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Shoot morphology and leaf gas exchange of *Fagus sylvatica* as a function of light in Slovenian natural beech forests

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Abstract: Five plots with young beech trees of the same age (13–15 years) were established to study the threshold, where plagiotropic growth becomes evident as the consequence of the reduced light intensity. Trees were equally distributed along the light gradient and were divided according to light conditions (Indirect Site Factor, ISF) into three groups of stand conditions: close canopy stand (ISF<20), edge (20<ISF<25) and open area conditions, without the sheltering effect of a mature stand (ISF>25).

Morphological and physiological responses of young beech were studied between managed and old growth forest and between different forest complexes (Pohorje and Kočevje region) on natural beech sites. Criteria for the plagiotrophic growth was the relation between tree length and tree height (l/h) under various light conditions.

Under controlled conditions (temperature, flow and CO_2 concentration, RH, light intensity) light saturation curves of leaf net photosynthesis were measured on same trees to compare both responses between different light categories and different plots within comparable light conditions.

Our study confirmed different thresholds for morphologic response between two forest complexes as well as between old growth and managed forest. Results were in accordance with physiological responses: the value of limiting light for a plagiotropic response was lower in Kočevje (17% ISF) than on Pohorje (25% ISF).

Additional key words: light, plagiotropic growth response, light saturation curves, managed and old growth beech forest

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Introduction

Forest management is facing higher risk-rates and an increasing number of extreme events, especially on marginal and extreme sites. The importance of autochthonous tree species is emphasized in connection of more frequent and intensive pressures to which forests are exposed (Zerbe 2002, Hannah et al. 1995, Stanturf 2002). In Slovenia, where forests cover over 60% of the country, sites of mixed broadleaf species predominate; in particular natural beech forests (Kutnar 2003). The quality of existing and future beech forests is closely connected with our understanding of tree-response to different light conditions, especially in an environment of reduced light intensity under a mature canopy and in younger development stages. Such knowledge leads to correct and well-tuned spatial and temporal silvicultural measures, which may vary among different silvicultural systems. It is also directed at sustainable development and a better future quality of forests (Kazda 1997).

Increased risk is predicted in forest management, especially in forest ecosystems (Diaci 2007). In spite of the relatively wide and balanced presence of beech forests in Slovenia, several key questions about the future response of European beech (*Fagus sylvatica* L.) to expected changes, such as temperature increase, redistribution of precipitation and increase of atmospheric CO_2 concentration, remain open. Research results cited in the literature are in most cases unclear and sometimes even contradictory (Poorter 1998, Lloyd and Farquhar 1996).

Shade tolerant species such as beech are capable of adapting their growth and morphology to modest light conditions. In shade, they maximize light utilization by minimizing growth. Leaf distribution and the orientation of shoots are also different than in open light conditions. Plagiotropic growth, which results in deviation from the vertical axis, an assymetric shape of crown and knee-shaped growth of the stem in young trees, is the least useful and most unwanted effect with respect to future forest products that increases with the degree of shade (Lüpke et al. 2004). As indicated in a study by Huss (in Lüpke et al. 2004), the stem form of young beeches is more plagiotropic below dense shelter compared to plots with low or no shelter (Lüpke 2005). The consequences of such growth are seen in an almost horizontal orientation of the stem and minimum self-shading effect of leaves (Lüpke et al. 2004). In a study of different architectural factors effecting the formation of forks in beech under the presence or absence of forest canopy by Nicolini and Caraglio (1994) not only shelter, but also large variation and fluctuation of annual growth rate most strongly influenced the arrangement and formation of forked branches (vertical lateral axes), which are also an unwanted effect in terms of future stem quality. Nicolini (2000) connected a plagiotropic growth pattern with lack of light and also with lower vigour in young trees. Changes in crown morphology have been shown to play an important role in the acclimation capacity of species to different light environments, and crown morphological plasticity has been found to be especially important in shade-tolerant species (Canham 1988, 1989).

Our research goal was to define range of morphological response to different light intensity in naturally regenerated beech on different forest sites (1) and to test if the gas exchange e.g. photosynthetic response of same beech and sites is following the same pattern (2).

Methods

Research was performed on 10–15 year old beech trees at five selected natural forest stands: at Kladje and Bričká in the Pohorje area, at Vrhovo and in the karstic-dinaric area of Kočevski Rog – at Snežna jama (managed forest) and Rajhenav (virgin forest). The number of adult trees per hectare and growing stock was assessed on each research plot in conditions of complete canopy closure. Tree height was measured electronically with a Vertex III (Haglöf, Sweden) and breast height diameter (dbh) with callipers.

Both Bričká and Kladje belong to the acidophilous beech forest type Luzulo albidae-Fagetum (Urbančič and Kutnar 2006) while Snežna jama and Rajhenav to the dinaric silver fir and beech forest type Omphalodo-Fagetum (Kutnar and Urbančič 2008).

At each location, a research plot was established 100×100 m in size encompassing all light environments, ranging from complete closure to open sky conditions on all plots, with little or no exposure. The gradient of natural light conditions was obtained by selecting young trees under a range of canopy openness. On each fenced plot, the potential light environment of 24 young beech trees in comparable light-intensity conditions was estimated with hemispherical photos. Fine tuning was applied after pilot analysis, so that the light conditions on all plots were comparable. The parameter used for evaluation of light conditions was the indirect site factor (ISF) (Wagner 1994), which is the relative proportion of diffuse light intensity above a defined plant compared to open/gap conditions, without shading, in percentage (%). Photos were taken with a digital Nikon Coolpix 990 and calibrated fish-eye lens and analyzed with WinScanopy software. In the process of hemispherical photo analysis the vegetation period was defined for each plot group separately; a »Standard overcast sky« (SOC) model was applied for diffuse light distribution. For the calculation within the vegetation period, the sun's position was specified every ten (10) minutes. The solar constant was defined as 1370

Table 1. Research plots characteristics

Plot	Altitude (m)	Lat (0)	Long (0)	Annual precipitation (mm)	Annual average air T (°C)	Soil type	Number of trees (No/ ha)	Growing stock (m^3/ha)
Bričká	1093	46°28'40''	15°15'40'	1190	9,1	Dystric Cambisol	173	477
Kladje	1308	46°28'48''	15°23'24''	1066	9,2	Dystric Cambisol	126	302
Vrhovo	273	45°48'25''	15°18'11''	1138	9,4	Acric Luvisol	189	479
Sn. jama	875	45°39'15''	15°01'40''	1330	8,3	Rendzic Leptosol	166	612
Rajhenav	865	45°39'36''	15°03'36''	1330	8,3	Rendzic Leptosol	167	992

W/m^2, 0.6 for atmospheric transmissivity and 0.15 for the proportion of diffuse radiation compared to calculated direct potential radiation. Three groups were defined on the basis of light conditions: stand conditions (ISF<20), edge (20<ISF<25) and more open area conditions, without the sheltering effect of a mature stand (ISF>25). The height of trees on plots ranged from 40–70 cm under stand conditions, from 70–110 cm under edge conditions and from 110–220 cm in open area conditions.

In each group, eight trees were also randomly selected also for photosynthesis and leaf nutrient measurements (Leco CNS-2000 analizer).

Light saturation curves were established to define comparable the ecophysiological response of net assimilation (A) in beech to different light intensities in different plots and in comparable potential light conditions (Larcher 1995, Farquhar et al. 1980). All photosynthesis measurements were performed at a constant temperature of the measurement block (20°C), a CO_2 concentration of ambient 350 μmol/l, RH of 35–40% and different light intensities: 0, 50, 250, 600 and 1200 μmol/m^{2}s. Measurements were recorded manually after plant response reached equilibrium and coefficient of variability dropped below 5% (approximately 20–30 minutes for every measurement point), starting at ambient light conditions, which were reduced to reach zero, followed by a gradual increase toward maximum values, so that stomata could adapt. Maximum assimilation (A_{max}) rates were used in comparisons of trees among different plots. Responses were measured with an LI–6400 portable system on at least three sun leaves per plant, located in the upper third of the tree-crown height on every plot. Twelve trees were measured on each plot, four per same canopy light conditions. Measurements were restricted to the time period between 9.00–11.30 AM and were blocked by day to ensure proper replication through time.

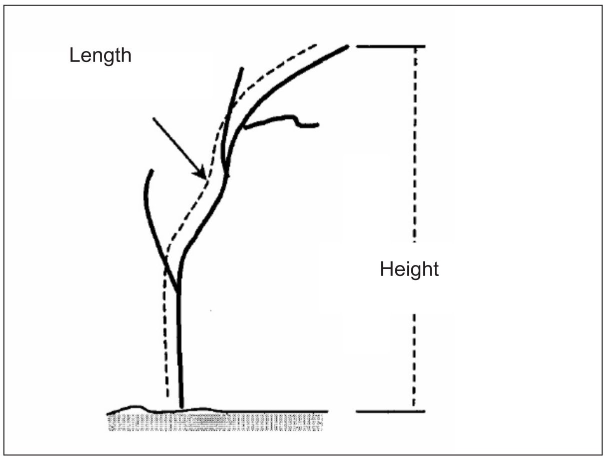

Fig. 1. Tree length and height as an indicator of plagiotropism (Lüpke et al. 2004)

To evaluate the morphological response the quotient between the length and height of trees (l/h) was used, which increased in the case of plagiotropic growth (> 1).

Since some young trees in the open also show a slight deviation in growth from the vertical axis, which is not necessarily a function of plagiotropy, a threshold value of l/h= 1.1 was chosen to separate plagiotropic from orthotropic growth. The limiting value of light was defined after measurements of the ratio in three sequential vegetation periods (2003, 2004 and 2005). In the analysis, the values under similar light-intensity conditions were compared between plots (how closed/open the mature stand was). Annual measurements of tree length were performed with a measuring tape and of tree height with an aluminium holder equipped with a measuring tape and perpendicular mounted profile to avoid paralaxis, with centimetre accuracy (cm).

The limiting value below which plagiotropic growth was observed was defined for each plot separately. Plagiotropic behavior between different plots was assesed by comparison of data into an exponential-decay-3 parameter curve (1),

$$Y = A + B^{*}\exp^{(-b^{*}x)} \qquad (1)$$

Differences among categories and plots were determined by analysis of variance (AVAR) and post-hoc analysis (LSD) after normality of data was confirmed by the program R (http://www.r-project.org/).

Results

Plagiotropic growth

Under favourable light conditions, the tree trunk was vertical, i.e., the ratio between tree length and height was close to 1 and the crown was symmetrical. Below the limiting light value, the proportion of light was reduced, the shape of the young trees became curved and, consequently, the ratio (l/h) higher. By fitting the data into an exponential type of curve, the point of different reaction to light was observed. The slope of the fitted curve and the ISF value at (l/h) a quotient of 1.1 observed on all plots showed that values from both Pohorje plots were higher than those in Kočevski Rog.

On all plots, young beech trees showed plagiotropic growth if light conditions dropped below 20% ISF. The reactions of beech at Brička and Kladje were different from trees on the remaining plots, the steepness of curves was less pronounced and the calculated limiting light values were higher than those from Snežna jama and Rajhenav. If the morphological reaction is compared to other light components (e.g., total openness or direct light), the connection is not so

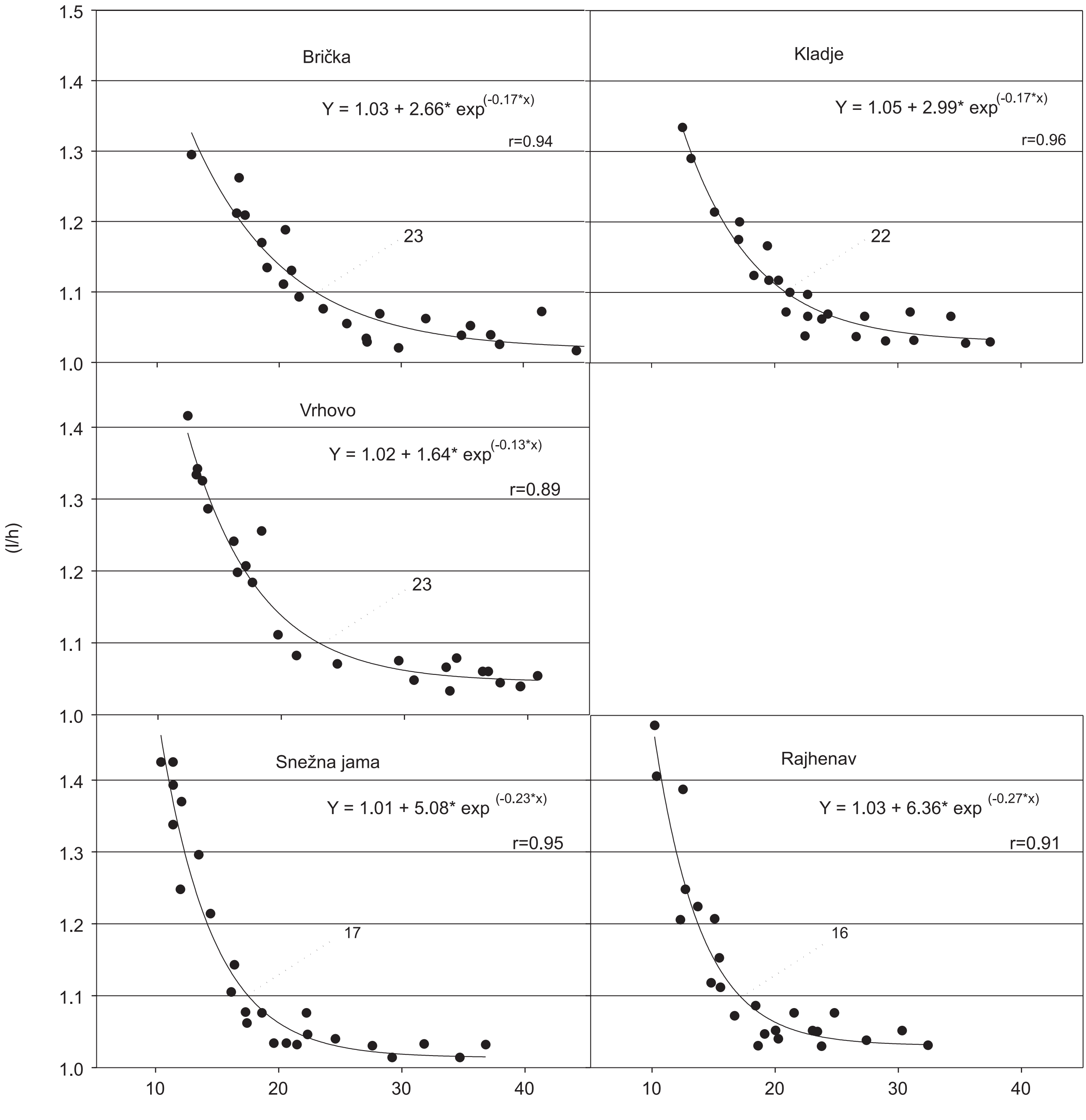

Fig. 2. Ratio between trunk length and tree height (l/h) in relation to light intensity (ISF %) on research plots with decaying exponential curve. Limiting ISF values for light intensity for each plot and exponential-decay type of function are presented with correlation coefficient (r)

pronounced as in the case of the indirect site factor (ISF in %). When data was compared between forest complexes, the difference between the two was clearly expressed (Fig. 3).

The ratio l/h on plots in the Kočevje complex achieved higher values than those from Pohorje. Comparison of data from plots also confirmed the differences between the two complexes. The reaction of trees was better explained with diffuse than with direct light components (Table 2).

Table 2. Correlation coefficients (r) for direct – diffuse light components and l/h ratio, presented for both forest complexes

Forest complex	Direct light	Diffuse light
Pohorje	0.34	0.86
Kočevje	0.79	0.92

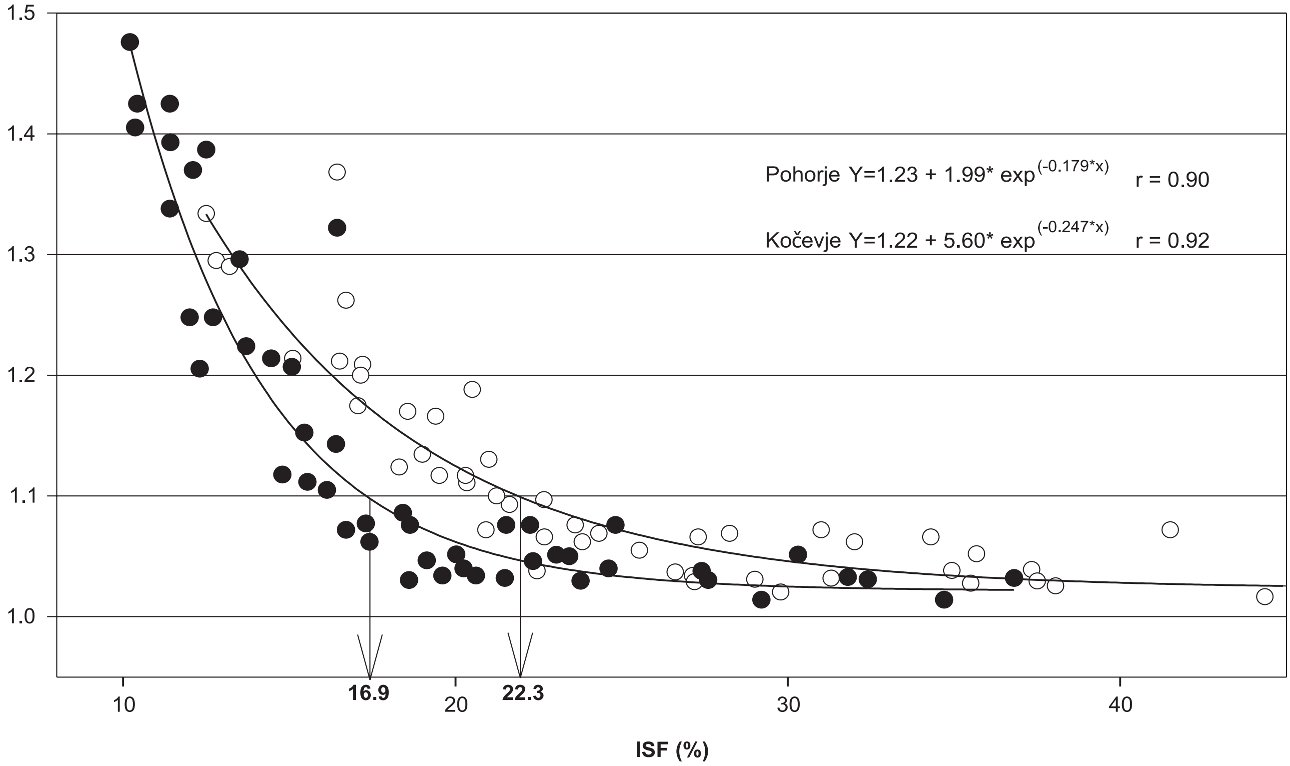

Fig. 3. Comparison of ratio between trunk length and tree height in relation to light intensity (ISF) between Kočevje and Pohorje, fitted by exponential decaying curve. Limiting ISF values for light intensity and forest complex intensity from exponential-decay type of function with correlation coefficient (r) are presented

Light response of photosynthesis

The highest light saturated values of photosynthesis (A_{max}) were measured in the open (gap) at Vrhovo, followed by the plots from the Pohorje complex (Brička and Kladje), while the lowest values were measured on plots in Kočevski Rog (Snežna jama, Rajhenav) (Table 3).

Differences among canopy, edge and open area responses were confirmed with high significance on all plots (Table 4) except in Rajhenav (virgin forest), where no differences between canopy and edge area conditions ($df_{1,14}$; F=0.13; NS… non significant) were confirmed (Table 4).

There was also no difference in response to maximum light under gap conditions between Snežna jama and Rajhenav. Assimilation responses to light were higher in all categories in the virgin forest. The assimilation response of young beech was also significantly different between the two forest complexes under canopy ($df_{1,30}$; F=285.99***), edge ($df_{1,30}$; F=171.68***) and gap conditions ($df_{1,30}$; F=93.30***).

Table 3. Maximum assimilation rates (A_{max}) for light saturation curves (means ± SE, n=24)

A_{max} (μmol /m^{2}s)	Canopy	Edge	Gap
Brička	7.3±0.4	9.8±0.8	11.9±1.1
Kladje	8.3±0.3	9.7±0.5	10.7±0.9
Vrhovo	6.1±0.4	9.3±0.4	13.2±0.6
Snežna jama	4.8±0.4	6.5±0.5	8.0±0.7
Rajhenav	7.1±0.3	7.2±0.5	8.2±0.6

Table 4. Differences in maximum assimilation rates (A_{max}) on plots (AVAR and *post hoc* LSD analysis): 1 – shelter; 2 – edge; 3 – open light conditions; NS… non-significant differences

Plot	df (2, 21)		
	F	*P*	LSD
Brička	58.681	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.000
Kladje	28.804	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.005
Vrhovo	442.675	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.000
Sn. Jama	75.266	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.000
Rajhenav	12.495	0.000	1–2 p=0.600 NS
			1–3 p=0.000
			2–3 p=0.0006

Table 5. Average leaf nitrogen content per leaf area on plots (means ± SE, n=8)

Plot	Nitrogen (N) [mg/cm^2]		
	Canopy	Edge	Gap
Brička	7.5±1.2	9.7±1.3	12.7±1.4
Kladje	8.8±1.0	12.4±1.7	18.2±1.9
Vrhovo	4.5±0.9	8.6±1.5	10.9±2.1
Sn. jama	4.7v±0.8	10.4±0.7	10.7±1.6
Rajhenav	3.4±0.8	9.0±0.6	8.9± 1.3

Table 6. Differences in leaf nitrogen between categories on plots (AVAR and *post hoc* LSD analysis): 1 – shelter; 2 – edge; 3 – open light conditions; NS… non-significant differences

Plot	df (2, 21)		
	F	*P*	LSD
Brička	37.173	0.000	1–2 p=0.002
			1–3 p=0.000
			2–3 p=0.000
Kladje	93.225	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.000
Vrhovo	70.205	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.000
Sn. Jama	68.914	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.742 NS
Rajhenav	88.634	0.000	1–2 p=0.000
			1–3 p=0.000
			2–3 p=0.742 NS

In the Kočevski rog area, differences among the tree light categories were smaller in the virgin forest, where no differences in response between canopy and edge were found (Post hoc LSD, p=0,097), than in the managed one (at Snežna jama). Assimilation rates were highest in all categories in virgin forest, despite the comparable amount of nitrogen in leaves on the two plots (Table 5).

The nitrogen content defined per leaf unit (mg/cm^2) was different between Pohorje and Kočevje plots under canopy ($df_{1,30}$; F=105.13***), edge ($df_{1,30}$; F=6.19*) and gap conditions ($df_{1,30}$; F=40.99***). On every plot, the amount was highest under forest gap and lowest under shelter conditions, except in virgin forest, with maximum values at the forest edge (Table 5). Differences between edge and open area conditions were not significantly different on the two plots from Kočevje (Table 6).

Comparison between maximal photosynthetic rates (A_{max}) and light conditions (ISF) (Fig. 4) also indicated differences between forest complexes.

Discussion

The ability of juvenile trees to adapt morphologically to various light levels is an important species-specific characteristic (Messier et al. 1999), as indicated in our study. Plants have evolved different adaptation strategies to optimize their growth in different light conditions (Kunstler et al. 2005). There is no clear evidence that shade-tolerant species are morphologically more plastic than less tolerant ones

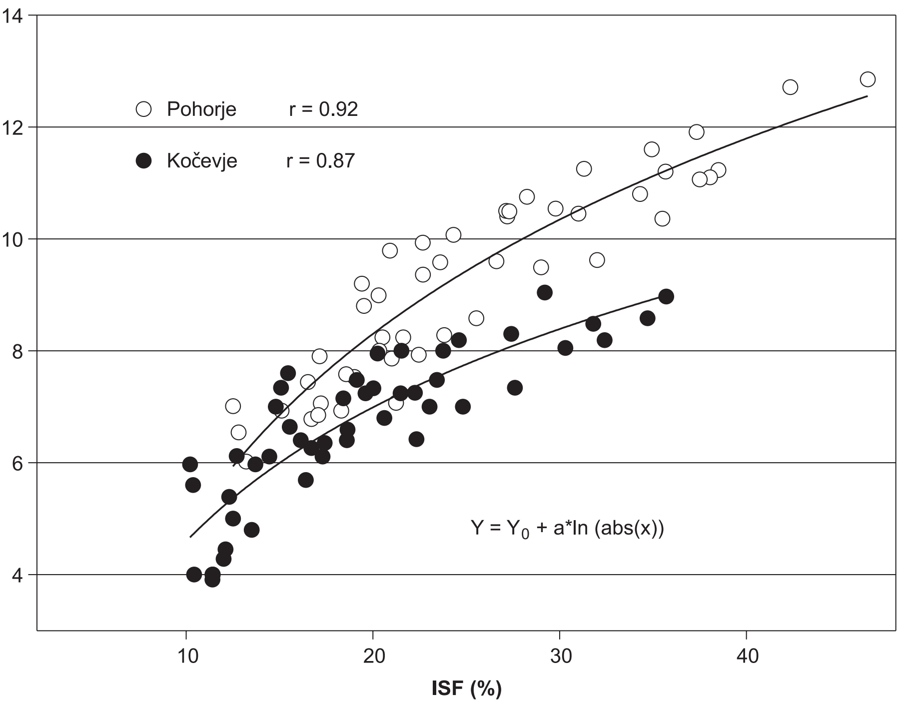

Fig. 4. A_{max} vs. light (ISF) in both forest complexes

(Canham 1988, Chen et al. 1996, Messier and Nikinmaa 2000, Paquette et al. 2007).

The Kočevje region (Snežna jama and Rajhenav) is well known for its forest management, with a long tradition of a sustainable and close-to-nature approach, with a single-tree selection method (Diaci 2006). In contrast, in the Pohorje complex, Norway spruce has been favoured in the last century on potential beech sites and beech is today gradually replacing spruce, either by underplanting or by natural regeneration (Diaci 2006). In the case of the response in young beech trees, differences in assimilation rate may reflect not only the different forest management history, but also a different genetic background.

The limiting value was defined as 22% relative light intensity for Brička and Kladje, while young beech responded at much lower values, below 16%, and showed a more shade-tolerant character than on plots in the Pohorje region. The ratio between tree length and height as the result of light conditions of the mature canopy and the position of each tree in forest stands, may indicate possible future quality and mechanical stability.

Our study confirmed differences in response among beech under shelter, at the forest edge and in the open. In spite of comparable light conditions, the highest assimilation rates were measured on the research plots of the Pohorje complex, where plagiotropic growth in beech started below higher values, compared to the highest assimilation rates and reaction of trees on Kočevski Rog. Results also indicate a different response of young beech between managed forest (Snežna jama) and virgin forest (Rajhenav). Differences in virgin forest between the same light categories were not very pronounced and were thus more homogenous than those observed in the managed forests. The photosynthetic yield in all categories was higher in virgin forest. There were no confirmed differences in the amount of leaf nitrogen among plots which, expressed in units per leaf area, which were highest on all plots in open conditions, without shade.

Von Lüpke, who confirmed the effect of density on plagiotropic growth in a mature spruce stand, with more vertical growth as the density was reduced (Lüpke et al. 2004), reached similar conclusions as those relating to the Pohorje complex. Wagner and Müller-Using (1997) quote a limiting value of 10%, while Schmitt et al. (1995) state 15% of relative light intensity, below which plagiotropic growth is evident, which is similar to our results for plots in Kočevski Rog, but significantly less than values measured and defined for Pohorje. Under conditions with lower light intensities, under dense canopies, in which the diffuse component of light radiation predominates, plagiotropic growth is more present (Lüpke et al. 2004) and it is also influenced by the forest management approach (Gralla et al. 1997, Pampe 2000, Pampe et al. 2003, Spellmann and Wagner 1993). Studies from Burschel and Schmaltz (1965) with beech seedlings showed a significant response in terms of a reduction of biomass, especially in the roots, with an increasing effect of shade; the height increment was reduced after relative light intensity dropped below 20% of open area solar radiation and the radial increment was only 50% of that under open light conditions. Below 10%, plagiotropic growth and a strong reduction in the number of seedlings were evident, while at 8% of relative light, biomass production dropped to 50%; seedlings survived for 2 years at 1% light intensity (Röhrig 1967). In our study, the plagiotropic growth responses of trees to different light intensity were non-linear; maximum relative changes were evident at the forest edge. The ratio between canopy density and plagiotropic shape increased exponentially, after light dropped below a certain point. With lower light, the inclination (degree) of terminal shoots also increases (Leder 1993, Schmitt et al. 1995, Wagner and Müller-Using 1997, Weihs and Klaene 2000), so future timber quality may be questionable. On Pohorje plots, the mature stand density was higher (180 trees/ha) than on plots in Kočevski Rog (166 trees/ha) (Table 1), but with a much higher growing stock in Kočevje region. It is difficult to extrapolate results from only a few research plots to a whole forest complex, but the reaction on young trees indicated a different response between and a homogenous response within forest complexes to different light. One would expect even smaller shade tolerance on plots from Kočevje because of the smaller leaf nitrogen amount (Table 5). An interesting aspect would be the genetic constitution of the studied (target) trees. Only differences between some sites with different pollution rates have been so far confirmed for beech in Slovenia (Brus 1996).

The physiological response of young beech on the studied plots was in accordance with morphological adaptation to light. In Kočevski Rog plots, young beech was more shade tolerant according to the threshold where plagiotropsm became evident, but the absolute response to the same light intensities was smaller than the response of young beech on Pohorje plots. Even though differences between virgin forest and managed forest were confirmed, this should be treated with caution, since the sample size was relatively small and the variables measured were very few.

We believe our results have some relevance to silvicultural measures (thinning, stand density) and regeneration processes, since the conclusions showed a different reaction of trees under the same light conditions, but this should be considered site-specifically. According to the observed stem quality (Lüpke 2005, Stancioiu and O'Hara 2006), below 25% ISF, beech had more pronounced plagiotropic growth, which was also accompanied by poorer stem quality and more forked and crooked saplings. In this regard, Lüpke (2005) suggested a threshold light value of 15% ISF, which also corresponds well with our findings. Avoiding light conditions below 15–25% ISF for longer periods in regeneration stages of beech and sufficient canopy openness may therefore be a precondition for the future of beech timber quality.

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