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The influence of orographical and bioclimatic factors on morphological variability of analyzed characters of *Jovibarba heuffelii* (Schott) A. Löve & D. Löve (Crassulaceae)

Danijela Nikolić[1*], Jasmina Šinžar-Sekulić[2], Vladimir Ranđelović[1], Dmitar Lakušić[2]

[1]University of Niš, Faculty of Sciences and Mathematics, Department of Biology and Ecology, Višegradska 33, 18000 Niš, Serbia
[2]University of Belgrade, Faculty of Biology, Institute of Botany and Botanical Garden „Jevremovac", Takovska 43, 11000 Belgrade, Serbia

** E-mail: danid@pmf.ni.ac.rs*

***Abstract*:**

Nikolić, D., Šinžar-Sekulić, J., Ranđelović, V., Lakušić, D.: *The influence of orographical and bioclimatic factors on morphological variability of analyzed characters of Jovibarba heuffelii (Schott) A. Löve & D. Löve (Crassulaceae). Biologica Nyssana, 6 (1), September 2015: 1-9.*

The goal of this paper was to determine the extent of morphological variability in species *J. heuffelii* caused by orographic and bioclimatic factors. Samples were collected from 14 populations of species *J. heuffelii*, from the territories of Serbia, Macedonia, Bulgaria and Romania. For this purpose cluster analysis (UPGMA) on bioclimatic parameters and regression analysis were performed. The cluster analysis of bioclimatic factors has shown that the study area was influenced by semiarid temperate-continental or subcontinental climate, continental mountain climate and humid mountain climate. Among the orographic factors, the greatest influence on morphological characters of species *J. heuffelii* was determined for altitude, exposition and slope of the terrain. The mean temperature of the wettest quartile (BIO8) and temperature seasonality (BIO4) have shown the greatest influence on the morphological characters of *J. heuffelii*.

Key words: *Jovibarba heuffelii*, morphological variability, environmental factors

***Apstrakt*:**

Nikolić, D., Šinžar-Sekulić, J., Ranđelović, V., Lakušić, D.: *Uticaj orografskih i bioklimatskih faktora na morfološku varijabilnost analiziranih karaktera Jovibarba heuffelii (Schott) A. Löve & D. Löve (Crassulaceae). Biologica Nyssana, 6 (1), Septembar 2015: 1-9.*

Cilj ovog rada je bio da se utvrdi u kolikoj meri je velika morfološka varijabilnost kod vrste *J. heuffelii* uslovljena uticajem orografskih i bioklimatskih faktora. Prikupljeni su uzorci 14 populacija vrste *J. heuffelii* sa područja Srbije, Makedonije, Bugarske i Rumunije. Urađena je klaster analiza (UPGMA) sa bioklimatskim parametrima i regresiona analiza. Klaster analiza bioklimatskih faktora je pokazala da je istraživano područje pod uticajem tri tipa klime: semiaridne umereno kontinentalne ili subkontinentalne klime, kontinentalne planinske klime i humidne planinske klime. Od orografskih faktora pored nadmorske visine, ekspozicija i nagib terena imaju najveći uticaj na morfološke karaktere vrste *J. heuffelii*. Srednja temperatura najvlažnijeg kvartala (BIO8) i temperaturna sezonalnost (BIO4) najviše utiču na morfološke karaktere *J. heuffelii*.

Key words: *Jovibarba heuffelii*, morfološka varijabilnost, ekološki faktori

Introduction

J. heuffelii (Crassulaceae) is a succulent xerophyte primarily inhabiting rocky habitats at various substrates (limestone, serpentinite, silicate) in a range of altitudes from the coastline to 2500 m above sea level (Barca & Niculae, 2005; Lakušić et al., 2005; Dimitrijević et al., 2011). Distribution of this species in Balkan Peninsula and the Southern Carpathians indicates that this is a European endemic species (Meusel, 1965; Jalas et al., 1999). According to the climatic division of southeastern Europe (Horvat et al., 1974) and division into main climate and biome types by Walter and Leith (1964), there are two main climate types within the range of *J. heuffelii* complex: temperate-continental climate (type VI) and mountain climate (type X). The temperate-continental climate is represented by subtype VI 3 - semiarid temperate-continental climate (Moesian-Carpathian variant). Within the mountain climate there are two subtypes: X 2 - humid mountain climate of alpine type (Illyrian variant) and X 3 – continental mountain climate (Moesian-Carpathian variant).

This species is characterized by a very high morphological variability, as evidenced by recent studies on variability of morphological characteristics of vegetative and reproductive organs (Dimitrijević et al., 2011) and analysis of morphological characteristics of nectaries (Nikolić et al., 2015a). The impact of orographic and bioclimatic habitat factors on morphological variability was analyzed in paper by Nikolić et al. (2015b), while this paper pertains only to populations from identical mountain habitats, while gorge and canyon populations were omitted from the analysis. Regression analysis and cluster analysis (UPGMA) based on matrix of bioclimatic parameters were performed in order to determine the extent of impact of orographic and bioclimatic factors on variability of morphological characteristics and differentiation of all analyzed populations.

Table 1. The list of population of *J. heuffelii* used in this study. Vouchers are deposited in the Herbarium of the Institute of Botany, Faculty of Biology, University of Belgrade (BEOU)

Population	Coordinate	Substrate	Altitude	Voucher	Individuals
1. RO-Domogled	44°52'41.70"N 22°25'54.11"E	limestone	1300	BEOU- 16510	20
2. SR-Gradac	44°15'17.98"N 19°53'23.00"E	limestone	490	BEOU-16458	21
3. SR-Suvaja	44°10'54.98"N 19°52'11.08"E	limestone	417	BEOU-16457	20
4. SR-Studenica	43°29'20.56"N 20°32'7.74"E	serpentinite	486	BEOU-16461	20
5. SR- Nebeske stolice	43°15'34.14"N 20°49'33.59"E	serpentinite	1907	BEOU-16468	22
6. SR-Treska	43°15'36.31"N 20°47'6.40"E	serpentinite	1628	BEOU-16462	20
7. SR-Basarski kamik	43° 9'37.29"N 22°42'9.57"E	limestone	1350	BEOU- 16460	25
8. SR-Radan	42°55'4.99"N 21°33'25.74"E	silicate	802	BEOU-16456	20
9. SR-Pljačkovica	42°34'47.20"N, 21°53'31.09"E	silicate	674	BEOU-16465	21
10. SR- Besna Kobila	42°31'45.08"N 22°13'51.10"E	silicate	1900	BEOU- 16463	30
11. SR-Stara planina	43°23'23.41"N 22°38'1.98"E	silicate	1840	BEOU-16459	20
12. BU-Trojanski prolaz	42°46'1.62"N 24°37'2.30"E	silicate	1400	BEOU-16509	20
13. MA-Treskavec	41°24'14.73"N 21°32'14.44"E	silicate	1250	BEOU- 16511	20
14. MA- Mavrovo	41°38'14.33"N 20°42'29.90"E	limestone	1300	BEOU- 16512	20

Table 2. Morphological characters investigated using the populations of *J. heuffelii* described in Table 1.

	MORPHOLOGICAL CHARACTERS	ABBREVIATIONS
1	Diameter of rosette (mm)	Ros_D
2	Number of leaves in rosette	LeRos_N
3	Length of biggest leaf (mm)	LeRos_L max
4	Width of biggest leaf (mm)	LeRos_W max
5	Distance of widest part of leaf from the top of the leaf (mm)	Apex_D_Ros
6	Length of spike (mm)	LeRos_Sp_L
7	Length of cilia (mm)	LeRos_Ci_L
8	Width of cartilaginous leaf edge (mm)	LeRos_Ed_W
9	Height of stem to lowest flower branch (mm)	Ste_H
10	Number of leaves at stem	LeSte_N
11	Length of middle leaf on stem (mm)	MidLeSte_L
12	Width of middle leaf on stem (mm)	MidLeSte_W
13	Distance of widest part of leaf from the top of the leaf (mm)	Apex_D_Ste
14	Number of floral branches	FloBra_N
15	Number of flowers at stage of ripening fruit	Flo_N
16	Length of longest branch in fruit (mm)	FloBra_L
17	Length of sepal (mm)	Sep_L
18	Width of sepal (mm)	Sep_W
19	Length of petal (mm)	Pet_L
20	Width of petal (mm)	Pet_W
21	Length of longest filament (mm)	Fil_L max
22	Height of ovary (mm)	Ova_H
23	Height of stylus (mm)	Sty_H
24	Height of central tooth on petal (mm)	CenToo_H
25	Height of lateral tooth on petal (mm)	LatToo_H
26	Height of fruit (mm)	Fru_H
27	Width of fruit (mm)	Fru_W
28	Length of rostrum (mm)	Rost_L
29	Total seed length (mm)	See_L
30	Total seed width (mm)	See_W
31	Width of central longitudinal fold (costa) (mm)	Cos_W
32	Width of nectary (mm)	Nect_W
33	Height of nectary (mm)	Nect_H
34	The angle between carpels and nectaries (degree)	Nect-Ang

Material and methods

Plant material

Fourteen populations (299 individuals) of *J. heuffelii* were collected for morphological analysis. The samples were taken from Serbia, Macedonia Bulgaria and Romania (during two growing seasons 2010, 2011).

The voucher specimens are deposited in the Herbarium of the Institute of Botany and Botanical Garden “Jevremovac", Faculty of Biology, University of Belgrade - BEOU (**Tab. 1**).

Morphometric analyses

Morphometric analyses were performed on dissected plant organs (leaves, stems, flowers, fruits and seeds). Leaves and inflorescences were stored in a glycerol: 96% ethanol solution (50:50). For measuring of flowers, the microscope slides were used, where all flower parts (sepals, petals, stamens, carpels) were separated and individually placed on the microscope slide. Slides were first scanned (ScanExpress A3 USB, Mustek) and then measured by using the LeicaQWin image analyzing program (Leica image software). For purposes of measuring the smallest details on leaves, flowers and nectaries, these organs were photographed with the LEICA DM 1000 microscope while seeds were photographed with the LEICA MZ16 A stereomicroscope.

Thirty four morphological characters were used in these analyses (**Tab. 2**).

Statistical analysis

Cluster analysis (UPGMA) was performed in order to evaluate the bioclimatic differentiation between the habitats of the 14 investigated populations. Each location was characterized using 19 bioclimatic parameters, extracted from the WorldClim set of global climate layers (Hijmans et al., 2005). The extraction of bioclimatic parameters was done with DIVA-GIS 7.5 software (Hijmans et al., 2012).

Regression analysis (linear regression) was performed in order to estimate the correlations between the variation of morphological characters of *J. heuffelii* and basic orographic, geological, and bioclimatic habitat characteristics, as well as the geographic position of each population. The geographic positions were recorded using a hand-held Global Positioning System (GPS Garmin eTrex Vista® C). Orographic characteristics including altitude, slope and aspect were calculated from the Shuttle Radar Topography Mission (Reuter et al., 2007) at an approximate 90 m pixel resolution using ARCGIS 10 Spatial Analyst. Prior to the regression analysis, habitat characteristics were tested for multicollinearity. Bioclimatic predictors that have shown significant correlations with other predictors were not used in regression analysis of morphological characters.

All statistical analyses were performed using the package Statistica 5.1 (Statsoft, 1996).

Results and discussion

Cluster analysis of bioclimatic data

Cluster analysis based on bioclimatic factors showed presence of 3 clusters (**Fig. 1**). The first cluster (C1) included localities with semiarid, temperate-continental climate or subcontinental climates. These habitats appear in gorges of rivers Gradac, Suvaja and Studenica as well as at Domogled in Romania. This cluster also included populations from Bulgaria (BU-Trojanski prolaz - central part of Stara planina) and the population from Mt. Stara planina in the E part of Serbia. The second cluster (C2) contained localities with continental mountain climates (SR-Besna Kobila, SR-Radan, SR-Basarski kamik, SR-Pljačkovica and MA-Treskavec). The third cluster (C3) includes localities with humid mountain climate (SR-Treska, SR-Nebeske stolice and MA-Mavrovo).

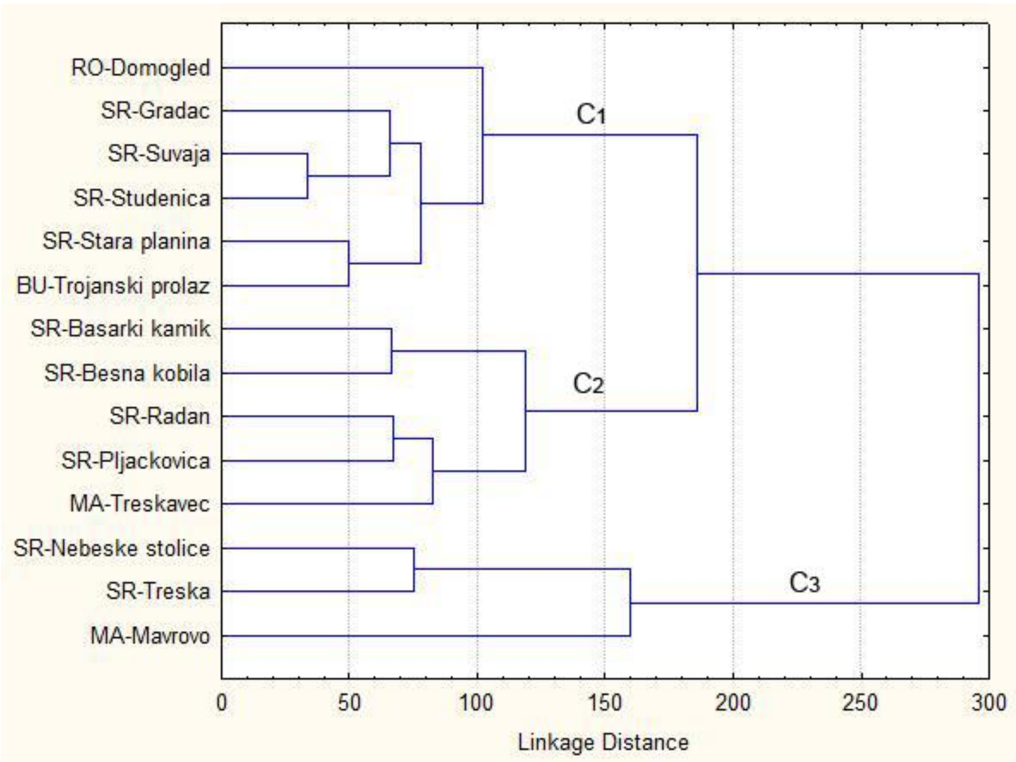

Fig. 1. Results of cluster analysis for populations of *J. heuffelii* based on habitat climatic characteristics (C1, C2, C3, climate type, for details see **Tab. 2.**)

Table 3. Minimal, average and maximal value of 19 bioclimatic parameters of the studied localities. C1, C2 and C3 represent climate types correspond to the groupings obtained from the cluster analysis of bioclimatic parameters (see Fig. 1). The bioclimatic variables that were used as predictors in regression analysis are marked with asterisk (*).

Bioclimatic parameters	**C1**			**C2**			**C3**		
	semi -arid moderately continental climate			continental mountain climate			humid mountain climate		
	Min	Avg	Max	Min	Avg	Max	Min	Avg	Max
Annual mean temperature (1)	3.37	7.71	11.33	3.30	7.74	9.72	2.87	4.23	4.98
Mean monthly temperature range (2) *	7.98	9.1	10.1	8.73	9.1	10.36	7.48	8.16	9.04
Isothermality (2/7) (* 100) (3) *	29.49	31.74	33.67	31.64	33.30	34.64	29.34	30.88	33.49
Temperature seasonality (STD * 100) (4) *	676.60	724.84	755.92	661.08	721.52	750.39	645.84	668.49	691.64
Max. temperature of the warmest month (5)	17.2	22.65	26.8	17.6	23.48	24.1	16.4	18.3	19.6
Min. temperature of the coldest month (6)	-3.2	-5.97	-8.9	-4.4	-5.93	-9	-7.4	-8.1	-9.1
Annual temperature range (5–6) (7) *	26.1	28.62	30.2	26.6	29.4	30.4	25.5	26.4	27
Mean temperature of the wettest quarter (8)	9.6	14.61	18.45	3.93	10.29	13.55	-1.3	6.36	11.32
Mean temperature of the driest quarter (9) *	-0.92	3.45	9.58	1.8	11.27	16.52	-2.75	6.06	12.63
Mean temperature of the warmest quarter (10)	11.48	16.36	20.17	11.25	16.35	18.58	10.85	12.26	13.12
Mean temperature of the coldest quarter (11)	-4.95	-1.42	2.01	-3.3	-1.34	0.17	-5.38	-4.02	-2.9
Annual precipitation (12) *	778	815.17	849	606	665.75	742	950	1001.67	1045
Precipitation of the wettest month (13)	87	100.33	121	68	76.75	84	104	113.67	127
Precipitation of the driest month (14) *	42	50	55	40	42.75	46	56	62.67	69
Precipitation seasonality (CV) (15) *	17.57	23.13	34.40	16.67	19.10	21.29	15.13	18.9	26.24
Precipitation of the wettest quarter (16)	255	269.13	310	172	200.75	231	285	312.33	348
Precipitation of the driest quarter (17)	147	162.17	175	127	136.25	147	178	202	222
Precipitation of the warmest quarter (18) *	220	245.17	291	136	161.75	204	179	235	272
Precipitation of the coldest quarter (19) *	158	177.5	187	147	160	194	218	255	310

Table 4. Sumary statistics of regression (R^2) for independent bioclimatic, geographical and geological variables

Acronym	ALT	ASP	SLO	BIO2	BIO3	BIO4	BIO7	BIO8	BIO9	BIO12	BIO13	BIO14	BIO15	BIO18	BIO19
Ros_D	0.07**	0.02	0.01	0.02	0.07**	0.05	0.00	0.26	0.11	0.01	0.00	0.05	0.01	0.16	0.02
LeRos_N	0.26*	0.13*	0.02	0.25*	0.13*	0.19*	0.28*	0.08**	0.01	0.02	0.00	0.04	0.02	0.01	0.02
LeRos_L max	0.09*	0.02	0.01	0.00	0.05	0.13*	0.02	0.22*	0.01*	0.00	0.03	0.00	0.09*	0.16*	0.09*
LeRos_W max	0.12*	0.02	0.00	0.00	0.04	0.16*	0.04	0.20*	0.19*	0.01	0.05	0.02	0.03	0.14*	0.02
Apex_D1	0.06	0.02	0.00	0.00	0.00	0.07	0.02	0.10*	0.04	0.00	0.00	0.00	0.02	0.04	0.04
LeRos_Sp_L	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.01	0.00	0.01	0.02
LeRos_Ci_L	0.00	0.01	0.07	0.00	0.01	0.04	0.01	0.00	0.01	0.00	0.02	0.02	0.10*	0.00	0.02
LeRos_Ed_W	0.03	0.04	0.04	0.00	0.00	0.01	0.01	0.03	0.01	0.00	0.03	0.07**	0.14*	0.01	0.01
Ste_H	0.17*	0.04	0.01	0.00	0.04	0.17*	0.05	0.30*	0.12*	0.00	0.00	0.04	0.01	0.08**	0.05
LeSte_N	0.00	0.01	0.00	0.06	0.12*	0.00	0.01	0.05	0.07**	0.03	0.00	0.16*	0.13*	0.03	0.00
MidLeSte_L	0.00	0.01	0.00	0.03	0.05	0.00	0.01	0.04	0.03	0.00	0.02	0.00	0.04	0.10*	0.02
MidLeSte_W	0.00	0.00	0.01	0.09*	0.19*	0.02	0.02	0.10*	0.20*	0.06	0.07**	0.09*	0.00	0.22*	0.00
Apex_D2	0.05	0.00	0.01	0.00	0.05	0.07**	0.01	0.23*	0.08**	0.01	0.02	0.01	0.04	0.07**	0.10*
Sep_L	0.03	0.00	0.09*	0.00	0.00	0.01	0.00	0.08**	0.02	0.06	0.10*	0.00	0.06	0.00	0.06
Sep_W	0.02	0.00	0.07	0.00	0.01	0.01	0.00	0.07**	0.00	0.01	0.00	0.00	0.00	0.01	0.03
Pet_L	0.22*	0.06	0.04	0.02	0.01	0.19*	0.09*	0.31*	0.05	0.01	0.01	0.02	0.03	0.03	0.06
Pet_W	0.01	0.01	0.04	0.03	0.08**	0.01	0.00	0.04	0.04	0.01	0.00	0.11*	0.09*	0.01	0.00
Fil_L max	0.23*	0.11*	0.00	0.02	0.00	0.17*	0.08**	0.34*	0.08**	0.00	0.01	0.05	0.05	0.06	0.03
Ova_H	0.23*	0.13*	0.04	0.01	0.01	0.15*	0.07**	0.31*	0.04	0.00	0.00	0.03	0.02	0.04	0.03
Sty_H	0.29*	0.15*	0.00	0.04	0.00	0.29*	0.16*	0.36*	0.10*	0.00	0.00	0.02	0.01	0.09*	0.07**
CenToo_H	0.02	0.00	0.05	0.01	0.00	0.00	0.01	0.02	0.01	0.02	0.09*	0.00	0.12*	0.03	0.01
LatToo_H	0.01	0.04	0.01	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.09*	0.00	0.17*	0.08**	0.00
Fru_H	0.31*	0.14*	0.02	0.03	0.00	0.22*	0.12*	0.42*	0.06	0.00	0.02	0.05	0.07	0.04	0.05
Fru_W	0.31*	0.14*	0.04	0.03	0.00	0.21*	0.12*	0.40*	0.05	0.00	0.02	0.04	0.07	0.03	0.05
Rost_L	0.25*	0.37*	0.08**	0.04	0.00	0.26*	0.13*	0.19*	0.00	0.00	0.07**	0.00	0.21*	0.11*	0.06
FloBra_N	0.03	0.02	0.00	0.01	0.05	0.03	0.00	0.11*	0.07**	0.01	0.01	0.03	0.00	0.09*	0.00
Flo_N	0.09	0.05	0.00	0.01	0.00	0.06	0.03	0.10*	0.04	0.00	0.01	0.00	0.01	0.04	0.01
Fil_L max	0.11	0.00	0.00	0.00	0.06	0.13*	0.02	0.38*	0.20*	0.02	0.07	0.02	0.11*	0.06	0.10*
See_L	0.07**	0.08**	0.02	0.00	0.00	0.02	0.01	0.07**	0.06	0.02	0.06	0.00	0.06	0.09*	0.00
See_W	0.13*	0.03	0.00	0.05	0.02	0.05	0.06	0.08**	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Cos_W	0.02	0.00	0.02	0.01	0.00	0.01	0.01	0.07	0.01	0.01	0.17*	0.03	0.41*	0.01	0.00
Nect_W	0.08**	0.10*	0.03	0.17*	0.13*	0.05	0.14*	0.00	0.06	0.06	0.11*	0.02	0.04	0.12*	0.02
Nect_H	0.04	0.04	0.00	0.00	0.01	0.07**	0.03	0.04	0.05	0.03	0.03	0.03	0.00	0.04	0.00
Nect-Ang	0.04	0.01	0.03	0.08**	0.08**	0.01	0.05	0.00	0.01	0.05	0.04	0.04	0.00	0.05	0.01

Abbreviations: ALT-altitude, ASP- aspect, SLO-slope, BIO- bioclimatic characteristics (see Table 3)

* *$p < 0.05$, ** $p < 0.01$*

The analysis of the three clusters regarding the values of bioclimatic parameters (**Tab. 3**) shows that type C1 is characterized by the highest values of BIO1 bioclimatic parameter, the mean annual temperature within the range 3.37-11.33 °C. C2 type has shown variation in this character in range of 3.30-9.72 °C, while C3 climate type has shown the lowest values of this parameters, 2.87 - 4.98 °C (**Tab. 3**). A similar trend was noticed in bioclimatic parameters BIO5, BIO6, BIO8, BIO10 and BIO11, while in the bioclimatic parameter BIO9 (mean temperature of the driest quarter) the highest values were recorded for the second type of climate C2 (1.8-16.52 °C), followed by the third type C3 (–2.75 -12.63 °C) while the lowest values were recorded in the first climate type C1 (–0.92-9.58 °C). The analysis of these three clusters according to bioclimatic factors (**Tab. 3**) indicated that the greatest differences between clusters were present in the amount of precipitation, as measured by the factors Annual precipitation (BIO12), Precipitation of the driest month (BIO14) and Precipitation of the wettest quarter (BIO16). The largest amount of precipitation was present in the third cluster, the second had the lowest amount of precipitation, while the first cluster was intermediate. Considering the temperature, the highest values were recorded in canyons and river gorges (C1) and the lowest values in the third cluster (C3).

There is an important question: to which extent do bioclimatic factors in analyzed habitats cause the differentiation in populations? The answer to this question may be provided by cluster analysis including both the bioclimatic characters and the morphological characteristics of individuals from the analyzed populations. If the position of populations in the cluster analysis of bioclimatic factors matches the position obtained from morphometric characters, it may be concluded that such grouping is a result of impact by various bioclimatic factors and vice versa (Kuzmanović et al., 2011).

As cluster analysis of bioclimatic factors have shown that the study area is strongly differentiated into three main clusters: one with semiarid temperate continental or subcontinental climate, another with continental mountain climate and the third cluster with humid mountain climate, it might be expected that the cluster analysis of morphological characters would also produce three main clusters. However, the analysis has shown that within the cluster analysis of morphological characters all populations were divided into four clusters (Nikolić et al., 2015b), while the distribution of individual clades (populations) was not matched to the distribution of populations obtained in the cluster analysis of bioclimatic parameters. This type of distribution indicates that bioclimatic factors are not the single reason for such morphological differentiation of populations.

Results of the cluster analysis performed solely on mountain populations were similar. The effect of microclimatic differences caused by orography on morphological differentiation was avoided in this analysis, as all mountain populations inhabit open grassland habitats from classes Festuco-Brometea and Elyno-Seslerietea. Although both cluster analyses, of morphological characters and bioclimatic parameters, have shown separation into two groups, the placement of individual populations into these groups is different, indicating that bioclimatic parameters are not crucial in differentiation of populations (Nikolić et al., 2015b).

Regression analysis (Linear regression)

Regression analysis showed that orographic factors (altitude, aspect and slope) influenced the morphological characters of the species *J. heuffelii*. The geological substrate was not analyzed, as this factor showed a high level of co-linearity with other factors (**Tab. 4**).

Altitude had the greatest influence on the following morphological characters: length of rostrum, height of fruit, height of stylus, width of fruit, number of leaves in rosette, length of the longest branch in floral maturation stage, length of the longest filament. Exposition aspect is also one of the key abiotic factors, with the greatest impact on morphological characters of reproductive organs (ovary stylus, fruit and nectary).

The morphological differentiation of the analyzed populations is also highly influenced by the bioclimatic factors precipitation and temperature. The greatest correlation with the analyzed characters was shown by Mean temperature of driest quarter (BIO8) and Temperature seasonality (BIO4). These two bioclimatic factors have the highest influence on the same characters that are highly influenced by altitude. There is a somewhat smaller but still significant impact of Precipitation seasonality (BIO15), with the greatest impact on following characters: length of petal, height of ovary, height of the stem to the lowest flower branch, width of the nectary, width of the middle leaf on the stem, width of the largest leaf, length of the largest leaf, width of the central longitudinal fold (costa). There is a somewhat smaller but still significant impact of Precipitation of warmest quarter (BIO18) and Mean Temperature of driest quarter (BIO9).

The geographic variability in plant morphology is the result of phenotypic changes expressed as an answer to local ecological conditions, genetic variability and evolution among the populations, as well as the biogeographic history of species (Ellison et al., 2004). Some of the morphological characteristics have genetic origins, for example leaf shape, but they may also be strongly influenced by local conditions in which the plants develop (Thompson, 1991; Schlichting & Pigliucci, 1998). Altitude is a factor with significant impact on variability of morphological characteristics of analyzed populations, as shown by regression analysis. Change in altitude causes changes in other factors, including temperature, air humidity, precipitation and partial pressure of gasses in the atmosphere, causing the adaptive response in plants and therefore also changes in morphology and physiology (Körner, 1999). Altitude may have a strong impact on both leaf morphology and physiology in individuals from various populations within the same species (Hovenden & Vander Schoor, 2004). With increase of altitude the length and width of leaves generally decrease (Körner *et al.*, 1986), while thickness of leaves increases (Körner *et al.*, 1989; Roderick *et al.*, 2000). Regression analysis has supported the hypothesis that altitude has the greatest impact on variability of morphological characters in *J. heuffelii* populations.

Conclusion

The regression analysis has shown that morphological characteristics are under stronger influence by seasonal dynamics in temperature and precipitation than by the total amount of precipitation or mean annual temperature, which are the most commonly analyzed climatic factors for any geographic area. In addition to altitude, the orographic factors with the strongest impact on morphological characters of species *J. heuffelii* are exposition and slope of terrain. The bioclimatic parameters may also influence the variability in morphological characters. The greatest impact was recorded in mean temperature of wettest quartile (BIO8) and temperature seasonality (BIO4). They are mostly influencing the following characters: height and width of fruit, height of stylus, length of rostrum, number of leaves in the rosette, length of the longest flowering branch and length of longest filament of the stamen.

The seasonal character of precipitation (BIO15) was shown to influence size of leaves, height of stem and reproductive characters: length of petal, height of ovary and width of nectary.

These results suggest that temperature conditions and precipitation may contribute to plant phenotype in various habitat types. This trend was also recorded in the populations from canyons and river gorges with C1 type of climate. Populations with the highest value of BIO15 parameter (seasonality of precipitation) show greater dimensions of leaves than the populations from localities with C2 and C3 types of climate, where values of BIO15 parameter are lower.

It remains to be determined if the large morphological variability of *J. heuffelii* populations in the territory of central Balkans and Southern Carpathians was caused by phenotype plasticity or by genetically caused characteristics. The ongoing molecular analyses will help in solving this question.

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