Growth and physiological state of beech seedlings grown in a nursery in different light conditions

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ABSTRACT: Seedlings of European beech of two populations (from the 4th and 7th forest altitudinal zone) were grown in a shaded and unshaded plastic greenhouse. The objective was to compare seedling growth and the function of assimilatory organs and to determine their reactions after transfer to different light conditions. Seedlings grown in the unshaded plastic greenhouse (the sun variant) were taller and stronger at the end of the first growing season and had the higher weight and volume of shoots and root systems than seedlings grown in the shade. A higher number of leaves, larger total leaf area and higher dry matter of leaves per 1 plant were determined in seedlings grown in the sun. The average area of one leaf was larger in seedlings grown in the shade. The higher photosynthetic electron transport rate (ETR) determined from the light curves of chlorophyll fluorescence in seedlings grown in the sun was apparently connected with the higher photosynthetic rate and more intensive growth of these seedlings. The transfer of seedlings from full sun to shade resulted only in small changes in chlorophyll fluorescence (*Fv*/*Fm*, ETR). On the contrary, the transfer of seedlings from the shaded plastic greenhouse to the sun induced photoinhibition leading to a significant reduction in the maximum quantum yield of photochemistry *Fv*/*Fm* and in the photosynthetic electron transport rate (ETR).

Keywords: beech; chlorophyll fluorescence; *Fagus sylvatica*; light conditions; morphology; seedlings

The augmentation of the beech proportion in artificial regeneration is connected with many problems for the time being. Besides protection from game the support of faster growth after outplanting and mortality reduction are important. The European beech is used for reforestation on clear-cut areas and in underplantings. If plants grown in the shade in a nursery are outplanted onto unprotected clear-cut areas or, vice versa, if beech plants from a sunny nursery are set out in gaps and underplantings, they are subjected to marked changes in light conditions. Plants grown in the sun and in the shade differ in a number of morphological, anatomic and physiological characteristics (Welander, Ottosson 1997; Wyka et al. 2007). They have to adapt themselves to different light conditions after outplanting. Many data are available on reactions of seedlings growing in the shade to a sudden increase in light access. Some characteristics change very rapidly, within hours or several days. E.g. processes associated with photosynthesis and chlorophyll fluorescence react quickly (Tognetti et al. 1997). Reactions of growth, mainly height growth, are much slower, where differences were observed in several successive growing seasons (Collet et al. 2001). There is very little information on reactions of seedlings grown in a nursery in the sun after their outplanting to the shade or semi-darkness. However, the knowledge of these reactions is not less important because plants produced in nurseries in the sun are also used for underplantings or for outplantings onto partly shaded sites. We should know how quickly and in what way they are able to adapt themselves to this change. The objective of the present paper is to compare the growth and function of assimilatory organs of beech seedlings grown in a nursery in the sun or in the shade and to determine their reactions after transfer to different light conditions.

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MATERIAL AND METHODS

Beechnuts originating from the 4th forest altitudinal zone (FAZ) (seed lot CZ-1-2C-BK-20008-21-4-L) and from the 7th FAZ (seed lot CZ-2-2B-BK-03012-3-7-K) were used for the sowing of European beech (*Fagus sylvatica* L.). Germinated beechnuts were sown into HIKO V-265 trays of the cell capacity 265 ml of peat substrate enriched with 1 kg of Multicote slow-release fertilizer (with 6-month solubility at 20°C) per m^3 of substrate. Seedlings were grown in a plastic greenhouse at Opočno Research Station of the Research Institute of Forest and Game Management. A half of the plastic greenhouse was shaded in such a way that ca 25% of full sunlight was let through. Seedlings grown in the unshaded part are designated below in the text as the "sun" variant; seedlings from the shaded part are the "shadow" variant. To determine the reaction to a change in light conditions, in mid-September a part of trays from the unshaded plastic greenhouse was transferred to the shade and *vice versa*. The reaction of assimilatory organs was evaluated in them within two weeks by measuring chlorophyll fluorescence.

Evaluation of morphological characteristics

Detailed evaluation of morphological parameters in one-year planting material prepared for outplanting onto research plots was done in the accredited laboratory Nursery Control according to Standard Methods. In partial samples assimilatory organs (number of leaves, their area and dry matter) were evaluated in detail in relation to the other parts of seedlings.

Measurement of chlorophyll fluorescence

The method of chlorophyll fluorescence measurement is used most frequently to study reactions to illumination in dark-adapted leaves. Before measurement leaves are left in darkness for 20 min at least. It is ensured that all chlorophyll is in the steady state and electron transmission pathways are empty before a light impulse is intercepted. In this stage fluorescence has the minimum (basic) value (*Fo*). After strong saturation illumination all acceptors and reaction centres of the photosystem are filled with electrons very quickly (100–200 ms) and fluorescence increases to the maximum value (*Fm*). The activation of photochemical processes follows (3–5 s). Electron energy is gradually conducted and stored to highly energetic bonds and subsequently used for CO_2 assimilation (Lichtenthaler et al. 2005).

The *Fv*/*Fm* ratio is the most important diagnostic element when *Fv* is so called variable fluorescence calculated as the difference between *Fm* and *Fo*. The maximum quantum yield of the photochemistry of photosystem 2 (PSII), which is a designation of the *Fv*/*Fm* ratio, provides the exact estimation of PSII efficiency. The parameter *Fv*/*Fm* is the most frequently cited result of chlorophyll fluorescence measurement (Ritchie, Landis 2005).

Chlorophyll fluorescence was measured with an Imaging-PAM 2000 instrument (Walz, Effeltrich, Germany) on samples of beech leaves adapted to darkness for 20 min at least in a humid dark environment. The light intensity of 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and saturation impulse of the intensity 2,400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 800 ms were applied for measurements.

The determination of leaf reaction to increasing radiation intensity (the light curve) was another used method. The intensity of photosynthetically active radiation (PAR) was increased from 0 to 1,414 $\mu mol \cdot m^{-2} \cdot s^{-1}$ while the interval between the impulses of saturation light was 10 s. The evaluated parameter was the photosynthetic electron transport rate (ETR) indicating the velocity of electron conduction from photosystem 2 (PSII) and their utilization for further processes of photosynthesis. This parameter is used especially because its curves have a similar course like the curves of photosynthetic fixation of CO_2 (Maxwell, Johnson 2000).

Statistical evaluation

The results were processed in Excel programme. Statistical significance of the differences in characteristics between the two variants was determined by *t*-test. The confidence interval with 5% confidence level is used to represent variability in graphs.

RESULTS AND DISCUSSION

Morphological traits of one-year-old seedlings

The basic morphological traits of one-year-old container seedlings of European beech coming from seed from the 4th FAZ and grown for the whole growing season in an unshaded or shaded plastic greenhouse are shown in Table 1 while Table 2 shows data on seedlings originating from the 7th FAZ.

Seedlings grown in the unshaded plastic greenhouse (the sun variant) were taller and stronger; they had a larger volume of shoots and root systems compared to seedlings from the shaded plas-

Table 1. The comparison of morphological traits of one-year seedlings of European beech originating from the 4th FAZ grown in an unshaded (sun) and shaded (shade) plastic greenhouse (the number of evaluated plants in each variant N = 100)

Variant	Sun		Shade		t-value	Significance
	mean	SD	mean	SD		
Height (cm)	29.80	6.724	23.50	4.061	0.005	–
Root length (cm)	16.20	1.089	15.60	1.209	3.872	**
Collar diameter (mm)	5.10	0.940	3.73	0.780	11.257	**
Shoot volume (ml)	4.00	1.428	2.40	0.929	9.159	**
Volume of thick roots (ml)	3.70	1.504	2.10	0.911	8.786	**
Volume of fine roots (ml)	1.10	0.593	0.70	0.365	6.550	**
Root/shoot ratio	1.20	0.371	1.10	0.277	1.707	–
Proportion of fine root volume (%)	22.60	7.643	22.70	5.968	–0.181	–

SD – standard deviation, – significance level α = 0.05, **significance level α = 0.01

Table 2. The comparison of morphological traits of one-year seedlings of European beech originating from the 7th FAZ grown in an unshaded (sun) and shaded (shade) plastic greenhouse (N = 43 in the sun, N = 32 in the shade)

Variant	Sun		Shade		t-value	Significance
	mean	SD	mean	SD		
Height (cm)	33.90	8.343	23.10	4.804	6.513	**
Root length (cm)	16.00	1.068	15.70	1.023	1.338	–
Collar diameter (mm)	4.79	0.710	4.13	0.690	4.069	**
Shoot volume (ml)	5.60	2.685	3.00	1.099	5.230	**
Volume of thick roots (ml)	3.30	1.020	2.50	0.954	3.244	**
Volume of thin roots (ml)	1.00	0.617	0.70	0.338	2.695	**
Root/shoot ratio	0.90	0.296	1.10	0.233	–3.739	**
Proportion of fine root volume (%)	23.20	8.943	22.80	7.368	0.183	–

SD – standard deviation, – significance level α = 0.05, **significance level α = 0.01

tic greenhouse. The differences were highly statistically significant. The differences in the root to shoot ratio were not unambiguous.

The above-described trend corresponds to observations of other authors. Dziemidek and Tarasiuk (2005) reported a decrease in the final size of one-year beech seedlings when shading reducing the daily light intensity to 40% was used. Faster growth at increasing light availability under shelterwood from 1% to 50% of full light was observed by Beaudet and Messier (1998) in *Fagus grandifolia*. Johnson et al. (1997) produced container beech seedlings in the open area, in a gap and under shelterwood. Seedlings from the open area were taller than those from the other variants. A marked decrease in height, diameter, dry matter of stems, branches, leaves and roots with decreasing light quantity were also reported by Ammer (2003) or Bobinac (2003). A strong negative influence of the shelterwood density on diameter growth and a much smaller influence on height growth were described by Collet and Chenost (2006).

Burschel and Huss (1964) observed a reduction in shoot growth only when the light intensity was lower than 12%. However, the root weight was reduced by shading strongly and progressively. On the contrary, Curt et al. (2005) stated that unlike the other morphological traits only a small influence of light conditions was exerted on the shoot to root ratio and on biomass distribution. Our experiments provided similar findings. The reaction of growth and root to shoot ratio to the light intensity may be

Table 3. The comparison of morphological traits of one-year seedlings of European beech grown in an unshaded (sun) and shaded (shade) plastic greenhouse ($N = 21$)

Variant	Sun		Shade		Significance
Morphological trait	mean	SD	mean	SD	
Shoot height (cm)	28.1	4.259	24.1	3.458	**
Number of branches per 1 seedling	1.4	1.137	0.7	1.084	*
Number of leaves per 1 seedling	14.9	6.018	8.7	3.399	**
Leaf area per 1 seedling (cm^2)	198.6	63.670	160.2	35.214	*
Average area of 1 leaf (cm^2)	14.1	3.104	19.6	4.096	**
Leaf dry matter per 1 seedling (g)	0.98	0.322	0.65	0.156	**
Average leaf area weight ($g \cdot cm^{-2}$)	0.0049	0.0009	0.0041	0.0005	**
Average dry matter of 1 leaf (g)	0.0697	0.0207	0.0806	0.0200	–
Ratio of leaf area to seedling height	7.2	2.877	6.7	1.304	–

SD – Standard deviation, – significance indifferent, *significance level $\alpha = 0.05$, **significance level $\alpha = 0.01$

markedly influenced by other environmental factors, e.g. by water availability (Madsen 1994).

Detailed analysis of assimilatory organs was done on samples of seedlings from the shaded and unshaded plastic greenhouse (21 samples of either type) (Table 3).

Seedlings grown in the sun were larger and had more branches and leaves. Their total leaf area and dry matter of all leaves per 1 seedling were higher. But average leaf area and average dry weight of one leaf were higher in seedlings grown in the shade.

Significantly lower dry matter of leaves per plant and leaf area weight in the shade were described by Špulák (2008) in beeches from natural regeneration in the Jizerské hory Mts. Leaf area was much smaller in these conditions. Larsen and Buch (1995) reported an increase in leaf area and a decrease in the number of buds and leaves when the light quantity was diminished; Bobinac (2003) observed a higher number of assimilatory organs in seedlings grown in the sun.

Chlorophyll fluorescence in beech seedlings growing in different light conditions

The state and function of assimilatory organs were evaluated by measuring chlorophyll fluorescence (Fig. 1). The comparison of chlorophyll fluorescence of seedlings grown in the unshaded and shaded plastic greenhouse showed higher values of the maximum quantum yield of photochemistry Fv/Fm in beeches grown in the shade. This trend was evident for the whole period of observation (from June to October), in seedlings from both the 4th and 7th FAZ. But the differences were small and usually statistically insignificant.

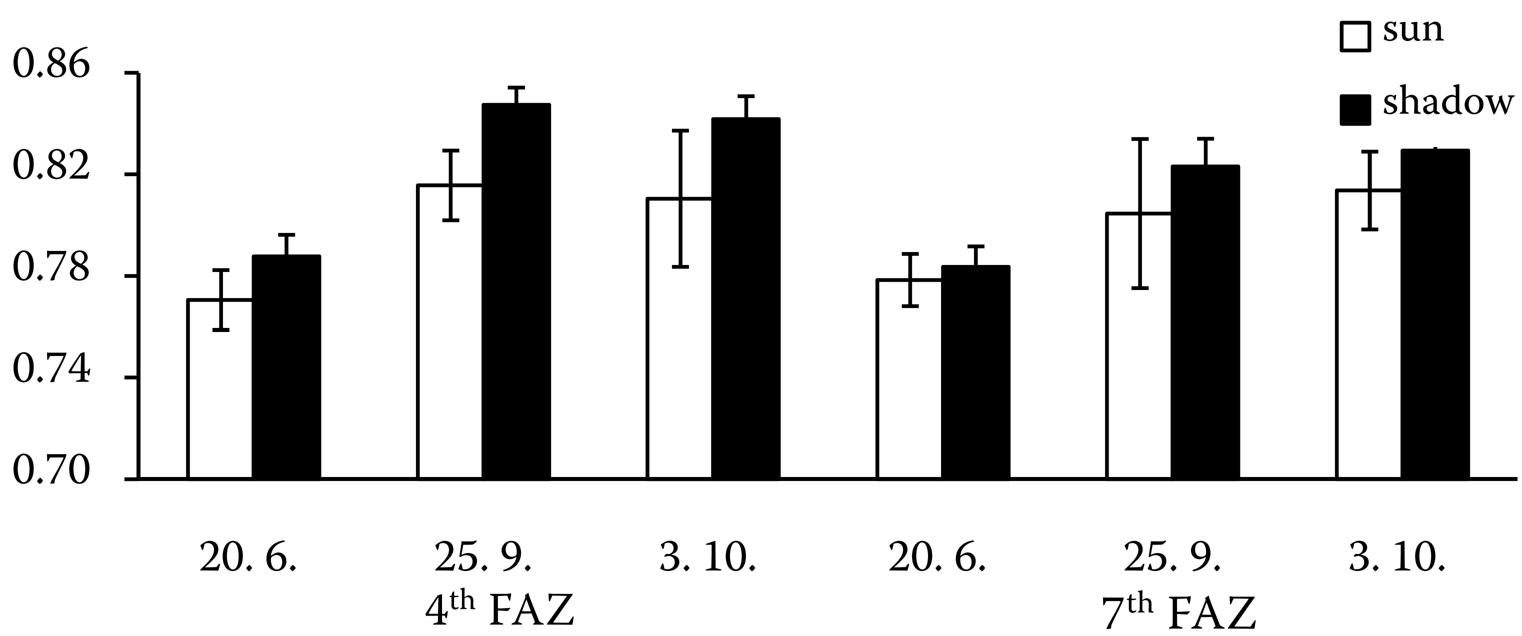

Fig. 1. The maximum quantum yield of photosystem 2 (PSII) Fv/Fm of European beech seedlings originating from the 4th and 7th FAZ grown in an unshaded (sun) and shaded (shade) plastic greenhouse. Vertical line segments represent the confidence on 5% of signinificance

Einhorn et al. (2004), who measured the lowest values of *Fv*/*Fm* in beech seedlings growing in the open area, higher values in the gap and the highest values in seedlings growing under shelterwood, explained these differences by increased photoinhibition in beeches in the gap and in the open area. But the higher photoinhibition did not have a negative influence on total biomass accumulation. They stated that such photoinhibition was of adaptive character and did not damage the assimilatory organs.

Higher values of the maximum quantum yield of PSII (*Fv*/*Fm*) photochemistry in beech seedlings in the shade compared to seedlings on the area with higher light access were reported by Špulák (2008). Significantly higher values in shaded beech plants compared to plants growing in direct sun were also measured by Valladares et al. (2002). They concluded that these were species-specific differences as they did not observe this trend in oak.

In beech seedlings from both the 4th and the 7th FAZ the evaluation of the reaction of assimilatory organs to increasing light intensity revealed statistically significant differences in the photosynthetic electron transport rate (ETR) between the sun and shade variant in the plastic greenhouse. Seedlings exposed to full sunlight had the markedly higher ETR especially at lower and medium values of photosynthetically active radiation (PAR) and higher maximum values of ETR. A similar course of ETR curves and differences between plants grown in the sun and in the shade were observed in seedlings from both the 4th and the 7th FAZ during the whole growing season (Fig. 2).

Higher maximum values of ETR in unshaded seedlings of various tree species including the European beech compared to heavily shaded plants were described by Wyka et al. (2007). Schreiber (1997) reported that shady leaves showed the saturation of ETR at lower values of PAR than did sunny leaves and they were characterized by the lower ETR. These results support the findings of the higher photosynthetic rate of beech plants growing in high light compared to shaded plants (Tognetti et al. 1997).

Reaction of assimilatory organs to changes in light conditions

To determine the reaction of seedlings grown in a plastic greenhouse to a sudden change in light conditions (e.g. after outplanting) a part of trays (56 plants) with seedlings from sunny conditions was transferred to the shade in mid-September, and vice versa, the same number of plants from the shade was transferred to an unshaded plastic greenhouse. Chlorophyll fluorescence was repeatedly measured during two subsequent weeks.

A slight increase in the values of the maximum quantum yield of fluorescence *Fv*/*Fm* was observed

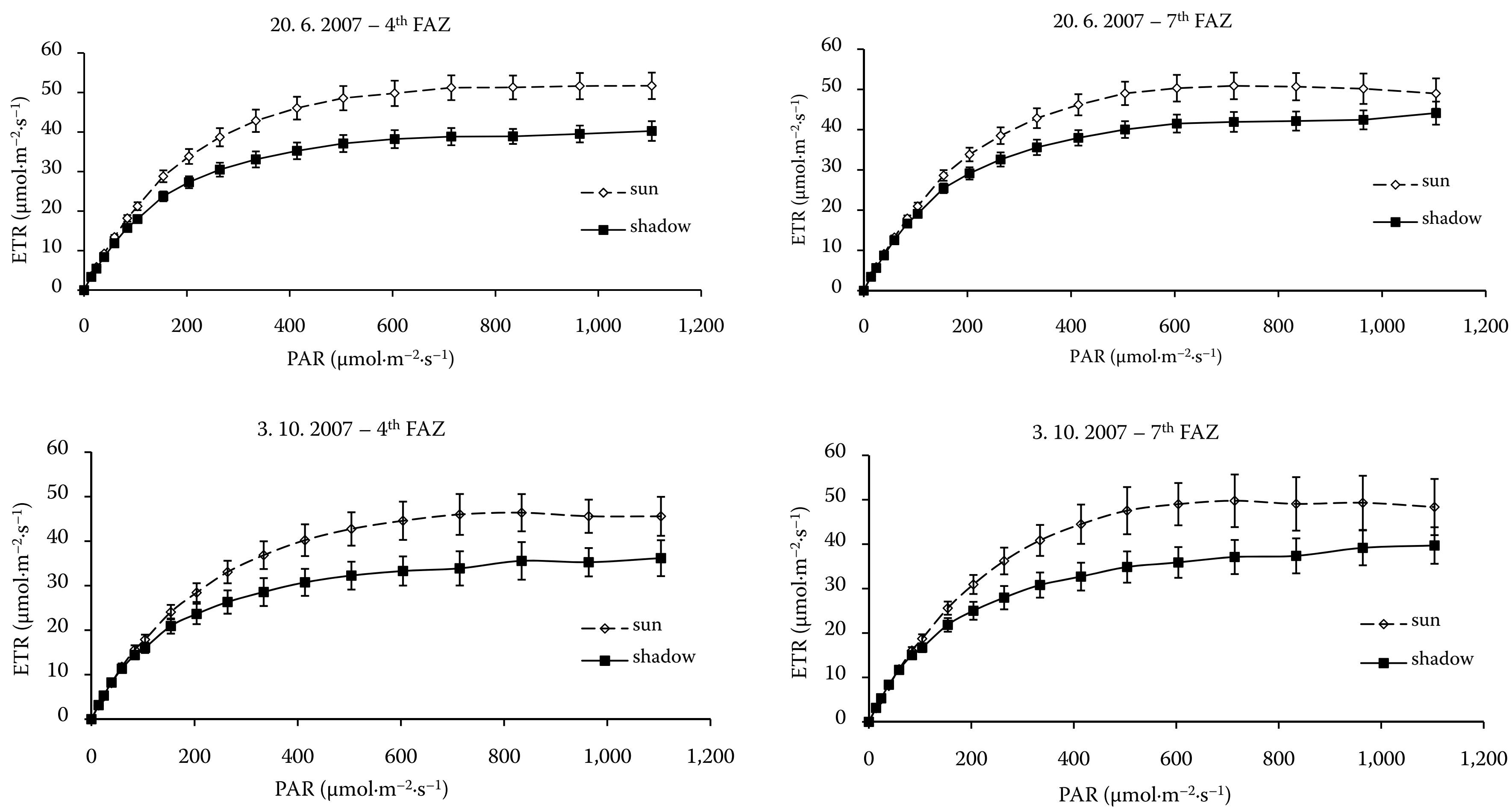

Fig. 2. The photosynthetic electron transport rate (ETR) at the increasing intensity of photosynthetically active radiation (PAR) in beech seedlings from the 4th and 7th FAZ grown in an unshaded (sun) and shaded (shade) plastic greenhouse. Vertical line segments represent the confidence on 5% of signinificance

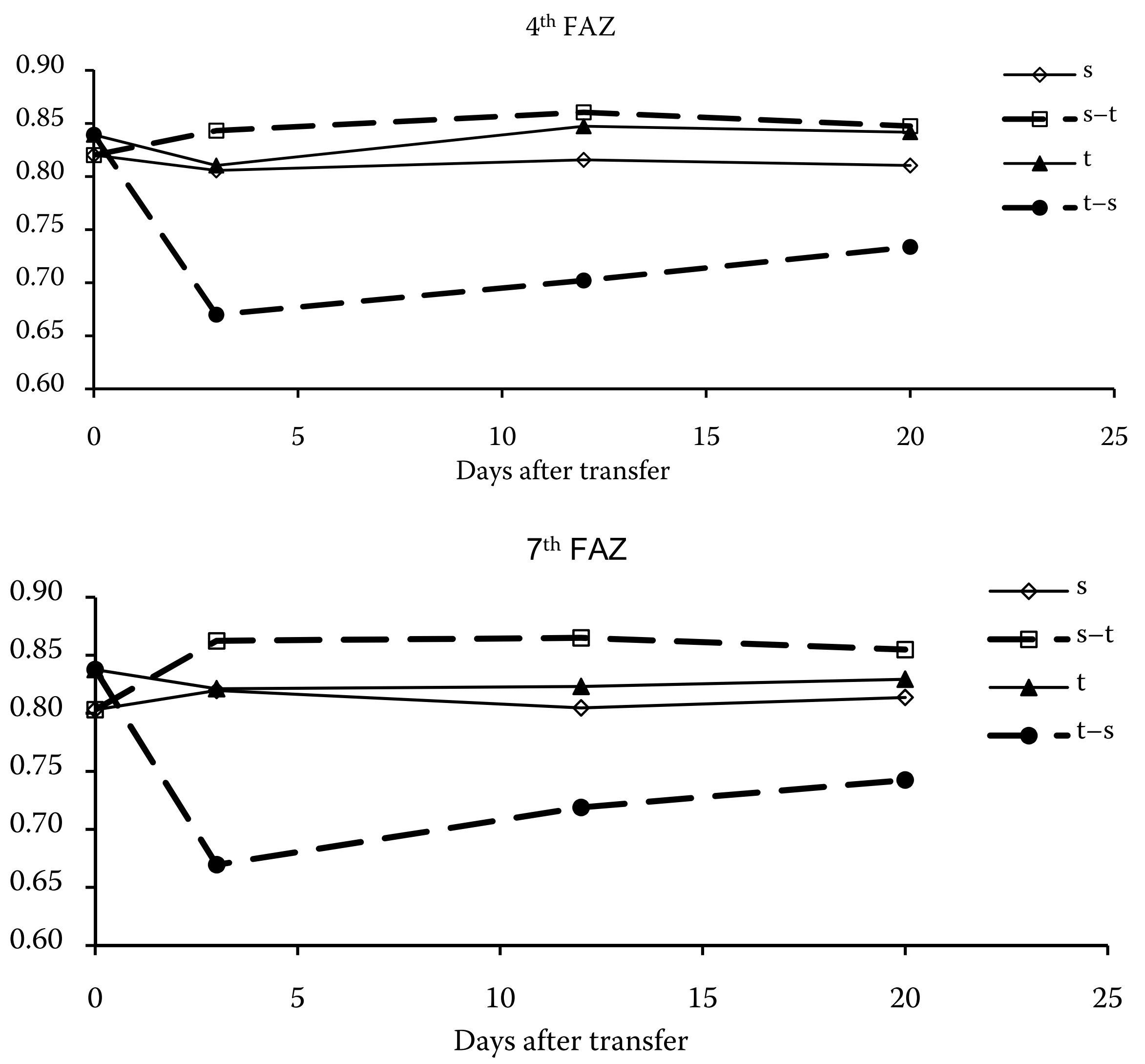

Fig. 3. Changes in chlorophyll fluorescence *Fv*/*Fm* after the transfer of beech seedlings from shade to sun and vice versa compared to seedlings left in the initial light conditions (s = seedlings in the sun, s–t = transport from sun to shade, t = left in the shade, t–s = transport from shade to sun)

after transfer from the sun to the shade that persisted until the last evaluation at the beginning of October (Fig. 3).

On the contrary, after seedlings grown in the shade were transferred to the unshaded plastic greenhouse, there occurred high photoinhibition that caused a decrease in the *Fv*/*Fm* values. Within two weeks after the transfer of beech seedlings from the shade to the sun the values of the maximum quantum yield of fluorescence *Fv*/*Fm* were slightly increasing and significant differences from the other variants were observed until the beginning of October (the last measurement). The described trend was found out in seedlings from both the 4th and 7th FAZ.

A similar reaction of shade-adapted beech plants after transfer to high light was described by Wyka et al. (2007). The rate and duration of photoinhibition (measured as a decrease in the maximum quantum yield *Fv*/*Fm*) were species specific; they were highest in beech, much lower in spruce and fir and the lowest in maple. Higher values of *Fv*/*Fm* in beech seedlings growing at a low radiation intensity compared to seedlings growing at a high light intensity in the growth chamber were observed by Tognetti et al. (1997). After a change in light conditions from low to high radiation intensity there was a significant decrease in the *Fv*/*Fm* values. Within another three weeks following the change in light conditions these values continued to decrease.

A decrease in the *Fv*/*Fm* values of seedlings growing in the shade that occurred immediately after transfer to a gap was also reported by Naidu and DeLucia (1997) in oak and maple. The decrease was followed by a slow return to the initial values. The maximum quantum yield of *Fv*/*Fm* of leaves growing in the shade after transfer to a gap was still lower after 30 days than in the leaves of plants left in the shade and in control seedlings growing in the gap.

Photoinhibition in beech seedlings grown in the shade and transferred to full light caused a reduction in the photosynthetic electron transport rate (ETR) measured during the increasing intensity of photosynthetically active radiation (PAR). Fig. 4 illustrates the maximum values of ETR obtained from light curves at PAR increasing from 0 to 1,414 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Seedlings grown in the sun (variant s) reached significantly higher values of ETR compared to seedlings from the shaded plastic greenhouse (variant t). The reactions of seedlings from various environments to transfer to different light conditions were different. While the seedlings grown in the unshaded plastic greenhouse (sun) did not show any greater changes in ETR after their transfer to the shade (variant s–t), there was a marked reduction in the photosynthetic electron transport rate in the seedlings grown in the shade after their transfer to the sun (variant t–s). The results were similar in seedlings from both the 4th and 7th FAZ.

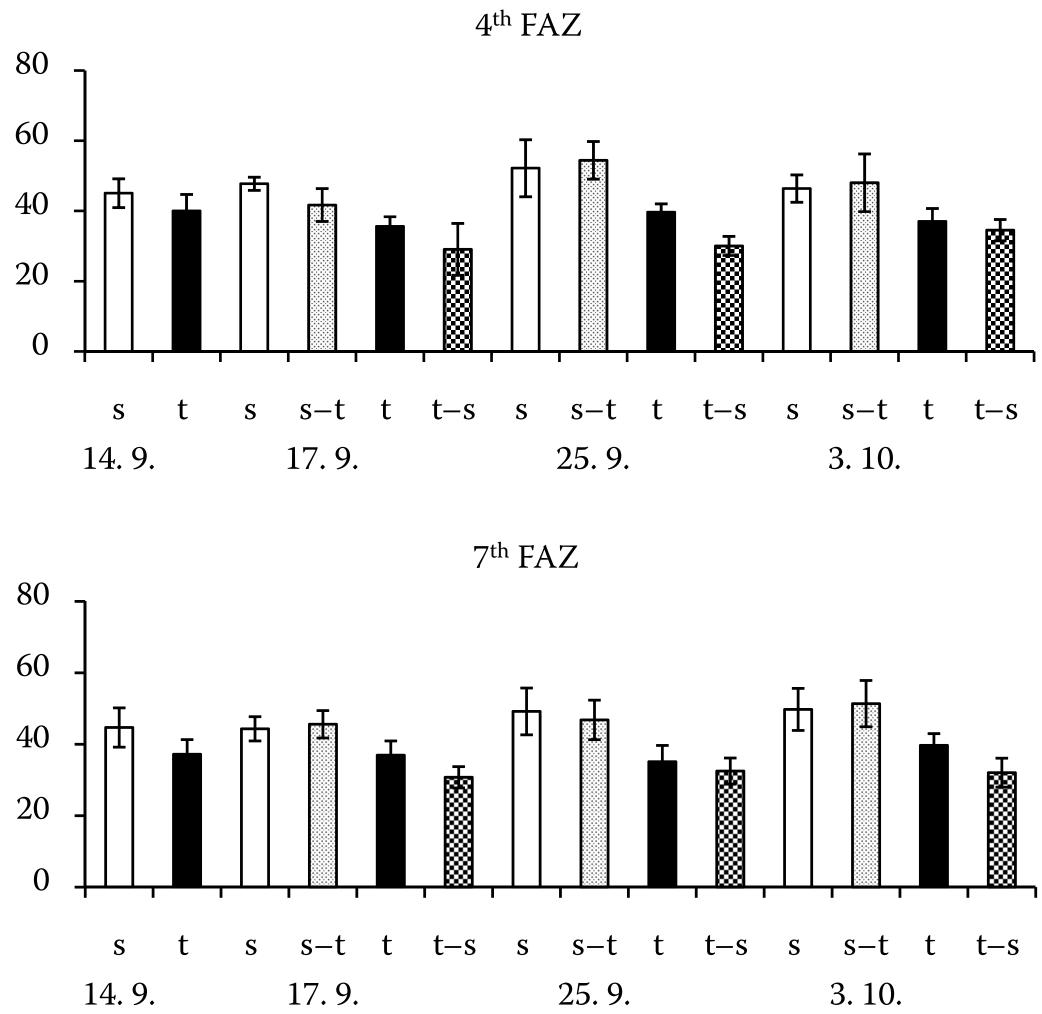

Fig. 4. Maximum values of photosynthetic electron transport rate (ETR) obtained from light curves in beech seedlings grown in the sun and in the shade within 2 weeks after a change in light conditions (description of the variants see Fig. 3). Vertical line segments represent the confidence on 5% of signinificance

The measurement of ETR is used mainly for its close relationship with the CO_2 assimilation rate. Under certain conditions the electron flow through PSII is an indicator of the total photosynthetic rate (Maxwell, Johnson 2000). Tognetti et al. (1997) studied the photosynthetic rate in beech seedlings grown in a growth chamber at low and high light intensity. They also investigated the reaction of seedlings adapted to low light intensity after their exposure to high radiation intensity. The photosynthetic rate was highest in seedlings permanently grown at high light intensity. After the light intensity changed (from low to high intensity), a steady reduction in the photosynthetic rate was observed within several weeks. The authors ascribed these changes to photoinhibition that occurred after the leaves were exposed to light conditions exceeding the intensity that may be used for photosynthesis. Photoinhibition is also indicated by a marked decrease in the values of chlorophyll fluorescence *Fv*/*Fm* following the change in light conditions.

During photoinhibition the photosynthetic capacity is reduced on the level of the light phase of photosynthesis, i.e. in processes of the capture and transmission of radiant energy quanta. The long-term effect of excessive PAR leads to the photodestruction of assimilatory organs when the bleaching of photosynthetic pigments occurs (Šprtová, Marek 1996).

The evaluation of chlorophyll fluorescence of European beech seedlings grown under different light conditions showed significantly higher values of the photosynthetic electron transport rate (ETR) in seedlings grown in the unshaded plastic greenhouse. From such values the higher photosynthetic rate can be deduced in these seedlings. It also implies more intensive growth and larger size of seedlings grown in the sun compared to seedlings in the shade.

The evaluation of chlorophyll fluorescence after beech seedlings were transferred to different light conditions demonstrated the relatively small reaction of seedlings transferred from the sun to the shade. Only small changes in the evaluated parameters of chlorophyll fluorescence (*Fv*/*Fm*, ETR curves) were observed. On the contrary, the transfer of shade-adapted seedlings to the sun led to a marked decrease both in the maximum yield of photochemistry *Fv*/*Fm* and in the photosynthetic electron transport rate (ETR). These results document the high photoinhibition of assimilatory organs.

The full acclimatization of beech seedlings is a gradual process observable during several subsequent growing seasons (Reynolds and Frochot 2003). Further evaluation of the survival and growth of seedlings grown in the sun and in the shade after their outplanting to different conditions will show to what extent the need of adaptation to different light conditions will influence their performance.

CONCLUSION

European beech seedlings grown in an unshaded plastic greenhouse were larger at the end of the first growing season than seedlings grown in the shaded part. They had taller shoots, larger root collar diameters and higher weight and volume of shoots and root systems. In seedlings grown in the sun a higher number of leaves, larger total leaf area and higher dry matter of leaves per 1 plant were determined. The average area of one leaf was larger in seedlings grown in the shade.

Different light conditions during growing did not usually influence the root to shoot ratio, the proportion of fine roots in the root system and the ratio of leaf area to seedling height.

The measurement of chlorophyll fluorescence showed lower values of the maximum quantum yield of photosystem PSII (*Fv*/*Fm*) in seedlings grown in the sun that indicate partial photoinhibition. The higher photosynthetic electron transport rate (ETR) evaluated at the increasing intensity of photosynthetically active radiation (PAR) in seedlings grown in the sun was apparently connected with the higher photosynthetic rate and more intensive growth of these seedlings.

The transfer of seedlings from full sun to shade resulted only in small changes in chlorophyll fluorescence (*Fv*/*Fm*, ETR). On the contrary, the transfer of seedlings from the shaded plastic greenhouse to the sun induced photoinhibition leading to a significant decrease in the maximum quantum yield of photochemistry *Fv*/*Fm* and photosynthetic electron transport (ETR), which also indicates a reduction in the photosynthetic rate.

The described results document that the outplanting of the beech planting material to different light conditions from those in which it was grown requires its overall adaptation to the new environment. How serious the need of such adaptation of beech seedlings grown in the sun and in the shade is after their outplanting to different conditions must be tested in further research.

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