Assimilation apparatus variability of beech transplants grown in variable light conditions of blue spruce shelter

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ABSTRACT: The paper valuates the differences in the selected characteristics of the assimilation apparatus of beech transplants growing in various light conditions of blue spruce small pole stage in the Jizerské hory Mts. in the Czech Republic. The leaf area, chemical parameters, and photosynthetic capacity measured by the method of chlorophyll fluorescence were established. Light conditions of individual beech trees were determined by means of processing a hemisphere photograph of the crown space. The research revealed a significant trend of decreasing nitrogen content with increasing irradiance of the beech. The foliage of the sheltered beech trees exhibited higher contents of phosphorus and potassium. The average specific leaf mass (SLM) of the beech under crowns was lower (0.303 contrary to 0.499 g/dm^2 in gap) and the respective variants did not differ in average leaf size. A significantly higher maximum fluorescence and a maximum quantum yield (0.854 contrary to 0.803 in gap) were found under crowns. A significant variance was also observed in the absorption capacity. It follows that the beech showed adaptation to the light conditions defined by its location within the stand of blue spruce.

Keywords: beech transplants; light; nutrient content of leaves; fluorescence of chlorophyll; leaf area

Admission of light is one of the factors affecting the forest regeneration quantity and the growth. Apart from the yew and fir, the beech is one of the tree species rather tolerant to shade. The shade tolerance is particularly important during juvenile stages, because juveniles in the understorey are likely to be subject to the shade suppression (Peters 1997). Juvenile beeches can quickly adapt their leaf morphology to changes in the light environment, i.e. in the year following the change (Burschel, Smaltz 1965 in Peters 1997).

One of indirect methods to assess the stand canopy and the light penetration into forest stands is the method of the hemisphere sky photograph. The method dwells on the taking of photographs with a wide-angle (fish-eye) objective, and on the processing of the photograph and calculation of a range of parameters depending on the size, location, and character of gaps in forest stands (see details in Rich 1990; Frazer et al. 1997, 1999, etc.). The results of the evaluation of the light conditions by using this method strongly correlate e.g. with the values obtained from photodiodes (% of photosynthetic proton flux density – Battaglia et al. 2003) and by pyranometers (Hardy et al. 2004).

For the survival and growth of tree species, the degree of illumination must be above the compensation point of photosynthesis (Silvertown, Charlesworth 2001). The value of this compensation point depends not only on the plant species and its general light requirements, but also on the degree of maturity of a concrete assimilatory organ and its accommodation to the light conditions in the dependence on the developmental stage of the individual and on

Supported by the Ministry of Agriculture of the Czech Republic, Project No. MZe 0002070201.

the impact of other environmental factors. On the other hand, a high intensity of radiation may lead to serious changes in the structure and function of the photosynthetic apparatus that are commonly known as photoinhibition (Ögren 1990) and manifest them selves in the reduced maximum rate of photosynthesis. The decrease is as a rule fully reversible, although only after a lapse of several hours or days (Gloser 1998). Photoinhibition particularly shows in plants adapted to dark. According to some researchers (Einhorn et al. 2004), the beech inclines to photoinhibition more than for example the ash. However, our study did not reveal any negative influence of the photoinhibition periods on the accumulation of total biomass in the beech individuals concerned.

The plants are capable of physiological adaptation to concrete light conditions (Tognetti et al. 1997). Irradiance affects also the shape and size of the assimilation apparatus of tree species. For example, Hamerlynck and Knapp (1994) observed dissimilar shapes of irradiated and shaded oak leaves with the shaded leaves exhibiting approximately a double size than the sunlit leaves thanks to a higher number of lobes in the sun leaves reducing the leaf area.

Being measured and analysed adequately, the fluorescence of chlorophyll makes it possible to provide detail information on what is going on inside the photosynthetising organism (Schreiber 2004). One of the applications of chlorophyll fluorescence is monitoring differences in the physiology of the sun and shade leaves and their adaptation to altered conditions (Gamper et al. 2000; Lichtenthaler et al. 2000; Einhorn et al. 2004). A basis for the application of this method is the relation of chlorophyll fluorescence to the capacity of photosynthesis. Theoretical rudiments of chlorophyll fluorescence processes at the biological level and the methods of measuring the chlorophyll fluorescence have been described in a number of fundamental physiological works (e.g. Lichtenthaler et al. 2005).

The objective of this work is to compare some morphological, chemical and physiological parameters of the assimilation apparatus of the beech individuals planted in diverse light conditions within a small pole stage of a blue spruce stand.

METHODOLOGY

The research into the relation of the light conditions to the characteristics of the assimilation apparatus of the beech underplanted in the stand of blue spruce was conducted in 2007 on the research plot Plochý in the Jizerské hory Mts., Czech Republic (880 m a.s.l., slope 5°, area 0.12 ha, acidic spruce forest site type). The stand of blue spruce was planted in this locality in 1985–1990 as a substitution of autochthonous species, whose planting at the time of air-pollution disaster failed. The research plot was established in 1995 in order to investigate the possibilities of using the substitutive blue spruce stand for beech underplanting. The beech was planted in a pseudoregular arrangement of plants in stand gaps, on crown borders and under crowns of blue spruce trees. The stand of blue spruce was not subjected to any release during the research period.

Preceding works revealed a positive effect of the blue spruce on the survival of beech individuals (Balcar, Kacálek 2008). In 2006, the average heights of the blue spruce and the beech on the research plot were 4 m (Špulák 2007) and 72 cm (137 cm for 20% of the highest trees), respectively.

In 2007, leaves were sampled from the upper crown parts of equably high 10 individuals growing under the crown of blue spruce and 10 individuals growing in the gaps. Chlorophyll fluorescence in the samples was analysed using the Imaging-PAM Chlorophyll Fluorometer. The total number of leaves analysed per variant was 44, i.e. 3–5 leaves per transplant. The measurement was made simultaneously in 2 leaves of each variant. Following the adaptation of leaves to darkness, maximum fluorescence yield Fv/Fm and the absorption capacity were measured, followed by the measurements of rapid kinetics and light curve (Walz 2004).

Furthermore, the complete assimilation apparatus was sampled from 11 approximately average beech individuals growing under the crown, on the crown border, and in the gap. The assimilation apparatus area and the parameters of an average leaf were determined by scanning and analysis using the ImageJ 1.38x programme. The individual 33 samples were analysed for DM content, the contents of nutrients (N, P, K, Ca, Mg), sulphur, and silicon.

Concrete crown light conditions of the above beech trees analysed were established by the method of hemisphere photograph assessment (e.g. Rich 1990). The photographs were taken at a hight of 80 cm above the ground at the growth point of the analysed beech with the image being processed by the Gap Light Analyser SW (version 2.0, Frazer et al. 1999).

The data were evaluated by ANOVA and Kruskal-Wallis tests (at $\alpha = 0.05$ if not stated otherwise).

RESULTS AND DISCUSSION

The light conditions of the beeches in the respective variants exhibited statistically significant differ-

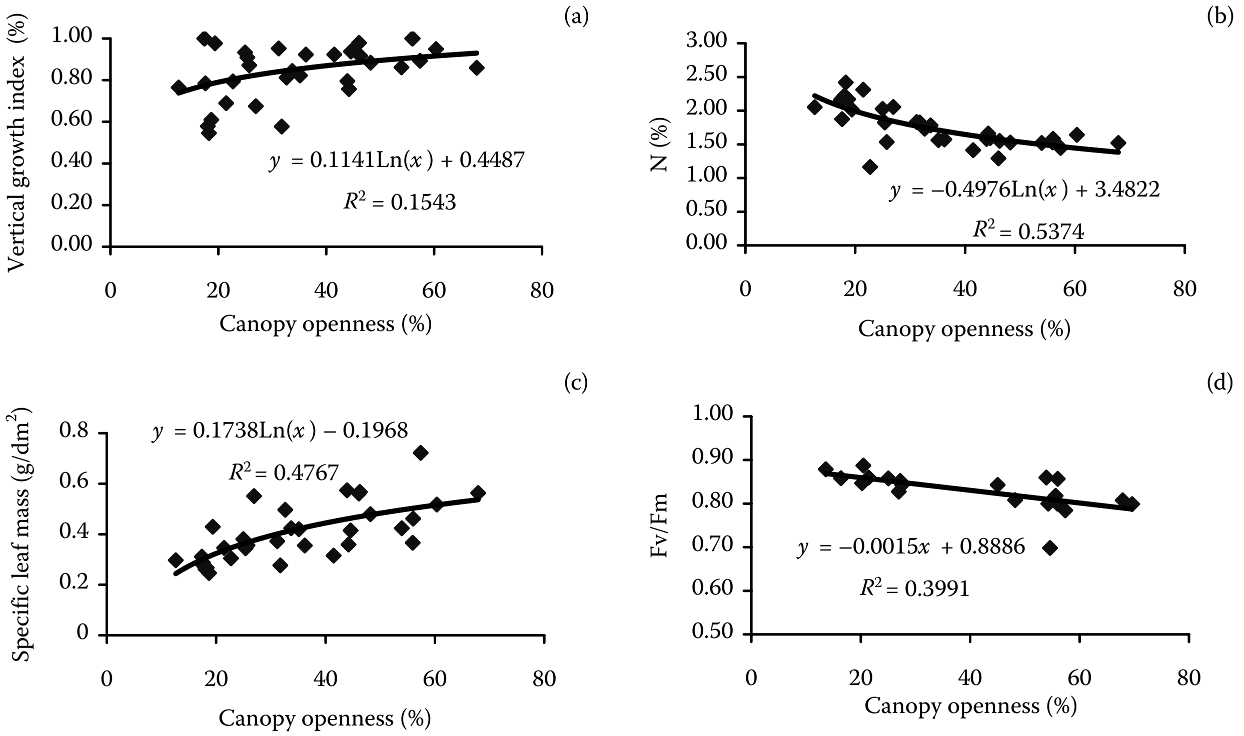

Fig. 1. Canopy openness relations obtained through the analysis of hemisphere photographs to the selected parameters of beech assimilation apparatus: a – vertical growth index (ratio of the perpendicular height of beech to the longest shoot length), b – nitrogen content (%), c – specific leaf mass (g/dm^2), d – maximum quantum yield of chlorophyll a fluorescence

ences. Average canopy openness under the crown, on the crown border, and in the gap was 22.1%, 30.7%, and 53.5%, respectively. With the increasing irradiance, the share of individuals with the tendency towards horizontal growth was decreasing. The Vertical Growth Index trend (ratio between beech tree height and the length of the longest shoot) was not conspicuous, though (Fig. 1a). Peters (1997) describes two extreme growth strategies of *Fagus sylvatica* in the shade: (1) mainly (pseudo)sympodial branching with long shoots and absent top-shoot, and (2) a monopodial top-shoot consisting of short shoots. Thus, the individuals with the strategy of short shoots disturb the above characterised trend.

Chemical analysis of the beech assimilation apparatus showed a statistically significant trend of decreasing nitrogen content in the direction from individuals growing under crown to individuals growing in the open (Table 1, Fig. 1b). The trend corresponds to the findings published in literature from the research of natural regeneration under forest stand and in forest stand gap (Johnson et al. 1997). Beech trees growing in the shade exhibited significantly higher concentrations of phosphorus and potassium. A similar trend of decreasing concentrations with the increasing irradiance was recorded with other elements, too (Ca, Mg). The higher capacity of nutrients accumulation in the assimila-

Table 1. Average contents of nutrients in the foliage of beech trees planted under blue spruce crowns, on crown perimeter and in gaps. Different letter between locations indicates a different group of statistic homogeneity

Location		N	P	K	Ca	Mg	S	Si	Dry matter
					(%)				(g)
Crown	mean	2.114a	0.076a	0.575a	0.971	0.194	0.167	0.758a	3.829a
	s. d.	0.167	0.024	0.079	0.260	0.046	0.031	0.312	2.910
Perimeter	mean	1.703b	0.043b	0.415b	0.819	0.180	0.139	0.374b	4.111ab
	s. d.	0.237	0.019	0.085	0.133	0.050	0.022	0.181	2.370
Gap	mean	1.517c	0.038b	0.368b	0.797	0.163	0.162	0.520ab	7.742b
	s. d.	0.090	0.016	0.047	0.204	0.042	0.074	0.264	4.520

Table 2. Leaf area parameters, the average height of beech trees and the leaf area/height ratio

Location		Mean leaf (cm^2)	Mean total leaf area (cm^2)	Mean height (cm)	Leaf area/height ratio
Crown	mean	7.28	1,321.7	63.9	18.6
	s. d.	*1.55*	*1,094.0*	*24.4*	*11.2*
Perimeter	mean	7.64	1,066.6	61.5	17.0
	s. d.	*1.95*	*663.4*	*16.0*	*8.3*
Gap	mean	7.42	1,572.8	71.1	21.1
	s. d.	*1.86*	*878.8*	*17.3*	*8.2*

tory organs of sheltered beech trees is a prerequisite for their faster recycling by leaf-fall.

In the case of silicon, a statistic difference was observed between the under-crown variant and the crown-border variant. The markedly higher values in the crown may be caused by the spruce canopy drift as it is well known that spruce needles, particularly if the spruce is under stress, have a higher content of silicon (Godde et al. 1991). The beech trees growing in the respective variants differed by neither average height nor their average leaf area, showed a convincing gradient (Table 2); statistically significant was however the difference in the DM content of the assimilatory organs, the weight of which was increasing with the increasing irradiance (Table 1). This corresponds to the findings published by Mészáros et al. (1998), who recorded in the research into natural regeneration that the specific weight of the beech as well as those of *Fraxinus excelsior* and *Carpinus betulus* were highest in the sunlit clearcut and lowest in the understory. This also corresponds to the ratio of the leaf area to the beech tree height in the case of the under-crown and in-gap variants (Table 2).

The average leaf size of the beech trees growing under crown and in gap was comparable; average leaf area did not exhibit any statistically significant difference between the variants (Table 2). In contrast to this, Majer (1989) observed in mature beech individuals the area of shade leaves larger by 20% than that of sunlit leaves. Significantly larger but thinner shade leaves in the mature beech were reported also by Hladká and Čaňová (2005). The leaf thickness was not measured in our study. However, the comparison of average leaf dry weight points to a significantly lower weight of leaves as well as the weight of the square decimetre (Specific Leaf Mass) of beech leaves growing under crowns (Table 3, Fig. 1c), which can be considered an indication of the leaf thickness differences, too.

Comparing the basic parameters of chlorophyll fluorescence, we found highly significant differences between the under-crown and in-the-open variants (Table 4). The shaded individuals exhibited both a higher maximum fluorescence and the Fv/Fm ratio (maximum quantum yield), which corresponds to the findings in adult (Hladká, Čaňová 2005). The decreasing maximum quantum yield with the increasing irradiance can be expressed by a linear trend (Fig. 1d). The respective variants also differed in their capacity of absorption – the ratio of reflected R and NIR radiation. Absorptivity measured by the Imaging-PAM instrument may be considered a close estimate of PAR-Absorptivity (Walz 2004).

Table 3. Dry weight of average leaf and dry specific leaf mass (SLM) in beeches planted under blue spruce crowns, on crown perimeter and in gaps. Different letter between locations indicates a different group of statistic homogeneity

Location		Mean dry matter weight of leaf (g)	Specific leaf mass (g/dm^2)
Crown	mean	0.0221a	0.303a
	s. d.	*0.0058*	*0.043*
Perimeter	mean	0.0289bc	0.400b
	s. d.	*0.0057*	*0.078*
Gap	mean	0.0362c	0.499c
	s. d.	*0.0101*	*0.110*

Table 4. Minimum and maximum fluorescence, maximal fluorescence yield and absorptivity (Abs) of the leaves of beech trees planted under blue spruce crowns and in gaps

Location		F0	Fm**	Fv/Fm**	Abs*
Crown	mean	0.087	0.594	0.854	0.888
	s. d.	0.027	0.099	0.036	0.020
Gap	mean	0.086	0.451	0.803	0.878
	s. d.	0.022	0.101	0.075	0.019

**Significance at $\alpha = 0.01$, *significance at $\alpha = 0.05$

CONCLUSION

In our research into the impact of the light conditions on the assimilation apparatus characteristics of the beech underplanted in a blue spruce small pole stage of about 4 m in height, a significant influence was observed of the shelter on the selected parameters. Chemical analysis revealed a statistically significant trend of decreasing nitrogen content with increasing irradiance (from 2.1% to 1.5%). The beech trees growing in the shelter exhibited significantly higher phosphorus and potassium contents. Magnesium and calcium showed a decreasing trend, which was insignificant though. Average dry weight of leaves under crowns was significantly lower than the dry weight of the leaves of the beech trees growing in gap with the two variants showing no difference in the leaf size. The beeches growing under crowns showed significantly higher maximum fluorescence (0.594 and 0.451) as well as significantly higher maximum quantum yield (0.854 as compared with 0.803); absorptivity also exhibited a significant variance. Thus, the beech demonstrated its capacity of adaptation to the light conditions defined by its location within the blue spruce stand.

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Received for publication June 10, 2008
Accepted after corrections July 11, 2008

Proměnlivost asimilačního aparátu prosadeb buku do porostu smrku pichlavého rostoucích v různých světelných podmínkách

ABSTRAKT: Příspěvek hodnotí rozdíly ve vybraných charakteristikách asimilačního aparátu sazenic buku, rostoucích v různých světelných poměrech tyčkoviny smrku pichlavého v Jizerských horách v České republice. Hodnotila se listová plocha, chemické parametry a fotosyntetická kapacita metodou měření fluorescence chlorofylu. Světelné poměry jednotlivých buků byly stanoveny pomocí zpracování hemisférické fotografie korunového prostoru. Z výzkumu vyplynul průkazný trend poklesu obsahu dusíku s rostoucí ozářeností buku; listy zastíněných buků měly vyšší obsah fosforu a draslíku. Průměrná specifická hmotnost listí (SLM) buků rostoucího pod korunami byla nižší (0,303 proti 0,499 g/dm^2), velikostí průměrného listu se varianty nelišily. Pod korunou byla zjištěna průkazně vyšší hodnota maximální fluorescence a maximálního výtěžku fluorescence (0,854 proti 0,803), také v absorptivitě byl zjištěn významný rozdíl. Buk tak vykazoval adaptaci na světelné podmínky definované jeho polohou vůči prosazovanému porostu smrku pichlavého.

Klíčová slova: buková prosadba; světlo; obsah živin v listech; fluorescence chlorofylu; listová plocha

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