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Morpho-anatomical differentiation of the species *Teucrium montanum* (Lamiaceae) in the Central Balkan Peninsula

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ABSTRACT: Inter-population differentiation of the species *Teucrium montanum* was analyzed on the basis of morpho-anatomical variability of its thirteen populations distributed between 60 and 1750 m above sea level in the Mediterranean and Continental region of the central Balkan Peninsula.

Descriptive statistics were performed for each of 28 continuous quantitative characters related to leaf and stem morphology and anatomy. The hypothesis of morphological separation of populations was tested using canonical discriminant analysis (CDA), and discriminant function analysis was used to estimate the contribution of individual characters to overall discrimination. The discrimination between groups in CDA was predominantly based on characteristics of the external structure on the leaf surface, while the internal structure of the leaf and stem did not show such significant differences between the 13 populations.

The morpho-anatomical analysis of plants from these populations has confirmed that the species *T. montanum* belongs to evergreen microphyllic xeromorphic semi-bushes. Statistical analysis revealed four group of populations with significant morphological differentiation. One part of the observed anatomical variability could be explained as an adaptive response to different geographical and recent environmental factors, and another part seemed to be caused by genetic or evolutionary factors.

Key words: *Teucrium montanum,* evergreen shrub, morphology, anatomy, indumentums, differentiation.

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INTRODUCTION

T. montanum L. is distributed in southern and central Europe, to Holland in the north, and from Ukraine to the west (Tutin & Wood 1976). It is also distributed in Algeria in Africa (Greuter 1986), and in Asia Minor (Diklić 1974). In the Balkan Peninsula, it is widely distributed, extending from the Montenegro coast in the south-west to the Danube river in the north-east, and from the Adriatic coast to altitudes of over 2100 m a. s. l. in the Dinaric mountains (Lakušić 2000).

T. montanum is an evergreen suffruticose caespitosa chamaephytes (fo semp Mi-MesCh suffrut caesp). The species have a preference for limestone and a soil derived from dolomitic rock, though it is equally vital on serpentinites, and on acid siliceous soil. Previous physiological-ecological (Pavlović 1975) and morpho-anatomical research of *T. montanum* from different habitats has shown that this species possesses a pronounced phenotype plasticity manifested through more- or less-expressed xeromorphic characters (Stevanović & Stevanović 1985).

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The species inhabit altitudinal ranges, from the coastal area up to 2100 m a. s. l., with the highest number of occurrences in the zone between 500 and 1000 m. Their ecological optimum is in the vegetation of continental rocky grounds (*Festuco-Brometea)* and xerophyllous deciduous forests (*Querco-Fagetea* pro parte). It is also relatively common in the vegetation of open coniferous forests (*Pinetea nigrae-heldreichi*), alpine and subalpine grasslands (*Festuco-Seslerietea*) and chasmophytic vegetation (*Asplenietea rupestris*). Rarely it inhabits vegetation of Mediterranean rocky grounds (*Cymbopogono-Brachypodietea*), garigue (*Cisto-Ericetea*) and Mediterranean evergreen forests (*Quercetea ilicis*), as well as dark boreo-montane coniferous forests (*Vaccinio-Picetea*) and alpine and subalpine screes (*Drypetea spinosae*). Quite exceptionally, rare individuals of *T. montanum* have been recorded in wet meadows (*Molinio-Arrhenatheretea)* and hygrophyllous deciduous salix-populus forests (Lakušić 2000).

Due to its high morphological variability, *T. montanum* represents a complex of more or less well-defined infraspecific taxa, some of which were basically described as separate species. Currently, there is a wealth of species and infraspecies taxa connected within *T. montanum*: *T. supinum* L., *T. skorpilii* Vel., *T. helianthemoides* Adamović, *T. jailae* Juz., *T. praemontanum* Klokov, *T. pannonicum* A. Kerner *T. montanum* var. *parnassicum* Čel., *T. montanum* var. *hirsutum* Boiss., etc. However, regardless of the morphological specificities, recent literature treats all these taxa mostly as synonyms for the broadly defined species *T. montanum* (Tutin & Wood 1976).

Taking into account the pronounced morphological variability and heterogeneity of *T. montanum* habitats, the aim of this study was to quantify morphological variation among populations and to describe differentiations among populations based on multivariate statistics on characters related to the leaf and stem morphology and anatomy.

MATERIAL AND METHODS

Plant material and morpho-anatomical analysis. Morpho-anatomical analysis was carried out on plant samples from 13 populations collected in the sub-Mediterranean vegetation of the Adriatic coastal region of Montenegro, and in the continental region of the central and northern part of the Balkan Peninsula (Serbia and Montenegro). All populations inhabited open grassland communities on limestone rocks. The collected plant material was either placed in a herbarium or fixed in 50% alcohol and deposited in the Herbarium of the Institute of Botany and Botanical Garden "Jevremovac", Faculty of Biology, University of Belgrade (BEOU) and Herbarium of the Department of Botany, Faculty of Pharmacy, University of Belgrade (HFF). Sample provenances and voucher numbers are given in Table 1.

Anatomical sections of leaves and stems were preserved on permanent slides, prepared by a standard method for light microscopy. Epidermal peels (10 samples per population), for the surface structures were prepared using Jeffrey's solution.

All morpho-anatomical measurements were made with the Image Analyzer System Ozaria 2004 and data processed with the statistical package Statistica 4.5 for Windows. For each of the quantitative characters, 30 leaf samples and 10 stem samples were obtained from different individuals belonging to each of the 13 populations analyzed.

Twentyeight quantitative characters for statistical analysis were grouped into three categories: I. Leaf anatomy characters (19); II. Leaf shape characters (4) and III. Stem anatomy characters (5). Characters included in the analysis are listed in Table 2.

Statistical analysis. For each of the quantitative characters, a univariant statistical analysis was performed on the basis of the following parameters: mean, minimum, maximum, standard deviation and standard error of the mean. The hypothesis of morphological separation of individual populations and biogeographical groups of population was tested using canonical discriminant analysis (CDA) conducted on the resulting data matrix comprising 21 characters, after character reduction and standardization to zero mean and unit variance. Character reduction was envisaged by computing pair-wise Spearman correlations and retaining only one of the character pairs with absolute values of correlation coefficients exceeding 0.8. Characters included in the CDA are listed in Table 3. The CDA for individual populations was performed with 13 *a priori* defined groups × 420 measurements × 21 characters, while CDA for biogeographical groups of populations was performed with 6 *a priori* defined groups × 420 measurements × 21 characters. Biogeographical groups were defined according to biogeographical regionalization of the Balkan Peninsula defined by Stevanović (1995, 1996). Informal names of biogeographical groups "submediterranean", "illyrian", "moesian", "oromediterranean", "oroillyrian" and "oromoesian", correspond to the formal names of biogeographical provinces and regions explained in Table 1. Discriminant function analysis (Table 3) was carried out to estimate the contribution of individual characters to overall discrimination. Canonical scores for each case were calculated with the aim to measure distances between individuals, and a scatter plot of canonical scores

Table 1. Sample provenances and voucher numbers of investigated plant material.

	Locality	Population	Biogeographical group	Biogeography	Coordinate	Habitat	Voucher
1	MONTENEGRO: Canyon of Cijevna	Cijevna	submediterranean	Adriatic province of Submediterranean region	42. 39 N, 19. 39 E	rocky grounds, limestone, 100 m a. s.l.	BEOU-771/90
2	MONTENEGRO: Canyon of Morača, Dromira	Morača	submediterranean	Adriatic province of Submediterranean region	42. 61 N, 19. 38 E	rocky grounds, limestone, 150 m a. s. l.	HFF-2625
3	MONTENEGRO: Canyon of Sušica	Sušica	illyrian	Illirian province of Central European region	43. 19 N, 18. 99 E	rocky grounds, limestone, 1300 m a.s.l.	BEOU-613/94
4	MONTENEGRO: Canyon of Tara, Ćurovac	Tara	illyrian	Illirian province of Central European region	43. 19 N, 19. 08 E	rocky ground, limestone, 1400 m a.s.l.	BEOU-1078/96
5	MONTENEGRO: Mt. Prokletije, Ropojana	Prokletije	illyrian	Illirian province of Central European region	42. 50 N, 19. 83 E	screes, limestone, 1100 m a.s l.	BEOU-250/94.
6	SERBIA: Canyon of Derventa	Derventa	illyrian	Illirian province of Central European region	43. 96 N, 19. 36 E	rocky grounds, limestone, 300 m a. s. l.	HFF-2641
7	SERBIA: Canyon of Trešnjica	Trešnjica	illyrian	Illirian province of Central European region	44. 14 N, 19. 60 E	rocky grounds, limestone, 800 m a. s. l.	BEOU-44/93
8	SERBIA: Miljkovačka gorge	Miljkovac	moesian	Moesian province of Central European region	43.45 N, 21.90 E	rocky grounds, limestone, 500 m a. s. l.	HFF-2650
9	SERBIA: Sićevačka gorge, above sv. Petka	Sićevo	moesian	Moesian province of Central European region	43. 34 N, 22. 14 E	rocky grounds, limestone, 900 m a. s. l.	HFF-2635
10	SERBIA: Đerdap gorge, Kazan	Djerdap	moesian	Moesian province of Central European region	44. 62 N, 22. 28 E	rocky grounds, limestone, 90 m a. s. l.	BEOU-1716/94
11	MONTENEGRO: Mt. Orjen, Orjenske lokve	Orjen	oromediterranean	Dinaric province of of South European mountan region	42. 56 N, 18. 55 E	subalpine pastures, limestone, 1600 m a.s.l.	HFF-2643
12	MONTENEGRO: Mt. Durmitor, Inđini dolovi	Durmitor	oroillyrian	Dinaric province of Central and South European mountan region	43. 14 N, 19. 07 E	subalpine pastures, limestone, 1750 m a.s.l.	HFF-2640, 2647
13	SERBIA: Mt. Rtanj, Šiljak	Rtanj	oromoeisan	Balkan province of Central and South European mountan region	42. 39 N, 19. 39 E	subalpine pastures, limestone, 1550 m a.s.l.	HFF-2637

Table 2. Characters used for morphometric analysis of *Teucrium montanum*. Descriptive statistics for all measured morphometric characters. Abbreviations: **N** - valid number of measuremens, **Mean** – average value, **Min** - minimum, **Max** - maximum, **Std.Dev**. standard deviation, **Std.Err.** standard error of the mean, * - character with absolute values of Spearman correlation coefficients >0. 8 and excluded from Discriminant Function Analysis

	N	Mean	Min	Max	Std.Dev.	Std.Err.
Height of adaxial epidermal cells	420	22.02	12.99	36.01	4.28	0.21
*Thickness of palisade tissue	420	127.57	48.21	225.08	29.87	1.46
Thickness of adaxial palisade tissue	420	122.96	48.21	225.08	34.37	1.68
Thickness of spongy tissue	121	35.67	12.99	73.40	13.02	1.18
Thickness of abaxial palisade tissue	72	26.91	10.47	43.23	7.68	0.90
Height of abaxial epidermal cells	420	10.69	5.19	26.26	2.67	0.13
*Number of palisade layers	420	3.20	2.00	5.00	0.67	0.03
Number of adaxial palisade layers	420	3.05	2.00	5.00	0.80	0.04
Number of abaxial palisade layers	235	0.28	0.00	1.00	0.45	0.03
Surface area of adaxial epidermal cells	420	1621.0	461.88	4763.0	674.55	32.91
Surface area of adaxial stomata	24	415.61	150.11	760.62	174.87	35.69
Number of adaxial stomata	420	1.21	0.00	21.95	3.62	0.18
Surface area of abaxial epidermal cells	246	732.68	277.57	1412.3	228.30	14.56
*Surface area of adaxial stomata	246	424.62	196.87	750.43	78.54	5.01
Number of abaxial stomata	359	227.47	109.74	334.71	44.31	2.34
Number of adaxial glandular hairs	420	16.94	0.00	53.99	12.85	0.63
Number of abaxial glandular hairs	420	69.24	0.00	142.69	39.53	1.93
Number of adaxial non-glandular hairs	420	102.33	11.57	286.41	73.90	3.61
Number of abaxial non-glandular hair	420	592.20	361.22	715.22	93.78	4.58
Leaf length	140	16.21	7.42	25.86	4.21	0.36
Distance between the largest leaf width point and the leaf top	140	5.51	1.38	12.29	2.08	0.18
*The largest width of the leaf	140	3.57	1.38	7.42	1.14	0.10
*Leaf surface area	140	43.22	10.97	124.72	22.35	1.89
The stem diameter	140	1213.3	759.2	2085.4	285.54	24.13
*The stem diagonal	140	1272.7	143.62	2183.0	357.37	30.20
The stem cortex thickness	140	163.54	80.21	460.92	43.72	3.70
*The stem vascular cylinder thickness	140	306.39	102.53	884.23	157.94	13.35
The stem pith diameter	140	156.84	47.85	359.58	57.74	4.88

(Fig. 1) was made to visualize the relationship between the *a priori* defined groups. Overall differences between the compared groups are presented as Mahalanobis distances, which are used for clustering on the basis of the UPGMA method. To establish relationships between morpho-anatomical and bioclimate variables, another cluster analysis (UPGMA) was performed to evaluate the bioclimatic differentiation between the habitats of the 13 populations. Each location was characterized by 19 bioclimatic parameters, extracted from the WorldClim set of global climate layers. The extraction of bioclimatic parameters was done with DIVA-GIS 7.5 software (Hijmans *et al.*, 2012). These statistical analyses were performed using Statistica 5.1 (StatSoft 1996).

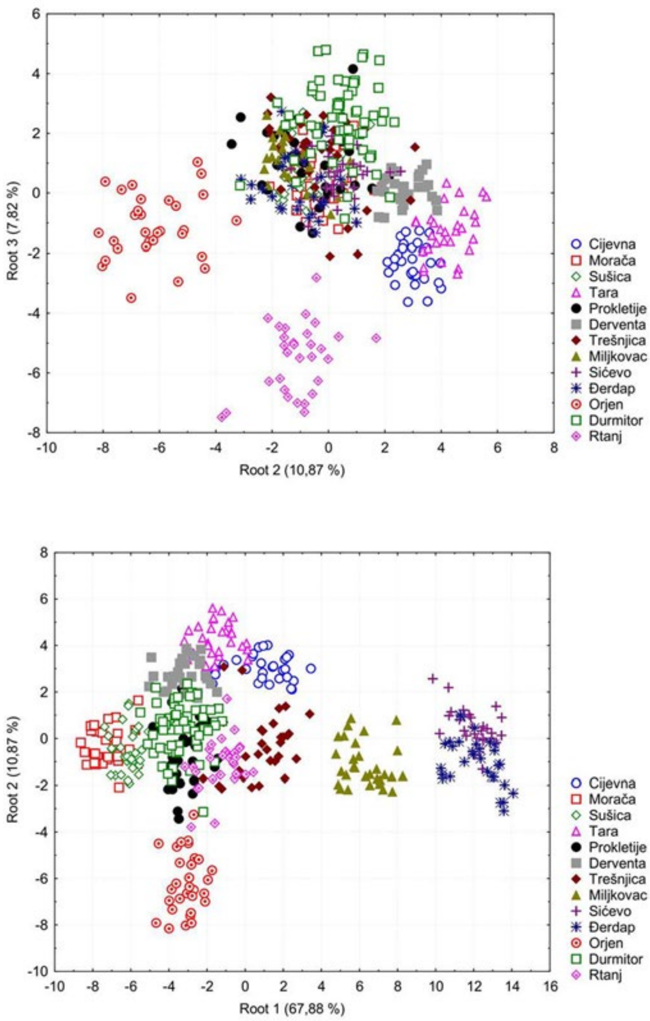


Fig. 1 Canonical discriminant analysis (CDA) of *Teucrium montanum* for individual populations.

RESULTS

Basic Morpho-anatomical Characteristics of T. montanum - The leaves of *T. montanum* are elliptic, from broad to narrow elliptical, or almost linear. In general, in all 13 populations the leaf length was between 12 and 26 mm, and the leaf width ranged between 2 and 6 mm. The leaf surface area varied between 24 and 125 mm^2. The leaf margin was entire and more or less enrolled towards the abaxial side of the leaf.

The leaf indumentum of all plants was composed of glandular and non-glandular hairs. Glandular hairs were peltate and capitate. Capitate hairs were with one or two stalk cells and a secretory head of one or two cells. Nonglandular hairs were unicellular and multicellular, uniseriate and unbranched. On the adaxial side of the leaf, non-glandular hairs dominated. The abaxial surface was white due to a dense indumentum of long, entwined, non-glandular hairs. In some populations both leaf surfaces were white.

The epidermis of adaxial and abaxial sides of the leaf was single-layered. The cuticle on the adaxial epidermis was thicker than on the abaxial epidermis. The outer epidermal cell walls were thickened, particularly in the adaxial epidermis, occupying 2/3 of the cell lumen. Anticlinal walls of epidermal cells on the adaxial and abaxial sides were undulated with more or less deep amplitudes.

The leaves were hypostomatic or hypoamphistomatic; the stomata anomocytic and diacytic.

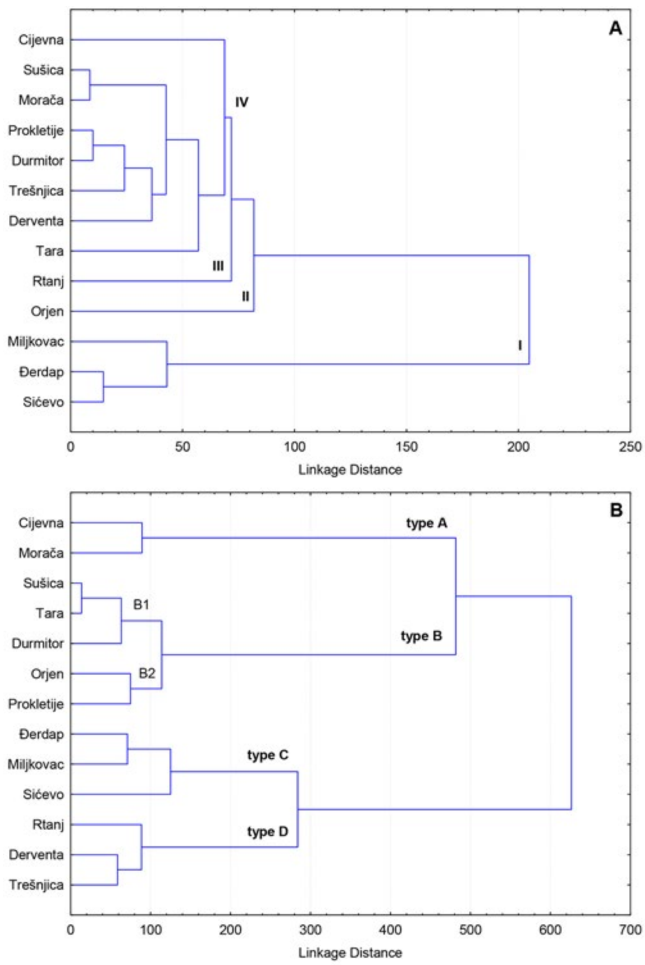
The mesophyll consisted of only palisade cells or was differentiated into palisade and spongy tissues. Idioblasts (oil cells) could be found above the xylem.

The stem structure in all populations was more or less uniform. The stem surface indumentum had the same structure as the indumentum of the leaf. In cross-section, the stem was round with a two- or three-layered hypodermis. A pericycle was made of bundles of sclerenchymatous elements and small groups of parenchyma cells. The vascular elements were located in concentric circles. The center of the stem was filled with pith parenchyma (for more details of the morpho-anatomy of *T. montanum* see Lakušić 2000; Lakušić *et al.* 2010).

Descriptive statistics are presented in Table 2.

Statistical Analysis of Morphometric Data - The CDA largely supported the hypothesis of morpho-anatomical separation of some groups of populations.

The CDA for individual populations (13 *a priori* defined groups × 420 measurements × 21 characters) shows that the first three discriminant axes explained 86.67 % of discrimination between groups (Fig. 1). On discriminant axis 1 (explaining 67.88 % of discrimination), the scores of individuals from lowland populations from eastern Serbia (Đerdap, Sićevo, Miljkovac) were separated from scores of all other individuals from the remaining populations. On discriminant axis 2 (explaining 10.87 % of discrimination), the scores of individuals from subalpine grasslands from Mt. Orjen formed an almost separated group. On discriminant axis 3 (explaining 7.82 % of discrimination), the individuals from subalpine grasslands from Mt. Rtanj were completely separated (Fig. 1). The scores of individuals of other populations, on the first three discriminant axes were grouped and strongly overlapped, suggesting their high morpho-anatomical similarity. An identical pattern of differentiation between individual populations was also clearly observed on the basis of the overall Mahalanobis distances presented in Fig. 2A.



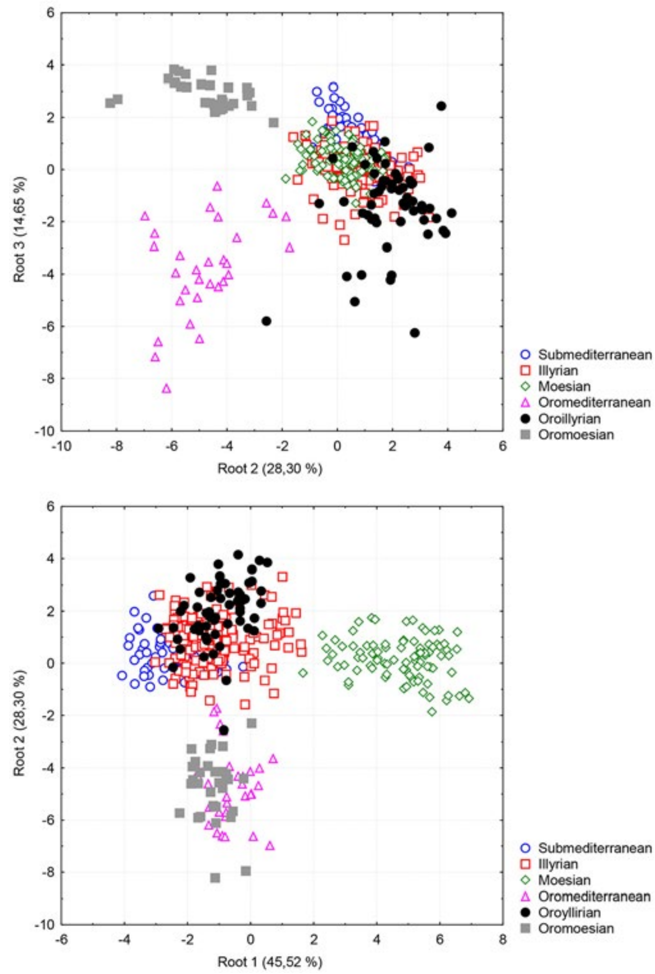


Fig. 2 Cluster analysis (UPGMA) of *Teucrium montanum* for individual populations. A) analysis for morphological data, and B) analysis for bioclimatic data

Fig. 3 Canonical discriminant analysis (CDA) of *Teucrium montanum* for biogeographical groups of populations.

The CDA for biogeographical groups of populations (6 *a priori* defined groups × 420 measurements × 21 characters) showed that the first three discriminant axes explained 88.47 % of discrimination between the groups (Fig. 3). On discriminant axis 1 (explaining 45.52 % of discrimination), the scores of individuals from the "moesian" group were completely separated. The scores of individuals from "oromediterranean" and "oromoesian" groups were separated on the negative part, while the scores of individuals from "submediterranean", "illyrian" and "oroillyrian" groups were separated on the positive part of discriminant axis 2 (explaining 28.3 % of discrimination). Finally, on discriminant axis 3 (explaining 14. 65 % of discrimination), the scores of individuals from "oromediterranean" and "oromoesian" groups were completely separated (Fig. 3). As in CDA for individual populations, the cluster analysis based on Mahalanobis distances showed an identical pattern of differentiation between biogeographical groups of populations (Fig. 4).

Thus, CDA on both levels (individual populations and biogeographical groups of population) resolved four groups of morpho-anatomically separated populations: 1st group (Đerdap, Sićevo, Miljkovac - "moesian" group), 2nd group (Rtanj - "oromoesian" group), 3rd group (Orjen - "oromediterranean" group) and 4th group (Cijevna, Morača, Sušica, Tara, Derventa, Trešnjica, Prokletije, Durmitor - "submediterranean", "illyrian" and "oroillyrian" groups)

Discriminant function analysis showed that characters of the indumentum, especially adaxial non-glandular hairs had a dominant contribution to the overall discrimination. Most of the discrimination was contributed by the number of abaxial glandular hairs, number of abaxial non-glandular hairs, surface area of adaxial epidermal cells, number of adaxial stomata and number of adaxial glandular hairs (Table 3, Fig. 5). This would suggest that the discrimination between groups in CDA was predominantly based on characteristics of the external structure on the leaf surface, while the internal

Table 3. Discriminant Function Analysis Summary. Wilks lambda is a multivariate generalisation of the univariate F-distribution; F-remove represents a measure of the extent to which a variable makes a unique contribution to the prediction of a group membership. p-values < 0.05 are printed in bold.

	Wilks Lambda	F-remove 13,379	p-level
Height of adaxial epidermal cells	0.000006	5.80	**0.0000**
Thickness of adaxial palisade tissue	0.000007	14.82	**0.0000**
Thickness of spongy tissue	0.000005	3.25	**0.0001**
Thickness of abaxial palisade tissue	0.000005	3.81	**0.0000**
Height of abaxial epidermal cells	0.000005	4.42	**0.0000**
Number of adaxial palisade layers	0.000006	7.30	**0.0000**
Number of abaxial palisade layers	0.000005	4.72	**0.0000**
Surface area of adaxial epidermal cells	0.000010	33.80	**0.0000**
Surface area of adaxial stomata	0.000005	4.24	**0.0000**
Number of adaxial stomata	0.000010	33.12	**0.0000**
Surface area of abaxial epidermal cells	0.000006	7.37	**0.0000**
Number of abaxial stomata	0.000008	23.33	**0.0000**
Number of adaxial glandular hairs	0.000010	30.80	**0.0000**
Number of abaxial glandular hairs	0.000015	66.73	**0.0000**
Number of adaxial non-glandular hairs	0.000123	750.22	**0.0000**
Number of abaxial non-glandular hairs	0.000012	44.09	**0.0000**
Leaf length	0.000005	3.92	**0.0000**
Distance between the largest leaf width point and the leaf top	0.000005	2.99	**0.0003**
The stem diameter	0.000006	6.89	**0.0000**
The stem cortex thickness	0.000005	3.12	**0.0002**
The stem pith diameter	0.000006	8.94	**0.0000**

structure of the leaf and stem did showed no significant differences between the 13 populations.

Cluster Analysis of Bioclimatic Data - Cluster analysis based on bioclimatic data (Fig. 2B) showed that four main "types" (clusters) could be differentiated: the habitats of the **Mediterranean climate** of lowland south-eastern Montenegro (type A), the habitats of the **transitional humid submediterranean-continental** climate of the mountain region of Montenegro (type B), the habitats of the **semiarid continental** climate of lowland eastern Serbia (type C), and the habitats of the **temperate continental** climate of Serbia (type D). The transitional humid submediterranean-continental type of climate showed a fine differentiation of varieties: continental (B1 – Durmitor, Sušica, Tara) and oromediterranean (B2 – Orjen, Prokletije) climate.

These four clusters of locations differed in several bioclimatic characteristics (Table 4). Generally, the Mediterranean climate (type A) was characterized by considerably warmer and more humid conditions. Namely, this climate type had a significantly higher annual mean temperature (BIO1), mean temperature of the driest (BIO9) and the warmest quarter (BIO10), positive minimum temperature of the coldest quarter (BIO10), and significantly higher annual precipitation (BIO12), as well as the precipitation of the coldest (BIO19) and wettest quarters (BIO16). In relation to the continental climates (types C and D), the transitional humid submediterranean-continental climate (type B) had a considerably higher mean temperature for the driest quarter (BIO9) and lower mean temperature for the wettest quarter (BIO8), as well as significantly higher annual precipitation (BIO12), and precipitation of the

Table 4. Mean values for bioclimatic variable for basic climate types resolved in cluster analyses of bioclimatic data (see Fig. 2B)

Bioclimatic parameters	Mediterranean	Transitional humid submediterranean-continental		Semiarid continental	Temperate continental
	Type A	Type B1	Type B2	Type C	Type D
Annual mean temperature (1)	13.68	5.88	6.90	9.65	7.88
Mean monthly temperature range (2)	9.84	8.38	7.98	9.71	8.84
Isothermality (2/7) (* 100) (3)	32.53	31.67	30.90	32.26	31.18
Temperature seasonality (STD * 100) (4)	742.52	663.79	659.05	762.25	722.46
Max. temperature of the warmest month (5)	30.15	20.03	20.90	25.77	22.67
Min. temperature of the coldest month (6)	-0.10	-6.37	-4.90	-4.30	-5.60
Annual temperature range (5–6) (7)	30.25	26.40	25.80	30.07	28.27
Mean temperature of the wettest quarter (8)	6.07	2.69	1.93	16.98	14.73
Mean temperature of the driest quarter (9)	22.89	13.68	14.94	1.49	0.08
Mean temperature of the warmest quarter (10)	22.89	13.88	14.94	18.67	16.49
Mean temperature of the coldest quarter (11)	4.67	-2.30	-1.08	-0.02	-1.24
Annual precipitation (12)	1563	1181	1233	644	889
Precipitation of the wettest month (13)	208	127	146	79	101
Precipitation of the driest month (14)	50	80	68	42	57
Precipitation seasonality (CV) (15)	39	14	23	22	20
Precipitation of the wettest quarter (16)	573	347	396	210	284
Precipitation of the driest quarter (17)	194	255	222	131	179
Precipitation of the warmest quarter (18)	194	261	222	185	259
Precipitation of the coldest quarter (19)	520	304	354	141	195

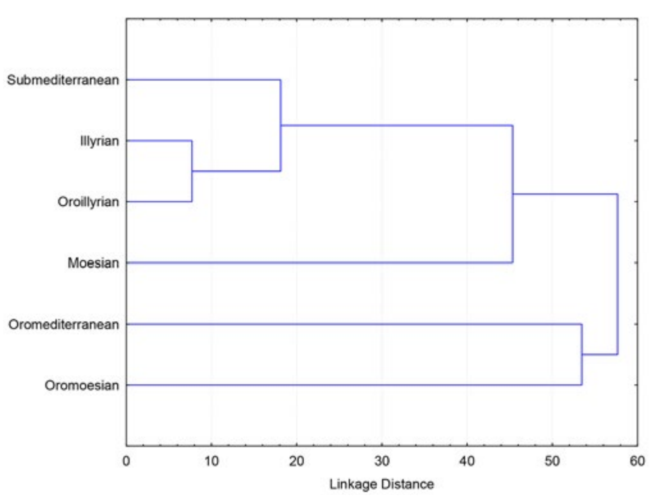


Fig. 4 Cluster analysis (UPGMA) based on Mahalanobis distances of *Teucrium montanum* for biogeographical groups of populations

coldest (BIO19) and wettest quarters (BIO16). Finally, the semiarid continental climate of lowland eastern Serbia (type C) was slightly warmer than the temperate continental climate (type D) and also with a considerably lower precipitation (BIO12-BIO19), especially during the warmest quarter (BIO18).

DISSCUSION

Morpho-anatomical analysis of plants from the thirteen distant populations confirmed that the species *T. montanum* is an evergreen, xeromorphic, microphyllic, semi-shrub (Stevanović & Stevanović 1985; Lakušić *et al.* 2010). As for most of the other species of the genus *Teucrium* (Lakušić 2000; Lakušić *et. al.* 2006, 2007, 2010), as well as in many other xeromorphic plants (Todorović & Stevanović 1994; Fahn & Cutler 1992; Kästner 1979; Yiotis *et al.* 2006), leaf shape and dimension, the nature of the leaf and stem indumenta, number of stomata, structure of epidermal cells, characteristics of

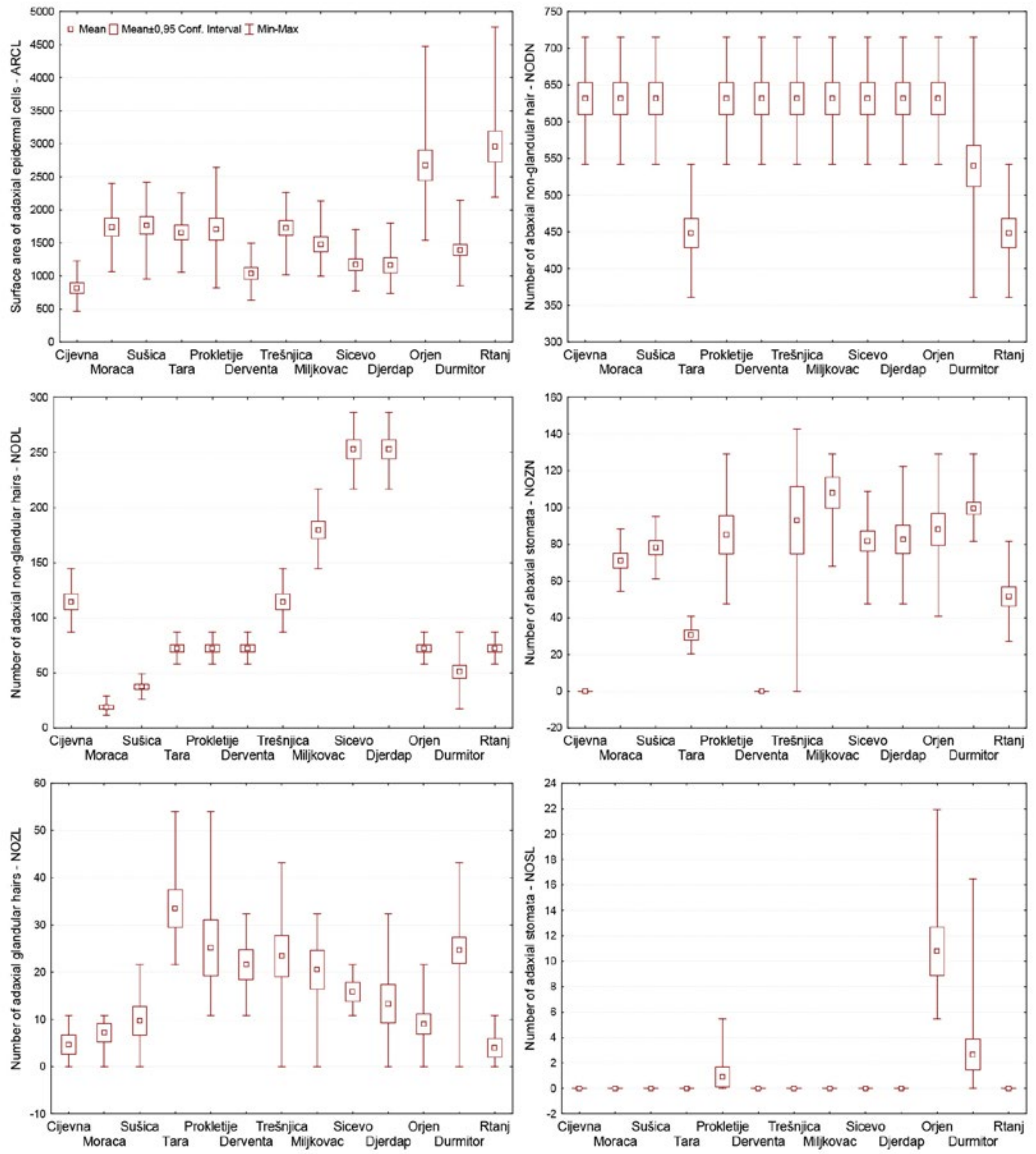


Fig. 5 Box and whisker plots of basic statistic parameters for characters with dominant contribution to the overall discrimination (see Table 3). Legend: Middle point – Mean, Box – Mean±0.95 Confidence Interval, Whisker – Minimum and Maximum

the mesophyll as well as the stem structure, represent the most prominent xeromorphic adaptations of the plants of these 13 populations of *T. montanum*.

The xeromorphic characteristics of this species were chiefly determined by the nature of the habitat that its populations inhabit. Irrespective of whether the habitats of the populations were located within a humid or perhumid climate variant, the precipitation quantity during the summer was extremely low, which consequently, in addition to high temperatures, provokes the occurrence of pronounced droughts that, in these habitats, could last one to two, and in extreme cases up to three months during the vegetation season.

The relationship of populations that were resolved into distinct groups generally corresponded to the biogeographical position of the populations, indicating that this grouping could be explained by geographical proximity and environmental similarity of their habitats. In addition, this showed that the observed anatomical variability represented an adaptive response to different geographical and environmental factors, as suggested also by Stevanović & Stevanović (1985). However, the discrepancy between the resolved morphological groups and climatic types, suggest that the recent climate was not having a determining influence on the differentiation. Namely, the cluster analyses, which included morphological and bioclimatic data, showed that only morphological group I (moesian) strictly corresponded to the climate type C (semiarid continental), while all other groups irregularly overlapped across the dendrogram (Fig. 2). Consequently, we conclude that the recent climatic conditions did not have a determining impact on the occurrence of distinct morphological groups of *T. montanum* in the Central Balkans. Also, the fact that different morphological groups inhabited the same open grassland communities on limestone rocks, suggests that we should not exclude the possibility that the anatomical differentiation in *T. montanum* could be caused by genetic or evolutionary factors.

Similar variations of morpho-anatomical characters have recently been registered within other ecologically plastic complexes such as *Edraianthus graminifolius* and *Edraianthus serpyllifolius* (Rakić *et al.* 2012), *Sesleria rigida* (Kuzmanović *et al.* 2011) and *Carex humilis* (Jakovljević et al 2013). It is important to point out, that within these complex groups, a few new cryptic species have recently been described (Surina *et al.* 2009; Lakušić *et al.* 2013b) and a few neglected plant taxa have recently been reaffirmed (Surina *et al.* 2009; Kuzmanović *et al.* 2013a, 2013b). Furthermore, many recent studies on cryptic and neglected species (Kučera *et al.* 2010; Mereda *et al.* 2011; Schönswetter & Schneeweiss 2009; Stevanović & Lakušić 2000; Lakušić *et al.* 2006; Lakušić & Conti 2004, Lakušić *et al.* 2013a) have confirmed the view that the phenomenon of cryptic speciation, i.e., the presence of two or more distinct species that were previously classified as a single species due to their morphological similarity (Bickford *et al.* 2007), is an important factor in assessing species diversity on the Balkan Peninsula. In this sense, it would not be too surprising if a number of previously-described and currently suppressed taxa within *T. montanum* represent a "good species". To confirm this opinion, it would be necessary to carry out a comparative morphological analysis of the reproductive organs, to perform experiments with cultivated plants, and to complete a comprehensive molecular and phylogenetic study.

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REZIME

Morfo-anatomska diferencijacija vrste *Teucrium montanum* (Lamiaceae) na prostoru centralnog Balkana

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Interpopulaciona diferencijacija vrste *Teucrium montanum* je analizirana na osnovu varijabilnosti morfo-anatomskih karakteristika lista i stabla u okviru 13 populacija koje su rasprostranjene između 60 i 1750 m nadmorske visine, u mediteranskom i kontinentalnom delu Centralnog Balkana (Crna Gora i Srbija).

Statističkom analizom je obuhvaćeno 28 kvantitativnih karaktera anatomije i morfologije lista i stabla. Hipoteza o morfo-anatomskoj diferencijaciji populacija testirana je kanonskom diskriminantnom analizom (CDA), dok je diskriminantnom funkcijskom analizom procenjen značaj pojedinačnih karaktera u diferencijaciji populacija. Razdvajanje grupa je pretežno zasnovano na karakterima površinske strukture listova, dok unutrašnja građa lista i stabla nije pokazala tako značajne uticaj na ustanovljene razlike između analiziranih populacija.

Na osnovu morfo-anatomskih analiza, utvrđeno je da vrsta *T. montanum* pripada grupi zimzelenih, mikrofilnih kseromorfnih polužbunova. Statistička analiza je pokazala postojanje četiri grupe populacija čija se varijabilnost, s jedne strane, može tumačiti kao adaptivni odgovor na različite ekološke uslove staništa kao i geografski položaj istraživanih populacija. S druge strane, deo ustanovljene varijabilnosti se izgleda može objasniti i odredjenim genetičkim i evolutivnim faktorima.

Ključne reči: *Teucrium montanum,* morfologija, anatomiija, indumentum, diferencijacija