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ORIGINAL PAPER

GAS EXCHANGE CAPACITY OF CROATIAN COMMON BEAN LANDRACES (*PHASEOLUS VULGARIS* L.) IS RELATED TO THEIR ORIGIN AND GROWTH TYPE*

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Abstract

The long tradition of common bean (*Phaseolus vulgaris* L.) cultivation in Croatia has resulted in the development of many landraces, which create a valuable basis for screening different physiological traits. Studying gas exchange parameters could provide valuable information that could be useful in creating new crop germplasm with enhanced agronomic attributes. Variability of gas exchange parameters, such as the net photosynthetic rate (A), transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), light use efficiency (LUE), and water use efficiency (WUE) were studied on the collection of 226 common bean accessions and the relationship of the gas exchange parameters with the origin and morphological traits was tested. The highest variability among all landraces was found for the WUE and g_s, and lowest for the A and LUE traits, indicating high potential of these traits to be used for selection and breeding programs. Accessions of the Mesoamerican origin had higher A and LUE and lower C_i values compared to accessions of the Andean origin. Accessions with the determinate growth had higher g_s and C_i values and lower A, LUE and WUE values compared to accessions with the indeterminate growth. The variance components analysis showed that the growth type has a more pronounced effect on g_s, C_i and WUE, whereas the origin has a stronger impact on A and LUE. The principal component analysis (PCA) showed that A separates accessions according to their origin, whereas C_i separates accessions according to their growth type. Accessions with higher C_i had lower A, indicating possibly higher rates of carboxylation per active site on

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the enzyme and/or higher regeneration capacity of Ribulose-1,5-bisphosphate (RuPB) in the Calvin cycle in accession with high A.

Keywords: common bean, landraces, origin, determinante growth, indeterminate growth, gas exchange capacity.

INTRODUCTION

The global population growth, especially in developing countries, requires an increase in crop productivity to meet current demands. Common bean (*Phaseolus vulgaris* L.) is one of the most important grain legumes for direct human consumption (Broughton et al. 2003), and it is grown and consumed principally in developing countries. According to FAOSTAT (2017), in 2014 dry common bean was cultivated on more than 30 million ha. The highest producer were Myanmar and India with more than 40 million tonnes, then Brazil with more than 30 million tonnes and USA, Mexico, Tanzania and China with more than 10 million tonnes.

In Croatia, common bean is a traditional crop, although neglected nowadays, and the production is based on landraces. In 2015, production of dry common bean equalled 1 156 t, harvested from 1 475 ha (Statistical Yearbook of the Republic of Croatia, 2016). Common bean was domesticated in Mesoamerica and the Andes (Gepts 1998). Following the discovery of the Americas, the plant achieved widespread popularity in Europe (Piergiovanni, Lioi 2010). Over centuries, European farmers have selected numerous landraces for different morpho-productive traits (Rodiño et al. 2009). Similarly, the old tradition of common bean cultivation in Croatia has resulted in the development of many landraces adapted to restricted areas. Therefore, landraces present an interesting, genetically diverse material for screening physiological traits.

Almost all dry matter of crop plants is produced by CO_2 assimilation in the process of photosynthesis (McCree 1986). The lack of correlation between crop yield and leaf photosynthesis rates, along with some evidence that yield is sink-, rather than source-limited have led to the conclusion that crop yields cannot be improved by increasing leaf photosynthetic rates (Borrás et al. 2004).

However, yielding potential of agricultural crop is determined by available light energy and by genetically determined properties such as the efficiency of light capture, efficiency of the conversion of intercepted light into biomass, and the proportion of biomass partitioned into grain. In addition, as was pointed out by Long et al. (2006), the efficiency of the conversion of intercepted light into biomass seems to represent a major factor of the possible increase in crop yield potential. Thus, the study of gas exchange parameters provides valuable information on the state of dry matter production in a crop plant which gives clear insight into plant performance.

Recent studies on common bean have shown that increased photosynthetic rate and stomatal conductance could lead to the increased yields and enhanced drought tolerance (Ribeiro et al. 2004, Wentworth et al. 2006). However, photosynthetic machinery represents a huge investment of resources and the extent of this investment responds to the economy of the whole plant, thus many of the plant's morphological and physiological traits can influence its photosynthetic capacity (Paul, Foyer 2001).

The aim of this study was to evaluate the genetic variability in gas exchange parameters, such as the net photosynthetic rate (A), transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), light use efficiency (LUE), and water use efficiency (WUE), among Croatian common bean accessions, and to test possible relationships between gas exchange parameters, growth type and origin.

MATERIAL AND METHODS

Plant material

In total, 226 accessions belonging to seven most widespread Croatian common bean landraces (Biser, Tetovac, Kukuruzar, Visoki Trešnjevac, Niski Trešnjevac, Zelenčec, Puter) were included in the analysis. Seed samples were obtained from the producers from all over Croatia. The list of accessions with their passport data is available in Supplementary Table S1. Research was carried out in 2014, at the experiment field of the Department of Seed Science and Technology, Faculty of Agriculture, University of Zagreb, Croatia. The accessions were grown in non-replicated field plots. Seeds were planted on 6 May 2014, at 70 cm inter-row distance, and 10 cm and 25 cm distance in rows for determinate and indeterminate growth, respectively. Each plot was 2 m long. During the plant growing season, mechanical weed control was performed.

The climatic conditions during the growth season are presented in Figure 1. The soil at the experimental site is classified as Cambisol according to IUSS Working Group WRB (2014), and the soil's characteristics are shown in Table 1.

Phaseolin type determination

Total genomic DNA extraction and phaseolin type determination were performed using standard methods as described in Carović-Stanko et al. (2017).

Gas exchange parameters measurements

Leaf gas exchange parameters, such as net photosynthetic rate (A), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i), were measured with a LCpro portable photosynthesis system (ADC, Bio Scientific Ltd., UK) equipped with a 6.25 cm^2 clamp-on leaf

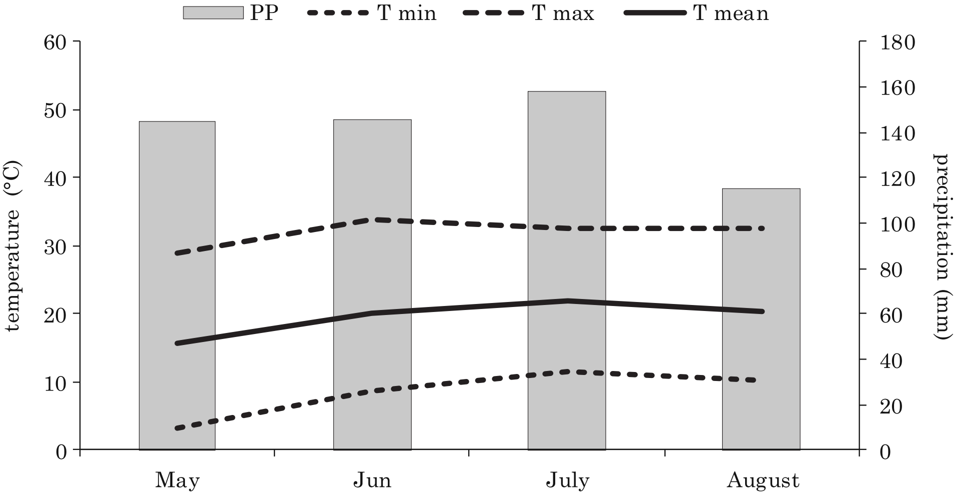

Fig. 1. Sum of precipitation (PP) and minimum (Tmin), maximum (Tmax) and mean (Tmean) air temperature conditions during the experiment

Table 1

Physical and chemical properties of the soil used in the study (Zagreb, Croatia) – AOAC 2015

San^{d}a	Silt^{a}	Clay^{a}	pH^{b}		C_{org}^{c}	N^{d}	P^{e}	K^{e}
(%)			H_2O	KCl	(g kg^{-1})		(mg kg^{-1})	
17.2	67.4	15.4	6.31	5.09	8.9	0.9	51.1	134.5

Basic soil characteristics were determined by standard methods: ^{a} Soil particle size distribution was determined by pipette-method with sieving and sedimentation; ^{b} pH potentiometrically; ^{c} Organic carbon content (C_{org}) determination after dry combustion; ^{d} Total nitrogen by a modified Kjeldahl method; ^{e} Phosphorus and potassium by ammonium lactate method

cuvette. Measurements were performed on the main leaflet of the topmost, fully expanded trifoliate leaf, on three plants per accession. Average values per plant were calculated from three recorded measurements per leaf. Measurements were performed at the bloom stage, given that the genotypes differed in their vegetation; 20 measurements were carried out during a period of 30 days (from 23 June to 23 July 2014).

Measurements were carried out on cloudless days, between 9:15 and 11:30 h a.m., at 1200 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) and at 380 ± 5 μmol mol^{-1} CO_2 concentration. During measurements, leaf temperature and leaf-to-air vapour pressure difference ($VPD_{leaf\text{-}to\text{-}air}$) were continuously monitored. All measurements were obtained at 21-25°C and 1.0-1.8 kPa $VPD_{leaf\text{-}to\text{-}air}$.

Water use efficiency was calculated as WUE = net photosynthetic rate (A) / transpiration rate (E), and light use efficiency was calculated as LUE = net photosynthetic rate (A) / photosynthetically active radiation (PAR).

Data analysis

PROC MIXED in SAS (SAS Institute Inc., 2011) was used for the analysis of each trait. In the preliminary analyses, landraces (morphotypes) were treated as fixed effects and accessions, nested in landraces, as random to test for significant differences among landraces. *Post-hoc* comparisons of the landrace means were carried out using the Tukey's Studentized Range test at $P < 0.05$.

In the subsequent analyses, the models included origin, growth and their interaction as fixed effects. The landraces were nested in origin and growth while the accessions were nested in landraces, origin and growth. Both landraces and accessions were treated as random effects. Random effects were removed from the model if not significant, one at a time, noting the goodness of fit across models using the value of the Akaike Information Criteria (AIC) statistics. The model with the lowest AIC value was considered the best model and was then used to test the significance of the fixed effects.

Variance components were estimated for each trait using the Restricted Maximum Likelihood method (REML) as implemented in PROC VARCOMP.

Principal component analysis (PCA) based on four gas exchange parameters (C_i, E, g_s, A, whereas LUE and WUE, as derived variables were excluded from the analysis) was performed using PROC PRINCOMP in SAS. The biplot was constructed by two principal components showing accessions and traits (as vectors).

RESULTS

The number of accessions per landrace ranged from 10 (Puter) to 78 (Niski Trešnjevac). The phaseolin type analysis of 226 accessions revealed that 75 accessions (33%) were of phaseolin type I (Mesoamerican; S), 29 (13%) of II (Andean; H or C) and 122 (54%) of type III (Andean; T). The accessions of the Mesoamerican origin belonged to landraces Biser, Tetovac or Kukuruzar, while those of the Andean origin belonged to Visoki Trešnjevac, Niski Trešnjevac, Zelenčec or Puter (Table 2). All the accessions belonging to landraces Biser, Niski Trešnjevac, Zelenčec and Puter were of determinate growth (93 accessions; 41%), while those belonging to landraces Tetovac, Kukuruzar and Visoki Trešnjevac were of indeterminate growth (133 accessions; 59%).

Preliminary data analysis was performed to test differences among the landraces and accessions for different gas exchange parameters. Mean values and CVs for gas exchange parameters of each landrace are shown in Table 3. The distribution of the gas exchange parameters for each landrace is shown in Figure 2, together with the results of *post-hoc* comparisons of landrace means. Accessions differed significantly ($P < 0.001$) in all the gas exchange parameters (Table 3). Highly significant differences ($P < 0.001$) were found

Table 2

Landrace, growth type and origin of 226 Croatian common bean accessions

No.	Landrace	Growth type[a]	Origin[b]	Number of accessions
L1	Biser	D	MA	11
L2	Tetovac	I	MA	25
L3	Kukuruzar	I	MA	39
L4	Visoki Trešnjevac	I	AN	29
L5	Niski Trešnjevac	D	AN	78
L6	Zelenčec	D	AN	34
L7	Puter	D	AN	10

[a] Growth: D – determinate; I – indeterminate
[b] Origin: MA – Mesoamerican; AN – Andean

among landraces for all the traits except WUE ($0.05 > P > 0.01$) and E ($P > 0.05$).

The highest A as well as LUE were determined in landraces Biser and Kukuruzar. Kukuruzar also showed the highest g_s, while Visoki Trešnjevac had the highest values of C_i. Results of *post-hoc* comparisons of the landrace means for E and WUE were not significant in any of the pairwise comparisons.

There was broad variation in all measured gas exchange parameters across the accessions of each landrace (Table 3, Figure 2). The highest CV across accessions of all the landraces (24%) was found for WUE and g_s (23%), whereas the smallest one was found for A (16.2%) and LUE (16.2%). When comparing different landraces, the highest variability for A, g_s and LUE was found in Tetovac (20%, 27% and 20%, respectively). The highest variability for E was found in Biser (22%), for C_i in Puter (24%), while for WUE in Kukuruzar (26%).

In the subsequent analyses, the models included origin, growth and their interaction as fixed effects. The final models for all the traits included origin, growth and their interaction as fixed effects and accessions, nested in origin and growth, as random effects (Table 4).

Significant effect of origin was determined for A, C_i, and LUE. Mesoamerican accessions had higher average A (26.7 μmol CO_2 m^{-2} s^{-1}) and LUE (0.03), and lower C_i (153.3 μmol mol^{-1}) compared to accessions from the Andean gene pool (24.6 μmol CO_2 m^{-2} s^{-1}, 0.02, and 158.3 μmol m^{-2} s^{-1}, respectively). Growth type was significant for all gas exchange parameters except for E. Compared to accessions with the indeterminate growth, accessions with the determinant growth had higher A (26.13 vs. 24.91 μmol CO_2 m^{-2} s^{-1}), LUE (0.03 vs. 0.02), and WUE (4.98 vs. 4.46), and lower g_s (0.29 vs. 0.33 mol H_2O m^{-2} s^{-1}) and C_i (145 vs. 171 μmol mol^{-1}).

Table 3

Means and coefficients of variation (CV) for gas exchange parameters in Croatian common bean landraces

Parameter[a]	Land.[b]	Access.[c]	Landraces													
			Biser		Tetovac		Kururuzar		Visoki Trešnjevac		Niski Trešnjevac		Zelenčec		Puter	
			mean	CV	mean	CV	mean	CV	mean	CV	mean	CV	mean	CV	mean	CV
A	***	***	28.1	14.3	25.2	20.3	26.9	13.1	22.3	15.5	26.3	14.6	24.0	13.6	26.1	17.0
E	ns	***	5.6	21.9	5.8	15.8	5.9	19.5	5.6	20.1	5.5	16.9	5.4	16.8	5.1	18.0
Ci	***	***	127.2	20.2	166.6	16.7	166.0	14.9	180.4	19.0	144.6	21.3	157.0	20.2	151.1	23.9
g_s	***	***	0.29	21.0	0.320	26.8	0.350	22.1	0.310	27.4	0.290	16.5	0.270	17.1	0.290	20.4
LUE	***	***	0.027	14.3	0.024	20.3	0.026	13.1	0.021	15.5	0.025	14.6	0.023	13.6	0.025	17.0
WUE	*	***	5.160	21.2	4.450	24.8	4.800	26.2	4.130	23.9	4.940	23.0	4.580	21.3	5.230	23.2

[a] Gas exhange parameters: A – net photosynthetic rate; E – transpiration rate; C_i – intercellular CO_2 concentration; g_s – stomatal conductance, LUE – light use efficiency; WUE – water use efficiency;

[b] Significance of ANOVA *F*-test for landraces: ns – non-significant value; *significant at $P < 0.05$; **significant at $P < 0.01$; ***significant at $P < 0.001$;

[c] Significance of ANOVA *F*-test for accessions (nested in landraces): as above

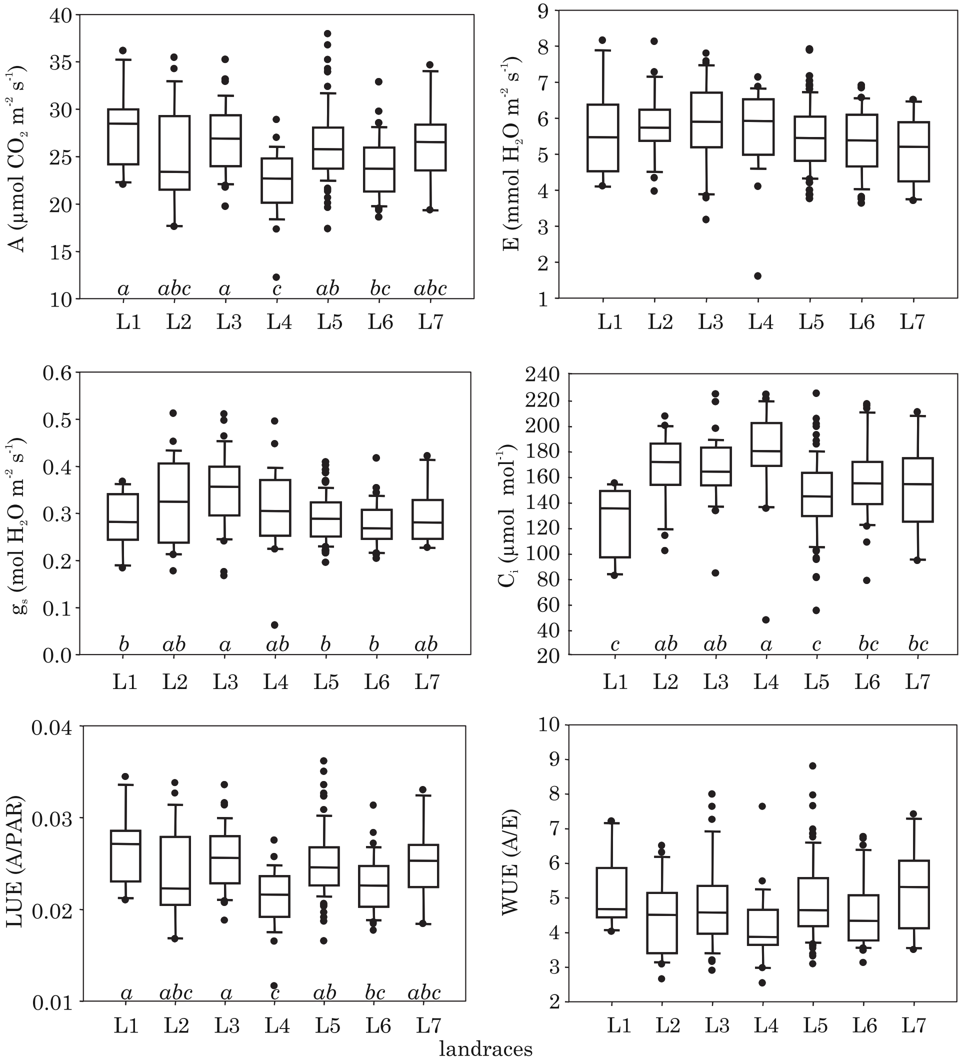

Fig. 2. Box-plots of gas exchange parameters in Croatian common bean landraces: L1 – Biser; L2 – Tetovac; L3 – Kukuruzar; L4 – Visoki Trešnjevac; L5 – Niski Trešnjevac; L6 – Zelenčec; L7 – Puter (the same letter indicates that the mean values are not significantly different among landraces at $P > 0.05$), A – net photosynthetic rate, E – transpiration rate, g_s – stomatal conductance, C_i – intercellular CO_2 concentration, LUE – light use efficiency, WUE – water use efficiency

Variance components were estimated to assess the amount of variation for dependent variables associated with random effects (Figure 3). The highest percent of the total variance for all gas exchange parameters could be attributed to differences among accessions. In addition, significant percentage of the total variance for A (9%), C_i (30%), g_s (10%) LUE (9%), and WUE (8%) could be attributed to the growth type, and for A (16%) C_i (7%), and LUE

Table 4

Analysis of variance for gas exchange parameters

Source of variability	df[a]	Gas exchange parameters[b]					
		A	E	g_s	C_i	LUE	WUE
Origin	1	***	ns	ns	**	***	ns
Growth	1	***	ns	**	***	***	**
Origin x growth	1	ns	ns	ns	ns	ns	ns
Acession (landrace origin growth)	225	***	***	***	***	***	***

[a] df – degrees of freedom

[b] gas exchange paramters: A – net photosynthetic rate, E – transpiration rate, g_s – stomatal conductance, C_i – intercellular CO_2 concentration, LUE – light use efficiency, WUE – water use efficiency, ns – non-significant value, * significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$

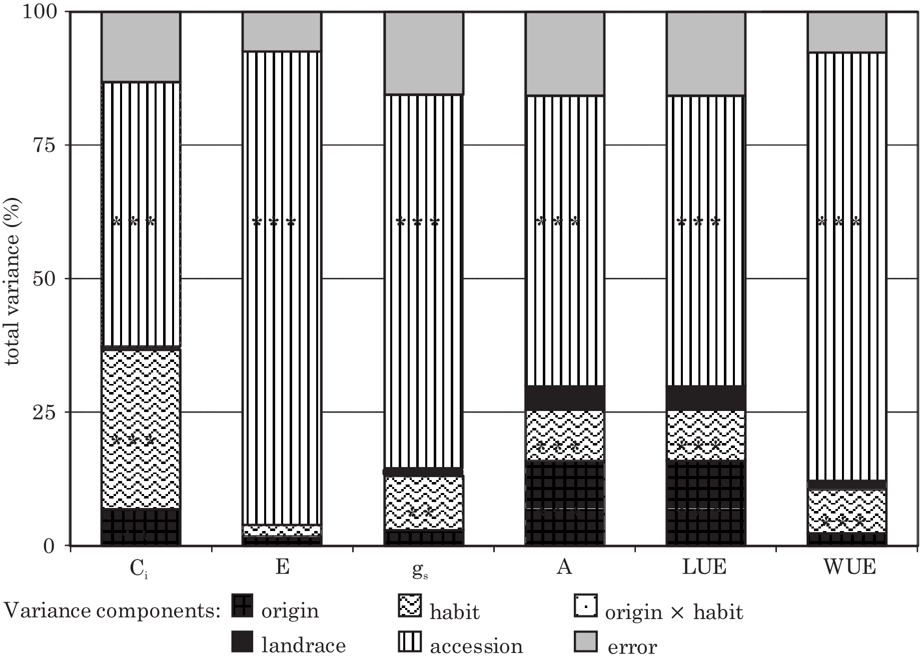

Fig. 3. Variance components of gas exchange parameters in Croatian common bean landraces: A – net photosynthetic rate, E – transpiration rate, g_s – stomatal conductance, C_i – intercellular CO_2 concentration, LUE – light use efficiency, WUE – water use efficiency; Significance levels: ns – non-significant value, * significant at $P < 0.05$, ** significant at $P < 0.01$, *** significant at $P < 0.001$

(16%) to the origin. With the origin having greater effect on the A and LUE, whereas the growth type had greater effect on g_s, C_i and WUE (Figure 3).

The biplot constructed by the first two axes of principal component analysis showed the relationships among origin (Mesoamerican vs. Andean) and growth (determinate vs. indeterminate) of the accessions and the values of the four quantitative gas exchange parameters shown as vectors (Figure 4). First two principal components had the eigenvalue higher than 1, jointly explaining 78% of the total variation. A strong positive correlation ($r = 0.66$) was observed between the first principal component (PC1) and A, separating accessions according to their origin. The second principal component (PC2) was strongly correlated with C_i ($r = 0.77$), separating accessions according to their growth type.

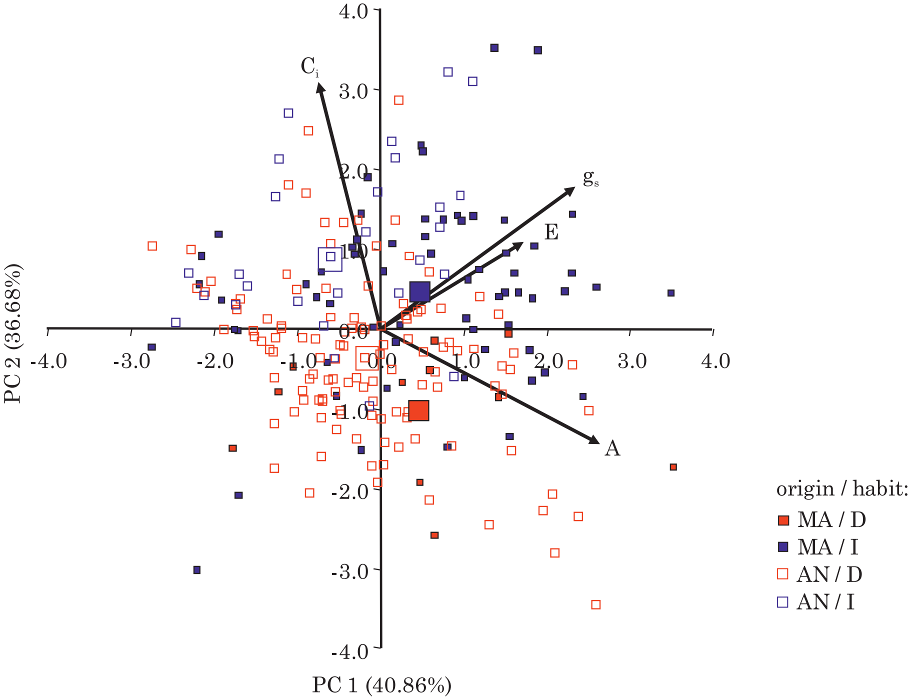

Fig. 4. Principal component analysis of Croatian common bean accessions based on four gas exchange parameters shown as vectors. Accessions were designated according to their origin (Mesoamerican vs. Andean) and growth (determinate vs. indeterminate)

DISCUSSION

Common bean germplasm is genetically diverse and includes a high number of different landraces (GEPTS 1998). As it is true for several physiological traits such as phosphorus efficiency (BEEBE et al. 1997), drought tolerance (WENTWORTH et al. 2006), salinity tolerance (DASGAN, KOC 2009), considerable variability could also be found in gas exchange parameters. Wherein the highest variability among all landraces was found for WUE and g_s, and lowest for A and LUE.

Gas exchange parameters are highly influenced by environmental conditions, thus during the measurements special care was given to the uniformity of environmental conditions, especially to $VPD_{leaf\text{-}to\text{-}air}$ and leaf temperature. In addition, a high number of accessions representing each landrace, and even a higher number when we consider differences between different growth type (133 with determinate and 93 with indeterminate growth) or origin (151 of the Andean and 75 of the Mesoamerican gene pool), grown under the same environmental conditions for sufficient time to show steady physiological behaviour, allow us to address differences in gas exchange parameters to genotypic differences among the studied common bean accessions. Moreover, the measured values of gas exchange parameters are comparable to those obtained in other research conducted in growing chambers (Wentworth et al. 2006) or greenhouses (Lobato et al. 2010), suggesting favourable environmental conditions on the field during the plant growing season.

Analysis of variance indicates differences in the measured gas exchange parameters between the different growth types and different origins. Possible explanation of the higher g_s and consequently higher C_i found in indeterminate accessions compared to determinate ones could be the differences in their ontogeny and senescence (Lewis et al. 2002) and related higher cytokinin and auxin activity in indeterminate accessions. Several studies have reported a positive effect of low cytokinin (Pospíšilová et al. 2001, 2005) and auxin (Eamus 1986) concentrations on the stomatal opening in common bean. This explanation is supported by the non-significant differences in g_s between accessions of different origin and by the results of variance component analysis, which show that significant variation in g_s, C_i and WUE is related to differences in the growth type, and that a high percentage of variability in these traits could be attributed to different growth types.

Although there were significant differences in g_s between accessions with different growth types, there were no significant differences in E, suggesting that plants were well watered and that stomatal aperture was sufficient to support maximal E. Despite lower g_s and C_i, accessions with the determinant growth had higher A, LUE and WUE. Higher LUE and WUE of determinant accessions are caused by significantly higher A found in determinate accessions compared to accessions with the indeterminate growth. Similarly, higher A, and LUE, and lower Ci was found in the Mesoamerican compared to Andean origin. In addition, higher percentage of the total variability in A and LUE could be addressed to different origin. Significantly higher A and lower g_s and C_i in determinant compared to indeterminate accessions, as well as significantly higher A and lower C_i in the Mesoamerican compared to Andean accessions, without differences in g_s between accessions of different origin, indicate a possible difference in their photochemical efficiency. Similar results were obtained by Ribeiro et al. (2004), who reported a drop in A without changes in g_s when genotypes had been transferred from controlled to natural conditions. However, in one genotype they reported a simultaneous drop in g_s and A. These authors concluded that bean cultivars showed different physiological responses when submitted to the same environmental changes. The differences in photosynthetic capacities may be caused by differences in the Rubisco carboxylation capacity, improved regeneration rates of CO_2 acceptor molecule (ribulose bisphosphate), higher rates of the catalysis of carboxylation (Long et al. 2006) or a different number of mesophyll cells per unit surface leaf area (Nobel 1999) including different leaf acclimation plasticity (Wentworth et al. 2006).

Results of the PCA analysis showed that the first principal component was correlated with A separating accessions according to the origin, and the second one was highly correlated with C_i, separating accessions according to growth. Vectors of A and C_i were pointed in opposite directions. These results indicate that despite the difference in g_s, accessions with higher A had lower C_i, indicating possibly higher rates of carboxylation per active site on the enzyme and/or higher regeneration capacity of RuPB in the Calvin cycle (Long et al. 2006) or possible differences in the thickness of leaf mesophyll. The latter could be a reasonable explanation at least for the differences found between accessions with different growth types. Namely, leaf development is highly controlled by signals perceived by mature leaves and transduced to newly developing leaves (Yano, Terashima 2004). Therefore, it is possible that different environmental stimuli such as the quantity and quality of light spectra, temperature, relative humidity, etc., which are different under canopies of plants with determinate and indeterminate growth, change the leaf morphology and consequently change the leaf photosynthetically capacity.

CONCLUSIONS

Results of this research showed high variability of gas exchange parameters among Croatian common bean landraces. In addition, the relationship between origin and/or growth type with different gas exchange parameters was found. Further experiments should be conducted to reveal the photochemical or morphological background of the relationship between a higher net photosynthetic rate found in the Mesoamerican and determinant accessions, as well as to check the effect of higher photosynthetic rates on the yield production.

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