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PHOTOSYNTHETIC RESPONSE OF YOUNG BEECH (*Fagus Sylvatica* L.) ON RESEARCH PLOTS IN DIFFERENT LIGHT CONDITIONS

FOTOSINTETSKI ODZIV MLADIH STABALA BUKVE (*Fagus sylvatica* L.) NA ODABRANIM PLOHAMA U RAZLIČITIM SVJETLOSNIM UVJETIMA

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*ABSTRACT: In view of evident changes in the reaction of European beech (*Fagus sylvatica* L.) to environmental changes, five plots with young trees of the same age were established and studied on natural beech sites. Beech trees were equally distributed along the light gradient and were divided according to light conditions. The parameter used for evaluation of light conditions was the indirect site factor (ISF) obtained by the WinScanopy analysis. Three groups of canopy – light conditions were defined: stand conditions (ISF<20), edge (20<ISF<25) and open area conditions, without the sheltering effect of a mature stand (ISF>25). In all categories light saturation curves and curves describing dependence between intercellular CO_2 concentration in leaves and assimilation rate (A-Ci) were measured under the same fixed parameters (temperature, flow and CO_2 concentration, humidity, and light intensity) with Li-6400, to compare responses between different light categories and different plots within comparable light conditions.*

Differences between canopy, edge and open area responses were confirmed with high significance on all plots as well as between studied forest complexes. On plots from Kočevje region, young beech indicated more shade tolerance, the response to increased light intensity and different CO_2 concentration was greater than the response of young beech on Pohorje plots within the same light intensities. Responses of trees on plots in managed and virgin forest were also different: young beech response in virgin forest plot was more shade-tolerant, compared to response of young beech from plots in managed forest.

Key words: Beech, photosynthesis, light, CO_2, response

INTRODUCTION – Uvod

The more frequent and intensive pressures to which forests are exposed are connected with an increasing number of extreme events and consequently higher risk-rates of forest management decisions, especially on marginal and extreme sites. The importance of autochthonous tree species in preserving dynamic equilibrium and stability in forest ecosystems is frequently emphasized (Zerbe 2002, Hannah et al. 1995, Stanturf and Madsen 2002). In Slovenia, where forests cover over 60 % of the country, sites of mixed broadleaf species predominate; in particular natural beech forests (*Fagus sylvatica* L.) (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). Solar radiation, temperatures and precipitation which influence the distribution of plants are getting in times of intensive climatic extremes and climatic changes a new

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dimension. Evident changes in distribution of plants and species diversity consequently affect primary productivity (Callaghan et al. 2004).

Several key questions about the future response of beech to expected changes such as temperature increase, redistribution of precipitation and increase of atmospheric CO_2 concentration remain open and without answers. Quotations in literature and research results are in most cases unclear and sometimes even contradictory (Poorter 1998, Lloyd and Farquhar 1996). Photosynthesis, the first estimate of net productivity could be measured as the response of plants to different light intensity or the response to different concentration of CO_2 which is entering the system in the controlled environment. In spite of good understanding of processes of carbon dynamics at leaf level in a changed CO_2 environment, it is difficult to make a prognosis of the future response of the whole plant, also because of the short time interval of observations and numerous possible interactions that have not yet been recognized. According to Batič (2007) most changes by the increased amount of atmospheric CO_2 could be expected for C3 plants at the beginning of saturation curves, especially for the plants that grow in reduced or minimal light conditions, close to compensation point. We may therefore expect most changes in shade tolerant species.

The research goal was to define range of photosynthetic response in young beech in dependence of light intensity and different concentration of CO_2 between three canopy conditions (shelter, forest edge and gap) on different forest sites.

MATERIAL AND METHODS – Materijali i metode

Research was performed on 10–15 year old beech trees at five selected natural forest stands: at Kladje and Brička in the Pohorje area, at Vrhovo and the karstic-dinaric area in Kočevski Rog – at Snežna jama (managed forest) and Rajhenav (virgin forest) (Table 1).

Table 1 Research plots characteristics
Tablica 1. Značajke pokusnih ploha

Plot *Ploha*	Altitude *Nadmorska visina* (m)	Lat (º)	Long (º)	Annual precipitation *Oborina* (mm)	Annual average air T *Prosječna godišnja T* (ºC)	Soil type *Tip tla*	Growing stock *Drvna zaliha* (m³/ha)
Brička	1093	46º28'40"	15º15'40'	1190	9,1	Dystric Cambisol	477
Kladje	1308	46º28'48"	15º23'24"	1066	9,2	Dystric Cambisol	390
Vrhovo	273	45º48'25"	15º18'11"	1138	9,4	Acric Luvisol	479
Sn. jama	875	45º39'15"	15º01'40"	1330	8,3	Rendzic Leptosol	612
Rajhenav	865	45º39'36"	15º03'36"	1330	8,3	Rendzic Leptosol	992

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

At each location a research plot was established 100x100m in size, reaching 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, for 24 young beech trees in comparable light-intensity conditions, their potential light environment was estimated with hemispherical photos (Anonymous 2003). 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; for the diffuse light distribution a "Standard overcast sky" (SOC) model was applied. For the calculation within the vegetation period, the sun's position was specified every ten (10) minutes. The solar constant was defined as 1370 W/m², 0.6 for atmospheric transmissivity and 0.15 for the proportion of diffuse radiation compared to calculated direct potential radiation. According to light conditions three groups were defined: stand conditions (ISF<20), edge (20<ISF<25) and open area conditions, without the sheltering effect of a mature stand (ISF>25). 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, four trees were randomly selected for measurement of photosynthesis. In the same leaves nitrogen concentration [mg/cm²] was determined to compare macronutrient status in different light categories (Leco CNS-2000 analyzer) (Anonymous, 2007).

Light saturation curves were established to define comparable ecophysiological response of net assimilation (A) in beech leaves to different light intensities in different plots and in comparable potential light conditions, as described by Potočić et al. (2009). All photosynthesis measurements were performed at a constant temperature of the measurement block (20ºC), a CO_2 concentration of 350 μmol/l, flow 500 µmol/s and different light intensities: 0, 50, 250, 600 and 1200 $\mu mol/m^2s$. Measurements started at ambient light conditions that were reduced to reach zero, then followed by a gradual increase toward maximum values, so that stomata could adapt.

A-Ci curves were established to compare and define assimilation response of trees (A) to different intercellular CO_2 concentrations (Ci): measurements were performed at constant light 600 $\mu mol/m^2s$, humidity, constant block temperature 20 ºC and flow 500 μmol/s, while ambient CO_2 was varied as 0, 50, 100, 350, 700 and 1000 μmol/l. Maximal assimilation (A_{max}) rates and calculated compensation points (CP) for the light saturation and A-Ci curves were used in comparisons of trees between different plots. Both types of response 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.

Water use efficiency of photosynthesis (WUE), a quantitative measure of the instantaneous gas exchange in leaves was expressed as the ratio of carbon gain per water lost [mol $H_2O/\mu mol\ CO_2$] (Larcher 1995, Lambers et al., 1998), while photosynthetic-use efficiency (PNUE) as the carbon gain per unit leaf nitrogen [$\mu mol\ CO_2/gN$] (Larcher 1995, Lambers et al., 1998) for each light category, respectively. A total of 20 leaves were sampled per seedling in the upper crown position, then cool-stored in airtight conditions. Fresh leaves were weighed and scanned for the leaf area. Leaves were dried at 105º for 24 hours until constant weight and weighed for the dry mass.

Analyses of variance (ANOVA) and post hoc LSD analysis were used after testing data to meet conditions of normality. Probability values of P<0.05 (*), P<0.01 (**) and P<0.001 (***) were considered significant. Statistical data analysis was done with the programme R (http://www.r-project.org/).

RESULTS – Rezultati istraživanja

The nitrogen content defined per leaf unit (mg/cm^2) was different between Pohorje and Kočevje plots in 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 in forest gap and lowest under shelter conditions, except in virgin forest, with maximum values at the forest edge (Table 2). Differences between edge and open area conditions were not significantly different on both plots from Kočevje (Table 3).

Table 2 Average leaf nitrogen content per leaf area, water use efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE) on plots (means ± SE, n=8)

Tablica 2. Prosječni sadržaj dušika po jedinici površine lista, efikasnost uporabe vode (WUE) i fotosintetska efikasnost uporabe dušika (PNUE) na plohama (sredine ± SE, n=8)

	Nitrogen (N) [mg/cm^2]			WUE [mol $H_2O/\mu mol\ CO_2$]			PNUE [$\mu mol\ CO_2/gN$]		
Plot *Ploha*	Canopy *Zastor*	Edge *Rub*	Gap *Otvoreno*	Canopy *Zastor*	Edge *Rub*	Gap *Otvoreno*	Canopy *Zastor*	Edge *Rub*	Gap *Otvoreno*
Brička	7.5±1.2	9.7±1.3	12.7±1.4	20.0±2.1	18.7±2.3	16.6±2.8	0.04±0.002	0.03±0.002	0.04±0.004
Kladje	8.8±1.0	12.4±1.7	18.2±1.9	22.9±2.4	20.4±1.5	15.8±2.2	0.04±0.005	0.03±0.003	0.02±0.003
Vrhovo	4.5±0.9	8.6±1.5	10.9±2.1	17.9±1.8	12.2±2.7	8.9±1.8	0.06±0.008	0.06±0.003	0.04±0.005
Sn. jama	4.7±0.8	10.4±0.7	10.7±1.6	19.9±3.3	18.8±3.2	15.2±1.9	0.10±0.006	0.08±0.002	0.08±0.003
Rajhenav	3.4±0.8	9.0±0.6	8.9± 1.3	20.3±2.6	20.9±3.1	19.9±3.3	0.08±0.006	0.06±0.002	0.04±0.006

The values for water use-efficiency (WUE) were highest under shelter on all plots, ranging from 17.9-22.9 mol $H_2O/\mu mol\ CO_2$, with the exception Rajhenav, where maximum values were measured at the forest edge (20.9 mol $H_2O/\mu mol\ CO_2$) (Table 2). Although the value measured at the forest edge in Rajhenav was greater from that measured in gap it was statistically not significant (20.9 mol $H_2O/\mu mol\ CO_2$ compared to 20.3 mol $H_2O/\mu mol\ CO_2$, respectively). A similar relation was determined for photosynthetic nitrogen use efficiency (PNUE), highest under shelter at Snežna jama (0.10 $\mu mol\ CO_2/gN$). The highest values for the maximum assimilation rate (A_{max}) was 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 4).

Table 3 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

Tablica 3. Razlike u sadržaju dušika u lišću izmedju različitih kategorija na plohama (AVAR i post hoc LSD analiza): 1- zastor; 2 - rub; 3 - otvoreno; NS… nesignifikantne razlike

	df (2, 21)		
Plot *Ploha*	F	p	LSD
Brička	37.173	0.000	1-2 p=0.0021 1-3 p=0.0000 2-3 p=0.0001
Kladje	93.225	0.000	1-2 p=0.0000 1-3 p=0.0000 2-3 p=0.0000
Vrhovo	70.205	0.000	1-2 p=0.0000 1-3 p=0.0000 2-3 p=0.0001
Sn. Jama	68.914	0.000	1-2 p=0.0000 1-3 p=0.0000 2-3 p=0.7419 NS
Rajhenav	88.634	0.000	1-2 p=0.0000 1-3 p=0.0000 2-3 p=0.7419 NS

Differences between canopy, edge and open area responses were confirmed with high significance on all plots (Table 5) except in Rajhenav (virgin forest), where no differences between canopy and edge area conditions ($df_{1,14}$; F=0.13; NS) were confirmed.

The response to maximum light in gap conditions between Snežna jama and Rajhenav showed also no differences. Assimilation responses to light were higher in all categories in the virgin forest. The calculated light compensation point (LCP) for edge and gap conditions in Rajhenav and Snežna jama were practically the same (20μmol/m^{2}s), values on other plots followed maximal assimilation rates, respectively (data not shown).

The assimilation response of young beech between the two forest complexes was also significantly different between canopy ($df_{1,30}$; F=285.99***), edge ($df_{1,30}$; F=171.68***) and gap conditions ($df_{1,30}$; F=93.30***).

Table 4 Average values of maximum assimilation rates (A_{max}) (means ± SE, n=24)

Tablica 4. Prosječne vrijednosti maksimalne asimilacije (A_{max}) (sredine ± SE, n=24)

A max (µmol /m^{2}s)	Canopy *Zastor*	Edge *Rub*	Gap *Otvoreno*
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 5 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

Tablica 5. Razlike u maksimalnoj asimilaciji (A_{max}) na plohama (AVAR i post hoc LSD analiza): 1- zastor; 2 - rub; 3 - otvoreno; NS… nesignifikantne razlike

	df (2, 21)		
Plot *Ploha*	F	p	LSD
Brička	58.681	0.000	1-2 p=0.0000 1-3 p=0.0000 2-3 p=0.0001
Kladje	28.804	0.000	1-2 p=0.0002 1-3 p=0.0000 2-3 p=0.0049
Vrhovo	442.675	0.000	1-2 p=0.0000 1-3p=0.0000 2-3 p=0.0000
Sn. Jama	75.266	0.000	1-2 p=0.0000 1-3 p=0.0000 2-3 p=0.0000
Rajhenav	12.495	0.000	1-2 p=0.6002 NS 1-3p=0.0002 2-3 p=0.0006

Maximum assimilation values for A-Ci curves ($A_{max\ A\text{-}Ci}$) (Table 6) showed similar reaction of trees as in the case of maximum assimilation values measured for the light curves (A_{max}) (Table 4).

The response of young beech was greatest in the category of canopy gap and lowest under shelter on all plots. The highest response to increased CO_2 concentration was evident at Vrhovo, followed by plots on Pohorje (Brička and Kladje) and lowest in Kočevski Rog (Rajhenav, Snežna jama). Comparison of the calculated compensation point for CO_2 between light categories showed no significant differences (data not shown). Differences between forest complexes were statistically different in all categories: canopy ($df_{1,30}$; F=6.47**), edge ($df_{1,30}$; F=13.17**) and gap conditions ($df_{1,30}$; F=33.41***).

Table 6 Maximum assimilation values for A-Ci curves ($A_{max\ A\text{-}Ci}$); (means ± SE, n=24 trees).

Tablica 6. Maksimalna asimilacija ($A_{max\ A\text{-}Ci}$); (sredine ± SE, n=24 stabla).

A max $_{A\text{-}Ci}$ (µmol /m^{2}s)	Canopy *Zastor*	Edge *Rub*	Gap *Otvoreno*
Brička	6.1±0.7	7.7±0.6	12.3±0.5
Kladje	8.8±0.6	9.6±0.5	10.4±0.6
Vrhovo	5.4±0.4	7.1±0.8	13.4±1.0
Snežna jama	3.4±0.4	5.4±0.4	9.4±0.6
Rajhenav	7.8±0.4	8.3±0.6	9.7±0.6

In the Kočevski Rog area, differences among the tree light categories are smaller in the virgin forest where no differences in response between canopy and edge were confirmed (Post hoc LSD, p=0.0969) than in the managed one (at Snezna jama). Assimilation rates were highest in all categories in virgin forests, despite the comparable amount of nitrogen in leaves on the two plots.

DISCUSSION AND CONCLUSIONS – Rasprava i zaključci

Sensitivity of photosynthesis is similar for all C_3 plants and is in proportion with mesophyll CO_2 concentration (Farquhar et al. 1980). Many studies indicate that trees have higher mesophyll resistance for CO_2, consequently lower photosynthesis and are therefore more susceptible to the increase of atmospheric CO_2 concentration. In the view of climatic changes numerous and often contradictory conclusions are being presented about the response of plants and future development of tree adaptation to environmental changes, especially due to temperature increase (Körner, 2006), decrease in amount of precipitation and changes in water supply (Davies 2006) and increase of atmospheric CO_2 concentration (Ziska and Bunce 2006).

Light, nutrients, water and CO_2 are abiotic parameters, necessary for the plant growth. Efficiency and photosynthetic regulation are governed by ribulose-1,5 biphosphat carboxylase (rubisco), which is genetically defined (Cheng et al. 1998). In general, by higher atmospheric CO_2; protein synthesis in leaves increases, stomatal aperture decreases, water use-efficiency and C/N relation on the leaf level are increased, while on the whole plant level growth is stimulated (Kimball 1993, Ghannoum et al. 2000).

By the increased amount of CO_2 photosynthesis per unit of the leaf area would increase, which is dependent on the nitrogen supply. Respiration and root activities would also increase, while biomass would be allocated into roots (sweet chestnut) or increased proportionally over whole plant (beech), which indicates a species-specific response (Kohen et al. 1993).

In spite of relatively good insight into processes of carbon dynamics on the leaf level in changed CO_2 environment it is difficult to make a prognosis of future response of the whole plant also because of a short-time interval of observations and numerous possible interactions that haven't been recognized yet (Increased WUE might stimulate development of foliar fungi (Thompson and Drake 1994) while more sugars in assimilation apparatus might stimulate the development of pathogens and infections (Hibberd et al. 1996) etc.). Recent research quote up to 30 % increase of growth in ambient with two times higher CO_2 environment (Medylin et al. 2001). A smaller probability that such increase would reflect in long term growth in assimilation was confirmed by Batič 2007, where growth only increased at the beginning, and was later reduced in time. Our analysis conirmed the differences in response between beech under shelter, at the forest edge and in the open. In spite of these differences, the highest assimilation rates were measured on the research plots of Pohorje complex and lowest on the plots of Kočevski Rog. Results also indicate a different response of young beech between managed forest (Snežna jama) and virgin forest (Rajhenav); differences between light categories were more pronounced in the managed forest, while in virgin forest response to same light conditions was more intense than in managed forest. Photosynthetic yield in all categories was higher in virgin forest. Light compensation point was higher on plots of Pohorje complex compared to plots in Kočevski Rog (data not shown).

Water use efficiency (WUE) was in all cases highest under shelter and lowest in open conditions, similar to photosynthetic nitrogen use-efficiency (PNUE).

Self shading and nitrogen redistribution within whole plant could potentially underlie the degree of photosynthetic acclimation to elevated CO_2 (Takeuchi et al. 2001); it is clear that interactions with other potential environmental variables (light, nutrients) will determine the regulation of carbon sources and sinks at the leaf level (Lewis et al. 2002), but the ability to utilize the knowledge and predict a whole plant response is still limited and subject of controversy (Poorter 1998, Lloyd and Farquhar 1996).

There were no significant differences in the content of leaf nitrogen between plots. Leaf nitrogen values were on all plots (expressed in units per leaf area) highest in open conditions, without shading. Response of young beech to different CO_2 concentrations was similar to response of young beech to different light intensity; differences between managed and virgin forest were even bigger under canopy and edge conditions.

In Kočevski Rog young beech is more shade tolerant, relative response to increased light intensity and different CO_2 concentration is higher than response of young beech in Pohorje within same light intensities. Responses in managed and virgin forest are different: in the virgin forest young beech trees are more shade-tolerant, reaction of different light categories to elevated CO_2 concentration is similar and more homogenous, compared to managed forest where differences between categories are more pronounced. 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, with potential beech sites, Norway spruce has been favored in the last century and nowadays beech is gradually replacing spruce either by underplanting or by natural regeneration (Diaci 2006). In 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.

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*SAŽETAK: Glede uočenih promjena u reakciji bukve (*Fagus sylvatica *L.) u odnosu na ekološke promjene, odabrano je pet ploha mlade bukve jednake starosti na prirodnim staništima, koje su bile jednakomjerno raspoređene na svjetlosnom gradijentu od zastora odrasle sastojine, šumskog ruba do svjetlosnih uvjeta na otvorenome. Kriterij za grupiranje bio je neizravni stanišni* *čimbenik (ISF), dobiven analizom hemisfernih snimaka pomoću sustava WinScanopy: zastor krošanja (ISF<20), rub sastojine (20<ISF<25) i otvoreno, bez zastora krošanja (ISF>25), koji su bili jednaki na svim plohama. Za izmjere fotosintetskog kapaciteta, krivulje svjetlosnog zasićenja (0, 50, 250, 600 i 1200 μmol/m2s) i A-Ci krivulje (0, 100, 400, 700 i 1000 μmol CO_2/l) dobivene su pomoću Li-Cor LI-6400 u kontroliranom okruženju (temperatura, protok i koncentracija CO_2, zračna vlaga). Analize sadržaja dušika u lišću napravljene su Leco CNS-2000 analizatorom.*

Potvrđene su signifikantne razlike u reakciji mladih bukava između odabranih kategorija, kao i između različitih šumskih kompleksa. Mlade bukve na plohama iz Kočevskog pokazale su veću toleranciju na sjenu, a odziv na porast koncentracije CO_2 je pri istim intenzitetima osvijetljenosti bio veći nego kod mladih bukava iz Pohorskog kompleksa. Odziv mladih bukava bio je signifikantno različit između prašume (Rajhenav) i gospodarske šume unutar istog šumskog kompleksa: odziv u prašumi pokazuje veću toleranciju na sjenu.

Ključne riječi: Bukva, fotosinteza, svjetlo, CO_2, odziv