

Provenance by site interaction and stability analysis of European beech (*Fagus sylvatica* L.) provenances grown in common garden experiments

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Abstract

Fifteen provenances of European beech (*Fagus sylvatica* L.) were evaluated for stability and adaptability by height growth at four test sites in Bosnia and Herzegovina (1), Croatia (1) and Serbia (2). Provenance trials were established in spring 2007 by planting 2- and 3-year-old seedlings and arranged in a randomized complete block design. The data from seven 6-year-old and eight 5-year-old provenances were obtained in 2009 and analyzed separately. Finlay and Wilkinson's regression analysis and Additive main effects and multiplicative interaction model (AMMI model) were used to assess provenance by site interaction ($P \times S$) and to identify beech provenances that have high and stable performance in different environments, at the juvenile stage of development. Analysis of

variance showed that effects of provenance, site, and $P \times S$ interaction are highly significant ($p < 0.001$) in both age groups. Linear regression model evidenced that most of the provenances had regression coefficients not significantly different from unity ($b = 1.0$), except for provenances Sjeverni Dilj Cagliniski (HR24) and Vranica-Bistrica (BA59). The partitioning of the total sum of squares (SS) exhibited that the site effect was the predominant source of variation in both age groups of provenances (50.7% and 38.5%, respectively). Additionally, regression analysis explained 15.8% and 33.2% of provenance by site interaction terms, in provenances age six and five years, respectively, while the AMMI analysis accounted for 62.2% and 78.7% in $P \times S$ interaction. The results of AMMI showed that the first principal component (PC1) was statistically significant in both age groups. Adaptability and stability of provenances to the test sites were estimated with AMMI1 and AMMI2 biplots. Provenance Sjeverni Dilj Cagliniski (HR24) showed constant performance over tested sites, characterizing with above-average height growth at low yielding environments. Provenances HR25 and BA61 showed the opposite type of adaptation, being adapted to high yielding sites. Provenance Valkonya (HU42) was characterized by IPCA1 score close to zero and above average mean height growth, suggesting general adaptation to the tested environments. The implication of $P \times S$ was discussed in light of impact of climate change on beech and selection of most suitable provenances for future reforestation programs.

Key words: European beech, provenance trial, provenance \times site interaction, linear regression model, AMMI analysis, biplot.

Introduction

European beech (*Fagus sylvatica* L.) is one of the main tree species in Europe. Covering an

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area of approximately 14 million ha (VON WUEHLISCH, 2010a), beech is ecologically and economically one of the most important species for European forestry. Due to its known sensitivity to drought, beech is threatened by climate change. It is assumed that most endangered beech populations are those at the southern limit of the species distribution (JUMP *et al.*, 2006). On the other hand, in large parts of temperate and boreal regions, natural conifer forests (e.g. Norway spruce stands) are supposed to be replaced with the more competitive European beech forests (BUGMANN, 1997; AMMER *et al.*, 2008).

Provenance trials may provide a good basis for evaluation of genetic diversity and potential of various provenances to adjust to given climate conditions (STOJNIC *et al.*, 2013a). Recent studies demonstrated that beech populations from Southern Europe might be potential targets in the search for drought-resistant ecotypes (THIEL *et al.*, 2014). For example, ROBSON *et al.* (2013) showed that southern provenances from Spain and Bulgaria maintained high rates of assimilation even in mid-summer, whereas provenances from cooler sites in central and north Europe demonstrated reduced photosynthetic capacity under such conditions. Similarly, studying physiological differences of beech provenances exposed to drought stress, DOUNAVI *et al.* (2016) reported that Greek population showed better adaptability to future environmental conditions in comparison with provenances from central Europe.

International beech provenance trials were established in five series in 1986, '87, '89, '95 and '98 (VON WUEHLISCH, 2004). Unfortunately, within these series, the provenances from the central Balkan region (Bosnia and Herzegovina, and Serbia) were omitted, while the provenances from Croatia were poorly represented. Due to the expected genetic variation in this region, new trial series were established in order to cover this area (VON WUEHLISCH, 2004). The most recent series of international beech provenance trials were established in 2007. For this purpose, seven provenance trials were established across a range of environments: Bosnia and Herzegovina, Croatia, Italy, Germany (2) and Serbia (2), involving 32 provenances from eight countries (VON WUEHLISCH *et al.*, 2010b). Contrary to previously established series, this was the first time that the majority of the provenances originated from the Balkan

region (20 provenances). Such an approach provided the opportunity to compare performance in the field trials among the Balkan provenances and provenances originating from the core of Europe. Due to the fact that experiments were established across several sites, it also provided possibility to assess genotype by environment interaction ($G \times E$). The magnitude of $G \times E$ interaction is essential in a tree breeding programs for decision making about testing and deployment strategies (PSWARAYI *et al.*, 1997; ZAS *et al.*, 2004). Thus, the key objective in studies of $G \times E$ interaction is the assessment of stability and adaptability of provenances against a series of stressors that prevail at given environments.

Analysis of variance (ANOVA) is certainly the most frequently used method for studying $G \times E$ interaction, besides regression models and multivariate techniques (HANNRUP *et al.*, 2008). It is primarily used in determination and testing of sources of variability (e.g. genotype, environment, $G \times E$ interaction). However ANOVA allows adequate interpretation of main effects, it does not offer the insight into the response of the genotypes in the non-additive (interaction) term (SHAFII and PRICE, 1998; ZOBEL *et al.*, 1988). In other words, ANOVA does not provide information about the performances of single genotype against environmental variations (ABBOTT *et al.*, 2012). Thus, it is necessary to apply other methods to identify interaction relationships.

Linear regression analysis was reviewed by numerous authors (FINLAY and WILKINSON, 1963; EBERHART and RUSSELL, 1966; PERKINS and JINKS, 1968, etc.). The method is based on the regression of genotypic means against the mean values of an environmental effect at each site (environmental index), and could be used for the identification of good general performers across a wide range of sites (FINLAY and WILKINSON, 1963; MATHESON and RAYMOND, 1986). This approach is widely used in plant breeding, although the analysis has several limitations. CROSSA (1990) provided a comprehensive review of statistical and biological limitations of regression analysis in studying of $G \times E$ interaction.

The most commonly used multivariate technique is additive main effects and multiplicative interaction method (AMMI) (BOSE *et al.*, 2014a). AMMI analysis integrates analysis of variance and principal components analysis

(PCA) into a unified approach (GAUCH, 1988). AMMI has several models: AMMI0 which estimates additive main effects of genotypes and environments and does not include any principal component axis (IPCA); AMMI1 which combines additive main effects from AMMI0 with provenance by site interaction effect estimated from the first principal component axis (IPCA1); AMMI2 which combines additive main effects plus interaction effect for axes 1 and 2 (IPCA1 versus IP2A), and so forth, until the full model with all IP2A axis (GAUCH, 1988). Principal component analysis-based biplots were used in numerous studies due to easy visualization of responses and relationships (RAMBURAN *et al.*, 2011). In most cases, AMMI1 and AMMI2 biplots were selected for graphical assessment of provenance adaptability and stability.

Studies on genotype by environment interaction and stability analysis were used intensively in breeding programs of agricultural crops (BABIĆ *et al.*, 2010; MOHAMMADI and AMRI, 2011; KARIMIZADEH *et al.*, 2012; BOSE *et al.*, 2014b), even though numerous experiments were performed on forest tree species, as well. Apart from the most frequently studied growth parameters (PSWARAYI *et al.*, 1997; KARLSSON and HOGBERG, 1998; ZAS *et al.*, 2004; HANNRUP *et al.*, 2008; RWEYONGEZA *et al.*, 2011), analyses of genotype by environment interaction in forest tree species successfully implemented other traits, e.g. fruit mass (LITVAY, 2011), wood chemical properties (SYKES *et al.*, 2006), stem and crown form (FALKENHAGEN, 1996), wood density (BALTUNIS *et al.*, 2009), and water use efficiency (PONTON *et al.*, 2002).

Due to certain statistical and biological limitations of above mentioned methods, it is suggested that $G \times E$ interaction should be quantified using at least two different approaches together (KIM *et al.*, 2008). Therefore, in the present study, FINLAY and WILKINSON's regression analysis and AMMI model were adopted in order to: a) examine the influence of provenance, site and provenance by site interactions on height growth of fifteen European beech provenances, and b) determine adaptability and stability of certain provenances for height growth across test sites. The results were discussed in terms of climate change impact on beech and selection of suitable provenances for future reforestation programs in different regions.

Material and methods

Provenance by site interaction ($P \times S$) of 15 European beech (*Fagus sylvatica* L.) provenances, growing in common garden experiments, was analyzed to identify stable provenances with good height growth in juvenile stage of development (*Fig. 1*). The provenances were grown at four test sites, established in Bosnia and Herzegovina (Kakanj), Croatia (Medvednica) and Serbia (Fruska Gora and Debeli Lug) (*Tab. 1*).

Trial site Kakanj is situated in the region that belongs to temperate continental climate, characterized by cold winters and moderately warm summers, with high level of precipitation. The climate on the Medvednica mountain is temperate continental, as well, typical for Central European mountain region. In comparison to the surrounding lowland area, the mountain behaves as an „island“ in its climate characteristics, with more precipitation, lower temperatures, longer duration and greater snow cover. As for the trial localities in Serbia, both sites are under the influence of temperate continental climate (STOJNIC *et al.*, 2012). Fruska Gora Mountain is located in the Northern part of Ser-

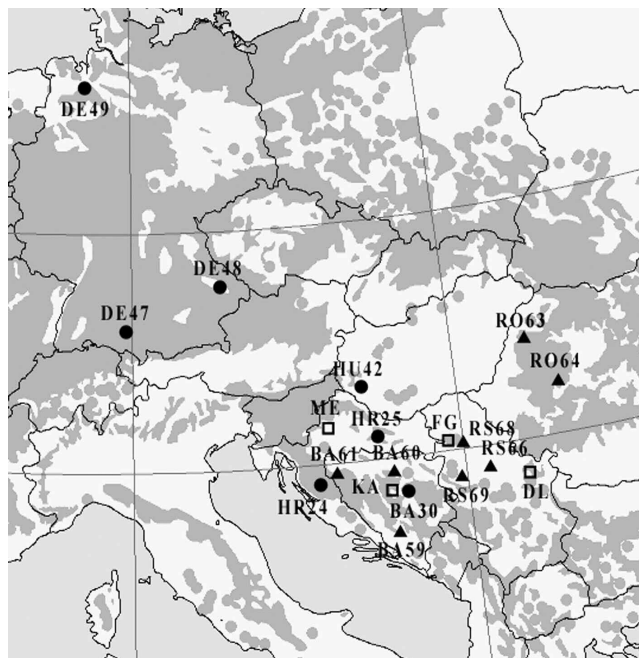


Figure 1. – The distribution of European beech provenances involved in the study. The abbreviation indicates six-year-old provenances (●), five-year-old provenances (▲) and trial sites (□) as shown in *Tab. 1* and *Tab. 2*. The dark shaded area represents natural distribution range of beech (VON WUEHLISCH, 2008).

bia. Similarly to Medvednica, the mountain appears as an “island” and it is surrounded by lowland agricultural land and floodplain forests of pedunculate oak and poplar plantations.

Debeli Lug is located in Northeastern part of Serbia. According to KRSTIĆ *et al.* (2002), 27% of pure beech forests in Serbia are situated in this region.

Table 1. – General data about four sites of European beech provenance trials.

Abbrev.	Locality	Country	Latitude	Longitude	Altitude (m)	Mean annual air temperature (°C)	Annual sum of precipitation (mm)
KA	Kakanj	Bosnia	44°04'	18°11'	538	10.7	960
ME	Medvednica	Croatia	45°53'	15°55'	730	6.6	1240
FG	Fruska Gora	Serbia	45°10'	19°47'	366	11.0	624
DL	Debeli Lug	Serbia	44°19'	21°52'	742	8.8	829

Table 2. – European beech provenances in the study.

Abbrev.	Provenance	Country	Latitude	Longitude	Altitude (m)	Mean annual air temperature (°C)	Annual sum of precipitation (mm)
Six year old provenances							
HR24	Sjeverni Dilj Caglinski	Croatia	45°17'	18°01'	350	10.8	779
HR25	Vrani Kamen	Croatia	45°37'	17°19'	600	8.5	972
BA30	Tajan, Zepce	Bosnia	44°23'	18°03'	700	10.3	804
HU42	Valkonya	Hungary	46°30'	16°45'	300	9.5	800
DE47	Schelklingen	Germany	47°59'	09°59'	650	6.0	840
DE48	Höllerbach	Germany	49°01'	13°14'	755	5.0	1200
DE49	Hasbruch	Germany	53°08'	08°26'	35	8.6	760
Five year old provenances							
BA59	Vranica-Bistrica	Bosnia	43°33'	17°49'	750	8.8	826
BA60	Crni Vrh	Bosnia	44°33'	17°59'	500	9.6	1069
BA61	Grmec	Bosnia	44°45'	16°14'	720	10.3	1304
RO63	Alesd	Romania	47°11'	22°15'	490	8.5	800
RO64	Alba-Iulia	Romania	46°10'	23°05'	860	8.0	850
RS66	Avala	Serbia	44°23'	20°45'	475	11.9	668
RS68	Fruska Gora	Serbia	45°10'	19°50'	370	11.2	782
RS69	Cer	Serbia	44°12'	19°50'	745	10.9	837

The trials were established in spring 2007 by planting 2- and 3-year-old saplings. They were arranged in a randomized complete block design replicated three times. Fifty saplings per plot were planted with 1×2 m spacing. The saplings were grown and distributed by the Thünen-Institute for Forest Genetics in Grosshansdorf, Germany. Survival and height of all plants at each site were obtained from measurements conducted in 2009, which involved provenances of both ages (7 provenances were 6 years old, whereas 8 provenances were 5 years old). For that reason, we classified provenances into two age groups and analyzed them separately (*Tab. 2*).

The first group of provenances (the „older“ group) consisted of geographically distant provenances, representing different geographic origins, covering a gradient in climate conditions from the North to the South of Europe. In contrast to the first group, the second,

„younger“ group, was more homogenous with respect to the provenances' geographic origin, as it included only South-eastern provenances - two provenances from Romania and three provenances from Bosnia and Serbia, respectively. Although aforementioned provenance trials were established from more than 20 provenances each, the present study involved only provenances that were common for all trials.

In order to evaluate adaptability and stability of beech provenances in different environments, the data of provenance height were subjected to linear regression models (FINLAY and WILKINSON, 1963) and Additive main effects and multiplicative interaction analysis (AMMI model).

Simple linear regression is one of the most frequently used statistical approach in genetics and plant breeding (CROSSA, 1990). In this model, the regression coefficient (b) of the geno-

Table 3. – Mean percentage survival of provenances at Kakanj (BA), Medvednica (HR), Fruska Gora (RS) and Debeli Lug (RS).

Provenance	Kakanj	Medvednica	Fruska Gora	Debeli Lug	Mean
Six-year-old provenances					
HR24	87.3	87.3	86.0	96.0	89.2
HR25	84.0	98.7	90.3	92.7	91.4
BA30	73.3	96.7	92.0	98.3	90.1
HU42	85.3	95.3	94.7	98.0	93.3
DE47	82.7	94.7	92.3	94.3	91.0
DE48	74.0	92.0	96.0	90.3	88.1
DE49	90.7	94.0	88.7	94.0	91.9
Five-year-old provenances					
BA59	43.3	75.3	86.0	84.0	72.2
BA60	50.0	70.0	84.7	78.7	70.9
BA61	75.3	81.3	90.0	94.0	85.2
RO63	75.7	64.7	76.0	82.3	74.7
RO64	53.3	80.0	78.0	90.0	75.3
RS66	72.0	79.3	80.3	90.0	80.4
RS68	71.0	64.7	78.0	90.3	76.0

types is used to determine the stability of genotypes over environments. Slope or b coefficient is interpreted as the amount of change in the dependent variable that is associated with a change in one unit of the independent variable. According to FINLAY and WILKINSON (1963) mean height of entries, across all environments, and regression coefficients are important indicators of genotype adaptation. The linear regression model equation is (eqn. 1):

$$Y_{ij} = \mu + g_i + E_j + b_i E_j + e_{ij}$$

where Y_{ij} is the mean of provenance i in environment j ; μ is the general mean; g_i is the mean of provenance i over all environment; E_j is the environmental index for environment j ($Y_{.j} - Y_{..}$); b_i is the slope of regression specific for provenance i ; and e_{ij} is the residual variation which is assumed to be zero for the values averaged over replications (KIM *et al.*, 2008).

AMMI partitions the overall variation into genotype main effects (G), environment main effects (E) and genotype environment (GEI) effects and utilize principal components analysis (PCA) to study $G \times E$ (KARIMIZADEH *et al.*, 2012). The AMMI model equation is (eqn. 2):

$$Y_{ij} = \mu + G_i + E_j + \sum_{n=1}^N \lambda_n \gamma_{in} \delta_{jn} + e_{ij}$$

where, Y is the height of the i^{th} genotype in the j^{th} environment; μ is the overall mean; G_i is the i^{th} genotype main effect; E_j is the j^{th} environment main effect; λ_n is the singular value of n^{th} PCA axis; γ_{in} is the genotypic eigenvector values for n^{th} PCA axis; δ_{jn} is the environmental eigenvector values for n^{th} PCA axis and e_{ij} is the residual (KIM *et al.*, 2008).

To test the significance of $G \times E$ effects, data pooled across the four sites were analyzed using analysis of variance (ANOVA) in program Statistica for Windows Version 12 (StatSoft, Inc.). Linear regression and AMMI analyses were performed using SAS version 9.1.3 (SAS Institute, Cary, NC 2011). The biplots were created in order to provide simple and effective means of illustrating the $P \times S$ interaction. The AMMI1 biplot was generated from main effects of provenances and environments and the IPCA1 scores. The abscissa shows the main effects and the ordinate shows the IPCA1 scores that capture interaction effects (ODEWALE *et al.*, 2013).

AMMI2 biplots were produced to visualize the $P \times S$ interactions for height growth. AMMI2 biplots are characterized by the projection of the genotype and environment IPCA1 and IPCA2 scores onto a two-dimensional biplot (RAMBURAN *et al.*, 2011). The genotypic IPCA scores in the AMMI analysis are considered indicators of the yield stability (PURCHASE *et al.*, 2000).

Results and discussion

Survival of plants

The survival percentage of provenances varied considerably from trial to trial. The lowest survival percentage was observed at the trial site Kakanj (72.7%), whereas the highest percentage was recorded at the trial Debeli Lug (90.9%). Lower mean survival rate observed in Bosnian trial was mainly the consequence of surprisingly low survival rate of five-year-old provenances BA59, BA60 and RO64 (43.3%, 50.0% and 53.3%, respectively). Provenance HU42 characterized with the highest survival percentage (93.3%). Among the five-year-old provenances notably higher survival percentage was observed in provenances BA61 and RS66 (85.2% and 80.4%, respectively).

Stability from Finlay and Wilkinson's linear regression analysis

Results of the present study showed significant provenance effect ($p < 0.001$) for height growth of seedlings in both age groups, which was probably the result of differences in the genetic makeup of the studied provenances (Tab. 4).

Significant effects of site ($p < 0.001$) and provenance by site interaction ($p < 0.001$) in both age groups indicated high phenotypic plasticity of height growth and existence of genetic variation in plastic response to environmental conditions. This is in agreement with the results of other studies on growth parameters in these beech provenance trials (JEZBEC *et al.*, 2007; IVANKOVIĆ *et al.*, 2011). As for the linear regression model, the regression line was not significant in six- and five-year-old provenances, probably because different environments were affected by different factors (ALIA *et al.*, 2010). The partitioning of total sum of squares (SS) exhibited that the site effect was a predominant

Table 4. – Two-way ANOVA for height growth with site regression among six-year-old and five-year-old provenances.

Source	df	SS	MS	F < P	% of SS
Six-year-old					
Provenance (P)	6	1413.13	235.52	<0.001	33.5
Site (S)	3	2141.12	713.71	<0.001	50.7
P × S	18	668.96	37.16	<0.001	15.8
P × S regression	6	375.99	62.66	ns	(56.2)
Deviation	12	292.97	24.41		(43.8)
Total	27	4223.21			100.0
Five-year-old					
Provenance (P)	7	1122.81	160.40	<0.001	28.3
Site (S)	3	1530.25	510.08	<0.001	38.5
P × S	21	1317.83	62.75	<0.001	33.2
P × S regression	7	163.57	23.37	ns	(12.4)
Deviation	14	1154.26	82.45		(87.6)
Total	31	3970.89			100.0

Legend: ns – not significant at $p < 0.05$.

source of variation in both age groups of provenances (50.7% and 38.5%, respectively). The interaction term explained 15.8% and 33.2% of the total variation, in provenances at ages of six and five years, respectively. The greater sum of squares of the $P \times S$ term compared to the effects of provenances (28.3%), observed in the „younger“ group of provenances, indicates larger differences in provenance response across environments than in the “older” group of provenances (REZENE *et al.*, 2014).

Regression coefficients for most of the provenances were not significantly different from unity ($b = 1.0$), except for provenances HR24 (0.158) and BA59 (1.371) (Tab. 5).

Provenance HR24 showed constant performance over environments, with very small changes in mean height despite substantial changes in environments. It means that this provenance was characterized by above average height growth in low yielding environments, yet insensitive to environmental change and with relatively small height growth in high yielding environments. Contrary to this, another prove-

nance from Croatia (HR25) exhibited the opposite type of adaptation. This provenance was characterized by high mean plant height and regression coefficient higher than 1.0 (1.454), indicating a better than average response to favorable environments, but worse than average response to unfavorable environments (below average stability). In the “younger” group provenances BA59 (1.371), BA61 (1.492) and RS66 (1.345) exhibited a similar pattern of response. In these provenances small changes in the environment caused large changes in tree height (FINLAY and WILKINSON, 1963). Hence, these provenances can be described as specifically adapted to high-yielding environments. The provenance from Hungary (HU42) was characterized by above average height and regression coefficient close to 1.0 (0.959) showing an average stability over all environments. This indicates that the response of this provenance to diverse environments is the same as the average response of all provenances in the experiment. In other words, it indicates that it has general adaptability. Finally, provenances RO63, RO64 and RS69 characterized by below

Table 5. – The mean height of provenances, slopes of regression of provenance means on site index and standard error of slopes.

Provenance	Mean height (cm)	Slope	Standard error
Six-year-old provenances			
HR24	96.93	0.158 *	0.122
HR25	103.39	1.454	0.326
BA30	103.63	0.833	0.250
HU42	97.67	0.959	0.209
DE47	85.37	1.398	0.131
DE48	84.90	0.867	0.390
DE49	93.32	1.331	0.287
Five-year-old provenances			
BA59	78.61	1.371 *	0.011
BA60	79.91	0.808	0.720
BA61	77.63	1.492	1.230
RO63	66.14	0.600	0.444
RO64	66.29	0.811	0.518
RS66	82.27	1.345	0.405
RS68	76.11	0.913	0.578
RS69	69.55	0.659	0.147

Legend: * – slopes significantly different from 1.00.

average mean heights and regression coefficient less than 1.0 (0.600, 0.811 and 0.659, respectively), which points to poor adaptability to all trial sites.

Adaptability from AMMI model

While the regression analysis explained 15.8% and 33.2% of provenance by site interaction, the AMMI analysis accounted for 62.2% and 78.7% of $P \times S$ interaction in six- and five-year-old provenances, respectively (Tab. 6).

These results are in agreement with the findings of PURCHASE *et al.* (2000), who compared several stability analysis procedures and concluded that AMMI analysis provides more adequate biological and statistical explanation of

$G \times E$ interaction than Finlay and Wilkinson regression analysis.

In the AMMI1 biplot, the x-axis represents the main effects (means) and y-axis represents the effects of the interaction (IPCA1) (MIROSAVLJEVIC *et al.*, 2014). Fig. 2 represents the AMMI1 biplot of PCA axis 1 versus mean height growth (cm) of both provenances and environments. The figures illustrate wide discrepancy between the variability of environments and genotypes.

Stable provenances (with less GEI) are those which have IPCA1 values closer to zero regardless of their sign. The best provenances are those placed on the right side of the AMMI1 biplot origin – the junction of IPCA1 at zero and

the mean height. Moreover, provenances appearing closer to the vertical reference line at $IPCA1=0$ indicate greater relative stability (SHAFII and PRICE, 1998). Concerning the „older“ group of beech provenances, there was clear separation of German provenances (DE47, DE48 and DE49) on the left side of the AMMI1 biplot and the rest of provenances on the right (Fig. 2). Hence, it can be concluded that German provenances showed below average performances in the environmental conditions of Southern Europe (Balkan Peninsula). Similar results were reported by VIŠNJIĆ (2010) who conducted the research on 16, nine-years-old beech provenances originating from Bosnia, Germany, Italy, Romani and Slovenia. The author demonstrated that beech provenances from Southern part of distribution range showed better height growth in comparison to Northern provenances. This phenomenon might

be the result of a strong local adaptation of Northern provenances to environmental conditions at the place of their origin or, rather, maladaptation to the environments in Southern Europe. Provenance HU42 was characterized by $IPCA1$ score close to zero and above average mean height growth, reflecting general adaptation to the tested environments. According to ALIA *et al.* (2010), existence of provenances that perform better across a range of different environments, points to caution in some generalizations on local adaptation in beech. The locality Fruska Gora was quite distinct from the other sites by its large interaction score (+3.83). Other sites had smaller and negative interaction scores. Regarding the „younger“ group of provenances, $IPCA1$ values close to zero were shown by provenances BA59 and RS69, although their position in the AMMI1 biplot was on the opposite sides along the x-axis

Table 6. – Combined ANOVA with AMMI model for height growth among six-year-old and five-year-old provenances.

Source	df	SS	MS	F value	% of P × S SS
Six-year-old					
Provenance (P)	6	1413.13	235.52		
Site (S)	3	2141.12	713.71		
P × S	18	668.96	37.16		
IPCA 1	8	415.81	51.98	2.053 *	(62.2)
IPCA 2	6	157.80	26.30	1.103 ns	(23.6)
P × S residual	4	95.15	50.14		(14.2)
Total	27	4223.21			
Five-year-old					
Provenance (P)	7	1122.81	160.40		
Site (S)	3	1530.25	510.08		
P × S	21	1317.83	62.75		
IPCA 1	9	1037.31	115.26	4.930 **	(78.7)
IPCA 2	7	197.90	28.27	1.711 ns	(15.0)
P × S residual	5	82.61	16.52		(6.3)
Total	31	3970.89			

Legend: * $p < 0.05$; ** $p < 0.01$; ns – not significant at $p < 0.05$.

(Fig. 2). Site Fruska Gora had the largest positive (+4.42) and Debeli Lug the largest negative (−3.53) score, in comparison to the other sites that displayed lower values of interaction scores.

The AMMI2 biplot (IPCA1 versus IPCA2 biplot) exhibits the magnitude of interactions of each provenance and environment (Fig. 3).

The environments with long vectors had greater influence in determination of provenance by site interaction and environments with short vectors contributed less to $P \times S$ (FARSHADFAR *et al.*, 2012). Also, the angles between the environmental vectors in the biplot represent the phenotypic correlation between the environments (MOHAMMADI and AMRI, 2011). Smaller angle between interaction vectors indicates greater similarity in the interaction response (BABIĆ *et al.*, 2010). Our results showed that sites Fruska Gora (RS) and Medvednica (HR) had the greatest influence on determination of $P \times S$, in both age groups of provenances. Also, smaller angle between environmental vectors of sites Kakanj (BA) and Debeli Lug (RS) indicates greater phenotypic correlation between these environments, especially for six-year-old provenances. Highly posi-

tively correlated vectors indicate that provenances had similar responses and rank positions in these two sites. Conversely, non-correlated vectors (angles approaching 90°) or highly negatively correlated vectors (angles approaching 180°) indicate that provenances respond differently at sites (MURILLO, 2001). Provenance trial Fruska Gora exhibited strong negative correlation with vectors of other test sites. The provenances and environments with IPCA values of same sign show positive interaction, suggesting adaptation of provenances to those environments and the opposite (KIM *et al.*, 2008). Also, provenances positioned closer to the biplot origin have higher stability (MIROSAVLJEVIC *et al.*, 2014). Within the „older“ group, provenances DE47, DE49 and HR25 expressed high interaction with the locality Fruska Gora, and therefore better adaptation to this site (Fig. 3). Unlike German provenances, provenance HR25 showed above average height growth, demonstrating specific adaptability to high yielding sites. On the other hand, provenances DE48 and BA30 showed high interaction with site Kakanj. Position of provenance HU42 closer to the biplot origin indicates higher stability of this provenance, which is already observed by AMMI1 biplot and linear

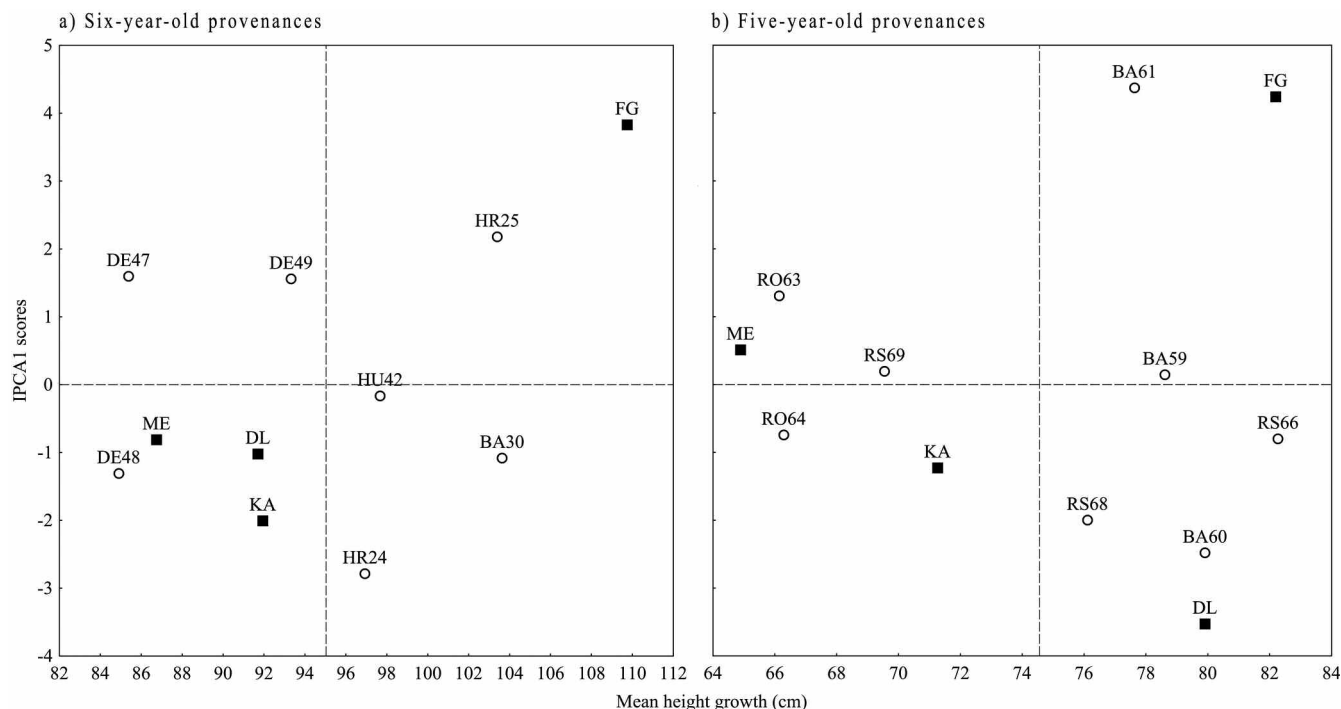


Figure 2. – AMMI1 biplot of mean height (cm) and IPCA1 scores of tested beech provenances across four environments, among: a) seven six-year-old and b) eight five-year-old provenances. The abbreviation indicates test sites (■) and provenances (○) as shown in Tab. 1 and Tab. 2. The vertical dash line is the grand mean of experiment and the horizontal dash line is IPCA = 0.

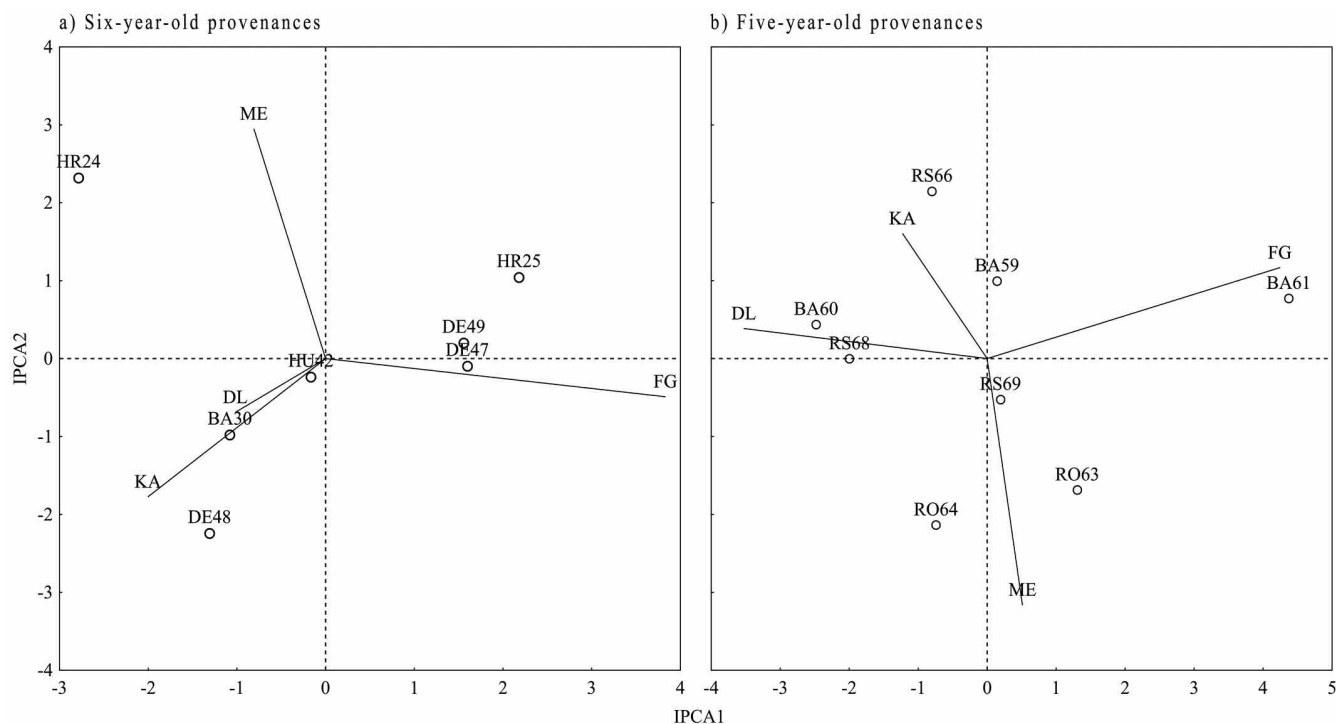


Figure 3. – Interaction biplot for the AMMI2 model on height growth among: a) seven six-year-old and b) eight five-year-old provenances, grown in four environments. The abbreviations represent the test sites and provenances as shown in Tab. 1 and Tab. 2.

regression analysis. Among the provenances which belong to „younger“ group, provenance BA61 showed high interaction with Fruska Gora, provenances RO63 and RO64 with site Medvednica, provenances BA60 and RS68 with Debeli Lug and BA59 and RS66 with site Kakanj, pointing out their narrow adaptability to certain environments (Fig. 3).

Implication of provenance by site interaction in light of climate change impact on beech

Two general approaches were proposed to deal with genotype by environment interaction (RAYMOND and NAMKOONG, 1990; ZAS *et al.*, 2004). The first approach is to define breeding zones with relatively uniform impact on genotypes and then choose the best, specifically adapted genotypes for each zone, independently (MCKEAND *et al.*, 1990; BALTUNIS *et al.*, 2010). The second approach is to find stable genotypes and to use them across a range of environments (FINLAY and WILKINSON, 1963). However, stability *per se* is not necessarily a positive factor and it is desirable only when associated with high mean yield (ADUGNA *et al.*, 2011). Present study evidenced that Hungarian provenance Valkonya (HU42) showed average stability over tested

environments, as well as above average mean height growth. This provenance also showed the highest survival percentage. Thus, provenance HU42 could provide a tradeoff between maximizing growth in one environment and ensuring resilience across a range of environments. However, selection for generally adapted provenances based on overall performance and stability across sites would reduce genetic diversity (ZAS *et al.*, 2004) and thereby decrease capacity of species to adapt to ongoing climate changes (MCLACHLAN *et al.*, 2007). For that reason, introduction of new provenances should be seen as complementing local seed sources, and never as replacing local provenance. In such a manner, fitness of local population may be enhanced via gene flow and changes in the genetic composition (LENORMAND, 2002). Furthermore, presence of increased genetic diversity might ensure faster response to rapid climatic changes, which will allow forest trees to survive, adapt and evolve in new environments (KOSKELA *et al.*, 2007).

Provenances HR25 and BA61 could be specifically adapted to high-yielding environments, as they showed the greatest height growth under the most favorable site conditions. These prove-

nances demonstrated high survival percentage, as well. Recently, STOJANIĆ *et al.* (2013a) evidenced that provenance HR25, growing at the Fruska Gora site, showed similar pattern in radial increment and wood anatomical structure as the local provenance, which points to a high potential of this provenance to adjust their wood-anatomical variables to these environmental conditions. However, because of low stability, performances of provenances HR25 and BA61 could be reduced under the influence of projected global warming, due to deterioration of site conditions for beech growth in Southeastern Europe (VON WUEHLISCH, 2004). Therefore, decision makers should decide whether to favor the provenances best adapted for current conditions or those for the expected future climatic conditions (LINDNER, 2007). For example, provenances occupying the sites characterized by certain climatic conditions, which might be expected to be similar to climate of other sites in the future (based on climate model predictions), should be considered as candidate sources for seed collection dedicated to those sites in the future (LINDNER *et al.*, 2008). LINDNER *et al.* (2010) believe that beech populations from more southern latitudes may be a valuable pollen source in terms of increasing local adaptation at species level.

Climate change is projected to not only reduce productivity of beech stands, but also increase mortality in certain areas (EILMANN *et al.*, 2014). Because of global warming, beech may no longer be adapted to the set of environmental conditions in a given natural range and could therefore fall outside its climatic niche (BELLARD *et al.*, 2012). STOJANOVIĆ *et al.* (2013) demonstrated that compared to the present distribution of beech in Serbia, up to 90% of the beech forests may be located outside their 20th century bioclimatic niche until the end of 21st century. Therefore, the establishment of new forests with genotypes and/or provenances of the same species that are better adapted to changing conditions would be of primary importance (WORTEMANN *et al.*, 2011). Results of the present study evidenced that Croatian provenance (HR24) was quite insensitive to environmental changes, showing potential of producing above average height growth in low yielding environments. This result confirms the findings of STOJANIĆ (2013b), who followed variability of certain physiological parameters in two beech provenance trials (Fruska Gora and Debeli Lug), over two growing seasons (wet and dry).

The author reported that despite the reduction of gas exchange in beech saplings during drought stress, provenance HR24 exhibited higher rates of stomatal conductance and net photosynthesis, compared to other provenances. Moreover, this provenance showed higher water use efficiency in comparison with other provenances involved in study. Owing to the fact that ability of plants to acclimate to different environmental conditions is directly or indirectly associated with their potential to adjust photosynthetic capacity to match those conditions (ATHANASIOU *et al.*, 2010), gas exchange parameters are important indicators of vitality and competitive ability of species or single genotype at the particular site (ARANDA *et al.*, 1996). Similarly, water use efficiency is considered an important component in assessment of plant drought resistance (BLUM, 2009). Bearing in mind these results, it is likely that provenance HR24 could be efficiently used in reforestation programs for more dry sites in Europe (e.g. sites in Southern Europe). CZAJKOWSKI and BOLTE (2005) recommended the introduction of drought-adapted provenances to decrease the vulnerability of Central European beech stands to drought.

Nevertheless, before making recommendations regarding seed transfer, meta-analysis of all existing beech provenance trials should be considered (LINDNER *et al.*, 2008). Furthermore, at this early developmental stage, height growth does not fully reflect growth potential of the provenances and the effect of the local environment on the provenances. Several authors demonstrated that early growth assessments may not be reliable for predicting G × E at mature age (HOGBERG and KARLSSON, 1998; HANNERZ *et al.*, 1999; GWAZE *et al.*, 2001). Similarly, MUHS *et al.* (2010) consider that the growth potential of beech can be estimated reliably only after 60 years in the field. For that reason, it is too early to reach a conclusion regarding provenance potential (VON WUEHLISCH, 2004). Instead, long-term monitoring of height growth is required.

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