Benjamín Jarčuška

Growth, survival, density, biomass partitioning and morphological adaptations of natural regeneration in *Fagus sylvatica*. A review

Abstract: Beech is an important woody species in terms of ecology, and it also has a considerable commercial value. This fact is also reflected in a high number of scientific papers handling the issue of natural regeneration of this woody plant. The aim of this review is to analyse influence of resources availability and impact of other factors (competition) on height and diameter growth, survival, density, biomass partitioning and morphological adjustment in naturally regenerated beech seedlings and saplings. It pays a particular attention to light – the factor that influences, directly or indirectly, other environmental factors, and consequently, has the key influence on the performance of beech natural regeneration. This contribution includes information about e.g. shade tolerance and mortality-light relationships, ability to increase growth under improved light conditions, dependence of trees growth on their individual size and age etc. In spite of a large number of papers handling the issue of research on beech natural regeneration, growth responses in individual plants are difficult to predict, because the factors involved are numerous. Thus, the process of natural regeneration is in fact interactive, and even retroactive: any change in one of the involved factors induces adjustments of the others.

Introduction

European beech (*Fagus sylvatica* L.) is one of the most thoroughly investigated European tree species, treated in numerous scientific studies in diverse fields of interest. Reasons for this interest include its wide distribution range and high ecological and economical importance (Gömöry et al. 2003). The same also holds for research oriented on natural regeneration of this woody species.

Forest life cycle is ensured by tree regeneration. Natural regeneration is a process by which an existing stand is replaced by a new generation of trees (Mountford et al. 2006). This process requires favourable conditions in appropriate time and spatial constellation. Comprehensive knowledge (and study) of these conditions enables us to understand dynamics of the forest ecosystems (e.g. Emborg 1998). The obtained information can also be used in regeneration of managed forest stands (Madsen 1995a, Modrý et al. 2004).

Main advantages of naturally regenerated forests are better plant establishment (Mauer and Palátová 2000), native regeneration material and high seedling densities (Madsen and Larsen 1997, Szymura et al. 2007, Jaworski and Podlaski 2007). However, there are many examples of unsuccessful natural regene-

rations which indicate the unreliability of the method (Watt 1923, Korpeľ 1978, Saniga 1987, Madsen 1995a, Agestam et al. 2003, Madsen and Hahn 2008), in spite of the fact that natural regeneration in temperate forests, dominated by shade-tolerant tree species, has been thoroughly studied for many decades (e.g. Madsen and Larsen 1997). This reveals the intricate and complex nature of the whole natural regeneration process – mechanisms involved in it are still poorly understood (Szwagrzyk et al. 2001).

The aim of this contribution is to provide a overview about recent regeneration research into *Fagus sylvatica* (L.), focussing on growth, development and morphological responses of beech natural regeneration (seedlings and saplings) to differences in belowground and aboveground resources availability – beginning with seed release to the seedbed, seed germination, seedling establishment, up to survival and growth.

Preconditions initiating forest natural regeneration

The necessary condition for establishment of beech natural regeneration is presence of primary prerequisites in appropriate time and spatial constellation: sufficient number of appropriately spaced parent trees with corresponding fruiting capacity, mast year, and suitable status of seedbed, favourable stand microclimate and climatic conditions from the seed fall up to the seedling establishment (Korpeľ et al. 1991, Saniga 2007).

The future existence of the established individuals depends on presence of individual factors and their combinations. These factors are related, directly or indirectly to the distribution of solar radiation components throughout the canopy (Beaudet and Messier 1998, Aussenac 2000) – representing, in such a way, the basic tool for their regulation. This factor (synonyms: light, above canopy light, irradiation), consequently, will be focussed on in this survey with most attention.

Height growth

The height growth (together with lateral growth) of the seedlings enables them to exploit available space, forage for higher light micro-sites, and possibly overtop surrounding vegetation (Beaudet and Messier 1998). Tree growth reflects the interdependence of physiological processes, biomass allocation patterns and growth rates as influenced by the individual's genome and the environment in which the individuals are growing (Martin et al. 2005). It has been commonly recognised that beech (or plant) height increment normally increases up to a certain light point, and then level out or decline when the

light is increased further (Watt 1923, Aussenac 2000). The range between 5 and 40% of above canopy light encompasses most of the variation in growth of beech seedlings associated with changes in light conditions: growth is extremely low below 5% and reaches saturation for light values well below 40% (Madsen 1995a, Emborg 1998, Coll et al. 2003, Collet and Chenost 2006, Balandier et al. 2007) of incident radiation at ground level. Below the lower limit, the main factor inhibiting regeneration is light; the upper limit, in contrast, means lack of underground resources (water, mineral nutrients) – caused by the surrounding vegetation, but also by elevated atmospheric water vapour deficit (Lendzion and Leuschner 2008). Agestam et al. (2003) and Kunstler et al. (2005) report maximum growth rates for irradiation values between 10 and 20%, while Collet and Chenost (2006) speak about 30 and 35%. This discrepancy may result from different site conditions, especially water availability to beech seedlings. Water and light availability are known to interact (Madsen 1994, 1995a), with a positive effect of increasing water availability at the light threshold values at which growth saturates. This relation between the tree growth and amount of available irradiation has mostly been fitted with quadratic, hyperbolic, negative exponential or Michaelis-Menten functions (e.g. Kobe 1999, Collet and Chenost 2006).

Morphological and physiological response of beech seedlings to an abrupt change in environmental conditions (e.g. increased light supply) is manifested with a lag of up to one year (Ammer 2003, Balandier et al. 2007). Löf and Welander (2000) have found that shoot length was mainly affected by drought in the previous year, seedling dry mass, leaf area, and number of leaves was affected by drought in the previous and in the current year and the decrease in area per leaf was due only to the current-year drought. Ability of beech trees to acclimate to current and changing light conditions is strongly limited by their leaf anatomy via mesophyll plasticity, which in beech is generally determined during bud formation at former light conditions (Eschrich et al. 1989). The diameter growth, with dynamics different from the monocyclic height growth, is an exception (Collet et al. 2001, Collet and Chenost 2006, see below). It continues during the most part of vegetation period, being, in such a way, more influenced by climatic conditions in the current year.

The capacity of beech seedlings to survive deep shade for a long period, and then respond rapidly to canopy opening has since long been recognised in forestry (Watt 1923, Collet et al. 2001). After canopy opening, the above canopy light supply had increased to 25%. The studied beech individual – twenty year old and 50 cm high at that time, reached, after the following seven years a height of almost 250 cm

(Jarčuška, personal observation). Emborg (2007) explains the growth pattern of beech as a "stop and go" competitive strategy, step by step slowly approaching a dominant position in the canopy.

Negative effect of competition from herbaceous vegetation on seedling growth is also dependent on size of the seedlings and on the resources that are present in minimal amounts only. Low soil water potential had a strong influence on seedling growth, although the competing vegetation at the same time reduced light, soil temperature, and the soil nitrogen concentration (Löf 2000). At the beginning of their existence, the seedlings had major part of their root biomass in the same soil layer as the herbal vegetation that they competed for resources with. In the following years, the ability of beech roots to escape herbaceous competition was increasing gradually – by exploiting deeper (non colonized) soil horizons (Curt and Prévosto 2003a, Coll et al. 2003).

Effect of competition of roots of old beech trees on relative growth rate in beech seedlings was tested by a trenching experiment (Wagner 1999). Two years after trenching, the six-year-old saplings showed an improved growth performance compared to the growth before trenching. Prévosto and Curt (2004) observed that beech saplings growing under silver birch (*Betula pendula* Roth.) exhibited – despite slightly higher light availability – slower growth and smaller dimensions than under Scots pine (*Pinus sylvestris* L.), primarily due to their fine root biomass that was clearly more abundant under birch than under pine. This trend, however, later tended to decrease because beech saplings were aging and started to penetrate the upper tree layers and deeper soil layers.

Apart from the biotic and abiotic factors, the seedling growth is also influenced by seedling size and age. The height growth in recently germinated seedlings growing under the canopy was more affected by belowground resources availability than by light (Szwagrzyk et al. 2001, Ammer et al. 2008). During subsequent stages of seedling development, apart from initial seedling size, light supply increasingly determined the seedling growth. Löf and Welander (2004) examining one-year old beech seedlings did not detected influence either of herb competition or increased nutrient supply on the seedling growth. This influence was only manifested over the next growing season. A possible explanation is that the seeds had sufficient resources to support them in early phases of seedling emergence (Moles and Westoby 2004). In seedlings identical in initial size but differing in age, the increase in height growth with increasing light was more pronounced in older seedlings than in younger ones (Ammer et al. 2008). Collet and Chenost (2006) and Ammer et al. (2008) showed that effect of resource availability on height growth varied with tree size.

Stem diameter growth

In presence of limited resources, these are primarily invested in tree height growth (Ammer 2003, Prévosto and Balandier 2007) promoting access to light, but at expense of building up and maintaining the stem (Falster and Westoby 2003). The result is higher variability in stem diameter increment compared to the height growth (Collet et al. 2001) as well as more sensitive response to competition (Collet and Chenost 2006). Petritan et al. (2007) used radial growth of saplings as an indicator for plant vigour and whole-plant carbon balance. Wagner (1999) and Balandier et al. (2007) consider stem diameter to be a better indicator for irradiance impact on seedling's growth than height growth, because the second is disturbed by confounding effects such as stem curvature with increasing shade, and because there is a close relationship between the annual increment in stem diameter and the total biomass of seedlings (Curt et al. 2005). The authors consider stem diameter as a rather sensitive predictor of probability of mortality (Collet and Le Moguedec 2007).

Balandier et al. (2007) also found out that annual stem diameter increment in beech saplings was significantly related to the amount of foliage participating in harvesting a fraction of light (spatial display of foliage), to the total leaf area and amount of radiation. This dependence is getting stronger with age (time), which has also been confirmed by Ammer et al. (2008). Light demands in beech trees are increasing with tree age (size). This is reflected in a decreasing rate of diameter increment over time with tree age under the same light conditions. Moreover, it is also associated with decreasing proportion of photosynthetic tissues to the total sapling biomass.

Diameter growth in shade-adapted beech seedlings exposed to higher irradiation levels increased in the first year after the canopy opening, and exhibited considerable inter-annual variations related to climatic conditions – unlike the height growth. Increase in diameter growth, however, was not as significant as in height growth (Collet et al. 2001). Variability in the individual growth variables increased with better availability of resources. Before the canopy opening, the diameter growth – unlike the height growth, was significantly influenced by competition. After the opening, the second one was also turned dependent on competition; nevertheless, the variability in diameter growth was still more than three times bigger compared to the height growth. After the canopy opening, diameter growth decreased regularly – as the local competition increased, whereas height growth increased up to the threshold value of competition, and then it decreased (Collet and Chenost 2006, Prévosto and Balandier 2007).

Influence of the surrounding vegetation, competing for soil resources, on the diameter growth was studied by Coll et al. (2003) and Curt et al. (2005) in the same experiment, but carried out on beech trees of different age. The authors observed that this influence was variable depending on tree size, competing species (grasses or dicotyledons, arborescent or non-arborescent) and availability of other resources. The differences in competitive abilities were due to different root dynamics, root architecture, soil-colonising strategy of roots and also the capacity of roots to absorb water more efficiently. Grasses are in general considered more competitive than the other herb species (e.g. Provendier and Balandier 2008).

Survival

Young forest stands that are naturally regenerated are characterized by a large number of seedlings and high mortality rates (Collet and Le Moguedec 2007). The cause of mortality can be either in reducing the available resources (e.g. soil water and nutrients, light) associated with increasing intra- and inter-specific competitions, or in presence of various abiotic and biotic harmful agents.

The wide range of seedling age observed in natural beech regeneration is related to the capacity of young beech seedlings to survive under poor light conditions (Collet et al. 2001). This ability of beech makes it vigorous also in competition with other woody plants – beech is an important component of climax forests, and it often dominates the regeneration of managed forests as well (Löf et al. 2007, Collet et al. 2008, Barna et al. 2009, in press). Beech is a strong competitor in forests with prevailing single tree disturbance pattern. Studies on naturally regenerated stands showed that beech seedlings could survive at approximately 3 to 5% of incident radiation (Watt 1923, Madsen and Larsen 1997, Emborg 1998, Szwagrzyk et al. 2001). The minimum light intensity required for young beech seedlings to survive in controlled conditions is around 1% of total radiation (Watt 1923). In such extreme conditions (suppressed state), beech seedlings can survive for a rather long period. Quantitative data, however, concerning persistence of these individuals in seedling bank are insufficient (Collet et al. 2002).

Reports on mortality-light relationships are scarce. Kunstler et al. (2005) observed a yearly mortality rate of 25% for a plot with 1% light supply, while mortality on the plot where the light supply was 10% was zero. Petritan et al. (2007) reported zero mortality in case of 12% above canopy light.

Apart from amount of incident light, mortality or survival of seedlings is also influenced by seedling size, recent seedling growth, local competition, soil moisture content, vegetation cover, distance to ma-

ture trees, browsing etc. Chances of the seedlings survival under its intraspecific competition were strongly determined by their dominance status within the first 5 years after the establishment (Ammer et al. 2008). Seedling establishment and growth is one of the most critical stages because it is particularly sensitive to reduced environmental resources (Kozlowski 2002). Consequently, this stage is characterized by high mortality rates (Korpeľ 1978, Szwagrzyk et al. 2001). Collet and Le Moguedec (2007) identified evident relationship between the probability of seedling mortality and their recent diameter growth, local competition and initial size. Their study revealed a clear shift toward higher mortality values when local competition increases. Kunstler et al. (2005) established growth mortality relationships for beech seedlings of similar size as Collet and Le Moguedec (2007) but growing on a drier site and under a much lower level of intraspecific competition and their models predicted a probability of mortality three times lower than models of Collet and Le Moguedec (2007). However, these relations are unstable – due to considerable inter-annual variability of a range of factors associated with changing growth conditions. For this reason, their use in regeneration models can be disputable (Collet and Le Moguedec 2007). Studying relations between size of individuals and probability of mortality, Dreyer et al. (2005) as well as Delagrange et al. (2004) found that morphological and allocational plasticity of shade-tolerant trees seedlings was greatest in small plants, up to 1 m tall. They summarized that being small in a shaded environment may be advantageous for survival. Kunstler et al. (2005) hypothesized in accordance with the findings of Delagrange et al. (2004) that the high morphological plasticity of smaller seedlings may not allow them to survive long after a sudden reduction in light; however, taller trees may be able to survive such an event because of their ability to store larger amounts of reserves in perennial tissues.

Density

Density of natural regeneration is dependent on more factors than height growth and biomass allocation, which results in higher variability of this characteristic (Szwagrzyk et al. 2001). For this reason, the distribution of seedlings is often extremely patchy (Mountford et al. 2006).

The state of seedbed had a strong influence on number of over-wintering nuts and sprouting seedlings (Madsen 1995b). Peltier et al. (1997) reports that beech seedlings were most abundant where litter did not accumulate. Artificial created mineral soil seedbeds, compared with the mixed soil and undisturbed seedbeds, provide better conditions for win-

tering. Difference is caused by small rodents, because the environment of mixed soil seed bed provides the animals with better shelter possibilities. Covering beechnuts with soil has a positive influence on germination, mainly during poor mast years. On the other hand, the survival in post-establishment stage and growth are not influenced by site preparation, any more (Madsen 1995b; Agestam et al. 2003; Olesen and Madsen 2008).

Apart from rodents, the number of over-wintered, sprouted and established seedlings is also influenced by various fungal infestations, several insect species, snails, birds and other mammals, by ground vegetation cover; from abiotic factors there are late frosts and droughts (Madsen 1994, 1995b, Agestam et al. 2003, Mountford et al. 2006). Mammals (especially hoofed game) seem to be the most important factor for reduction of the number of beech seedlings (Olesen and Madsen 2008), less, however, than in other woody plants (Ammer 1996).

Germination of beech seedlings depends to a large extent on soil moisture content, especially in the first weeks of their existence (Ammer et al. 2002, Löf and Welander 2004). The most critical for the seedling density is the period from sprouting up to reaching mineral soil layers with their roots (Korpeľ 1978). Since canopy density as well as fine root biomass of neighbouring trees/plants determines the soil moisture content, very dense stands – equally as much opened stands are characterised by lower numbers of emerged seedlings (c.f. Saniga 1983). Six years after the shelterwood cutting resulting in broken canopy, Agestam et al. (2003); Barna and Dobrovič (2008) and Barna (2008) observed the highest density under a dense shelter (most profitable for regeneration in case of repeating mast years), while the lowest was found for a clear-cut. As for the height growth, the individuals growing on clear-cut caught up with seedlings under sparse shelter only 6 years after the shelterwood application (Agestam et al. 2003). Occurrence frequency of various damage agents decreased with increasing sheltering by the crown canopy (clear-cut > sparse shelter > dense shelter). Survival (density) of natural regeneration is mainly dependent on precipitation. Consequently, the number of beech seedlings was dependent on light conditions in the stand, nevertheless, this dependence was found case-specific (e.g. Korpeľ 1978).

Biomass allocation and morphological plasticity

Reduction in growth and survival in response to shade and competition (belowground resource availability) in developing beech seedlings and saplings were reported several times (e.g. Welander and Ottoson 1998, Ammer 2003, Löf et al. 2005). In this process, the way of biomass distribution and morphological characteristics adjustment might be the key factors determining the growth rate and performance of the species under shaded conditions (Van Hees and Clerkx 2003).

European beech responded to changes in light environment by adjusting its leaf and root morphology, especially by extending its specific leaf area (SLA) under shade (e.g. Aranda et al. 2001, Van Hees and Clerkx 2003), by reducing specific root length (SRL) (Curt et al. 2005), and by reducing self-shading by means of spatial distribution of its leaves within the crown (Planchais and Sinoquet 1998, Kunstler et al. 2004). Together with leaf area ratio and lateral crown expansion (Van Hees and Clerkx 2003), these adjustments are hypothesized to maximize light capture (Planchais and Sinoquet 1998, Walters and Reich 2000, Curt et al. 2005). Enhanced light supply together with increasing competition in the root space, also influence underground organs – natural regeneration roots that turn thinner and more ramified, adjusted in such a way for better exploitation of soil resources (Curt and Prévosto 2003b).

Balandier et al. (2007) reports that some traits (variables) as leaf number, total leaf area (LA) and silhouette to total leaf area (STAR) are responsed more for the seedlings age than the light conditions, in spite of the fact that the differences in dependence strength are not big (see Löf and Welander 2000). Total leaf area is a good predictor for total plant height and diameter at root collar (Kazda et al. 2004). Mean leaf area and leaf inclination are independent of sapling size, which indicates that these variables can be good markers of light conditions (Balandier et al. 2007). In a similar way, the beech leaf mass per area basis (LMA) was correlated with soil moisture and nitrogen content, light and growth, confirming that LMA is a sensitive functional trait integrating the degree of stress experienced by saplings (Provendier and Balandier 2008).

While handling the issue of morphological plasticity of beech seedlings related to different levels of resources availability, the authors are more or less of the same opinion; they differ considerably in hypothesizing about the strategy of biomass allocation within the plants. The question whether the changes in biomass allocation are conditioned by biotic (e.g. competition) or abiotic stress (e.g. shade) or their nature is mostly ontogenetic maintains a subject of vital discussion. Ammer et al. (2008) suggests that the cause is in short study duration – less than 3 years. Most studies indicated that these changes were more dependent on tree age than on limited resources (Van Hees 1997, Curt et al. 2005).

Curt et al. (2005) studied six-year-old beech seedlings growing for four years under different irradiance levels. The authors confirmed that the light regime

and competition from herbaceous species had little effect on shoot-to-root ratio and on biomass allocation (see Ammer 2003, Agestam et al. 2003), but their impact on above- and belowground morphological variables was undisputable. Both light presence and herbaceous competition promoted biomass allocation to fine and coarse roots at expense of taproots, in agreement with findings of Machado et al. (2003). Curt et al. (2005) also observed that plant mass was not influenced biomass allocation except for leaves. The results obtained by these authors are in contradiction with theory on global allocation for biomass partitioning in plants (Sack et al. 2002).

Different results were obtained e.g. by Madsen (1994) in two-year-old seedlings, Van Hees and Clarkx (2003) in three-year-old seedlings and Löf et al. (2005) in one-year-old seedlings. Madsen (1994) reports that in case of high levels of soil moisture content, the root/shoot ratio decreased with light intensity, but at low levels of soil water content, this ratio slightly increased with increasing light. These contradictory results may be caused by different size and/or age of individuals studied in the individual experiments, as well as by the differences in observation length, because with increasing tree size, the proportion of non-photosynthetic tissues increased faster than that of photosynthetic ones. Consequently, it is generally assumed that tall individuals have higher light requirements than short individuals – due to increased respiration and construction costs.

Conclusions

Beech is considered to be the most shade-tolerating European broadleaved woody plant. Young trees can even tolerate long-lasting shade, and this negative history has no adverse impact on their further development after improving environmental conditions. This feature makes them strong competitors in forests with a prevailing single tree disturbance pattern. While in the first year the growth of natural regeneration depends mainly on belowground resources, with advancing time also the light influence gains increasing importance, as the principal determining agent of growth process. Another factor limiting natural regeneration in case of accruing above-canopy light is water – both soil and atmospheric. Apart from these factors, the growth of trees in natural regeneration also depends on their individual size and age. Under limited access to resources, the processes of biomass partitioning and morphologic characteristics adjustment (e.g. specific leaf area, specific root length) are driving ones – from the viewpoint of species performance under these conditions. These processes, however, are not only dependent on external environmental factors, they are also attributed – as recognised by the recent knowledge, to the ontogenesis. In case of an abrupt change in external conditions, the beech response can be manifested with a time lag of up to one year. This holds for the height growth, morphological and physiological adaptations, except for diameter growth. The influence of interrelated mutually linked factors together with their cumulative and synergic effects is the most distinct in case of density and in case of survival of beech natural regeneration.

In spite of a large number of papers handling the issue of research on beech natural regeneration, implementation of the relevant knowledge in silvicultural practice is often unsuccessful. Growth responses in individual plants are difficult to predict, because, as mentioned above, the factors involved are numerous. Thus, the process of natural regeneration is in fact interactive, and even retroactive: any change in one of the involved factors induces adjustments of the others. Apart from numerous external – environmental factors, the natural regeneration is also influenced by internal factors – genetically conditioned properties of the species. For example, substantial differences between provenances of beech trees in response to differences in soil water content was recorded by Nielsen and Jorgensen (2003) and Czajkowski and Bolte (2006).

Acknowledgments

References

Agestam E., Eko P.M., Nilsson U., Welander N.T. 2003. The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. Forest Ecology and Management 176: 61–73.

Ammer C. 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. Forest Ecology and Management 88: 43–53.

Ammer C. 2003. Growth and biomass partitioning of *Fagus sylvatica* L. and *Quercus robur* L. seedlings in response to shading and small changes in the R/FR-ratio of radiation. Annals of Forest Science 60: 163–171.

Ammer C., Mosandl, R., El Kateb H. 2002. Direct seeding of beech (*Fagus sylvatica* L.) in Norway spruce (*Picea abies* [L.] Karst.) stands – effects of canopy density and fine root biomass on seed germination. Forest Ecology and Management 159: 59–72.

Ammer C., Stimm B., Mosandl R. 2008. Ontogenetic variation in the relative influence of light and belowground resources on European beech seedling growth. Tree Physiology 28: 721–728.

Aranda I., Bergasa L.F., Gil L., Pardos J.A. 2001. Effects of relative irradiance on the leaf structure of *Fagus sylvatica* L. seedlings planted in the understory of a *Pinus sylvestris* L. stand after thinning. Annals of Forest Science 58: 673–680.

Aussenac G. 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Annals of Forest Science 57: 287–301.

Balandier P., Sinoquet H., Frak E., Giuliani R., Vandame M., Descamps S., Coll L., Adam B., Prevosto B., Curt T. 2007. Six-year time course of light-use efficiency, carbon gain and growth of beech saplings (*Fagus sylvatica*) planted under a Scots pine (*Pinus sylvestris*) shelterwood. Tree Physiology 27: 1073–1082.

Barna M. 2008. The effects of cutting regimes on natural regeneration in submountain beech forests: species diversity and abundance. Journal of Forest Science 54: 533–544.

Barna M., Dobrovič J. 2008. Diverzita a abundancia semenáèikov prirodzenej obnovy v bukovom ekosystéme. In: Boltižiar M. (ed.) Ekologické štúdie VII, Nitra, SEKOS, pp. 20–27.

Barna M., Schieber B., Cicák A. 2009. Effect of post-cutting changes in site conditions on the morphology and phenology of naturally regenerated beech seedlings (*Fagus sylvatica* L.). Polish Journal of Ecology 57: in press.

Beaudet M., Messier C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. Canadian Journal of Forest Research 28: 1007–1015.

Coll L., Balandier P., Picon-Cochard C., Prévosto B., Curt T. 2003. Competition for water between beech seedlings and surrounding vegetation in different light and vegetation composition conditions. Annals of Forest Science 60: 593–600.

Collet C., Chenost C. 2006. Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. Forestry 79: 489–502.

Collet C., Le Moguedec G. 2007. Individual seedling mortality as a function of size, growth and competition in naturally regenerated beech seedlings. Forestry 80: 359–370.

Collet C., Lanter O., Pardos M. 2001. Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. Annals of Forest Science 58: 127–134.

Collet C., Lanter O., Pardos M. 2002. Effects of canopy opening on the morphology and anatomy of naturally regenerated beech seedlings. Trees 16: 291–298.

Collet C., Piboule A., Leroy O., Frochot H. 2008. Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. Forestry 81: 135–150.

Curt T., Prévosto B. 2003a. Root biomass and rooting profile of naturally regenerated beech in mid-elevation Scots pine woodlands. Plant Ecology 167: 269–282.

Curt T., Prévosto B. 2003b. Rooting strategy of naturally regenerated beech in Silver birch and Scots pine woodlands. Plant and Soil 255: 265–279.

Curt T., Coll L., Prévosto B., Balandier P., Kunstler G. 2005. Plasticity in growth, biomass allocation and root morphology in beech seedlings as induced by irradiance and herbaceous competition. Annals of Forest Science 62: 51–60.

Czajkowski T., Bolte A. 2006. Different reaction of beech (*Fagus sylvatica* L.) provenances from Germany and Poland to drought. Allgemeine Forst- und Jagdzeitung 177: 30–40.

Delagrange S., Messier C., Lechowicz M.J., Dizengremel P. 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. Tree Physiology 24: 775–784.

Dreyer E., Collet C., Montpied P., Sinoquet H. 2005. Characterisation of beech seedling tolerance to shade – comparison with associated species. Revue Forestiere Francaise 57: 175–188.

Emborg J. 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 106: 83–95.

Emborg J. 2007. Suppression and release during canopy recruitment in *Fagus sylvatica* and *Fraxinus excelsior*, a dendro-ecological study of natural growth patterns and competition. Ecological Bulletins 52: 53–67.

Eschrich W.R., Burchardt R., Essiamah S. 1989. The induction of sun and shade leaves of the European beech (*Fagus sylvatica* L.): anatomical studies. Trees 3: 1–10.

Falster D.S., Westoby M. 2003. Plant height and evolutionary games. Trends in Ecology and Evolution 18: 337–343.

Gömöry D., Paule L., Shvadchak I.M., Popescu F., Sułkowska M., Hynek V., Longauer R. 2003. Spatial patterns of the genetic differentiation in European beech (*Fagus sylvatica* L.) at allozyme loci in the Carpathians and the adjacent regions. Silvae Genetica 52: 78–83.

Jaworski A., Podlaski R. 2007. Structure and dynamics of selected stands of primeval character in the Pieniny National Park. Dendrobiology 58: 25–41.

Kazda M., Salzer J., Schmid I., von Wrangell P. 2004. Importance of mineral nutrition for photosynthesis and growth of *Quercus petraea, Fagus sylvatica* and *Acer pseudoplatanus* planted under Norway spruce canopy. Plant and Soil 264: 25–34.

Kobe R.K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. Ecology 80: 187–201.

Korpeľ Š. 1978. Začiatočné fázy prirodzenej obnovy bukových porastov. In: Vedecké práce VÚLH Zvolen XXIII – Pestovanie a produkcia buka. Bratislava, Príroda, pp. 109–141.

Korpeľ Š., Peňáz J., Saniga M., Tesař V. 1991. Pestovanie lesa. Príroda, Bratislava, 465 p.

Kozlowski T.T. 2002. Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. Forest Ecology and Management 158: 195–221.

Kunstler G., Curt T., Lepart J. 2004. Spatial pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus pubescens* Mill.) seedlings in natural pine (*Pinus sylvestris* L.) woodlands. European Journal of Forest Research 123: 331–337.

Kunstler G., Curt T., Bouchaud M., Lepart J. 2005. Growth, mortality and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. Canadian Journal of Forest Research 35: 1657–1668.

Lendzion J., Leuschner C. 2008. Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. Forest Ecology and Management 256: 648–655.

Löf M. 2000. Establishment and growth in seedlings of *Fagus sylvatica* and *Quercus robur*: influence of interference from herbaceous vegetation. Canadian Journal of Forest Research 30: 855–864.

Löf M., Welander N.T. 2000. Carry-over effects on growth and transpiration in *Fagus sylvatica* seedlings after drought at various stages of development. Canadian Journal of Forest Research 30: 468–475.

Löf M., Welander N.T. 2004. Influence of herbaceous competitors on early growth in direct seeded *Fagus sylvatica* L. and *Quercus robur* L. Annals of Forest Science 61: 781–788.

Löf M., Bolte A., Welander N.T. 2005. Interacting effects of irradiance and water stress on dry weight and biomass partitioning in *Fagus sylvatica* seedlings. Scandinavian Journal of Forest Research 20: 322–328.

Löf M., Karlsson M., Sonesson K., Welander N.T., Collet C. 2007. Growth and mortality in underplanted tree seedlings in response to variations in canopy closure of Norway spruce stands. Forestry 80: 371–384.

Machado J.L., Walters M.B., Reich P.B. 2003. Below-ground resources limit seedling growth in forest understories but do not alter biomass distribution. Annals of Forest Science 60: 319–330.

Madsen P. 1994. Growth and survival of *Fagus sylvatica* seedlings in relation to light intensity and soil water content. Scandinavian Journal of Forest Research 9: 316–322.

Madsen P. 1995a. Effects of soil water content, fertilization, light, weed competition and seedbed type on natural regeneration of beech (*Fagus sylvatica*). Forest Ecology and Management 72: 25l–264.

Madsen P. 1995b. Effects of seedbed type on wintering of beech nuts (*Fagus sylvatica*) and deer impact on sprouting seedlings in natural regeneration. Forest Ecology and Management 73: 37–43.

Madsen P., Larsen J.B. 1997. Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. Forest Ecology and Management 97: 95–105.

Madsen P., Hahn K. 2008. Natural regeneration in a beech-dominated forest managed by close-to-nature principles – a gap cutting experiment. Canadian Journal of Forest Research 38: 1716–1729.

Martin T.A., Dougherty P.M., Topa M.A., McKeand S.E. 2005. Strategies and case studies for incorporating ecophysiology into southern pine tree improvement programs. Southern Journal of Applied Forestry 29: 70–79.

Mauer O., Palátová E. 2000. Root system response to stress in artificially established Norway spruce stands. Ekológia (Bratislava) 19: 151–161.

Modrý M., Hubený D., Rejšek K. 2004. Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. Forest Ecology and Management 188: 185–195.

Moles A.T., Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology 92: 372–383.

Mountford E.P., Savill P.S., Bebber D.P. 2006. Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. Forestry 79: 389–408.

Nielsen C.N., Jorgensen F.V. 2003. Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. Forest Ecology and Management 174: 233–249.

Olesen C.R., Madsen P. 2008. The impact of roe deer (*Capreolus capreolus*), seedbed, light and seed fall on natural beech (*Fagus sylvatica*) regeneration. Forest Ecology and Management 255: 3962–3972.

Peltier A., Touzet M.C., Armengaud C., Ponge J.F. 1997. Establishment of *Fagus sylvatica* and *Fraxinus excelsior* in an old-growth beech forest. Journal of Vegetation Science 8: 13–20.

Petritan A.M., von Lüpke B., Petritan I.C. 2007. Effect of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. Forestry 80: 397–412.

Planchais I., Sinoquet H. 1998. Foliage determinants of light interception in sunny and shaded branches of *Fagus sylvatica* (L.). Agricultural and Forest Meteorology 89: 241–253.

Prévosto B., Curt T. 2004. Dimensional relationships of naturally established European beech trees beneath Scots pine and Silver birch canopy. Forest Ecology and Management 194: 335–348.

Prévosto B., Balandier P. 2007. Influence of nurse birch and Scots pine seedlings on early aerial development of European beech seedlings in an open-field plantation of Central France. Forestry 80: 253–264.

Provendier D., Balandier P. 2008. Compared effects of competition by grasses (*Graminoids*) and broom (*Cytisus scoparius*) on growth and functional traits of beech saplings (*Fagus sylvatica*). Annals of Forest Science 65: ARTN 510.

Sack L., Maranon T., Grubb P.J. 2002. Global allocation rules for patterns of biomass partitioning. Science 296: 1923.

Saniga M. 1983. Prirodzená obnova buka v rámci kombinovanej obnovy v skupine lesných typov *Fagetum pauper* na ŠLP Zvolen. Acta Facultatis Forestalis Zvolen 25: 89–97.

Saniga M. 1987. Prirodzená obnova lesných porastov v stredoslovenských štátnych lesoch Banská Bystrica a príčiny jej malého podielu. Lesnícky časopis 33: 229–234.

Saniga M. 2007. Pestovanie lesa. ES TU Zvolen, 310 p.

Szymura T.H., Dunajski A., Aman I., Makowski M., Szymura M. 2007. The spatial pattern and microsites requirements of Abies alba natural regeneration in the Karkonosze Mountains. Dendrobiology 58: 51–57.

Szwagrzyk J., Szewczyk J., Bodziarczyk J. 2001. Dynamics of seedling bank in beech forest: results of a 10-year study on germination, growth and survival. Forest Ecology and Management 141: 237–250.

Van Hees A.F.M. 1997. Growth and morphology of pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) seedlings in relation to shading and drought. Annals of Forest Science 54: 9–18.

Van Hees A.F.M., Clerkx A.P.P.M. 2003. Shading and root-shoot relations in saplings of silver birch, pedunculate oak and beech. Forest Ecology and Management 176: 439–448.

Wagner S. 1999. Ökologische Untersuchungen zur Initialphase der Naturverjüngung in Eschen-Buchen-Mischbeständen. Schriftenreihe der Forstlichen Fakultät der Univ. Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt Göttingen, Sauerländer's Verlag, 262 p.

Walters M.B., Reich P.B. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology 81: 1887–1901.

Watt A.S. 1923. On the ecology of British beechwoods with special reference to their regeneration. Journal of Ecology 11: l–48.

Welander N.T., Ottosson, B. 1998. The influence of shading on growth and morphology in seedlings of *Quercus robur* L. and *Fagus sylvatica* L. Forest Ecology and Management 107: 117–126.