and natural disturbances in the long-term ecosystem functioning, generation of structural and compositional heterogeneity at multiple scales and the decrease of likelihood of unexpected catastrophic changes. The purpose of the natural-disturbance-based management is then to foster the processes that retain desired structural states, while discouraging processes that lead to undesired states (Drever et al. 2006). This management principle can be used to achieve diversity of structure and composition at large scale forest landscapes, by applying simultaneous silvicultural treatments to specific forest zones. The method allows the practice of selective harvesting for encouragement of late successional species and clear-cutting for early successional species favoring, which in fact simulates the occurrence of severe fires (Harvey et al. 2002). According to Larsen and Nielsen (2007), the transformation of forest from age-class forests to nature-based ones requires the collaboration of professionals and scientist in the definition of long-term goals in terms of stand structure and dynamics, which often remains as an objective very difficult to clarify. One of the benefits of near nature forest structure is the presence of deadwood, which favors biodiversity conservation by providing food and shelter to endangered species, especially invertebrates (Mountford 2002). For Bergeron et al. (2006) natural disturbance based management can be used in fire dominated forests as a way to substitute fire by harvesting, to retain the natural forest spectrum of compositions and structures at different scales. The profitability of near-natural beech stand management is primarily achieved through the utilization of natural ecological processes, with the purpose of producing valuable timber at low establishment costs (Nord-Larsen 2003).

Kuuluvainen (2009) exposed the structural variation of natural boreal forests of northern Europe in comparison with clear-cut forests, which have been traditionally defined by others as very structurally similar to natural conditions. The author expressed concern for the unlikely biodiversity conservation and ecological sustainability of areas under similar management models. In practice, the application of forest vegetation management environmentally friendly in Europe during the present century displays limitations. That is the case of a persistent use of herbicides in some degree especially

in the southern and central region, though other means of vegetation control like mechanical cut, overstorey manipulation for reduction of light in the understorey, application of mulches and biological control are also applied, in some cases regardless of the higher costs (Mccarthy et al. 2011).

The aim of the study was to evaluate the current conditions of the main stand structures and quantify the effect that particular management treatments have had in their growth parameters.

## 5.3.2. Materials and methods

In 1980, five 1 ha permanent research plots (PRP) were established in stands of even-aged beech forest in the NNR, in order to analyze their stand structure and production. In 2004, four of these plots (plots 01, 03, 04 and 05) were used again for a broader evaluation of their structure (Table 2), involving the measurement of dbh (diameter at breast height), total height, crown height, species, social status (dominant, codominant, subdominant and less than 20 m) and horizontal distribution using the Fieldmap equipment (IFER Monitoring and Mapping Solutions Ltd.). The evaluation of horizontal distribution included the description of crown projection of each live stem by measuring a minimum of five cardinal crown radii per tree. For the evaluation of stands with near nature characteristic (unmanaged), permanent research plots (PRP "Virgin forest" 06 and 07) were established in 2005 for the study of the stand and regeneration structure, both plots are 100 × 100 m (1 ha) of area, and represent 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). In 2007 a third PRP was established in the forest stand 436B17, forest type 4K3 and forest age 180. The topographical digitalization of the plots included the mapping of all woody stems ≥ 3 cm dbh. For each stem, we measured the dbh (double measurement in NS and EW), the height, the crown height and recorded the species, tree status (living, dying or dead), and social status (dominant, codominant, subdominant, less than 20 m, and broken tree). We also mapped the crown projection of each live stem. The data distribution was not normal.

The volume of dead wood ≥ 10 cm (logs and snags) was estimated by complete enumerations and mapping within permanent plots. For logs we measured the length and diameter at both ends. Deadwood was classified according to decay classes as follows:

1) wood hard, branches present, rind on more than 50% of the surface, profile oval
2) wood hard, branches present, rind on less than 50% of the surface, profile oval
3) soft, cut 1 - 5 cm, profile oval
4) soft, small fragments missing, profile elliptic
5) soft, contours deformed, profile elliptic
6) soft, reduced, no contours, wood covered by soil

The formula after Smalin was used for the estimation of log volume:

$$V = (go + gn)L/2 \quad (1)$$

go, gn ...basal areas on both ends
L ... length

With the formula after Denzin we estimated volume of snags:

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

Since the equation is valid for standing trees of height around 25 m, there was a volume reduction of 3% for each meter of difference.

Dendrometrical methods from Korf (1972) and Šmelko (2000) were use for quantification of production. Diameter and height distribution, arithmetic mean, standard deviation, and coefficient of variation for both variables were calculated.

Stand basal area (G) was by individual tree calculations of $g = (\pi/4)\ DBH^2$, and stand density by $\rho = (G_{SK})/(G_{RT})$ or the relation between the standard basal area value and the observed one. The standard values were taken from ÚHÚL – Brandýs nad Labem and VÚLHM Zbraslav Strnady, valid from 1. 1. 1990.

Volume increment was calculated by the formula:

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

$CPB$ = 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.

Distance dependant indices of spatial distribution: Hopkins-Skellam, Pileou-Mountford and Clark-Evansův were calculated by the software PointPro 2.1 developed at the Department of forest management at CULS Prague (Zahradník). The results of the calculations are assessed by the following criteria:

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

### 5.3.3. Results

*Tree species composition*

The monospecific characteristic of the managed plots (01 to 05) remains, with the exception of the two oaks present in PRP 05 and one larch present in PRP 01. Those three individuals have been the only representation of additional tree species in the managed plots from the beginning of the establishment of the research plots. Regarding the unmanaged plots, since the mortality in PRP 06 has been very low, there has not been much change in its species composition. In terms of number of individuals and without counting the inclusion of new young individuals classifying into the smallest diameter class (the so called, ingrowth), beech passed from being 90.2% of the total of individuals to be 90.7%; hornbeam came from 6.4 to 6.2; the only registered birch is now part of the dead ones; and the percentages of larch and spruce remain very similar since the last measurement (2.1% and 1% resp.). Similar results are obtained for PRP 07, which keeps a 73% of beech, one specimen of birch and sycamore maple (0.4% each), 15% of hornbeam, and 6% of both larch and spruce. Counting the ingrowth in both plots did not get to affect the species proportions in a larger way, which could be expected considering that its numbers are higher than the registered mortality. The 38 new individuals in PRP 06 (all of them beech) only increased beech dominance to 92.2% (1.5% more than without counting ingrowth). In the case of PRP 07, the 17 new individuals (16 beeches and 1 hornbeam) only got to increase beech dominance to 73.8% (0.8% more than without counting ingrowth). Strange enough, if the number of new trees represented by ingrowth belonged to another species, the change in the proportion of a very dominant species like beech would have changed in a little more noticeable way. That is to say, beech dominance would have decreased 14.8% in PRP 06 and 4.8 % in PRP 07. Similarly, in such case, the percentage of the particular secondary species would have increased even 16% in PRP 06 and 6% in PRP 07. These results point out the disadvantage that some calculations may hide, and the need to consider different variables and presentations of the data when the analysis is to be done. The first measurement of PRP 08 in 2007 showed that the 723 live trees are constituted by 88.7% of beech, 9.5% of fir, 1.2% of spruce and less than 1% of oak, hornbeam and larch with 1 and 2 individuals. The unmanaged stands, then, keep a beech dominance of 70% to 90%, at the considered scale, regardless of the density of trees.

*Dead wood account*

The spatial digitalization of PRP 02 did not evidence the existence of remaining logs on the forest ground, just as it is expected for most of the managed plots. In the course of 4 years, only two new logs were found in the managed plots; one in PRP 05 that was classified as snag in 2003, and one in PRP 01 that was alive in 2005. Those two logs accounted for 7.9 m$^3$ and 1.24 m$^3$ resp. In terms of snags, the recount of the managed plots showed three remaining individuals in PRP 03, and two in PRP 01 that were classified in the same condition in previous measurements. Two of those snags in PRP 03 were classified as such in 2005 and the other one in 1997. The ones in PRP 01 became snags in 2002 and 2005. Two other snags of PRP 03, one in PRP 04 and one in PRP 01 reported in previous measurements are now missing. No newer snags were

added to these plots. The total count of snags in the managed plots for 2009 is then 7.02 $m^3$ in PRP 03, 4.61 $m^3$ in PRP 01 and 1.72 $m^3$ in PRP 02.

Higher mortality in PRP 06 created an increment in snags from 18.27 $m^3$ in 2005 to 44.65 $m^3$ (six more beech trees) in addition to an increment in logs from 21.52 $m^3$ to 21.91 $m^3$ (three beech trees and one hornbeam). There was no change in the number of snags for PRP 07, with the only one registered in 2005 still standing (4.23 $m^3$), though three dead hornbeams changed the amount of logs from 46.27 $m^3$ to 48.66 $m^3$. The difference in number of snags of PRP 08 in comparison with the other unmanaged plots is much higher than the difference of total live trees could predict. A total of 31 snags (including two spruces and one fir) amounted for 10.13 $m^3$ (68% of the snags had DBH smaller than 17 cm). Though the number of logs found was larger than the other two plots (35 logs, compared to 18 in PRP 06 and 25 in PRP 07, during their first measurement) the volume of wood they represented was similar to the other two cases (28.25 $m^3$, compared to 21.52 $m^3$ and 46.27 $m^3$ for PRP 06 and 07). All of them were beech logs, which also differ from the other two plots that included one or two logs of spruce, birch, hornbeam or larch. Half of the log volume in PRP 06 belongs to decay class one, while 20 to 25% belongs to decay class two and three and the rest to classes four and five. In general, classes two and three are among the most common decay classes in the three unmanaged stands.

*Diameter distributions and Total count*

In the almost 30 years of measurements, PRP 03 has had the lowest reduction in total number of individuals (33), followed by PRP 04, while the rest of the managed plots have had reductions among 93 and 110 trees ((Table 9). Also, though PRP 02 currently keeps the highest number of trees (an average of 167 trees more than the other managed plots), this difference has been similar since 1980. Which means that the absolute mortality and harvesting executed in the plot have been similar to what has occurred in the analogous plots, and that such superior density is not due to disregard on management. The reduction in the total number of trees in all plots is described by a discreet negative arch that is marked by a higher rate of reduction from 1997 to 2003. The average reduction rate for the managed plots ranges from 6% to 21%, with annual values of 5% to 30%. Annual extraction of trees ranges from 1 to 13, with an average of 4.

There are no big differences in the diameter averages for the managed plots over the years, though PRP 01, 03 and 04 have kept a much close similarity than the others (values between 51 and 63). PRP 02 has the lowest values and PRP 05 is placed in a middle rank. Minimum, maximum and range diameters go according to the last classification, including PRP 02 having the smallest range values (an average of 48 cm), while the others have ranges from 48 cm to 77 cm. Likewise, standard deviations in PRP 02 are slightly lower than the rest, although its coefficient of variation values are more alike the other plots, which means that the standard deviations keep a similar rate in relation to the diameter averages. There is a slight increase in the values of standard deviation for the managed plots (except in PRP 05), and yet all of them show a small decrease in their C.V. That is explained by the fact that, as both standard deviation and range change little over time values of diameter average grow at a higher rate than the standard deviation. In general, values of standard deviation and C.V. have remained much equal and in relatively low values over time, which is a manifestation of the level

of predictability implanted by the management regime. PRP 01 has been decreasing its skewness to almost neutral values, while the other managed plots have increased their skewness to almost neutral or more to the right, which describes distributions with equal number of individuals to both sides of the mean, or under the average value. A gradual increment in the kurtosis values suggests a general tendency to accumulate individuals in middle diameter classes in all managed plots.

The inclusion of ingrowth in the unmanaged plots 06 and 07 keeps average values from increasing. In fact, the level of reduction of this value is proportional to the number of new young trees registered. The standard deviation is stable at higher values than managed plots, but the reduction of the average causes an increment of the already much higher C.V. than in managed plots. Skewness and kurtosis increase their values revealing the yet higher accumulation of trees in smaller classes. Statistical numbers for PRP 08 describe similar characteristics to 06 and 07, but skewness and kurtosis reveal larger number of trees in smaller classes.

Table 9. Summary of diameter statistics.

| Plot | Year | Count | Average | Standard deviation | C. of V. (%) | Minimum | Maximum | Range | Stnd. skewness | Stnd. kurtosis |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1980 | 170 | 51,332 | 12,4891 | 24,33 | 24,5 | 93 | 68,5 | 1,001 | 0,078 |
| | 1997 | 149 | 55,158 | 13,7026 | 24,84 | 25,6 | 91,8 | 66,2 | 0,543 | -0,87 |
| | 2002 | 114 | 59,05 | 13,9322 | 23,59 | 27,8 | 105,1 | 77,3 | 1,942 | 2,014 |
| | 2005 | 93 | 59,572 | 13,4385 | 22,56 | 28,75 | 95,6 | 66,85 | 0,244 | -0,21 |
| | 2009 | 65 | 63,465 | 14,0432 | 22,13 | 29,4 | 97 | 67,6 | -0,09 | 0,045 |
| 2 | 1980 | 399 | 33,009 | 8,69989 | 26,36 | 14,8 | 62,85 | 48,05 | 2,895 | 0,041 |
| | 1997 | 346 | 37,139 | 9,47252 | 25,51 | 15,35 | 68,75 | 53,4 | 2,939 | 0,039 |
| | 2003 | 321 | 40,045 | 9,21977 | 23,02 | 22,25 | 67 | 44,75 | 3,186 | -0,71 |
| | 2007 | 306 | 40,913 | 9,10476 | 22,25 | 22,35 | 69,95 | 47,6 | 3,495 | 0,096 |
| 3 | 1980 | 149 | 55,419 | 11,7446 | 21,19 | 26,6 | 81 | 54,4 | -1,14 | -1,04 |
| | 1997 | 138 | 60,111 | 12,6027 | 20,97 | 32,3 | 87,35 | 55,05 | -0,96 | -1,47 |
| | 2002 | 132 | 61,601 | 12,4118 | 20,15 | 32,1 | 87,15 | 55,05 | -1,11 | -1,08 |
| | 2005 | 126 | 62,658 | 12,7363 | 20,33 | 33 | 95 | 62 | -0,67 | -0,92 |
| | 2009 | 116 | 62,758 | 12,9964 | 20,71 | 33,3 | 96,5 | 63,2 | 0,011 | -0,82 |
| 4 | 1980 | 139 | 53,2 | 10,6554 | 20,03 | 27,6 | 87,2 | 59,6 | 0,622 | 0,11 |
| | 1997 | 127 | 57,76 | 11,7197 | 20,29 | 28,6 | 91,65 | 63,05 | -0,03 | -0,42 |
| | 2003 | 112 | 60,259 | 12,6194 | 20,94 | 30,75 | 105,8 | 75 | 1,179 | 1,413 |
| | 2005 | 110 | 60,486 | 12,2472 | 20,25 | 31,5 | 102,1 | 70,6 | 0,754 | 0,872 |
| | 2009 | 90 | 61,979 | 12,3325 | 19,90 | 31,75 | 108,1 | 76,35 | 1,804 | 2,967 |
| 5 | 1981 | 220 | 44,549 | 11,3381 | 25,45 | 18,85 | 72,15 | 53,3 | 0,798 | -1,92 |
| | 1998 | 195 | 49,056 | 11,8907 | 24,24 | 21,95 | 78,7 | 56,75 | 0,925 | -1,78 |
| | 2003 | 142 | 51,474 | 11,8296 | 22,98 | 24,55 | 84,1 | 59,55 | 1,39 | -0,68 |
| | 2005 | 117 | 54,999 | 10,4171 | 18,94 | 35,15 | 83,5 | 48,35 | 1,095 | -1,08 |
| | 2009 | 110 | 55,687 | 10,6518 | 19,13 | 33,75 | 85,1 | 51,35 | 1,544 | -0,24 |
| 6 | 2005 | 204 | 32,086 | 35,4642 | 110,53 | 3,6 | 146 | 142,4 | 6,807 | -0,55 |
| | 2009 | 231 | 27,773 | 34,1441 | 122,94 | 3,2 | 148,3 | 145,1 | 8,903 | 1,826 |
| 7 | 2005 | 272 | 29,617 | 23,7806 | 80,30 | 3,1 | 108,2 | 105,1 | 7,15 | 1,506 |
| | 2009 | 286 | 28,347 | 23,9276 | 84,41 | 3,2 | 109,5 | 106,3 | 7,721 | 1,982 |
| 8 | 2007 | 708 | 18,393 | 17,3758 | 94,47 | 4 | 84,7 | 80,7 | 14,56 | 3,99 |

* Values of average, standard deviation, minimum, maximum and range are in cm.
 C. of V. (%) – Coefficient of variation, Stnd. skewness – Standard skewness, Stnd. kurtosis – Standard kurtosis
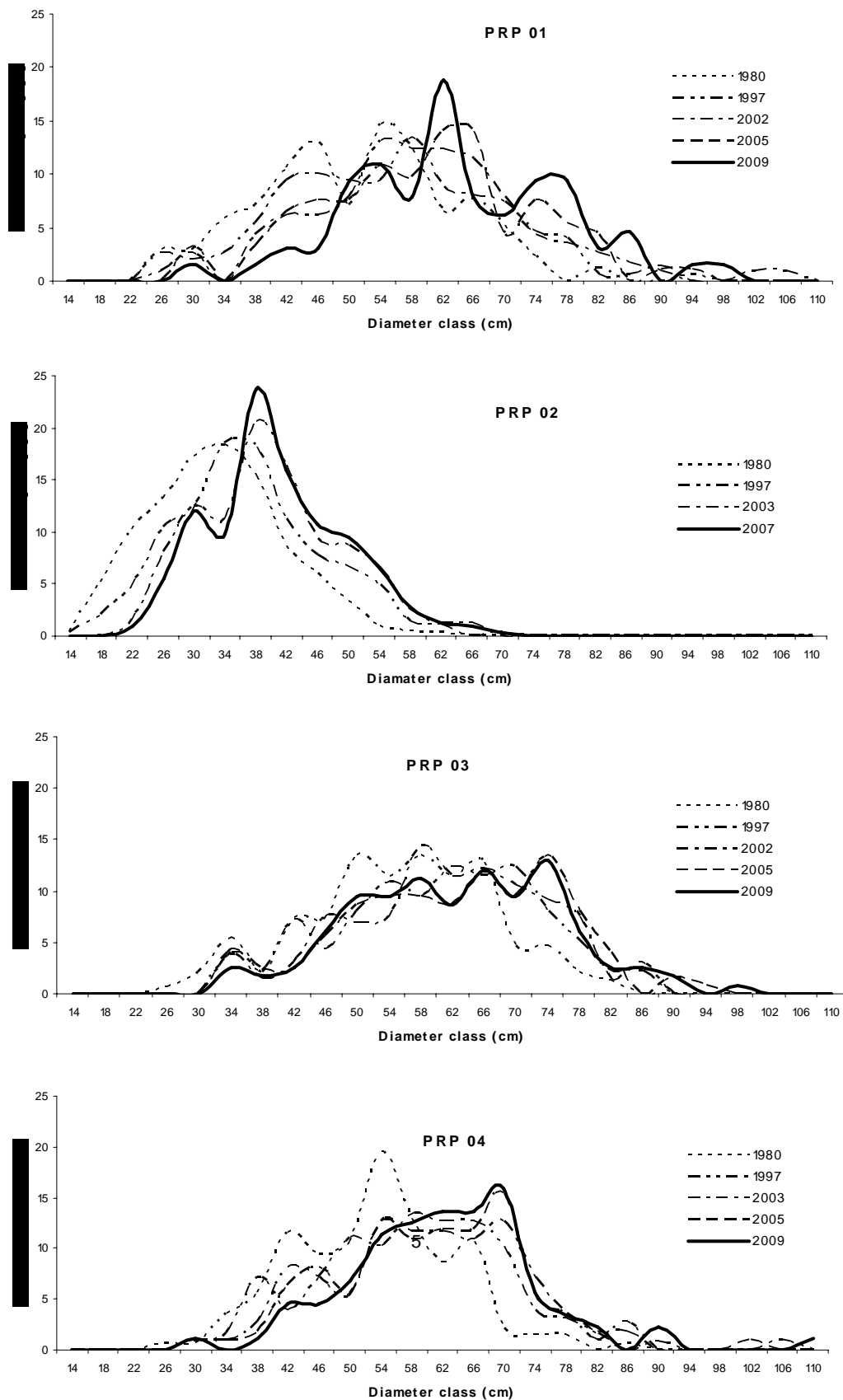
Fig. 8. Successive diameter distributions for PRP 01 to 04.
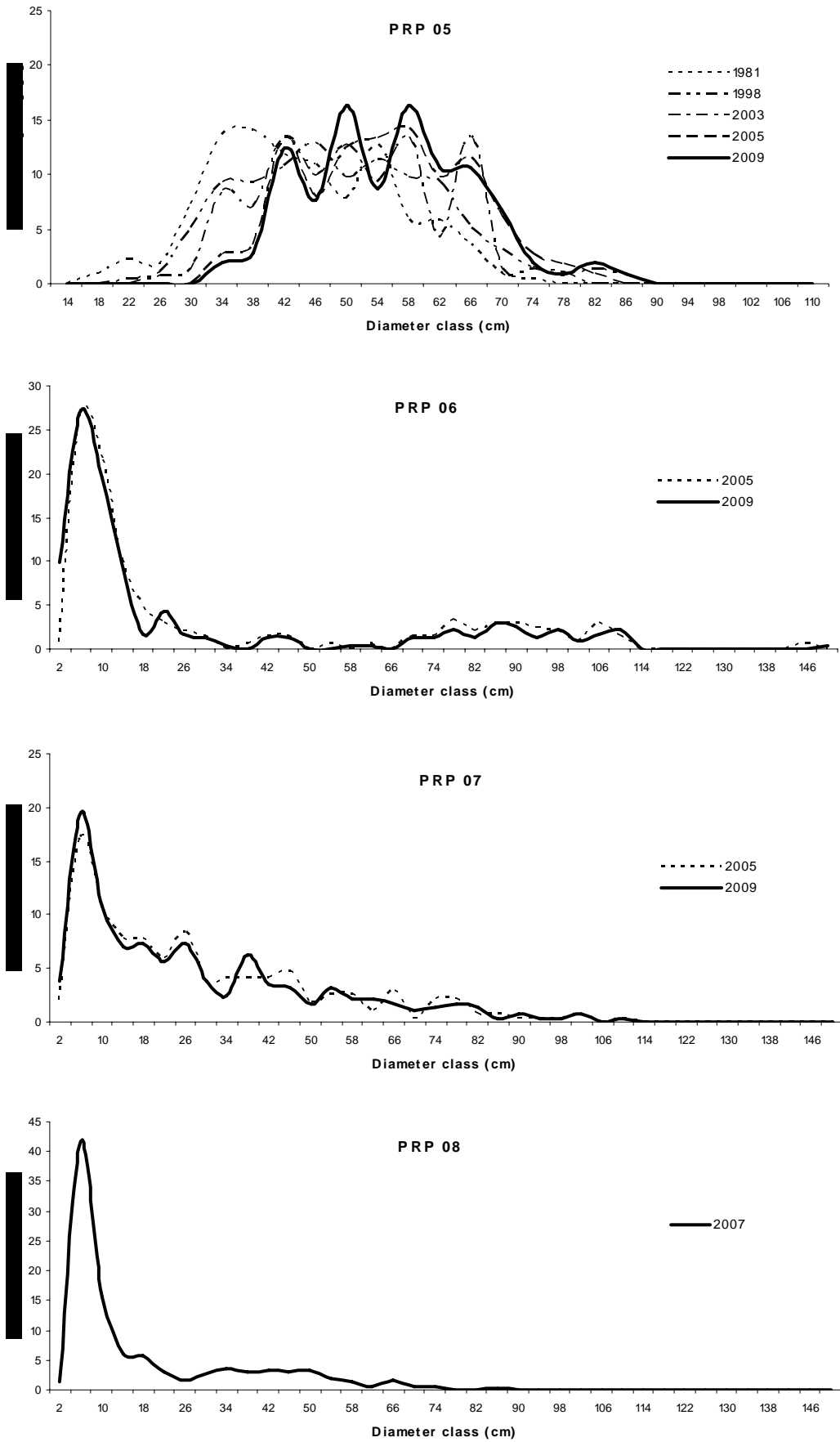
Fig. 9. Successive diameter distributions for plots 05 to 08.

The gradual diameter growth and transition from one diameter class to the next one is evident for all plots in figures 1 and 2. The largest accumulations of trees are clear by observing the highest peaks of the distributions, which varies from plot to plot. Classes 50 to 78 account for the 80% of the trees in PRP 01; 81% of the trees are placed in classes 30 to 50 in PRP 02; PRP 03 keeps 79% of the trees in classes 46 to 74; in PRP 04, classes 50 to 70 hold the 74% of trees; and in PRP 05, 83% of trees are in classes 42 to 66. A perfectly regular transition of distributions that preserves its shape unaffected year by year would have to maintain the relative proportions of individuals at each side of the mean as the trees grow and advance to higher classes. For that purpose, the population of trees would need to keep equal mortality and harvesting for particular size classes, and the size increment should remain constant for all trees. In practice, this hypothetical behavior does not occur, but it is possible to observe cases where the progress of a data set resembles this principle. One clear case is the one observed in PRP 02, where the characteristic peaks of the distribution show similar relative proportions for the classes over time. Plots 06 and 07 also preserve pretty well most of the peaks in the distribution, though the low level of mortality, total number of trees and the limited number of measurements reduce the possibility of major changes. Similar developments in the rest of the plots are more difficult to observe in the charts, because of the number of peaks in the distributions and the more conspicuous degree of fluctuation of proportions in particular classes. Nevertheless, considering the difficulty in controlling factors like diameter increment and mortality in subsequent years, it is still interesting to see that some characteristic patterns remain present in the plots. Alike plots 06 and 07, the most important diameter classes of PRP 08 are 6 and 10, though in this case, 57% of the trees are present in these two classes. Comparatively, plots 06 and 07 needed three and six classes to put together an equal percentage of trees. Eighty one individuals of PRP 08 (11.3% of the total) belong to a species different to beech. Sixty eight of them are fir and their DBH range from 4 to 17,5 cm. The nine spruce trees are 4.15 to 9.55 cm, and the only larch reaches 52.15 cm. Comparatively, the eleven hornbeam trees of plot 06 are 12.85 to 43.8 cm of DBH. As for plot 07, the forty one trees of hornbeam range from 6.8 to 50.25 cm, seventeen spruce trees are 19.6 to 72.45 cm, and fifteen larch trees are 40.3 to 83.3 cm of DBH.

A first inspection of the horizontal distribution of diameters exhibited in figures 3 to 6 evidences the necessary dimensional progress of the individuals by recognizing an increase in the sizes and colors of their respective symbols in the latest year in relation to the earliest one. A closer look to the managed plots does not reveal an obvious aggregation of individuals of similar diametric sizes, in spite of the fact that some plots show localized empty areas of increasing extension that could potentially segregate elements of particular common characteristics. After 29 years of growth and harvesting, common structural patterns of this attribute between two different stages of the same plot are not easily recognizable, to the point that the identification of a plot by its previous map description could likely be mistaken. The visual examination indicates that an elimination of trees of all diameter classes has taken place after the establishment of the plots. Though proportions of trees from each class being removed may appear equal, a significant removal of trees of the smaller classes in PRP 05 at the lower part of the plot is also apparent at a first look. Longer distances between trees of the largest sizes are also evident (around 50 m for class 95) as compared to smaller classes, though the total number of trees in each class is logically related to this matter. Greater contrasts between diameters of the trees are visible for PRPs 06 to 08, due to the
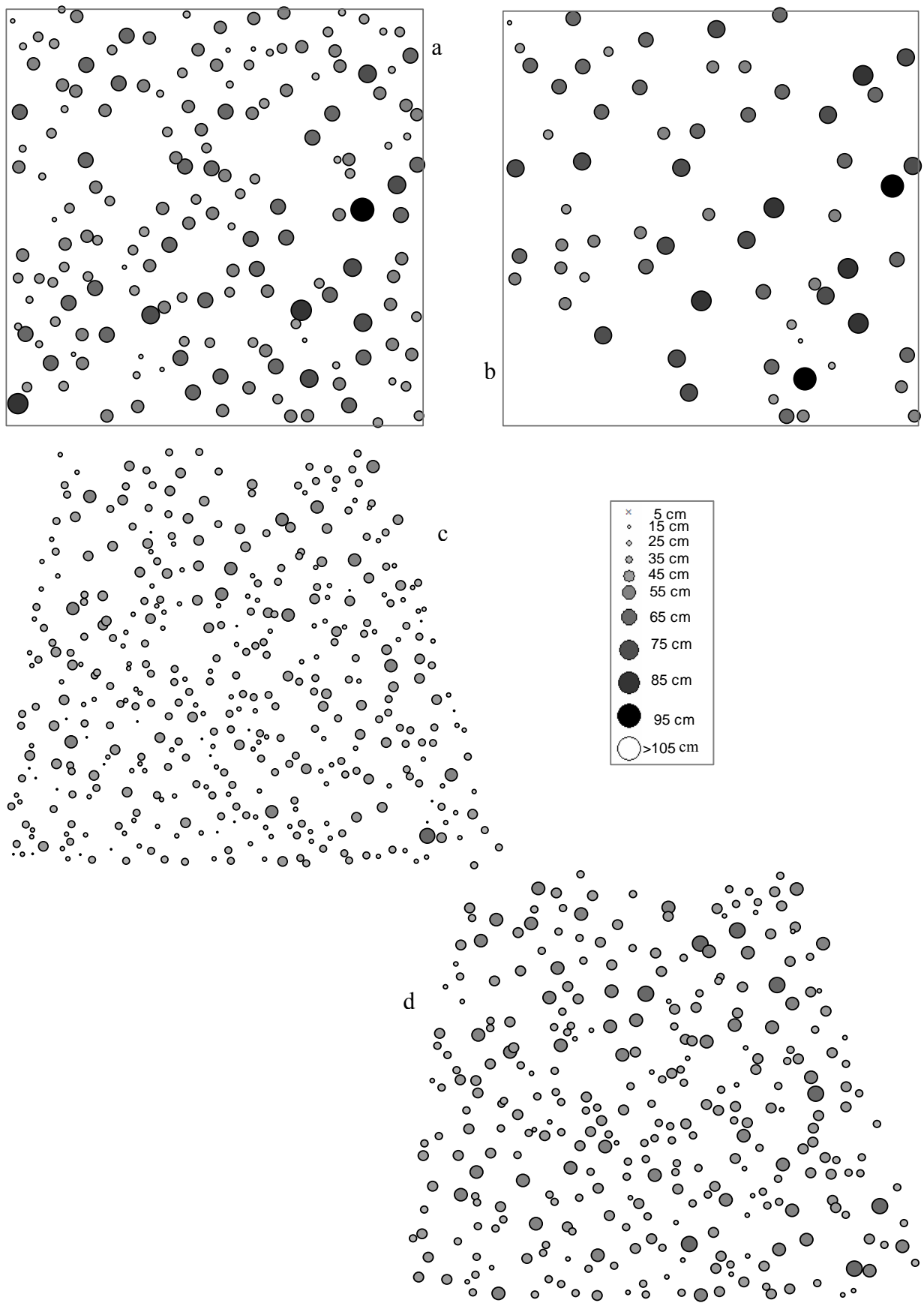
Fig. 10. Horizontal diameter distributions for PRPs 01 [1980 (a), 2009 (b)] and 02 [1980 (c), 2007 (d)].
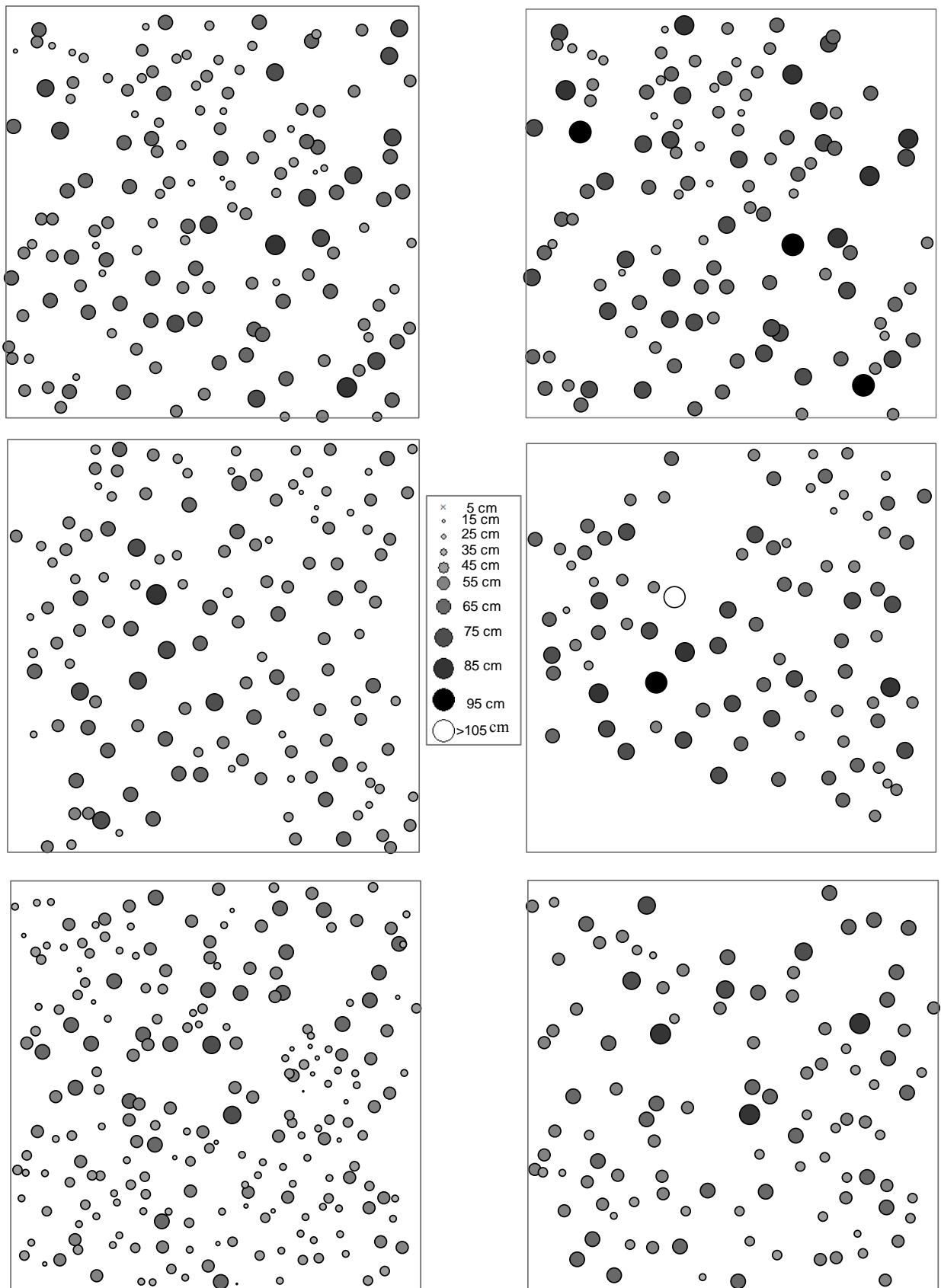
Fig. 11. Horizontal diameter distributions for PRPs 03 (up), 04 (middle), and 05 (down) [1980 (left), 2009 (right)].
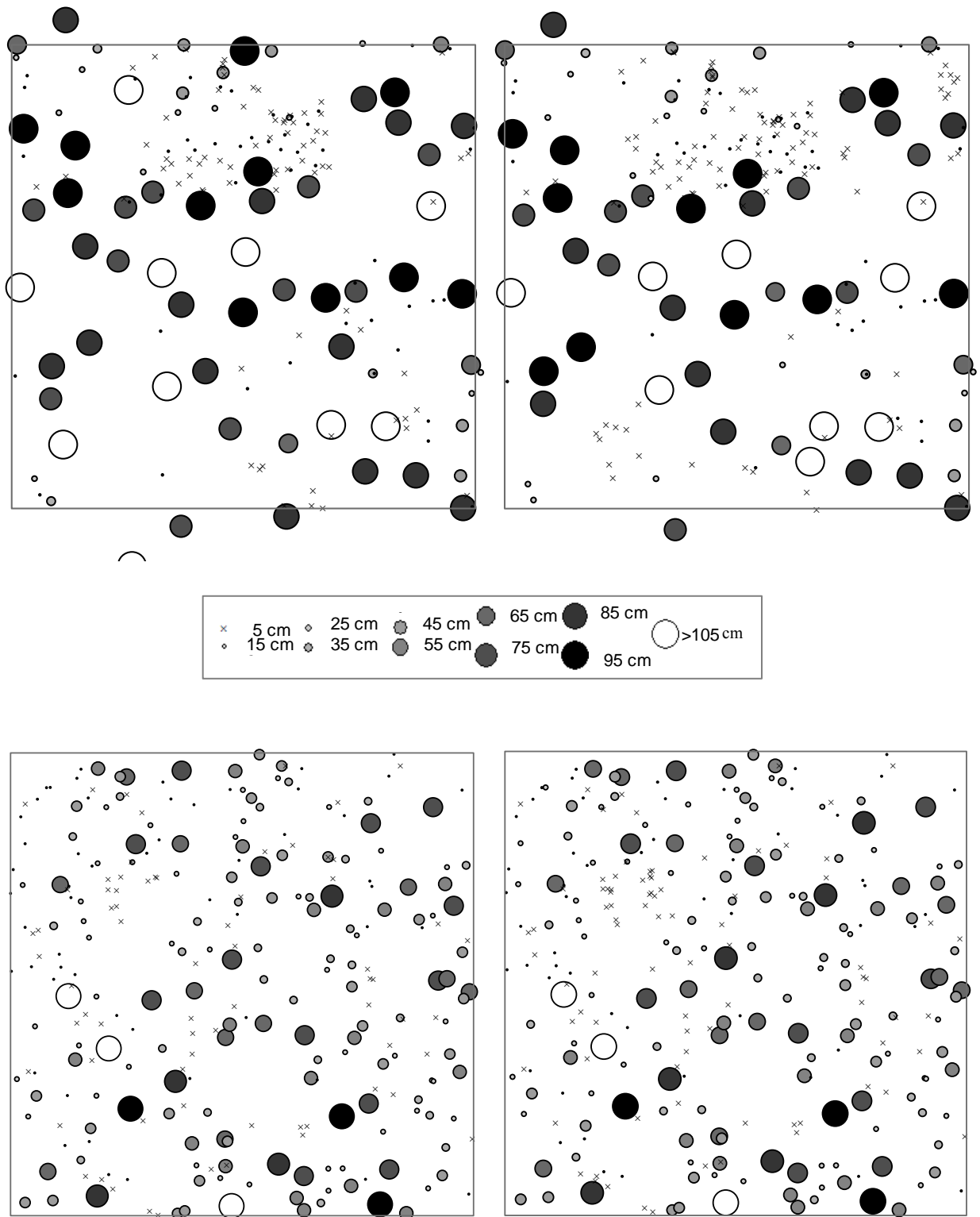
Fig. 12. Horizontal diameter distributions for PRPs 06 (up) and 07 (down) [2005 (left), 2009 (right)].
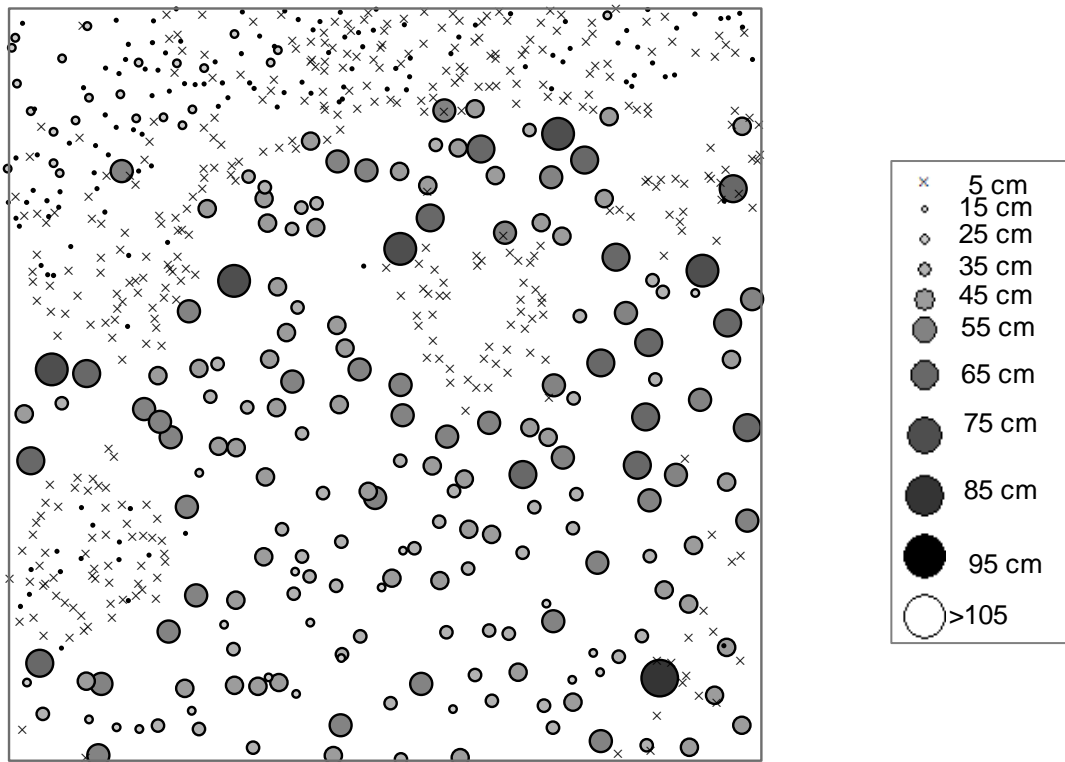
Fig. 13. Horizontal diameter distribution for PRP 08 (2007).

presence of elements in diameter classes 5 and 15. Aggregation in the smaller classes is clear in plots 06 and 08 but not so in 07. In plot 06, large areas with big number of trees in classes 85, 95 and > 100 are visibly associated to absence of trees of the smaller classes, which in turn eventually fill open large gaps. In plot 08, a lower density of trees of the biggest classes allows more presence of middle and small class ones. In this case, the higher total tree density is connected to an absence of big canopy gaps.

For a better understanding of the horizontal distribution of diameters, the determination of the size of the respective nearest neighbor tree for each individual of a plot was considered. This examination is based on the premise that the more aggregated a distribution is the higher the probability for two neighboring trees to belong to the same diameter class. Table 10 shows the number of trees in each diameter class and the classification of the corresponding nearest neighbor trees in equal number of classes as percentages. For the managed plots, the table displays a general visible trend of percentages mostly distributed in diameter classes closer to the one of the nearest neighbor. This pattern responds to the higher abundance of individuals in middle classes, which is also common for this plots. Trees in the smaller classes have a higher chance to find trees of larger diameters close to them and the opposite is true for larger ones. The low abundance in both extremes of the distribution reduces the chances to find elements of both groups next to each other. Plots with a fewer number of diametric classes and a more equal distribution throughout them will increase those chances. For most of the cases in the managed plots, the table shows that the percentages of trees

Table 10a. Trees in diameter classes (10 cm wide) and percentage of nearest neighbor trees (one per tree) in each class, for each plot in two different years.

| Plot | Year | Class (cm) | n | Class of the nearest neighbor tree (cm) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | > 100 |
| 1 | 1980 | 25 | 9 | 0 | 0 | 0 | 22.2 | 44.4 | 22.2 | 11.1 | 0 | 0 | 0 | 0 |
| | | 35 | 23 | 0 | 0 | 4.3 | 8.7 | 26.1 | 43.5 | 17.4 | 0 | 0 | 0 | 0 |
| | | 45 | 43 | 0 | 0 | 9.3 | 11.6 | 25.6 | 32.6 | 16.3 | 0 | 4.7 | 0 | 0 |
| | | 55 | 53 | 0 | 0 | 9.4 | 13.2 | 28.3 | 32.1 | 11.3 | 3.8 | 0 | 1.9 | 0 |
| | | 65 | 31 | 0 | 0 | 0 | 19.4 | 22.6 | 35.5 | 16.1 | 6.5 | 0 | 0 | 0 |
| | | 75 | 6 | 0 | 0 | 0 | 16.7 | 0 | 50 | 33.3 | 0 | 0 | 0 | 0 |
| | | 85 | 2 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 95 | 1 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 |
| | 2009 | 25 | 2 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 35 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 |
| | | 45 | 7 | 0 | 0 | 14.3 | 0 | 0 | 28.6 | 42.9 | 14.3 | 0 | 0 | 0 |
| | | 55 | 15 | 0 | 0 | 0 | 0 | 6.7 | 46.7 | 20 | 20 | 6.7 | 0 | 0 |
| | | 65 | 20 | 0 | 0 | 0 | 0 | 30 | 25 | 25 | 10 | 10 | 0 | 0 |
| | | 75 | 13 | 0 | 0 | 0 | 0 | 15.4 | 38.5 | 7.7 | 15.4 | 15.4 | 7.7 | 0 |
| | | 85 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 60 | 0 | 0 | 0 |
| | | 95 | 2 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 50 | 0 | 0 | 0 |
| 2 | 1980 | 15 | 23 | 0 | 8.7 | 34.8 | 39.1 | 13 | 0 | 4.3 | 0 | 0 | 0 | 0 |
| | | 25 | 128 | 0 | 3.1 | 35.9 | 45.3 | 13.3 | 2.3 | 0 | 0 | 0 | 0 | 0 |
| | | 35 | 169 | 0 | 7.1 | 36.7 | 44.4 | 10.7 | 1.2 | 0 | 0 | 0 | 0 | 0 |
| | | 45 | 65 | 0 | 4.6 | 36.9 | 38.5 | 15.4 | 3.1 | 1.5 | 0 | 0 | 0 | 0 |
| | | 55 | 13 | 0 | 7.7 | 38.5 | 30.8 | 23.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 65 | 1 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2007 | 25 | 36 | 0 | 0 | 13.9 | 50 | 27.8 | 2.8 | 5.6 | 0 | 0 | 0 | 0 |
| | | 35 | 124 | 0 | 0 | 10.5 | 49.2 | 30.6 | 8.1 | 1.6 | 0 | 0 | 0 | 0 |
| | | 45 | 96 | 0 | 0 | 13.5 | 40.6 | 36.5 | 9.4 | 0 | 0 | 0 | 0 | 0 |
| | | 55 | 42 | 0 | 0 | 4.8 | 45.2 | 35.7 | 4.8 | 9.5 | 0 | 0 | 0 | 0 |
| | | 65 | 8 | 0 | 0 | 37.5 | 12.5 | 0 | 50 | 0 | 0 | 0 | 0 | 0 |
| 3 | 1980 | 25 | 3 | 0 | 0 | 0 | 33.3 | 33.3 | 33.3 | 0 | 0 | 0 | 0 | 0 |
| | | 35 | 12 | 0 | 0 | 8.3 | 0 | 16.7 | 33.3 | 41.7 | 0 | 0 | 0 | 0 |
| | | 45 | 32 | 0 | 0 | 3.1 | 6.3 | 21.9 | 46.9 | 18.8 | 3.1 | 0 | 0 | 0 |
| | | 55 | 47 | 0 | 0 | 0 | 14.9 | 23.4 | 29.8 | 21.3 | 8.5 | 2.1 | 0 | 0 |
| | | 65 | 40 | 0 | 0 | 2.5 | 10 | 15 | 30 | 27.5 | 15 | 0 | 0 | 0 |
| | | 75 | 13 | 0 | 0 | 7.7 | 0 | 30.8 | 15.4 | 30.8 | 15.4 | 0 | 0 | 0 |
| | | 85 | 2 | 0 | 0 | 0 | 50 | 0 | 50 | 0 | 0 | 0 | 0 | 0 |
| | 2009 | 35 | 5 | 0 | 0 | 0 | 0 | 20 | 20 | 20 | 20 | 20 | 0 | 0 |
| | | 45 | 14 | 0 | 0 | 0 | 0 | 14.3 | 21.4 | 42.9 | 21.4 | 0 | 0 | 0 |
| | | 55 | 31 | 0 | 0 | 0 | 16.1 | 9.7 | 16.1 | 29 | 25.8 | 0 | 3.2 | 0 |
| | | 65 | 31 | 0 | 0 | 0 | 0 | 19.4 | 35.5 | 19.4 | 19.4 | 3.2 | 3.2 | 0 |
| | | 75 | 26 | 0 | 0 | 0 | 3.8 | 3.8 | 34.6 | 30.8 | 19.2 | 3.8 | 3.8 | 0 |
| | | 85 | 6 | 0 | 0 | 0 | 16.7 | 0 | 33.3 | 16.7 | 33.3 | 0 | 0 | 0 |
| | | 95 | 3 | 0 | 0 | 0 | 0 | 0 | 66.7 | 33.3 | 0 | 0 | 0 | 0 |
| 4 | 1980 | 25 | 2 | 0 | 0 | 0 | 50 | 50 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 35 | 13 | 0 | 0 | 7.7 | 0 | 15.4 | 53.8 | 15.4 | 7.7 | 0 | 0 | 0 |
| | | 45 | 34 | 0 | 0 | 5.9 | 11.8 | 32.4 | 23.5 | 20.6 | 0 | 5.9 | 0 | 0 |
| | | 55 | 53 | 0 | 0 | 0 | 15.1 | 28.3 | 39.6 | 13.2 | 3.8 | 0 | 0 | 0 |
| | | 65 | 27 | 0 | 0 | 0 | 11.1 | 25.9 | 40.7 | 18.5 | 3.7 | 0 | 0 | 0 |
| | | 75 | 6 | 0 | 0 | 0 | 0 | 16.7 | 50 | 16.7 | 16.7 | 0 | 0 | 0 |
| | | 85 | 1 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2009 | 35 | 2 | 0 | 0 | 0 | 0 | 50 | 50 | 0 | 0 | 0 | 0 | 0 |
| | | 45 | 11 | 0 | 0 | 0 | 9.1 | 0 | 18.2 | 54.5 | 18.2 | 0 | 0 | 0 |
| | | 55 | 24 | 0 | 0 | 0 | 0 | 25 | 20.8 | 20.8 | 25 | 4.2 | 0 | 4.2 |
| | | 65 | 29 | 0 | 0 | 0 | 3.4 | 17.2 | 27.6 | 31 | 20.7 | 0 | 0 | 0 |
| | | 75 | 17 | 0 | 0 | 0 | 0 | 11.8 | 23.5 | 47.1 | 11.8 | 5.9 | 0 | 0 |
| | | 85 | 3 | 0 | 0 | 0 | 0 | 33.3 | 33.3 | 0 | 33.3 | 0 | 0 | 0 |
| | | 95 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 |
| | | > 100 | 1 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 |
| 5 | 1981 | 15 | 2 | 0 | 0 | 0 | 0 | 0 | 50 | 50 | 0 | 0 | 0 | 0 |
| | | 25 | 17 | 0 | 0 | 5.9 | 23.5 | 52.9 | 17.6 | 0 | 0 | 0 | 0 | 0 |
| | | 35 | 69 | 0 | 0 | 5.8 | 40.6 | 21.7 | 27.5 | 4.3 | 0 | 0 | 0 | 0 |
| | | 45 | 57 | 0 | 0 | 12.3 | 28.1 | 40.4 | 10.5 | 8.8 | 0 | 0 | 0 | 0 |
| | | 55 | 51 | 0 | 0 | 3.9 | 25.5 | 25.5 | 23.5 | 21.6 | 0 | 0 | 0 | 0 |
| | | 65 | 22 | 0 | 4.5 | 0 | 18.2 | 22.7 | 45.5 | 9.1 | 0 | 0 | 0 | 0 |
| | | 75 | 2 | 0 | 0 | 0 | 50 | 0 | 50 | 0 | 0 | 0 | 0 | 0 |
| | 2009 | 35 | 5 | 0 | 0 | 0 | 0 | 80 | 20 | 0 | 0 | 0 | 0 | 0 |
| | | 45 | 26 | 0 | 0 | 0 | 11.5 | 38.5 | 26.9 | 19.2 | 0 | 3.8 | 0 | 0 |
| | | 55 | 39 | 0 | 0 | 0 | 2.6 | 23.1 | 46.2 | 23.1 | 5.1 | 0 | 0 | 0 |
| | | 65 | 28 | 0 | 0 | 0 | 3.6 | 21.4 | 25 | 42.9 | 7.1 | 0 | 0 | 0 |
| | | 75 | 4 | 0 | 0 | 0 | 0 | 0 | 75 | 0 | 25 | 0 | 0 | 0 |
| | | 85 | 3 | 0 | 0 | 0 | 0 | 66.7 | 0 | 33.3 | 0 | 0 | 0 | 0 |

Table 10b. Trees in diameter classes (10 cm wide) and percentage of nearest neighbor trees (one per tree) in each class.

| Plot | Year | Class (cm) | n | Class of the nearest neighbor tree (cm) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | > 100 |
| 6 | 2005 | 5 | 80 | 48.8 | 36.3 | 2.5 | 0 | 2.5 | 1.3 | 0 | 1.3 | 1.3 | 3.8 | 2.5 |
| | | 15 | 51 | 49 | 21.6 | 2 | 3.9 | 3.9 | 2 | 0 | 5.9 | 7.8 | 3.9 | 0 |
| | | 25 | 11 | 36.4 | 18.2 | 9.1 | 9.1 | 0 | 0 | 18.2 | 0 | 0 | 9.1 | 0 |
| | | 35 | 3 | 0 | 66.7 | 33.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 45 | 6 | 50 | 16.7 | 16.7 | 0 | 0 | 0 | 0 | 0 | 0 | 16.7 | 0 |
| | | 55 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 65 | 3 | 0 | 0 | 66.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33.3 |
| | | 75 | 10 | 50 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 |
| | | 85 | 14 | 21.4 | 35.7 | 0 | 0 | 0 | 0 | 0 | 14.3 | 7.1 | 14.3 | 7.1 |
| | | 95 | 11 | 45.5 | 36.4 | 0 | 0 | 0 | 0 | 0 | 9.1 | 9.1 | 0 | 0 |
| | | > 100 | 10 | 40 | 10 | 10 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 |
| | 2009 | 5 | 109 | 56 | 29.4 | 4.6 | 0 | 1.8 | 0.9 | 0 | 0.9 | 1.8 | 1.8 | 2.8 |
| | | 15 | 49 | 49 | 24.5 | 2 | 2 | 4.1 | 2 | 0 | 4.1 | 6.1 | 6.1 | 0 |
| | | 25 | 16 | 50 | 0 | 18.8 | 6.3 | 0 | 0 | 12.5 | 6.3 | 0 | 6.3 | 0 |
| | | 35 | 2 | 0 | 50 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 45 | 6 | 50 | 16.7 | 16.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16.7 |
| | | 55 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 65 | 4 | 25 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 |
| | | 75 | 7 | 42.9 | 28.6 | 14.3 | 0 | 0 | 0 | 0 | 0 | 14.3 | 0 | 0 |
| | | 85 | 12 | 25 | 33.3 | 0 | 0 | 0 | 0 | 0 | 8.3 | 0 | 16.7 | 16.7 |
| | | 95 | 11 | 36.4 | 27.3 | 0 | 0 | 0 | 0 | 9.1 | 0 | 18.2 | 9.1 | 0 |
| | | > 100 | 11 | 72.7 | 9.1 | 0 | 0 | 0 | 0 | 0 | 0 | 18.2 | 0 | 0 |
| 7 | 2005 | 5 | 70 | 37.1 | 21.4 | 11.4 | 7.1 | 11.4 | 2.9 | 1.4 | 4.3 | 1.4 | 1.4 | 0 |
| | | 15 | 54 | 35.2 | 27.8 | 13 | 9.3 | 5.6 | 5.6 | 0 | 3.7 | 0 | 0 | 0 |
| | | 25 | 44 | 27.3 | 9.1 | 15.9 | 20.5 | 6.8 | 11.4 | 0 | 4.5 | 0 | 0 | 4.5 |
| | | 35 | 27 | 40.7 | 7.4 | 33.3 | 7.4 | 3.7 | 3.7 | 0 | 3.7 | 0 | 0 | 0 |
| | | 45 | 26 | 23.1 | 15.4 | 23.1 | 0 | 19.2 | 7.7 | 11.5 | 0 | 0 | 0 | 0 |
| | | 55 | 17 | 5.9 | 29.4 | 23.5 | 5.9 | 11.8 | 11.8 | 5.9 | 0 | 0 | 5.9 | 0 |
| | | 65 | 11 | 27.3 | 18.2 | 0 | 0 | 36.4 | 9.1 | 0 | 9.1 | 0 | 0 | 0 |
| | | 75 | 13 | 23.1 | 38.5 | 7.7 | 15.4 | 0 | 7.7 | 7.7 | 0 | 0 | 0 | 0 |
| | | 85 | 4 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 |
| | | 95 | 3 | 33.3 | 0 | 0 | 0 | 0 | 33.3 | 0 | 33.3 | 0 | 0 | 0 |
| | | > 100 | 3 | 66.7 | 0 | 33.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 2009 | 5 | 86 | 47.7 | 17.4 | 11.6 | 9.3 | 3.5 | 3.5 | 1.2 | 2.3 | 2.3 | 1.2 | 0 |
| | | 15 | 53 | 37.7 | 20.8 | 15.1 | 9.4 | 5.7 | 7.5 | 0 | 3.8 | 0 | 0 | 0 |
| | | 25 | 43 | 25.6 | 16.3 | 16.3 | 16.3 | 7 | 9.3 | 0 | 2.3 | 2.3 | 0 | 4.7 |
| | | 35 | 30 | 50 | 3.3 | 23.3 | 13.3 | 3.3 | 3.3 | 0 | 0 | 3.3 | 0 | 0 |
| | | 45 | 22 | 9.1 | 18.2 | 27.3 | 0 | 18.2 | 13.6 | 13.6 | 0 | 0 | 0 | 0 |
| | | 55 | 17 | 11.8 | 23.5 | 23.5 | 5.9 | 11.8 | 11.8 | 5.9 | 0 | 0 | 5.9 | 0 |
| | | 65 | 13 | 23.1 | 30.8 | 0 | 0 | 30.8 | 7.7 | 0 | 7.7 | 0 | 0 | 0 |
| | | 75 | 10 | 30 | 40 | 0 | 10 | 0 | 10 | 10 | 0 | 0 | 0 | 0 |
| | | 85 | 6 | 66.7 | 0 | 0 | 16.7 | 0 | 0 | 0 | 16.7 | 0 | 0 | 0 |
| | | 95 | 3 | 33.3 | 0 | 0 | 0 | 0 | 33.3 | 0 | 33.3 | 0 | 0 | 0 |
| | | > 100 | 3 | 66.7 | 0 | 33.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 2007 | 5 | 367 | 74.4 | 18.3 | 1.4 | 1.1 | 2.5 | 1.9 | 0.3 | 0.3 | 0 | 0 | 0 |
| | | 15 | 130 | 58.5 | 34.6 | 6.2 | 0 | 0.8 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 25 | 44 | 15.9 | 22.7 | 25 | 18.2 | 11.4 | 2.3 | 2.3 | 2.3 | 0 | 0 | 0 |
| | | 35 | 54 | 9.3 | 0 | 16.7 | 35.2 | 27.8 | 3.7 | 3.7 | 3.7 | 0 | 0 | 0 |
| | | 45 | 57 | 26.3 | 1.8 | 12.3 | 22.8 | 24.6 | 8.8 | 3.5 | 0 | 0 | 0 | 0 |
| | | 55 | 35 | 37.1 | 2.9 | 2.9 | 8.6 | 20 | 20 | 8.6 | 0 | 0 | 0 | 0 |
| | | 65 | 15 | 20 | 0 | 6.7 | 26.7 | 6.7 | 26.7 | 0 | 13.3 | 0 | 0 | 0 |
| | | 75 | 5 | 40 | 0 | 20 | 20 | 0 | 0 | 20 | 0 | 0 | 0 | 0 |
| | | 85 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

belonging to the same class of their nearest neighbors are roughly proportional to the number of trees in the class in relation to the plot. In other words, classes with the highest abundance register more individuals next to each other, because a greater frequency represents a better probability to find an element on any specific place. Also, most of the values displayed in the table are lower than 50% and values higher than that correspond to trees in classes with less than eleven trees that are closer to elements of a different class. All these characteristics concur with the usual description of random distributions. Unmanaged plots (06 to 08) exhibit very different patterns. As it was illustrated before in the figures of diametric distribution, these plots keep their highest abundance in the smaller classes, and this feature also has an influence in the values of Table 10. That is to say that most of the highest percentages of nearest neighbor trees are also placed in the smaller classes. There is a notorious absence of middle sized trees

closer to each other in plot 06 due to their very small numbers and wide dispersion. The notable abundance of trees in classes five and fifteen is associated to the large percentages of individuals found next to each other. The illustration of the plot in Fig. 12 makes evident the existence of one cluster with trees of both classes and another one only with trees of class fifteen. The appearance of new trees of the smallest size in 2009 shows the attachment of some of them to the already established cluster and the formation of another two small ones in separate parts of the plot. The new increment in the number of trees from this class and their formation in clusters consequently increases the percentage displayed in Table 10 for trees of the class being next to each other. Even though there is a clear separation between small and large individuals in the plot, such separation is not manifested in the values of Table 10. Instead, large trees appear to be closer to the small ones than to themselves. Apparently, the longer distance among large trees and the capacity of the very abundant small trees to fill spaces make it more probable to find both kinds of sizes next to each other. Plot 07 has a more regularly decreasing diameter distribution, and such decrement is also reflected in the overall values of Table 10, specifically in the number of nearest neighbor trees with same sizes, suggesting a rather random distribution. Nevertheless, the ingrowth from 2009, in the same way like in plot 06, appears around the location of a number of trees of the same kind already established, materializing the formation of a cluster. PRP 08 follows the pattern of PRP 07, but the frequencies in the smallest classes are much higher. The 74.4% reached by class five reflects its remarkable density visible in the formation of four small clusters and a very large one. The density, frequency and dispersion of this class affect the detection of clusters in the two following classes, which are present in the same area of the referred class.

Table 11. Averages of the differences of diameters between two nearest neighbor trees (cm). Values are given for the actual diameters of the trees, and after the randomization of the diameters along the same horizontal structure of the plot.

| Plot | Year | Observed average | After randomization | | |
|------|------|------------------|-----------------|-----------------|-----------------|
| | | | Mean average | Minimum average | Maximum average |
| 1 | 1980 | 13.25 | 14.15 | 12.35 | 16.37 |
| | 2009 | 14.67 | 15.91 | 12.97 | 20.14 |
| 2 | 1980 | 9.09 | 9.89 | 8.95 | 10.88 |
| | 2007 | 9.25 | 10.29 | 8.85 | 11.13 |
| 3 | 1980 | 13.05 | 13.28 | 11.24 | 15.50 |
| | 2009 | 15.58 | 14.85 | 11.89 | 17.87 |
| 4 | 1980 | 12.07 | 12.07 | 10.20 | 14.40 |
| | 2009 | 12.75 | 13.42 | 9.79 | 15.78 |
| 5 | 1981 | 11.73 | 12.98 | 11.22 | 14.89 |
| | 2009 | 9.30 | 11.54 | 8.59 | 14.09 |
| 6 | 2005 | 27.30 | 34.85 | 27.33 | 40.17 |
| | 2009 | 24.73 | 31.44 | 24.35 | 37.71 |
| 7 | 2005 | 22.25 | 25.78 | 23.14 | 28.77 |
| | 2009 | 21.49 | 25.74 | 22.84 | 28.82 |
| 8 | 2007 | 8.80 | 17.56 | 16.26 | 18.99 |

The following step in the evaluation of the horizontal diametric distribution was to compare the actual dispersal of the observed list of diameters with the dispersal after repeated randomizations (Table 11). To do that, the list of diameters was randomly dispersed a hundred times along the actual geometrical position of the trees. After each randomization, the difference of diametric size between two nearest neighbor trees was calculated, as well as the average of differences for the plot. Mean, maximum and minimum averages were recorded for the comparison with the observed averages. Additionally, the diametric values were also arranged in an organized dispersion, forming a few large clusters, with the intention to establish the minimum averages that hypothetical very well aggregated plots could display. The results show that theoretically well aggregated managed plots can reach an average between 1 cm and 2 cm, while unmanaged plots show a range between 2 cm and 13 cm. The observed values for all the unmanaged plots, both at the first and last measurement, lay between the range of minimum and maximum averages, reinforcing the assertion that their diametric dispersion follows a random pattern. Both plots 06 and 07 show observed values close to the lower average of the randomizations, but values of plot 06 are a little closer and even inside the range, compared with plot 07. This is unexpected, considering that plot 06 displays clearer formation of aggregation than its counterpart. The explanation is found on the fact that the higher percentage of medium and large individuals closer to small ones, in plot 06, affects the distribution of diametric differences. Additionally, the maximum diameter found in the plot is much bigger than in plot 07, along with the diametric difference with its closest neighbor, which also influences the average. In contrast, plot 07 allocates diameters in a more even way, at the time that keeps a closer distance between small class trees. Plot 08 exhibits the smallest observed average, and with it, the clearest aggregation pattern of all plots, reiterating the findings of the previous observations.

*Diametric increments*

As seen in Table 12 and Fig. 14, most of the managed plots show a prominent augment in their diameter increment values for a period between 2002 and 2005, that reaches around the double of the value in 1997/1998. After 2005, the increments are reduced to values equal, lower or still higher than the ones before the increment rise. To avoid influence of the relative size of the trees on the evaluation of the growth, values are also shown in terms of percentage of the increment in relation to the previous recorded diameter. The arrangement of increments in percentage shows differences between years similar to the ones in the regular units. 1% per year appears to be a virtual limit for mean annual diametric growth per hectare in these stands. In general, values of DBH and diametric increment in centimeters of managed and unmanaged plots are positively correlated, though not always significantly. The dispersion of increments in percentage for managed plots shows similar arrangements to the ones of increments in centimeters, suggesting that growth is proportional to the size. Unmanaged plots, on the other hand, display very dissimilar dispersions of increments in both units. In fact, the dispersion of increments in percentage against DBH resembles very much the diametric distribution. That is to say, smaller trees have higher increments in proportion to their initial size than medium and large ones. This is also evident by observing the mean values in Table 12, where relatively small averages of increments in centimeters (affected by the small absolute increment of small trees) correspond to relatively higher averages of increments in percentages.

Table 12. Average diametric increments for the plots.

| Plot | Year | Periodic mean increment (cm) | Periodic mean increment (%) | Periodic mean annual increment (cm/year) | Periodic mean annual increment (%/year) |
|---|---|---|---|---|---|
| 1 | 1997 | 3.28 | 6.00 | 0.19 | 0.35 |
|   | 2002 | 2.49 | 4.46 | 0.50 | 0.89 |
|   | 2005 | 1.55 | 2.58 | 0.52 | 0.86 |
|   | 2009 | 1.23 | 1.92 | 0.31 | 0.48 |
| 2 | 1997 | 2.56 | 6.85 | 0.15 | 0.40 |
|   | 2003 | 2.01 | 5.35 | 0.33 | 0.89 |
|   | 2007 | 0.48 | 1.20 | 0.12 | 0.30 |
| 3 | 1997 | 4.07 | 7.05 | 0.24 | 0.41 |
|   | 2002 | 1.17 | 1.96 | 0.23 | 0.39 |
|   | 2005 | 1.39 | 2.20 | 0.46 | 0.73 |
|   | 2009 | 0.57 | 0.89 | 0.14 | 0.22 |
| 4 | 1997 | 4.44 | 8.20 | 0.26 | 0.48 |
|   | 2003 | 2.91 | 5.48 | 0.48 | 0.91 |
|   | 2005 | 0.81 | 1.40 | 0.41 | 0.70 |
|   | 2009 | 0.72 | 1.12 | 0.18 | 0.28 |
| 5 | 1998 | 2.93 | 6.07 | 0.17 | 0.36 |
|   | 2003 | 2.20 | 4.46 | 0.44 | 0.89 |
|   | 2005 | 1.26 | 2.39 | 0.63 | 1.19 |
|   | 2009 | 0.84 | 1.51 | 0.21 | 0.38 |
| 6 | 2009 | 0.64 | 4.19 | 0.16 | 1.05 |
| 7 | 2009 | 0.39 | 1.9 | 0.10 | 0.48 |
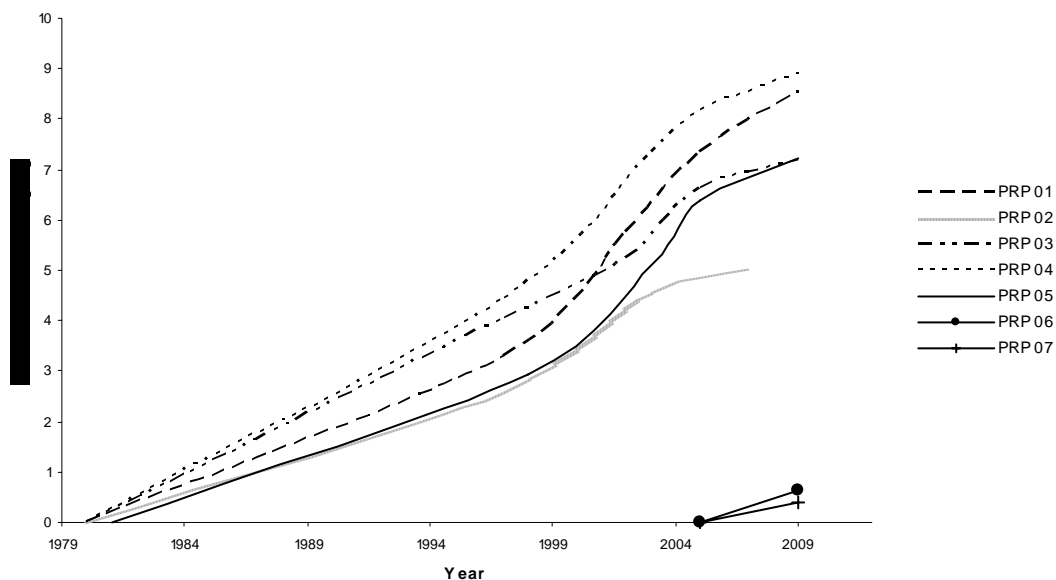


Fig. 14. Accumulated periodic diametric increments

With the intention to identify possible exterior factors that influence diametric increment in percentage, correlation analyses involving the presence of surrounding trees were performed. Distance to the nearest tree, its diameter, its height, the difference

in diameter and height between both trees, the average distance to the four nearest trees, and the difference in diameter and height between the referred tree and the average of the four nearest trees, were the factors considered in this process. Additionally, the influence of the cenotic position (dominance) of the referred tree on the diametric increment was calculated by an analysis of variance (ANOVA). All the factors involving the difference between tree dimensions (DBH and height of the one nearest and four nearest trees) proved statistically significant Spearman rank correlation to the increment (probability smaller than 0.05) at the first year of remeasurement for almost all the managed plots. The following years, those factors only show occasional importance in an irregular way. Irregular and occasional importance was also displayed for the other analyzed factors. In order to evaluate these factors in smaller diametric ranges, it was necessary to combine the elements of all the five managed plots into one single set of data, and to classify trees in three diametric classes (< 30 cm, 30 to 60 cm, and > 60 cm). the results showed no effect of any factor in class 60, significant correlation by the distance to the one nearest tree in class > 30, and seven factors significantly correlated to the increment in class 30 to 60 (factors involving the difference between tree dimensions (DBH and height of the one nearest and four nearest trees), plus diameter and height of the nearest tree and the average distance to the four nearest trees). Unmanaged plots (06 and 07) exhibited very dissimilar results. Plot 06 showed correlation to the distance to the one nearest tree and average of distances to nearest trees, while plot 07 showed correlation to height difference to the nearest trees, as well the diameter and height of the closest tree. The ANOVA performed to evaluate the influence of the social status proved statistical significance in plots 01, 03, 06 and 07. Nonetheless, the unmanaged plots show highest increments in percentage in trees less than 20 m height, while all the managed plots show higher increments in percentage in codominant trees.

*Height and crown characterization*

The Distance separating height distributions of plots 01, 03, 04, and 05 in relation to plot 02 (Fig. 15) is even larger than the distance found between the diameter distributions of the same groups of plots. 75% to 80 % of the trees in plots 01, 03, 04, and 05 are in height classes 37 to 43, while 74% of the trees in PRP 02 belong to classes 27 to 31. There is also a narrower range of classes holding most of the trees in plot 02 (6 m between the limits of the range), than in the rest of the managed plots (8 m between the limits of the range). This feature is, of course, an indication of the higher homogeneity characteristic of PRP 02, which is related to its high density.

Three different expressions are observed in the case of the unmanaged plots 06 to 08. As PRP 07 allocates similar proportions of trees in a wide range of classes, PRP 06 accumulates more trees in the lower and higher classes, and PRP 08 reduces its range to distribute rather even proportions in high and middle classes, while gathering most of the trees in the lowest ones. Two characteristic features seem to be present in the three distributions. There is an abrupt variation in the proportion of trees in classes 6 to 9, and a similar variation of proportions in the last three classes. Both traits are present in the unmanaged plots, and can be expected for many kinds of size distributions, but in the case of unmanaged plots, the fist trait does not seem so obviously expected.
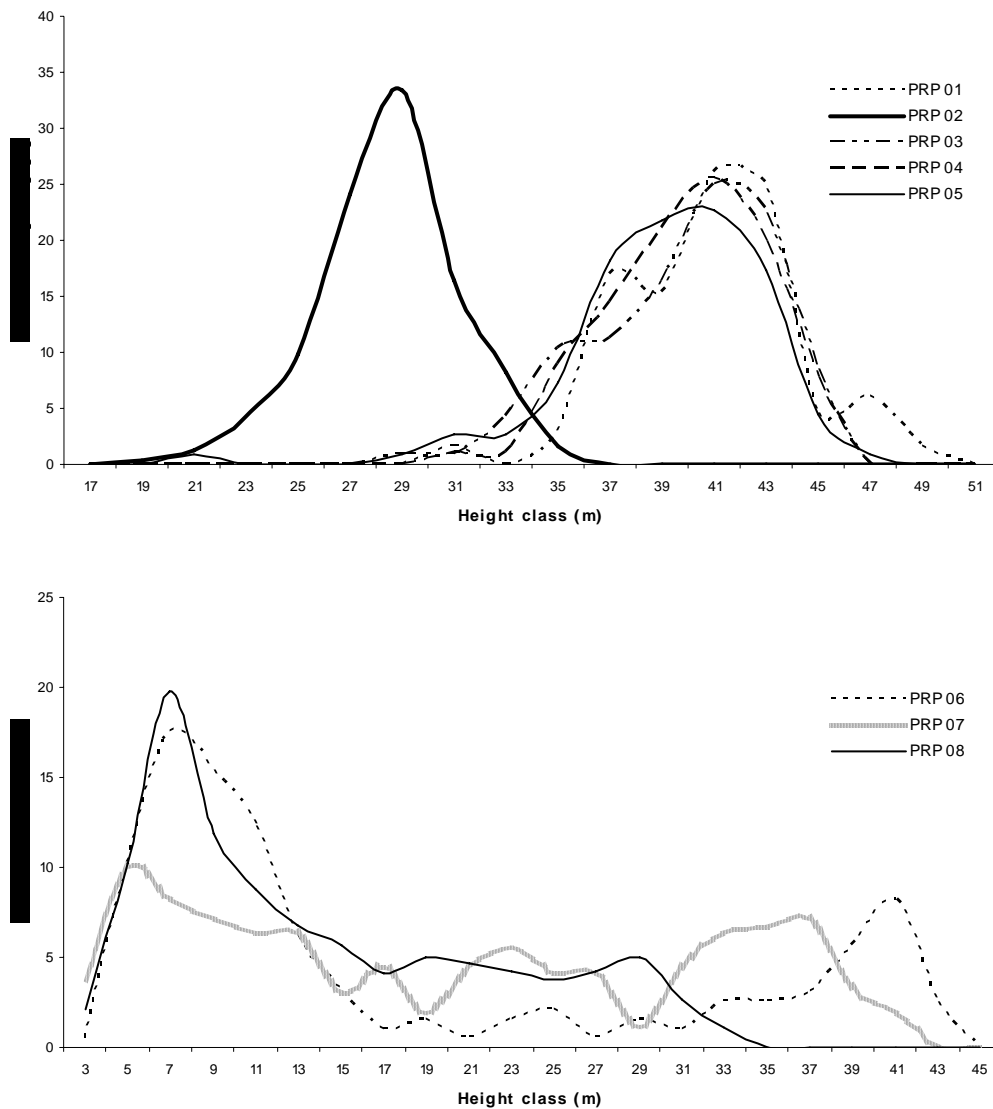
Fig. 15. Height distributions for PRPs 01 to 05 (up) and 06 to 08 (down). Values recorded in 2005 for PRPs 01, 03, 04, 05, 06 and 07, and in 2007 for PRP 02 and 08.

There is a very close similarity in the display of the polynomial linear regressions for the crown area in relation to the diameter in plots 01 to 05 (Fig. 16). The extension of the regression lines varies according to the ranges of diameters in each plot, and the fitting and course of the lines get affected by points at both extremes of the range. Moreover, comparing the arrangement of these relations for each plot requires considering the distribution of the distances from the fitting line to each one of the points. To combine both considerations, additional regressions were made for a range of diameters common for the group of plots (35 cm to 70 cm, in the case of managed plots, and less than 30 cm in the case of unmanaged plots), and the calculation of mean absolute errors (MAE) for the fitting lines was also carried out. Values of MAE from 16 cm to 18.5 cm were common for most of the managed plots, except for PRP 02, for which the mean absolute error reached half of the aforementioned values. These results should be related to the fact that total heights are also mostly dispersed in a smaller range of classes in this plot. The differences found in the case of unmanaged plots were much smaller, since the crown areas of trees below 30 cm of DBH are as well smaller,

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though it is still possible to observe a wider dispersion of the crown areas in the trees of PRP 07 in comparison to PRP 08. The slope of the fitting lines of managed and unmanaged plots are very similar, though the last ones are placed somewhat lower than the first ones. As a result, a tree with 60 cm of DBH in a managed plot has a crown area of 100 m$^2$ in average, while a tree with similar DBH in an unmanaged plot has 80 m$^2$ in average.
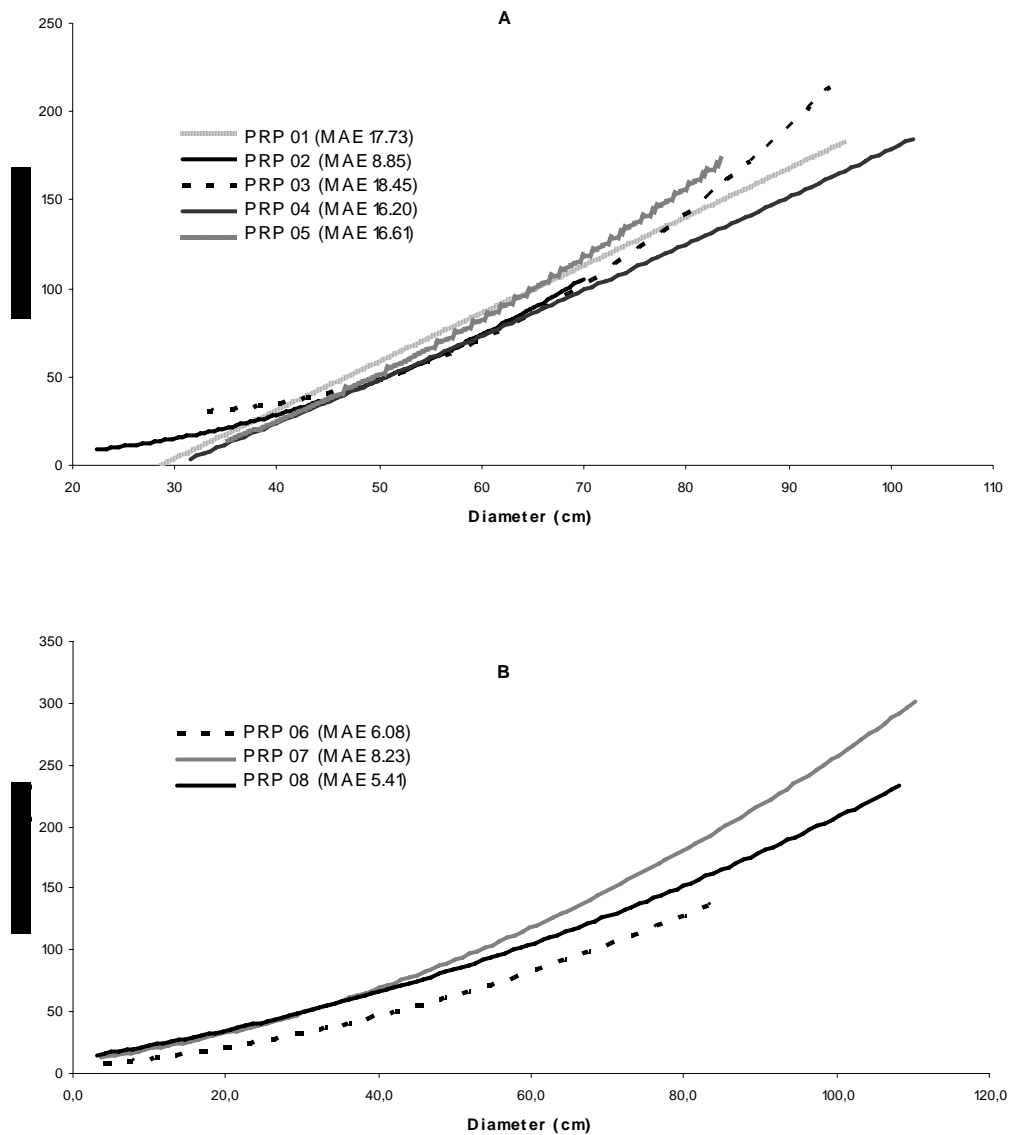


Fig. 16. Relation between crown area and diameter of beech in managed plots (A) and unmanaged plots (B).
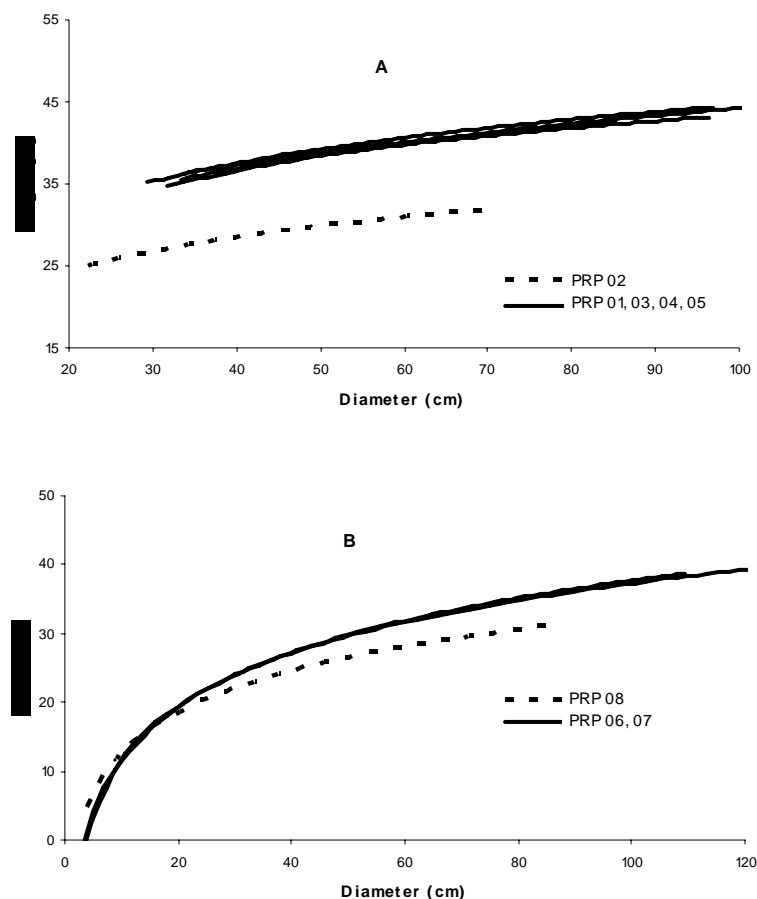
Fig. 17. Relation between height and diameter in managed plots (A) and unmanaged plots ( B).

The relation between height and diameter does not show big differences in terms of deviation of the dispersed points from each fitting line (Fig. 17). PRPs 01, 03, 04 and 05 express one common pattern when they are put together, but a closer look shows that the small differences can be related to the density of dispersed points present in the graph for each plot (in other words, the total number of trees). A visual inspection indicates a wider vertical separation of the point dispersion of plots 01 and 03. In fact, from the group of plots 01 to 05 (except 02) plots 01 and 03 have the lowest and highest number of trees (65 and 116 resp.). The larger separation between PRP 02 and the other managed plots seems to respond to the bigger difference in total number of tress of the first one. A linear regression for the average heights against total number of trees, with $R^2=0.98$, supports this view. Unmanaged plots converge for small diameters and describe a higher proportion of height growth against DBH for trees smaller than 20 cm of diameter. PRP 08 displays a separation of its fitting line from the other two plots, though in this case much smaller. The slope of the biggest part of the fitting lines for unmanaged plots coincides with the one for managed plots, but in the first case, height values reach about 10 m less in average than for the second one.

The differences found in the relations between height and DBH illustrated before resemble the ones observed in the relations between h/d ratio and DBH (Fig. 18).

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Values of h/d ratio for PRP 02 are in average 0.18 lower than for the other managed plots. For the unmanaged plots, plots 06 and 07 hold the highest density of trees in values approximately lower than 25 cm of DBH and 1.2 of h/d ratio, while plot 08 holds most of its trees in values lower than 20 cm of DBH and 0.9 to 1.7 of h/d ratio. In general, it is clear to see an exponential increase of the variability of h/d ratio values inversely related to the sizes of DBH. Trees with the smallest diameters are also the slenderest. As diameter grows, height grows increasingly slower and when trees reach about 20 to 30 cm of DBH the reduction of height growth in relation to the diameter stabilizes to a minimum. There is a virtual lower limit of h/d ratio for the unmanaged plots defined as 0.4, under which only occasional trees are found.
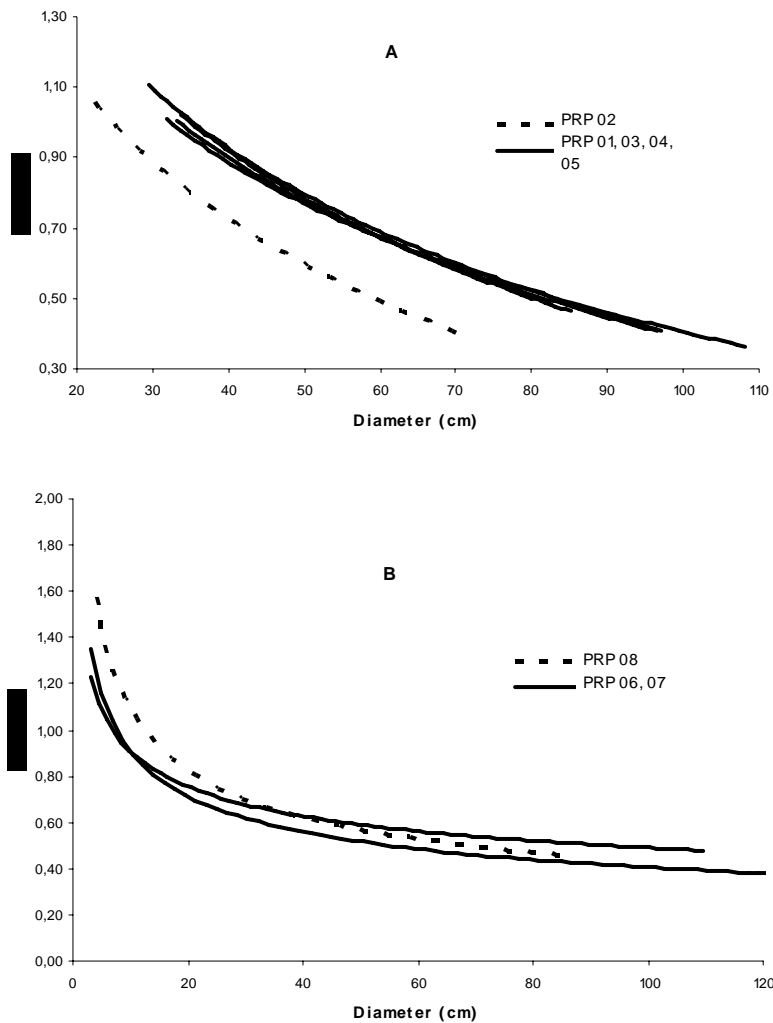


Fig. 18. h/d ratio against DBH for managed (A) and unmanaged plots (B).


*Volume and stand characteristics.*

Basal areas per hectare reached maximum values between 1997 and 2003 in plots 01, 03, 04 and 05, after which annual values decline (Table 13). Plots 01 and 05 suffer the strongest decline, while 03 and 04 display a similar and slower pattern. On the other

hand, plot 02 shows a steadier progress in basal area formation till 2003, followed only by a very discreet reduction. After 4 years, the unmanaged plots (06 and 07) exhibit little change in their total count of basal area, due to a very low mortality, whereas the value for the most recently established plot 08 comes out close to its counterparts. Small changes in basal area coincide with low reductions in stand density in plots 03 and 04, while plots 01 and 05 have reduced 42 and 27% resp. since the beginning of measurements. PRP 02 is the only plot that has maintained a higher basal area in relation to a fully stocked stand, as shown by the value of stand density, in response to only minor variation of diameter and height averages. With 87.37% of its surface covered by tree crowns, plot 02 maximize the use of the upper space without being able to reach a complete closure, while unmanaged plots rise above this number by means of overlaying trees of different stratums. In this way, unmanaged plots can keep a very high canopy cover and occurrence of canopy gaps at the same time. Reductions in canopy cover for the managed stands have been according to the level of harvesting performed since the prior measurement, ranging from 200 m$^2$ to more than 1200 m$^2$.

Table 13. General stand characteristics.

| Plot | Year | Age (years) | n | G (m$^2$/ha) | $\rho$ | Crown Cover (m$^2$/ha) | d mean (cm) | h mean (m) | h 10% (m) | V (m$^3$/ha) | Harvest/ Mortality (m$^3$/ha) | Periodic annual volume production (m$^3$/ha/year) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 01 | 1980 | 158 | 170 | 37.25 | 0.88 | - | 51.33 | 38.24 | 43.71 | 757.99 | - | - |
| | 1997 | 175 | 149 | 37.79 | 0.84 | - | 55.16 | 40.7 | 44.1 | 816.23 | 78.14 | 8.02 |
| | 2002 | 180 | 114 | 32.94 | 0.74 | - | 59.05 | 38.58 | 45.20 | 688.88 | 152.00 | 4.93 |
| | 2005 | 183 | 93 | 27.23 | 0.60 | 6604.20 | 59.57 | 40.89 | 46.11 | 597.48 | 151.21 | 19.94 |
| | 2009 | 187 | 65 | 21.55 | 0.46 | 5355.49 | 63.46 | 40.97 | 46.36 | 477.49 | 139.23 | 4.81 |
| 02 | 1980 | 147 | 399 | 36.51 | 1.11 | - | 33.01 | 26.37 | 32.20 | 508.11 | - | - |
| | 1997 | 164 | 346 | 39.91 | 1.12 | - | 37.14 | 29.56 | 34.60 | 617.48 | 23.41 | 7.81 |
| | 2003 | 170 | 321 | 42.56 | 1.14 | - | 40.04 | 31.90 | 35.38 | 687.20 | 16.40 | 14.35 |
| | 2007 | 174 | 306 | 42.21 | 1.21 | 8737.45 | 40.91 | 28.41 | 33.13 | 684.03 | 14.40 | 2.81 |
| 03 | 1980 | 168 | 149 | 37.54 | 0.89 | - | 55.42 | 37.41 | 42.57 | 745.31 | - | - |
| | 1997 | 185 | 138 | 40.87 | 0.92 | - | 60.11 | 39.5 | 41.54 | 859.29 | 36.26 | 8.84 |
| | 2002 | 190 | 132 | 40.93 | 0.89 | - | 61.60 | 40.82 | 45.80 | 898.71 | 28.88 | 13.66 |
| | 2005 | 193 | 126 | 40.44 | 0.89 | 8304.96 | 62.46 | 39.95 | 44.97 | 863.72 | 43.41 | 2.81 |
| | 2009 | 197 | 116 | 37.41 | 0.82 | 7670.94 | 62.76 | 39.88 | 44.85 | 800.64 | 76.74 | 3.41 |
| 04 | 1980 | 163 | 139 | 32.13 | 0.74 | - | 53.2 | 38.76 | 43.04 | 659.23 | - | - |
| | 1997 | 180 | 127 | 34.64 | 0.77 | - | 57.76 | 40.07 | 43.5 | 737.06 | 54.22 | 7.77 |
| | 2003 | 186 | 112 | 33.33 | 0.74 | - | 60.26 | 40.40 | 43.37 | 716.35 | 94.39 | 12.28 |
| | 2005 | 188 | 110 | 32.89 | 0.73 | 6850.69 | 60.49 | 39.99 | 44.91 | 711.05 | 10.63 | 2.66 |
| | 2009 | 192 | 90 | 28.22 | 0.62 | 5926.13 | 61.98 | 40.08 | 44.84 | 605.41 | 115.04 | 4.10 |
| 05 | 1981 | 148 | 220 | 36.50 | 0.90 | - | 44.55 | 35.67 | 41.55 | 691.72 | - | - |
| | 1998 | 165 | 195 | 39.01 | 0.91 | - | 49.05 | 38.76 | 42.05 | 790.56 | 32.36 | 7.72 |
| | 2003 | 170 | 142 | 31.10 | 0.71 | - | 51.47 | 38.51 | 42.34 | 626.30 | 200.13 | 7.17 |
| | 2005 | 172 | 117 | 28.78 | 0.66 | 6689.83 | 55.18 | 39.47 | 44.72 | 583.2 | 74.88 | 15.89 |
| | 2009 | 176 | 110 | 27.76 | 0.63 | 6477.15 | 55.69 | 39.25 | 44.35 | 575.99 | 37.29 | 7.52 |
| 06 | 2005 | 155 | 204 | 35.61 | - | 8657.07 | 32.09 | 17.92 | 41.36 | 706.26 | - | - |
| | 2009 | 159 | 231 | 35.06 | - | 8505.69 | 27.77 | 15.79 | 41.42 | 685.78 | 41.85 | 5.34 |
| 07 | 2005 | 155 | 272 | 30.71 | - | 8413.00 | 29.62 | 20.20 | 38.4 | 494.06 | - | - |
| | 2009 | 159 | 286 | 30.79 | - | 8422.94 | 28.35 | 19.36 | 38.4 | 495.45 | 2.71 | 1.03 |
| 08 | 2007 | 180 | 708 | 35.58 | - | 9217.44 | 18.39 | 14.10 | 29.73 | 461.66 | - | - |

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Different quantities of dead trees and ingrowth have resulted in dissimilar variations of crown cover in the unmanaged plots. Ten trees died in PRP 06 by 2009 and only three in PRP 07, whereas thirty eight small trees grew into plot 06 and seventeen in 07. Though the amount of ingrowth in 06 is more than the double than 07, the proportionally very small crowns of these new trees do not add much to the total of each plot, giving that the level of mortality is much superior. In the same way like the basal area, the volumes of the plots reached their highest point between 1997 and 2003. In fact, plots 01, 03, 04 and 05 maintain almost the same rank and pattern in terms of volume as the ones observed for basal area. Plot 02 also keeps the same pattern for both variables, but its lower volume values place it in a lower position (in comparison to the other plots) than in the case of the basal area. Relatively lower diameters and heights limit the scope of volume values in this plot, though its latest total amount, affected by enduring accumulation, is the second highest value.

Harvesting during the first seventeen years was the lowest registered in all plots (less than three trees per year till 1997). After that point, plots 01 and 05 had the most intense harvests (7 in average till 2009 for plot 01, and 11 till 2005 for plot 05). Plot 02 has had the most regular harvest with four trees per year. Disparity in the volumes of periodic harvest, in correspondence to the number of harvested trees, indicates variability in the sizes of the removed individuals. Nearly all the harvests performed in plot 01 through the years consist of a selection of trees along the different size classes of the existing distribution, with larger number of trees from the middle and more abundant classes. It was only by 2009 that a restricted selection, which excluded trees from the five larger diameter classes of the plot, was registered. Apart of the notoriously lower extraction in comparison with plot 01, the evenly distributed size selection, evident in all years but 2009, was also present in plot 03. The variable quantities harvested in plot 04, in consecutive years, do not reveal uneven selection. As for plot 05, a restricted harvest to middle and smaller sized trees seems to have taken place by 2009 as well as 1997, while softer emphasis in restriction was carried out between those years. On the other hand, plot 02 is a very particular case, where the eight largest diametric classes went virtually untouched by the harvesting measures through all the years. The selective removals are perceived in the values of periodical harvest, especially in the case of plot 02, where large numbers of harvested trees make only fractions of volume of what smaller numbers represent in other plots. The steeper decline in stand volume in plot 01 is a consequence of a combination of large diameters and heights (also manifest in the h10% periodic values), and larger numbers of harvested trees. Though similar numbers of trees were removed in plot 05, the relatively smaller size of its individuals and the performance of a more selective harvest result in a lower amount of removed volume. The periodic annual volume production reaches values between 2.4 and 19.9 $m^3$ among the managed plots. Accumulated growth for the total period of 27/29 years range from 229 to 240 $m^3$ (plots 01 and 03 have the highest values). Nevertheless, the total relative volume production reveals different effective growth, since plots 01, 03, 04 and 05 increased 32 to 33% of their original volumes, while plot 02 obtained 45%.

The increment in the number of small trees reduces both the diameter and height averages of plots 06 and 07. Volume values are not really affected, since the total amount of wood represented by ingrowth reaches only 0.12 to 0,16 $m^3$. The 9.3% of individuals in plot 06, which represent species different to beech, account for the 3.7% (25.52 $m^3$) of the total volume of the plot (a change of -0.7 $m^3$ since 2005), the majority of which comes from larch and hornbeam. As for plot 07, the 27% of individuals,

representing species different to beech, account for 2.8% (138.11 m$^3$) of the total of the plot (a change of -3.7 m$^3$ since 2005), the majority of which comes from larch, spruce and hornbeam. The 11.3% of individuals in plot 08, representing species different to beech, account for 1.2% (5.45 m$^3$) of the total of the plot, the majority of which comes from one big larch (3.22 m$^3$) and 68 small firs (1.82 m$^3$). Five of the dead trees in plot 06 in 2009 are less than 10 cm of diameter, four are between 10 and 100 cm, and one is bigger than 100 cm of diameter. The three dead trees of plot 07 are between 5 and 26 cm of DBH. Very different wood production was registered in both plots. 21.4 m$^3$ in plot 06 against 4.1 m$^3$ in plot 07 (5.3 m$^3$ and 1.0 m$^3$ annually resp.) represent 3.0% and 0.8% of the total growth.
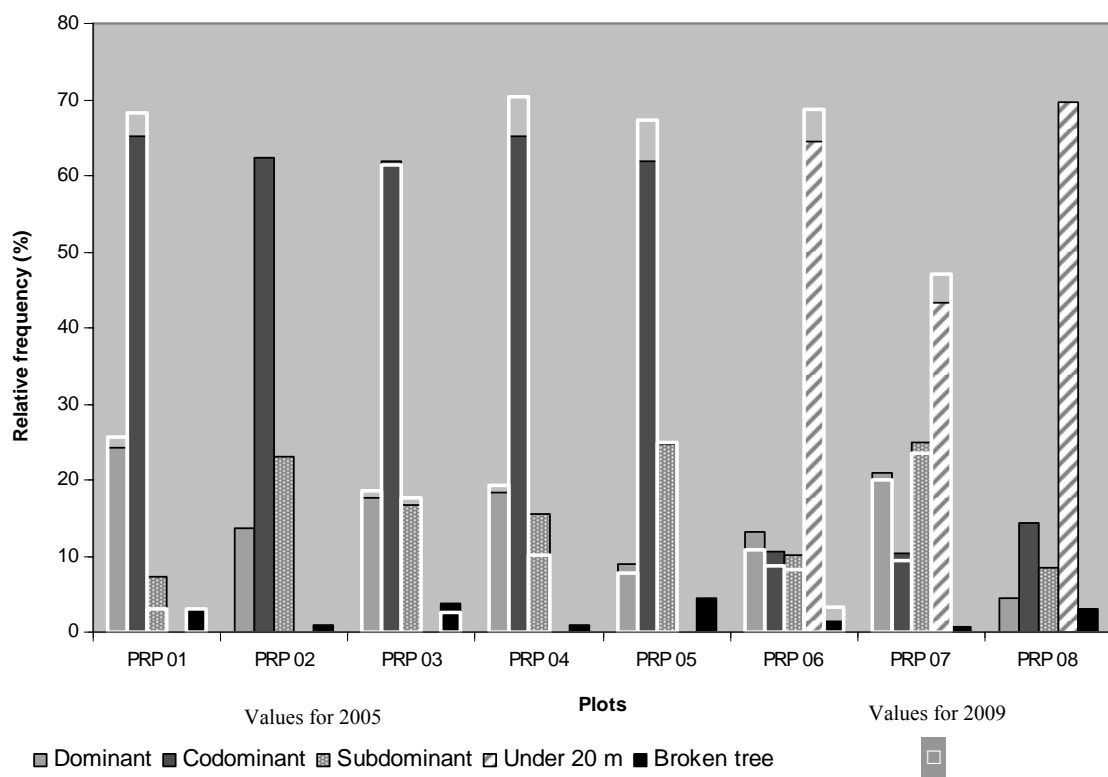
*Cenotic position.*



Fig. 19. Cenotic positions for 2005 and 2009. Data of PRPs 02 and 08 only available for 2007.

The broken trees in plots 04 and 05 were removed by 2009, while in the other two managed plots a small reduction in this class was registered (Fig. 19). Dominant, codominant and subdominant trees were extracted in almost all managed plots. Though the quantities were different in each case, a bigger proportion of harvested trees is observed in the codominant class, which is also the most abundant. Despite the greater density, values for plot 02 appear in the same ranges as the ones observed in the other managed plots, including the absence of trees under 20 m of height and the very small proportion of broken trees. Appearance of new broken trees and fell of existing ones occurred in plots 06 and 07, in addition to an increment of trees under 20 m, as a result of the registering of ingrowh. Proportional numbers of disappeared individuals from the

other classes is also observed. A particularly superior abundance of trees under 20 m is distinctive of PRP 08, complemented by a relatively small proportion of dominant ones, at the same time that the codominant class gains relative importance.


*Spatial distribution of trees.*

PRP 01 evidences a regular pattern of the dispersion of individuals during the first 25 years, adopting a random tendency by 2009 (Table 14). Harvest of the plot proved to be aggregated only by 2005, while the rest of the time it has occurred quite randomly. Plot 02 has been decidedly regular from the beginning, which is perhaps expected for a plot of such density. The harvesting has happened randomly, except by the last year, when a tendency to aggregation of the extraction was observed. Changes from regular to random are noticed for plot 03 under recurrent random harvest. Plot 04 has remained rather random under changing aggregated-random tree removals. Conversely and under fairly random harvests, plot 05 has kept very regular distributions over time.

Several different group analyses were made in the case of the unmanaged plots, motivated by the high variability in the classification of the trees (Table 15). By 2005, plot 06 showed an aggregated tendency when considering all species. All beech trees showed a stronger aggregated pattern that was restricted to trees smaller than 20 m when analyzing trees by sizes. In the same process, beech trees higher than 20 m registered regularity. The most representative secondary species (hornbeam) revealed a dispersion with inclination to aggregation. By 2009, the dispersions of both groups of all beech trees and all species were unaltered by the presence of ingrowth, showing aggregation patterns in every case. This fact is partly explained by the aggregated pattern of the ingrowth itself. Beech trees of less than 20 m kept their aggregated spatial distribution, but bigger beech trees passed from regular to random. The aggregated inclination of hornbeam was moved to the regular side, while the pattern of all the dead trees of the period was clearly random.

Randomness was a characteristic shared by the groups of all trees, all beech trees, beech more than 20 m and hornbeam trees in the case of plot 07 in 2005 (Table 16). Both larch and spruce showed an aggregated inclination, whereas beech trees smaller than 20 m shared the aggregation pattern on plot 06. Similarly to plot 06, the inclusion of the ingrowth in 2009 did not alter the dispersion description of larger groups consisting of trees of all species and beech of all sizes, despite the fact that the first group is displayed as random and the second as aggregated. Ingrowth itself was described as aggregated, which was a pattern clearly sustained by beech trees less than 20 m, spruces and larches. Beech trees higher than 20 m as well as hornbeams kept their random dispersion description.

In plot 08, the separation of the trees of all species in categories reveals strong aggregation distribution for individuals smaller than 20 m, as well as aggregation tendency in trees bigger than 20 m and the combinations of the categories (Table 17). Identical results were obtained for beech trees in separated categories and as a single group. The most abundant secondary species (fir) confirmed a strong aggregated pattern, while spruce described a random tendency.

Table 14. Spatial distribution indices for managed plots.

| Plot | Year | Index | Index value for alive trees | | | | Index value for harvested trees | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Observed | Expected | Lower bound | Upper bound | Observed | Expected | Lower bound | Upper bound |
| 1 | 1980 | Hopkins-Skellam | 0.303 | 0.5 | 0.428 | 0.575 | - | - | - | - |
| | | Pielou-Mountford | 0.654 | 1.086 | 0.883 | 1.358 | - | - | - | - |
| | | Clark-Evans | 1.338 | 1.034 | 0.95 | 1.116 | - | - | - | - |
| | 1997 | Hopkins-Skellam | 0.364 | 0.5 | 0.425 | 0.578 | 0.471 | 0.492 | 0.306 | 0.715 |
| | | Pielou-Mountford | 0.861 | 1.089 | 0.876 | 1.37 | 1.163 | 1.206 | 0.653 | 2.218 |
| | | Clark-Evans | 1.328 | 1.035 | 0.944 | 1.124 | 1.058 | 1.106 | 0.827 | 1.376 |
| | 2002 | Hopkins-Skellam | 0.36 | 0.499 | 0.416 | 0.594 | 0.581 | 0.496 | 0.351 | 0.674 |
| | | Pielou-Mountford | 0.805 | 1.1 | 0.853 | 1.438 | 2.795 | 1.172 | 0.732 | 1.882 |
| | | Clark-Evans | 1.288 | 1.042 | 0.936 | 1.144 | 1.154 | 1.078 | 0.875 | 1.277 |
| | 2005 | Hopkins-Skellam | 0.343 | 0.498 | 0.403 | 0.604 | 0.772 | 0.495 | 0.302 | 0.724 |
| | | Pielou-Mountford | 0.807 | 1.108 | 0.838 | 1.49 | 2.582 | 1.216 | 0.643 | 2.225 |
| | | Clark-Evans | 1.331 | 1.047 | 0.931 | 1.167 | 0.915 | 1.104 | 0.823 | 1.386 |
| | 2009 | Hopkins-Skellam | 0.46 | 0.497 | 0.387 | 0.622 | 0.484 | 0.495 | 0.33 | 0.7 |
| | | Pielou-Mountford | 1.286 | 1.128 | 0.794 | 1.606 | 1.102 | 1.195 | 0.708 | 2.086 |
| | | Clark-Evans | 1.331 | 1.056 | 0.912 | 1.202 | 1.126 | 1.092 | 0.863 | 1.321 |
| 2 | 1980 | Hopkins-Skellam | 0.37 | 0.5 | 0.439 | 0.567 | - | - | - | - |
| | | Pielou-Mountford | 0.846 | 1.074 | 0.894 | 1.305 | - | - | - | - |
| | | Clark-Evans | 1.248 | 1.029 | 0.955 | 1.101 | - | - | - | - |
| | 1997 | Hopkins-Skellam | 0.33 | 0.5 | 0.436 | 0.572 | 0.517 | 0.495 | 0.322 | 0.707 |
| | | Pielou-Mountford | 0.712 | 1.078 | 0.891 | 1.321 | 0.986 | 1.206 | 0.681 | 2.153 |
| | | Clark-Evans | 1.245 | 1.03 | 0.948 | 1.107 | 1 | 1.097 | 0.848 | 1.343 |
| | 2003 | Hopkins-Skellam | 0.346 | 0.499 | 0.43 | 0.573 | 0.366 | 0.493 | 0.276 | 0.76 |
| | | Pielou-Mountford | 0.798 | 1.08 | 0.877 | 1.332 | 0.761 | 1.26 | 0.593 | 2.513 |
| | | Clark-Evans | 1.279 | 1.033 | 0.952 | 1.116 | 1.242 | 1.134 | 0.797 | 1.479 |
| | 2007 | Hopkins-Skellam | 0.35 | 0.498 | 0.43 | 0.571 | 0.923 | 0.483 | 0.189 | 0.854 |
| | | Pielou-Mountford | 0.833 | 1.076 | 0.882 | 1.32 | 2.457 | 1.284 | 0.401 | 3.089 |
| | | Clark-Evans | 1.295 | 1.033 | 0.949 | 1.113 | 0.489 | 1.224 | 0.639 | 1.81 |
| 3 | 1980 | Hopkins-Skellam | 0.39 | 0.498 | 0.425 | 0.581 | - | - | - | - |
| | | Pielou-Mountford | 0.929 | 1.086 | 0.877 | 1.361 | - | - | - | - |
| | | Clark-Evans | 1.277 | 1.036 | 0.944 | 1.126 | - | - | - | - |
| | 1997 | Hopkins-Skellam | 0.357 | 0.499 | 0.423 | 0.588 | 0.511 | 0.485 | 0.245 | 0.793 |
| | | Pielou-Mountford | 0.783 | 1.092 | 0.874 | 1.395 | 1.721 | 1.254 | 0.533 | 2.727 |
| | | Clark-Evans | 1.26 | 1.038 | 0.943 | 1.133 | 1.215 | 1.16 | 0.755 | 1.577 |
| | 2002 | Hopkins-Skellam | 0.387 | 0.5 | 0.418 | 0.585 | 0.732 | 0.487 | 0.195 | 0.858 |
| | | Pielou-Mountford | 0.865 | 1.096 | 0.865 | 1.405 | 1.99 | 1.293 | 0.406 | 3.098 |
| | | Clark-Evans | 1.244 | 1.038 | 0.944 | 1.137 | 0.883 | 1.218 | 0.628 | 1.812 |
| | 2005 | Hopkins-Skellam | 0.476 | 0.499 | 0.416 | 0.592 | 0.513 | 0.489 | 0.189 | 0.85 |
| | | Pielou-Mountford | 1.15 | 1.096 | 0.862 | 1.42 | 1.71 | 1.305 | 0.401 | 3.195 |
| | | Clark-Evans | 1.195 | 1.039 | 0.939 | 1.141 | 1.069 | 1.217 | 0.663 | 1.843 |
| | 2009 | Hopkins-Skellam | 0.444 | 0.499 | 0.417 | 0.596 | 0.763 | 0.489 | 0.244 | 0.796 |
| | | Pielou-Mountford | 1.014 | 1.101 | 0.86 | 1.446 | 2 | 1.263 | 0.516 | 2.728 |
| | | Clark-Evans | 1.191 | 1.04 | 0.939 | 1.144 | 0.802 | 1.161 | 0.73 | 1.599 |
| 4 | 1980 | Hopkins-Skellam | 0.422 | 0.498 | 0.422 | 0.583 | - | - | - | - |
| | | Pielou-Mountford | 1.03 | 1.089 | 0.863 | 1.385 | - | - | - | - |
| | | Clark-Evans | 1.299 | 1.038 | 0.944 | 1.131 | - | - | - | - |
| | 1997 | Hopkins-Skellam | 0.405 | 0.498 | 0.418 | 0.586 | 0.952 | 0.493 | 0.257 | 0.781 |
| | | Pielou-Mountford | 0.918 | 1.092 | 0.859 | 1.406 | 4.898 | 1.268 | 0.555 | 2.589 |
| | | Clark-Evans | 1.275 | 1.041 | 0.943 | 1.139 | 0.529 | 1.146 | 0.766 | 1.539 |
| | 2003 | Hopkins-Skellam | 0.484 | 0.498 | 0.413 | 0.596 | 0.706 | 0.495 | 0.285 | 0.752 |
| | | Pielou-Mountford | 1.19 | 1.101 | 0.854 | 1.453 | 5.772 | 1.245 | 0.614 | 2.474 |
| | | Clark-Evans | 1.233 | 1.043 | 0.934 | 1.154 | 0.845 | 1.12 | 0.794 | 1.439 |
| | 2005 | Hopkins-Skellam | 0.462 | 0.498 | 0.411 | 0.592 | - | - | - | - |
| | | Pielou-Mountford | 1.123 | 1.101 | 0.851 | 1.438 | - | - | - | - |
| | | Clark-Evans | 1.245 | 1.043 | 0.936 | 1.149 | - | - | - | - |
| | 2009 | Hopkins-Skellam | 0.554 | 0.498 | 0.401 | 0.606 | 0.757 | 0.492 | 0.3 | 0.728 |
| | | Pielou-Mountford | 1.518 | 1.113 | 0.834 | 1.533 | 1.624 | 1.21 | 0.644 | 2.219 |
| | | Clark-Evans | 1.207 | 1.049 | 0.929 | 1.17 | 0.759 | 1.107 | 0.824 | 1.393 |
| 5 | 1981 | Hopkins-Skellam | 0.397 | 0.499 | 0.436 | 0.568 | - | - | - | - |
| | | Pielou-Mountford | 0.859 | 1.071 | 0.897 | 1.299 | - | - | - | - |
| | | Clark-Evans | 1.223 | 1.029 | 0.954 | 1.102 | - | - | - | - |
| | 1998 | Hopkins-Skellam | 0.403 | 0.499 | 0.432 | 0.57 | 0.401 | 0.494 | 0.331 | 0.684 |
| | | Pielou-Mountford | 0.833 | 1.077 | 0.885 | 1.316 | 1.01 | 1.184 | 0.709 | 1.969 |
| | | Clark-Evans | 1.181 | 1.031 | 0.952 | 1.111 | 1.231 | 1.09 | 0.856 | 1.323 |
| | 2003 | Hopkins-Skellam | 0.385 | 0.499 | 0.425 | 0.584 | 0.417 | 0.498 | 0.375 | 0.64 |
| | | Pielou-Mountford | 0.837 | 1.09 | 0.876 | 1.389 | 0.922 | 1.147 | 0.783 | 1.693 |
| | | Clark-Evans | 1.215 | 1.037 | 0.941 | 1.13 | 1.152 | 1.062 | 0.902 | 1.216 |
| | 2005 | Hopkins-Skellam | 0.398 | 0.5 | 0.414 | 0.594 | 0.634 | 0.493 | 0.329 | 0.682 |
| | | Pielou-Mountford | 0.935 | 1.103 | 0.858 | 1.438 | 1.629 | 1.181 | 0.692 | 1.995 |
| | | Clark-Evans | 1.291 | 1.041 | 0.936 | 1.147 | 0.919 | 1.091 | 0.867 | 1.318 |
| | 2009 | Hopkins-Skellam | 0.344 | 0.498 | 0.414 | 0.593 | 0.567 | 0.484 | 0.201 | 0.832 |
| | | Pielou-Mountford | 0.744 | 1.102 | 0.855 | 1.448 | 1.036 | 1.28 | 0.42 | 3.054 |
| | | Clark-Evans | 1.297 | 1.042 | 0.935 | 1.147 | 0.984 | 1.205 | 0.691 | 1.742 |

\*     Bigger than uooer bound      Smaller than lower bound

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Table 15. Spatial distribution indices for PRP 06.

| Year | Class of trees | Index | Index value for alive trees | | | |
|------|---------------|-------|----------|----------|-------------|-------------|
| | | | Observed | Expected | Lower bound | Upper bound |
| 2005 | All trees | Hopkins-Skellam | 0,561 | 0,5 | 0,434 | 0,571 |
| | | Pielou-Mountford | 1,511 | 1,077 | 0,89 | 1,31 |
| | | Clark-Evans | 0,94 | 1,03 | 0,951 | 1,109 |
| | Beech, all sizes | Hopkins-Skellam | 0,662 | 0,499 | 0,432 | 0,571 |
| | | Pielou-Mountford | 2,146 | 1,079 | 0,886 | 1,341 |
| | | Clark-Evans | 0,916 | 1,033 | 0,947 | 1,113 |
| | Beech, less than 10m | Hopkins-Skellam | 0,75 | 0,498 | 0,402 | 0,609 |
| | | Pielou-Mountford | 3,389 | 1,116 | 0,837 | 1,535 |
| | | Clark-Evans | 0,781 | 1,049 | 0,93 | 1,171 |
| | Beech, 10 to 20 m | Hopkins-Skellam | 0,921 | 0,499 | 0,366 | 0,655 |
| | | Pielou-Mountford | 10,13 | 1,16 | 0,775 | 1,782 |
| | | Clark-Evans | 0,676 | 1,067 | 0,892 | 1,242 |
| | Beech, more than 20 m | Hopkins-Skellam | 0,34 | 0,497 | 0,364 | 0,64 |
| | | Pielou-Mountford | 0,705 | 1,148 | 0,769 | 1,717 |
| | | Clark-Evans | 1,29 | 1,066 | 0,896 | 1,238 |
| | Hornbeam | Hopkins-Skellam | 0,855 | 0,49 | 0,23 | 0,81 |
| | | Pielou-Mountford | 2,73 | 1,281 | 0,499 | 2,834 |
| | | Clark-Evans | 0,618 | 1,17 | 0,72 | 1,634 |
| 2009 | All trees (Without Ingrowth) | Hopkins-Skellam | 0,611 | 0,5 | 0,434 | 0,571 |
| | | Pielou-Mountford | 1,83 | 1,08 | 0,889 | 1,323 |
| | | Clark-Evans | 0,929 | 1,031 | 0,951 | 1,113 |
| | All trees (With Ingrowth) | Hopkins-Skellam | 0,592 | 0,499 | 0,436 | 0,567 |
| | | Pielou-Mountford | 1,625 | 1,072 | 0,893 | 1,296 |
| | | Clark-Evans | 0,913 | 1,029 | 0,958 | 1,103 |
| | Beech, all sizes (Without Ingrowth) | Hopkins-Skellam | 0,626 | 0,499 | 0,43 | 0,573 |
| | | Pielou-Mountford | 1,802 | 1,079 | 0,878 | 1,328 |
| | | Clark-Evans | 0,905 | 1,033 | 0,95 | 1,118 |
| | Beech, all sizes (With Ingrowth) | Hopkins-Skellam | 0,611 | 0,5 | 0,435 | 0,568 |
| | | Pielou-Mountford | 1,735 | 1,076 | 0,897 | 1,306 |
| | | Clark-Evans | 0,895 | 1,03 | 0,953 | 1,106 |
| | Ingrowth | Hopkins-Skellam | 0,942 | 0,496 | 0,356 | 0,664 |
| | | Pielou-Mountford | 4,568 | 1,167 | 0,755 | 1,867 |
| | | Clark-Evans | 0,466 | 1,075 | 0,882 | 1,267 |
| | Beech, less than 10m | Hopkins-Skellam | 0,709 | 0,499 | 0,399 | 0,612 |
| | | Pielou-Mountford | 2,924 | 1,115 | 0,827 | 1,524 |
| | | Clark-Evans | 0,771 | 1,047 | 0,921 | 1,175 |
| | Beech, 10 to 20 m | Hopkins-Skellam | 0,932 | 0,496 | 0,363 | 0,651 |
| | | Pielou-Mountford | 11,78 | 1,152 | 0,765 | 1,779 |
| | | Clark-Evans | 0,682 | 1,071 | 0,891 | 1,246 |
| | Beech, more than 20 m | Hopkins-Skellam | 0,407 | 0,498 | 0,371 | 0,653 |
| | | Pielou-Mountford | 0,969 | 1,153 | 0,777 | 1,761 |
| | | Clark-Evans | 1,301 | 1,065 | 0,893 | 1,227 |
| | Hornbeam | Hopkins-Skellam | 0,623 | 0,485 | 0,222 | 0,811 |
| | | Pielou-Mountford | 0,812 | 1,272 | 0,474 | 2,888 |
| | | Clark-Evans | 0,635 | 1,193 | 0,718 | 1,691 |
| | Dead trees | Hopkins-Skellam | 0,63 | 0,49 | 0,217 | 0,824 |
| | | Pielou-Mountford | 2,479 | 1,295 | 0,472 | 2,96 |
| | | Clark-Evans | 1,131 | 1,184 | 0,699 | 1,688 |

\* ▭ Bigger than uooer bound　　▭ Smaller than lower bound

Table 16. Spatial distribution indices for PRP 07.

| Year | Class of trees | Index | Index value for alive trees | | | |
|---|---|---|---|---|---|---|
| | | | Observed | Expected | Lower bound | Upper bound |
| 2005 | All trees | Hopkins-Skellam | 0,487 | 0,5 | 0,446 | 0,561 |
| | | Pielou-Mountford | 1,066 | 1,068 | 0,907 | 1,258 |
| | | Clark-Evans | 1,068 | 1,026 | 0,959 | 1,095 |
| | Beech, all sizes | Hopkins-Skellam | 0,57 | 0,499 | 0,436 | 0,569 |
| | | Pielou-Mountford | 1,3 | 1,076 | 0,892 | 1,303 |
| | | Clark-Evans | 0,981 | 1,031 | 0,952 | 1,109 |
| | Beech, less than 10m | Hopkins-Skellam | 0,685 | 0,498 | 0,397 | 0,617 |
| | | Pielou-Mountford | 1,707 | 1,12 | 0,818 | 1,553 |
| | | Clark-Evans | 0,803 | 1,051 | 0,919 | 1,179 |
| | Beech, 10 to 20 m | Hopkins-Skellam | 0,662 | 0,496 | 0,373 | 0,64 |
| | | Pielou-Mountford | 1,921 | 1,137 | 0,778 | 1,698 |
| | | Clark-Evans | 0,85 | 1,064 | 0,899 | 1,227 |
| | Beech, more than 20 m | Hopkins-Skellam | 0,52 | 0,498 | 0,383 | 0,629 |
| | | Pielou-Mountford | 1,255 | 1,129 | 0,796 | 1,635 |
| | | Clark-Evans | 1,077 | 1,056 | 0,911 | 1,2 |
| | Spruce | Hopkins-Skellam | 0,951 | 0,492 | 0,295 | 0,729 |
| | | Pielou-Mountford | 6,142 | 1,237 | 0,63 | 2,404 |
| | | Clark-Evans | 0,579 | 1,12 | 0,811 | 1,424 |
| | Horbeam | Hopkins-Skellam | 0,443 | 0,497 | 0,361 | 0,656 |
| | | Pielou-Mountford | 0,953 | 1,158 | 0,771 | 1,788 |
| | | Clark-Evans | 1 | 1,069 | 0,884 | 1,25 |
| | Larch | Hopkins-Skellam | 0,804 | 0,49 | 0,285 | 0,748 |
| | | Pielou-Mountford | 2,153 | 1,237 | 0,611 | 2,41 |
| | | Clark-Evans | 0,667 | 1,131 | 0,801 | 1,459 |
| 2009 | All trees (Without Ingrowth) | Hopkins-Skellam | 0,468 | 0,499 | 0,444 | 0,56 |
| | | Pielou-Mountford | 0,994 | 1,064 | 0,907 | 1,255 |
| | | Clark-Evans | 1,076 | 1,027 | 0,956 | 1,094 |
| | All trees (With Ingrowth) | Hopkins-Skellam | 0,477 | 0,499 | 0,447 | 0,559 |
| | | Pielou-Mountford | 1,053 | 1,063 | 0,911 | 1,257 |
| | | Clark-Evans | 1,072 | 1,025 | 0,962 | 1,088 |
| | Beech, all sizes (Without Ingrowth) | Hopkins-Skellam | 0,603 | 0,499 | 0,431 | 0,569 |
| | | Pielou-Mountford | 1,49 | 1,076 | 0,885 | 1,319 |
| | | Clark-Evans | 0,981 | 1,031 | 0,952 | 1,113 |
| | Beech, all sizes (With Ingrowth) | Hopkins-Skellam | 0,568 | 0,499 | 0,437 | 0,567 |
| | | Pielou-Mountford | 1,335 | 1,072 | 0,896 | 1,289 |
| | | Clark-Evans | 0,986 | 1,029 | 0,953 | 1,104 |
| | Ingrowth | Hopkins-Skellam | 0,894 | 0,492 | 0,287 | 0,739 |
| | | Pielou-Mountford | 7,037 | 1,229 | 0,617 | 2,377 |
| | | Clark-Evans | 0,58 | 1,119 | 0,811 | 1,426 |
| | Beech, less than 10m | Hopkins-Skellam | 0,669 | 0,5 | 0,395 | 0,615 |
| | | Pielou-Mountford | 1,587 | 1,128 | 0,834 | 1,581 |
| | | Clark-Evans | 0,803 | 1,049 | 0,918 | 1,179 |
| | Beech, 10 to 20 m | Hopkins-Skellam | 0.665 | 0.498 | 0.374 | 0.641 |
| | | Pielou-Mountford | 1.949 | 1.148 | 0.785 | 1.715 |
| | | Clark-Evans | 0.850 | 1.064 | 0.906 | 1.230 |
| | Beech, more than 20 m | Hopkins-Skellam | 0,469 | 0,498 | 0,385 | 0,628 |
| | | Pielou-Mountford | 1,02 | 1,13 | 0,805 | 1,61 |
| | | Clark-Evans | 1,077 | 1,057 | 0,907 | 1,203 |
| | Spruce | Hopkins-Skellam | 0,969 | 0,495 | 0,292 | 0,744 |
| | | Pielou-Mountford | 9,736 | 1,241 | 0,632 | 2,357 |
| | | Clark-Evans | 0,579 | 1,115 | 0,81 | 1,417 |
| | Horbeam | Hopkins-Skellam | 0,483 | 0,497 | 0,357 | 0,657 |
| | | Pielou-Mountford | 1,145 | 1,159 | 0,758 | 1,779 |
| | | Clark-Evans | 1,052 | 1,073 | 0,885 | 1,264 |
| | Larch | Hopkins-Skellam | 0,895 | 0,491 | 0,281 | 0,749 |
| | | Pielou-Mountford | 4,502 | 1,235 | 0,611 | 2,457 |
| | | Clark-Evans | 0,667 | 1,127 | 0,792 | 1,459 |

\* ▭ Bigger than uooer bound  ▭ Smaller than lower bound

Table 17. Spatial distribution indices for PRP 08.

| Year | Class of trees | Index | Index value for alive trees | | | |
|---|---|---|---|---|---|---|
| | | | Observed | Expected | Lower bound | Upper bound |
| | All trees, all sizes | Hopkins-Skellam | 0,511 | 0,5 | 0,465 | 0,535 |
| | | Pielou-Mountford | 1,313 | 1,041 | 0,943 | 1,15 |
| | | Clark-Evans | 1,074 | 1,016 | 0,976 | 1,055 |
| | All trees, less than 10 m | Hopkins-Skellam | 0,916 | 0,499 | 0,448 | 0,555 |
| | | Pielou-Mountford | 7,012 | 1,061 | 0,912 | 1,242 |
| | | Clark-Evans | 0,725 | 1,024 | 0,963 | 1,087 |
| | All trees, 10 - 20 m | Hopkins-Skellam | 0,843 | 0,5 | 0,439 | 0,568 |
| | | Pielou-Mountford | 5,052 | 1,074 | 0,899 | 1,302 |
| | | Clark-Evans | 0,79 | 1,029 | 0,954 | 1,102 |
| | All trees, more than 20 m | Hopkins-Skellam | 0,58 | 0,5 | 0,431 | 0,576 |
| | | Pielou-Mountford | 1,644 | 1,08 | 0,882 | 1,347 |
| | | Clark-Evans | 1,132 | 1,031 | 0,949 | 1,111 |
| | Beech, all sizes | Hopkins-Skellam | 0,517 | 0,5 | 0,463 | 0,539 |
| | | Pielou-Mountford | 1,324 | 1,044 | 0,938 | 1,165 |
| | | Clark-Evans | 1,064 | 1,017 | 0,971 | 1,06 |
| | Beech, less than 10m | Hopkins-Skellam | 0,898 | 0,499 | 0,44 | 0,564 |
| | | Pielou-Mountford | 6,343 | 1,069 | 0,896 | 1,28 |
| | | Clark-Evans | 0,719 | 1,028 | 0,955 | 1,098 |
| | Beech, 10 to 20 m | Hopkins-Skellam | 0,884 | 0,501 | 0,437 | 0,567 |
| | | Pielou-Mountford | 6,973 | 1,079 | 0,894 | 1,309 |
| | | Clark-Evans | 0,772 | 1,03 | 0,954 | 1,106 |
| | Beech, more than 20 m | Hopkins-Skellam | 0,578 | 0,499 | 0,431 | 0,574 |
| | | Pielou-Mountford | 1,606 | 1,08 | 0,885 | 1,324 |
| | | Clark-Evans | 1,123 | 1,033 | 0,947 | 1,116 |
| | Fir | Hopkins-Skellam | 0,993 | 0,496 | 0,385 | 0,627 |
| | | Pielou-Mountford | 14,869 | 1,125 | 0,8 | 1,609 |
| | | Clark-Evans | 0,327 | 1,057 | 0,913 | 1,201 |
| | Spruce | Hopkins-Skellam | 0,79 | 0,489 | 0,232 | 0,812 |
| | | Pielou-Mountford | 4,311 | 1,286 | 0,498 | 2,805 |
| | | Clark-Evans | 0,893 | 1,177 | 0,727 | 1,625 |

\*  Bigger than uooer bound    Smaller than lower bound

## 5.3.4. Discussion

Forest stands with little to non periodic entries, like the managed stands of this study, basically depend on natural and artificial removals to alter the pattern of dispersion of its individuals, which otherwise would remain unchanged with the pass of the years. The pattern of the disruption also determines the future characteristics of the modified unit, which means that an intended modification can be designed according to particular purposes. Plots 01 to 05 can be taken as long term examples of this fact. The majority of the observed cases started as regular dispersions, which given the very homogeneous sizes of the existing trees are the most probable arrangement to be adopted by the set of components. Trees of similar sizes that have been left to grow and compete in a specific area will likely require equivalent proportion of resources and occupy a similar range of space, which results in regularity of distance between the elements. In the present case, the harvesting actions in originally regular plots have been performed randomly in addition to occasional aggregated ones. The occurrence of these random harvests have not had noticeable effect on the dispersion patterns found at the subsequent measurements, whereas aggregated ones do create a noticeable effect on the further years, depending on the specific level of aggregation applied to the harvesting. It is yet particularly interesting that, though the repeated execution of random harvests could logically lead a transformation from regular to random pattern of the remaining trees, such transformation has not clearly been observed in the many years of the study in the particular plots. However, this outcome is not meant to be expected in every kind of plot, as it is observed in PRP 03. The variation of dispersions expressed by this plot under steady random harvesting suggests that slightly irregular interventions may eventually emphasize small existing irregularities, which ultimately will create a more visible change in the dispersion. Given that random patterns represent an intermediate point between perfectly regular and aggregated distributions, it is expected that a gradual transformation from one extreme to its opposite will require the necessary and perhaps transitory conversion to a random dispersion, as it is observed in PRP 01 by 2009. The dimension of the resulting change caused by a particular intervention is also likely to be proportional to the amount of removed trees in relation to the remaining ones. This is easily observed in the case of PRP 02, where a rather aggregated harvest did not have a perceivable effect on the established dispersion in 2007. The effects of harvest interventions of specific patterns cannot be generalized in few different cases. The level of aggregation, regularity or randomness will have a great importance in the possible changes, and the exact dispersion of a specific stand should be considered to calculate these changes.

The aggregated pattern of beech trees shorter than 20 m in unmanaged stands is more clearly appreciated in individuals shorter than 10 m, due to the restricted size area at which their clusters are likely to appear (canopy gaps). As suggested by Nagel et al. (2010), trees emerging from these spots have probably been there already prior to the gap occurrence, since the require time span to attain these sizes would not correspond to the age of the gap. Aggregated patterns displayed by ingrowth indicate the existence of conditions in which small beech individuals are more likely to settle. However, despite the occasional connection between log degradation and development of the regeneration inside gaps, the decay class of logs inside a gap is not a good indicator of the advancement of regeneration. One of the main gaps in PRP 07, for example, registers about 20 young trees of less than 10 cm of diameter and a log in decay class 5 (soft, contours deformed, profile elliptic), while another gap in PRP 08, with about 40 young

trees of less than 10 cm of DBH, has a log in decay class 3 (soft, profile oval). The fact that one hornbeam was the only secondary species appearing as ingrowth during the four years after establishment of PRP 07 would suggest that the dominance of beech in the stand will change from 74% to 96%. Giving that PRP 06 is attached to PRP 07, we could then consider both plots as a single one and state that the future proportion is changing to a 98% of dominance of beech. Four years of results do not certainly give much precise confidence of the possible future, but the observed proportions are at least a logical reaffirmation of the status permanence of the dominant species.

Concurrence in the findings of horizontal distributions of sizes in terms of diameter and height confirms the simultaneous development of both factors in the different kinds of stands. Though the results of both kinds of evaluations come to be similar, the approaches are very much complementary. Aggregation or regularity of separated groups of elements does not necessarily imply combination or disjointing among groups. Particularly important is the dispersion evaluation of very uniform stands like the even aged managed plots, for which separated examination of independent size classes would require the categorization of groups with very small quantity of individuals. The dispersion analysis of such small groups would not probably be much accurate. The size regularity-randomness found in the managed plots is very much independent of kind of harvest executed in the latest years. Trees of different sizes in a very uniform combination will validate such condition even when observed at different scales. In consequence, the evaluation of a stand with very uniform mixture of sizes, both before and after an intensely localized harvest, would remain equivalent. In fact, harvesting does not really have much immediate influence in the dispersion of sizes of an old age stand, but potentially on the further regeneration. On the other hand, dispersion pattern is a characteristic dependant on the scale but also on the natural requirements and limitations of the individuals. Trees of small sizes have a wider range of possible manifestations in terms of number and dispersal, due to their reduced volume and need of resources, which allows them to form bigger clusters in smaller spaces. In contrast, larger requirements of large trees limit the possibility to find them at shorter distances from trees of same or different sizes. In consequence, older even aged stands with aggregated pattern of sizes are a more difficult thing achieve.

There were 99 trees with less than 5 cm of DBH in PRP 08, while PRPs 06 and 07 registered 43 and 29 resp. in the last measurement. Representing two or three times the amount found in its counterparts, this group of very young trees is a manifestation of the earlier developmental stage at which a big part of the stand is. Although it can be expected to keep finding relatively large numbers of new trees as ingrowth for many more years, the increasing reduction of space availability along with the canopy closure will eventually reduce quantities of periodic ingrowth to a minimum. Additionally, important levels of mortality, which are already significantly higher, will help to keep running the process of regeneration.

Species diversity is found quite irregular among plots 06 to 08. Apart of the reiterated dominance of beech, quantities, proportions and even dimensions of secondary species do not display evident similarities. It is yet interesting to see levels of aggregation of larch, fir and spruce in particular plots. The intolerant quality of larch explains its convenient presence and abundance at the south east border of plot 07 where availability of light satisfies its requirements, allowing it to reach large sizes. Fir and spruce concentrate high numbers of young trees in two particular spots of regeneration

of plot 08. The high density of fir trees thriving in the middle of an equally high density of beech trees should be connected to the presence of older firs. In the case of the spot at the border of the plot, one older fir was registered standing right outside of the plot. The spot in the middle of the plot does not register any living older fir, but it is fairly possible that the progenitor of that cluster was actually the creator of the original gap.

It has been shown how plots with different densities of trees display dissimilarities in the relations of height and h/d ratio with DBH, which lead to think that high densities reduce height growth expectations. Comparison between densities of managed and unmanaged plots could also be useful to appreciate this phenomenon. The reiterated superior density of PRP 08 is unevenly spread in different regions of the plot. There are at least two distinct regions separating most of the large and small trees. The region with large trees keeps a density of approximately 325 individuals per hectare, and sizes of 15 to 31 m of height and 23 to 65 cm of diameter. These numbers can be compared to the ones from PRP 02, which held 321 trees per hectare, with heights of 19 to 36 m, and diameters of 22 to 70 cm in 2003. While there is a bigger difference in height averages (23.3 m in the first area and 31.9 m in PRP 02), DBH averages are much similar (38.5 cm in the first area and 40.4 cm in PRP 02). Though this apparent behavior seems somewhat verifiable, it would be very valuable to discard soil property conditions as an influencing factor.

Higher diametric increments between 2002 and 2005 in the managed plots coincide with higher levels of harvesting. However, the reductions in diametric increment during the last period go against the continuation of harvesting levels similar to the prior period. In consequence, the observed periodical variation of diametric increment should be attributed mainly to regional variations of the environmental conditions. Furthermore, DBH and height of the one nearest and four nearest trees are factors that can be considered correlated to diametric growth in every stage of the stand, even though the statistical evaluation only validated their influence during the first period. Factors describing the individuals and space surrounding the tree are more homogeneous at higher densities in earlier stages. Increasing variation of these factors over time, and the change in density, may have affected the results of the evaluation. It is very difficult to give a full explanation of the diversity of outcomes obtained in the plots in the different periods, but a combination of selective harvesting, size and site characteristics can be related to particular cases. Relatively smaller increments registered in plots 01 and 05 during the first period could have been affected positively by the more intense harvesting in the following two periods. In plot 05, particularly, harvesting from below was more prominent. Space availability and favoring of larger trees could have helped achieving the bigger contrast between following periods. Though a similar process was performed in plot 02, the big proportion of middle and small size trees may have not allowed changing the average value of increments in the same degree.

Progressive decline of basal area in most of the managed plots responds very well to the intensity of harvesting from the second period of measurements. Harvest of smaller individuals in Plot 02 had the intention to increase the volume of the stand in relation to its counterparts, by favoring already grown trees and eliminating underdeveloped ones. The relative growth superiority of plot 02 occurs surprisingly among more developed ones. Its higher volume production comes in a somewhat detriment of periodic harvests.

Nevertheless, the total relative growth of the plot may not be considered much different to the one in the other plots, and therefore the approach would not be quite justifiable.

## 5.3.5. Conclusions

Patterns of spatial dispersion of the stands are regulated by natural or artificial dynamic processes, which are also classified in dispersion classes. Even aged stands under shelterwood treatment keep a regular or random dispersion. The most common dispersion pattern used during harvest (random) can preserve regular dispersions of stands pretty much well during consecutive periods. Aggregated patterns of regeneration and small proportion of mortality do not change significantly the aggregated patterns of unmanaged stands over a short period of years. Quantities of ingrowth and mortality can display wide differences among near stands, and new young saplings are likely to increase the size of already established clusters for prolonged periods. General size spatial dispersion of managed stands displays regular to random pattern, and the mixture of sizes do not appear to be notably affected by harvesting patterns. High densities of beech are not impediment to create clusters of regenerating fir or spruce when a canopy gap is created near the progenitor. High tree densities appear to be an impediment for height development of matured tree cohorts both in manage and unmanaged stands. Differences among the sizes of neighboring trees have a direct correlation with diametric increment, and high tree densities combined with low harvest can have a positive affect on relative volume production.

## 6. General conclusions

The results of the study help giving answer to specific questions formulated beforehand.

- *What is the importance of secondary fructification, different to mast seeding, in the regeneration process of beech forests?*

In most of the cases, when the establishment and survival of mast regeneration is expectedly successful, secondary fructifications will keep proportions that can reach 30% of the mast generation. We observed that locations with relatively low proportion of seedlings established from prior generations can have better chances to receive and support the development of secondary generations even to higher densities than in other locations. In view of that, secondary fructifications can be thought as permanent mechanisms of self maintenance that a species with great adaptation uses to remain dominant. Besides, the occasional increment of seed density can help reducing the negative impact of recurring herbivore attacks on repeated individuals.

- *What is the influence of the emergence of new gaps in the overstorey on the nearby establishment of seedlings?*

We observed that seedlings germinating near a canopy gap may have better chances of long term development. However, newly established gaps offer immediate availability of resources that most of the species are willing to use, at least temporarily. If the area is conveniently free of woody debris, there may be a larger number species able to start their participation in the regeneration of the place. Adaptation characteristics will determine their future permanence. Nevertheless, a more important thing to consider is the existence of seed sources in close proximity. The prominent dominant quality of beech is greatly due to its seed productivity, which have better chances to establish under its canopy. Alternative scenarios of regeneration occur when equally developed species set at the surroundings of the gap, which dimensions favor the adaptation of more intolerant species. If an important amount of seedlings of another tolerant species come from a nearby progenitor, the arriving species may have decent chances to thrive.

- *What is the difference between the rate of diameter growth of managed stands and non interventional ones?*

Differences in periodical increment in the same stand and among managed and non interventional stands correspond to different levels of percentual growth. Averages in both kinds of stands reach maximums near 1% per year, but proportional growth expresses different behavior in both kinds of stand. Managed stands have a clear tendency to elevate the proportional diametric increment in a positive correlation to the variation in DBH, while non interventional stands keep clear negative correlation between proportional diametric increment and variations in DBH, due to intense growth of the smaller diametric classes. In general, diametric growth of both kinds of stand is expected to keep a positive correlation with the sizes of the closest trees.

- *What is the long-term development of an even-aged beech stand like, under lower levels of intervention?*

Long term superior accumulation of individuals delays diametric development. Resuming more appropriate levels of intervention can potentially bring diametric growth to proportional rates similar to more intensively intervened ones. Height development also seems to be affected negatively by irregularly high tree density. Higher proportion of canopy closure and reduced distance among trees hinder natural regeneration to the almost absolute absence of seedling banks. Though selective diameter harvest from below can improve diameter growth, a corresponding relatively higher periodic productivity of wood volume comes in detriment of periodic volume extraction.

- *What is the influence of soil moisture under different kinds of canopy cover on the development of the natural regeneration?*

Though different kinds of canopy cover may show important differences in terms of seedling development, the high variability of soil moisture levels during a particular growing season and among kinds of canopy cover does not allow identifying soil water content as an important factor for seedling development. On the contrary, it was possible to determine that relatively high numbers of seedling establishment can persist in spots where given microclimate conditions and soil properties cause lower water depletion during eventual dry events, as well as in spots where water depletion does not reach critical levels. Percentual is the fact

- *What is the relation between age structure of the main stand and seedling development?*

The permanent promotion of an even aged structure eliminates individuals from consecutive successions. The creation of a single layer reduces spaces among the crowns and with that, the amounts of direct solar radiation reaching the ground. Moreover, the standardization of high levels of tree density decreases soil suitability by the depletion of resources. Natural dynamics of forest communities keeps smaller proportions of older trees for the benefit of the process of regeneration. Allowing the formation of large, frequent and spontaneous canopy gaps, guarantees the preservation of appropriate conditions for a more permanent self regulation of the ecosystem. The absence of regeneration under restricted areas of dense old aged beech trees in unmanaged stands supports this view.

It might be valid to consider that the near nature forests we were able to observe are at least 150 year old and have not been under management for more than 50 years, which means that the current naturally developed processes are probably not representative of a whole life cycle. It could be said that the aggregation size pattern observed is only characteristic of an initial phase to a more complex series of stages that would show mixed horizontal dispersions. However, what might be truer is that the observed size aggregation is an expression of necessary dynamically complex disruptions that can

reach different sizes and have different frequencies, but will normally generate size aggregated patterns at some scale.

Logically, heterogeneous properties of communities cause increasing variation in the number of manifestations that can be described in terms of strength, which is translated to variation of disease resistance and rate of growth increment. Communities with individuals of similar genetic characteristic but with age and size differentiation will not behave in the same way like the first ones. The selection process in the first case will have an obvious tendency to eliminate the most unfitted elements as well as the ones in plain microsite disadvantage. In the case of even genetic potential, only microsite disadvantages will be considered in the process of selection. This is visible in even aged stands, where similar high developmental properties may prolong the process of deterioration. The arrangement of specific changes to be performed in order to lead a stand towards a more near nature structure will require the retention of those imperfect and otherwise undesired attributes remaining in the community to some extension. The preservation of this property will help the ecosystem to achieve the necessary rates of self regulation.

Historical records highlight the particular transformation of forest in the region, which resulted in opposite variation of proportional representation of spruce and fir. Taking those previous stages as a pattern, there should be special attention granted to the recovery of the ecological status of fir. From the species with previous recognized presence in the region, we found important numbers of newly arriving fir and pine under wide gap formation with high diversity at its surroundings. The response of fir is such conditions in earlier developmental stages is not expected to show immediate disadvantage (Jonášová et al. (2006). However the given environmental circumstances may not be suitable for the definitive progress of fir. As stated by Nagel et al. (2010), fir attributes represent advantages for its development under canopy, waiting for small canopy disturbances, in which case it would achieve competitive advances. We have observed the localized persistence of fir in advanced regeneration under and in proximity of canopy that indicates positive and prolonged response to this kind of arrangement.

If these observations are widely applicable, multiple reproductions of this pattern could be reproduced along the extension of the beech stands. However, an intense and radical transformation of the current structure would not probably be recommended if the outcome is to be controlled. This of course means that important alterations should not be expected to occur in the short term. Moreover, the success of the species under these conditions lies on its comparative endurance in particular situations. In fact, processes encouraging the development of tolerant species necessarily take into consideration the longer term characteristic of their common growth habits. The recognized weakness of natural regeneration of fir implies contemplating special protection and artificial supply of seedlings, besides focalization of seedling establishment in areas with minimum understorey presence to reduce the undesirable competition, which the species is known to reject.

It is necessary to remember that genetic characteristics of the species of these communities have unavoidably changed due to anthropogenic interventions, by means of selective harvesting. Species with different level of genetic improvement caused by centuries of tending should have increased their relative adaptability and

competitiveness. In consequence, the potential development of specific proportions of different species in a common area should not be expected to produce the same ecological interactions as proportionally similar communities living centuries ago. Although comparative levels of adaptation of the species to specific conditions have probably not changed radically, achieving the same proportions of individuals registered in ages prior to more intense human impact may prove more unrealistic than we think, due in part to evident practical difficulties related to the responses of the species to the intended objectives.

In the process of selection of areas to be left in the non interventional category, it is highly recommended to consider both the variability of landforms and the interconnectivity of their locations. While it is true that interconnectivity facilitates the mobilization of harmful agents, like different kinds of herbivores, the considerable benefit of having the presence of disseminating and pollinating agents commuting widely through greater extensions of area, inhabited by largely diverse organisms, increases the chances to create communities truly representative of the ecological zone. In addition, encouraging the natural movement of organisms multiplies the possibilities to enrich the pool of genetic expressions within the species, and helps automating the process of species diversification.

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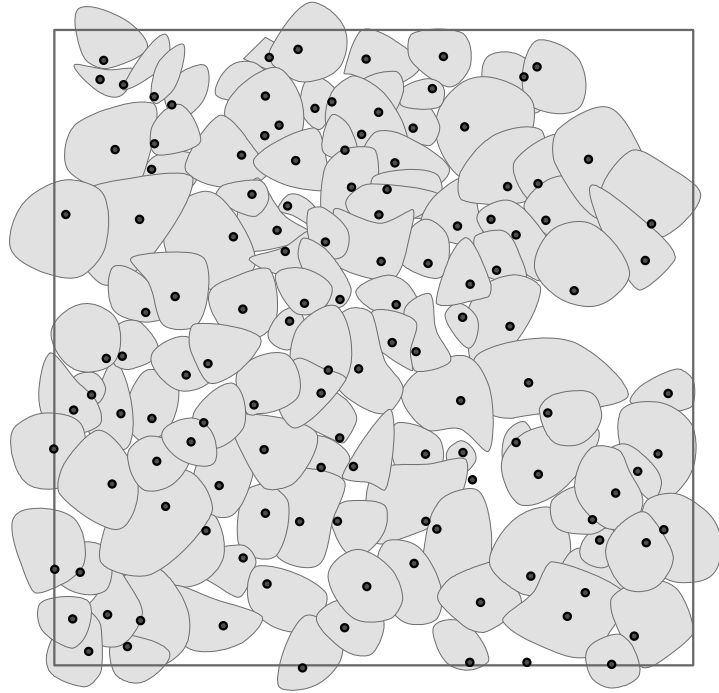
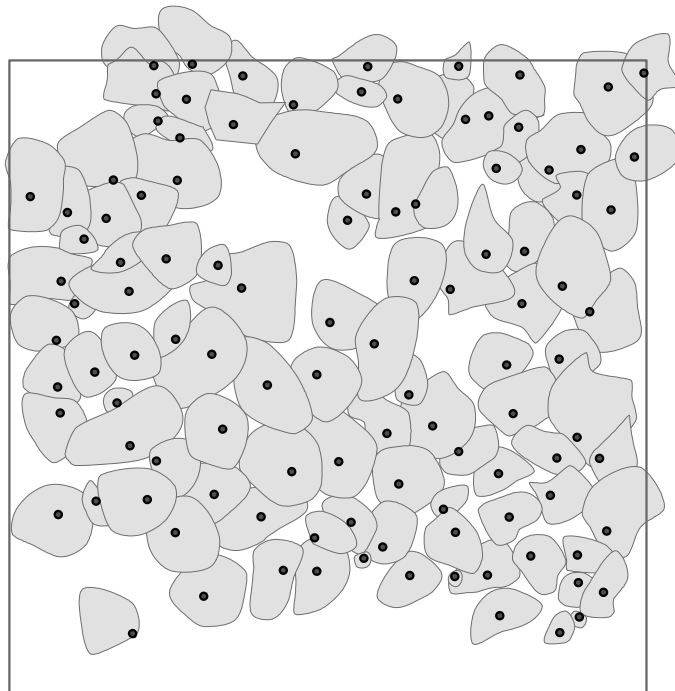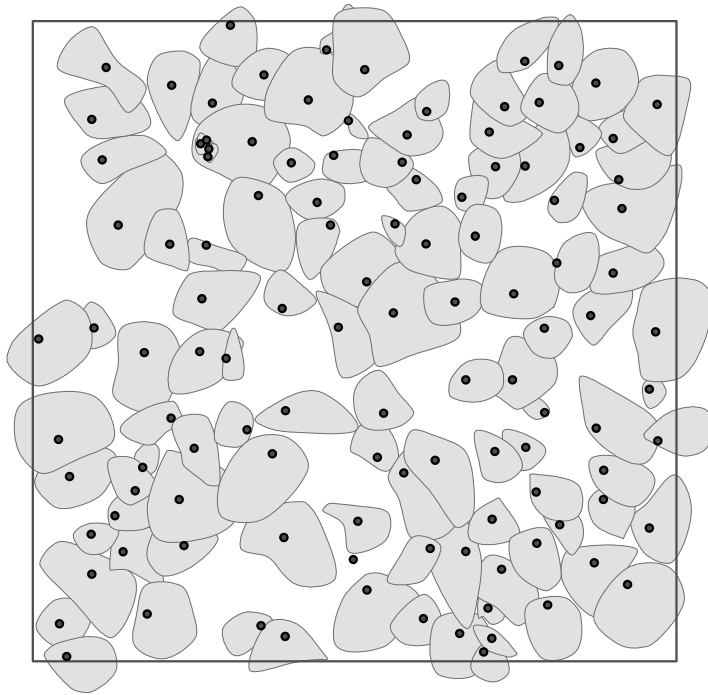# 7. APPENDIX

**Horizontal descriptions of PRPs.**
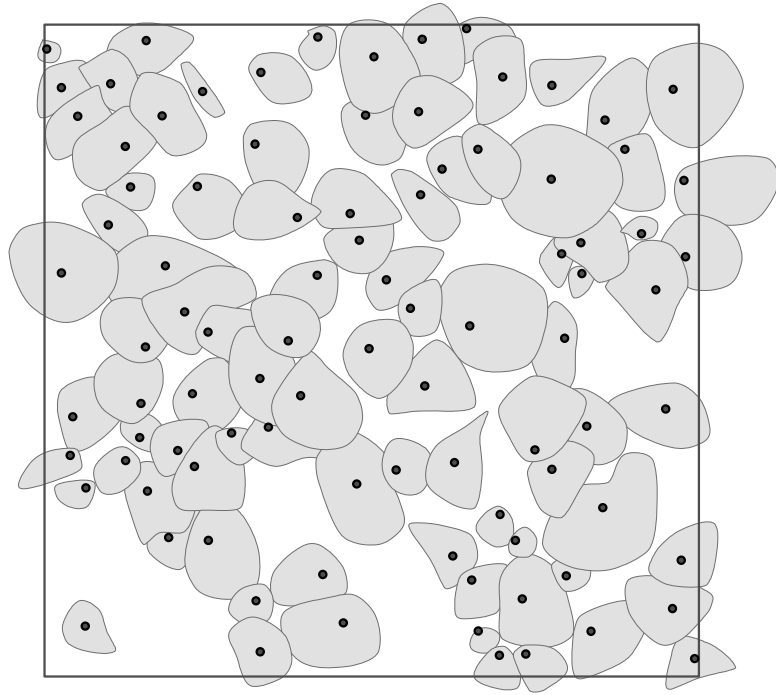


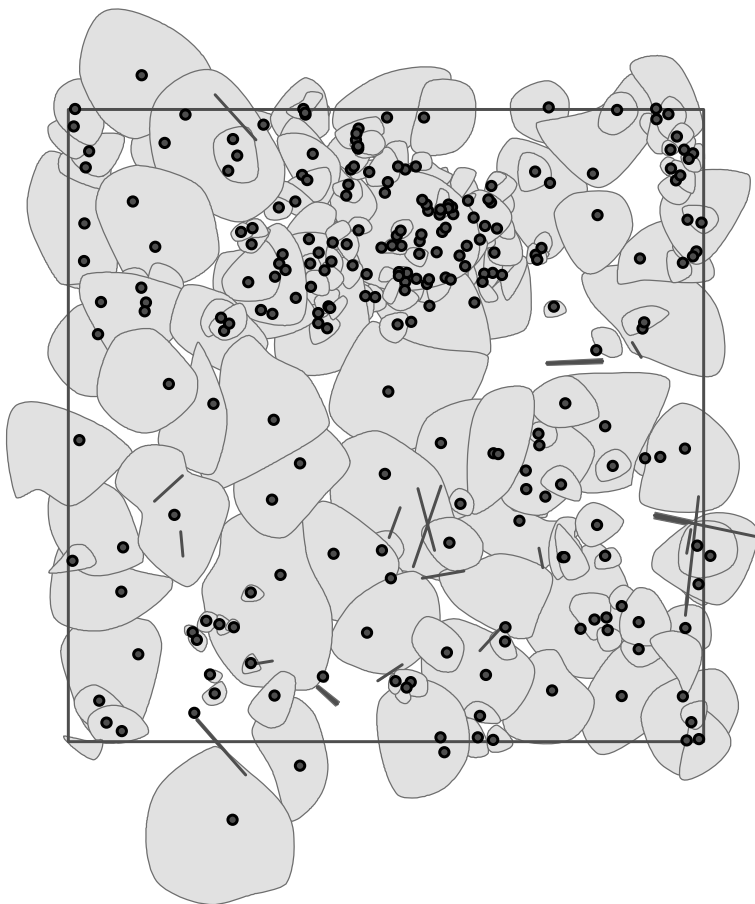**PRP 01**
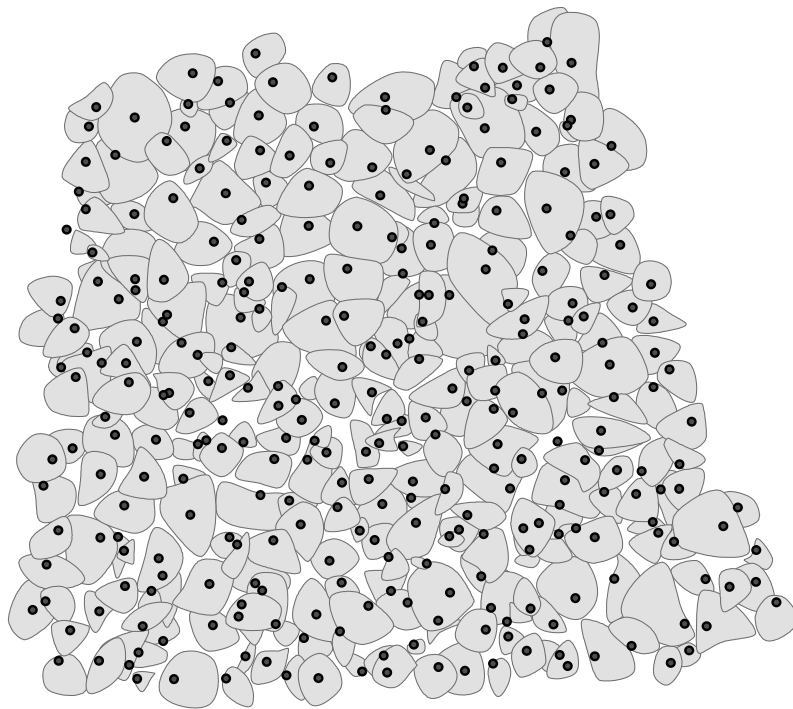


**PRP 02**

**PRP 03**

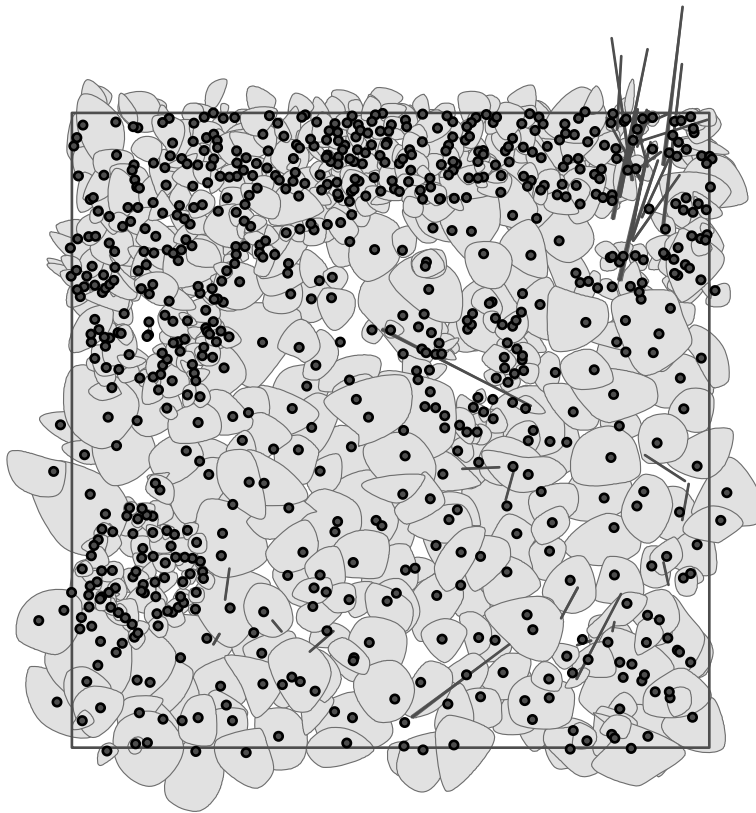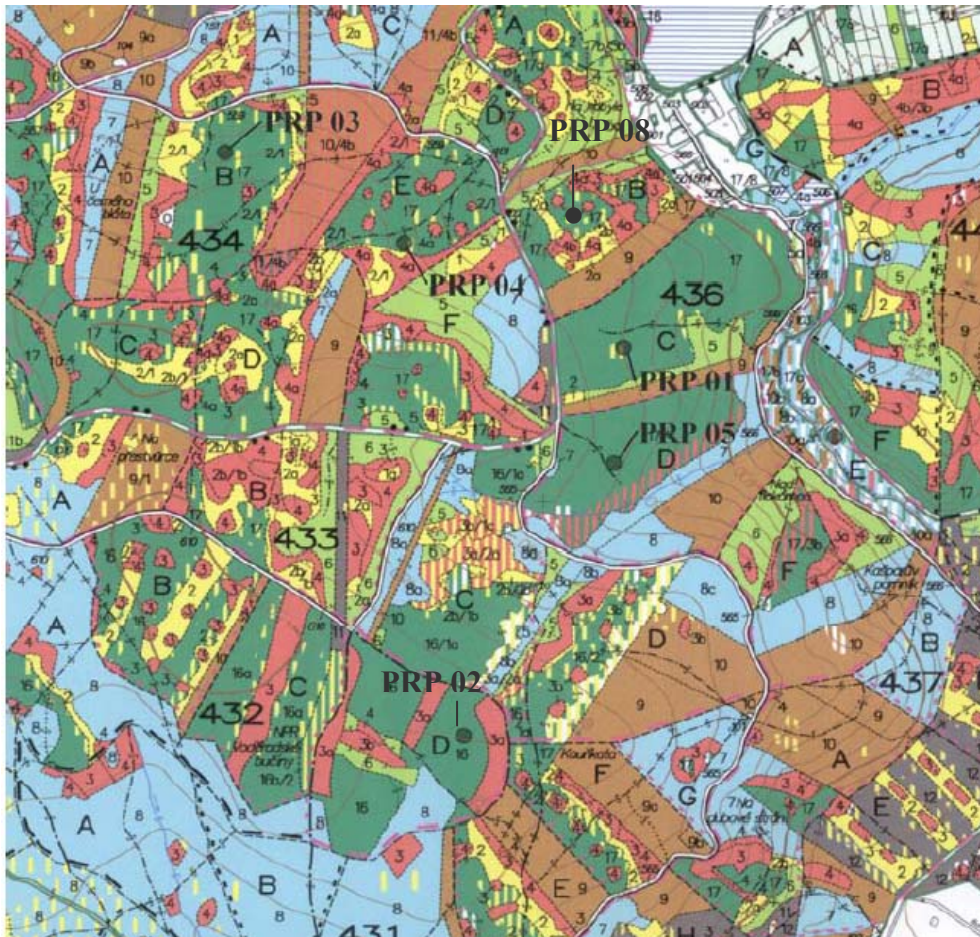

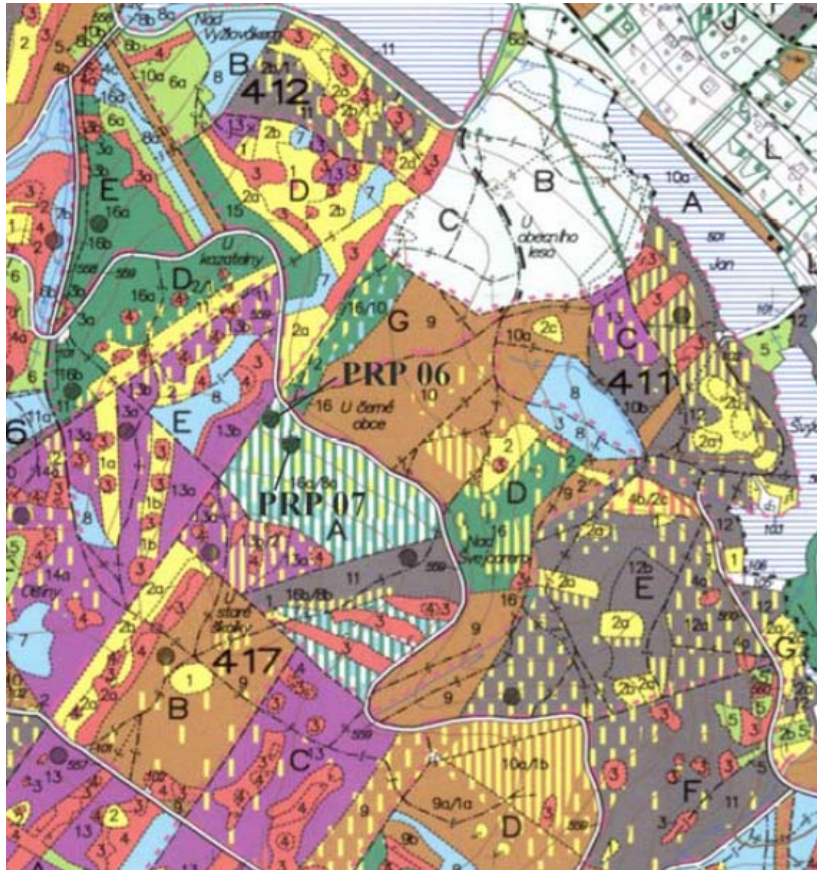**PRP 04**

**PRP 05**



**PRP 06**
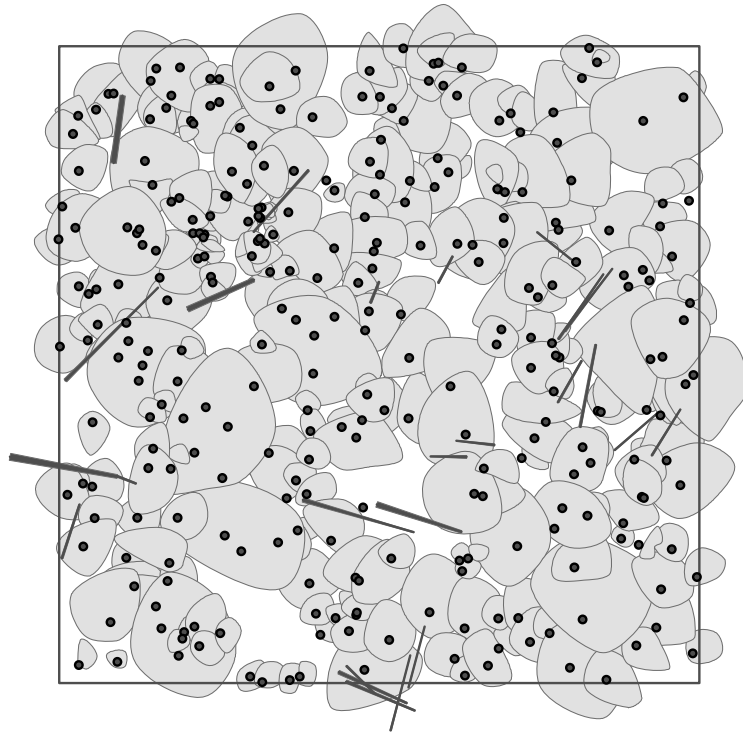
**PRP 07**



**PRP 08**

**Localization of PRPs 01, 02, 03, 04, 05, and 08**

**Localization of PRPs 06 and 07**

**Regular aspect of the stand structure of a managed stand. (PRP 05)**

**Aspect of a gap formation in an unmanaged stand (PRP 06).**