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PHOTOSYNTHETIC EFFICIENCY OF EUROPEAN BEECH *(FAGUS SYLVATICA* L.) INDIVIDUALS THAT GROW WITHIN THE PLANTATIONS OF THE NORWAY SPRUCE *(PICEA ABIES* KARST.)

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A large complex of beech forests on the Maljen mountain was afforested and replaced by the Norway spruce *(Picae abies* Karst.) sylvicultures. Ecophysiological investigations performed in the natural beech forest and the Norway spruce sylvicultures clearly indicate that the modified microclimate conditions within the sylvicultures significantly affected the photosynthetic efficiency of European beech. Examinations of the induced chlorophyll fluorescence kinetics revealed that the photosynthetic efficiency of beech individuals was considerably greater in the control sample plot (natural beech forest) than in the plantations of the Norway spruce, throughout the whole vegetation season. The greatest difference of photosynthetic efficinecy was recorded in early spring. Excessive light simultaneously causes the heliophilous acclimation of beech leaves and the lowering of the photosynthetic efficiency.

Key words: *Fagus sylvatica* L., Photosynthetic efficiency, *Picea abies* Karst., Sylviculture

Ključne reči: *Fagus sylvatica* L., fotosintetička efikasnost, *Picea abies* Karst., silvikulture

INTRODUCTION

The forest vegetation on Maljen mountain may be grouped in nine zonal, azonal and extrazonal associations (G a j i ć et al., 1954; K a r a d ž i ć, 1994). The main forest types significantly differ with respect to the intensity of their exploitation and forestry management. The mixed black hornbeam-black ash forests as well as mixed Scots pine-black pine forests that are developed on extremely poor soils (litosoles on dolomites and serpentines, respectively) have a low economic value, and therefore they are not affected by the forestry practice. It should be noted that these, low productive, forests have considerably greater biodiversity than economically more important beech and oak forests that are strongly affected by the forestry management. The greatest afforestation on Maljen mountain was performed within the belt of beech communities. The afforested habitats have been frequently replaced by the Norway spruce, *Picea abies* Karst. plantations. The photosynthetic efficiency of European beach, *Fagus sylvatica* L. growing in the Norway spruce sylvicultures and the native beech forest were investigated in the present study.

The photosynthetic efficiency was evaluated on the basis of the chlorophyll fluorescence. The chlorophyll fluorescence includes several components. The variable fluorescence (Fv) is closely correlated to the availability of the primary electron acceptor (quinone molecules termed Q_A) of photosystem II. Oxidized Q_A of dark-adapted leaves provides minimum fluorescence (Fo), and the reduction of Q_A will increase fluorescence until all Q_A molecules are reduced when the fluorescence reaches its maximum (Fm). The photochemical effiiciency of PSII is proportional to Fv/Fm (B u t l e r, 1978; Ö q u i s t & W a s s, 1988). The Fv/Fm ratio is inversely correlated with the non-photochemical quenching of chlorophyll fluorescence. It has been shown that the function of thylakoid membranes is sensitive to environmental stress (drought, excessive irradiance, high temperatures frost) (B e r r y & B j ö r k - m a n 1980; K e c k & B o y e r, 1974; C o r l e t t et al., 1992).

This paper aims at detecting a relationship between the modified environmental conditions and the photosynthetic efficiency of the European beech, *Fagus sylvatica* L.

MATERIAL AND METHODS

Investigations were performed in three adjacent forests, near the „Kaona" locality. The forests are located between 800 and 850 m a.s.l. Two forests (sample plots I and II) represent planted sylvicultures of Norway spruce *(Picea abies* Karst.). The bar-like segments of the Norway spruce plantations are incorporated within a natural zone of beech communities. Individual trees of *Fagus sylvatica* grow between the bars of the Norway spruce sylvicultures. Due to both the „forest edge" effect and very sparse distribution of beech individuals the light intensity in the zone between two adjacent sylvicultures is considerably greater than in the natural beech forest. As a consequence of the modified light climate, the relative air humidity is a lower in the zone between the sylvicultures.

The third sample plot (control) represents a native, undisturbed and non-exploited beech forest.

The photosynthetic efficiency of beech individuals was assessed on the basis of the chlorophyll fluorescence induced kinetics. The photochemical efficiency (Fv/Fm) of photosystem II and $t_{1/2}$ (half rise time from Fo to Fm) were measured using an induction fluorimeter („Plant Stress Meter", Biomonitor AB S.C.I. Umea, Sweden).

The water saturation deficit (W.S.D.) was determined as:

W.S.D. = 100*(FTW-FW)/(FTW-DW) 1), where
FTW is fully turgid weight, FW fresh weight and DW dry weight of a whole leaf (Stocker, 1928; Barrs, 1968; Slavik, 1974).

Relative effects of spatial and temporal changes in the photosynthetic efficiency were tested using a one-way ANOVA. Relationship between different parameters was assessed using a linear regression.

RESULTS AND DISCUSSION

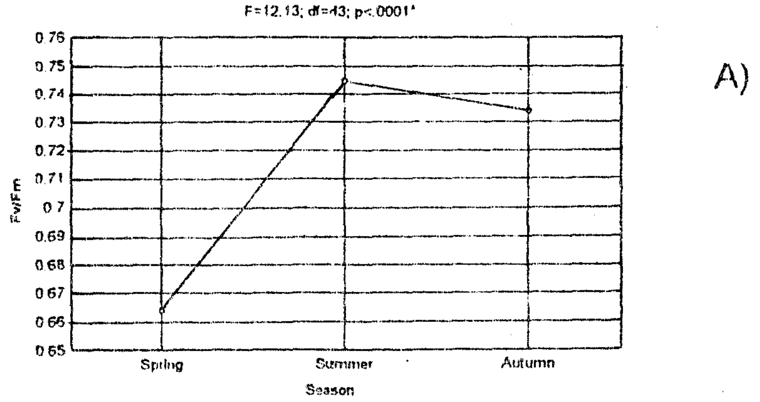
The photosynthetic efficiency considerably increased from early spring to summer months, and slightly decreased at the end of the vegetation season (Fig. 1). The low photosynthetic efficiency during spring months is usually attributable to both the low chlorophyll content and the nitrogen deficiency in young leaves. The ontogenetic trend in leaf N and chlorophyll content is strongly correlated with the seasonal changes in the leaf photosynthetic efficiency (Šestak, 1977; Jurik et al., 1979; Chapin et al., 1987). The slight decline in photosynthetic efficiency during autumn months may be explained by the leaf damages that are accumulated during the vegetation season. Our results could be conneced to the data of Drake & Read (1981) who detected a similar seasonal variation of the photosynthetic efficiency.

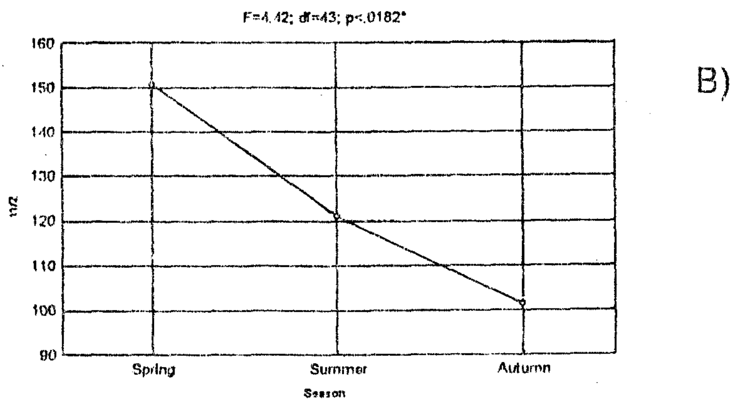
The half rise time from Fo to Fm continuously decreased from spring to autumn. Under identical excitation conditions the shade-adapted plants generally show a smaller $t_{1/2}$ than do sun-adapted plants (Oquist and Wass, 1988). Experiments with DCMU, a herbicide which acts as a blocker of the electron transport from PSII, clearly indicate that $t_{1/2}$ is a suitable indicator for antenna size of PSII (Malkin & Fork, 1981). As compared to sun-adapted plants, the shade-adapted plants have, a larger light harvesting complex, as well a smaller plastoquinone pool. This causes a faster increase from Fo to Fm in shade-adapted plants (or shade-adapted leaves). Our results clearly indicate that young leaves of European beech are adapted to the full day light conditions. Seasonal changes in the canopy structure directly affect the light microclimate. The light intensity continuously declined from spring to autumn months. As $t_{1/2}$ values indicate, the modified light microclimate induced an acclimation of beech leaves to shade conditions.

The lowest water saturation deficit in leaves was observed in early spring. This is an expected result since the greatest quantity of the available soil water was recorded at the beginning of the vegetation season. The water saturation deficit was considerably greater in summer and autumn.

Applying a one way ANOVA, we found statistically significant difference ($p < 0.05$) between Fv/Fm, $t_{1/2}$, and W.S.D. for different seasons during the vegetation period.

The synergistic effects of drought and light stresses usually inactivate the primary PSII-associated photochemistry (Powles, 1984; Masojidek et al., 1990; Chaves, 1991). Our analyses clearly indicate that the water saturation deficit is inversely correlated to the photochemical efficiency (Fig. 2). The greatest influence of water saturation deficit on the photosynthetic efficiency was observed in early spring. Both, Person's correlation coefficinet ($r = -0.7585$) and the regression line between W.S.D. and Fv/Fm indicate that young leaves are very sensitive to drought.





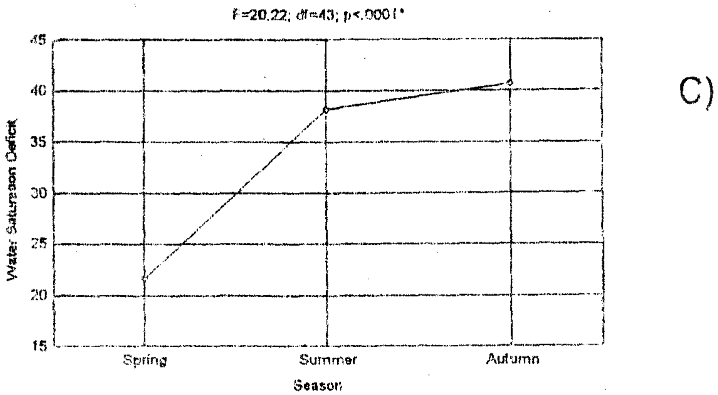


Fig. 1. – Seasonal dynamics of the photsynthetic efficiency (Fv/Fm), half rise time from Fo to Fm ($t_{1/2}$) and the water saturation deficit (W.S.D.) of *Fagus sylvatica*

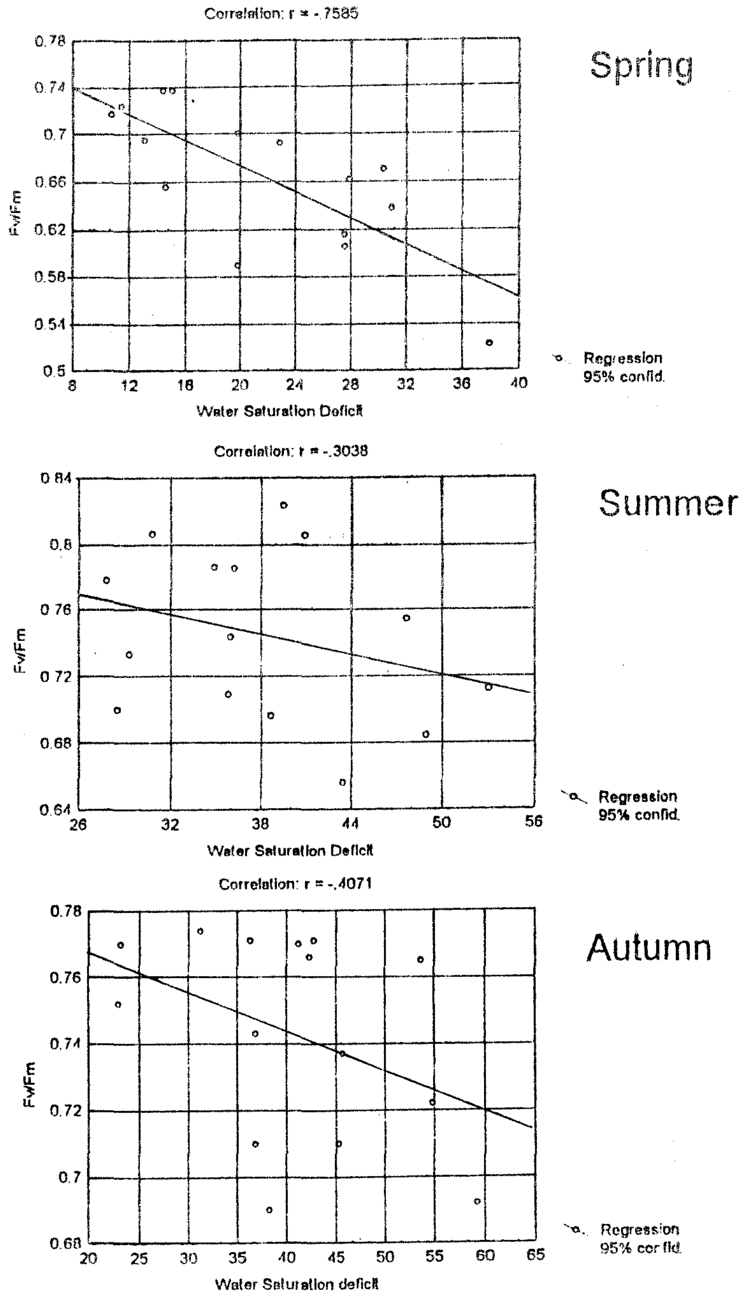


Fig. 2. - The relationship between the water saturation deficit and the photosynthetic efficiency of *Fagus sylvatica*

A poor correlation between W.S.D. and Fv/Fm (r = - 0.3038) indicates that the resistance of leaves to water saturation deficit considerably increased during the summer months. These results may be explained considering the synergistic interaction of stress factors. Björkman and Powels (1984) have revealed that water stress has a little effect on photochemistry of PSII when plants are kept in deep shade. During the spring months the young leaves of *Fagus sylvatica* are exposed to the full sunlight. Excessive light in combination with drought may cause photoinhibitory damages and lowering of the photosynthetic efficiency. Due to the increased shade during the vegetation period, the mature leaves are not exposed to the light stress. Consequently, the photosynthetic efficiency of mature leaves is almost insensitive to low and moderate water saturation deficits.

Water saturation deficit more strongly affected the photosynthetic efficiency during the autumn months. It may be explained by the excessive drought in the end of vegetation season. Regardless on the low light intensity, the increase of the water saturation deficit above a critical level significantly deceases the photosynthetic efficiency of *Fagus sylvatica*.

The photosynthetic efficiency is inversely related to $t_{1/2}$ (Fig. 3). This clearly indicates that the *Fagus sylvatica* is a shade-adapted species. The European beech is a typical sciophylous species (Janković, 1970; Ellenberg, 1979; Kojić et al., 1994). Consequently, any acclimation to the increased light of *Fagus sylvatica* results in the lowering of the photosynthetic efficiency. The strongest correlation between Fv/Fm and $t_{1/2}$ was observed in young leaves, during the spring months.

Photosynthetic efficiency of beech individualas was a greater in the control sample plot than in the plantations of the Norway spruce, throughout the whole vegetation season (Fig. 4). The greatest difference of photosynthetic efficiency was recorded in early spring (Tab. 1). As it was pointed out, individuals of *Fagus sylvatica* growing between the bars of the Norway spruce sylvicultures are exposed to the direct light. Excessive light simultaneously causes the heliophilous acclimation of beech leaves and the lowering of the photosynthetic efficiency. Moreover the water saturation deficit of beech leaves was considerably greater in the plantations of the Norway spruce than in the control sample plot.

CONCLUSIONS

A large complex of beech forests on the Maljen mountain was afforested and replaced by the Norway spruce (*Picea abies* Karst.) sylvicultures. The individual trees of *Fagus sylvitica* frequently grow between the bars of the Norway spruce sylvicultures. Due to both, the „forest edge" effect and the sparse distribution of European beech individuals, the light intensity in the zone between two adjacent sylvicultures is considerably greater than in the natural beech forest.

Ecophysiological investigations performed in the natural beech forest and the Norway spruce sylvicultures clearly indicate that the modified microclimate conditions significantly affected the photosynthetic efficiency of European beech. The excessive light in sylvicultures during spring months caused a heliophilous acclimation of beech leaves and simultaneous decrease of the photosynthetic efficiency. Moreover, the water saturation deficit of beech leaves was considerably greater in the Norway spruce sylvicultures than in the control sample plot.

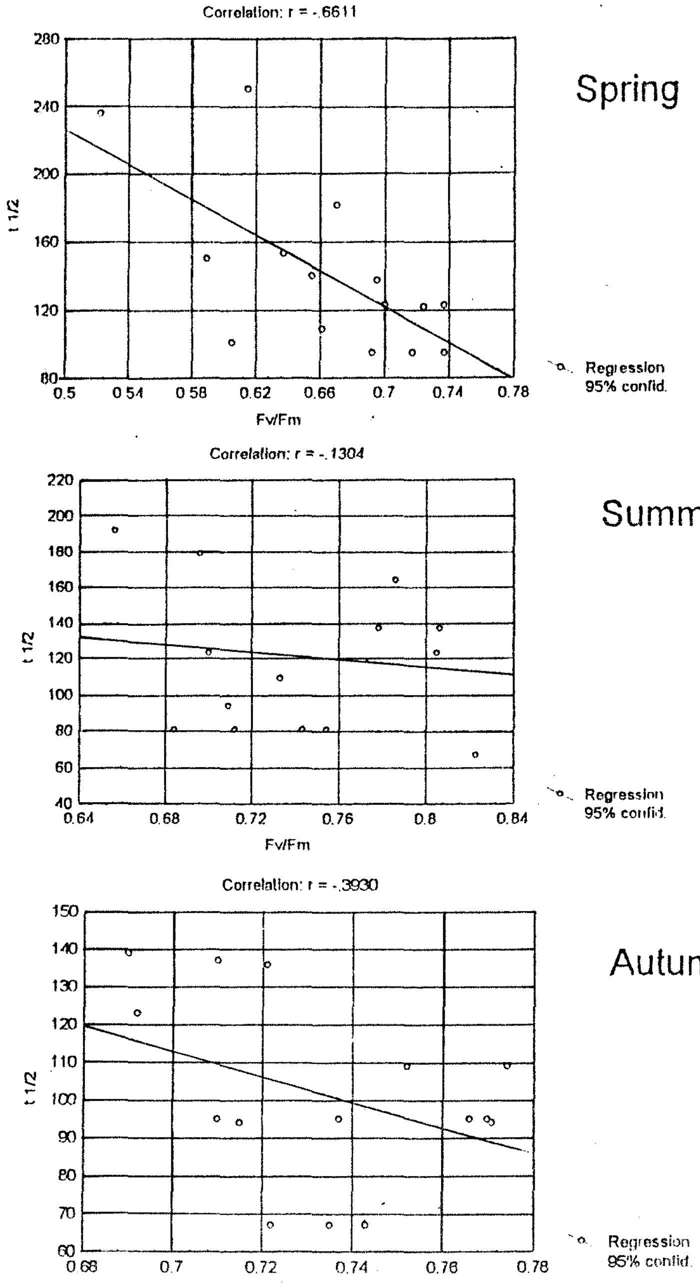


Fig. 3. – The relationship between the photosynthetic efficiency (Fv/Fm) and the half rise time from Fo to Fm ($t_{1/2}$) of *Fagus sylvatica*. The shade adapted leaves have a smaller $t_{1/2}$

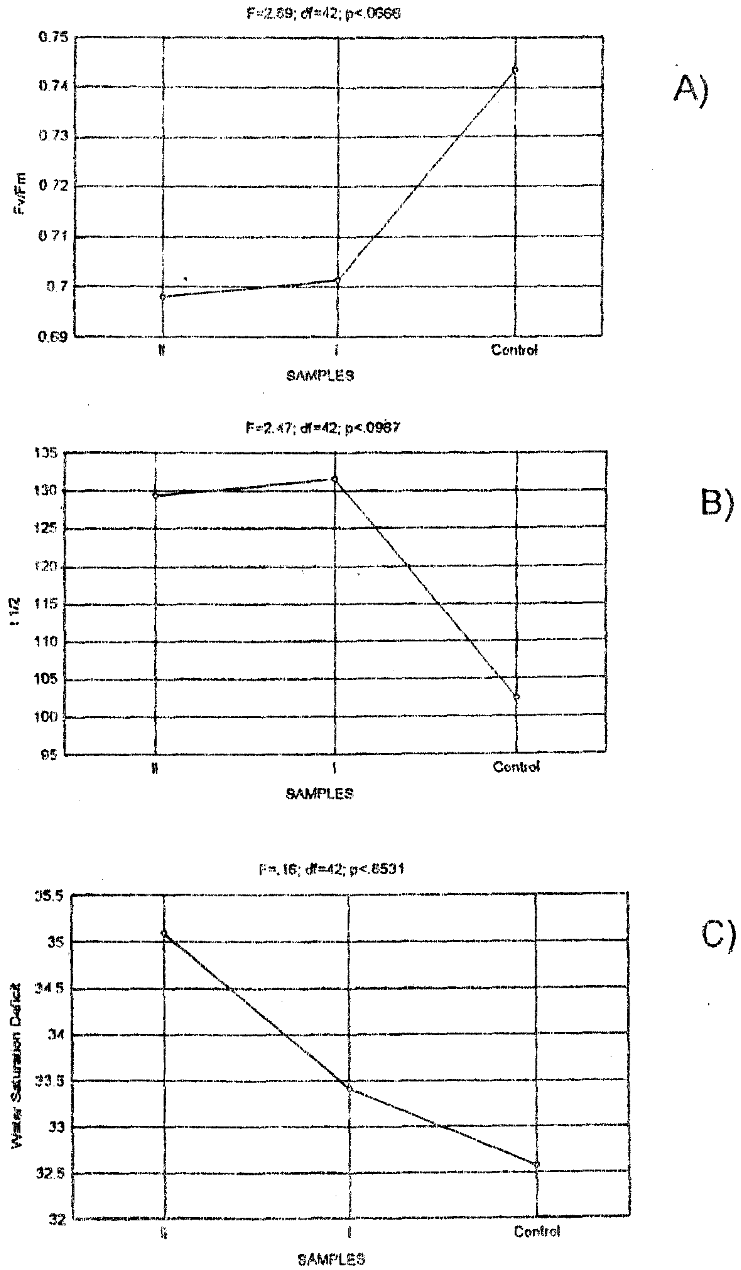


Fig. 4. – Relative effects of sylvacultures (samples I and II) on the photosynthetic efficiency (Fv/Fm), the half rise time from Fo to Fm ($t_{1/2}$) and the water saturation deficit in leaves of *Fagus sylvatica*

Tab. 1. – Seasonal dynamics of the photochemical efficiency (Fv/Fm), half rise time from Fo to Fm ($t_{1/2}$) and the water saturation deficit (W.S.D.) of the European beech growing in plantations of the Norway spruce (sample plots I and II) and in the control sample plot

Season		Samples				
		Control	I	II	F	p
Spring	Fv/Fm	0.724 ± 0.015	0.645 ± 0.041	0.628 ± 0.066	6.392	0.013*
	$T_{1/2}$	111.6 ± 15.16	157.2 ± 54.06	153.2 ± 58.61	1.451	0.272
	W.S.D.	14.11 ± 3.585	20.85 ± 6.982	29.92 ± 5.473	10.11	0.002*
Summer	Fv/Fm	0.753 ± 0.043	0.742 ± 0.052	0.737 ± 0.066	0.115	0.898
	$T_{1/2}$	108.6 ± 35.41	117.2 ± 36.18	136.8 ± 51.17	0.604	0.562
	W.S.D.	42.61 ± 7.778	38.23 ± 6.636	35.79 ± 6.839	1.132	0.354
Autumn	Fv/Fm	0.734 ± 0.023	0.717 ± 0.022	0.731 ± 0.035	1.502	0.2624
	$T_{1/2}$	86.23 ± 18.78	120.1 ± 18.02	97.86 ± 25.89	3.214	0.0762
	W.S.D.	40.66 ± 13.84	41.38 ± 13.19	39.62 ± 3.888	0.032	0.9669

The light intensity continuously declined from spring to the end of the vegetation season. It attenuated differences of Fv/Fm and $t_{1/2}$ between the control sample plot and the plantations of Norway spruce, during summer and autumn months.

REFERENCES

Bars, H.D. (1968): Determination of water deficit in plant tissues. Pages 236-369 in: Kozlowski, T.T. (ed.) *Water deficits and plant Growth*. Academic Press, New York.

Berry, J.A. & Björkman, O. (1980): Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol. 31*, 491-543.

Butler, W.L. (1978): Energy distribution in the photochemical apparatus of photosynthesis. *Annu. Rev. Plant Physiol. 29*, 345-378.

Drake, B.G. & Read, M. (1981): Carbon dioxide assimilation, photosynthetic efficiency and respiration of a Chesapeake Bay salt march *J. Ecol. 69*, 405-423.

Chapin, F.S., Bloom, A.J., Field, C.B. & Waring, R.H. (1987): Plant responses to multiple environmental factors. *Bio. Science 37*, 49-57.

Chaves, M.M. (1991): Effects of water deficits on carbon assimilation. *Journal of Experimental Botany, 42*, 1-16.

Corlett, J.E., Jones, H.G., Masojidek, J.M. & Massacci, A. (1991): Chlorophyll fluorescence in the field grown sorghum. Instrument discrepancies. *Photosynthetica, 27*, 257-260.

Gajić, M., Ivanović, M. and Kojić, M. (1954): Pregled šumskih fitocenoza planine Maljen. *Glas. Šum. fak. Univ. u Beogradu, 7*, 255-276.

Janković, M.M. (1970): Rod *Fagus* L. Pages 70-74 in: Josifović, M. (ed.) *Flora SR Srbije*. SANU, Beograd.

Jurik, T.W., Chabot, J.F., Chabot, J.F. (1979): Ontogeny of photosynthetic performance in *Fragaria virginiana* under changing light regimes. *Plant Physiol. 63*, 542-547.

Karadžić, B. (1994): *Fitocenološka analiza šumske vegetacije Maljena*. Doktorska disertacija. Biološki fakultet Univerziteta u Beogradu.

Keck, W. & Boyer, J.S. (1974): Chloroplast response to low leaf water potentials. III. Differing inhibition of electron transport and photophosphorylation. *Plant Physiol. 53*, 474-479.

Kojić, M., Popović, R. and Karadžić, B. (1954): *Fitoindikatori i njihov značaj u proceni ekoloških uslova staništa*. Nauka, Beograd.

Malkin, S. & Fork, D.C. (1981): Photosynthetic units of sun and shade plants. *Plant Physiol. 67*, 580-583.

Masojidek, J., Trivedi, S., Halshaw, L., Alexiou, A. and Hall, D.O. (1991): The synergetic effect of drought and light stresses in sorghum and pearl millet. *Plant Physiol. 96*, 198-207.

Oqist, G. & Wass, R. (1988): A portable, microprocessor operated instrument for measuring chlorophyll fluorescence kineticks in stress physiology. *Physiol. Plant. 73*, 211-217.

Powles, S.B. (1984): Photoinhibition of photosynthesis induced by visible light. Ann. Rev. of Plant Physiol. *35*, 15-44.

Slavik, B. (1974): *Methods of studying plant water relations*. Academia, Prague

Stocker, O. (1928): Das Wasserhaushalt ägyptischer Wüsten – und Salzpflanzen. *Bot. Abhandl.* (Jena. *13*, 1-200.

Šestak, Z. (1977): Photosynthetic characteristics during ontogenesis of leaves. I. Chlorophylls. *Photosynthetica 11*, 367-448.

Rezime

RANKA POPOVIĆ, MIROSLAVA MITROVIĆ, PAVLE PAVLOVIĆ, BRANKO KARADŽIĆ

FOTOSINTETIČKA EFIKASNOST INDIVIDUA BUKVE (*FAGUS SYLVATICA* L.) U SILVIKULTURAMA SMRČE (*PICEA ABIES* KARST.)

Institut za biološka istraživanja „Siniša Stanković", Beograd

Veliki kompleks bukovih šuma na Maljenu uništen je i zamenjen silvikulturama smrče *(Picea abies* Karst.). Ekofiziološka istraživanja koja su vršena u silvikulturama smrče i u prirodnoj bukovoj sastojini (kontrola) jasno ukazuju da modifikovani mikroklimatski uslovi u silvikulturama značajno utiču na fotosintetičku efikasnost bukve. Indukcijom hlorofilne fluorescencije utvrđeno je da, tokom cele vegetacione sezone, fotosintetička efikasnost bukve znatno veća u prirodnim sastojinama nego u silvikulturama smrče. Najveća razlika u fotosintetičkoj efikasnosti utvrđena je u rano proleće. Prekomerna svetlost u prolećnim mesecima izaziva heliofilne modifikacije listova i istovremeno smanjenje fotosintetičke efikasnosti.

Veća zasenčenost u postvernalnom periodu ujednačava fotosintetičku efikasnost bukve u prirodnoj sastojini i u silvikulturama smrče.