



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 & Liebster 2007).

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, Sorong & 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 $\frac{2}{3}$ 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 11°–26° S and 65°–75° 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](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. Sorong. (2005) Phylogenetic 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. & Sorong, 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, Poaeae) based on nuclear ITS and plastid 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](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 anfanensis*, una nueva especie de Poaceae de la Argentina. *Darwiniana* 35: 159–162.
- Negritto, M.A. & Anton, A.M. (2000) Revisión de las especies 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/>