UDC 575:630
DOI: 10.2298/GENSR1202341S
Original scientific paper

VARIATION IN LEAF PHYSIOLOGY AMONG THREE PROVENANCES OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.) IN PROVENANCE TRIAL IN SERBIA

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Stojnić S., S. Orlović, A. Pilipović, D. Vilotić, M. Šijačić Nikolić, and D. Miljković (2012): *Variation in leaf physiology among three provenances of european beech (Fagus sylvatica L.) in provenance trial in Serbia.* - Genetika, Vol 44, No. 2, 341-353.

The paper presents the results of investigation of variability of net photosynthesis (A), transpiration (E), stomatal conductance (gs) and water use efficiency (WUE) of three European beech (*Fagus sylvatica* L.) provenances in the provenance trial established on Fruska Gora Mt. Provenances originate from three localities along a gradient from the north to the south of Europe: Pfalzgrafenweiler (Germany), Grenchen (Swiss) and Valkonya (Hungary). Results indicate that observed parameters were

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influenced both by environmental conditions of sites and genetic constitution of provenances. On the basis of ANOVA procedure it was observed significant differences among provenances in terms of rate of transpiration ($p \leq 0.037$) and water use efficiency ($p \leq 0.011$), while differences regarding net photosynthesis and stomatal conductance were not statistically significant. Canonical discriminant analysis (CDA) was performed in order to estimate multivariate relations among analyzed physiological parameters. Provenances were separated by the first canonical axis (CD1), which described 96.4% of variability. Provenance from the driest site (Valkonya) showed the highest water use efficiency, indicating on high potential for afforestation programmes in more arid areas.

Key words: Fagus sylvatica, provenance trial, net photosynthesis, transpiration, stomatal conductance, water use efficiency.

INTRODUCTION

European beech is the most abundant tree species in Serbia. Pure beech forests cover about 660,400 ha or 29.3% of total forest coverage area (NATIONAL FOREST INVENTORY, 2009), while mixed forests of beech and other deciduous and coniferous tree species occupy an area of 379,302 ha, or 16.4% of forest coverage area (VUČIĆEVIĆ, 2004). Starting from the climate scenarios and by taking into account the fact that the beech is a tree species sensitive to drought, VON WUEHLISCH (2004) estimated that natural range of beech is going to decrease, and that the most threatened habitats will be those at lower elevations in southern and southeastern parts of its range, where Serbia is located, too. According to ISAJEV *et al.* (2009), stability of the forest ecosystem depends on population's ability to adapt to changing environmental conditions. The same author further state that regardless of the adaptation mechanism, genetic diversity plays a key role, and that without its appropriate level adaptation processes would not be possible. Provenance trials are therefore used as a method for assessment of the degree of diversity and potential of indigenous and non-indigenous tree species, and for determination of differences in genetic variability both between and within different provenances (ŠIJAČIĆ-NIKOLIĆ and MILOVANOVIĆ, 2010). Provenance trials are also important from the point of selection of appropriate provenances for future afforestation. According to GÖMÖRY (2010), the main objective of researches in the provenance trials is to identify populations that are characterized by good growth and adaptability, in order to use it as a seed source for future reforestations.

Due to the high percentage of coppice and degraded beech forests in the total growing stock of Serbia (about 50%), KRSTIĆ and STOJANOVIĆ (2003) suggests artificial regeneration by using beech seeds and seedlings, as one of the method of forest regeneration, especially on the localities where natural regeneration cannot be carried out. During the processes of reforestation, seedlings are often transplanted to harsh planting sites, where drought and other environmental factors limit their success (RAJASEKARAN and BLAKE, 1998). Successful forest establishment depends on the use of seedlings whose morphological and physiological characteristics meet targets associated with favorable growth and survival under an anticipated range of site conditions (DAVIS and JACOBS, 2005).

Numerous studies conducted in controlled and field conditions have shown that the beech is very sensitive to drought and that shortage of water in the soil leads to a reduction of its physiological activity (PEUKE *et al.*, 2002; GELLE and FELLER, 2007; ROSE *et al.*, 2009). Therefore, special attention should be paid to the selection of appropriate provenances for reforestation of drier sites.

The paper presents results of investigation of variability of net photosynthesis, transpiration, stomatal conductance and water use efficiency among three beech provenances planted at Fruska Gora Mountain. This investigation had two aims: 1) to assess genetic variation of observed physiological parameters among given provenances and 2) that on the bases of some physiological characteristics distinguish provenances, in the juvenile stage of development, able to adapt to the drier habitat conditions, which will be a key factor for success of future reforestation programs.

MATERIALS AND METHODS

Beech provenance trial was established at the Fruska Gora Mountain (N 45°10'09.86", E 19°47'53.45"), in the spring of 2007, within the COST Action E52: "*Evaluation of the Genetic Resources of Beech for Sustainable Forestry*". Site characteristics of the Fruska gora Mt. are shown in Table 1. At the time of planting beech seedlings were 3 years old.

Table 1. The altitude, climate characteristics and Ellenberg's climate quotient of Fruska Gora Mt.

Locality	Altitude (m)	Mean annual temperature (°C)	Mean July temperature (°C)	Mean annual precipitations (mm)	Ellenberg's climate quotient
Fruška gora	370	11.0	21.4	782	27.4

The suitability of habitat for beech growing is expressed through Ellenberg's climate quotient (EQ). It is a simple index that represents the joint effect of temperature and precipitations, and serves to convey site humidity. EQ is calculated by using the formula: $EQ=1000\ T_{07}\ P_{ann}^{-1}$, where T_{07} – mean air temperature in July, P_{ann} – mean annual precipitations (MÁTYÁS *et al.*, 2009).

Study included three provenances, originating from Germany (Pfalzgrafenweiler), Hungary (Valkonya) and Swiss (Grenchen). General data about provenances are given in Table 2.

Net photosynthesis (A), transpiration (E) and stomatal conductance (gs) were recorded by using an ADC Bioscientific Ltd. LCPro+ portable gas analysis system. Measurements were carried out in August 2010, on the three plants from each provenance, in five replications per single plant. Measured leaves were fully formed, south-southwest oriented and located in the upper third part of the crown. Measurements were conducted by the clear, sunny weather, in the period between 09:00 and 11:00 hours a.m. Photosynthetic active radiation (PAR) has been set to volume of 1000 μmol m^{-2} s^{-1}, while the temperature, humidity and the concentration of CO_2 in the device's chamber were measured on the spot. Water use efficiency (WUE) was calculated as a ratio between net photosynthesis and transpiration (WUE=A/E [μmol $mmol^{-1}$]) (ZHANG *et al.* 2004).

Table 2. Location and geographic characteristics of three provenances: the origin, altitude and climatic characteristics.

Provenance	Country	Longitude		Latitude		Altitude	Mean annual temperature	Annual precipitations
		deg	min	deg	min	(m)	(°C)	(mm)
Pfalzgrafenweiler	Germany	8	35	48	46	700	7.4	1100
Grenchen	Swiss	7	21	47	13	1050	5.3	1274
Valkonya	Hungary	16	45	46	30	300	9.5	800

All statistical tests were accomplished by using the SAS program (SAS 2003) and the Statistica 10. Descriptive statistics (mean and SD) and one-way analysis of variance (ANOVA) with Sheffe's test (post hoc analysis) were provided for each parameter in order to verify the significance of differences among provenances. In order to define the differences among the analyzed provenances, for the observed physiological parameters, it was used canonical discriminant analysis (CDA).

RESULTS AND DISCUSSION

On the basis of ANOVA procedure we found statistically significant differences among provenances in terms of intensity of transpiration ($p \leq 0.037$) and water use efficiency ($p \leq 0.011$), indicating that these parameters were primarily conditioned by the genetic specificity of provenances. On the other hand, net photosynthesis and stomatal conductance did not differ significantly among the observed provenance, referring to the assumption that in this case, differences in genetic constitution of the provenances were masked by the effect of site conditions of the locality where the provenance trial is established (Table 3). This confirmes previous results (STOJNIĆ *et al.*, 2010), in which certain physiological parameters, in the beech provenance trials in Serbia, were influenced both by hereditary factors of provenances as well as by site characteristics of locality. Apart from physiological parameters, similar results were reported by other authors who have studied the variability of certain morphological characteristics and growth parameters of seedlings in the beech provenance trials (ŠIJAČIĆ-NIKOLIĆ *et al.*, 2006; IVANKOVIĆ *et al.*, 2008; MEKIĆ *et al.*, 2010; IVANKOVIĆ *et al.*, 2011).

Table 3. Results of ANOVAs for four physiological traits (net photosynthesis (A), transpiration (E), stomatal conductance (gs) and water use efficiency (WUE)) of three European beech (Fagus sylvatica L.) provenances cultivated on Fruska gora Mt. The values of different letters are significantly different at the 0.05 probability level according to the results of the Scheffe's test.

Provenance	A (µmol m^{-2} s^{-1})		E (mmol m^{-2} s^{-1})		gs (mol m^{-2} s^{-1})		WUE (µmol $mmol^{-1}$)	
	$\overline{X}$	CV (%)	$\overline{X}$	CV (%)	$\overline{X}$	CV (%)	$\overline{X}$	CV (%)
Pfalzgrafenweiler	9.77 b	6.06	2.33 b	4.69	0.24 c	10.02	4.20 b	5.68
Grenchen	9.29 c	10.47	2.63 a	8.50	0.25 b	14.94	3.54 c	8.66
Valkonya	10.24 a	8.32	2.00 c	10.94	0.28 a	17.75	5.15 a	10.85
F value		0.84^{ns} (p>0.05)		6.01* (p≤0.037)		0.58^{ns} (p>0.05)		10.38* (p≤0.011)

* P<0.05, ** P<0.01, *** P<0.001, ns- non significant.

Canonical discriminant analysis (CDA) was applied in order to estimate the multivariant relationship among analyzed physiological parameters at three beech provenances (Table 4 and 5, Figure 1). Provenances are separated by the first canonical axis (CD1) that describes 96.4 % of variability (Table 5). According to that axis, there is a separation of provenance Valkonya, which differs from other two provenances in the values of stomatal conductance ($gs_{Valkonya}$=0.28 mol m^{-2} s^{-1}, comparing to $gs_{Grenchen}$= 0.25 mol m^{-2} s^{-1}, and $gs_{Pfalzgrafenweiler}$=0.24 mol m^{-2} s^{-1}) (Figure 1). This separation is explained by the highest value of standardized coefficient for the first axis, which amounts for 5.501 (Table 5). Separation of provenance Valkonya by the second axis (CD2) is based on the absolute value of standardized coefficient of -3.302 for the net photosynthesis ($A_{Valkonya}$=10.24 µmol m^{-2} s^{-1}, comparing to $A_{Grenchen}$=9.28 µmol m^{-2} s^{-1}, and $A_{Pfalzgrafenweiler}$=9.74 µmol m^{-2} s^{-1}).

Table 4. A chi-*squared test (χ2) of significance obtained CD axes for the four observed physiological parameters in three provenances of beech (Fagus sylvatica L.)*

Root removed	Eigenvalue	Canonicl R	Wilks' Lambda	Chi-Sqr.	df	p-level
0	96.385	0.995	0.007	201.261	8	0.000
1	0.478	0.569	0.677	15.825	3	0.001

Figure 4 shows that plants within the provenance Grenchen are not grouped, as it is the case with the provenances Valkonya and Pfalzgrafenweiler. In the first mentioned provenance (Grenchen) there is a separation of one of the plants on the second canonical axis. This phenomenon could explained by two factors: 1) the high genetic differentiation of plants at the level of provenance and 2) differences in micro-habitat conditions of the locality where the provenance trial is established.

Table 5. Standardized canonical coefficients on two axes from a canonical discriminant analysis (CDA) based on four physiological characteristics of Fagus sylvatica L. leaf among three provenciences.

Variable	Root 1	Root 2
WUE	1.494	2.965
gs	5.501	0.711
E	-4.242	2.813
A	-1.098	-3.302
Eigenvalue	96.385	0.478
Cum.Prop.	0.995	1.000

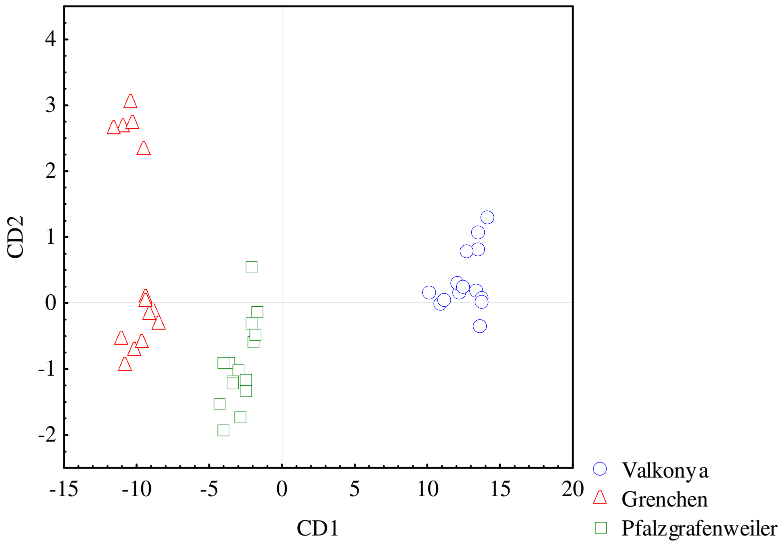

Figure 1. The scaterplot of first two CD axes obtained by Canonical distribution analysis analysis (CDA) on four physiological characteristics of Fagus sylvatica L. leaf among three provenances cultivated on Fruska gora Mt.

ROSE *et al.* (2009) found greater genetic diversity within a single beech stand, than between the different stands. Numerous studies conducted in provenance trials and various populations have shown that the differences among families at the intra-population level were often statistical significant (SABUNCU, 2006; ŠIJAČIĆ-NIKOLIĆ *et al.*, 2007; BALLIAN *et al.*, 2009), sometimes even larger than differences among populations (BALLIAN *et al.*, 2010). Also, provenance trials are usually established on forest land with variable soil conditions, often surrounded or bordered by older stands that affect the micro climate modifying the solar radiation and air currents (GÖMÖRY *et al.*, 2011). All these factors lead to the formation of environmental patches or gradients which may seriously affect the estimation of treatment effects in trials (YE and JAYAWICKRAMA, 2008).

Besides from the aspect of genetic variability of the investigated parameters, our results are interesting from the point of impact of habitat conditions at the site Fruška Gora Mt. on the gas exchange and water use efficiency of individual provenances. Figure 2 shows the mean value, standard deviation (SD) and standard error (SE) for net photosynthesis, transpiration, stomatal conduction and water use efficiency at observed provenances.

From the aspect of optimal climatic conditions for the growth of beech, Fruska Gora Mt. is characterized by quiet xeric conditions, which can best be seen by the value of Ellenberg's climate quotient for this site. FANG and LECHOWICZ (2006) report that sites with EQ value below 20 represent the most favorable habitat for beech growth. Vitality of the species begins to decline as the index increases between 20 and 30, and finally beech disappeares in the regions where the index is above the 30. The value of EQ of 27.4 indicates that Fruska Gora Mt. is a site that is almost borderline habitat for beech. Since drought stress affects many aspects of physiology in plants, such as gas exchange, water use efficiency and biomass production (CHALAPATHI RAO and REDDY, 2008), RAFTOYANNIS *et al.* (2003) states that physiological characteristics of seedlings determine their ability to overcome the transplanting stress. According to LEUSCHNER *et al.* (2001) photosynthesis is an important indicator of the vitality and competitive ability of a species at a given site. For this reason, net photosynthesis and related gas exchange parameters have been suggested as early selection criteria, in order to be able to assess the genotype potential as soon as possible (ORLOVIĆ *et al.*, 2003; ORLOVIĆ *et al.*, 2010).

In the present study, the highest values of net photosynthesis and stomatal conductance were registered at the provenance Valkonya (HUN), which originates from the most xeric site. On the other hand, the lowest value of net photosynthesis was recorded in plants of the provenance Grenchen, while the lowest intensity of stomatal conductivity was measured at the provenance Pfalzgrafenweiler (Figure 2a and 2c). According to ABRAMS *et al.* (1994) xeric genotypes generally have a higher net photosynthesis and stomatal conductance, during the drought, comparing to more mesic genotypes. Research conducted by ROSE *et al.* (2009) on beech provenances from the central part of its range (Germany) and from the eastern border areas (Poland), showed that in the drought treatment central provenance plants from a humid environment responded more sensitively to soil drought by partial stomatal closure. ABRAMS *et al.* (1990), observing the intensity of net photosynthesis and stomatal conductance in 5 populations of *Fraxinus pennsylvanica* Marsh., found that during drought periods populations originated from the most xeric habitat maintained the highest values of these parameters, while opposite her, population originated from the most mesic habitat, had the lowest values of net photosynthesis and stomatal conductance. In contrast to net photosynthesis and stomatal conductance, the lowest intensity of transpiration was measured at the provenance that originates from the drier region (Valkonya, HUN), while the highest intensity of transpiration was observed by the provenance Grenchen (CH), which comes from the most mesic habitat (Figure 2b). This is in agreement with the findings by PEUKE *et al.* (2002).

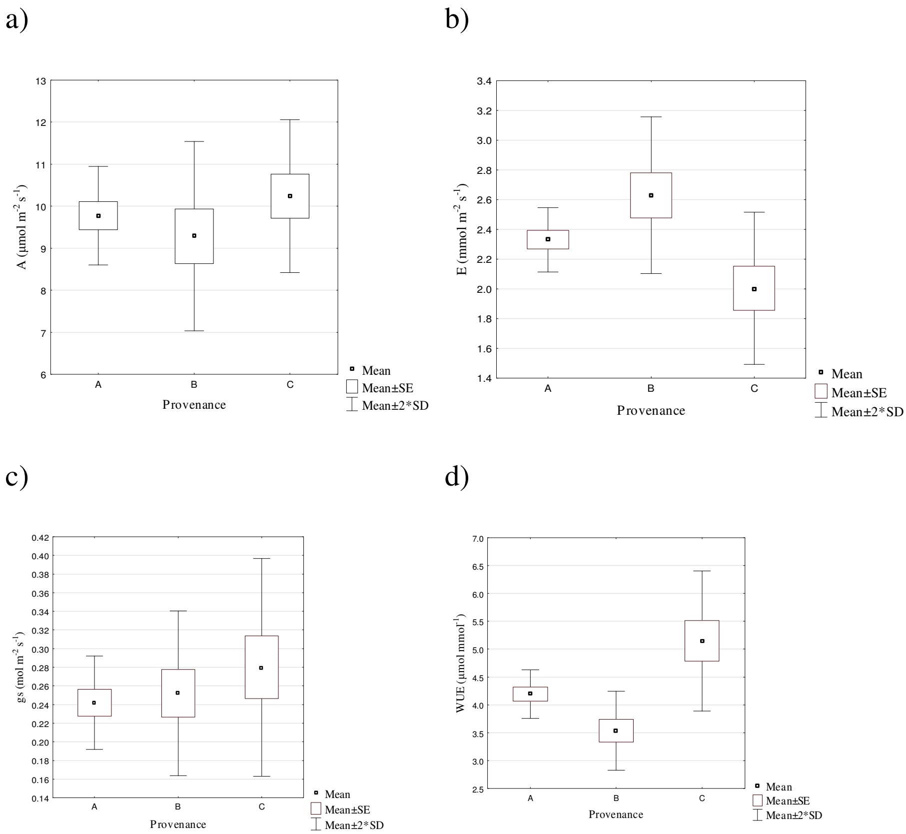

Figure 2. Mean, standard deviation and standard error for four physiological characteristics: a) net photosynthesis (A), b) rate of transpiration (E), c) stomatal conductance (gs) and d) water use efficiency (WUE) among three provenances which marked with (A) Pfalzgrafenweiler, (B) Grenchen, (C) Valkonya.

These autors looking for the impact of induced drought on 11 beech provenances, came to the conclusion that beech seedlings originating from areas with limited water availability in the soil, had a lower intensity of transpiration, and thus used water more economically than provenances from the more humid regions. Similar results are presented by ZHANG *et al.* (2004), who investigated the impact of drought on seedlings of three populations of *Populus davidiana*. Both mentioned studies have shown that seedlings originating from dry habitats had the lowest transpiration intensity, while the highest intensity of transpiration had plants originating from the wet site. ZHANG *et al.* (2004) explained that this is a consequence of adaptation of populations to contrasting soil water regimes. Dry climate population is adapted to conditions where drought periods are prolonged, and it is associated with high capacity for drought resistance. On the other side, wet climate population used to mild drought of short duration, which allows these plants intensive use of available water from the soil. PEUKE *et al.* (2002) also found that the beech provenances which originate from the drier sites maintained low transpiration both in control and drought treatments.

Plants achieve high water use efficiency through lower transpiration or high net photosynthesis, or both (ROUH *et al.*, 2007). In the present study, the highest WUE was registered at the provenance Valkonya, which is characterized by the largest net photosynthesis, and the lowest intensity of transpiration (Figure 2d). GRATANI *et al.* (2003) followed the variability of structural-functional characteristics of leaves in three provenances of *Quercus ilex* originating from different ecological conditions in Italy and they found that under conditions of high air temperatures (31-33^{o}C), provenance from dry habitat had the highest water use efficiency and net photosynthesis, indicating greater resistance of drought stress. MÉSZÁROS *et al.* (2007) considered that plants maintaining a high level of WUE show a water-saving strategy that allows avoidance of larger water losses and moderates water absorption. Therefore this species may be more successful in prolonged drought periods. Opposite to Hungarian provenance, provenance Grenchen had the lowest WUE, which was the result of the lowest net photosynthesis and highest intensity of transpiration (compared with the other two provenances). The water-use strategy of this provenance permits absorption of water from the soil at the expense of a larger loss of water through transpiration. However, such strategy cannot be sufficient in long-lasting drought periods.

CONCLUSION

The existence of genetically conditioned differences among the studied provenances is an important prerequisite for the preservation of beech genetic resources in Serbia. The variability among populations is generally associated with geographic and climatic gradient and therefore can be interpreted as the result of their adaptation to the given differences in the air temperature, soil moisture and other environmental conditions, while the variation within populations provides the basis how selection, natural or artificial, acts (MARSHALL *et al.*, 2001). Obtained statistically significant differences among provenances in terms of intensity of transpiration and water use efficiency indicate the possibility of choosing the best provenance for breeding program in dry habitats. Provenance Valkonya (Hungary) showed the best strategy of using of available water from the soil, possessing the smallest intensity of transpiration and the highest water use efficiency, indicating the potential of this provenance for adaptation on the more xeric site conditions. If we consider the predictions related to global climate changes, and the fact that the regions in temperate continental zone will be affected by frequent summer droughts in the future, than this findings could be a key factor for success of future reforestation at the sites, characterized by insufficient content of water in the soil.

Finally it should be noted that due to the long life span of trees, at this stage of research we can only discuss about the possible potential of a given provenance for adaptation to specific site and climatic conditions. For more reliable conclusions it is necessary to implement a studies which will last for several years, and even, in some cases and for certain parameters and several decades of research.

ACKNOWLEDGEMENTS

This paper was realized as a part of the project "Biosensing Technologies and Global System for Long-Term Research and Integrated Management of Ecosystems" (43002) financed by the Ministry of Education and Science of the Republic of Serbia within the framework of integrated and interdisciplinary research for the period 2011-2014.

Received November 11th, 2011

Accepted July 07th, 2012

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VARIJABILNOST FIZIOLOŠKIH PARAMETARA LISTA KOD TRI PROVENIJENCIJE BUKVE (*FAGUS SYLVATICA* L.) U PROVENIJENIČNOM TESTU U SRBIJI

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U radu su prikazani rezultati istraživanja varijabilnosti neto fotosinteze (A), transpiracije (E), stomatalne provodljivosti (gs) i efikasnost korišćenja vode (WUE) kod tri provenijencije bukve (*Fagus sylvatica* L.) u provenijeničnom testu osnovanom na Fruškoj gori. Provenijencije obuhvaćene istraživanjem potiču sa tri lokaliteta koji se protežu duž areala bukve od severa prema jugu Evrope: Pfalzgrafenweiler (Nemačka), Grenchen (Švajcarska) i Valkonya (Mađarska). Rezultati ukazuju da su posmatrani fiziološki parametri bili pod uticajem kako stanišnih karakteristika lokaliteta, tako i genetičke konstitucije provenijencija. Na osnovu analize varijanse, konstatovane su statistički značajne razlike između provenijencija u pogledu intenziteta transpiracije ($p \leq 0.037$) i efikasnosti korišćenja vode ($p \leq 0.011$), dok razlike u pogledu neto fotosinteze i stomatalne provodljivosti nisu bile statistički značajne. Primenom kanonijske diskriminantne analize (CDA) izvršena je procena multivarijantnog odnosa između analiziranih fizioloških parametara. Provenijencije su se odvajaju po prvoj kanonijskoj osi (CD1) koja je opisivala 96.4 % varijabilnosti. Postojanje genetski uslovljenih razlika između istraživanih provenijencija je važan preduslov u očuvanju genetskih resursa bukve u Srbiji. Dobijene statistički značajne razlike između provenijencija u pogledu intenziteta transpiracije i efikasnosti korišćenja vode ukazuju na mogućnost izbora najboljih provenijencija za program oplemenjivanja na sušnim staništima. Provenijencija koja potiče sa najsušnijeg staništa (Valkonya) je imala najveću efikasnost korišćenja vode, što upućuje na visok potencijal ove provenijencije za primenu u programima pošumljavanja suvljih staništa.

Primljeno 11. XI 2011.
Odobreno 07. VII. 2012.