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MORPHOLOGICAL DIFFERENTIATION OF *POLYGONUM VIVIPARUM* (POLYGONACEAE) IN EUROPEAN POPULATIONS

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Abstract. The variation of *Polygonum viviparum* L. in Europe was studied in 584 plants sampled from 14 populations at different altitudes and from different substrates in the Carpathians, Alps, Dinaric Alps, Pyrenees and Scandinavian Mts. The samples were analyzed biometrically, using 12 measured stem and inflorescence characters and 10 characters calculated from those 12. The obtained ranges of values were only slightly wider than those given in the literature. All characters significantly differed between populations and six characters were statistically significant in identifying differences between regions. Altitude, substrate and the interactions between them significantly affected the differences in characters between samples. The values of most of the measured characters were lower in samples from higher locations and on poor substrate than in those from lower localities and on rich substrate. Substrate type affected the calculated characters less but it influenced the shift between vegetative and generative reproduction. Multidimensional analyses confirmed the proximity of samples from regions either geographically close or linked via routes of postglacial migrations, despite altitude and substrate differences between them.

Key words: arctic-alpine plants, biogeography, biometry, plant morphology, plant variation, vegetative reproduction

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INTRODUCTION

Polygonum viviparum L. (Polygonaceae) is a circumpolar arctic-alpine plant (Zając & Zając 2009). It is a perennial geophyte with short rhizomes giving rise to erect unbranched leafy stems with slender inflorescence spikes at the top (Pawłowski 1956; Webb & Chater 1964). The species is known for its frequent asexual – 'viviparous' – reproduction by bulbils formed in place of flowers (Wookey *et al.* 1994). The bulbils are red or brown, a character apparently not associated with any other traits of the plant (Dormann *et al.* 2002). Despite the dominance of vegetative propagation, medium to high genetic diversity has been recorded in alpine and subarctic populations from Europe (Law *et al.* 1983; Bauert 1993, 1996) and the Rocky Mountains (Diggle *et al.* 1998). Its seeds are recorded only occasionally, primarily due to a low fertilization rate and abortion of young sporophytes (Diggle *et al.* 2002), but its seed production is enough to maintain the observed genetic diversity (Diggle *et al.* 1998).

The species is tolerant to $CaCO_3$ and to pH from 6.5 to 9.0, but its occurrence is limited to harsh climatic conditions; it grows in arctic tundra or in the (subalpine) alpine zone in mountains, on meadows and open areas (Wookey *et al.* 1994; Diggle 1997; Diggle *et al.* 1998; Totland & Nyléhn 1998).

Several studies have described the effect of the environment on *P. viviparum* morphology. Warmer conditions appear to have only a weak or even no influence on the width of the largest leaf on the stem or on the number of flowers and bulbils (Totland & Nyléhn 1998; Gugerli & Bauert 2001). In one study, experimentally increased mean temperature did not influence vegetative parameters significantly but caused allocation of biomass to reproductive structures (Wookey *et al.* 1994). In plants grown under experimentally increased temperature in open-top chambers, bulbil biomass and flowering stem height were increased (Gugerli & Bauert 2001). The overall impact of temperature on plants is difficult to assess, particularly in cold climates. Chapin III (1983) concluded that temperature does not strongly limit plant growth in the Arctic. It is generally known that in the mountains of Central Europe plant size decreases with altitude (Fabbro & Körner 2004), and this has been confirmed for *Polygonum viviparum* (Bauert 1993).

Allocation of biomass to reproductive organs is a very important parameter for plants. *Polygonum viviparum* shows a trade-off between sexual and asexual reproduction reflected in a negative correlation between number of flowers and number of bulbils (Totland & Nyléhn 1998). The results for these traits are ambiguous, however: an increase in allocation to vegetative reproduction with increasing altitude has been reported in *Polygonum viviparum* from the Swiss Alps (Bauert 1993), but in the Qinghai-Tibet Plateau sexual reproduction increased with elevation (Fan & Yang 2009). It has also been suggested that growing season length influences the mode of reproduction: in the mountains of southern Japan, the ratio of flowers to bulbils was found to be smaller in plants from places where snow melted later (Tomita & Masuzawa 2010).

The present European arctic-alpine range of *Polygonum vivparum* arose as a consequence of glacial and postglacial migrations. The observed intraspecific variability of arctic-alpine plants is the result of these migrations, and recent molecular studies of this variability have revealed the phylogeography of several arctic-alpine species (Skrede *et al.* 2006; Schönswetter *et al.* 2007; Alsos *et al.* 2009). The question of whether this isolation leads to variability on the morphological level is much less well investigated. Recent research on the morphological diversity of two arctic-alpine plants (*Salix herbacea*, *S. reticulata*) within their European range indicated that the biogeographic structure of this variation was consistent with existing proposals for pathways of the plants' migrations (Marcysiak 2012a, b).

Current findings on the biogeography of arctic-alpine species and the above-mentioned studies suggest a number of working hypotheses for this study, formulated below.

Populations of *P. viviparum* from isolated mountain ranges should show morphological differences. The differences should be greater between more distant massifs than between populations connected with migration routes. Environmental factors may influence species morphology, so plants from populations growing in the subalpine zone should be larger than those from the alpine zone, substrate rich in calcium (limestone, schist) should positively affect plant size, environmental factors should have a stronger effect on the size of the plant and its parts than on its shape, and a trade-off between vegetative and generative reproduction should be evident.

MATERIAL AND METHODS

MATERIAL AND MEASUREMENTS

Fourteen samples each consisting of 19–55 complete flowering stems of *P. viviparum*, provided a total of 584 individuals (Table 1). Plants growing more than three meters apart were sampled to minimize the possibility of collecting the same genet. The sampled populations grew on limestone, granite or schist at sites in distant regions: the Southern Carpathians (CS), Western Carpathians (CW), Central Alps (AC), Northern Alps (AN), Western Alps (AW) Dinaric Alps (AD), Pyrenees (P) and Scandinavian Mountains (SW) (Fig. 1). The plant material was dried and is preserved in the herbarium of the Department of Botany, Kazimierz Wielki University in Bydgoszcz, Poland.

For analyses, samples were divided into groups with regard to substrate and altitudinal zone: P – growing on poor granite bedrock, R – growing on substrate rich in calcium (limestone or schist); and SA – growing in subalpine zone, A – growing in alpine zone (Table 1). The 22 analyzed characters (Table 2) were selected specifically for the study, some following already published data on the diversity of *P. viviparum* (Law *et al.* 1983; Bauert 1993; Totland & Nyléhn 1998; Gugerli & Bauert 2001; Fan & Yang 2009). Measurements were taken from dried plants with the use of standard graph paper. Character values (means ±SD) are in APPENDIX 1.

ANALYSES

The unimodality of data was assessed with frequency histograms, then descriptive statistics were calculated for the entire data set, for regions, for particular samples and for groups of samples (SA, A, P, R). The level of character variation was tested with variation coefficients (Cv = 100SD/M), separately for the whole data set, dis-

Table 1. Collection data for the studied *Polygonum viviparum* L. populations. SA – subalpine; A – alpine, P – poor, granite substrate; R – substrate rich in calcium

Location of population	Acronym	Number of individuals	Altitude [m a.s.l.]	Altitudinal zone	Substrate	N [°]	E [°]
Southern Carpathians, Romania, Parâng Mts.	CS	19	2390	A	P	42.354	23.524
Western Carpathians, Poland, Tatra Mts., Kondracka Przełęcz	CW1	50	1700	SA	R	49.263	19.954
Western Carpathians, Slovak Rep., Tatra Mts., Rysy	CW2	19	2130	A	P	49.174	20.079
Dinaric Mountains, Montenegro, Komovi massif	AD	28	2345	A	R	42.687	19.669
Central Alps, Austria, Oetztal, Obergurgl	AC1	44	2042	SA	P	46.880	11.041
Central Alps, Austria, Oetztal, Kreuz Kogel	AC2	50	2300	SA	P	46.842	10.895
Central Alps, Austria, Oetztal, Gaislacher Kogel	AC3	49	2820	A	P	46.939	10.969
Northern Alps, Austria, Grubigstein	AN	53	2100	A	R	47.382	10.842
France, Western Alps, Col du Galibier	AW	33	2620	A	R	42.056	6.405
Andorra, Pyrenees, Rialb	P1	34	2330	SA	R	42.636	1.568
Andorra, Pyrenees, Arcalis	P2	54	2600	A	P	42.617	1.485
Andorra, Pyrenees, Casamanya	P4	46	2700	A	R	42.584	1.568
Andorra, Pyrenees, Casamanya	P3	50	2700	A	R	42.584	1.568
Norway, Hardangevidda, Hallingskarvet	SW	55	1300	SA	R	60.559	8.079

tinguished regions, site groups and particular samples. To find highly related or redundant traits, correlations between character values within the whole data set were assessed using Pearson's correlation coefficient.

Student's *t* test was performed to compare pairs of groups SA-A and P-R to find the characters differing significantly between groups. Univariate analysis of variance (ANOVA/ANCOVA) was performed to assess the significance of differences between samples. The level of difference between regions and between samples within regions was determined by nested ANOVA. Two-way ANOVA was used to examine the effects of substrate type, altitude zone, and the interaction between them. The results of this variance analysis are given in least squares means charts (Sokal & Rolf 2003).

Discriminant analysis was performed to determine multidimensional relations between samples (Sokal & Rohlf 2003). Under the assumption that the calculated characters are more stable and less sensitive to external factors (Marcysiak 2012c), they were used as the basis of this analysis.

RESULTS

The stem of *P. viviparum* was *ca* 143 mm long and had 2.72 leaves on average. The upper leaf was 17.5 mm long and 2.3 mm wide, and the biggest leaf 29 mm long and 5.6 mm wide. Some plants from the Central and Northern Alps were devoid of the small upper leaf. The biggest leaf petiole (*blp*) was 9.9 mm long on average and was present on all plants from CS, AD, CW2, WA, P2 and P4. In the other samples, *blp* was missing from 2–34% of individuals. Of the 584 plants, 560 possessed the upper leaf (24 did not), only 131 individuals pos-

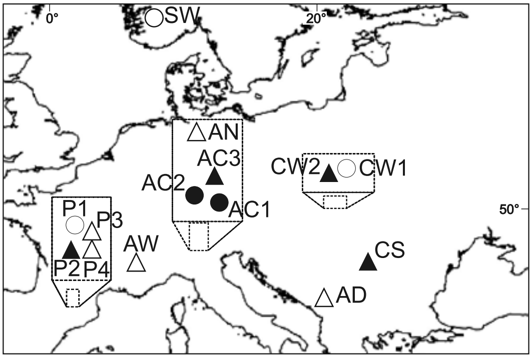


Fig. 1. Location of *Polygonum viviparum* L. samples; triangles – alpine zone; circles – subalpine zone; black – samples collected from poor granite substrate; white – samples collected from calcium-rich substrate. CS – Southern Carpathians CW – Western Carpathians, AD – Dinaric Alps, AC – Central Alps, AN – Northern Alps, AW – Western Alps, P – Pyrenees, SW – Scandinavian Mountains.

Table 2. Analyzed characters of *Polygonum viviparum* L. and their statistical characteristics.

Character category	Character	Acronym	M	Min	Max	Cv
Measured characters of stem and leaves	Length of stem [mm]	*stl*	143.15	28.00	396.00	40.86
	Number of leaves on stem	*ln*	2.72	1.00	5.00	24.72
	Length of upper leaf blade [mm]	*ull*	17.47	2.00	66.00	55.13
	Width of upper leaf blade [mm]	*ulw*	2.26	1.00	15.00	73.65
	Length of biggest leaf blade [mm]	*bll*	29.41	3.00	71.00	35.77
	Width of biggest leaf blade [mm]	*blw*	5.66	1.00	26.00	51.92
	Petiole length of biggest leaf [mm]	*blp*	9.91	1.00	43.00	74.29
Calculated characters of stem and leaves	Number of leaves/stem length	*ln/stl*	0.02	0.01	0.11	56.36
	Length of upper leaf blade/stem length	*ull/stl*	0.13	0.01	0.52	52.94
	Length/width of upper leaf	*ull/ulw*	8.71	0.47	33.00	42.33
	Length of biggest leaf blade/stem length	*bll/stl*	0.23	0.02	0.72	42.80
	Length/width of biggest leaf	*bll/blw*	6.23	0.31	21.00	53.28
	Proportion of petiole in biggest leaf length	*blp/bllp*	0.25	0.02	0.77	55.74
Measured and counted characters of spike	Length of spike [mm]	*spl*	34.94	10.00	84.00	40.78
	Length of part of spike with bulbils [mm]	*sp-bl*	28.70	5.00	83.00	42.87
	Number of flowers	*fn*	7.05	0.00	50.00	142.73
	Number of bulbils	*bn*	27.16	2.00	86.00	42.55
	Number of flower and bulbils	*fbn*	34.25	4.00	86.00	36.72
Calculated characters of spike	Spike length/stem length	*spl/stl*	25.60	10.24	80.00	29.06
	Number of bulbils/number of flowers and bulbils	*bn/fbn*	0.82	0.09	1.00	27.85
	Number of bulbils/length of part of spike with bulbils	*bn/spbl*	0.99	0.07	2.36	31.48
	Number of flowers and bulbils/length of spike	*fbn/spl*	1.02	0.12	2.33	27.14

sessed the upper leaf petiole, and 512 possessed the biggest leaf petiole. The spike was almost 35 mm long and yielded 27 bulbils and 7 flowers on average. Sample CA2 did not have any flowers on the spikes. The share of specimens lacking flowers in particular samples ranged from 2% to 60%; 339 individuals had flowers on the spikes.

Analysis of the frequency histograms confirmed that the distributions of the analyzed characters in the whole data set were similar to normal but slightly right-skewed and narrow. This trend was evident for the whole set of data, for particular regions, altitudinal and site groups (data not shown).

The Cv values calculated for the whole data set were highest for *fn, ulw* and *blp*, and most stable for *ln*, *fbn/spl* and *bn/fbn* (Table 2).

Many of the characters depended on each other and these relationships varied between the examined populations. Correlations between *stl* and *ln/stl*, *blp* and *blp/bllp* or *spl* and *sp-bl* were most common in the analyzed data set. The most frequent linkages were those between stem length (*stl*) and spike length (*spl*), all the measured characters pertaining to them, and the characters calculated from them (Table 3).

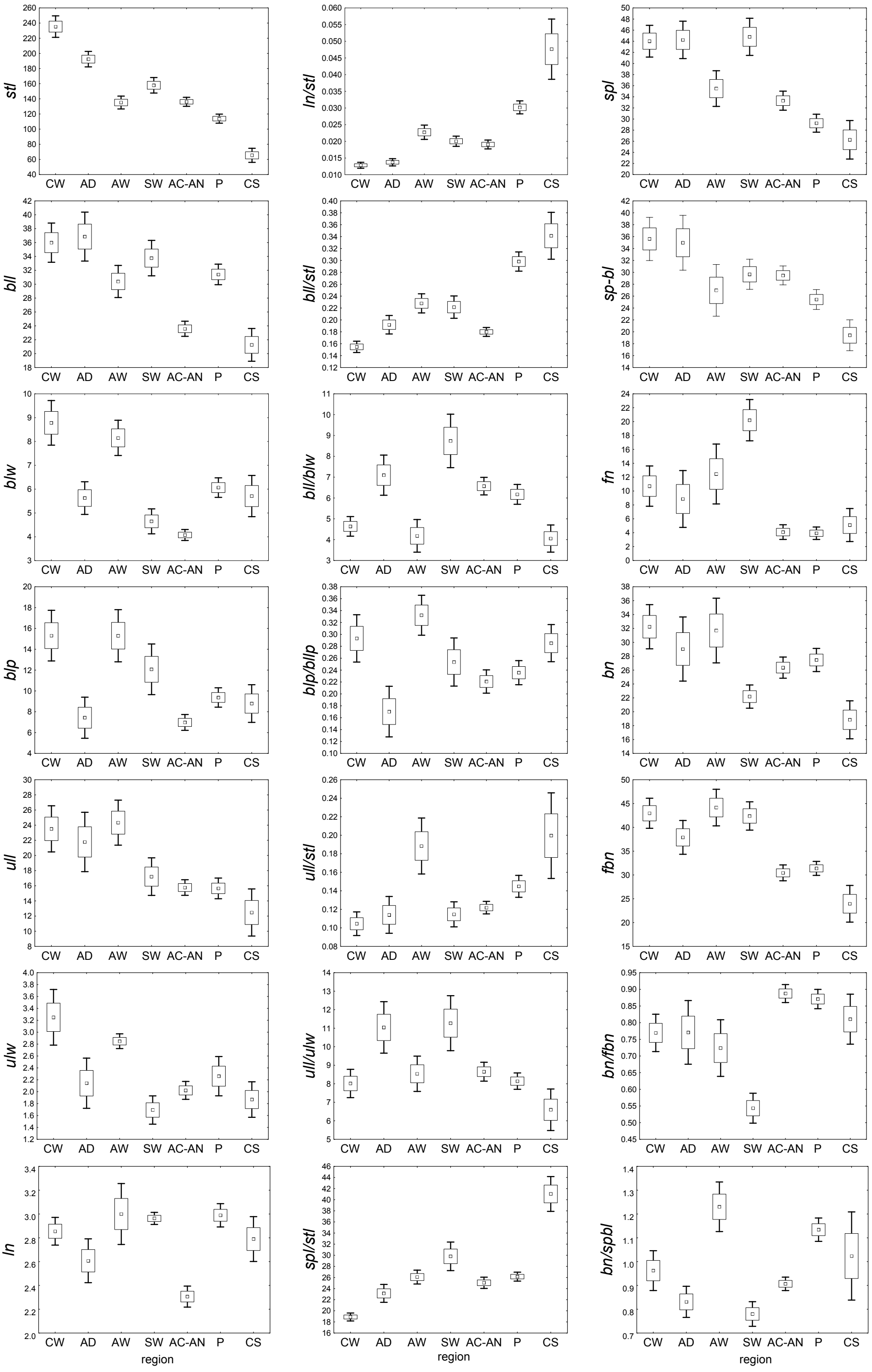
Certain character values were similar between some of the regions. Plants from the Western Carpathians (CW), Dinaric Alps (AD) and Western Alps (AW) were tallest, and those from the Central and Northern Alps (AC, AN), Pyrenees (P) and Southern Carpathians (CS) were smaller (Fig. 2).

The groups connected with altitudinal zones SA-A differed significantly with regard to 16 characters, both measured and calculated, but the differences between groups of substrate type P-R were related mainly to measured characters (Table 4).

ANOVA indicated that all the characters differed significantly between populations (not shown). Nested ANOVA showed that variation

Table 3. Correlations between characters of *Polygonum viviparum* L. for the whole data set: italics – correlations significant at p<0.01, bold – medium and strong correlations; character abbreviations as in Table 2.

Character	*stl*	*ln*	*ull*	*ulw*	*bll*	*blw*	*blp*	*ln/stl*	*ull/stl*	*ull/ulw*	*bll/stl*	*bll/blw*	*blp/bllp*	*spl*	*sp-bl*	*fn*	*bn*	*fbn*	*spl/stl*	*bn/fbn*	*bn/spbl*
ln	-0.04																				
ull	***0.49***	*-0.16*																			
ulw	*0.24*	-0.08	***0.47***																		
bll	***0.63***	0.15	*0.38*	0.11																	
blw	*0.32*	0.13	*0.30*	*0.24*	*0.25*																
blp	*0.30*	*0.23*	*0.35*	*0.18*	*0.18*	***0.41***															
ln/stl	***-0.78***	***0.50***	***-0.44***	-0.09	***-0.40***	-0.14	-0.14														
ull/stl	*-0.23*	-0.12	***0.64***	*0.26*	-0.05	0.04	0.09	*0.18*													
ull/ulw	0.15	0.08	*0.32*	*-0.37*	*0.21*	-0.05	*0.18*	-0.14	*0.27*												
bll/stl	***-0.55***	*0.23*	*-0.21*	-0.12	*0.23*	-0.06	-0.14	***0.64***	*0.28*	-0.02											
bll/blw	0.05	0.01	-0.05	*-0.20*	*0.39*	**-0.57**	*-0.31*	-0.06	-0.05	*0.23*	0.29										
blp/bllp	0.02	*0.18*	0.16	0.15	*-0.27*	0.30	***0.83***	0.05	0.11	0.06	-0.27	***-0.53***									
spl	***0.73***	-0.02	**0.46**	0.11	***0.58***	0.15	*0.27*	**-0.59**	-0.07	*0.33*	-0.29	*0.20*	-0.01								
sp-bl	***0.63***	*-0.20*	0.34	0.10	***0.40***	0.06	0.13	-0.59	-0.11	*0.19*	-0.36	0.11	-0.07	***0.77***							
fn	*0.32*	*0.23*	0.28	0.04	***0.41***	0.11	*0.29*	*-0.16*	0.03	*0.26*	0.04	*0.23*	0.09	***0.51***	-0.02						
bn	***0.45***	-0.07	0.25	0.09	*0.29*	0.12	*0.18*	***-0.40***	-0.08	0.13	*-0.24*	-0.01	0.03	***0.45***	***0.68***	-0.14					
fbn	***0.56***	0.15	**0.40**	0.09	***0.54***	0.17	*0.36*	*-0.39*	-0.02	*0.31*	-0.12	*0.19*	0.10	***0.73***	***0.43***	***0.76***	***0.53***				
spl/stl	*-0.37*	0.02	-0.06	*-0.15*	-0.05	-0.20	-0.07	*0.36*	*0.27*	0.14	***0.46***	*0.25*	-0.08	*0.28*	0.10	*0.23*	-0.05	*0.16*			
bn/fbn	-0.09	*-0.29*	-0.12	0.01	*-0.27*	-0.07	*-0.19*	-0.06	-0.05	*-0.16*	*-0.18*	*-0.20*	-0.05	*-0.26*	*0.29*	***-0.88***	***0.47***	***-0.45***	*-0.21*		
bn/spbl	*-0.27*	*0.26*	-0.11	0.01	-0.11	0.10	0.08	*0.37*	0.08	-0.06	*0.26*	-0.15	0.14	***-0.41***	***-0.49***	-0.08	*0.24*	0.09	-0.15	0.09	
fbn/spl	-0.21	*0.29*	-0.09	0.03	-0.01	0.06	*0.16*	*0.33*	0.04	-0.03	*0.28*	-0.03	*0.17*	*-0.33*	***-0.43***	*0.31*	0.13	*0.35*	*-0.16*	*-0.28*	***0.74***


stl
ln/stl
spl
bll
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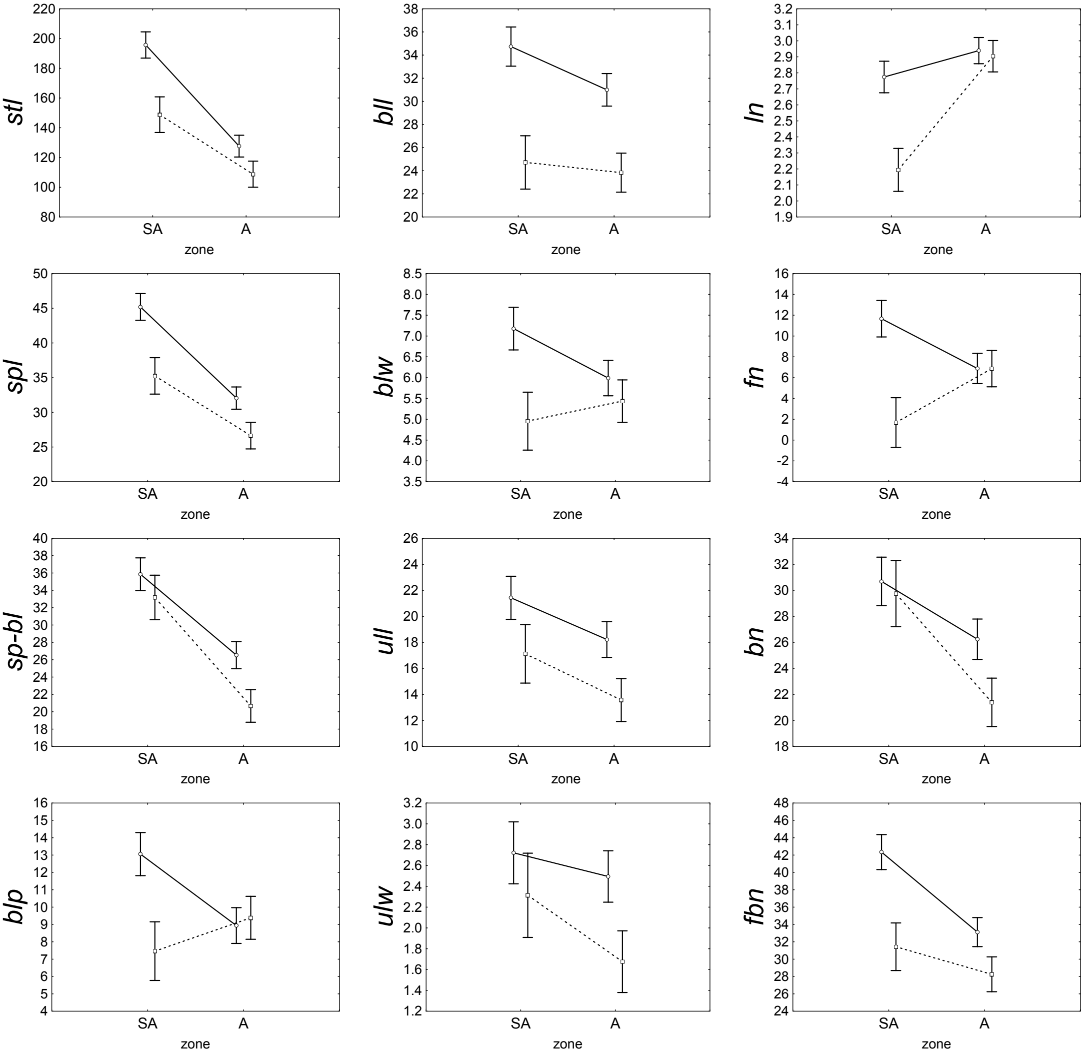

Fig. 3. ANOVA results – interaction between altitude and substrate group for measured and calculated characters of *Polygonum viviparum* L., based on least square means; SA – alpine zone; A – alpine zone; dashed line – samples collected from poor granite substrate; solid line – samples collected from calcium-rich substrate; character abbreviations as in Table 2.

was highest within samples, that is, large differences between individual plants in the samples (Table 5). Six characters significantly distinguished regions; the percentage of variance of these characters (*bll*, *blw*, *blp*, *ull/stl*, *spl/stl*, *bn/spbl*) was greater between regions than between populations within regions.

Altitudinal zone had a stronger effect than substrate type on the differences between characters, and the interaction between the two factors affected

←

Fig. 2. Mean values for characters of *Polygonum viviparum* L. for regions: CW – Western Carpathians, AD – Dinaric Alps, AW – Western Alps, SW – Scandinavian Mountains, AC-AN – Central and Northern Alps, P – Pyrenees, CS – Southern Carpathians; character acronyms as in Table 2; point – arithmetic mean; box – standard error; whiskers – 1.96 standard error.

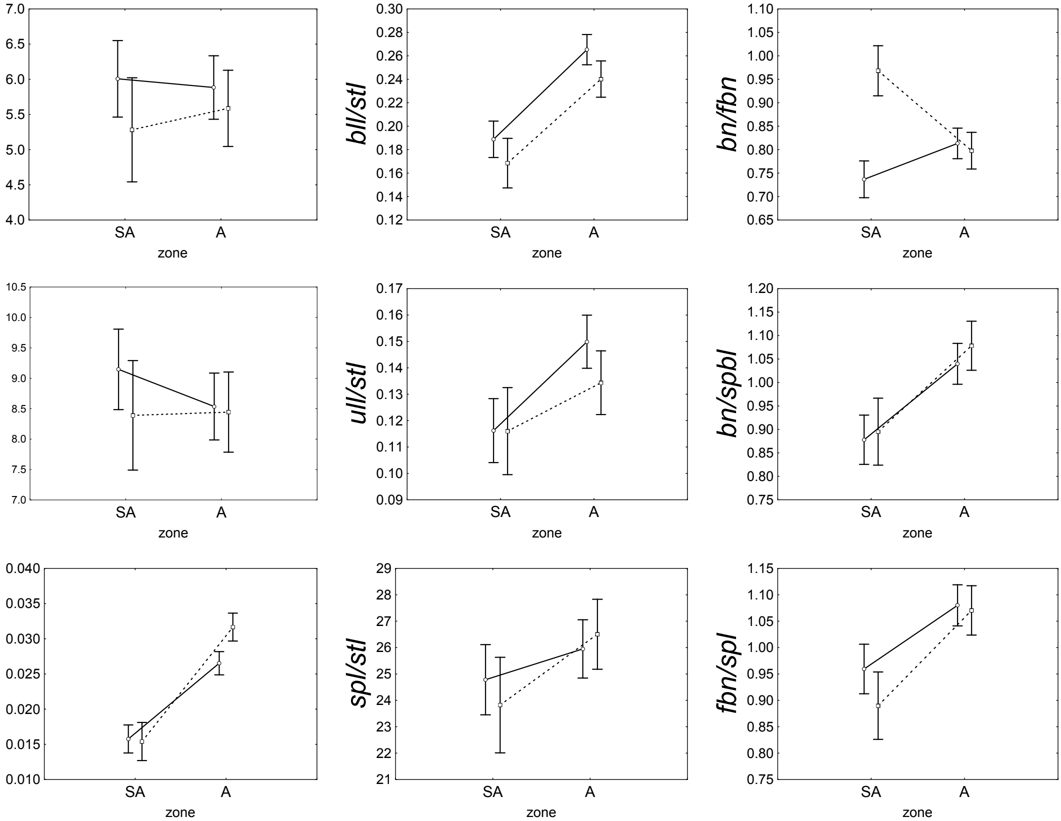

Fig. 4. ANOVA results – graphs of interaction between altitude and substrate groups for calculated characters of *Polygonum viviparum* L., based on least square means; SA – alpine zone; A – alpine zone; dashed line – samples collected from poor granite substrate; solid line – samples collected from calcium-rich substrate; character abbreviations as in Table 2.

the characters the least. The values of most of the measured characters were lower in the alpine zone and on poor substrate than in the subalpine zone and on rich substrate. The substrate-based differences were less evident for calculated characters, whose values usually were lower in the subalpine zone (Figs 3 & 4).

Multidimensional grouping in discriminant analysis clustered together the samples from the Western Carpathians, Northern and Central Alps and Dinaric Alps, regardless of substrate type or altitude. The Pyrenean samples also clustered together except for sample P1, which joined the Alpine–Carpathian group, and the population from the Western Alps took a position between those two groups. The samples from the Western Scandinavia and the Southern Carpathians were the most distant (Fig. 5). The first canonical variable described over 37% of variability and was most strongly correlated with *ln/stl*, *bll/stl* and *spl/stl*; the second, determining the distinctiveness of the SW sample, was most strongly connected with *bn/fbn*.

DISCUSSION

Most of the characters were selected specifically for the study, and morphological analyses of the species are scarce, so only a few characters could be compared with other data. The range of values of measured *Polygonum viviparum* characters in this study was only slightly wider than given in floras and other published data. Stem length varied from 28 to 396 mm and spike length from 10 to

Table 4. Results of t-test for two pairs of groups of *Polygonum viviparum* L.; statistically significant results are bolded; SA – subalpine zone, A – alpine zone; P – poor granite substrate; R – calcium-rich substrate, df – degrees of freedom, p – probability; character acronyms as in Table 2.

Character	Altitudinal zone					Substrate type				
	Mean		t	df	p	Mean		t	df	p
	SA	A				R	P			
stl	**176.00**	**121.48**	**12.3944**	**581**	**0.0000**	**155.10**	**125.52**	**6.18888**	**581**	**0.0000**
ln	**2.45**	**2.89**	**-8.1545**	**581**	**0.0000**	**2.84**	**2.54**	**5.47540**	**581**	**0.0000**
ull	**19.73**	**16.06**	**4.4778**	**558**	**0.0000**	**19.28**	**14.74**	**5.60918**	**558**	**0.0000**
ulw	**2.53**	**2.09**	**3.0415**	**558**	**0.0025**	**2.51**	**1.88**	**4.46482**	**558**	**0.0000**
bll	**30.80**	**28.49**	**2.6061**	**581**	**0.0094**	**32.83**	**24.34**	**10.41545**	**581**	**0.0000**
blw	5.95	5.49	1.8742	581	0.0614	**6.24**	**4.84**	**5.78162**	**581**	**0.0000**
blp	**11.23**	**9.07**	**3.2643**	**510**	**0.0012**	**10.63**	**8.71**	**2.88858**	**510**	**0.0040**
ln/stl	**0.02**	**0.03**	**-13.6097**	**581**	**0.0000**	0.02	0.02	-2.11908	581	0.0345
ull/stl	**0.12**	**0.14**	**-3.7322**	**578**	**0.0002**	0.14	0.13	1.65714	578	0.0980
ull/ulw	8.96	8.53	1.3733	571	0.1702	8.83	8.51	1.00702	571	0.3144
bll/stl	**0.18**	**0.26**	**-9.7525**	**580**	**0.0000**	**0.24**	**0.21**	**3.48068**	**580**	**0.0005**
bll/blw	6.23	6.22	0.0067	580	0.9947	6.28	6.15	0.47234	580	0.6369
blp/bllp	0.25	0.24	1.2840	510	0.1997	0.24	0.26	-1.55005	510	0.1217
spl	**41.19**	**30.54**	**10.5997**	**581**	**0.0000**	**37.51**	**30.74**	**6.38919**	**581**	**0.0000**
sp-bl	**35.18**	**24.39**	**11.4351**	**575**	**0.0000**	**30.59**	**26.02**	**4.46539**	**575**	**0.0000**
fn	7.12	7.00	0.1417	581	0.8874	**8.49**	**4.91**	**4.28662**	**581**	**0.0000**
bn	**31.19**	**24.56**	**7.0478**	**581**	**0.0000**	**28.52**	**25.24**	**3.38571**	**581**	**0.0008**
fbn	**38.31**	**31.56**	**6.5722**	**581**	**0.0000**	**37.02**	**30.15**	**6.70798**	**581**	**0.0000**
spl/stl	**24.46**	**26.35**	**-3.0278**	**581**	**0.0026**	25.51	25.72	-0.33187	581	0.7401
bn/fbn	0.84	0.80	1.8674	581	0.0623	**0.79**	**0.86**	**-3.64666**	**581**	**0.0003**
bn/spbl	**0.90**	**1.06**	**-6.0347**	**575**	**0.0000**	0.98	1.01	-1.07756	575	0.2817
fbn/spl	**0.94**	**1.07**	**-5.5848**	**581**	**0.0000**	1.03	1.00	1.45956	581	0.1450

84; European literature data gives 50–400 mm and 20–75 mm respectively (Pawłowski 1956; Webb & Chater 1964; Villar 1990; Bauert 1993). The number of bulbils ranged from 2 to 86; in other studies that number fluctuates around 20–40 (Wookey *et al.* 1994; Totland & Nyléhn 1998; Gugerli & Bauert 2001). The differences probably are attributable to the large and multi-sourced pool of samples used in this study.

BIOGEOGRAPHIC STRUCTURE

Although many aspects of *Polygonum viviparum* have been examined there has been no phylogeographic analysis of it, so the similarities between regions found in my work can be compared only with general findings on postglacial migrations. The closeness of the *P. viviparum* populations from the Northern and Central Alps well fits the division of the Alps obtained from phylogeographic studies and with the posited distribution of glacial refugia (Schönswetter *et al.* 2005). Previous studies on the biogeography of the Alps showed the division of the massif into western and central-eastern parts, the latter further divided into central and eastern parts, evident on both interspecific and intraspecific levels (Schönswetter *et al.* 2005, Thiel-Egenter *et al.* 2011). Studies have also suggested that the phylogeographic structure of Alpine plant species is associated with substrate (Alvarez *et al.* 2009), the distribution of bedrock types and refugia on the margins of the Alps (Schönswetter *et al.* 2005). However, interspecific differentiation on the molecular level between the western and central-eastern parts of the massif has been found in plant species bound to siliceous, calcareous and intermediate substrate (Alvarez *et al.* 2009). This may explain the evident distance between

Table 5. Results of nested ANOVA of *Polygonum viviparum* characters (% – percentage of total variance, SS – sum of squares, MS – mean square, df – degrees of freedom, F – F statistics, Prob > F – probability).

Character	Component	%	SS	MS	df	F	Prob > F
bll	between regions	20.511	13648.90	2274.810	6	3.9377	0.0439*
	between samples in regions	12.067	4963.44	709.063	7	8.9541	<00001*
	within samples	67.423	44979.10	79.1886	568		
blw	between regions	27.197	1227.07	204.5110	6	6.4158	0.0113*
	between samples in regions	8.222	271.196	38.7423	7	6.6580	<0.0001*
	within samples	64.581	3305.12	5.81887	568		
blp	between regions	18.441	4734	789.000	6	5.6646	0.0151*
	between samples in regions	5.3	1107.98	158.283	7	3.6233	0.0008*
	within samples	76.26	21711.4	43.685	497		
ull/stl	between regions	10.172	0.29666	0.04944	6	3.6261	0.0486*
	between samples in regions	5.329	0.11236	0.01605	7	3.7810	0.0005*
	within samples	84.499	2.39865	0.00425	565		
spl/stl	between regions	26.503	8014.83	1335.8	6	5.5190	0.0178*
	between samples in regions	9.939	2072.03	296.004	7	7.9502	<0.0001*
	within samples	63.557	21147.9	37.2323	568		
bn/spbl	between regions	18.907	9.71695	1.61949	6	6.1809	0.0113*
	between samples in regions	5.116	2.15709	0.30816	7	3.9505	0.0003*
	within samples	75.976	43.838	0.078	562		

samples from the Central and the Western Alps in my research.

Relationships between the Alpine and the Western Carpathian plant populations have been described for several species as proof of a shared postglacial origin (Zhang *et al.* 2001; Kropf *et al.* 2003, 2006). The clustering of the samples from the Central Alps and Western Carpathians in my discriminant analysis (Fig. 5) might therefore be interpreted as resulting from their origin in a common refugium.

Likewise, the Alps and mountains in Western Scandinavia were connected with the migration routes of several species (Schönswetter *et al.* 2003; Alsos *et al.* 2009). In my study the samples from the Alps and the Scandinavia grouped with regard to the first discriminant variable (Fig. 5).

During the Pleistocene the Carpathians were far less covered with glaciers than most of the mountain chains of Europe (Kondracki 1978) and could serve as a refugium for alpine plants (Ronikier 2011). Recent phylogeographic studies confirmed the classical biogeographic divisions, with the main boundary between the western and south-eastern parts of the mountains (Ronikier 2011). Thus the observed separateness of the Southern Carpathian sample in my study could be due to protracted isolation of this population.

The overall conclusion is that, in conformity with my working hypothesis, the grouping obtained from discriminant analysis reflects the closeness of samples from regions either geographically close or linked via migration routes despite the differences in altitude and substrate between them. However, molecular studies are needed to confirm the suggestion that the morphological diversity of *P. viviparum* is connected with its postglacial history.

RELATION TO ENVIRONMENTAL FACTORS

The influence of altitude on some characters of *Polygonum viviparum* has been described by other authors for particular massifs (Bauert 1993; Totland & Nyléhn 1998). This study of the whole European geographic range confirmed the decrease of most measured characters with increasing altitude (Fig. 3). Such is common among arctic plants (Fabbro & Körner 2004) and is interpreted as an adaptation to harsh alpine conditions. What may be puzzling is that the effect of altitude on characters differed dramatically between substrate types: biggest leaf width (*blw*), length of petiole of biggest leaf (*blp*) and number of flowers (*fn*) decreased with altitude on the calcium-rich substrate (LS) but increased on granite (GR) (Fig. 3). Was this result influenced by the location of the samples? Only two samples collected on granite in the subalpine zone originated from the Central Alps, so the results might be specific to that massif (Fig. 1). An analysis of all altitude groups on all types of substrate in one mountain range probably would yield a reliable answer but that was not the design of this study. Note that the dependence of bulbil production on environmental factors has been reported (Law *et al.* 1983; Bauert 1993).

The present results did confirm some clear relations between *P. viviparum* characters and substrate type. Most of the measured characters reached higher values for plants from limestone substrate than for those from granite, the only exceptions being number of leaves (*ln*) and biggest leaf petiole (*blp*) in the alpine zone (Fig. 2). Previous analyses have pointed out the influence of substrate type on species biodiversity, migration, and the possibility of survival in refugia for a population of a species with specific substrate requirements (Schönswetter *et al.* 2005; Arnesen *et al.* 2007; Alvarez *et al.* 2009); in general, biodiversity is greater on limestone (Wohlgemuth & Gigon 2003).

The results also demonstrated the greater stability of calculated characters than measured characters. The greater reliability of calculated characters versus morphological traits has been noted in different species (Kremer *et al.* 2002; Marcysiak 2012c).

VEGETATIVE VERSUS GENERATIVE REPRODUCTION

Vegetative reproduction is of key importance for the survival of plants in difficult high mountain and arctic conditions; more than 50% of species occurring there reproduce that way (de Witte *et al.* 2012). So far the results on a shift to vegetative or sexual reproduction, which in the case of *P. viviparum* means increased production of bulbils or flowers, are equivocal. Studies of material from the Alps indicated a decrease of sexual reproduction with increasing altitude (Bauert 1993), while results from Norway and the Qinghai-Tibet Plateau showed the opposite trend (Law 1983; Fan & Yang 2009). In my work these relations look different on different substrates, but as mentioned already only two samples from granite substrate and the subalpine zone originated from the Central Alps. Perhaps the declining role of sexual reproduction with increasing elevation is typical for the Alps, in accordance with previous findings (Bauert 1993), or perhaps it is connected with granite substrate.

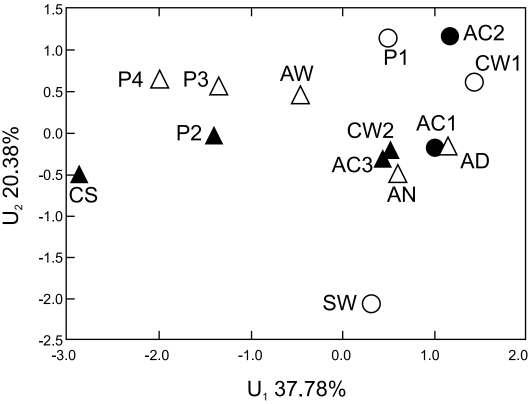

Fig. 5. Results of discriminant analysis for *Polygonum viviparum* L. samples – means of samples on the plane of the first two variables; triangles – alpine zone, circles – subalpine zone, black – samples collected from poor granite substrate, white – samples collected from calcium-rich substrate. For abbreviations see Table 1.

The morphological differentiation of *Polygonum viviparum* in Europe is determined genetically but also depends on environmental factors, among which altitude and substrate fertility play important roles. Substrate type may also influence the shift between vegetative and generative reproduction. Environmental conditions connected with substrate had less of an effect on the calculated characters that describe the shape of the plant.

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