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Phenotypical variation and taxonomic correlates of five closely related Andean species of *Poa* (Poaceae) along geographic and climatic gradients

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Abstract

Poa anfamensis, P. jujuyensis, P.lilloi, P. parviceps and *P. scaberula* (Poaceae) are a group of morphologically similar species. These species inhabit cool grasslands and mesic puna. They are highly polymorphic and their circumscriptions are uncertain, especially the entities around *P. scaberula*. Univariate and multivariate analyses (PCA and DA) were conducted to evaluate the morphological variation among 150 herbarium specimens identified as *P. anfamensis, P. jujuyensis, P. lilloi, P. parviceps* and *P. scaberula*. Forty morphological characters were included and their patterns of variation were analyzed among specimens, together with their relationship with environmental variables, using correlation analysis. The relationships between morphological variation and geographical distance, and climatic variables among specimens, were compared with Mantel permutation tests. Taxa were delimited according to the observed clustering of specimens in the PCA plots and DA, and diagnostic characters were identified. The five taxa showed continuous morphological variation. Morphological variation is explained by geographical and climatic factors such as elevation, geographical distance, latitudinal and longitudinal gradients, temperature and precipitation in the different sites in the Andes. Altitudinal and geographical distance are apparently more decisive factors in phenotypic differentiation and could have played a large role in interspecific differentiation among *Poa* entities, as shown by the stronger and significant association between vegetative and reproductive phenotype and altitudinal distance, and between vegetative and reproductive phenotype and geographical distance. In addition, we observed uncoupling among vegetative and floral characters in *Poa* specimens that grow along environmental gradients; these characters are responding independently to different abiotic forces promoting genetic divergence and speciation. Based on the results, *P. anfamensis* and *P. parviceps* are synonymised with *P. scaberula*, and *P. jujuyensis* is synonymised with *P. lilloi*.

Keywords: environmental gradients, geographic variation, Gramineae, morphological variation, multivariate analysis, reproductive characters, vegetative characters

Introduction

Plant morphology is a function of phenotypic changes in response to geographical variation and local climatic conditions, genetic variation within and among taxa, and the biogeographic history of an individual species. Morphological variation and geographical separation among individuals are also necessary for the formation of subspecies and species (Ellison *et al*. 2004). Individuals within a species typically differ in phenotype, and although some of this variation may be random, a large proportion of this variation may represent adaptive matching of phenotypes to variable environments (Clausen *et al*. 1948). This variation can arise from phenotypic plasticity, in which different morphologies are produced from the same genotypes in different environments (Richards *et al*. 2005, Scheepens *et al*. 2010).

Abiotic and biotic environmental processes acting upon isolated taxa are thought to be key factors in species divergence (Still *et al.* 2005). Processes of geographical divergence occur by isolating mechanisms, in part due to the restriction of gene flow between taxa. Among individuals of a widespread species, different ecological environments and independent evolution of individuals through genetic drift may lead to divergence. Many plant species grow in a range of different habitats and have developed adaptive strategies suited to the particular habitats in which they occur (Coyne & Orr 2004). Several studies have shown that plants growing along altitudinal and latitudinal gradients, and under different climatic conditions, are characterized by fixed, locally adapted phenotypes, which have a genetic background (Linhart & Grant 1996, Briggs & Walters 1997, Hufford & Mazer 2003, Schneller & Liebst 2007).

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The genus *Poa* Linnaeus (1753: 67) includes 575 species occurring mostly in temperate and cool regions of the world (Clayton & Renvoize 1986, Gillespie & Soreng 2005, Giussani *et al.* 2012). The genus is extremely uniform, with numerous infraspecific taxa, marked phenotypic plasticity and wide ecological tolerance (Fernández Pepi *et al.* 2008), resulting in a complex taxonomy. The most recent molecular phylogenetic studies recognize five subgenera; most endemic species of South America are part of subgenus *Poa*, which includes five sections (*Anthochloa* (Nees & Meyen 1835: 14) Soreng & Gillespie (2007: 431), *Dasypoa* (Pilger 1898: 716) Soreng (1998: 187), *Dioicopoa* Desvaux (1854: 413), *Homalopoa* Dumortier (1823: 110, 113) and *Poa*) and an informal group ("Punapoa") (Gillespie & Soreng 2005, Gillespie *et al.* 2007, Soreng *et al.* 2010, Giussani *et al.* 2012). According to Gillespie & Soreng (2005) and Gillespie *et al.* (2007, 2008), *Poa scaberula* Hooker f. (1846: 378) and *P. parviceps* Hackel (1914: 298) are included within section *Dasypoa*, while *P. lilloi* Hackel. (1911: 153) is included in the informal group "Punapoa". *Poa jujuyensis* (Parodi ex Nicora 1997: 143) Giussani, Soreng & Anton (2011: 91) was previously treated as variety of *P. parviceps* (sect. *Dasypoa*) (Nicora 1997). *Poa anfamensis* Negritto & Anton (1998: 159) was recently treated as synonym of *P. scaberula* (sect. *Dasypoa*) in the Flora Argentina (Giussani *et al.* 2012); however, here we treat it at species level to corroborate its identity. These five native species are highly polymorphic and morphologically very similar and are difficult to distinguish from each other. Their distinguishing characters are expressed to varying degrees among specimens, especially in *P. scaberula* (Soreng & Peterson 2012). These characters are spikelets bearing hermaphrodite flowers (monoclines), except *P. lilloi*, which has pistillate and hermaphrodite flowers (gynomonoecious), presence of a callus with short or woolly hairs on the basal florets, lemmas with cilia in the middle or basal portion of the keel, caryopsis strongly adhered to palea and small oval anthers (ca. 0.5 mm long). In addition, the species have overlapping geographic distributions along the Andes from Colombia to southern of Chile and Argentina (Fig. 1). They inhabit cool temperate forests and mesic puna, range in elevation from 0–5004 m, and occur in areas with average annual precipitation ranging from 88.33–2195.83 mm years^{-1} and average temperature from 1.6–16.8°C (Hijmans *et al*. 2005). Across their ranges, climatic and geographic variables such as elevation vary along north-south and east-west gradients.

We investigate the relationship among geographic, climatic and morphological variation among specimens of *P. anfamensis, P. jujuyensis, P. lilloi, P. parviceps* and *P. scaberula*. Our main goal is to establish whether phenotypic variation is associated with environmental and climatic gradients, and whether the specimens of these five closely related Andean species of *Poa* respond morphologically to local environmental conditions. In addition, we use multivariate statistical analysis to reassess the morphological variation among these taxa and clarify the identity of species closely related to *P. scaberula*.

Materials and Methods

Study area

The study area covers 3,368.970 km^2 of the Andes from northwestern South America (Peru) to Patagonian regions of southern Argentina and Chile. Elevation ranges from 0 to 5004 m, average annual precipitation from 88.33 to 2195.83 mm years^{-1} and average temperature from 1.6 to 16.8°C (Hijmans *et al*. 2005). The total distribution of the five species based on geographical coordinates corresponding to each collection site ranges from 1°14' to 52°51'S, and 79°15' to 64°25'W.

Study species

One hundred and fifty herbarium specimens from BAA, CORD, LIL, LP, LPB, SI, USM and US (Thiers 2014) were identified: two as *P. anfamensis*, 19 as *P. jujuyensis*, three as *P. lilloi*, 31 as *P. parviceps* and 95 as *P. scaberula* (Appendix 1). The tentative identifications were based on regional treatments according to the geographic origin of the material (Negritto & Anton 2000, Giussani *et al.* 2012). These specimens were selected to cover the geographic range and the morphological variability of each species. Thirteen vegetative and twenty-seven reproductive morphological characters were analyzed to detect variable characters (Table 1). Vegetative traits were measured on flowering culms. Reproductive traits were measured in complete mature panicles. Spikelet characters were measured in the middle portion of the panicle on hermaphrodite spikelets. Specimens with missing values were excluded.

Climate data

When not available on herbarium specimen labels, the geographic locations of the specimens examined were determined manually using Google Earth. The locations of each specimen were visualized in DIVA-GIS 7.5 (Hijmans *et al.* 2012)

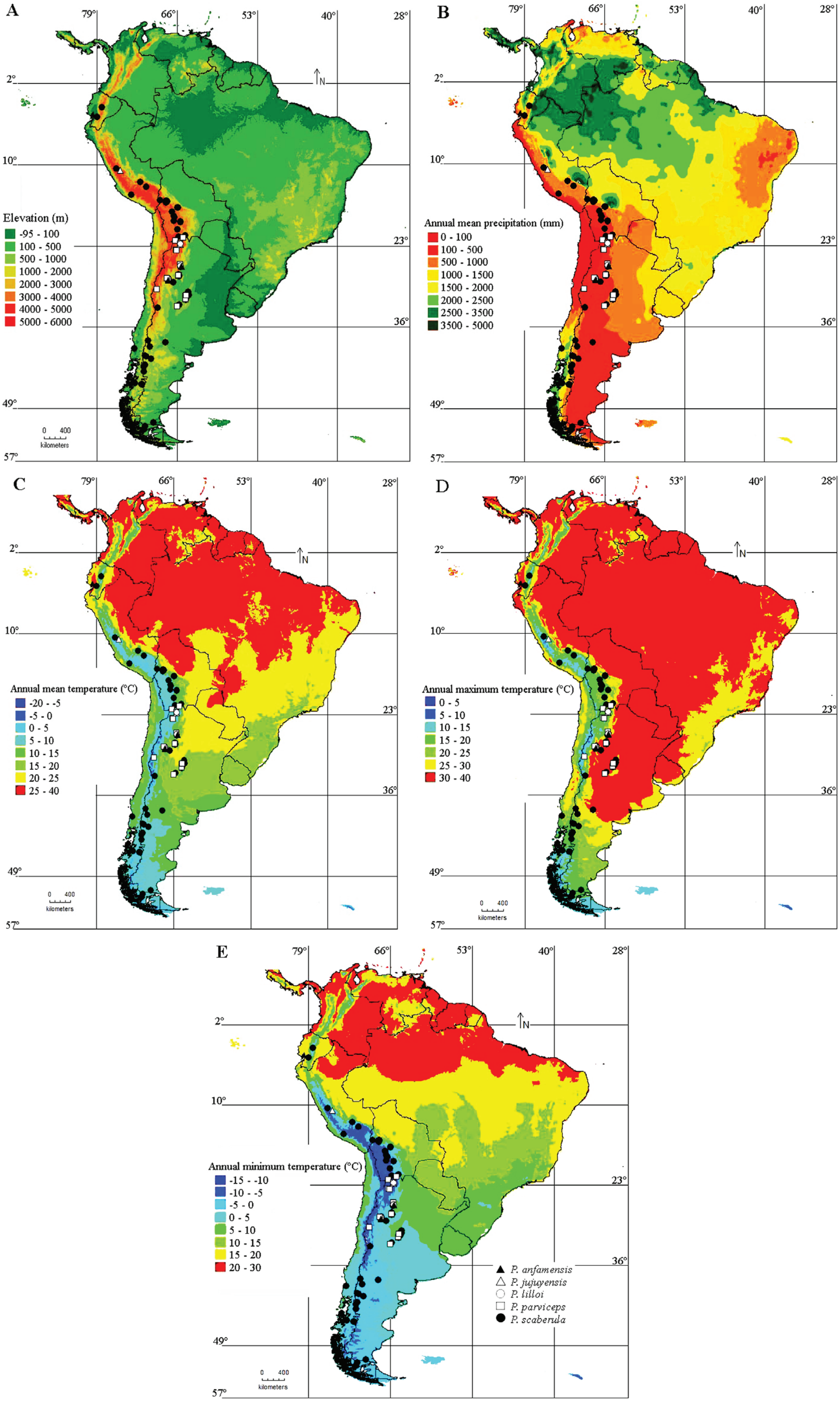

FIGURE 1. DIVA-GIS map of environmental variables and 150 collection sites of *Poa* specimens from the Andes in South American. A. Elevation. B. Annual mean precipitation. C. Annual mean temperature. D. Annual maximum temperature. E. Annual minimum temperature. Symbols for the *Poa* species are described in E.

using the WGS84 datum (Fig. 1, Appendix 2). We used 19 GIS data layers from the WorldClim Global Climate GIS database 5 arc minute grid resolution (Hijmans *et al.* 2005). These included geographic and bioclimatic variables representing elevation (m), annual mean temperature (AMT) (ºC), annual maximum temperature (AMAXT) (ºC), annual minimum temperature (AMINT) (ºC) and annual mean precipitation (AMP) (mm). Data on elevation was taken from herbarium collections; when this information was lacking, it was inferred using the WorldClim database. All topographic and climatic data were log10-transformed to standardize it for statistical analyses.

TABLE 1. List of the fourteen binary or multistate characters (marked with asterisks) and the twenty-six quantitative characters measured in the study. Thirteen characters were excluded from analyses because of the lack of variation (marked with the letter "a").

Code	**Characters**
	Vegetative
CHAR1	Culm length (mm)
CHAR2	Blade length (mm)
CHAR3a	Blade width (mm)
CHAR4*	Blade folding: flat (0), convolute (1), conduplicate (2)
CHAR5*a	Blade apex: acute (0), obtuse (1)
CHAR6*a	Adaxial blade surface: glabrous (0), scabrous (1), pilose (2)
CHAR7*a	Abaxial blade surface: glabrous (0), scabrous (1), pilose (2)
CHAR8 a	Sheath length (mm)
CHAR9*a	Abaxial sheath surface: glabrous (0), scabrous (1), pilose (2)
CHAR10 a	Ligule length (mm)
CHAR11*	Ligule shape: obtuse (0), truncate (1)
CHAR12	Number of large internodes
CHAR13	Uppermost internode length (mm)
	Reproductive
CHAR14	Panicle length (mm)
CHAR15a	Panicle width (mm)
CHAR16a	Number of branches of the proximal node of the panicle
CHAR17	Number of nodes along the axis of the panicle
CHAR18	Length of the longest branch at proximal node of the panicle (mm)
CHAR19	Spikelet length (mm)
CHAR20	Spikelet width (mm)
CHAR21a	Number of florets per spikelet
CHAR22*	Glumes overlapping the florets to: 1/2 (0), 2/3 (1), 3/4 (2), 4/4 (3)
CHAR23*a	Glumes relative size: equal (0), slightly unequal (1), unequal (2)
CHAR24	Number of lower glumes nerves
CHAR25	Lower glume length (mm)
CHAR26	Lower glume width (mm)
CHAR27	Upper glume length (mm)
CHAR28	Upper glume width (mm)
CHAR29*a	Glumes surface: glabrous (0), slightly scabrous (1), scabrous (2), pilose (3)
CHAR30*	Callus vestiture: glabrous (0), shortly woolly (1), largely woolly (2)
CHAR31	Lemma length (mm)
CHAR32	Lemma width (mm)
CHAR33a	Number of lemma nerves
CHAR34*	Lemma apex: acute (0), obtuse (1), truncate (2)
CHAR35*	Lemma nerve vestiture: glabrous (0), slightly scabrous (1), scabrous (2), pubescent (3), ciliate (4)
CHAR36*	Vestiture between the nerves of the lemma: glabrous (0), slightly scabrous (1), scabrous (2), pubescent (3), ciliate (4)
CHAR37	Palea length (mm)
CHAR38	Distance between the nerves of the palea (mm)
CHAR39*	Palea vestiture: glabrous (0), slightly scabrous (1), scabrous (2), pubescent (3), ciliate (4)
CHAR40	Anther length (mm)

Statistical analyses

Principal component analysis (PCA) was used to evaluate the morphological variation among species and specimens. Discriminant analysis (DA) was performed to examine multivariate differentiation among five tentative species and to identify the morphological characters most useful in distinguishing taxa. The clustering method used was average linkage (UPGMA) using Euclidean distance. Because both qualitative and quantitative characters were analyzed, the Gower similarity measure was used. We performed a multivariate analysis of variance (MANOVA) on morphological characters (measurements) to detect between-species differences in all characters with interaction and posterior Hotelling's comparisons based on Bonferroni correction to test the differences found in the MANOVA (Hotelling 1936, Pillai 1960, Johnson & Wichem 1998). The mean, standard deviation, and range of variation of quantitative variables were calculated for each group of individuals detected in the multivariate analysis. Significance of differences among groups for each trait was assessed with a one-way ANOVA (significance level of 5%) after Bartlett's test of homogeneity. Also, the Tukey's test was used to assess significance of differences between each pair of means (significance level of 5%). Four specimens with missing values were excluded.

Geographical patterning of morphological variation was assessed by relating phenotypic distance matrixes of morphological characters and geographical distance, and altitudinal distance within each of the main groups resulting from multivariate analyses with a Mantel test using PC-ORD (McCune & Mefford 1995). This statistic verifies whether a correlation exists between two matrices by pair-wise comparison of the cells at corresponding positions. Under the null-hypothesis of no correlation, the values should not deviate significantly from the distribution of corresponding values obtained by repeatedly comparing one of the original matrices with 999 randomly generated matrices (Mantel 1967, Bonnet & Van de Peer 2002). Each matrix was constructed by subtracting the differences in values between specimens. The null hypothesis is rejected when the Mantel statistic falls outside the 0.05 confidence level. Phenotypic dissimilarities were calculated as the Euclidean distances between each pair of specimens based on morphological data, whereas linear geographical distances between each pair of specimens were calculated using DIVA-GIS v. 7.5. To estimate the proportion of morphological differentiation that could be associated with the climatic variables AMT, AMAXT, AMINT and AMP, dissimilarity matrices were subjected to a Mantel test. Likewise, the relationship between geographic distance and each climatic variable was tested with a Mantel test, as described above.

To examine whether characters exhibited clinal variation across altitudinal, latitudinal and longitudinal gradients and climatic variables, we conducted a Pearson's correlation analysis, performed between each of the first PCA axes of the quantitative morphological variables and the elevation, latitude, longitude, AMT, AMINT, AMAXT, and AMP of the collecting sites for each of the species groups identified in the PCA, as well as a correlation between geographical and climatic variables. Values of $p < 0.05$ were considered to be statistically significant. The data were standardized and analyzed using InfoStat version 12 (Group InfoStat 2012).

Results

Morphological variation analysis among taxa

Variation along the first three axes from the PCA incorporating all specimens of *P. anfamensis, P. jujuyensis, P. lilloi, P. parviceps* and *P. scaberula* is illustrated in Fig. 2. The first three components explain 59% (36, 17 and 6%, respectively) of the total variation in the dataset (Table 2). The cophenetic correlation is r = 0.90, indicating a good fit between the Euclidean distance among OTUs. Two groups can be recognized in the PCA, one consisting of all specimens of *P. anfamensis, P. parviceps* and *P. scaberula*, and another consisting of all specimens of *P. jujuyensis* and *P. lilloi* (Fig. 2). Loading on the first component (PC1) was contributed mainly by the following characters: upper glume length (CHAR27) and width (CHAR28), callus vestiture (CHAR30), palea length (CHAR37) and anther length (CHAR40) (Table 2). Loading on the second component (PC2) was contributed mainly by culm length (CHAR1), blade length (CHAR2), uppermost internode length (CHAR13), panicle length (CHAR14), length of the longest branch at proximal node of the panicle (CHAR18), spikelets length (CHAR19) and lemma length (CHAR31) (Table 2). All specimens showed continuous morphological variability along this component (Fig. 2). In the plot of components 1 and 2 there is overlap among specimens of *P. scaberula*, *P. anfamensis* and *P. parviceps*, and between *P. jujuyensis* and *P. lilloi*. Loading on the third component (PC3) was contributed mainly by blade length (CHAR2), number of lower glumes nerves (CHAR24), lemma apex (CHAR34), vestiture between the nerves of the lemma (CHAR36) and palea vestiture (CHAR39). The plots of components 1 and 3 shows the same pattern of overlap as above.

Discriminant analysis classified specimens with 95.27% success (Fig. 3). The absolute values of the coefficients of the first two standardized discriminant functions are shown in Table 2. The first canonical axis explained 78.02% of the morphometric variation and the second canonical axis explained 14.86%. The plot of canonical axes 1 and 2 group the specimens into the same two groups identified in the PCA: (1) *P. anfamensis, P. parviceps* and *P. scaberula*; (2) *P. jujuyensis* and *P. lilloi* (Fig. 3). The specimens of *P. jujuyensis* and *P. lilloi* overlapped and had positive canonical coefficients for the first axis (Fig. 3); the characters that best discriminate them are upper glume width (CHAR28), lemma width (CHAR32), palea length (CHAR37), distance between the nerves of the palea (CHAR38) and anther length (CHAR40) (Table 2). High negative values on the first axis are mainly determined by blade folding (CHAR4), panicle length (CHAR14), ratio of the glumes overlapping the florets (CHAR22) and callus vestiture (CHAR30). Most specimens of *P. parviceps* grouped together on the lower middle portion of the graph, while specimens of *P. scaberula* and *P. anfamensis* grouped in the upper left with overlap among them; this cluster included a few individuals of *P. parviceps*.

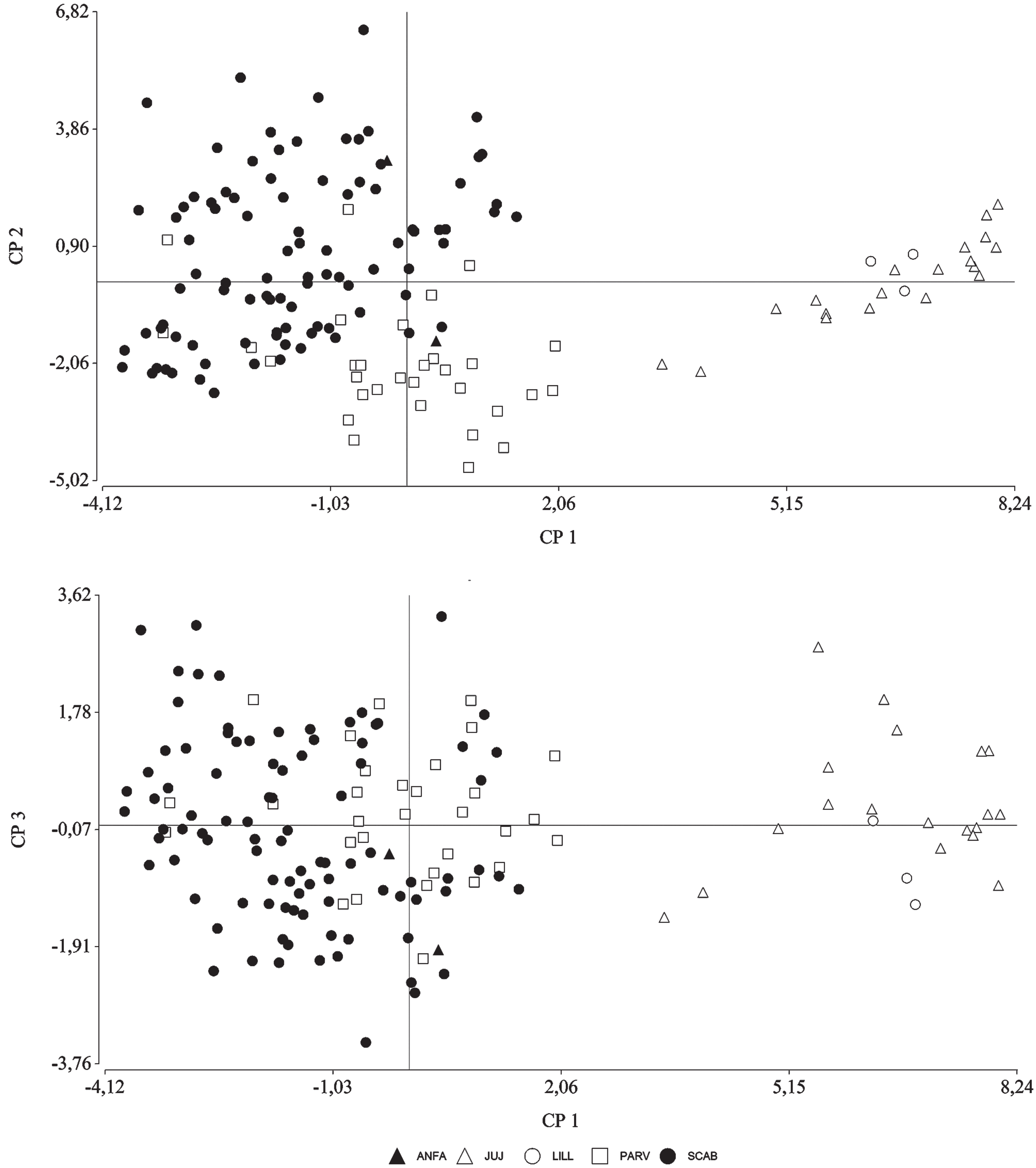

FIGURE 2. Plots of PC1 × PC2 and PC1 × PC3 from principal components analysis (PCA) of all specimens in the study. ANFA: *P. anfamensis*; JUJ: *P. jujuyensis*; LILL: *P. lilloi*; PARV: *P. parviceps*; SCAB: *P. scaberula*.

High positive values on the second canonical axis corresponded with panicle length (CHAR14), lemma length (CHAR31), lemma nerve vestiture (CHAR35), vestiture between the nerves of the lemma (CHAR36) and anther length (CHAR40) (Table 2), which align with almost all specimens of *P. jujuyensis* and *P. lilloi*, and most specimens of *P. scaberula* and *P. anfamensis*. High negative values on the second canonical axis are characterized by spikelet length (CHAR19), length of the longest branch at proximal node of the panicle (CHAR18) and upper glume length (CHAR27) (Table 2), which separate almost all specimens of *P. parviceps* (Fig. 3).

The distribution of the average values and standard deviation of the quantitative characters and one-way analysis of variance for each of the species groups is shown in box plots (Fig. 4, Appendix 3). Seven vegetative (CHAR3, CHAR5, CHAR6, CHAR7, CHAR8, CHAR9 and CHAR10) and six reproductive (CHAR15, CHAR16, CHAR21, CHAR23, CHAR29 and CHAR33) characters showed no variability between the two groups (Table 1).

TABLE 2. Contributions of individual characters to the first three multivariate axes of the principal components analysis (PCA) and two canonical axes of the discriminant analysis (DA) of the five species of *Poa* studied. The horizontal line divides the vegetative and reproductive characters. The codes for the morphological characters are provided in Table 1.

Characters*	PCA			DA	
	PC1	**PC2**	**PC3**	**C1**	**C2**
CHAR1	-0.15	0.35	-0.01	-0.13	0.06
CHAR2	-0.13	0.26	0.29	0.22	-0.07
CHAR4	-0.20	0.07	-0.15	-0.32	-4.1E-03
CHAR11	0.02	-0.08	-0.06	0.05	-0.09
CHAR12	-0.12	0.24	-0.07	-0.24	-0.11
CHAR13	-0.15	0.32	-0.09	-0.20	0.08
CHAR14	-0.16	0.36	0.10	-0.47	0.25
CHAR17	-0.21	0.16	0.08	-0.04	-0.08
CHAR18	-0.12	0.28	0.10	-0.05	-0.33
CHAR19	0.21	0.26	0.15	-0.04	-0.42
CHAR20	0.20	0.20	0.07	-0.06	0.14
CHAR22	-0.12	-0.11	0.06	-0.46	-0.07
CHAR24	0.08	0.07	-0.26	0.11	-0.07
CHAR25	0.24	0.21	0.15	0.06	0.03
CHAR26	0.26	-0.01	-0.05	-0.15	0.17
CHAR27	0.24	0.20	0.09	0.12	-0.64
CHAR28	0.26	0.02	0.02	0.25	-0.13
CHAR30	-0.25	0.13	-0.11	-0.40	0.01
CHAR31	0.24	0.25	0.11	-0.02	1.17
CHAR32	0.24	0.06	-0.01	0.03	0.03
CHAR34	-0.13	-0.09	0.54	0.10	0.22
CHAR35	-0.15	0.21	-0.16	-0.18	0.72
CHAR36	0.10	0.21	-0.42	0.02	0.25
CHAR37	0.27	0.12	0.09	0.27	0.11
CHAR38	0.24	-0.02	0.11	0.27	-0.23
CHAR39	0.13	0.07	-0.42	0.24	-0.10
CHAR40	0.25	0.03	0.03	0.28	0.25
Total variance explained (%)	36.0	17.0	6.0	78.02	14.86

Geographical variation in climate and vegetative and reproductive characters in P. lilloi s.l. (*P. lilloi* and *P. jujuyensis*)

The Mantel tests showed significant positive associations between the phenotypic distance matrix (PHEN) and both geographic and altitude distance matrices (DIST and ALT, respectively) (Table 3). Thus, distant specimens had the greatest differences in phenotype, meaning that differences in phenotypic distances were structured by altitudinal and geographic distances (Table 3). The phenotype distance matrix (PHEN) showed a significant positive association with annual mean precipitation (AMP) and annual minimum and maximum temperature (AMINT and AMAXT, respectively). However, the phenotypic distance matrix (PHEN) did not show association with the annual mean temperature (AMT) (Table 3). A significant positive relationship was detected between the geographic distance (DIST) and climatic variables (AMP, AMINT and AMT), and altitudinal distance (ALT). However, the geographic distance matrix did not show association with the annual maximum temperature (AMAXT) (Table 3). The altitudinal distance (ALT) showed strongest positive association with climatic matrices (AMINT, AMT and AMP), except for annual maximum temperature (AMAXT) (Table 3). Annual mean precipitation (AMP) showed strong positive association with annual minimum temperature (AMINT).

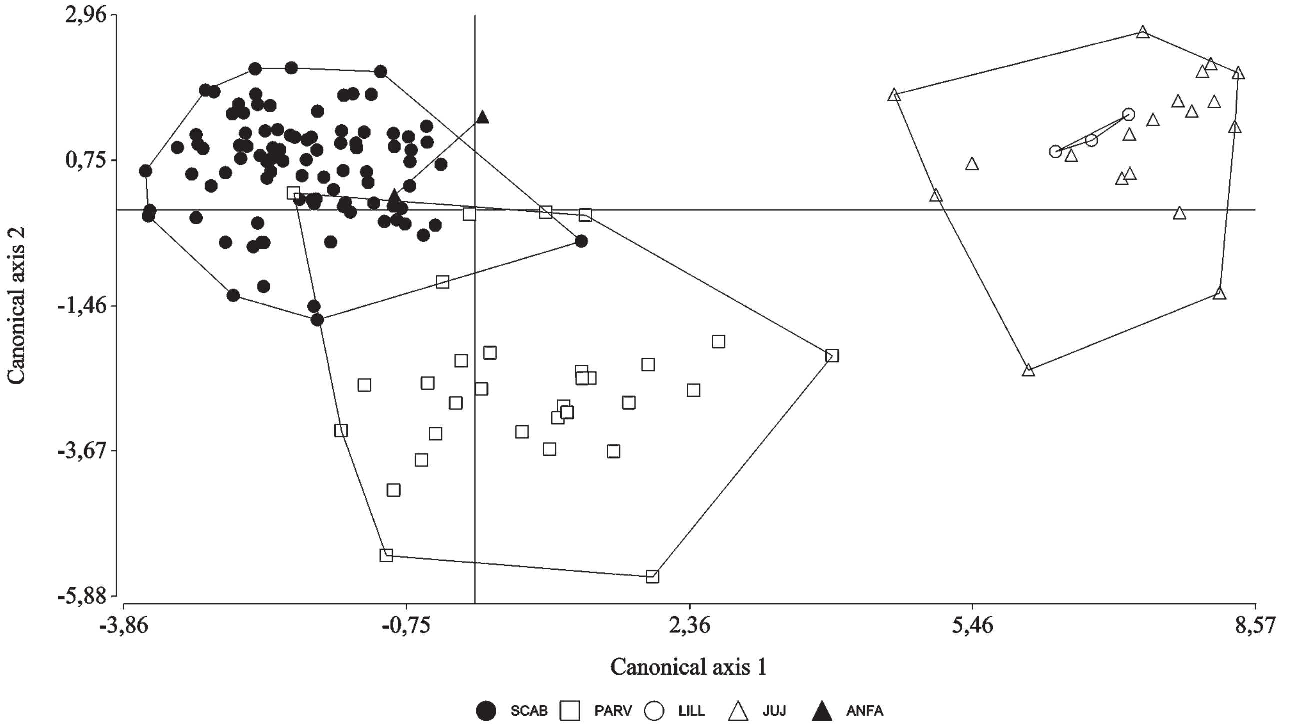

FIGURE 3. Plot of discriminant analysis (DA) along the first two discriminant axes obtained from all specimens pertaining to a priori defined species. ANFA: *P. anfamensis*; JUJ: *P. jujuyensis*; LILL: *P. lilloi*; PARV: *P. parviceps*; SCAB: *P. scaberula*.

TABLE 3. Mantel tests of association among phenotypic distances, geographic distance, altitudinal distance and climatic variables of specimens of *P. lilloi* and *P. scaberula*.

Matrix		***P. lilloi***		***P. scaberula***	
A	**B**	**R**	***p****	**R**	***p****
PHEN	DIST	0.510	0.0030	0.034	0.0941
PHEN	ALT	0.213	0.0025	0.230	0.0020
PHEN	AMT	-0.040	0.3684[a]	0.144	0.0010
PHEN	AMINT	0.403	0.0060	0.210	0.0010
PHEN	AMAXT	0.188	0.1241	-0.009	0.4324[a]
PHEN	AMP	0.489	0.0080	0.119	0.0020
DIST	ALT	0.577	0.0010	0.504	0.0010
DIST	AMT	0.073	0.2052	0.155	0.0010
DIST	AMINT	0.825	0.0010	0.079	0.0050
DIST	AMAXT	-0.118	0.2192[a]	0.221	0.0010
DIST	AMP	0.932	0.0010	0.368	0.0010
ALT	AMT	0.403	0.0010	0.200	0.0010
ALT	AMINT	0.576	0.0010	0.099	0.0060
ALT	AMAXT	-0.043	0.5656[a]	0.337	0.0010
ALT	AMP	0.517	0.0010	0.324	0.0010
AMP	AMT	0.098	0.2132	0.121	0.0010
AMP	AMINT	0.808	0.0010	0.136	0.0010
AMP	AMAXT	-0.097	0.4104[a]	0.081	0.0350

ALT, altitudinal distance; AMP, annual mean precipitation; AMT, annual mean temperature; AMAXT, annual maximum temperature; AMINT, annual minimum temperature; DIST, geographic distance; PHEN, phenotypic distance.

*Probability that a random Z < observed Z.

[a] Probability that a random Z > observed Z.

A Pearson's correlation analysis was performed between each of the first PCA axes of the quantitative vegetative and reproductive morphological variables and the geographic and climatic variables, as well as a correlation between the geographic variables and climatic variables of each of the sites (Table 4). Uppermost internode length (CHAR13) showed a negative correlation with elevation ($p < 0.10$). Although there is not a significant decrease in the size of the plant with increasing elevation, there is a significant shortening of the vegetative internodes. Reproductive characters such as panicle length (CHAR14) and length of the longest branch at proximal node of the panicle (CHAR18) showed a negative correlation with elevation ($p < 0.05$ and $p < 0.10$), suggesting a decrease in panicle size with increasing elevation (Table 4). However, spikelet characters such as spikelets width (CHAR20), lower glume length (CHAR25), lemma length (CHAR31), lemma width (CHAR32) and distance between the nerves of the palea (CHAR38) showed a positive correlation with elevation ($p < 0.10$), suggesting an increase in size of spikelets characters with increasing elevation.

Culm length (CHAR1) and number of large internodes (CHAR12) showed a strong positive correlation with latitudinal gradients ($p < 0.05$), and the same can be observed in panicle length (CHAR14), length of the longest branch at proximal node of the panicle (CHAR18), upper glume width (CHAR28) and anther length (CHAR40), which increase significantly in size along north-south latitude gradients (Table 4).

Culm length (CHAR1) showed a negative correlation with longitudinal gradients ($p < 0.05$), and the same can be observed for panicle length (CHAR14), spikelet length (CHAR19), lower glume length and width (CHAR25 and CHAR26, respectively), upper glume length (CHAR27), lemma length (CHAR31), palea length (CHAR37) and distance between the nerves of the palea (CHAR38), which decrease in size along east-west longitudinal gradients (Table 4).

The strong association observed between phenotypic variation and elevation, and the latitude and longitudinal gradients, indicate a pattern of north-south and east-west phenotypic variation corresponding to decreasing elevation in the Andes.

The vegetative characters culm length (CHAR1) and length of uppermost internode (CHAR13) showed a positive correlation ($p < 0.05$) with annual mean precipitation (AMP) and annual mean temperature (AMT), respectively (Table 4). The reproductive characters spikelet length (CHAR19), lower glume length and width (CHAR25 and CHAR26, respectively), upper glume length (CHAR27), lemma length (CHAR31), palea length (CHAR37) and distance between the nerves of the palea (CHAR38), showed a strong negative correlation with annual mean precipitation (AMP) ($p < 0.05$ and $p < 0.10$), indicating an decrease in the size of spikelet characters relative to an increase in rainfall. Lower glume length (CHAR25), distance between the nerves of the palea (CHAR38) and anther length (CHAR40) showed a negative correlation with annual mean temperature (AMT) ($p < 0.05$ and $p < 0.10$), indicating a decrease in these characters relative to decrease in temperature range.

Length of the longest branch at proximal node of the panicle (CHAR18), spikelet length (CHAR19) and palea length (CHAR37) showed positive correlation with annual maximum temperature (AMAXT) ($p < 0.05$ and $p < 0.10$), suggesting an increase in their lengths with increasing maximum temperatures. Vegetative characters were not correlated significantly with this variable. Vegetative and reproductive characters showed no significant correlation with minimum temperature (Table 4).

The elevation showed a strong significant negative correlation with annual mean temperature (AMT) ($p < 0.05$), indicating a decreasing temperature along an altitudinal gradient (Table 4, Fig. 1). In addition, elevation showed a significant negative correlation with latitude and longitude ($p < 0.10$). Correlation between longitude and annual mean precipitation (AMP) was very strong, positive and significant ($p < 0.05$), exhibiting an increase of rainfall along an east-west gradient. There is no significant correlation between latitude and climate variables, and between precipitation and temperature variables.

Geographical variation in climate and vegetative and reproductive characters in P. scaberula s.l. (*P. scaberula*, *P. anfamencis* and *P. parviceps*)

The Mantel tests showed significant positive associations between the phenotypic distance matrix (PHEN) and both geographic and altitude distance matrix (DIST and ALT, respectively) (Table 3). Thus, distant specimens had the greatest differences in phenotype, meaning that differences in phenotypic distances were structured according to altitudinal and geographic distances (Table 3). The phenotype distance matrix (PHEN) showed a significant positive association with climatic matrices such as annual mean temperature (AMT), annual minimum temperature (AMINT) and annual mean precipitation (AMP). However, the phenotypic distance matrix (PHEN) did not show association with the annual maximum temperature (AMAXT) (Table 3). A significant positive relationship was detected between the geographic distance (DIST) and climatic variables, and altitudinal distance (ALT). The association was strongest between geographic distance (DIST) and altitudinal distance (ALT), and between geographic distance (DIST) and annual mean precipitation (AMP), and between geographic distance (DIST) and annual maximum temperature (AMAXT). The altitudinal distance (ALT) showed strongest positive association with annual maximum and minimum temperature (AMAXT and AMINT, respectively), and annual mean precipitation (AMP) (Table 3). Annual mean precipitation (AMP) showed significant positive association with three temperature variables (AMT, AMINT and AMAXT).

TABLE 4. Pearson product-moment correlation coefficient between the first PCA axes of the morphological and environmental variables of the collecting localities of *P. lilloi*. The horizontal line divides the vegetative and reproductive characters.

Character	Elevation	Latitude	Longitude	AMP	AMT	AMINT	AMAXT
1	-0.12	0.63*	-0.40*	0.40*	0.20	0.00	0.17
2	-0.21	-0.06	-0.23	-0.23	0.15	0.00	0.03
12	-0.17	0.30*	0.01	0.01	0.29	0.00	0.08
13	-0.31**	0.05	-2.7E-03	-2.7E-03	0.47*	0.00	0.08
14	-0.43*	0.34*	-0.28**	-0.28	0.28	0.00	0.26
17	-0.14	-0.11	-0.25	-0.25	-0.02	0.00	-0.07
18	-0.28**	0.41*	-0.17	-0.17	0.09	0.00	0.39*
19	0.02	-0.16	-0.45*	-0.45*	0.01	0.00	0.33**
20	0.28**	-0.15	-0.21	-0.21	0.17	0.00	0.23
24	0.22	-0.07	-0.07	-0.07	-0.26	0.00	-0.02
25	0.31**	0.10	-0.54*	-0.54*	-0.34**	0.00	0.12
26	0.01	0.14	-0.36**	-0.36**	-0.02	0.00	0.14
27	0.19	0.04	-0.51*	-0.51*	-0.17	0.00	0.04
28	0.13	0.39*	-0.13	-0.13	-0.21	0.00	-0.20
31	0.34**	0.04	-0.60*	-0.60*	-0.22	0.00	0.27
32	0.26**	0.05	0.08	0.08	-0.17	0.00	0.23
37	-2.4E-03	0.04	-0.29**	-0.29**	0.14	0.00	0.39*
38	0.34**	-0.07	-0.53*	-0.53*	-0.46*	0.00	-0.03
40	-0.14	0.30*	0.13	0.13	-0.36**	0.00	0.09
Elevation	1.00						
Latitude	-0.32**	1.00					
Longitude	-0.32**	-0.05	1.00				
AMP	-0.32**	-0.05	0.99*	1.00			
AMT	-0.82*	0.26	0.26	0.26	1.00		
AMINT	0.00	0.00	0.00	0.00	0.00	1.00	
AMAXT	0.17	-0.01	-0.01	-0.01	0.07	0.00	1.00

Significant based on Tukey's test at significance level:*$p < 0.05$, **$p < 0.10$.

A Pearson's correlation analysis was performed between each of the first PCA axes of the quantitative vegetative and reproductive morphological variables and the geographic and climatic variables, as well as a correlation between the geographic variables and climatic variables of each of the sites (Table 5). Vegetative characters showed a negative correlation with elevation ($p < 0.10$). In addition, reproductive characters such as panicle length (CHAR14) and number of nodes along the axis of the panicle (CHAR17) showed a strong negative correlation with elevation ($p < 0.05$), suggesting a decrease in plant and panicle size with increasing elevation (Table 5). However, spikelet characters such as spikelet length (CHAR19), lower glume length (CHAR25), lower glume width (CHAR26), upper glume width (CHAR28), lemma length (CHAR31) and lemma width (CHAR32), showed a strong positive correlation with elevation ($p < 0.05$ and $p < 0.10$), suggesting an increase in size of spikelet characters with increasing elevation.

The vegetative characters showed no correlation with latitudinal gradient (Table 5). Reproductive characters such as number of nodes along the axis of the panicle (CHAR17), spikelet length (CHAR19), lower glume length (CHAR25), upper glume length (CHAR27) and lemma length (CHAR31), showed a positive correlation with latitudinal gradients ($p < 0.10$) (Table 5), suggesting an increase in size along a north-south latitudinal gradients.

Vegetative characters such as culm length (CHAR1), number of large internodes (CHAR12) and uppermost internode length (CHAR13) showed a positive correlation with longitudinal gradients ($p < 0.05$ and $p < 0.10$), and the same can be observed for panicle length (CHAR14), spikelet length (CHAR19), lower glume length (CHAR25), upper glume length (CHAR27), upper glume width (CHAR28), lemma length (CHAR31) and palea length (CHAR37), which increase in their size along an east-west longitudinal gradients (Table 5).

The strong association observed between phenotypic variation and altitudinal distance, and the latitude and longitudinal gradients, indicate a pattern of north-south and east-west phenotypic variation corresponding to decreasing elevation in the Andes.

The vegetative characters culm length (CHAR1), number of large internodes (CHAR12) and uppermost internode length (CHAR13) showed a positive correlation ($p < 0.10$) with annual mean precipitation (AMP) (Table 5). The reproductive characters panicle length (CHAR14), lower glume length (CHAR25) and lemma length (CHAR31), showed a positive correlation with annual mean precipitation (AMP) ($p < 0.05$ and $p < 0.10$), indicating an increase in their size relative to an increase in rainfall. Panicle length (CHAR14) showed a positive correlation with annual mean temperature (AMT) ($p < 0.10$). However, lower glume length (CHAR25), lower glume width (CHAR26), upper glume length (CHAR27), upper glume width (CHAR28) and lemma width (CHAR32), showed a negative correlation with annual mean temperature (AMT) ($p < 0.05$ and $p < 0.10$), indicating a decrease in these characters relative to decrease in temperature range. In addition, lower glume width (CHAR26) and lemma width (CHAR32) showed significant negative correlation with annual minimum temperature ($p < 0.10$). The majority of the spikelet characters showed a strong negative correlation with annual maximum temperature (AMAXT) ($p < 0.05$), indicating a decrease in spikelets characters size relative to decrease in temperature range.

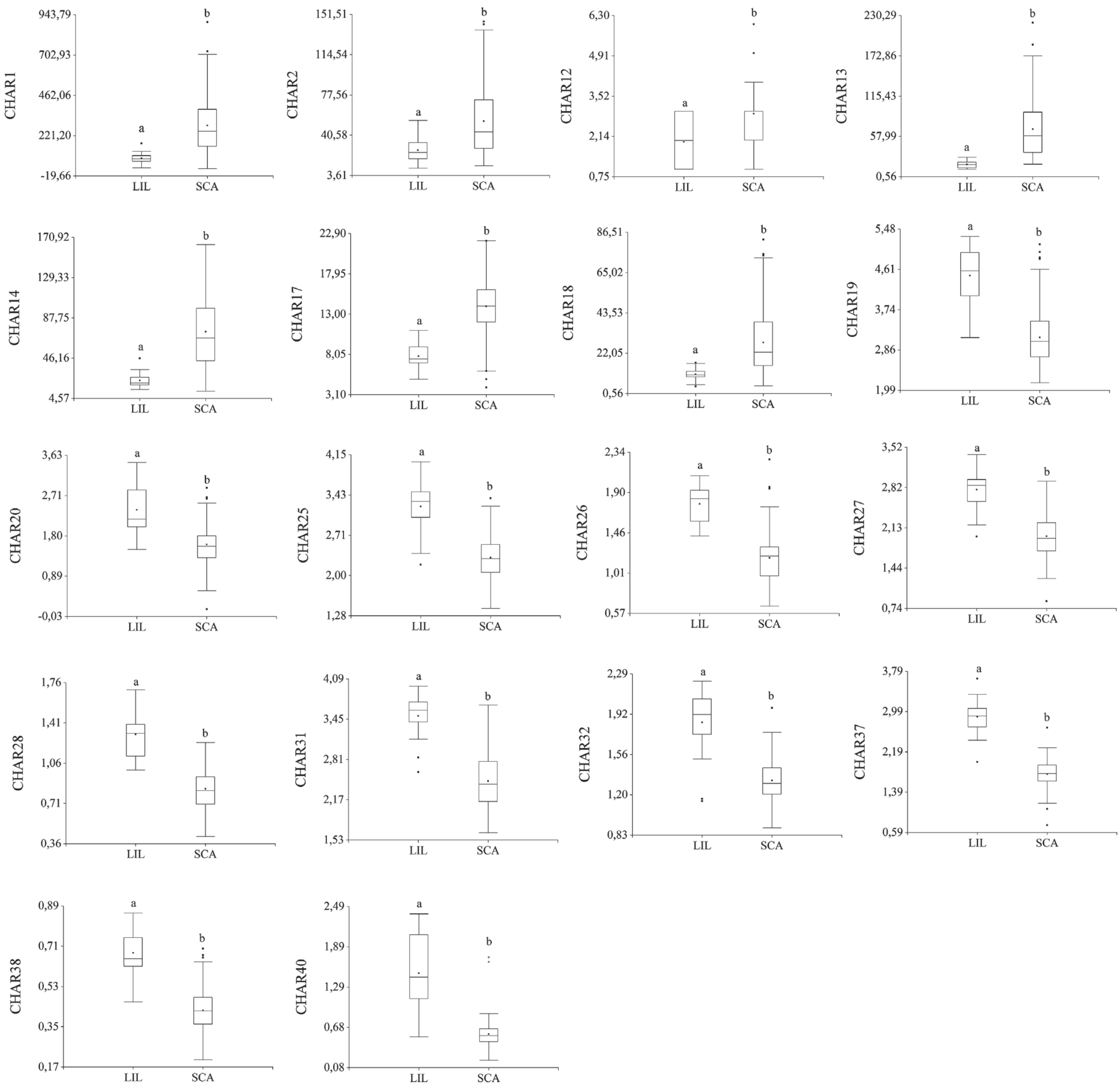

FIGURE 4. Box plots representing the mean, median, interquartile range, adjacent values (lines), and outliers (dots) of quantitative characters in *P. lilloi* and *P. scaberula*.

TABLE 5. Pearson product-moment correlation coefficient between the first PCA axes of the morphological variables and environmental variables of the collecting localities of *P. scaberula*. The horizontal line divides the vegetative and reproductive characters.

Characters	Elevation	Latitude	Longitude	AMP	AMT	AMINT	**AMAXT**
1	-0.24**	0.11	0.23**	0.20**	0.16	3.7E-03	-0.01
2	-0.24**	0.13	0.02	0.08	0.10	0.09	0.09
12	-0.32**	0.16	0.22**	0.22**	0.17	0.02	-0.04
13	-0.20**	0.15	0.29*	0.24**	0.02	-0.04	-0.17
14	-0.32*	0.16	0.20**	0.25**	0.22**	0.10	0.09
17	-0.33*	0.25**	0.06	0.16	0.19	0.11	0.04
18	-0.12	0.08	0.16	0.13	-1.2E-03	0.02	-0.02
19	0.33*	0.24**	0.29*	0.17	-0.01	0.07	-0.09
20	-0.17	0.17	0.23	0.08	-0.16	0.04	-0.14
24	0.05	-0.04	0.11	0.05	-0.08	-0.09	-0.11
25	0.25**	0.28*	0.32**	0.23**	-0.25**	-0.07	-0.27**
26	0.28**	-0.13	0.16	-0.04	-0.43*	-0.27**	-0.29*
27	-0.17	0.24**	0.30**	0.14	-0.32*	-0.09	-0.29*
28	0.25**	-0.08	0.25**	-0.05	-0.46*	-0.20	-0.32*
31	0.35*	0.26**	0.46*	0.31*	-0.10	0.03	-0.19**
32	0.19**	-0.08	0.19	0.07	-0.35*	-0.25**	-0.29*
37	-0.04	-0.01	0.26**	0.18	-0.14	0.06	-0.14
38	0.08	-0.03	-0.03	-0.09	-0.12	0.09	-0.02
40	0.05	-0.07	0.10	0.05	-0.15	1.6E-03	-0.11
Elevation	1.00						
Latitude	-0.84*	1.00					
Longitude	-0.19	0.14	1.00				
AMP	-0.51*	0.41*	0.48*	1.00			
AMT	-0.14	-0.21**	-0.25**	0.09	1.00		
AMINT	-0.30*	-0.02	-0.19	0.09	0.48*	1.00	
AMAXT	0.08	-0.44*	-0.54*	-0.26**	0.69*	0.64*	1.00

Significant based on Tukey's test at significance level: $*p < 0.05$, $**p < 0.10$.

The elevation showed a strong significant negative correlation with latitude; elevation declines from north to south along latitudinal gradient (Table 5, Fig. 1A). The correlation between elevation and annual mean precipitation (AMP), and between elevation and annual minimum temperature (AMINT) were significant and negative, indicating a decrease in minimum temperatures and precipitation along an altitudinal gradient, being the annual minimum temperature more noticeable (Table 5). Correlation between latitude and climatic variables, and longitude and climatic variables was positive significant for annual mean precipitation (AMP) and negative and significant for annual maximum temperature (AMAXT) and annual mean temperature (AMT), exhibiting an increase of rainfall along north-south and east-west gradients.

Discussion

Univariate and multivariate methods based on quantitative and qualitative morphological characters allow the differentiation of two related species groups. Plants from these groups are characterized by pronounced morphological variability that is related to its geographical distribution. The taxa distributed in the Andean mountains span a wide range of elevations and occur in ecologically diverse habitats with varying climates, from north of Ecuador to south of Argentina and Chile. The morphological variability described by PCA and DA shows that the specimens of five *Poa* species can be separated into two groups: (1) *Poa anfamensis, P. parviceps* and *P. scaberula* specimens, and (2) *P. jujuyensis* and *P. lilloi* specimens. Both groups are morphologically and ecologically distinguishable. *Poa anfamensis* and *P. parviceps* specimens showed significant morphological overlap with *P. scaberula* in the multivariate analyses and are therefore reduced to synonyms of that taxon. *Poa jujuyensis* specimens overlap with *P. lilloi* specimens, and are treated as synonyms.

The group of specimens treated here as *P. lilloi* comprise very small plants with short panicles but larger spikelets and anthers (Fig. 4), restricted to high elevations ranging from 4080 to 5004 m with annual mean temperature from

1.59 to 6.75°C, and an arid climate, with low annual mean precipitation of 93.33–196.67 mm, except one specimen of *P. jujuyensis*, which occurs in an area with mean rainfall of 653.33 mm (Appendix 2). The group of specimens treated here as *P. scaberula* are larger in vegetative and reproductive traits than *P. lilloi*. In addition, they are widely distributed at elevations from 41 to 4606 m with annual mean temperature from 2.94 to 16.75°C, and annual mean precipitation of 88.3–2195.83 mm (Appendix 2).

The phenotypic variation observed in *P. lilloi* and *P. scaberula* is associated with environmental conditions and geography characteristic of the Andean region of South America. In both species, Mantel tests indicate a strong association between phenotypic distances and altitudinal distance, and between phenotypic distances and geographic distance. Most of the vegetative and reproductive characters relative to panicle size decrease at higher elevations; however, spikelet characters increase with elevation. Decreasing plant size as an adaptation to increasing elevation is a well-known phenomenon. It results from a slower growth rate that may allow plants to use resources more efficiently in severe climatic environments (Grime 1979, Bennington & McGraw 1995). In addition, the decrease in growth with increasing elevation is interpreted to be symptomatic of increasing environmental stress (Cordell *et al*. 1998, Fabbro & Körner 2004, Macek *et al*. 2009, Jafari & Sheidai 2011, Milla & Reich 2011, Maad *et al*. 2013). However, a more interesting result is the increase in spikelet size along an altitudinal gradient despite a decrease in plant size. This has also been documented for other alpine plants species (Maad *et al*. 2013), and could be an adaptation to extreme climatic conditions.

Phenotypic variation showed a strong correlation with geographic distance in *P. lilloi*. In addition, vegetative and reproductive character size was correlated with a latitudinal gradient, increasing in size and height with increasing latitude towards the south (Table 4). The same was observed in the reproductive characters of *P. scaberula*, while vegetative characters were not correlated with a latitudinal gradient. In *P. lilloi* the vegetative and reproductive character sizes decrease along an east-west longitudinal gradient, while in *P. scaberula* the sizes of vegetative and reproductive characters increase along a longitudinal gradient. Vegetative and reproductive characters in both species showed differential responses to longitude.

Altitudinal and geographical distance are apparently important factors in phenotypic differentiation and could have played a large role in differentiation between *P. lilloi* and *P. scaberula*, as shown by the significant association between vegetative and reproductive phenotype and altitudinal distance, between vegetative and reproductive phenotype and latitudinal gradient, and between vegetative and reproductive phenotype and longitudinal gradient. Thus, the higher elevation and lower latitude of the north localities might have contributed to the separation of the two species (Fig. 1). *Poa lilloi* specimens are restricted to higher elevations above 4000 m, whereas those *P. scaberula* specimens are widely spread from sea level to 4600 m elevation. Other abiotic factors such as annual mean temperature and annual mean precipitation have an important role in phenotypic variation in both species and displayed patterns across the species' range (Fig. 1). These variables were associated with changes in vegetative and reproductive character size, and varied significantly between the drier and wetter regions of the Andes. In both species, the morphological characters and annual mean precipitation are strongly associated. Vegetative characters increase in size with increasing rainfall. A common pattern reported for many species is a reduction in plant height and leaf size as environmental aridity increases, representing an adaptive strategy because smaller leaves exhibit lower evapotranspiration (Dudley 1996, Parkhurst & Loucks 1972). However, reproductive characters of *P. lilloi* decrease with increasing rainfall, but in *P. scaberula* these increase with increasing rainfall. Therefore, both species respond differently to environmental changes in humidity and precipitation.

According to the Mantel test, in general in both species the three temperature variables are correlated with phenotypic variation. However, in *P. lilloi* vegetative characters were more influenced by variation in annual mean temperature, whereas vegetative characters of *P. scaberula* were not correlated with this variable. Nevertheless, reproductive characters were correlated with the annual mean, annual maximum and minimum temperatures, except in *P. lilloi*, which does not show changes with annual minimum temperature.

The morphological variation observed suggests that specimens of *P. lilloi* and *P. scaberula* are under the effect of strong forces that foster intraspecific variation. This is supported by the fact that these taxa show high morphological variation in size of culms, leaves, panicles and spikelet characters. This phenotypic plasticity, which is mediated by environmental factors such as geography, elevation, temperature and precipitation, may provide indirect evidence that gene flow is limited. Size and shape of morphological characters are primarily a function of elevation, which varies consistently with latitude and longitude.

The elevation of the Andes decreases along a north-south latitudinal gradient with increasing rainfall and a decreasing temperature range as a result of a decrease in the maximum temperatures towards the south (Fig. 1). At high elevations, the climate is drier and colder as a consequence of low rainfall and low temperatures. Towards the south of

Argentine Patagonia and south of Chile, the Andean mountain elevation decreases and the climate is more humid and cooler.

In summary, based on the results of the multivariate analysis based on morphological characters, we propose that *P. anfamensis* and *P. parviceps* be treated as synonyms of *P. scaberula,* and that *P. jujuyensis* is a synonym of *P. lilloi.* Morphology of *P. lilloi* and *P. scaberula* specimens is correlated with environmental factors. The within-species and morphological uncoupling between vegetative and reproductive characters suggests that both types of characters are responding independently to different forces, thus increasing the potential for evolutionary novelty. Moreover, the results denote uncoupling between vegetative and spikelet characters, and between panicle and spikelet characters, suggesting that spikelet morphology is able to evolve independently of variation in vegetative and panicle morphology, promoting genetic divergence and speciation. Based upon the information obtained, a new identification key for these taxa is proposed.

Taxonomic treatment

Key to the species of *P. lilloi* and *P. scaberula*:

1. Culms longer than 14 cm; blades longer than 3.5 cm, flat; uppermost internode 43–77 mm long; panicles longer than 39 mm; length of the longest branch of the first node of the panicle 20–30 mm; spikelets 2.8–3.6 mm; glumes up to ¾ the length of the florets; lower glume 3-nerved; lower glume less than 2.3 mm long and 1.6 mm wide; upper glume less than 2 mm long and 1 mm wide; callus usually long woolly; lemma 2.2–2.6 mm long, apex usually obtuse, nerves usually pubescent or ciliate, glabrous between the nerves; palea 1.7–1.8 mm long, nerves 0.4 mm apart, usually glabrous or scabrous; anthers 0.6–1.1 mm long .... 1. *P. scaberula*

- Culms not more than 11 cm long; blades less than 2.8 cm, convolute; uppermost internode 16–18 mm long; panicles less than 25 mm long; length of the longest branch of the first node of the panicle 10–12 mm long; spikelets 4.3–4.5 mm long; glumes less than ⅔ the length of the florets; lower glumes 3−5-nerved; lower glume up to 3.2 mm long and 1.8 mm wide; upper glume up to 2.8 mm long and 1.3 mm wide; callus usually glabrous; lemma 3.5–3.6 mm long, apex usually acute, nerves usually scabrous, between the nerves slightly scabrous; palea to 2.8 mm long, nerves 0.7 mm apart, usually scabrous or ciliate; anthers 1–1.6 mm long .... 2. *P. lilloi*

1. *Poa scaberula* Hooker f. (1846: 378). Type:—CHILE. Magallanes, Puerto del Hambre, no date, *King s.n.* (holotype K-433922!, isotypes BAA (fragm.), GH-243500!).

Poa dactyliformis Steudel (1854: 426). Type:—CHILE. Magallanes, Punta Arenas, no date, *Lechler s.n.* (holotype P!, isotypes US-89676!, LE, SGO, W!).

Poa micranthera Hackel (1911: 154). *Poa anfamensis* Negritto & Anton (1998: 159). Type:—ARGENTINA. Tucumán, Tafí, Cuesta de Anfama, no date, *Lillo 5468, Herb. T. Stuckert 19827* (holotype W!, isotypes LIL!, US-88758!).

Poa parviceps Hackel (1914: 298). Type:—ARGENTINA. Tucumán, Lara, 17 February 1912, *Lillo 11474, Herb. T. Stuckert 22531* (holotype W!, isotypes US-88749!, BAA!, SI!)

Culms 14.7–34.2 cm tall, caespitose; blades 3.6–5.9 cm long, flat; ligule obtuse; number of large internodes 2–4; uppermost vegetative internode 43.2–77.3 mm long. Panicle 39.3–85.1 mm long, number of nodes 12–15, length of the longest branch of the first node 20.3–29.9 mm. Spikelets 2.8–3.6 × 1.5–1.6 mm; glumes up to ¾ as long as the florets, lower glumes 2.2–2.4 × 1.1–1.6 mm, 3-nerved, upper glume 1.84–2.0 × 0.8–1 mm; callus usually long woolly; lemma 2.2–2.6 × 1.3–1.5 mm, apex usually obtuse, nerves usually pubescent or ciliate, between the nerves glabrous; palea 1.7–1.8 mm long, nerves 0.4–0.5 mm apart, usually glabrous or scabrous; anthers 0.6–1.1 mm long. Monoclinous, chasmogamous.

Distribution:—American native grass, distributed in North and South America in Argentina, Chile, Ecuador, México and Perú, from 1º–53º S and 64º–79º W. Inhabits moist soils and shady, common in fertile soils,pastures and slopes between 41 and 4606 m elevation.

Poa lilloi Hackel (1911: 153). Type:—ARGENTINA. Tucumán, Cumbres Calchaquies, 4000 m, 29 February 1907, *Lillo 5619*, *herb. T. Stuckert 17741* (holotype W, isotypes BAA, CORD, LIL, SI, US-88760 (fragm. ex W), US-1867542 (ex NY)

Poa parviceps var. *jujuyensis* Parodi ex Nicora (1997: 143). *Poa jujuyensis* (Parodi ex Nicora) Giussani, Soreng & Anton (2011: 91). Type:—ARGENTINA. Jujuy, Humahuaca, Mina Aguilar, no date, *Fernández s.n.* (holotype BAA!, isotype SI!)

Culms 8.2–11 cm tall, rhizomatous, caespitose; blades 2.1–2.8 cm long, convolute; ligule obtuse; number of large internodes 1–3; uppermost vegetative internode 18.3–16.4 mm long. Panicle 22.8–25.1 mm long, number of nodes 7–8, length of the longest branch of the first node 10.6–12 mm. Spikelets 4.3–4.5 × 2.3–2.4 mm; glumes up to ⅔ as long as the florets, lower glumes 3.2–3.3 × 1.8 mm, 3–5-nerved, upper glume 2.8 × 1.3–1.4 mm; callus usually glabrous; lemma 3.5–3.6 × 1.8–2 mm, apex usually acute, nerves usually scabrous, between the nerves slightly scabrous; palea 2.9 mm long, nerves 0.7 mm apart, usually scabrous or ciliate; anthers 1–1.6 mm long. Monoclines, chasmogamous.

Distribution:—South American native grass from Argentina, Bolivia and Perú, from 11º–26º S and 65º–75º W. Inhabits rocky soils in high mountain meadows between 4000 and 5004 m.

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References

Bennington, C.C. & McGraw, J.B. (1995) Natural-selection and ecotypic differentiation in *impatiens-pallida*. *Ecological Monographs* 65: 303–23.
http://dx.doi.org/10.2307/2937062

Bonnet, E. & Van de Peer, Y. (2002) zt: a software tool for simple and partial Mantel tests. *Journal of Statistical Software* 7: 1–12.

Briggs, D. & Walters, S.M. (1997) *Plant variation and evolution*. Cambridge University Press, Cambridge, UK, 512 pp.
http://dx.doi.org/10.1016/S0176-1617(99)80336-8

Clausen, J., Keck, D.D. & Hiesey, W.M. (1948) *Experimental studies on the nature of species. III. Environmental responses of climatic races of Achillea*. Carnegie Institute of Washington Publication 581. Washington, DC, 129 pp.

Clayton, W.D. & Renvoize, S.A. (1986) Genera Graminum. *Grasses of the World*. Royal Botanic Gardens, Kew, London, 389 pp.

Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D. & Vitousek, P.M. (1998) Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* 113: 188–196.
http://dx.doi.org/10.1007/s004420050367

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer, Sunderland, Massachusetts, 545 pp.

Desvaux, E. (1854) Gramineas. *In*: Gay, C. (ed.) Flora chilena (t.6): 1−551. Available from: http://botanicus.org/page/2271847.

Dudley, S.A. (1996) Differing selection on plant physiological traits in response to environmental water availability: a test of adaptive hypotheses. *Evolution* 50: 103–110.
http://dx.doi.org/10.2307/2410784

Dumortier, B.C. (1823) *Observations sur les Graminées de la Flore Belgique*. Casterman, J., Aîné, Tournay, 153 pp.
http://dx.doi.org/10.5962/bhl.title.346

Ellison, A.M., Buckley, H.L., Miller, T.E. & Gotelli, N.J. (2004) Morphological variation in *Sarracenia purpurea* (Sarraceniaceae): geographic, environmental, and taxonomic correlates. *American Journal of Botany* 91: 1930–1935.
http://dx.doi.org/doi:10.3732/ajb.91.11.1930

Fabbro, T. & Körner, C. (2004) Altitudinal differences in flower traits and reproductive allocation. *Flora* 199: 70–81.
http://dx.doi.org/10.1078/0367-2530-00128

Fernández Pepi, M.G., Giussani, L.M. & Morrone, O. (2008) Variabilidad morfológica de las especies del complejo *Poa resinulosa* (Poaceae) y su relación con las especies de la sección Dioicopoa. *Darwiniana* 46: 279–296.

Gillespie, L.J. & R.J. Soreng. (2005) Aphylogenetic analysis of the bluegrass genus *Poa* based on cpDNA restriction site data. *Systematic Botany* 30: 84–105.
http://dx.doi.org/10.1600/0363644053661940

Gillespie, L.J., Archambault, A. & Soreng, R.J. (2007) Phylogeny of *Poa* (Poaceae) based on trnT-trnF sequence data: major clades and basal relationships. *Aliso* 23: 420–434.

http://dx.doi.org/ 10.5642/aliso.20072301.33
Gillespie, L.J., Soreng, R.J., Bull, R.D., Jacobs, S.W.L. & Refulio Rodriguez, N.F. (2008) Phylogenetic relationships in subtribe Poinae (Poaceae, Poeae) based on nuclear ITS and plasta trnT-trnL-trnF sequences. *Botany* 86: 938–967. http://dx.doi.org/10.1139/B08-076
Giussani, L.M., Soreng, R.J. & Anton, A.M. (2011) Novedades nomenclaturales en Poaceae argentinas. *Darwiniana* 49: 90–93.
Giussani, L.M., Anton, A.M., Negritto, M.A. & Soreng, R.J. (2012) *Poa. In*: Zuloaga, F.O., Rúgolo, Z.E & Anton, A.M. (Eds.) *Flora Argentina. Flora vascular de la República Argentina*. Graficamente Ediciones, Córdoba, pp. 284–339.
Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, New York, 222 pp.
Hackel, E. (1911) Stuckert, T. Tercera contribución al conocimiento de las Gramíneas argentinas. *Anales del Museo Nacional de Buenos Aires* 21 (ser 3, t XIV): 1–214.
Hackel, E. (1914) Stuckert, T. Beiträge zur Kenntniss der Flora Argentiniens. II. Quatrième contribution a la connaissance des Graminées Argentines. *Annuaire du Conservatoire et Jardin Botaniques de Genève* 17: 278–309.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978. http://dx.doi.org/10.1002/joc.1276
Hijmans, R.J., Guarino, L. & Mathur, P. (2012) *DIVA-GIS*. Version 7.5. A geographic information system for the analysis of species distribution data.
Hooker, J.D. (1846) The Botany of the Antarctic Voyage. *Flora Antarctica* (2). Reeve, London, 574 pp. http://dx.doi.org/10.5962/bhl.title.16029
Hotelling, H. (1936) Relations between two sets of variables. *Biometrika* 28: 321–377. http://dx.doi.org/10.1093/biomet/28.3-4.321
Hufford, K.M. & Mazer, S.J. (2003) Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* 18: 147–155. http://dx.doi.org/10.1016/S0169-5347(03)00002-8
Jafari, S. & Sheidai, M. (2011) The role of elevation on *Alopecurus* L. speciation; Morphological evidence. *International Journal of Agriculture: Research and Review* 1(4): 164–167.
Johnson, R.A. & Wichern, D.W. (1998) *Applied multivariate statistical analysis*. 4th ed. Prentice Hall, Upper Saddle River, New Jersey, 834 pp. http://dx.doi.org/10.2307/2531032
Linhart, Y. & Grant, M.C. (1996) Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237–277. http://dx.doi.org/10.1146/annurev.ecolsys.27.1.237
Linnaeus, C. (1753) *Species plantarum* 1. Stockholm, L. Salvius, 560 pp.
Maad, J., Armbruster, W.S. & Fenster, C.B. (2013) Floral size variation in *Campanula rotundifolia* (Campanulaceae) along altitudinal gradients: patterns and possible selective mechanisms. *Nordic Journal of Botany* 31: 361–371. http://dx.doi.org/10.1111/j.1756-1051.2013.01766.x
Macek, P., Macková J. & de Bello, F. (2009) Morphological and ecophysiological traits shaping altitudinal distribution of three *Polylepis* treeline species in the dry tropical Andes. *Acta Oecologica* 35: 778–785. http://dx.doi.org/10.1016/j.actao.2009.08.013
Mantel, N.A. (1967) The detection of disease clustering and generalized approach. *Cancer Research* 27: 209–220.
McCune, B. & Mefford, M.J. (1995) *PC-ORD*. Multivariate analysis of ecological data, version 2.0. MjM Software Design, Gleneden Beach, Oregon, USA.
Milla, R. & Reich, P.B. (2011) Multi-trait interactions, not phylogeny, fine-tune leaf size reduction with increasing altitude. *Annals of Botany* 107: 455–465. http://dx.doi.org/10.1093/aob/mcq261
Nees von Esenbeck, C.G.D. & Meyen, F.J.F. (1835) *In:* Meyen, F.J.F. (Ed.) *Reise um die erde 2.* Conrad Feister, Berlin, 411 pp.
Negritto, M.A & Anton, A.M. (1998) *Poa anfamensis*, una nueva especie de Poaceae de la Argentina. *Darwiniana* 35: 159–162.
Negritto, M.A & Anton, A.M. (2000) Revisión de lase species de *Poa* (Poaceae) del noroeste Argentino. *Kurtziana* 28: 95–136.
Nicora, E.G. (1997) Notas sobre los géneros *Poa* y *Puccinellia* (Gramineae). *Hickenia* 2: 143–148.
Parkhurst, D.F. & Loucks, O.I. (1972) Optimal leaf size in relation to environment. *Journal of Ecology* 60: 505–537. http://dx.doi.org/10.2307/2258359
Pilger, R. (1898) Plantae Stübelianae novae. *In*: Engler, A. (Ed.) *Botanische Jahrbuecher fuer Systematik* 25: 709−721.
Pillai, K.C.S. (1960) *Statistical tables for tests of multivariate hypotheses*. Manila, The Statistical Center, University of the Philippines, Philippines, 46 pp.
Richards, C.L., Pennings, S.C. & Donovan, L.A. (2005) Habitat range and phenotypic variation in salt marsh plants. *Plant Ecology* 176: 263–273. http://dx.doi.org/10.1007/s11258-004-0841-3
Scheepens, J.F., Frei, E.S. & Stöcklin, J. (2010) Genotypic and environmental variation in specific leaf area in a widespread Alpine plant after transplantation to different altitudes. *Oecologia* 164: 141–150. http://dx.doi.org/10.1007/s00442-010-1650-0
Schneller, J. & Liebst, B. (2007) Patterns of variation of a common fern (*Athyrium filix-femina*; Woodsiaceae): Population structure along and between altitudinal gradients. *American Journal of Botany* 94: 965–971. http://dx.doi.org/10.3732/ajb.94.6.965
Soreng, R.J. (1998) An infrageneric classification for *Poa* in North America, and other notes on sections, species, and subspecies of *Poa*, *Puccinellia*, and *Dissanthelium* (Poaceae). *Novon* 8: 187−202. http://dx.doi.org/10.2307/3391995

Soreng, R.J. & Peterson, P.M. (2012) Revision of *Poa* L. (Poaceae, Pooideae, Poeae, Poinae) in Mexico: new records, re-evaluation of *P. ruprechtii*, and two new species, *P. palmeri* and *P. wendtii*. *Phytokeys* 15: 1–104.
http://dx.doi.org/10.3897/phytokeys.15.3084
Soreng, R.J., Bull, R.D. & Gillespie, L.J. (2010) Phylogeny and reticulation in *Poa* L. based on plastid trnTLF and nrITS sequences with attention to diploids. *In*: Seberg, O., Petersen, G., Barfod, A.S. & Davis, J.I. (Eds.) *Diversity, Phylogeny, and Evolution in the Monocotyledons*, Aarhus University Press, Aarhus, 619–643.
Still, D.W., Kim, D.-H. & Aoyama, N. (2005) Genetic variation in *Echinacea angustifolia* along a climatic gradient. *Annals of Botany* 96: 467–477.
http://dx.doi.org/10.1093/aob/mci199
Thiers, B. (2014) *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/

APPENDIX 1. Vouchers and specimens examined.

Taxa	**Specimens**	**Country**	**Province/State**	Collection
P. anfamensis	ANFA01	Argentina	La Rioja, Famatina	*Calderón 1171* (BAA)
	ANFA02	Argentina	Tucumán, Tafí del Valle	*Lillo 5468* (LIL)
P. jujuyensis	JUJ01	Argentina	Jujuy, Humahuaca	*Fernandez 50a* (CORD)
	JUJ02	Argentina	Jujuy, Rinconada	*Schwabe 405* (CORD)
	JUJ03	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA 4785a)
	JUJ04	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA 4785b)
	JUJ05	Argentina	Jujuy, Humahuaca	*Fernandez 52* (BAA)
	JUJ06	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA 4787a)
	JUJ07	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA 4787b)
	JUJ08	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA 4791)
	JUJ09	Argentina	Jujuy, Humahuaca	*Cabrera 9213* (BAA)
	JUJ10	Argentina	Jujuy, Humahuaca	*Fernandez 1017* (BAA)
	JUJ11	Argentina	Jujuy, Humahuaca	*Fernandez 5* (BAA)
	JUJ12	Argentina	Jujuy, Humahuaca	*Frangi 28* (CORD)
	JUJ13	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA 4761)
	JUJ14	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA)
	JUJ15	Perú	Junín, Junín	*Aguilar 994* (BAA)
	JUJ16	Argentina	Jujuy, Humahuaca	*s.n.* (BAA 7197)
	JUJ17	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA)
	JUJ18	Argentina	Jujuy, Humahuaca	*Fernandez s.n.* (BAA)
	JUJ19	Argentina	Salta, San Antonio de Los Cobres	*Werner 298* (LP)
P. lilloi	LIL01	Argentina	Jujuy, Humahuaca	*Fernandez 50b* (CORD, BAA 2592b)
	LIL02	Argentina	Jujuy, Humahuaca	*Fabris 1844* (BAA)
	LIL03	Argentina	Tucumán, Tafí del Valle	*Lillo 5619* (BAA)
P. parviceps	PARV01	Argentina	Jujuy, Susques	*Werner 211* (LP)
	PARV02	Argentina	Jujuy, Rinconada	*Schwabe 908* (CORD)
	PARV03	Argentina	Jujuy, Rinconada	*s.n.* (BAA 7148)
	PARV04	Argentina	Jujuy, Rinconada	*s.n.* (BAA 7162)
	PARV05	Argentina	Jujuy, Humahuaca	*Buthsatz s.n.* (BAA 14572)
	PARV06	Argentina	Jujuy, Humahuaca	*Fernandez 1007* (BAA)
	PARV07	Argentina	San Juan, Iglesia	*Carrizo 3* (BAA)
	PARV08	Argentina	La Rioja, Aguas Negras	*Calderón 1011* (BAA)
	PARV09	Argentina	Jujuy, Yavi	*Cabrera 7838* (BAA)
	PARV10	Argentina	Córdoba, Punilla	*Doering s.n.* (CORD 15616)
	PARV11	Argentina	Córdoba, Calamuchita	*Hunziker 9558* (CORD)
	PARV12	Argentina	San Luis, Junín	*Hunziker 11807* (CORD)
	PARV13	Argentina	Córdoba, San Alberto	*Lutti 5214* (CORD)
	PARV14	Argentina	Catamarca, Ambato	*Hunziker 19993* (CORD)
	PARV15	Argentina	Catamarca, Ambato	*Hunziker 19815* (CORD)
	PARV16	Argentina	Catamarca, Ambato	*Hunziker 20040* (CORD)
	PARV17	Argentina	Catamarca, Ambato	*Hunziker 20843* (CORD)
	PARV18	Argentina	Catamarca, Ambato	*Hunziker 21687* (CORD)
	PARV19	Argentina	Catamarca, Ambato	*Hunziker 22246* (CORD)
	PARV20	Argentina	Catamarca, Ambato	*Hunziker 20978* (CORD)
	PARV21	Argentina	Catamarca, Ambato	*Hunziker 20972* (CORD)
	PARV22	Argentina	Catamarca, Ambato	*Hunziker 20912* (CORD)
	PARV23	Argentina	Catamarca, Ambato	*Hunziker 20967* (CORD)
	PARV24	Argentina	Catamarca, Ambato	*Hunziker 20867* (CORD)
	PARV25	Argentina	Tucumán, Tafí del Valle	*Rodriguez 575* (CORD)
	PARV26	Argentina	La Rioja, Famatina	*Kurtz 13993* (CORD)
	PARV27	Argentina	La Rioja, Famatina	*Krapovickas 6265* (CORD)
	PARV28	Argentina	Catamarca, Ambato	*Hunziker 20835* (CORD)
	PARV29	Argentina	Catamarca, Ambato	*Hunziker 20901* (CORD)
	PARV30	Argentina	Córdoba, Calamuchita	*Hunziker 9627* (CORD)
	PARV31	Argentina	Córdoba, Punilla	*Hunziker 15616* (CORD)

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APPENDIX 1. (Continued)

Taxa	**Specimens**	**Country**	**Province/State**	Collection
P. scaberula	SCAB01	Argentina	Córdoba, Punilla	*Meyer 15536a* (LILL)
	SCAB02	Argentina	Córdoba, Punilla	*Meyer 15536b* (LILL)
	SCAB03	Argentina	Córdoba, Punilla	*Meyer 15536c* (LILL)
	SCAB04	Argentina	Tucumán, Tafí del Valle	*Lillo 3514* (LILL)
	SCAB05	Argentina	San Luis, Coronel Pringles	*Anderson 2007* (CORD)
	SCAB06	Argentina	Córdoba, San Alberto	*Cabido s.n.* (CORD 397)
	SCAB07	Argentina	Córdoba, San Alberto	*Lutti 5075* (CORD)
	SCAB08	Argentina	Córdoba, Punilla	*Hunziker 16304* (CORD)
	SCAB09	Argentina	Catamarca, Ambato	*Hunziker 19830* (CORD)
	SCAB10	Argentina	Catamarca, Ambato	*Hunziker 20067* (CORD)
	SCAB11	Argentina	Catamarca, Ambato	*Hunziker 19702a* (CORD)
	SCAB12	Argentina	Catamarca, Ambato	*Hunziker 19702b* (CORD)
	SCAB13	Argentina	Catamarca, Ambato	*Hunziker 20799* (CORD)
	SCAB14	Argentina	Córdoba, San Alberto	*Hieronymus s.n.* (CORD 471)
	SCAB15	Argentina	Córdoba, Punilla	*Hieronymu s.n.* (CORD)
	SCAB16	Argentina	La Rioja, Famatina	*Hieronymus s.n.* (CORD 670)
	SCAB17	Argentina	Córdoba, Punilla	*Hosseus s.n.* (CORD 729)
	SCAB18	Perú	Junín, Junín	*Petterson 35* (USM)
	SCAB19	Argentina	Córdoba, Punilla	*Hunziker 20997* (CORD)
	SCAB20	Argentina	Córdoba, Punilla	*Stuckert 20999* (CORD)
	SCAB21	Argentina	Córdoba, Punilla	*Stuckert 21000* (CORD)
	SCAB22	Argentina	Córdoba, Punilla	*Stuckert 21004* (CORD)
	SCAB23	Argentina	Córdoba, Cruz del Eje	*Stuckert 21091* (CORD)
	SCAB24	Argentina	Córdoba, Cruz del Eje	*Stuckert 20893* (CORD)
	SCAB25	Argentina	Córdoba, Cruz del Eje	*Stuckert 20739* (CORD)
	SCAB26	Argentina	Córdoba, Cruz del Eje	*Stuckert 20801* (CORD)
	SCAB27	Argentina	Córdoba, Cruz del Eje	*Stuckert 20803* (CORD)
	SCAB28	Argentina	Córdoba, Cruz del Eje	*Stuckert 20806* (CORD)
	SCAB29	Argentina	Córdoba, Cruz del Eje	*Stuckert 20879* (CORD)
	SCAB30	Argentina	Córdoba, Cruz del Eje	*Stuckert 20630* (CORD)
	SCAB31	Argentina	Córdoba, Cruz del Eje	*Stuckert 20707* (CORD)
	SCAB32	Argentina	Córdoba, Cruz del Eje	*Stuckert 20848* (CORD)
	SCAB33	Argentina	Córdoba, Cruz del Eje	*Stuckert 21017* (CORD)
	SCAB34	Argentina	Córdoba, Punilla	*Kurtz 2929* (CORD)
	SCAB35	Argentina	Córdoba, Punilla	*Kurtz 3856b* (CORD)
	SCAB36	Argentina	Córdoba, Punilla	*Kurtz 3885* (CORD)
	SCAB37	Argentina	Córdoba, Punilla	*Doering 15577* (CORD)
	SCAB38	Argentina	Jujuy, Santa Catalina	*Kurtz 11483* (CORD)
	SCAB39	Argentina	La Rioja, Famatina	*Kurtz 14972a* (CORD)
	SCAB40	Argentina	La Rioja, Famatina	*Kurtz 14972b* (CORD)
	SCAB41	Argentina	La Rioja, Famatina	*Kurtz 15028* (CORD)
	SCAB42	Ecuador	Azuay	*Peterson 8856* (US)
	SCAB43	Argentina	La Rioja, Chilecito	*Morello 5230* (LP)
	SCAB44	Chile	Magallanes	*Spegazzini 863* (LP)
	SCAB45	Argentina	Neuquén, Catan Lil	*Dawson 1174* (LP)
	SCAB46	Argentina	Chubut, Carranleufu	*Spegazzini 905* (LP)
	SCAB47	Argentina	Río Negro, Bariloche	*Cabrera 113* (LP)
	SCAB48	Argentina	Chubut, Carranleufu	*Spegazzini 901* (LP)
	SCAB49	Chile	Magallanes	*s.n.* (LP 7908)
	SCAB50	Argentina	Río Negro, Bariloche	*Maldonado 600a* (LP)
	SCAB51	Argentina	Córdoba, Punilla	*Kurtz 15661* (CORD)
	SCAB52	Bolivia	Cochabamba, Ayopaya	*Candia 3* (LPB)
	SCAB53	Bolivia	Oruro, Pagador	*Peterson 12772a* (LPB)
	SCAB54	Bolivia	La Paz, Murillo	*Solomon 16247* (LPB)
	SCAB55	Bolivia	Tarija, José María Aviléz	*Beck 27410* (LPB)

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APPENDIX 1. (Continued)

Taxa	Specimens	Country	Province/State	Collection
P. scaberula	SCAB56	Bolivia	Potosí, Frías	*Wood 10753* (LPB)
	SCAB57	Argentina	Córdoba, Punilla	*Doering 26* (CORD)
	SCAB58	Bolivia	La Paz	*Buchtien 8539* (US)
	SCAB59	Bolivia	Potosí, San Felipe	*Hitchcock 22598a* (US)
	SCAB60	Bolivia	Cochabamba, Tequiña	*Hitchcock 22860* (US)
	SCAB61	Bolivia	Oruro, Pagador	*Peterson 12772b* (LPB)
	SCAB62	Bolivia	La Paz	*Buchtien 8831* (US)
	SCAB63	Bolivia	La Paz	*Buchtien 370* (US)
	SCAB64	Bolivia	Oruro, Challapata	*s.n.* (US 1099682)
	SCAB65	Bolivia	Oruro	*s.n.* (US 1099683)
	SCAB66	Bolivia	La Paz, Pongo	*s.n.* (US 1388927)
	SCAB67	Bolivia	Potosí, San Felipe	*Hitchcock 22598b* (US)
	SCAB68	Argentina	Chubut, Cushamen	*Illín 259* (US)
	SCAB69	Argentina	Santa Cruz, Guer Aike	*Peterson 17091* (US)
	SCAB70	Argentina	Río Negro, Bariloche	*Peterson 17331* (LP)
	SCAB71	Argentina	Neuquén, Picunches	*Parodi 3164* (US)
	SCAB72	Argentina	Chubut, Futaleufú	*Burkart 19835* (US)
	SCAB73	Argentina	Mendoza, Tupungato	*Melis 79* (US)
	SCAB74	Argentina	Neuquén, Los Lagos	*Diem 218* (US)
	SCAB75	Chile	Magallanes	*Philippi 415* (US)
	SCAB76	Chile	Magallanes	*Andersson s.n.* (US 1717778)
	SCAB77	Chile	Valdivia	*Buchtien s.n.* (US 1099673)
	SCAB78	Chile	Aysén, Aysén	*Barros 5640* (US)
	SCAB79	Chile	Aysén, Aysén	*Barros 5638* (US)
	SCAB80	Chile	Aysén, Aysén	*Barros 5644* (US)
	SCAB81	Chile	Aysén, Aysén	*Barros 5643* (US)
	SCAB82	Chile	Aysén, Aysén	*Barros 5642* (US)
	SCAB83	Chile	Aysén, Aysén	*Dusén s.n.* (US 1161179)
	SCAB84	Chile	Magallanes	*s.n.* (US 1761387)
	SCAB85	Ecuador	Tungurahua, Patate	*Asplund 7968* (US)
	SCAB86	Argentina	Río Negro, Bariloche	*Maldonado 600b* (US)
	SCAB87	Perú	Cuzco, Espinar	*Vargas 11202* (US)
	SCAB88	Perú	Ayacucho, Parinacochas	*Peterson 16350a* (US)
	SCAB89	Chile	Aysén, Aysén	*Barros 5639* (US)
	SCAB90	Perú	Cuzco, Ollaantaytambo	*Hitchcock 22540* (US)
	SCAB91	Bolivia	Potosí, Frías	*Peterson 13148* (US)
	SCAB92	Bolivia	La Paz	*Buchtien 8844* (US)
	SCAB93	Bolivia	Cochabamba, Taquiña	*Hitchcock 22859* (US)
	SCAB94	Bolivia	Cochabamba, Taquiña	*Hitchcock 22865* (US)
	SCAB95	Bolivia	Potosí, Quijarro	*Peterson 12816* (US)

APPENDIX 2. Geographical locations, elevation, and environmental characteristics of Poa specimens studied. Population codes correspond to specimens listed in Appendix 1.

Taxa	Population	Latitude	Longitude	Elevation (m)	AMINT (°C)	AMAXT (°C)	AMT (°C)	AMP (mm)
P. anfamensis	ANFA01	-26.7411	-65.5986	2100	9.23	20.49	14.86	415.00
	ANFA02	-29.0063	-67.7004	3540	-1.54	12.67	5.56	173.33
P. jujuyensis	JUJ01	-23.1879	-65.7211	5004	-7.86	11.03	1.59	144.17
	JUJ02	-23.2292	-65.7281	4500	-6.58	12.32	2.87	140.00
	JUJ03	-23.2264	-65.7478	4600	-5.50	13.44	3.97	138.33
	JUJ04	-23.2264	-65.7478	4600	-5.50	13.44	3.97	138.33
	JUJ05	-23.2427	-65.7410	4500	-5.18	13.76	4.29	138.33
	JUJ06	-23.2193	-65.7482	4600	-6.22	12.73	3.25	139.17
	JUJ07	-23.2193	-65.7482	4600	-6.22	12.73	3.25	139.17
	JUJ08	-23.2520	-65.7424	4500	-3.91	15.05	5.57	135.83
	JUJ09	-23.2520	-65.7424	4500	-3.91	-3.91	5.57	135.83
	JUJ10	-23.2520	-65.7424	4500	-3.91	-3.91	5.57	135.83
	JUJ11	-23.2329	-65.7429	4650	-5.50	13.44	3.97	138.33
	JUJ12	-23.2520	-65.7424	4500	-3.91	15.05	5.57	135.83
	JUJ13	-23.2520	-65.7424	5000	-3.91	15.05	5.57	135.83
	JUJ14	-23.2520	-65.7424	5000	-3.91	15.05	5.57	135.83
	JUJ15	-11.3842	-75.4564	4120	-0.38	13.88	6.75	653.33
	JUJ16	-23.1803	-65.7182	4950	-7.28	11.63	2.18	143.33
	JUJ17	-23.1879	-65.7212	5000	-7.86	11.03	1.59	144.17
	JUJ18	-23.1879	-65.7211	5000	-7.86	11.03	1.59	144.17
	JUJ19	-24.2140	-66.3567	4080	-2.23	15.03	6.40	93.33
P. lilloi	LIL01	-23.1878	-65.7201	5000	-7.86	11.03	1.59	144.17
	LIL02	-23.1803	-65.7182	4900	-7.28	11.63	2.18	143.33
	LIL03	-26.6259	-65.7751	4200	-1.53	12.98	5.73	196.67
P. parviceps	PARV01	-24.0986	-66.4814	4450	-4.26	13.23	4.49	88.33
	PARV02	-22.6876	-66.5107	4300	-3.53	15.44	5.95	90.00
	PARV03	-23.2890	-65.7338	4200	-2.44	16.43	7.00	135.00
	PARV04	-23.2890	-65.7338	4200	-2.44	16.43	7.00	135.00
	PARV05	-23.2431	-65.7429	4450	-4.43	14.54	5.06	136.67
	PARV06	-23.2264	-65.7478	4606	-5.50	13.44	3.97	138.33
	PARV07	-30.3968	-69.5094	2800	-1.59	12.64	5.53	98.33
	PARV08	-29.0985	-67.5938	1710	7.65	23.51	15.58	173.33
	PARV09	-22.2121	-65.2839	4000	-1.63	18.39	8.38	241.67
	PARV10	-31.4242	-64.8096	2326	2.28	16.52	9.40	545.83
	PARV11	-32.0656	-64.9225	2400	0.68	15.08	7.88	554.17
	PARV12	-33.1477	-66.2152	2005	2.79	17.86	10.33	448.33
	PARV13	-31.5303	-64.8644	2181	2.67	16.88	9.78	543.33
	PARV14	-28.3241	-66.0219	3850	-0.67	13.48	6.40	270.00
	PARV15	-28.2740	-66.0234	3350	0.77	14.84	7.80	270.83
	PARV16	-28.2733	-66.0430	4050	-2.60	11.65	4.53	265.00
	PARV17	-28.2394	-66.0173	3917	-1.73	12.43	5.35	266.67
	PARV18	-28.1801	-65.9906	3500	1.23	15.22	8.23	269.17
	PARV19	-28.1803	-66.0152	3800	-0.43	13.65	6.61	264.17
	PARV20	-28.1885	-65.9904	3500	1.36	15.36	8.36	270.00
	PARV21	-28.1885	-65.9904	3500	1.36	15.36	8.36	270.00
	PARV22	-28.1885	-65.9904	3500	1.36	15.36	8.36	270.00
	PARV23	-28.1885	-65.9904	3500	1.36	15.36	8.36	270.00
	PARV24	-28.2509	-66.0333	4366	-4.24	10.12	2.94	269.17
	PARV25	-26.4130	-65.7444	3246	2.41	16.37	9.39	186.67
	PARV26	-28.8901	-67.6633	3000	1.81	16.29	9.05	168.33
	PARV27	-28.6711	-67.9161	4100	-3.39	10.52	3.56	149.17
	PARV28	-28.2409	-66.0182	3900	-1.73	12.43	5.35	266.67
	PARV29	-28.2206	-66.0182	3850	-1.81	12.38	5.28	265.83
	PARV30	-31.9886	-64.9318	2600	0.98	15.38	8.18	552.50
	PARV31	-31.4307	-64.8138	2400	2.11	16.34	9.23	545.83

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APPENDIX 2. (Continued)

Taxa	Population	Latitude	Longitude	Elevation (m)	AMINT (°C)	AMAXT (°C)	AMT (°C)	AMP (mm)
P. scaberula	SCAB01	-31.6094	-64.7575	2200	2.96	17.16	10.06	556.67
	SCAB02	-31.6094	-64.7575	2200	2.96	17.16	10.06	556.67
	SCAB03	-31.6094	-64.7575	2200	2.96	17.16	10.06	556.67
	SCAB04	-26.8342	-65.7875	3300	3.19	16.78	9.98	206.67
	SCAB05	-32.8625	-66.0039	1490	5.83	20.47	13.15	475.00
	SCAB06	-32.0453	-64.9378	2064	0.16	14.61	7.38	550.83
	SCAB07	-31.6812	-64.8737	2000	2.93	17.14	10.03	546.67
	SCAB08	-31.6227	-64.6781	1550	5.34	19.42	12.38	557.50
	SCAB09	-27.9676	-66.0644	3000	3.76	17.63	10.69	252.50
	SCAB10	-28.2873	-66.0284	3380	2.14	16.16	9.15	271.67
	SCAB11	-28.2681	-65.9992	3000	4.77	18.70	11.73	286.67
	SCAB12	-28.2681	-65.9992	3000	4.77	18.70	11.73	286.67
	SCAB13	-28.1833	-65.9505	2721	4.69	18.54	11.62	286.67
	SCAB14	-31.6446	-64.7256	1876	4.38	18.50	11.44	558.33
	SCAB15	-31.4040	-64.7804	1821	4.48	18.58	11.53	545.83
	SCAB16	-28.9545	-67.6440	3232	3.18	17.98	10.58	170.00
	SCAB17	-30.8444	-64.4993	1184	6.68	20.78	13.73	552.50
	SCAB18	-11.0630	-76.1628	4150	-1.73	11.96	5.11	815.00
	SCAB19	-31.3328	-64.6041	1081	7.63	21.72	14.67	547.50
	SCAB20	-31.3328	-64.6041	1081	7.63	21.72	14.67	547.50
	SCAB21	-31.3328	-64.6041	1081	7.63	21.72	14.67	547.50
	SCAB22	-31.3328	-64.6041	1081	7.63	21.72	14.67	547.50
	SCAB23	-31.2960	-64.7281	1783	4.66	18.77	11.71	546.67
	SCAB24	-31.2960	-64.7281	1783	4.66	18.77	11.71	546.67
	SCAB25	-31.3367	-64.6315	1120	15.08	43.27	14.59	542.50
	SCAB26	-31.3367	-64.6315	1120	15.08	43.27	14.59	542.50
	SCAB27	-31.3367	-64.6315	1120	15.08	43.27	14.59	542.50
	SCAB28	-31.3367	-64.6315	1120	13.64	41.83	14.59	542.50
	SCAB29	-31.2960	-64.7281	1783	4.66	18.77	11.71	546.67
	SCAB30	-31.2960	-64.7281	1783	4.66	18.77	11.71	546.67
	SCAB31	-31.2960	-64.7281	1783	4.66	18.77	11.71	546.67
	SCAB32	-31.2960	-64.7281	1783	4.66	18.77	11.71	546.67
	SCAB33	-31.3421	-64.7408	1700	5.22	19.30	12.26	545.83
	SCAB34	-31.2645	-64.4301	1000	7.00	21.11	14.05	571.67
	SCAB35	-31.3904	-64.7184	1521	5.58	19.66	12.62	546.67
	SCAB36	-31.3904	-64.7184	1521	5.58	19.66	12.62	546.67
	SCAB37	-31.4368	-64.8114	2300	2.28	16.52	9.40	546.67
	SCAB38	-21.9462	-66.0505	3832	-0.05	19.39	9.67	161.67
	SCAB39	-28.6600	-67.7333	2500	4.77	19.95	12.36	150.83
	SCAB40	-28.6600	-67.7333	2500	4.77	19.95	12.36	150.83
	SCAB41	-28.6600	-67.7331	2500	4.77	19.95	12.36	150.83
	SCAB42	-2.8161	-79.2581	3851	2.39	10.83	6.61	861.67
	SCAB43	-29.2932	-66.9431	2110	6.38	21.45	13.91	234.17
	SCAB44	-52.2989	-71.5129	118	0.41	9.22	4.81	329.17
	SCAB45	-39.5891	-70.7071	1225	1.55	15.40	8.48	349.17
	SCAB46	-43.5768	-71.6915	535	3.24	13.73	8.49	1.106.67
	SCAB47	-41.1296	-71.2687	790	2.82	14.55	8.68	779.17
	SCAB48	-43.5768	-71.6915	535	3.24	13.73	8.49	1.106.67
	SCAB49	-52.2989	-71.5129	118	0.41	9.22	4.81	329.17
	SCAB50	-41.1296	-71.2687	790	2.82	14.55	8.68	779.17
	SCAB51	-31.4368	-64.8114	2400	2.28	16.52	9.40	546.67
	SCAB52	-17.2858	-66.2119	3931	1.25	17.07	9.16	678.33
	SCAB53	-18.6718	-66.8776	3770	1.48	18.19	9.84	270.00
	SCAB54	-16.2	-68.1167	3900	0.36	14.38	7.37	560.00
	SCAB55	-21.7833	-64.95	3400	2.70	21.40	12.05	347.50
	SCAB56	-19.5892	-65.7535	4000	0.78	17.41	9.10	327.50

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APPENDIX 2. (Continued)

Taxa	Population	Latitude	Longitude	Elevation (m)	AMINT (°C)	AMAXT (°C)	AMT (°C)	AMP (mm)
P. scaberula	SCAB57	-31.4301	-64.8144	2400	2.11	16.34	9.23	545.83
	SCAB58	-20.7677	-66.2900	4070	0.11	17.75	8.93	125.83
	SCAB59	-20.7677	-66.2900	4070	0.11	17.75	8.93	125.83
	SCAB60	-17.3368	-66.1867	2772	8.35	24.80	16.58	510.83
	SCAB61	-17.9761	-67.1245	3901	-1.71	17.53	7.91	321.67
	SCAB62	-16.1618	-69.0918	3950	4.08	16.53	10.31	687.50
	SCAB63	-16.1626	-69.0922	3900	4.08	16.53	10.31	687.50
	SCAB64	-18.9007	-66.7502	4000	1.58	17.62	9.60	278.33
	SCAB65	-16.2068	-68.0164	3700	3.63	18.58	11.10	568.33
	SCAB66	-16.3298	-67.9360	3741	2.46	17.73	10.10	525.83
	SCAB67	-20.7677	-66.2900	4070	0.11	17.75	8.93	125.83
	SCAB68	-42.5263	-71.5216	641	2.32	14.46	8.39	725.00
	SCAB69	-51.7422	-70.1658	60	2.11	11.83	6.97	164.17
	SCAB70	-41.5125	-70.5306	1038	0.99	13.95	7.47	325.83
	SCAB71	-38.6526	-71.0059	1400	0.97	15.49	8.23	775.00
	SCAB72	-42.8172	-71.7157	528	3.25	14.63	8.94	1.040.00
	SCAB73	-33.3724	-69.4721	2353	1.01	15.57	8.29	278.33
	SCAB74	-38.9259	-68.1494	324	6.75	22.08	14.42	137.50
	SCAB75	-52.6241	-73.5389	176	2.15	8.87	5.51	2.195.83
	SCAB76	-52.6241	-73.5389	176	2.15	8.87	5.51	2.195.83
	SCAB77	-39.8808	-73.2429	41	6.87	16.57	11.72	1.820.00
	SCAB78	-45.5968	-72.0413	850	0.85	9.43	5.14	820.83
	SCAB79	-45.5968	-72.0413	850	0.85	9.43	5.14	820.83
	SCAB80	-45.5968	-72.0413	850	0.85	9.43	5.14	820.83
	SCAB81	-45.5992	-72.0320	1000	1.50	9.98	5.74	855.00
	SCAB82	-45.5992	-72.0320	1000	1.50	9.98	5.74	855.00
	SCAB83	-45.3909	-73.1582	808	2.94	9.75	6.35	1.915.00
	SCAB84	-52.8611	-71.7980	103	0.67	8.55	4.61	600.83
	SCAB85	-1.2500	-78.5000	2722	9.23	21.00	15.12	476.67
	SCAB86	-41.0506	-71.5365	782	2.73	14.24	8.48	1.023.33
	SCAB87	-14.0341	-71.3469	4500	-4.94	13.17	4.11	661.67
	SCAB88	-15.2464	-73.6931	3320	1.64	18.42	10.03	484.17
	SCAB89	-45.5990	-72.0354	1065	0.85	9.43	5.14	820.83
	SCAB90	-13.2740	-72.2687	3600	4.13	19.63	11.88	583.33
	SCAB91	-19.6291	-65.7706	4200	-0.67	16.17	7.75	304.17
	SCAB92	-16.4874	-68.0993	3900	1.00	16.38	8.69	475.83
	SCAB93	-17.3351	-66.1935	2742	8.48	25.01	16.75	495.83
	SCAB94	-17.3351	-66.1935	2742	8.48	25.01	16.75	495.83
	SCAB95	-19.4849	-66.8776	3796	1.39	17.86	9.63	160.83

APPENDIX 3. Descriptive statistics of nineteen quantitative variables calculated for each species. Data were taken from 150 herbarium specimens of *P. lilloi* and *P. scaberula* (22 and 128 specimens, respectively). Mean = mean value of the variable. SD = standard deviation. Min = minimum value. Max = maximum value. Characters are listed in Table 1. Significant differences between taxa are denoted with different letters at the 5% level of Tukey's test.

Species	Characters																		
	Vegetative				Reproductive														
	1	2	12	13	14	17	18	19	20	24	25	26	27	28	31	32	37	38	40
P. scaberula																			
Mean	281.21^{a}	53.37^{a}	2.92^{a}	68.48^{a}	73.45a	13.95^{a}	27.75^{a}	3.13^{a}	1.61^{a}	2.89^{a}	2.32^{a}	1.18^{a}	1.99^{a}	0.84^{a}	2.47^{a}	1.33^{a}	1.75^{a}	0.42^{a}	0.58^{a}
SD	175.40	32.27	1.08	40.78	38.16	3.45	15.91	0.62	0.43	0.68	0.40	0.26	0.39	0.18	0.40	0.19	0.27	0.10	0.20
Min	24.13	12.39	1.00	18.37	12.13	4.00	4.63	2.15	0.14	1.00	1.41	0.65	0.87	0.42	1.65	0.90	0.74	0.20	0.19
Max	900.00	144.79	6.00	219.85	163.36	22.00	82.60	5.15	2.89	5.00	3.38	2.26	2.93	1.24	3.67	1.98	2.67	0.70	1.73
Q1	157.11	28.25	2.00	35.00	43.30	12.00	15.28	2.71	1.30	3.00	2.05	0.98	1.73	0.70	2.14	1.20	1.61	0.36	0.47
Q2	378.50	73.12	3.00	92.67	97.59	16.00	38.74	3.49	1.80	3.00	2.55	1.30	2.22	0.94	2.78	1.44	1.93	0.48	0.66
P. lilloi																			
Mean	86.03^{b}	26.92^{b}	1.95^{b}	18.04^{b}	23.05^{b}	7.82^{b}	10.76^{b}	4.47^{b}	2.39^{b}	3.18^{b}	3.23^{b}	1.77^{b}	2.79^{b}	1.31^{b}	3.50^{b}	1.85^{b}	2.89^{b}	0.68^{b}	1.49^{b}
SD	31.35	12.65	0.79	5.41	7.34	1.65	3.33	0.62	0.59	0.59	0.43	0.20	0.35	0.19	0.33	0.29	0.35	0.09	0.55
Min	29.39	10.33	1.00	11.00	13.78	5.00	4.47	3.13	1.49	3.00	2.19	1.42	1.98	1.00	2.61	1.14	1.99	0.46	0.54
Max	174.86	54.02	3.00	28.01	45.80	11.00	16.92	5.32	3.46	5.00	4.02	2.08	3.39	1.70	3.97	2.22	3.64	0.86	2.38
Q1	67.54	18.83	1.00	13.29	18.52	7.00	9.41	4.03	2.00	3.00	3.03	1.58	2.58	1.12	3.40	1.74	2.68	0.62	1.11
Q2	100.92	33.79	3.00	21.50	26.44	9.00	12.32	4.97	2.84	3.00	3.49	1.92	2.96	1.40	3.72	2.06	3.05	0.75	2.07