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Regular research paper

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EFFECTS OF POST-CUTTING CHANGES IN SITE CONDITIONS ON THE MORPHOLOGY AND PHENOLOGY OF NATURALLY REGENERATED BEECH SEEDLINGS (*FAGUS SYLVATICA* L.)

ABSTRACT: We studied the response in growth and phenology of naturally regenerated beech seedlings to changed ecological conditions over 14 and 19-years after cutting with different intensity. Five different types of stand densities were modelled: plot C – control plot – no cut, L – low intensity cut, M – medium intensity cut, H – high intensity cut and CC – clear cut, with 1, 8, 22, 53 and 100% of relative irradiation, and 66, 68, 78, 92 and 100% of through fall, respectively. We were focussing on tree height growth and leaf area. Our phenological observations were aimed at onset and course of two spring vegetative phenophases: bud-burst and leaf unfolding. Already in two-year-old beech seedlings we found significant differences in height growth; the differences in mean leaf area, however, were observed later. From the viewpoint of phenotypic plasticity, the height growth in beech seedlings represented more sensitive response to the environment than the leaf area. According to leaf area size and height growth in the beech seedlings on control plot, the stress conditions were indicated, primarily from the lacking light. With stand opening, the development of recruitment was getting better, and beginning with plot M the increase of seedlings height and leaf area became continuously related to the amount of radiation. The results of phenological observations showed that the spring phenophases in the seedlings start first on control plot. The start of spring phenophases on the clear-cut was always observed the latest, even in com-

parison with the parent stand. Correlation analysis confirmed a significant correlation ($P < 0.05$, $r = -0.61$) between the mean air temperature in March and April and start of the phenophase leafing in the individual years. Analysis of long-term research showed that the trend of leafing's onset observed in course of 18 years was significant ($P < 0.05$), manifested a shift towards earlier dates.

KEY WORDS: seedling recruitment, height, leaf area, bud-burst, leaf unfolding, shelterwood cutting, phenotypic plasticity

1. INTRODUCTION

The adaptability of trees in forest stands is usually assessed based on their genetic diversity examined on the bio-chemical-molecular level, often at loci the adaptive importance of which is none or disputable. Response (growth, phenology) to ecological cues is frequently examined insufficiently, in spite of their considerable practical importance (Mátyás 2006). It is necessary to study quantitative parameters in field conditions where the case is not only validation of genetic markers but also identification of 'non-genetic' regulatory effects, e.g. phenotypic plasticity (external look of organisms) and ecological interactions – with the purpose to embed genetic

results into a meaningful ecological context. Results of investigated response can be utilized in forecasting the effects of the climate change, as the conditions at the test site can be interpreted as a simulation of environmental changes (Mátyás 2007).

The shelterwood cutting is one of the basic methods of enhancement of natural regeneration – both in terms of ecology and from the viewpoint of silvicultural management (Korpeľ *et al.* 1991). This method regenerates a new forest under the shelter of older trees. The profit of the method is in a loosening of the stand canopy closure, resulting in ecological conditions favourable for establishment and survival of the natural seedlings of the required woody plant on the clear-cut areas. In course of the regeneration period, the ecological conditions are gradually changing – beginning with a completely closed stand, up to an open area, parallel with changing light conditions that have a key impact on the leaf structure. Differences in leaf structure are mainly distinct when comparing the sun and shadow leaves (determined genetically), sun-exposed and shadowed leaves (instantaneous state of light-exposure). The first case is about the adaptation, the second is about acclimation of the leaves to the contrast light conditions (Masarovičová 1979).

After the tree felling, the remaining trees adapt quickly their photosynthesis and respiration. The process is mainly controlled by the intensity of accessible radiation at the moment of establishment and differentiation of assimilatory organs when important features for morphological development of the plant are determined. There parallel changes occur in cellular and sub-cellular structures and changes in bio-chemical processes that determine key parameters of CO₂ exchange in heliophilous and shade-tolerating forms. At certain values of CO₂ concentration, the sun leaves on beech trees can photosynthesize in higher rates than the shadow leaves – which is reflected in the tree growth. The stand growth after the stand opening gets more intensive and it proceeds for several years (Barna 2000). We can declare that, over the whole regeneration cycle, the remaining trees from the parent stand together with the natural regeneration are step-by-step adapted to

varying environmental conditions, and entail specific changes to the leaf structure and morphology.

Variable structure of the parent stand offers variable climatic-ecological conditions for the beech natural regeneration. This phyto-climatic diversity of the site is reflected, apart from the above-mentioned structural and morphological changes to leaves, also in changes in their phenological manifestations. Primary ecological factors influencing the phenology of beech seedlings are, at the first place, light and temperature conditions of the site (Tognetti *et al.* 1998, Schieber 2006). Biological properties (phenotypical plasticity) of beech – a shade-tolerating woody plant have also impact on phenological pattern in this species. Their influence is conspicuous, for example, in spring when different intensity of solar radiation affects significantly the variability of setting and course of spring vegetative phenological phases (Šindelář 1985, Cicák and Štefančík 1993). Several authors also suggest about an influence of genetic factors (*e.g.* provenance) on the beech's phenological variability (Chmura and Rożkowski 2002, Nielsen and Jørgensen 2003).

This paper reports on quantitative-adaptation response in growth and phenology of beech seedlings as the response to ecological conditions changed after shelterwood cutting with different intensities. The tree growth was monitored based on their vertical growth and leaf area development. Our phenological observations were focussing on the start and course of two spring vegetative phenophases: bud-burst and leafing. We expect that the above tree seedlings parameters will be – in the process of natural regeneration – continuously related to the amount of radiation, temperature and water available at the bottom of the forest plots treated with different rate of cutting.

2. STUDY AREA

We conducted research on a beech stand at the Ecological Experimental Site (EES) Kremnické vrchy Mts, Central Slovakia (48°38'N and 19°04'E). The age of the parent stand in 2002 was 105 years. The stand is situated on a west-oriented slope with an

Table 1. Basic data of beech stands on the plots after experimental cutting in 1989. Ecological Experimental Site (EES), Kremnické vrchy Mts (Slovakia).

Plot - treatment	Density stems (ha ⁻¹)	Height (m)	DBH ¹ (cm)	Stocking density	Relative irradiation ² (%)	Throughfall ³ (%)	Area (m ²)
C – control	700	23.6	23.9	0.9	1	66	1500
L – light cut	397	25.4	29.4	0.7	8	68	3500
M – medium cut	243	26.9	31.3	0.5	22	78	3500
H – heavy cut	160	27.7	32.0	0.3	53	92	3500
CC – clear cut	0	–	–	0	100	100	4000

¹ The mean diameter at breast height; ² Strělec 1992 (values measured on August 1, 1990);

³ Dubová 2001 (average for 1989-2001)

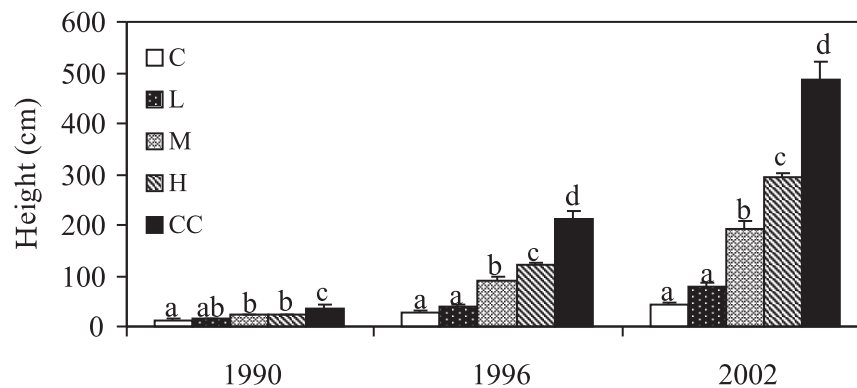


Fig. 1. Average height of beech seedling recruitment on the study plots (C, L, M, H, CC see Table 1) in years 1990, 1996 and 2002. Different letters (a, b, c, d) indicate statistically significant differences between means; tested by Duncan's test ($P \leq 0.05$). Vertical bars indicate \pm SE from the mean.

inclination of 20%, and altitude ranging between 450 and 510 m a.s.l. The mean annual temperature obtained for a 30-year period (1951–1980) is -6.8°C , in the growing season (April–September) -13.5°C . The mean annual precipitation total is 780 mm, in the vegetation period 449 mm (Strělec 1992). According to Kukla *et al.* (1998), the leading stand-forming association (central association) is *Dentario bubliferæ-Fagetum* Zlatník 1935 (Hartmann 1953) with locally admixed *Carici pilosæ-Fagetum* Oberd. 1957.

In February 1989, the stand was divided to five plots (Table 1). Four plots were subjected to shelterwood cutting with intensity adjusted in such a way as to obtain plots different in stocking and modelling the phases of shelterwood cutting. The former stocking of the stand (0.9) had been altered as follows: 0.7 – plot L (light cut), 0.5 – plot M (medium cut) and 0.3 – plot H (heavy cut). One plot was clear-cut (CC – clear-cut – 0.0) and one was left without intervention and without changing the original stocking of 0.9

(C – control plot). A brief description of the plots after the cutting intervention is in Table 1.

3. MATERIAL AND METHODS

In 2002, we measured the height growth of beech natural regeneration in groups consisting of 26 individuals randomly selected from each plot. The length of separate annual shoots were possible to measure down to the year 1989 (year of germination), thanks to scars after the fallen scales of terminal buds (Roloff 1986, 1999). The length was measured with a precision of 0.5 cm. The height growth of beech seedlings was assessed based on the cumulative height values obtained in years 1990, 1996 and 2002. In such a way, the increments were compared between two periods, the first: 1991–1996 (6 years) and the second: 1997–2002 (6 years). The average leaf size was determined three times, for leaves sampled in August 1990, 1996 and 2002, from 26 randomly selected plants from each plot. From each specimen, we sampled three leaves (one by one from the lower, medium and upper third of crown). The leaf sampling followed the method elaborated by Cicák (1998) – the method of a “representative leaf“. The method provides with the fact that the second leaf from the shoot’s base has an area representing the average area for all the leaves on the shoot. This property is independent of the actual number of leaves on the shoot. The leaf area was measured with a photo-planimeter LICOR LI-3000 A (USA).

Phenological observations on two spring phenophases: bud burst and leaf unfolding were carried out on sampling sets consisting of 25 specimens from each plot. We did not identify any differences in start of phenophases for adult beech trees of the parent stand between the plots. The set of parent trees represented 50 trees scattered uniformly across the whole EES area. Visual observations were running from March 1st towards the end of May, repeated each two- or three- days. The course of phenophases of the adult trees was observed with a telescope. The bud-burst phenophase represented cracking of scales enveloping the buds together with just discernible green leaf blade convoluted. The leaf unfold-

ing phenophase is defined as the phase, when the first regular surface of leaves becomes visible, the final leaf size, however, has not been attained yet. In both phases, the start was dated on the day when the phase first occurred in 50% individuals in the set, at least. The correlation analysis between air temperature and start of leafing phase in the natural regeneration on plot C revealed the significant effect of the cumulative positive average air temperature (CPAMAT) over March and April. Braslavská and Borsányi (1996) and Schieber (2005) declare this period as a very important for beech leafing. Results of phenological study on recruitment presented in paper were summarised from the papers given by Cicák and Štefančík (1993), Schieber (2006) and were supplemented by own recent observations.

The influence of changed ecological conditions modelled by the shelterwood cutting on morphological and growth parameters of the stand was tested using the analysis of variance (ANOVA). Homogeneity of the groups was determined based on the results of the Duncan’s test, comparing several times among the mean values. The characters a, b, c, or d express the homogeneity between the plots with a probability of $P < 0.05$. The correlation between the onset of leaf unfolding phase and air temperature could be fitted with a line (Pearson’s correlation).

4. RESULTS

4.1. Seedlings’ height and leaf area

The average height of the regenerating beech seedlings increased with increasing treatment intensity (Fig. 1). Already in 1990, two years after the germination, we found significant differences ($P < 0.05$) between the plots resulting in formation of three homogeneous groups. In year 1996, eight years after the regeneration cut, the situation was found different. Apart from a considerable increase in the regenerated individuals’ height, there were also recorded significant differences in average height among all the plots, except for C and L (Fig. 1).

The seedlings’ height markedly increased from the first period to the second one on all plots ($P < 0.05$, Fig. 2). More intensive was the stand opening, more vigorous was the incre-

Table 2. Results of ANOVA analysing: A. influence of cutting intensity on tree height and leaf area of seedling recruitment in years 1990, 1996 and 2002. B. increase of height and leaf area of seedling recruitment on plots in course of research periods. C. influence of age and cutting intensity and their interaction.

Variable	df	Height		Leaf area	
		F	P	F	P
A. Year					
1990	4	10.00	0.00004	0.96	0.43186
1996	4	75.00	<0.00001	9.98	<0.00001
2002	4	117.43	<0.00001	96.53	<0.00001
B. Treatment					
C	2	17.86	0.00003	2.42	0.09149
L	2	30.09	<0.00001	0.85	0.42726
M	2	37.68	<0.00001	9.23	0.00013
H	2	316.27	<0.00001	37.17	<0.00001
CC	2	105.4	<0.00001	287.96	<0.00001
C. Two-way ANOVA					
1. Year	2	134.87	<0.00001	56.49	<0.00001
2. Treatment	4	360.01	<0.00001	140.93	<0.00001
Interaction 1×2	8	46.08	<0.00001	55.54	<0.00001

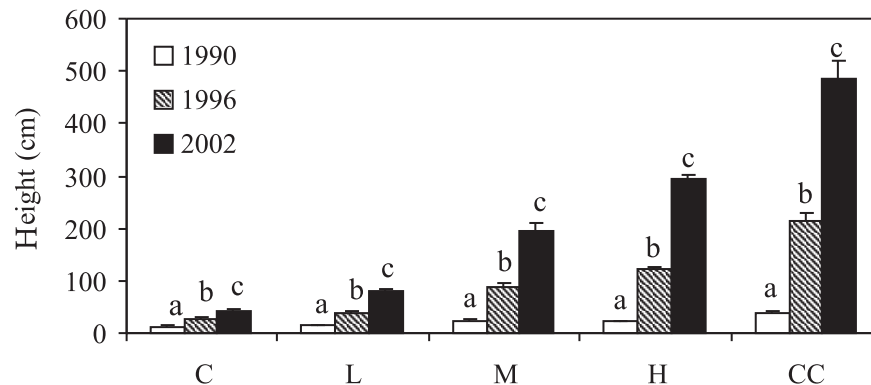


Fig. 2. Increase (absolute values) of average height of beech seedling recruitment on individual plots of different treatment (C, L, M, H, CC see Table 1).

ment (Table 2B). In the second period (1997–2002), we recorded an increase in growth rate compared to the first period (1991–1996 on all the plots: on plot CC – 154, H – 190, M – 159, L – 162%), except for the control plot (C – 93%) where we observed a decrease (Fig. 2). This fact manifests that the growth conditions on this plot were not favourable for development of beech natural regeneration, primarily as a result of insufficient light conditions.

Unlike in case of height we can see that in the year 1990, there was not found a significant difference in the leaf area size of beech seedlings between the plots (Fig. 3). All the tested groups belonged to one homogeneous group. In year 1996, the differences were found more conspicuous. There were occurred three homogeneous groups. The group with the largest average leaf area consisted of seedling recruitment situated on plots with

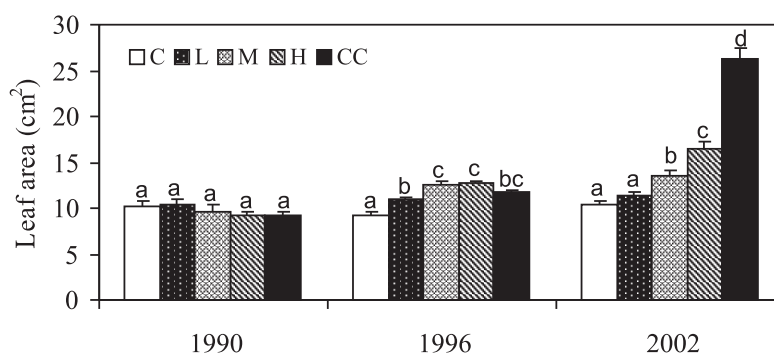


Fig. 3. Average leaf area of beech seedling recruitment on the research plots (C, L, M, H, CC see Table 1) in years 1990, 1996 and 2002.

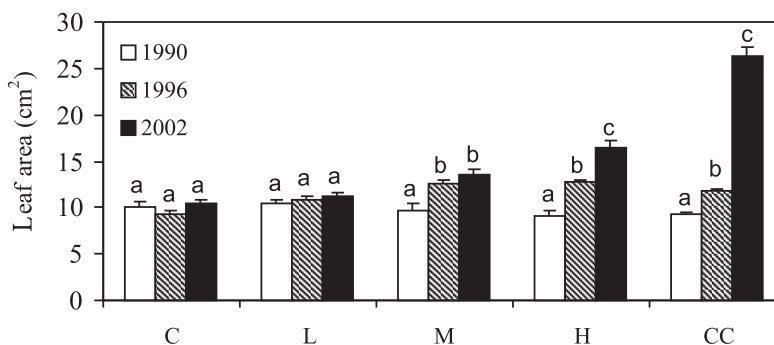


Fig. 4. Changes of average leaf area of beech seedling recruitment on individual plots (C, L, M, H, CC see Table 1).

the most open crown canopy (M, H, CC). In year 2002, there were already identified four homogeneous groups, because there the significant differences among the just mentioned plots occurred, and on the other hand, the differences between plots C and L disappeared. This fact can be explained as follows: 14 years after the cutting, beech trees on plot L had filled the gaps, and the growth conditions had turned similar to plot C. The data in Table 2A manifest that the influence of stand opening on leaf size increases in importance with time.

On all plots, except for C, we recorded the considerable increases in average leaf size (Fig. 4). On plot L, the change in this parameter was insignificant. On plot M, this change was significant only in the first study period. On plots H and CC, increase in leaf size was

significant in both periods. The results of ANOVA listed in Table 2B suggest the important influence of cutting intensity on increase in leaf area. Two-way ANOVA in Table 2C manifests an important influence of cutting intensity, time (research periods) and their interaction on growth dynamics of recruitment and on leaf area of the analyzed trees.

4.2. Leaf phenology

The earliest start of bud-burst phenophase in the recruitment was observed in year 1990 on plot C. The time delay of this phenophase on the other plots depended on the parent stand density. The difference between plot C and plot CC represented 22 days in 1990. In years 1996 and 2002 the start of bud-burst on control plot was observed 4-5

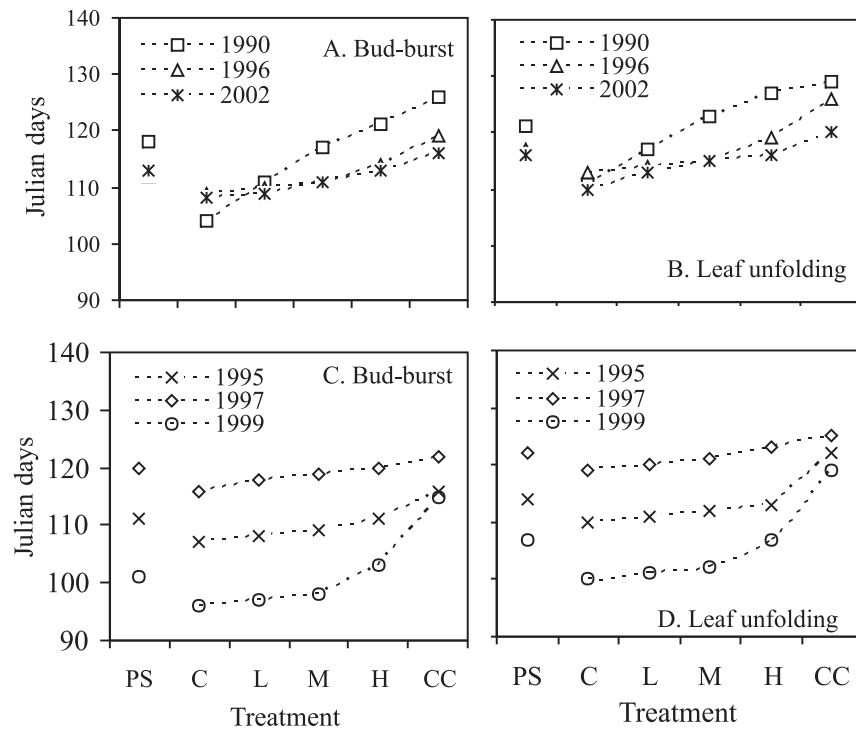


Fig. 5. Influence of treatment (C, L, M, H, CC see Table 1) on onset of bud-burst (A, C) and leaf unfolding (B, D) phenophases in recruitment and parent beech stand (PS) in selected years.

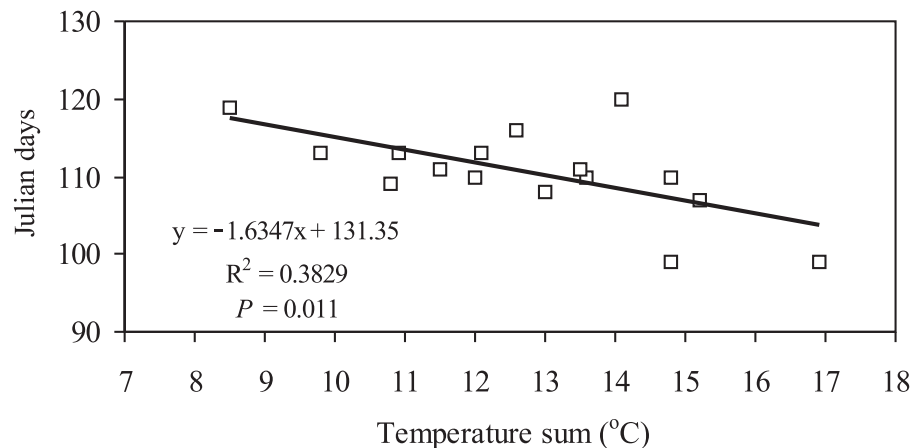


Fig. 6. Correlation between start of beech leaf unfolding and air temperature sums for relevant period (March-April).

days later compared to 1990 (Fig. 5). On the other plots, however, this phenophase started by 1 to 10 days earlier compared to 1990. The time delay in start of the phenophase on the plots L, M, H and CC was stabilised in com-

parison with the control plot. Nevertheless, it was less conspicuous compared to 1990 (Fig. 5A). The start of leaf unfolding had a similar course as was reported above. However, control plot was different, almost the same

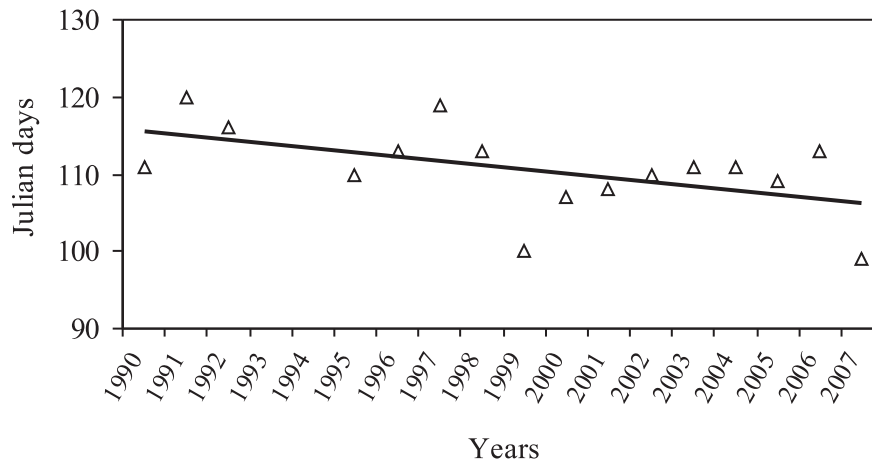


Fig. 7. The trend in onset of beech leafing over the 18-year period (own results).

course in start of leaf unfolding was kept in all three years of study (Fig. 5B). The timing of both phenophases in the parent stand was different from the natural regeneration. The earliest start, almost simultaneous of both phenophases was observed in years 1996 and 2002. In year 1990 there was a delay by 4–6 days compared to next years (Fig. 5A, B).

The year 1995 represents an ‘average’ year in which the phenophases started on dates close to the average date obtained for 16 years of observations (Fig. 5C, D). The years 1997 and 1999 were ‘extreme’ in context of these 16 years, because the earliest timing of the phenophases on the study plots (except for the former clear-cut) was observed in 1999, the latest, by contrast, in 1997. The picture shows that the time difference between the start of phenophases on the control plot and the former clear-cut was substantially smaller (6 days) in year 1997 than in year 1999 (19 days). On the other hand, in all these three contrast years, the phenophases started later in parent trees compared to the natural regeneration on plot C (Fig. 5C, D).

Temperature sum over the relevant period significantly correlated ($P = 0.01$) with the start of leafing in recruitment (Fig. 6). Statistically significant ($P < 0.05$) is also inter-annual trend in onset of leaf unfolding pointing out a positive (earlier) shift in beginning of this phenophase (Fig. 7).

5. DISCUSSION

5.1. Morphological pattern

Morphological analyses in stressed beech trees have confirmed that the leaf area was reduced (Bussotti *et al.* 1998). Also Korpel *et al.* (1991) point out that strong shading leads the decline in height increment and smaller buds and leaves. This phenomenon has also been confirmed in our case. Judging from development of tree vertical growth and leaf area size, we concluded that the natural regeneration on plot C (Control, without cut) was influenced by stress. We explain it by strong shadowing and the relative irradiation representing 1% of the value on the open plot (Střelec 1992). The parameters investigated on seedlings from plot L (Light cut, stocking density – 0.7, Table 1) did not manifest stress response. Significant increase in height growth and mean leaf area ($P < 0.05$) was observed beginning with plot M (Medium cut, stocking density – 0.5), and it still maintained even 14 years after the cutting intervention.

More favourable growth conditions on plots with more intensive cutting resulted in bigger leaf area and accelerated vertical growth. The trend is explicitly increasing beginning with plot C (completely shadowed plot) up to plot CC (clear-cut). The fact that the seedling recruitment is taller on more opened plots is primarily a consequence of

more favourable light conditions, more abundant throughfall and humification accelerated after the cutting.

Leaf area of beech is well adaptable to the local radiation climate (Larcher 1995). The sun leaves have different structure, they are thicker, and contain more chlorophyll per leaf area and they differ in morphology from the shadow leaves (Lichtenthaler *et al.* 1982, Uemura *et al.* 2000 and others). Moreover, the plants subjected to radiation with higher intensities create smaller leaf area (Masarovičová and Štefančík 1990). A question arises: why we observed that leaf area size in the beech naturally regenerated individuals increased with more opening of the stand canopy? This question might be answered by higher precipitation of water supply followed by higher soil moisture content during the whole vegetation period after opening of the stand canopy (Pichler 1998). Noticeable is also better humification under influence of other ecological factors. The netphotosynthesis in beech sun leaves is several times higher compared to the shade ones (Larcher 1995). The assimilated carbon that has not been released by respiration contributes to the dry mass amount. Accumulated assimilates are used according to the plant's requirements (*e.g.* growth). The most biomass is allocated to organs the most efficient for acquiring light, water and nutrients (Curt *et al.* 2005). Valldares *et al.* (2002) observed physiological plasticity in beech seedlings in a forest nursery – manifested by bigger leaf area responding to more irradiation. A similar phenomenon was also observed on research plots with contrast light conditions in adult subdominant trees (Barna 2004). It is generally well-known that leaves in crowns of adult beech trees in the main stand layer are markedly differentiated in a reverse way – the sun leaves have smaller leaf area, and the leaf area of shadow leaves is bigger. It is in contradiction with our results. Similar phenomenon was observed after the cutting on the same plots in adult subdominant trees (Barna 2004).

5.2. Phenological pattern

Variable phenological pattern of naturally regenerated seedlings on the studied plots is evident. Also in this case we can conclude

about the result of eco-morphological adaptation of beech trees to contrasting phyto-climatic conditions and factors resulting from differentiated structure of the parent stand (Cicák and Štefančík 1993). In all the study years, the two phases started first on the control plot with the highest density of the parent stand, the latest was the former clear-cut. The light conditions on the control plot (without cutting) are the least favourable compared to the other plots. The period after the leafing is associated with a conspicuous reduction in light energy supply to the lower stand layers (Střelec 1992). These conditions are responded by the regenerated seedlings develop of their foliage before the parent stand leafing. Another cause can be in different structure of scales enveloping shadow and sun buds. The scales of shadow buds are thinner, which can result in earliest bud-burst, and *vice versa* (Engler 1911). In a similar way, the temperature conditions of the site can control time shifts in phenophases starting in a given year (Schieber 2006). In the year with the earliest onset of vegetation (year 1999), there was observed the biggest difference in phenophases starting between the control plot and the former clear-cut (19 days). By contrast, in the year with the latest vegetation onset, the corresponding difference was substantially smaller (6 days). This can be explained by the fact that there were observed the best favourable light conditions on plot CC (clear cut). Also there were recorded the most conspicuous fluctuations in air temperature that may produce retardation effects on the phenophases beginning. At time of the start of the first phenophase in 1999 on the control plot, there was keeping snow cover on plot CC, the influence of which was also evident on average day temperatures being by 2–3°C lower compared to the control. On the other hand, in 1997, the start of phenophases on the control plot was delayed by 19–20 days compared to year 1999. At this time, also the temperature conditions on plot CC were more favourable (without snow cover), which was also reflected in noticeable reduction of time delay in phenophase starting between the two compared plots.

The inter-annual variability in onset of spring phenophases in a given species is significantly controlled by climatic factors as the

light, air temperature and humidity (Sparks *et al.* 2000). It is necessary to know the temperature sum accumulated over a certain) period preceding the phenophase development. The results show evidently that the earlier start of leafing is correlated with higher temperature sum values; on the other hand, in years with colder weather history (lower temperature sum), the onset was recorded later. The results also illustrate the trend of leafing start in the beech regeneration in course of 18 years. The shift of leafing towards earlier dates is evident. We suppose that this phenomenon may be connected with the global climate change, in Central Europe manifested, for example, by general increase in air temperature, longer growing season as well as changes in the precipitation regime (Ahas *et al.* 2002, Kożuchowski and Degirmendžić 2005). In this context, we need to point out a possible risk of changed ecological conditions (water-logging or flooding), with their possible negative influence on competition ability of beech in forest ecosystems (Geßler *et al.* 2007).

6. CONCLUSIONS

The regeneration cutting of various intensity performed in 1989 resulted in changes to the parent stand's canopy providing different conditions for development of beech recruitment. Leaf, in its morphology and anatomy the most variable plant organ, did not show significant changes in naturally regenerated beech seedlings between the plots after the second year follow the intervention. By contrast, there were found significant differences in seedlings height growth between the plots already two years after the cutting. Important differences in development of leaf area and tree height growth were found in the eighth year after the cutting, and then they increased even more intensively towards the end of the research. As for the phenotypic plasticity, we can say that the tree height respond the change of site conditions more sensitively than the leaf area.

Based on the data on leaf size and height growth of trees in the natural regeneration on plot C (1% relative enlightenment and 66% through fall compared to the open plot), we can conclude that their development was influenced by stress, mainly from the shortage

of light, soil water and nutrients if appropriate. The conditions on plot L (light cut) are more favourable, the seedlings development, however, does not manifest an increase in parameters comparable to the other plots. Significant differences in development of beech seedlings were recorded just from plot M with relative irradiation 22% and throughfall representing 78% of the open plot. We can conclude that these conditions became favourable for seedling recruitment.

Phenological pattern of the recruitment showed the earliest onset of the phenophases on control plot (without cutting) with the least favourable light conditions. Timing of the phenophases on the other studied plots was delayed in dependence on accruing relative irradiation. Also inter-annual variability in phenophase start timing was observed, influenced mainly by climatic conditions (primarily air temperature). The mean temperature in March and April significantly ($P < 0.05$, $r = -0.61$) correlated with onset of leafing in the individual years. In years with higher sums of active temperatures we usually observed earlier phenophase dating. The trend in onset of leafing over the 18-year period is statistically significant ($P < 0.05$) and manifests a shift towards earlier dates. We suppose that this phenomenon may be connected with the global climate change (general increase in air temperature sums, unbalanced precipitation regime, etc).

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7. REFERENCES

- Ahas R., Aasa A., Menzel A., Fedotova V.G., Scheifinger H. 2002 – Changes in European spring phenology – *Int. J. Climatol.* 22: 1727–1738.
- Barna M. 2000 – Impact of shelterwood cutting on twig growth in predominant beech trees (*Fagus sylvatica* L.) – *Ekológia* (Bratislava), 19: 341–353.
- Barna M. 2004 – Adaptation of European beech (*Fagus sylvatica* L.) to different ecological conditions: leaf size variation – *Pol. J. Ecol.* 52: 35–45.

- Braslavská O., Borsányi P. 1996 – Quality control of long series of phenological data with sum of cumulated average monthly air temperatures – International Symposium on Applied Agrometeorology and Agroclimatology – Proceedings Volos, Greece, 24 to 26 April: 305–310.
- Bussotti F., Gravano E., Grossoni P., Tani C. 1998 – Occurrence of tannins in leaves of beech trees (*Fagus sylvatica*) along an ecological gradient, detected by histochemical and ultrastructural analyses – *New Phytol.* 138: 469–479.
- Chmura D., J., Rożkowski R. 2002 – Variability of beech provenances in spring and autumn phenology – *Silvae Genetica*, 51: 123–127.
- Cicák A. 1998 – Knowledge of leaf area distribution in beech (*Fagus sylvatica* L.) spring shoots and possibility of its application in production ecology – *Lesnictví-Forestry*, 44: 250–255.
- Cicák A., Štefančík I. 1993 – Phenology of bud breaking of beech (*Fagus sylvatica* L.) in relation to stocking of its tree component – *Ekológia (Bratislava)*, 12: 441–448.
- 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 – *Ann. For. Sci.* 62: 51–60.
- Dubová M. 2001 – Sulphates dynamic of surface water in beech ecosystem of the Kremnické vrchy Mts. – *Folia oecol.* 28: 101–109.
- Engler A. 1911 – Untersuchungen über Blattaustausch und das sonstige Verhalten von Schatten- und Lichtpflanzen der Buche – *Mitt. Schweiz. Zent. Forst. Versuch.* 10, 106 pp.
- Geßler A., Keitel C., Kreuzwieser J., Matyssek R., Seiler W., Rennenberg H. 2007 – Potential risk for European beech (*Fagus sylvatica* L.) in a changing climate – *Trees*, 21: 1–11.
- Korpel' Š., Peňáz J., Saniga M., Tesař V. 1991 – Pestovanie lesa [Silviculture] – *Príroda, Bratislava*, 472 pp.
- Kożuchowski K., Degirmendžić J. 2005 – Contemporary changes of climate in Poland: Trends and variation in thermal and solar conditions related to plant vegetation – *Pol. J. Ecol.* 53: 283–297.
- Kukla J., Kontriš J., Kontrišová O., Gregor J., Mihálik A. 1998 – Causes of floristical differentiation of *Dentario bulbiferae-Fagetum* (Zlatník 1935) Hartmann 1953 and *Carici pilosae-Fagetum* Oberd.1957 associations – *Ekológia (Bratislava)*, 17: 177–186.
- Larcher W. 1995 – *Physiological plant ecology*, Third edition. Springer – Verlag, Berlin, Heidelberg, 506 pp.
- Lichtenthaler H.K., Kuhn G., Prenzel U., Buschmann C., Meier D. 1982 – Adaptation of chloroplast ultrastructure and of chlorophyll protein levels to high-light and low-light growth conditions – *Z Naturforsch* 37c: 464–475.
- Mátyás Cs. 2006 – Migratory, Genetic and Phenetic Response Potential of Forest Tree Populations Facing Climate Change – *Acta Silv. Lign. Hung.* 2: 33–46.
- Mátyás Cs. 2007 – Genetic background of response of tree populations to aridification at the xeric forest limit; consequences for climatic modelling. (In: *Bioclimatology and natural hazards*, International Scientific Conference, Eds. K. Štrelcová, J. Škvarenina, M. Blaženc – ISBN 978-80-228-17-60-8, 19 p.
- Masarovičová E. 1979 – Relationships between the CO₂ compensation concentration, the slope of CO₂ curves of net photosynthetic rate and the energy of irradiance – *Biol. Plant.* 21: 434–439.
- Masarovičová E., Štefančík L. 1990 – Some ecophysiological features in sun and shade leaves of tall beech trees – *Biol. Plant.* 32: 374–387.
- Nielsen CH.N., Jørgensen 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 – *For. Ecol. Manage.* 174: 233–249.
- Pichler V. 1998 – The changes of soil moisture and of soil moisture potential after the reduction of the stocking of beech stand – *Dissertation, TU Zvolen*, 83 pp. (in Slovak).
- Roloff A. 1986 – *Mitteilungen der Deutschen Dendrologischen Gesellschaft* – Verlag Eugen Ulmer Stuttgart, 5–47 pp.
- Rolloff A. 1999 – Tree vigor and branching pattern – *J. For. Sci.* 45: 206–216.
- Schieber B. 2005 – Onset and course of selected phenological phases in European beech (*Fagus sylvatica* L.) over the last 10 years – *Meteorol. J.* 8: 9–12.
- Schieber B. 2006 – Spring phenology of European beech (*Fagus sylvatica* L.) in submountain beech forest stand with various stocking between 1995–2004 – *J. For. Sci.* 52: 208–216.
- Sparks T.H., Jeffree E.P., Jeffree C.E. 2000 – An examination of the relationship between flowering times and temperature at the international scale using long-term phenological records from the UK – *Int. J. Biometeorol.* 44: 82–87.
- Střelec J. 1992 – Influence of cutting operation in a beech stand on changes in illumination – *Lesn. čas. – Forestry Journal*, 38: 551–558.

- Šindelář J. 1985 – Outline of the results of the phenological observation and some other elements of early diagnostics at provenances of beech *Fagus sylvatica* L. – Práce VÚLHM, 66: 9–43 (in Slovak with English abstract).
- Tognetti R., Minotta G., Pinzauti S., Michelozzi M., Borghetti M. 1998 – Acclimation to changing light conditions of long-term shade-grown beech (*Fagus sylvatica* L.) seedlings of different geographic origins – *Trees*, 12: 326–333.
- Uemura A., Ishida T., Nakano I., Terashima H., Tanabe H., Matsumoto Y. 2000 – Acclimation of leaf characteristics of *Fagus* species to previous-year and current-year solar irradiances – *Tree Physiol.* 20: 945–51.
- Valladares F., Chico J.M., Aranda I., Balaguer L., Dizengremel P., Manrique E., Dreyer E. 2002 – The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity – *Trees*, 16: 395–403.

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