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Leaf anatomy of *Carex humilis* (Cyperaceae) from Central and South Eastern Europe

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ABSTRACT: A detailed description of the total variability of leaf anatomical characters in different populations of the taxon *Carex humilis* Leysser from Austria, Hungary, Romania, Serbia, Bosnia & Herzegovina, Montenegro and Albania was made. Analyses were performed on the cross-section of 253 leaves collected from 18 populations. Statistical analyses were carried out for 33 quantitative characters related to the leaf anatomy. To identify the trends in anatomical differentiation, descriptive statistics, correlative variability and variations in regard to the geographical gradients, as well as analysis of variance (ANOVA) have been done.

Key words: *Carex humilis*, C & SE Europe, leaf anatomy

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INTRODUCTION

The genus *Carex* L. (commonly known as sedges) is one of the largest genera with species mainly distributed through the cold and temperate regions of the northern hemisphere. It belongs to the Cyperaceae, a family related to Poaceae and Juncaceae in many vegetative morphological features. Globally, the Cyperaceae is represented by 4500-5000 species in 100-105 genera (Goetghebeur 1987).

Together with the genera *Kobresia* Willd., *Uncinia* Pers. and *Schoenoxiphium* Nees, the genus *Carex* belongs to the tribe Cariceae of the sub-family Caricoideae Pax (Reznicek 1990). According to Dahlgren *et al*. (1985) *Carex* includes some 2000 species, 180 of them occurring in Europe (Chater 1980). Most species in the genus are most commonly associated with wet habitats.

The species *Carex humilis* Leysser range extends from S England, N Poland and S Russia southwards, but it is rare in the Mediterranean region (Chater 1980). Outside Europe, this species area covers marginal east parts of Asia (Meusel *et al*. 1965). In the Balkan peninsula and neighboring region, it inhabits different types of habitats. This species grows mostly in the vegetation of the hilly rocky grounds, mixed deciduous broadleaved woodland, as well as coniferous black pine forests and open alpine and subalpine high mountain pastures (classes Festuco-Brometea Br.-Bl. et R. Tx. 1943, Querco-Fagetea Br.-Bl. et Vilieger 1937, Erico-Pinetea Ht. 1959, Festuco-Seslerietea Barbero et Bonim 1969). This species occurs less frequently within the vegetation of the rocky crevices (Asplenietea trichomanis Br.-Bl. 1934 corr. Oberd. 1977) and open sandy grasslands (Festucetea vaginatae Soó 1968 emend. Vicherek 1972). Additionally, it is very tolerant to the type of geological substratum. It inhabits carbonate, serpentine as well as sandy substrates, in a very wide range of altitudes, between 87 and 2000 m a.s.l.

General anatomical characteristics of the genus *Carex* were studied in detail by Metcalfe (1971), but the species *C. humilis* was not further investigated. Therefore, the aim of this study was, on the basis of formal morphometric research, to describe the nature of variability of the anatomical structure of the leaves of *Carex humilis* and to establish existing trends in differentiation of its populations in C & SE Europe.

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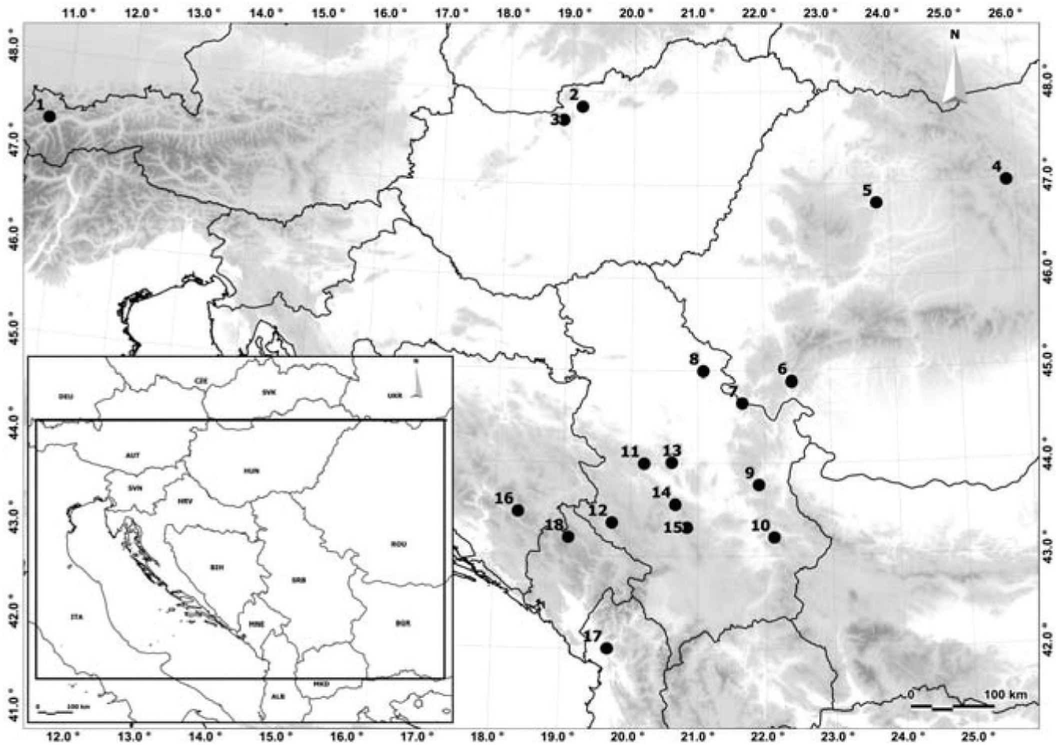

Fig. 1. Distribution of the populations of *Carex humilis* studied in this paper (1- AT-Imst; 2- HU-Mt Naszaly; 3- HU-Mt Pilis; 4- RO-Bicaz; 5- RO-Turda; 6- RO-Domugled; 7- RS-Đerdap's gorge; 8- RS-Deliblatska peščara; 9- RS-Mt Rtanj; 10- RS-Mt Suva planina; 11- RS-Ovčar-Kablar's gorge; 12- RS-Mileševka's gorge; 13- RS-Mt Vujan; 14- RS-Mt Studena planina; 15- RS-Mt Kopaonik; 16- BA-Gostović; 17- AL-Skadar; 18- ME-Mt Durmitor)

MATERIAL AND METHODS

Study Area and Plant Sampling. Eighteen populations of *Carex humilis* (253 individuals) from C & SE Europe were sampled for the analysis of leaf anatomical traits (for details, see Electronic Supplementary Material). The samples were taken from Serbia (9 populations, 146 individuals), Romania (3 populations, 34 individuals), Hungary (2 populations, 20 individuals), Austria (1 population, 10 individuals), Bosnia & Herzegovina (1 population, 15 individuals), Montenegro (1 population, 18 individuals) and Albania (1 population, 10 individuals) (Figure 1). All plant material was collected in the period 2009-2011.

The collected plant material was fixed in 50% ethyl–alcohol solution and voucher specimens were deposited in the Herbarium of the Institute of Botany and Botanical Garden "Jevremovac", Faculty of Biology, University of Belgrade – BEOU (Holmgren *et al.* 1990).

Leaf Cross-Section - Anatomical analyses of leaves were done on permanent slides, prepared by the standard method for light microscopy. Frozen sections of the leaves (253 samples) were cut on a Leica CM1859 cryostat (up to 45 μm thick). The sections were cleared in Parazone and thoroughly washed before staining in safranin (1% w/v in 50% ethanol) and alcian blue (1% w/v, aqueous). All slides were mounted in Canada balsam after dehydration. All anatomical measurements were made with Digimizer 3.7.0.; image analysis software.

Morphometric analysis - The measurements were performed on cross-sections of 253 leaves (each obtained from a different individual) collected in the field. A total of 33 characters (Figure 2) were measured:

1. WLL- Width of longer leaf blade; 2. WShL-Width of shorter leaf blade; 3. HCAdLL-height of cuticle of adaxial side of longer leaf blade; 4. HCAbLL-height of cuticle of abaxial side of longer leaf blade; 5. HEAdLL-height of epiderm of adaxial side of longer leaf blade; 6. HEAbLL-height of epiderm of abaxial side of longer leaf blade; 7. HPLL-height of parenchyma of longer leaf blade; 8. HCAdShL-height of cuticle of adaxial side of shorter leaf blade; 9. HCAbShL-height of cuticle of abaxial side of shorter leaf blade; 10. HEAdShL-height of epiderm of adaxial side of shorter leaf blade; 11. HEAbShL-height of epiderm of abaxial side of shorter leaf blade; 12. HPShL-height of parenchyma of shorter leaf blade; 13.

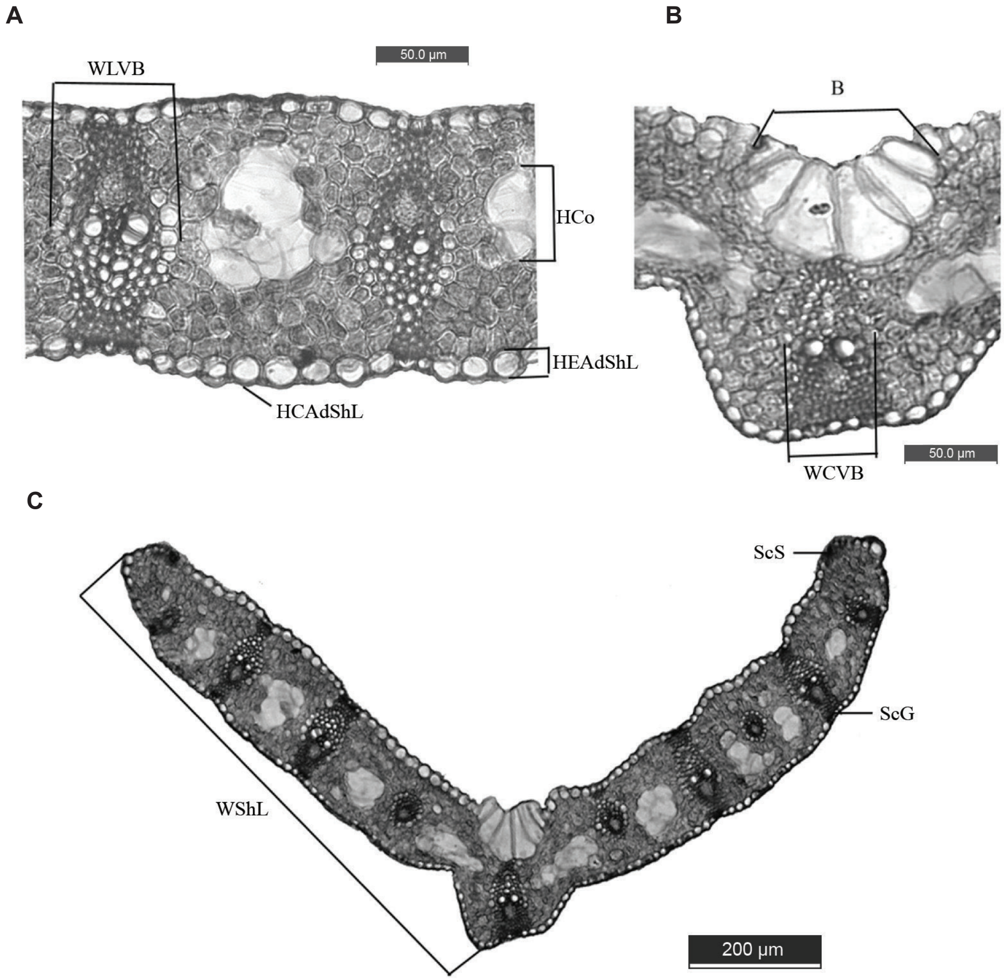

Fig. 2. Leaf cross-section of *Carex humilis* with some of the measured characteristics - A) leaf cross-section in total; B) central part of the leaf blade; C) region of central rib.
(WShL-length of shorter leaf blade; HEAdShL-height of epiderm of adaxial side of shorter leaf blade; HCAbShL-height of cuticule of abaxial side of shorter leaf blade; WCVB-width of the central vascular bundle; WLVB-width of the largest lateral vascular bundle; B- bulliform cells, HCo - height of the biggest colorless cell, ScS - sclerenchyma strand, ScG - sclerenchyma girder)

TL- Largest thickness of the leaf blade; 14. WCr-width of the central rib; 15. HSc-height of sclerenchyma at the widest part of the leaf; 16. HScCr-height of sclerenchyma at the central rib; 17. NoVB-number of vascular bundles; 18. NoVBmaj-number of major vascular bundles; 19. NoVBmin-number of minor vascular bundles; 20. HCVB-height of the central vascular bundle; 21. WCVB-width of the central vascular bundle; 22. HLVB-height of the largest lateral vascular bundle; 23. WLVB-width of the largest lateral vascular bundle; 24. S-total leaf surface; 25. SB-surface of bulliform cells; 26. NoB-number of bulliform cells; 27. HB-height of highest bulliform cell; 28. NoCo-number of colorless cells; 29. SCo-surface of the biggest colorless cell; 30. HCo-height of the biggest colorless cell; 31. NoScG-number of the sclerenchyma girders; 32. NoScS-number of sclerenchyma strands; 33. NoScB-number of sclerenchyma bundles;

Statistical analysis - For each of the quantitative characters descriptive statistics (mean, standard deviation, minimum, maximum and standard error, coefficient of variation) were calculated and variations in regard to the geographical gradients were performed to identify the trends in anatomical differentiation. The significance of differences between the populations studied was established by analysis of variance (ANOVA). All statistical analyses were performed with the statistical package Statistica 5.1 for Windows (1997), StatSoft.

Table 1. Basic statistic parameters of 18 populations of *Carex humilis* in the investigated area; Values are expressed in µm (Legend: Valid N – Number of measured cases, Min. – Minimum, Max. – Maximum, Std. Dev – Standard Deviation, Std. Error – Standard Error, CV% – coefficient of variation, F - F-ratio for distance between individual distributions, p - probability for differences amongst populations).

	Valid N	Mean	Minimum	Maximum	Std.Dev.	CV (%)	F	p
*Width of longer leaf blade	251	805.2	387.04	1375.8	194.70	24.17982	12.49722	0.000000
*Width of shorter leaf blade	251	655.4	314.90	1109.3	160.49	24.48567	9.04923	0.000000
*Height of cuticule of adaxial side of longer leaf blade	251	1.1	0.72	1.6	0.12	11.4966	3.77264	0.000002
*Height of cuticule of abaxial side of longer leaf blade	251	1.0	0.71	1.5	0.12	12.26957	2.57596	0.000815
*Height of epiderm of adaxial side of longer leaf blade	251	10.9	5.59	17.3	2.28	20.84745	12.47363	0.000000
*Height of epiderm of abaxial side of longer leaf blade	251	7.2	4.52	10.6	1.16	16.20056	5.04588	0.000000
*Height of parenchyma of longer leaf blade	251	143.8	75.45	252.8	39.32	27.35368	32.86474	0.000000
*Height of cuticule of adaxial side of shorter leaf blade	251	1.1	0.83	1.7	0.13	12.06727	4.53366	0.000000
*Height of cuticule of abaxial side of shorter leaf blade	251	1.0	0.72	1.5	0.12	11.51523	1.96069	0.014426
*Height of epiderm of adaxial side of shorter leaf blade	251	11.0	5.05	17.7	2.43	22.03857	14.61308	0.000000
*Height of epiderm of abaxial side of shorter leaf blade	251	7.4	3.81	11.9	1.33	17.89832	6.69144	0.000000
*Height of parenchyma of shorter leaf blade	251	144.1	72.64	256.3	39.16	27.18286	33.69400	0.000000
*Largest thickness of the leaf blade	251	190.7	115.34	357.1	50.99	26.74012	38.93605	0.000000
*Width of the central rib	251	188.5	93.49	389.3	62.97	33.41174	47.38291	0.000000
*Height of sclerenchyma at the widest part of the leaf	251	25.5	8.16	69.3	13.34	52.36801	41.75563	0.000000
*Height of sclerenchyma at the central rib	251	21.8	2.90	76.9	13.86	63.43774	42.71188	0.000000
*Number of vascular bundles	251	10.3	5.00	16.0	2.08	20.24275	5.26458	0.000000
*Number of major vascular bundles	251	5.2	3.00	9.0	1.35	26.09876	4.40729	0.000000
*Number of minor vascular bundles	251	5.1	2.00	9.0	1.21	23.98198	3.40258	0.000013
*Height of the central vascular bundle	251	87.6	45.63	151.9	25.56	29.18452	52.91023	0.000000
*Width of the central vascular bundle	251	48.6	21.60	82.8	13.71	28.18361	41.24241	0.000000
*Height of the largest lateral vascular bundle	251	103.9	60.68	169.9	24.48	23.56143	38.92572	0.000000
*Width of the largest lateral vascular bundle	251	56.5	27.02	82.1	12.22	21.62908	44.31551	0.000000

	Valid N	Mean	Minimum	Maximum	Std.Dev.	CV (%)	F	p
*Total leaf surface	251	236032.0	89839.06	419111.6	64905.54	27.49861	8.24254	0.000000
*Surface of bulliform cells	251	4076.0	0.00	12803.0	2866.80	70.33395	25.06923	0.000000
*Number of bulliform cells	251	5.8	0.00	15.0	3.11	53.72348	21.69973	0.000000
*Height of highest bulliform cell	251	38.4	0.00	81.8	20.34	53.03056	20.37894	0.000000
*Number of colorless cells	251	8.0	4.00	13.0	1.72	21.42964	11.43872	0.000000
*Surface of the biggest colorless cell	251	11663.2	1322.67	63015.7	9488.48	81.35417	33.04348	0.000000
*Height of the biggest colorless cell	251	105.0	23.28	277.3	55.45	52.82793	56.39747	0.000000
*Number of sclerenchyma girders	251	4.3	0.00	8.0	1.53	35.24849	10.16560	0.000000
*Number of sclerenchyma strands	251	3.9	1.00	8.0	1.30	33.19864	5.52466	0.000000
*Number of sclerenchyma bundles	251	2.0	0.00	6.0	1.25	61.99649	4.84508	0.000000
*ANOVA effects significant at $p < 0.05$								

RESULTS

Based on the measurements of anatomical characteristics of the cross-sections of leaves of the 18 populations of taxon *Carex humilis*, a detailed description was made covering the total variability of populations of this species on the territory of C&SE Europe.

Basic anatomical characteristics. Leaves of *Carex humilis* Leysser, like leaves of most members of the family Cyperaceae, are characterized by a specific structure. They are bilateral and V-shaped in cross-section with different blade width. They have one row of vascular bundles surrounded by sheaths composed of two layers: the inner sclerenchyma layer and the outer parenchyma layer. In the keel of the leaf, on the upper side hinge cells are located. Air spaces may be present between vascular bundles. Stomata are located on the adaxial surface; guard cells and subsidiary cells lie even with the surface of the epidermis. Epidermal cells do not form any trichomes; they are rectangular, slightly elongated, and on the edge of the leaf they have one or several silica bodies. Parenchyma is not differentiated: palisade mesophyll and hypodermis are missing. There is one layer of bulliform cells adaxial to the median vascular bundle, generally subtended by one layer of smaller translucent cells. The vascular bundles make just one row. They are different in size, therefore it is easy to differentiate the “major” (big) and “minor” (small) bundles which alternate in a regular way one after the other, going from the central nerve towards the margin of the leaf. All the bundles have elliptic form and are surrounded by one layer of cells, making the sheath of the vascular bundle. The major vascular bundles have clearly-differentiated big tracheas.

Measurement results. Cross-section surface of the leaves varied from 89839.06 to 419111.65 μm^2. Width of the longer blade varied from 387.04 to 1375.76 μm, and the shorter one from 314.90 to 1109.34 μm. The largest thickness of the leaf blades varied from 115.34 to 357.14 μm, and the central rib from 93.49 to 389.30 μm. The mesophyll was not differentiated into a spongy and palisade tissues. It consisted of the parenchyma cells which occupied all the space not covered by sclerenchyma or vascular bundles and their sheath layer. Its thickness varied from 72.64 to 256.30 μm. Epidermal cells on the upper side of the leaf were larger (up to 2x) than cells on the bottom. Their thickness varied from 5 to 17 μm on the adaxial side and from 4 to 11 μm on the abaxial side. Thickness of the cuticle layer was very uniform among the adaxial and abaxial sides, and varied from 0.7 to 1.6 μm for the adaxial and from 0.7 to 1.5 μm for the abaxial side of the leaf.

Bulliform cells, located only at the base of the central vascular bundle of the adaxial side of the leaf, were present in the great majority of leaves analyzed, being absent only in very young individuals. Their numbers ranged up to 15 per cross-section, diameter up to 81.84 μm, and total surface up to 12802.95 μm^2. Colorless cells were present in all individuals and their number varied from 4 to 13 per cross-section, diameter from 23.28 to 277.27 μm and surface area varied from 1322.67 to 63015.73 μm^2.

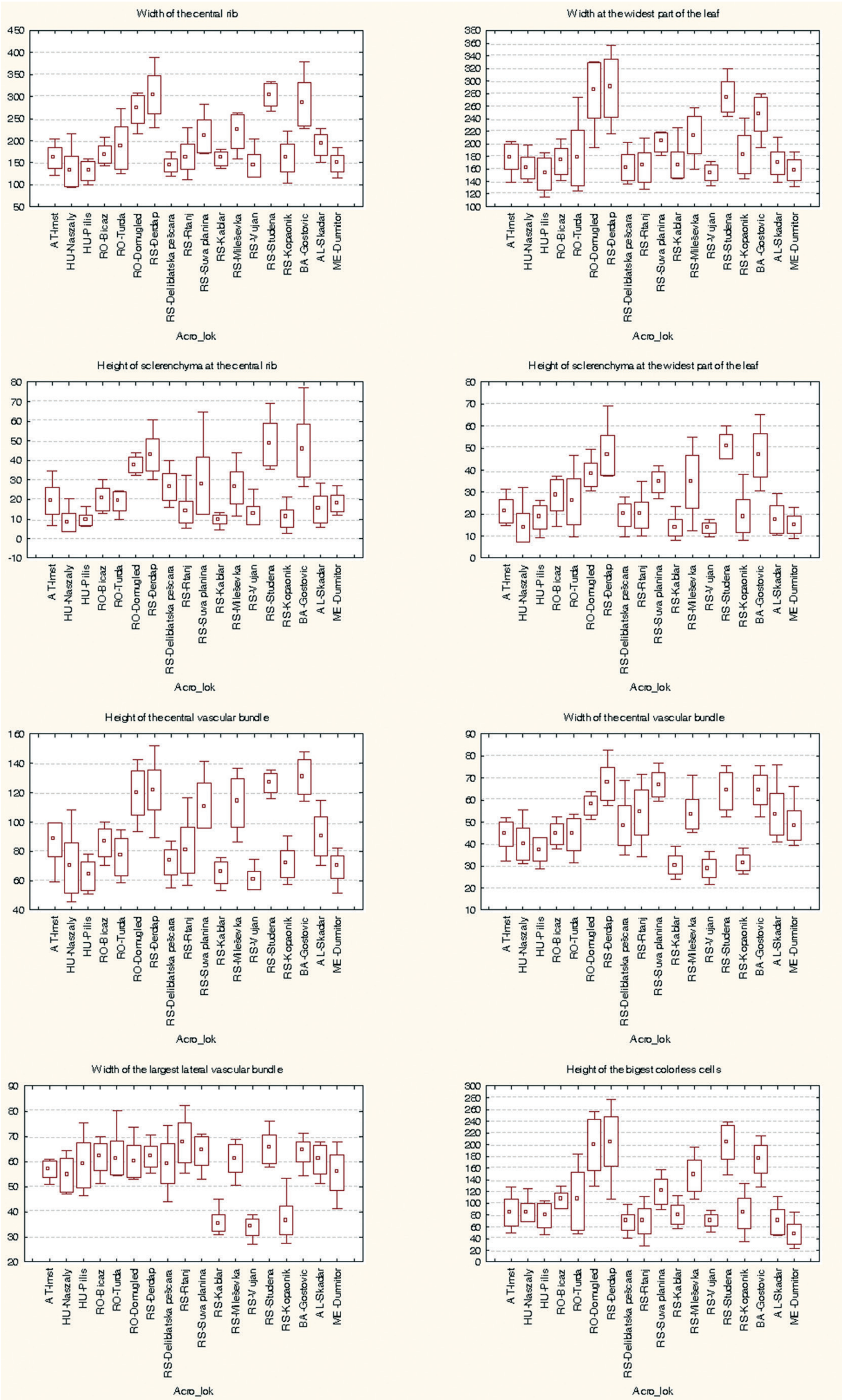

Fig. 3. Box and whisker plots of basic parameters of characters with the highest F-ratios - all measures in μm (Legend: Middle point = Mean, Box = Mean±SD, whisker = Min-Max, ☐ = Outliers)

Total number of vascular bundles per cross-section varied from 5 to 16. Number of major vascular bundles varied from 3 to 9. Minor vascular bundles were small, without or with hardly noticeably big tracheas. Number of minor vascular bundles varied from 2 to 9. Height of the central vascular bundle varied from 45.63 to 151.92 μm. Width of the central vascular bundle varied from 21.60 to 82.77 μm. Height of the largest lateral vascular bundle varied from 60.68 to 169.92 μm and width of the largest lateral vascular bundle varied from 27.02 to 82.12 μm.

STATISTICAL ANALYSIS

Coefficient of variation - The analysis of variation of particular anatomical characteristics in 18 populations of *Carex humilis* showed that the many characters exhibited moderate degrees of variability (CV=10-35% - Table 1) amongst populations. Within the group of highly variable characters, whose coefficients of variation (CV%) were higher than 35%, were the following: surface of the biggest colorless cell (81.35%), surface of bulliform cells (70.33%), height of sclerenchyma at the central rib (63.44%), number of sclerenchyma bundles (62.00%), number of bulliform cells (53.72%), height of highest bulliform cell (53.03%), height of the biggest colorless cell (52.83%), height of sclerenchyma at the widest part of the leaf (52.37%). In contrast, the lowest coefficients of variation were found for thickness of cuticle on the ad- and abaxial sides of both the longer and shorter leaf blade - height of cuticle of the abaxial side of the longer leaf blade (12.27%), height of cuticle of the adaxial side of the shorter leaf blade (12.07%), height of cuticle of the abaxial side of the shorter leaf blade (11.52%) and height of cuticle of the adaxial side of the longer leaf blade (11.50%).

Analyses of variance (ANOVA) - Analyses of variance showed that all the characters significantly contributed to differentiation of the 18 populations (Table 1). The characters that contributed to the minimum extent, though still significantly, to anatomical differentiation, were the following: thickness of cuticle on the adaxial and abaxial side of the leaf and the total number of vascular bundles. However, a post-hoc test showed that some characters, such as thickness of cuticle (HCAdLL, HCAbLL, HCAbShL), total leaf surface and number of vascular bundles (NoVB, NoVBmaj, NoVBmin), did not contribute significantly to differentiation. In contrast, height and width of the central vascular bundles, height of the biggest lateral vascular bundle as well as surface of bulliform cells highly contributed to differentiation of the populations. Regarding other characters, different populations contributed in varying degrees to general differentiation. For most characters, the populations from Djerdap and Domogled contributed the most to differentiation.

Analysis of correlation - The analysis of correlation of characters of leaf anatomy showed that the majority of characters were significantly correlated (for details, see Electronic Supplementary Material). The basic group of highly-correlated characters (coefficient of correlation >0.6) comprised width of leaf - height of parenchyma – largest thickness of the leaf blade– width of the central rib - number of vascular bundles – number of colorless cells – surface of the biggest colorless cell – diameter of the biggest colorless cell. Within this group, an extremely high level of correlation (>0.9) was shown between the following characters: height of parenchyma – largest thickness of the leaf blade, and surface of the biggest colorless cell - height of the biggest colorless cell. The largest negative correlations were between the number, size and diameter of the bulliform cells, and the height of parenchyma.

The correlation analysis showed that as the basic dimensions of the leaf (above all - thickness) increased, the dimensions of many other characters of leaf anatomy also regularly increased. The exception to this rule was thickness of cuticle (on the adaxial and abaxial sides of the leaf), which was not significantly dependent on other characters.

Variations in regard to geographical gradients. The results of detailed analyses in relation to the three groups of characters (those referring to leaf size, those referring to sclerenchyma and vascular elements, and those referring to the bulliform and colorless cells) are presented in Figure 3. Although there was local population differentiation among themselves on the anatomical level, there was no expressive trend of variation of anatomical characters of the leaf in the horizontal (“east-west”, “north-south”) and vertical gradients.

DISCUSSION

It is well known that climatic factors and geological substrate have very strong influences on the morpho-anatomical differentiation of plants. It is not rare that these environmental factors have a crucial influence on the development of special adaptive structures and the appearance of a well-defined anatomical differentiation. Highly distinct differences in thermal and hygric habitat characteristics generally result in significant anatomical differences between populations growing under different climatic conditions. These differences usually represent an adaptive response to habitat conditions, and generally do not have a distinct taxonomic significance (Fahn 1964; Kummerow 1973; Fahn & Cutler 1992; Todorović

& Stevanović, 1994; Stevanović & Janković 2001; Bosabalidis & Kofidis 2002; Lakušić *et al.* 2006, 2010; Kuzmanović *et al.*, 2011). Also, the significance of the serpentine geological substrate for the morpho-anatomical differentiation of plant populations, for plant speciation, and, finally, for the total florogenesis in wider geographical regions, was recognized a long time ago and studied in detail by several authors (Kruckenberg 1951, 1954, 1967, 1984; Walker 1954; Whittaker *et al.*, 1954; Tadros 1957; Ritter-Studnička 1968; Proctor & Woodell 1975; Karataglis *et al.*, 1982; Tatić & Veljović 1990; Stevanović *et al.*, 2003, Kuzmanović *et al.*, 2011).

In the Balkan peninsula and neighboring regions, *C. humilis* inhabits very different climatic conditions, geological substrate and habitat types, so it was expected that this species should show a significant inter-population variability and anatomical differentiation influenced by environmental factors.

The analysis of variation of particular anatomical characteristics in these populations of *Carex humilis* has shown that a large number of characters have moderate degrees of variability amongst populations and that particularly variable characters were the surface and height of the biggest colorless cell and bulliform cells, as well as height of the sclerenchyma at different parts of the leaf. The majority of characters showed highly-significant contributions to population differentiation, especially height of the biggest lateral vascular bundle and surface of bulliform cells, together with characters related to bulliform and colorless cells, as well as to lateral vascular bundles. In contrast, cuticle thickness proved to be the most stable character. It is also shown, by correlation analyses, that thickness of cuticle was not significantly dependent on other characters, being the exception to the rule that the dimensions of many other characters of leaf anatomy regularly increased with increase of basic dimensions of the leaf (above all - thickness).

If we consider the relatively wide range of climatic conditions and habitat types of *Carex humilis* in the study area, this plant shows a significant inter-population variability in leaf anatomical traits. However, given that regularity in the variation of characters was not observed in regard to geographic gradient, it is difficult to state whether the observed anatomical differences between these populations represent an adaptive response to habitat characteristics, or whether this differentiation was caused by historical and evolutionary factors.

Results of morpho-anatomical analyses suggest the possibility that *C. humilis* has maintained a stable, conservative morpho-anatomical structure. To confirm this, it is necessary to make a comparative morphological study of reproductive organs as well as a comprehensive molecular and phylogenetic study, which is in progress.

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Botanica SERBICA

REZIME

Lisna anatomija *Carex humilis* Leysser (Cyperaceae) sa područja centralne i jugo-istočne Evrope

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U radu je prikazan opis ukupne varijabilnosti anatomije listova u različitim populacijama vrste *Carex humilis* na području Austrije, Mađarske, Rumunije, Srbije, Bosne i Hercegovine, Crne Gore i Albanije. Analize su urađene na uzorku od 253 lista iz 18 populacija. Statističke analize su urađene za 33 kvantitativna karaktera koji se odnose na anatomiju lista. U cilju utvrđivanja trendova u anatomskoj diferencijaciji urađene su deskriptivna statistika, analiza varijanse (ANOVA), korelativna varijabilnost, kao i varijacija u odnosu na geografski gradijent.

Ključne reči: *Carex humilis*, C & JI Evropa, lisna anatomija