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Intraspecific variability of some functional traits of *Trigonocaryum involucratum* (Steven) Medw., a Caucasus endemic plant

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ABSTRACT:
Plant traits have been used to predict species and community responses to environmental gradients. We studied variation of leaf area (LA), specific leaf area (SLA), flowering shoot number and seed mass along an elevation gradient in the case of *Trigonocaryum involucratum*, a scree-growing plant endemic to the Caucasus ecoregion. The study had two major aims: (1) to compare the role of intra-population and inter-population variation of functional trait values; and (2) to ascertain dependence between elevation and trait values and their variation. We collected trait data in several populations in Dagestan (Russian Federation), where the species has about a 1000-m amplitude of elevational distribution. The intraspecific variability of trait values was assessed via standard statistical tools (one-way ANOVA and linear regression analysis). The trait values mostly have high inter-population variation (more than 90% for each of the trait values compared to intra-population variation of each trait), indicating adaptation of populations to site conditions. Much higher intra- vs. inter-population variation in SLA at subnival elevations indicates local micro-site diversity and may serve as a buffer against future stress related to climate change. All the trait values negatively but significantly correlate (weakly or moderately) with elevation. Negative correlation presumably shows a certain increase in the limiting effect of the elevation gradient associated with changes in temperature, soil nutrient availability and soil water content, as well as with high solar radiation. More evidence from a broader study of the species throughout its distribution range is needed for firmer conclusions about the intraspecific variability of *T. involucratum*.

Keywords:
leaf functional traits, specific leaf area (SLA), *Myosotis involucrata*, Dagestan, the North Caucasus

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INTRODUCTION

Functional trait variability enables plants to survive and reproduce in conditions of varying degrees of stress, disturbance and competition (Westoby 1998; Grime 2001; Lavorel & Garnier 2002; Westoby *et al.* 2002; Reich *et al.* 2003). Over the past decades, plant traits have been used to predict species and community responses to different environmental gradients. The majority of studies have focused on functional trait variability between species (i.e., interspecific variation), but recent developments in functional trait-based community ecology have shown the importance of studies of variation at both the interspecific and the intraspecific levels. Study of intraspecific variation may give answers to a number of questions about plant adaptations and enable us to predict the effects of environmental changes, thereby helping in plant conservation (Jung *et al.* 2010; Albert *et al.* 2011; Violle *et al.* 2012; Wellstein *et al.* 2013; Harzé *et al.* 2016; Campetella *et al.* 2019).

Endemic species occupying niches unavailable to others are interesting in connection with intraspecific variation and plasticity of the traits best reflecting plant ecological strategies, i.e., whether a species is developing a more competitive ecological strategy or adopting a more conservative strategy through adaptation of functional traits to specific habitat conditions (Westoby 1998; Tonin *et al.* 2020). We studied leaf area (LA) and specific leaf area (SLA) as measures of resource acquisition (Pérez-Harguindeguy *et al.* 2013), flowering shoot number as a measure of fecundity (see Scheiner 1989; Bazzaz *et al.* 2000) and seed mass as a measure of both survivorship and fecundity (Westoby *et al.* 1996) in the case of *Trigonocaryum involucratum* (Steven) Medw., a scree-growing plant endemic to the Caucasus ecoregion. Characterised by high endemism of vascular plants (more than 25% of the total flora) (Williams *et al.* 2006; Zazanashvili *et al.* 2012; Solomon *et al.* 2013), the ecoregion has a number of mono- and oligotypic endemic genera, including the genus *Trigonocaryum* Trautv. (Boraginaceae) with a single species, T. *involucratum*. In Dagestan (Russian Federation), the species has about a 1000m elevation amplitude. The plant is restricted to alpine grey slate screes of the northeastern Great Caucasus in the Russian Federation, Georgia and Azerbaijan (Gagnidze *et al.* 2002; Litvinskaya & Murtazaliev 2009). Existing literature only mentions *Trigonocaryum* among mono- and oligotypic endemic Caucasian genera, characterises *T. involucratum* as a scree-growing species and deals with its morphology or molecular genetics mainly in relation to the taxonomic position of the species (Gachechiladze & Kobakhidze 1996; Kerimov & Askerova 2005; Chacón *et al.* 2016), but no studies have been carried out on functional traits so far.

A large number of relevant traits can be considered for different research contexts. However, a few traits, viz., plant height, SLA and seed mass, have been considered relevant almost universally because they adequately reflect the ecological strategies of plants (Westoby 1998; Westoby *et al.* 2002; Pérez-Harguindeguy *et al.* 2013). SLA is known to be strongly correlated with other traits that measure stress tolerance (Poorter & Garnier 1999). Seed mass reflects the ability of a plant to cope with disturbance (Westoby 1998), but it is considered a so-called 'stable trait' with low intraspecific variation (Westoby *et al.* 1996; Garnier *et al.* 2007). In the case of *T. involucratum*, measuring plant height contains potential bias related to the semi-decumbent nature of the plant and largely uneven surface of its scree substrate, so this trait was not considered in the study design.

The present study has the following major aims: (1) to compare the role of intra-population (within a site) and inter-population variation of the trait values; and (2) to ascertain dependence between elevation (and/or other environmental factors) and trait values and their variation. Understanding how this species adjusts its functional traits according to the elevation can improve our knowledge about the ability of plants to cope with environmental changes, including climate change (see Tonin *et al.* 2020).

MATERIALS AND METHODS

Target species. *Trigonocaryum involucratum* is a 2-10 cm tall plant sparsely covered in all parts with sub-appressed, equal bristles borne on small tubercles, generally green. The root is thin but grows deep into the substrate. The main stem is up to 3 cm tall, and stem branches are semi-decumbent. Leaves are 1-1.5 cm long, up to 3-5 mm wide above, gradually tapering at the base. Terminal inflorescences are leafy, once or twice furcate, few flowered, 1-3 cm long and wide. Bracts are 1-2 cm long, similar to cauline leaves in shape. The calyx is ca. 2 mm long, sessile or on a short curved pedicel, campanulate. The plant fowers in June-August (Popov 1953). The type specimen of T. *involucratum* was initially described as *Myosotis involucrata* Steven (Steven 1812) but was later placed in a separate monospecific genus by Medvedev (1919); however, the traits which served as a basis for segregation of the genus (presence of blue-violet flowers, flat gynobase, basal oval cicatrix, seeds with a caruncle) as well as some other traits are observed in the genus *Myosotis* L. A recent molecular study of relationships of the major clades in Boraginaceae *s.str.* using plastid markers also supported synonymisation of *T. involucratum* as *M. involucrata* (Chacón *et al.* 2016). However, T. *involucratum* is still given as the accepted name for the taxon, for example in Euro+Med (2006–), and we follow this nomenclature for the studied plant in the present paper.

Study sites. The material was collected at six sites of three localities in Dagestan (Russian Federation) (Fig. 1) in 2016-2018: vicinity of the village of Jynykh, Rutul district (J, three sites), vicinity of the village of Kurush, Dokuzparin district (K, two sites) and vincinity of the village of Choroda, Tlyarata district (Ch, one site). Description of environmental conditions at each locality and descriptions of the respective sites are given below.

Vicinity of the village of Jynykh, Rutul district: the village is located in the Samur river valley surrounded by high mountain ranges (> 3 000 m a.s.l.). The northern slopes are covered by pine-birch forests and the southern slopes by dry steppe-like secondary meadows and scrub (Chilikina & Shiffers 1962). The local climate is strictly continental with cold winters and cool summers; the mean annual temperature is about 8°C, and annual precipitation is about 550 mm (Akaev *et al.* 1996).

Fig. 1. Study area: three locations of the six studied populations of *Trigonocaryum involucratum*.

Three sites were studied at the Jynykh locality. The site J1 is located at 1785 m a.s.l. on an eastern slope of 40° with scree particles 3-12 cm long and a vegetation cover of less than 5%. *Silene lacera* (Steven) Sims and *Satureja hortensis* L. were recorded at J1 along with the target species. The siteJ2 is located in a small stream basin at 1810 m a.s.l. on a northern 5–7° slope having scree particles 0.5–2 cm long with a silt admixture and a vegetation cover of about 30–40%. *Epilobium colchicum* Albov, *Delphinium gelmetzicum* Dimitrova, *Tussilago farfara* L., *Papaver fugax* Poir., etc., are recorded there. The site J3 is located at 1900 m a.s.l. on a southern 10° rocky slope with scree-covered portions. The scree particles are 2-5 cm long. The vegetation cover is about 10–15%. *Sempervivum caucasicum* Rupr. ex Boiss., *Silene saxatilis* Sims, etc., are also recorded.

The village of Kurush, Dokuzparin district: the sites are located on Mt. Nesindagh and are covered by alpine meadows with significant segments of rock-scree plant communities. The climate is strictly continental with cold winters and short cool summers; the mean annual temperature is about 6°C, and annual precipitation is about 600 mm (Akaev *et al.* 1996).

Two sites were studied at the Kurush locality. The site K1 is located in a small stream basin at 2450 m a.s.l. on a northeastern 5-7° slope having a silty substrate with pebble admixed and a vegetation cover of about 30%. *Trisetum rigidum* (M. Bieb.) Roem. & Schult. and *Epilobium colchicum* are recorded. The site K2 is located at 2750 m a.s.l. on a southwestern slope of 25–30° inclination with scree particles 2-5 cm long. *Campanula meyerana* Rupr., *Pseudobetckea caucasica* (Boiss.) Lincz., *Ranunculus arachnoideus* C. A. Mey., *Silene humilis* C. A. Mey., *Stachys pauli* Grossh., *Trisetum transcaucasicum* Seredin, *Valeriana daghestanica* Boiss., *Vavilovia formosa* (Steven) Fed. and *Cicer incisum* (Willd.) K. Malý are recorded (Murtazaliev *et al.* 2012).

The village of Choroda, Tlyarata district: the village is located in the Jurmut gorge. Northern slopes are covered by a pine-birch forest and subalpine meadows, southern slopes by shrub thickets and montane meadows enriched with steppe species and scattered individuals of *Pinus sylvestris* subsp. *hamata* (Steven) Fomin (Chilikina & Shiffers 1962). The local climate is continental with cold winters and cool summers; the mean annual temperature is about 6°C, and annual precipitation is about 750 mm (Akaev *et al.* 1996).

A single site was studied at the Choroda locality. The site Ch is located at 1950 m a.s.l. on a southwestern 30° slope with scree particles 5-12 cm long and a vegetation cover of less than 10%. *Silene lacera*, *Rumex scutatus* L., solitary plants of *Papaver fugax* Poir., *Scutellaria* sp. and *Crepis* sp. are recorded.

Sampling design and traits. Five to eight individuals of the target species were randomly selected at each study site. Five to six fully developed and undamaged leaves (Petruzzellis *et al.* 2017) as well as five seeds (Westoby 1998) were collected from each plant. Collected leaves were scanned, and these images were then used for calculation of leaf area, LA (mm^2) by ImageJ (Rueden *et al.* 2017). For dry mass measurements, leaves and seeds were oven-dried at 70°C for 72 h, then weighed to obtain leaf dry mass (mg) and seed mass (mg). To calculate specific leaf area, SLA (mm^2/mg), the ratio between fresh leaf area and leaf dry mass was pooled (Pérez-Harguindeguy *et al.* 2013).

The voucher specimens are stored in the herbarium of the Mountain Botanical Garden of the Dagestan Federal Research Centre RAS (DAG).

Statistical analysis. Descriptive statistical values (the minimum, maximum, mean and standard deviation) were obtained for each characteristic. Additionally, normality of trait values was rejected based on the Shapiro-Wilk test. These parameters were therefore log10-transformed prior to analyses in order to attain approximate normality and homogeneity of residuals. One-way analysis of variance (ANOVA) was used to analyse differences in trait values on the intra- and inter-population levels at three different locations of *T. involucratum* populations in Dagestan (Russian Federation, North Caucasus). Additionally, Tukey's HSD multiple comparisons were performed to investigate the significance of mean differences between pairs of populations. Regression analysis was conducted to evaluate the complex of environmental factors acting at each locality on the variability of all trait values.

All statistical analyses were performed using SPSS ver. 21.0 (https://www-01.ibm.com/).

RESULTS

Mean values of SLA in the single population at Choroda (8.4±2.1 mm^2/mg) and three populations at Jynykhare are higher (from 8.9±3.1mm^2/mg at J1 to 10.5±2.8 mm^2/mg at J3) compared to the two populations at Kurush (6±1.5 mm^2/mg at K1 and 5.8±0.9 mm^2/mg at K2); the mean for the six populations is 8.4±3 mm^2/mg. LA varies in a broad range (from 19.6±4.5 mm^2 at K2 to 57.2±17.9 mm^2 at J3); the mean for the six populations is 36.1±20.7 mm^2. The highest values are observed at J1 and J3, while the other four populations (Ch, J2, K1, K2) have mean values lower than the mean of the six populations. The mean number of shoots per plant ranges from 2.9±0.7 at Ch to 5.5±1.6 at J1; the mean for the six populations is 4.1±1.5. Seed mass ranges from 2.1±0.5 mg at K1 to 3.4±0.8 mg at J1; the mean for the six populations is 2.9±0.8 mg.

Mean values for each trait at each site and the entire set of populations are given in Table 1.

One-way ANOVA for *post-hoc* comparison of populations and breakdown of total variance into inter- and intra-population variance showed that for all the trait values inter-population variance is much higher compared to intra-population variance, in all cases exceeds 90% and is highest for LA (Table 2).

Comparison of the log10-transformed data (Supplementary Table 1) shows that statistically highly reliable differences (p<0.001 in 53% of pairs) in SLA are only observed between the populations at Choroda and Jynykh on the one hand and those at Kurush on the other. In the case of LA, statistically highly reliable differences (60% of pairs) are observed between all the pairs containing J1 and J3 on the one hand and those containing Ch, J2, K1 and K2 on the other. In the case of flowering shoot numbers, all three populations at Jynykh are different from Ch and K2, while K1 is only different from J1 (p<0.001 again in 53% of pairs). In the case of seed mass, all the three populations at Choroda and Jynykh are different from the populations at Kurush except for the pairs J3-K2 and Ch-K2 with no statistically highly reliable difference (p<0.001 in 40% of pairs).

Linear regression analysis based on three environmental factors (elevation, site and slope) showed that elevation has statistically significant linear influence on inter-population differentiation of all the trait values (p<0.001, Table 3). All the trait values correlate negatively but significantly (weakly or moderately) with elevation. The influence is strongest on LA and somewhat weaker on SLA (r^2 = 34.3, $p \leq 0.001$, r_{xy} = -0.59, $p \leq 0.001$ and r^2 = 31.1, $p \leq 0.001$, r_{xy} = - 0.56, $p \leq 0.001$; Supplementary Table 1). Influence of site conditions is observed to be even stronger for three of the four measured traits (SLA, LA, seed mass), being the strongest for LA (r^2 = 47.4, $p \leq 0.001$, r_{xy} = 0.69, $p \leq 0.001$; Supplementary Table 1). Average slope inclination significantly influenced seed mass and LA: the traits positively but weakly correlate with rising slope inclination in a statistically significant way (Table 3).

DISCUSSION

Our study showed that the trait values have high inter-population variability expressed by the per cent input of inter-population variation in relation to the total variation of each trait. For all the trait values, the input of inter-population variation exceeds 90%, being highest in the case of LA (98.7%), which points to adaptation of each population to the respective site conditions. High intra-population variability of certain traits, e.g., LA and SLA, reflecting resource acquisition would presumably serve as a buffer against climate change (Wellstein *et al*. 2013), which is considered to be particularly pronounced in mountainous regions (Körner 2003). Hence the conservative strategy of the studied plant, observed particularly for vegetative traits, may not be beneficial for the species in terms of survival in altered environmental conditions. However, further research needs to be focused on probable consequences of the observed inter- vs. intra-population variation in conditions predicted according to various climate change scenarios.

The very low input of intra-population variation in total variation of seed mass and relatively low proportion of statistically highly reliable differences in pairwise comparison of populations (p<0.001 in 40% of pairs, which is the lowest of values obtained for the four trait values) are consistent with the general observation of comparatively narrow variation of seed mass within species (Westoby *et al*. 1996; Garnier *et al*. 2007).

Elevation exerts linear influence on inter-population differentiation. Its significant effects were determined for all the traits: the trait values negatively correlate with elevation, which presumably shows a certain increase of the limiting effect of the elevation gradient in the localities at higher levels of the vertical distribution range. Elevation is associated with changes in temperature, soil nutrient availability and soil water content, as well as with high solar radiation. Interspecific changes observed in plant traits such as LA and SLA with increasing elevation are well known: alpine plants tend to have smaller leaves with lower SLA values compared to lowland plants, which indicates a more conservative resource use in the harsh conditions of highlands (Körner *et al*. 1989; Wright *et al*. 2001; Körner 2003; Pérez-Harguindeguy *et al*. 2013). Statistically highly reliable differences in SLA between the populations located at 1795 to 1950 m a.s.l. on the one hand and those at 2450 and 2750 m a.s.l. on the other support the conclusion on the effect of elevation.

The influence of site conditions is observed to be stronger than that of elevation. Heterogeneous environmental conditions at the study sites and the relatively small number of the populations within the study area

Table 1. Means (AV), standard deviations (SD) and minimum-maximum values of morphological/functional traits of *T. involucratum* in six studied populations in Dagestan (Russian Federation, North Caucasus).

Population/ N of samples	Elevation (m a.s.l.)	Parameters	Traits			
			SLA (mm^2/mg)	Leaf area (mm^2)	Shoot number	Seed mass (mg)
J1/44	1785	Mean±SD (min-max)	8.98±3.1 (3.8-16.2)	54.5±18.7 (28.1-105.9)	5.5±1.6 (3-8)	3.4±0.8 (2-5)
J2/37	1810	Mean±SD (min-max)	10±3.1 (5.3-18.3)	27.5±8.4 (9.8-45)	4.1±1.1 (2-6)	3.2±0.7 (2-5)
J3/40	1910	Mean±SD (min-max)	10.5±2.8 (4.7-17.9)	57.2±17.9 (19-93.9)	4.7±1.3 (2-6)	2.9±0.6 (1-4)
K1/33	2450	Mean±SD (min-max)	6±1.5 (2.3-13.4)	20.9±5 (8.8-32.4)	3.6±0.9 (2-5)	2.1±0.5 (1-3)
K2/28	2750	Mean±SD (min-max)	5.8±0.9 (2.9-19.3)	19.6±4.5 (11-34.7)	2.9±0.6 (2-4)	2.5±0.6 (1-4)
Ch/25	1950	Mean±SD (min-max)	8.4±2.1 (4.5-17.5)	21.7±7.3 (11-42.3)	2.9±0.7 (1-4)	2.88±0.3 (2-3)
Total/207		Mean±SD (min-max)	8.5±3 (2.3-19.3)	36.1±20.7 (8.8-105.9)	4.1±1.5 (1-8)	2.9±0.8 (1-5)

Table 2. One-way ANOVA results for six populations of *Trigonocaryum involucratum* at three different locations in Dagestan (Russian Federation, North Caucasus) (SS –sum of squares; df – degrees of freedom; MS – mean squares; *F* – F test statistics; asterisks indicate overall significance of *F*-statistics (*** - p<0.001). All parameters were $\log_{10}$-transformed to achieve normality.

		SS	df	MS	Proportion of intra and inter-population variance (%)	*F****
Log_{10} (SLA) Leaf specific area (mm^2/mg)	Between populations	1.8	5	0.37	94.9	24.72***
	Within populations	3	201	0.02	5.1	
	Total	4.8	206			
Log_{10} (LA) Leaf area (mm^2)	Between populations	7.9	5	1.57	98.7	88.8***
	Within populations	3.6	201	0.02	1.3	
	Total	11.5	206			
Log_{10} (ShN) Shoot number	Between populations	1.9	5	0.4	95.2	23.3***
	Within populations	3.3	201	0.02	4.8	
	Total	6.2	206			
Log_{10} (SM) Seed mass (mg)	Between populations	1.2	5	0.2	95.2	23.5***
	Within populations	3	201	0.01	4.8	
	Total	3.2	206			

Table 3. Results of regression analysis by elevation and slope inclination (r^2 – coefficient of determination; r_{xy} – coefficient of correlation between a given factor and a studied trait; '–' – r^2 below 0.001 (or 0%); *p<0.05; **p<0.01; ***p<0.001). All parameters were $\log_{10}$-transformed to achieve normality.

Trait	Elevation		Site		Slope	
	r^2(%)	r_{xy}	r^2(%)	r_{xy}	r^2(%)	r_{xy}
Log_{10} (SLA)	31.1***	-0.56***	16.8***	0.41	–	0.09
Log_{10} (LA)	34.3***	-0.59***	47.4***	0.69	18.6**	0.43**
Log_{10} (ShN)	18.3**	-0.43**	9.5***	0.31	–	0.19
Log_{10} (SM)	26.0***	-0.51***	11.3***	0.34	21.3**	0.46**

do not allow for clear differentiation of the effect of each environmental factor on the studied plant traits and clear explanation of the results of pairwise comparison of LA, shoot number and seed mass. It should be noted that biotic drivers appear to be more important at low elevations, while abiotic drivers appear to be more important at high elevations (Hulshof *et al*. 2013); in the case of *T. involucratum,* the question of trait variability and its connection with various environmental drivers requires coverage of a broader geographic range with more populations in further studies for a more accurate examination of the action of biotic and abiotic factors on the target traits.

CONCLUSION

The present study, which is a brief analysis of the variation of a few core functional traits of an alpine scree plant species along a vertical gradient, enables us to draw the following conclusions: (1) The trait values associated with resource acquisition (LA, SLA) and fecundity (flowering shoot number, seed mass) exhibit much higher inter-population vs. intra-population variation, indicating adaptation of each population to site conditions. The conservative strategy may not be beneficial for the species in terms of survival in conditions of the currently on-going climate change, but the assumption requires separate research. (2) Elevation exerts linear influence on inter-population differentiation of all the trait values: negative correlation presumably shows a certain increase of the limiting effect of the elevation gradient associated with changes in temperature, soil nutrient availability and soil water content, as well as with high solar radiation. Statistically highly reliable differences in SLA between elevations below 2000 m a.s.l. on the one hand and above 2400 m a.s.l. on the other support the conclusion on the effect of elevation. The observed stronger influence of site conditions also requires additional research to distinguish the leading environmental drivers that along with elevation direct plant trait variability in alpine areas.

REFERENCES

Akaev BA, Ataev ZV, Gadzhiev BS, Gadzhieva ZKh, Ganiev MI, Hasanguseynov MG, Zalibekov ZM, Ismailov ShI, Kasparov SA, Lepekhina AA, Musaev VO, Rabadanov RM, Soloviev DV, Surmachevsky VI, Tagirov BD, Eldarov EM. 1996. *Fizicheskaya Geografiya Dagestana. Uchebnoe Posobie.* Shkola, Moscow.

Albert CH, Grassein F, Schurr FM, Vieilledent G & Violle C. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* **13**(3): 217–225.

Bazzaz FA, Ackerly DD & Reekie EG. 2000. Reproductive allocation in plants. In: Fenner M (ed.), *Seeds: the Ecology of Regeneration in Plant Communities*, pp. 1–29, Cabi.

Campetella G, Velshtein S, Farris E, Calvia G, Simonetti E, Borsukiewicz L, Vanderplank S & Marigani M. 2019. Contrasting patterns in leaf traits of Mediterranean shrub communities along an elevation gradient: Measurements matter. *Plant Ecology* **220**(7–8): 765–776.

Chacón J, Luebert F, Hilger HH, Ovchinnikova S, Selvi F, Cecchi L, Guilliam CM, Hasenstab-Lehman K, Sutori K, Simpson MG & Weigend M. 2016. The borage family (Boraginaceae s.s.): a revised infrafamilial classification based on new phylogenetic evidence, with emphasis on the placement of some enigmatic genera. *Taxon* **65**: 523–546.

Chilikina LN & Shiffers EV. 1962. *Karta rastitel'nosti Dagestanskoi ASSR*. Izd-vo Akademii nauk SSSR, Moscow-Leningrad.

Euro+Med. 2006–. *Euro+MedPlantBase– the information resource for Euro-Mediterranean plant diversity*. Published on the Internet - http://ww2.bgbm.org/EuroPlusMed/ http://ww2.bgbm.org/EuroPlusMed/[Accessed 24/07/2019].

Gachechiladze M & Kobakhidze L. 1996. The formation of generative organs and character of pollination of *Trigonocaryum involucratum* (Stev.) Kuzn. (Boraginaceae). *Bulletin of the Georgian Academy of Sciences* **154**: 428–430.

Gagnidze R, Gviniashvili T, Shetekauri S & Margalitadze N. 2002. Endemic genera of the Caucasian flora. *Feddes Repertorium: Zeitschrift für Botanische Taxonomie und Geobotanik* **113**(7–8): 616–630.

Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C, Freitas H, Golodets C, Grigulis K, Jouany C, Kazakou

E, Kigel J, Klever M, Lehsten V, Leps J, Meier T, Pakeman R, Papadimitriou M, Papanastsaia VP, Quested H, Quétier F, Robson M, Roumet C, Rush G, Skarpe Ch, Sternberg M, Theau JP, Thébault A, Vile D & Zarovali MP. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* **99**: 967–985.

Grime JP. 2001. *Plant strategies, vegetation processes and ecosystem properties*, 2nd ed. John Wiley & Sons, Chichester, UK.

Harzé M, Mahy G & Monty A. 2016. Functional traits are more variable at the intra- than inter-population level: a study of four calcareous dry-grassland plant species. *Tuexenia* **36**: 321–336.

Hulshof CM, Violle C, Spasojevic MJ, McGill B, Spasojevic MJ, McGill B, Damschen E, Harrison S & Enquis BJ. 2013. Intraspecific and interspecific variation in specific leaf area reveals the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science* **24**(5): 921–931.

Jung V, Violle C, Mondy C, Hoffmann L & Müller S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**(5): 1134–1140.

Kerimov VN & Askerova RK. 2005. On the taxonomic position of the genera *Trigonocaryum* and *Suchtelenia*. *Botanical* Žurnal **90**: 264–267.

Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer Science & Business Media.

Körner C, Neumayer M, Menendez-Riedl SP & Smeets-Scheel A. 1989. Functional morphology of mountain plants. *Flora* **182**(5-6): 353–383.

Lavorel S & Garnier É. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**(5): 545–556.

Litvinskaya SA & Murtazaliev RA. 2009. *Kavkazskiy element vo flore Rossiyskogo Kavkaza: geografiya, sozologiya, ekologuiya*. Krasnodar.

Medvedev YaS. 1919. Semeystvo Boraginaceae. *Travaux du Jardin Botanique de Tiflis* **13**(part. 2): 368–381.

Murtazaliev RA, Musaev AM, Burlyaeva MO, Huseinova ZA, Rajabov GK, Aleksandrova TG & Kotseruba VV. 2012. *Vavilovia formosa* and *Cicer minutum* (Fabaceae) v Dagestane. *Botanical Žurnal* **97**(7): 961–966.

Pérez-Harguindeguy NS, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Poorter HS & Cornelissen JHC. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167–234.

Petruzzellis F, Palandrani C, Savi T, Alberti R, Nardini A. & Bacaro G. 2017. Sampling intraspecific variability in leaf functional traits: Practical suggestions to maximize collected information. *Ecology and Evolution* **7**(24):11236–11245.

Poorter H & Garnier E. 1999. Ecological significance of inherent variation in relative growth rate and its components. *Handbook of Functional Plant Ecology* **20**: 81–120.

Popov MG. 1953. Boraginaceae. In: Shischkin BK (ed.), *Flora USSR*, Vol. **19**, pp. 97–691, Izdatel'stvo Akademii Nauk SSR. Moscow & Leningrad.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M & Walters MB. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* **164**(S3): 143–164.

Rueden CT, Schindelin J, Hiner MC, Dezonia BE, Walter AE, Arena ET & Eliceiri KW. 2017. ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* **18**: 529.

Scheiner SM. 1989. Variable selection along a successional gradient. *Evolution* **43**(3): 548–562.

Solomon J, Shulkina T & Schatz GE. (eds.). 2013. *Red list of the endemic plants of the Caucasus: Armenia, Azerbaijan, Georgia, Iran, Russia, and Turkey*. Monographs in Systematic Botany from the Missouri Botanical Garden (MSB) 125. Missouri Botanical Garden Press, Saint Louis.

Steven C. 1812. Catalogue des plantes rares on nouvelles, observées pendant voyage autour du Caucase oriental. *Mémoires de la Société Impériale des Naturalistes de Moscou* **3**: 244–270.

Tonin R, Gerdol R & Wellstein C. 2020. Intraspecific functional differences of subalpine plant species growing in low-altitude microrefugia and high-altitude habitats. *Plant Ecology* **221**(3): 155–166.

Violle C, Enquist BJ, McGill BJ, Jiang LIN, Albert CH, Hulshof C, Jung V & Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**(4): 244–252.

Wellstein C, Chelli S, Campetella G, Bartha S, Galiè M, Spada F & Canullo R. 2013. Intraspecific phenotypic variability of plant functional traits in contrasting mountain grasslands habitats. *Biodiversity & Conservation* **22**(10): 2353–2374.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**(2): 213–227.

Westoby M, Falster DS, Moles AT, Vesk PA & Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology & Systematics* **33**(1): 125–159.

Westoby M, Leishman M & Lord J. 1996. Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society B: Biological Sciences* **351**(1345): 1309–1318.

Williams L, Zazanashvili N, Sanadiradze G & Kandaurov A (eds.). 2006. *Ecoregional Conservation Plan for the Caucasus. WWF, KfW, BMZ, CEPF, MacArthur Foundation. Tbilisi*. Retrieved from: http://assets.panda.org/downloads/ecp_second_edition.pdf

Wright IJ, Reich PB & Westoby M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high and low rainfall and high and low nutrient habitats. *Functional Ecology* **15**(4): 423–434.

Zazanashvili N, Garforth M, Jungius H, Gamkrelidze T & Montalvo Ch (eds.). 2012. *Ecoregion Conservation Plan for the Caucasus.* Revised and updated edition. WWF, KfW, Federal Ministry for Economic Cooperation and Development. Tbilisi.

REZIME

Botanica SERBICA

Intraspecijska varijabilnost određenih funkcionalnih karakteristika *Trigonocaryum involucratum* (Steven) Medw., endemične vrste sa Kavkaza

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Osobine vrsta su korišćene za predikciju odgovora biljnih vrsta i biljnih zajednica na sredinske gradijente. Istraživali smo površinu lista (LA), specifičnu površinu lista (SLA), broj cvetnih izdanaka i masu semena endmeične kavkaske vrste *Trigonocaryum involucratum* duž gradijenta nadmorskih visina. Studija je imala dva osnovna cilja: (1) upoređivanje intrapopulacionog i interpopulacionog variranja funkcionalnih osobina biljaka; (2) istraživanje zavisnosti između visine i vrednosti osobina, kao i variranja tih vrednosti. Podatke smo sakupili u nekoliko populacija u Dagestanu (Ruska federacija), gde vrsta ima visinski gradijent od 1000 m. Intraspecijska varijabilnost vrednosti osobina je istraživana pomoću standardnih statističkih analiza (One-way ANOVA i linearna regresiona analiza). Vrednost osobina je uglavnom imala visoku inter-populacionu varijabilnost (više od 90% za svaku od vrednosti osobina poređenu sa intra-populacionom varijabilnošću svake osobine) ukazujući na adaptaciju populacija osobinama staništa. Mnogo veća intra- u odnosu na inter-populacionu varijabilnost specifične površine lista ukazuje na lokalni diverzitet mikro-staništa i može poslužiti kao puffer stresa izazvanog budućim klimatskim promenama. Sve vrednosti osobina lista su negativno slabo ili umereno korelisane sa nadmorskom visinom. Negativna korelacija verovatno ukazuje na određeno povećanje ograničavajućeg uticaja visinskog gradijenta povezanog sa promenama temperature, dostupnosti nutrijenata, sadržaja vode i jakog sunčevog zračenja. U cilju donošenja sigurnijih zaključaka o intraspecijskoj varijabilnosti vrste *T. involucratum*, neophodna je šira studija vrsta duž njihovog visinskog gradijenta.

Ključne reči: funkcionalne osobine lista, specifična povšina lista, *Myosotis involucrata*, Dagestan, severni Kavkaz