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CHASMOPHYTIC VEGETATION AND MESOCLIMATES OF ROCK OUTCROPS IN VENTANIA (BUENOS AIRES, ARGENTINA)

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Summary: We studied the relationships between mesoclimate variations of rock outcrops and the composition of the chasmophytic communities over a W-E altitudinal gradient (500-1243 m a.s.l.) in the Sierras Australes (Ventania). In transitory weather stations located on 5 sites we recorded climatic variables hourly and simultaneously during 3-4 days at each season for 2 years. We used phytosociological data obtained with the *relevé* method by Frangi y Bottino (1995) in sites with same topography that weather stations. The analysis showed the influence of aspect on mesoclimates, since physical properties of rocks enhance thermal contrast originated in direct sun radiation, then, it showed altitudinal gradients. Sites to S (550 m a.s.l.) and SW (850 m a.s.l.) was shadowy, humid with low evaporation, and have a common species assemblage; at higher altitude lower temperatures favour microthermic species: endemic, Subantarctic or Andean. North-facing lower site was the hottest and driest biotope; includes endemisms, xerothermophilous southern-Brazilian, and northwestern Argentina species connected through the Andean-pampean mountainous arch. Northeast-facing mid-elevation outcrops were floristically and mesoclimatically transitional between both lower sites, lacking xerothermophilous and Subantarctic species. Summit outcrops, evaporative, sunny and relatively cold, had lower richness. These mountains enclose mesoclimates, species and communities exclusive to the Pampas, whose arrangement in the landscape are coherent with their lineage.

Key words: landscape arrangement of species, mountain mesoclimates, plant communities, Sierras Australes, species lineage.

Resumen: Vegetación casmofítica y mesoclimas de afloramientos rocosos en Ventania (Buenos Aires, Argentina). Estudiamos las relaciones entre las variaciones mesoclimáticas de roquedales y la composición de las comunidades casmofíticas sobre un gradiente altitudinal (500-1243 m s.n.m.) W-E en las Sierras Australes (Ventania). En 5 estaciones meteorológicas transitorias se registraron variables climáticas horaria y simultáneamente durante 3-4 días cada estación del año durante 2 años. Se utilizaron datos de censos fitosociológicos (20 *relevés)* realizados por Frangi y Bottino (1995) en sitios con topografía similar a las estaciones meteorológicas. El análisis mostró la influencia de la exposición sobre los mesoclimas, ya que las propiedades físicas de las rocas aumentan los contrastes térmicos causados por la radiación solar directa, luego evidenció gradientes altitudinales. Los sitios S (550 m s.n.m.) y SW (850 m s.n.m.) fueron sombríos, húmedos, poco evaporantes, y compartieron especies; a mayor altitud las bajas temperaturas favorecieron las especies microtérmicas: endémicas, subantárticas y andinas. El sitio basal al N fue el biotopo más caliente y seco; incluyó endemismos y especies xerotermófilas austrobrasileñas y del NW argentino. Los faldeos NE fueron florística y mesoclimáticamente transicionales entre los roquedales basales; sin especies subantárticas y xerotermófilas. Las cumbres, evaporantes, soleadas y frescas, poseyeron menor riqueza. Las sierras albergan mesoclimas, especies y comunidades exclusivas para las Pampas, cuya disposición en el paisaje es coherente con su linaje.

Palabras clave: disposición de especies en el paisaje, mesoclimas serranos, comunidades vegetales, Sierras Australes, linaje de especies.

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INTRODUCTION

The relationship between species and their environment has always been a central topic in ecology. Climate, with other environmental factors, has been widely used in predictive models of distribution of species and communities (Guisan & Zimmermann, 2000). It has been recognized that the spatial heterogeneity in climate, from mesoclimate to topoclimate scales, represents an important spatial buffer in response to climate change, and merits increased attention in conservation planning (Ackerly *et al*., 2010).

The elements of the macroclimate best correlated with the vegetation zones and distribution of the biomes are temperature and precipitation; additionally the concentration of rains and the minimum temperatures of the summer season play an important role. At this global level of analysis, the altitude offsets latitude, as it occurs in large mountain ranges (Whittaker, 1970; Walter, 1977; Holdridge, 1978).

At the local level, meso and microclimates play an important role probably increasing the complexity of the distributions and biodiversity. We conceive mesoclimate as resulting of the modification of regional climate - or macroclimate - caused by relief and substrate (Scaëtta, 1935). The relationship between local climates or mesoclimates, and mountain plant communities has been less studied and approached in several ways. Much of the early work concerning relief-induced changes on the climate and soils and segregation of vegetation was summarised by Cantlon (1953) and Geiger (1971). Topography (aspect and elevation) has been considered as indicative of moisture and temperature conditions, and related to species populations and vegetation types (Whittaker, 1956, 1960; Whittaker & Niering, 1965). Meso-microclimatic gradients within landscape play an important role in determining diversity and structure of the soil communities (Raschmanova *et al*., 2008). The substrate plays an important role also. In rock outcrops, different values of physical constants of particular rocks play a decisive role in the thermal balance of rock masses (Rejmánek, 1971) and so, aspect and inclination may also have great influence and may be used to explain the differences in climatic conditions, floristic composition and traits, between rock outcrops.

While the macroclimate – that responds to geographical constraints such as latitude, presence of high mountain ranges, distance to the sea, and the cyclone and anticyclone centers - represents the average condition of the atmosphere and it is based on continuous recordings for more than one decade, mesoclimatic studies could be based on shorter time recordings, fewer than ten years or a month or two in each season of the year (e.g. Capparelli *et al*., 2006). The analysis of microclimates, and frequently of mesoclimates, requires simultaneous and comparative data recorded during short periods. Therefore, the observed differences are an indicator of the modifier effect of local conditions on the climate.

In the province of Buenos Aires, emerge two orographic systems, Tandilia and Ventania. The latter emerges *ca.*1000 m above the Pampas plains and includes a high biodiversity and ecological heterogeneity. Indirect mapping of vegetation allowed Lizzi *et al*. (2007) to recognize sixteen units of vegetation there, whereas field studies identify twenty-four plant communities (Frangi & Bottino, 1995) and eleven mesoclimates, five of the latter for rock outcrops (Kristensen, 1992). The air temperature decreases 0.69 °C per 100 m elevation and above 750 m a.s.l. this could indicate a bioclimatic belt (*sensu* Holdridge, 1978) in the upper sierras, unique in the province (Kristensen, 1992; Kristensen & Frangi, 1995, 1996). The rock outcrops are an exclusive biotope of the range and are the habitat of chasmophytic groups of ferns, sub-shrubs, forbs, grasses and graminoids.

Floristic and phytogeographical studies reported that Tandilia and Ventania were an orographic station in migratory routes for chasmophytic vascular plants of different lineage, geographic distribution, and ecology, and a distinctive ecological place where some local endemisms evolved (Sota, 1967, 1973, 1985; Ponce, 1982, 1986). The historical analysis of biogeography of the Asteraceae from Tandilia and Ventania showed that while the species of Tandilia were more closely related to those of Uruguay, Southern Brazil and Pampas area, Ventania was more related to the Sierras Pampeanas (Crisci *et al*., 2001). Its flora shows different morpho-ecological characteristics and it has phytogeographical relationships with the tropical, subtropical and Subantarctic Andes, Southern Brazil and other mountainous areas in central and NW Argentina. In Lihue Calel (La Pampa, Argentina) Mazzola *et al.* (2008) proved that exposure N-S exerted more control over vegetation variation (380-547 m a.s.l.) than altitude, with higher altitudinal gradients in N slope. Frangi & Bottino (1995) demonstrated the importance of substrate type in segregating plant communities and suggested that differences in biotopes and local climates could explain the local spatial arrangement of species and communities. The identification of the environmental factors associated with species distribution could allow the recognition of the main stressors that determine the primary strategies in plants (*sensu* Grime, 2001), and many of them may be operating in the meso and microclimatic scales.

In order to explain the spatial arrangement of chasmophytic communities in the higher Buenos Aires mountain landscape, we focused on the recognition of the relationships between mesoclimate variations of rock outcrops and the composition of the chasmophytic communities over a W-E altitudinal gradient (500-1243 m a.s.l.). We attempted to describe the local spatial variation of vegetation units (and species) with the associated environmental variation to find matching patterns. We suppose that the main factor operating in mesoclimate differentiation of rock outcrops is the aspect and, that mesoclimatic variables are important in order to explain the current local distribution of taxa according to their lineage.

Material and Methods

Study area. This study was carried out in Ventania, located southwest of the province of Buenos Aires (Argentina), at Provincial Park Ernesto Tornquist (38° to 38° 10’ S and 61°45’ to 62° 8’ W). The climate is temperate and oceanic (Burgos, 1968). Annual mean temperature (at 260 m a.s.l.) is 14.5 °C and annual amplitude is 14-15 °C. Precipitation does not change significantly with elevation (Dascanio & Bianchi *pers. comm.*), but decreases from E to W and N to S, with 809 mm in Sierra de la Ventana (38° 08’ S and 61° 47’ W) and 659 mm in Tornquist (38° 06’ S and 62° 14’ W). The topography has a very limited effect as atmospheric humidity condenser. However, it has a cooling effect more pronounced during winter (the 6 and 7 °C July isotherm encompasses only the Sierras Australes), a shorter period free of frosts (< 160 days/yr), the hardest winter frosts (-10°C, with 5% of probability) and the greater risk of late (spring) frosts in the Province of Buenos Aires (Burgos, 1968). Phytogeographically they are at the Austral District of Pampean Province, near the limit of the Caldén District, Espinal Province (Cabrera, 1971).

Sites. We compared five sites placed in Cerro Ventana and in Cerro Destierro I, which represented the main chasmophytic asociations (Frangi & Bottino, 1985). They were located in a W-E transect across the altitudinal gradient (Fig. 1, Table 1).

Meteorological data. We used the meteorological data set obtained for the identification of mesoclimates (Kristensen, 1992; Kristensen & Frangi, 1996). Simultaneous records were obtained during two consecutive days at the beginning of every season during two years. Light intensity (luximeters), wet and dry bulb air temperatures (battery powered and Assmann type psychrometers), evaporative capacity (Piché evaporimeters), wind speed (microanemometers and anemometers) and soil temperature (geothermometers) were recorded hourly at temporary stations. Atmospheric data was obtained at 1.5 m, and interstitial-soil temperature at 1 and 10 cm depth. Relative humidity and deficit of water pressure saturation (SD) were obtained using psychrometric tables. Values for 21 annual mesoclimatic variables, expressed like indicators of simultaneous differentiation of sites, were defined (see Kristensen & Frangi, 1996).

Communities. We used a data set of 20 *relevés* (3-5 on each site) obtained in a regional phytosociological study (Frangi & Bottino 1995). To obtain a unique importance index for each species at each site, we multiplied its Braun Blanquet’s abundance-dominance and frequency (Braun-Blanquet, 1979). To enhance the non-abundant species and reduce the importance of dominants, we replaced the abundance-dominance classes by the following equivalencies: + and 1 = 1; 2 and 3 = 1.5; 4 and 5 = 2; we changed I to V frequency classes for its midpoint percent value. We used the nomenclature of the Catalog of vascular plants of the Southern Cone (Zuloaga *et al*. 2008 and its online updates at www.darwin.edu.ar). We explored in bibliography information of the lineage and geographical distribution of significant species in relation with mesoclimate and location in the range.

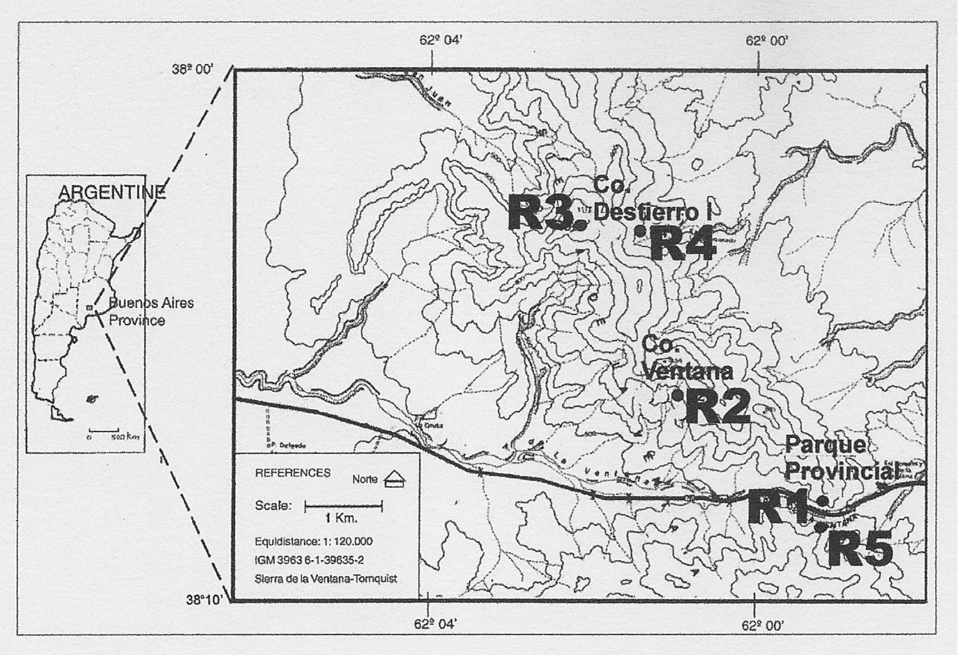


Fig. 1. Topographic map showing rock outcrops (R) sites. See table 1 for the description of sites.

Table 1. Characteristics of studied sites in rock outcrops of Ventania with chasmophytic vegetation

Site	Community	Geo-edaphic environment	Location	Elevation (m a.s.l.)	Aspect
R1	*Poa iridifolia* + *Pleopeltis pinnatifida*	Serrano	Tall blocks at steeply dipping fractured folds, caves; abundant sediments in cracks.	550	S
R2	*P. iridifolia* + *Polystichum plicatum*	Serrano	As above.	850	SW
R3	Scarcely vegetated with herbs + lichens	Serrano	Tall and low rocks with scarce sediments	1100	------
R4	Transitional community between *P. iridifolia* + *P. pinnatifida* / *Cheilanthes buchtienii* + *Zexmenia buphtalmiflora*	Serrano	Tall blocks, fractured abrupt or oblique; abundant sediments in cracks	850	NE
R5	*C. buchtienii* + *Z. buphtalmiflora*	Serrano	As above	550	N

Analysis. To highlight the relationships between floristic composition and mesoclimatic site conditions we analyzed and described the matching patterns found in both data sets (Tables 2, 3). Additionally we performed a canonical correspondence analysis (CCA, Canoco) (Ter Braak, 1988; Jongman *et al*., 1995). Multivariate analysis was exploratory since the data (few sites to compare) does not meet the conditions required by the method.

Table 2. Species list and their importance value for each site. Boulders highlight higher values.

Variables - species		Sites				
		R1	R2	R3	R4	R5
Altitude (m a.s.l.)		**550**	**850**	**1100**	**850**	**550**
Exposition		**S**	**SW**	**0**	**NE**	**N**
Woodsia montevidensis (Spreg.) Hieron.	**Generalist species**	**23.6**	1.2	7.5	1.2	0.6
Piptochaetium montevidense (Spreng.) Parodi		0.6	0.1	7.5	1.2	0.4
Hysterionica pinifolia (Poir) Baker		0.1	0.1	7.5	0.4	0.9
Stevia satureiifolia (Lam.) Sch. Bip.var. *ventanensis* Cabrera		**1.2**	0.4	**7.5**	0.1	0.4
Jarava juncoides (Speg.) Peñailillo		0.9	0.6	**1.2**	**1.2**	1.0
Luzula excelsa Buchenau		0.1	**1.2**	**1.2**	0.6	0.1
Pellaea ternifolia (Cav.) Link		**1.2**	7.5	**0.9**	**0.9**	0.6
Chascolytrum subaristatum (Lam.) Desv.		0.4	0.4	0.9	0.9	0.6
Senecio ventaniensis Cabrera		1.2	0.6	0.9	0.6	0.1
Danthonia cirrata Ack. & Arechav.		0.1	0.4	0.9	0.9	0.4
Gamochaeta stachydifolia (Lam.) Cabrera		0.4	0.6	0.6	0.1	0.1
Oxalis articulata Savigny		0.6	0.6		0.9	0.4
Nassella pampeana (Speg.) Barkworth.		1.2	0.4		0.9	0.1
Blechnum australe L. *ssp. auriculatum* (Cav.) de la Sota		0.9	0.4		0.9	0.1
Melica rigida Cav.		0.1	0.1		0.9	0.6
Cerastium mollissimum Poir.		0.6	0.1		0.6	0.4
Grindelia ventanensis A. Bartoli & Tortosa		0.1	0.4	**7.5**	13.1	
Vulpia bromoides (L.) Gray		0.1	0.1	7.5	0.6	
Cardionema ramosissima (Weinm.) A. Nelson & J.F. Macbr.		0.6	0.4	**23.6**	0.9	
Eryngium stenophyllum Urb		23.6	23.6	0.9	18.4	
Pseudognaphalium cheirantifoliun (Lam.) Hilliard & B.L. Burtt		0.4	0.4	0.9	0.9	
Hypochaeris variegata (Lam.) Baker		0.1	0.1	0.9	0.1	
Koeleria ventanicola A. M. Molina		0.1	0.6	0.6	0.4	
Hieracium palezieuxii Zahn			0.4	0.6	0.1	0.4
Nothoscordum gracile (Dryand. ex Aiton) Stearn			0.6	**7.5**		0.4
Euphorbia portulacoides L. *var. portulacoides*		0.6		**7.5**	0.6	0.6
Achyrocline satureioides (Lam.) DC.		0.9		0.9	0.9	0.9
Pavonia cymbalaria A. St.-Hil & Naudin		0.4		**7.5**	0.4	1.0
Zexmenia buphtalmiflora (Lorentz) Ariza		**22.5**		**Absent of colder sites**	0.6	**1.0**
Cuphea glutinosa Cham. & Schltdl.		0.1			0.6	0.4
Blumenbachia insignis Schrad.		**0.6**			0.4	**0.9**
Hybanthus parviflorus (Mutis ex L. f.) Baill.		0.4			0.4	0.6
Gomphrena perennis L. *var. perennis*		0.1			0.4	0.6
Eryngium paniculatum Cav. & Dombey ex F. Delaroche		0.4			0.4	0.4
Lucilia acutifolia (Poir.) Cass.		0.1			0.4	0.4
Cheilanthes hieronymi Herter		0.1			0.4	0.4
Acmella decumbens (Sm.) R.K. Jansen var *decumbens*		0.4			0.4	0.1
Dichondra sericea Sw. *var. sericea*		**1.2**			0.1	**7.9**
Cheilanthes myriophylla Desv.		0.1			0.1	**0.6**
Eupatorium tanacetifolium Gillies ex Hook. & Arn.		0.1			0.1	0.6
Baccharis articulata (Lam.) Pers.		0.6			0.1	0.4
Daucus pusilus Michx.		0.1			0.1	0.4
Nassella trichotoma (Nees) Hack. ex Arechav.		0.1			0.1	0.1
Crocanthemum brasiliense (Lam). Spach			0.1		0.4	0.6
Lathyrus tomentosus Lam.		0.1	0.1			0.1
Nassella megapotamia (Spreng. ex Trin.) Barkworth		0.6			0.1	
Lathyrus sp.		0.4			0.1	
Nassella ventanicola (Cabrera & Torres) Barkworth		0.1			0.4	
Geranium albicans A. St.-Hil		0.6	0.6		0.4	
Pleopeltis pinnatifida Gillies ex Hook. & Grev.		0.9	0.6		0.6	
Poa iridifolia Hauman		23.6	23.6		0.6	
Calceolaria parviflora Benth.		0.6	0.6			
Adiantum thalictroides Willd. ex Schltdl. f. *bottini* Giúdice & Ñieto		0.9	0.4			
Asplenium dareoides Desv.		0.1	0.4			
Elaphoglossum gayanum (Fée) T. Moore		0.4	0.1			

Variables - species	**Sites**				
	R1	**R2**	**R3**	**R4**	**R5**
Altitude (m a.s.l.)	**550**	**850**	**1100**	**850**	**550**
Exposition	**S**	**SW**	**0**	**NE**	**N**
Hypochaeris petiolaris (Hook. & Arn.) Griseb.	0.1		7.5		
Habranthus gracilifolius Herb.			**7.5**	0.6	
Pelletiera verna A. St.-Hill.			**7.5**	0.4	
Facelis retusa (Lam.) Sch. Bip.			0.6	0.1	
Sommerfeltia spinulosa (Spreng.) Less.			**7.5**	0.6	0.9
Sorghastrum pellitum (Hackk.) Parodi			**7.5**	0.4	0.4
Pfaffia gnafaloides (L.f.) Mart.			**7.5**	0.4	0
*Nassella filiculmi*s (Delile) Barkworth			**7.5**	0.1	0.4
Aristida spegazzinii Arechav.			0.6	0.6	0.6
Dichondra sericea Sw. var. *holosericea* (O'Donnell) Fabris				0.4	0.6
Mimosa rocae Lorentz & Niederl.				0.4	0.6
Krapovickasia flavescens (Cav.) Fryxell				0.4	0.4
Piptochaetium lejopodum (Speg.) Henrard				0.4	0.4
Cliococca selaginoides (Lam.) C.M. Rogers & Mildner				0.4	0.1
Schizachyrium spicatum (Spreng.) Herter				0.1	**1.2**
Wigginsia tephracantha (Link & Otto) D.M. Porter				0.1	0.6
Tillandsia sp.				0.1	0.4
Festuca ventanicola Speg.		0.4	1.2	0.4	
Cerastium chilense Bartl.		0.4	0.6	0.4	
Arjona tuberosa Cav.var. *tandilensis* (Kuntze) G. Dawson		0.1		0.4	
Nassella pampeana (Speg.) Barkworth		0.6		0.1	
Salpichroa origanifolia (Lam.) Baill.	0.2				0.6
Wahlenbergia linarioides (Lam.) A. DC.	0.1	**Basal**			0.4
Phalaris angusta Nees ex Trin.	0.1				0.4
Conyza sp.	0.1		0.9		0.1
Viola arvensis Murray sbsp *arvensis*	0.1				
Grindelia buphthalmoides DC.	22.5			0.1	
Melpomene peruviana (Desv.) J. Sm.		0.4			
Cirsium vulgare (Savi) Ten.		0.4			
Blechnum cordatum (Desv.) Hieron.		13.1			
Acaena ovalifolia Ruiz & Pav.		13.1			
Polystichum plicatum (Poepp. ex Kuntze) Hicken		1.2			
Asclepias sp.			7.5		
Dichondra mycrocalix (Hallier f.) Fabris				0.4	
Cheilanthes buchtienii (Rosensts.) R.M. Tryon					**23.6**
Anemia tomentosa (Savigny) Sw. var. *tomentosa*					0.9
Commelina diffusa Burm. F. var. *diffusa*					0.6
Oxalis refracta A. St.-Hil					0.4
Gamochaeta sp.					0.4
Oenothera sp,					0.4
Bulbostilys capillaris (L.) C.B. Clarke var. *capillaris*					0.4
*Nassella poeppigian*a (Trin. & Rupr.) Barkworth					0.4
Eupatorium subhastatum Hook. & Arn.					0.4
Croton parvifolius Müll. Arg.					0.4
Exclusive species of site (n°)	2	5	1	3	10
Exclusive species of site (%)	1.2	2.4	0.4	2.2	6.6
Richness	60	48	40	72	66

Exclusives of only one site

RESULTS

The distribution of species in sites highlights a group of generalist species, also each site had exclusive species and different richness (Table 2). Extreme values of mesoclimate variables of each site (Table 3) allow interpret the preferences of the species that there inhabit. Depending on their location in the landscape, we recognized some groups of species: basal, montane, exclusive – or absent - of shady and humid S-SW sites, typical of sites without interference to the sun as R3, R4 and

Table 3. Descriptive variables of mesoclimate of each site. LI = Light intensity, SD = water pressure saturation deficit, EVP = Piché evaporation. Note: all mesoclimate values were expressed on a daily basis; except those for winter and summer, values were annual means, absolutes or amplitudes. *measured in soils of interstices between rocks.

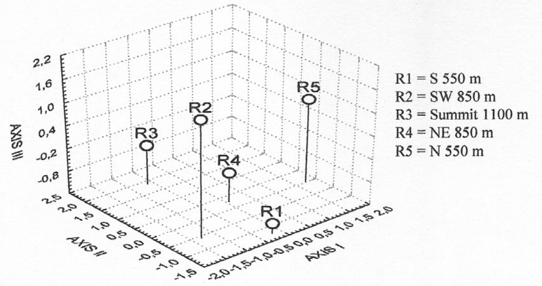
Mesoclimatic variable	**Sites**	**R1**	**R2**	**R3**	**R4**	**R5**
	(exposure-m a.s.l.)	**S-550**	**SW-850**	**1100**	**NE-850**	**N-550**
Ilumination Indicator	LI mean	116	164	443	461	450
	LI annual variation	253	**417**	**707**	273	379
Ligth Intensity (lux)	LI absolute maximum (lux)	56	69	**108**	92	**100**
	LI lowest maximum (lux)	5.10	4.60	6	**40**	**68**
Water Pressure Saturation Deficit	SD annual indicator	**142**	111	117	**143**	**171**
	SD indicator of variation	**205**	146	198	**201**	180
	SD maximum (hPa)	18.90	16.40	16.00	18.00	**22.80**
	SD minimum (hPa)	1.01	0.69	**0.07**	0.98	0.70
Air Temperature (°C)	TEMP absolute maximum	26.50	26.80	23.50	26.00	**29.50**
	TEMP absolute minimum	3.20	2.50	**0.20**	2.80	4.30
	TEMP annual amplitude	23.30	24.30	23.30	23.20	**25.20**
	TEMP maximum daily variation	10.50	9.90	11.20	**12.00**	**14.50**
	TEMP minimum daily variation	5.60	**3.20**	**3.70**	7.90	8.90
Air Evaporative Capacity (mm/h)	EVP absolute maximum	0.76	0.82	**1.50**	0.92	0.95
	EVP absolute minimum	0.17	0.16	0.29	0.27	0.46
	EVP mean	0.48	0.46	**0.81**	0.68	**0.79**
Superficial Soil Temperature* (°C)	maximum -1 cm	21.00	22.00	29.50	**34.90**	**35.50**
	minimum -1 cm	0.20	3.80	0.20	**5.90**	3.10
	thermal variation -1cm	20.80	**18.20**	29.30	29.00	32.40
Soil Temperature to -10 cm* (°C)	mean -10 cm	11.00	**9.00**	10.00	13.50	**17.00**
	annual thermal variation -10 cm	16.00	20.00	**28.00**	**26.20**	21.00

R5. The latter share a group of species, although some did not reach to summit (R3). Warm and sunny slopes (R4) and basal sites (R1, R5) had most richness. The most extreme environments hosted most unique species. They were, R5 for his condition of receive highest solar radiation, and R2 being cool and the most shady and moist.

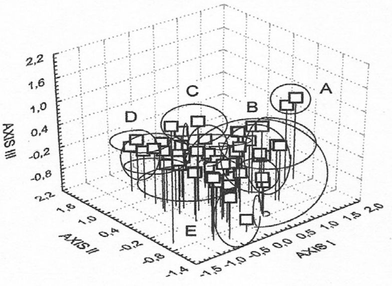
The exploratory analysis of CCA, despite of data did not meet the conditions required for this method, allowed recognized these patterns and highlight the variables and species with best contribution to the separation - or association - between sites. We used it for synthesis the copious information that we have. The first axis (Fig. 2a) separated R5 with the chasmophytic community *Cheilanthes buchtienii-Zexmenia buphtalmiflora* to the positive (right) extreme and R2 with *Poa iridifolia-Polystichum plicatum* to the negative (left) extreme. The second axis had at negative and positive extremes, respectively, R1 with *P. iridifolia-Pleopeltis pinnatifida* and R3 at the summit mainly with lichens and herbs. The third axis located R1 and R2 at the negative and positive extremes, respectively. R4 appeared towards the centre of the distribution of all axes.

The species that fitted better to the first axis were those with increasing importance towards the right extreme, like *Pavonia cymbalaria, Hybanthus parviflorus, Schizachyrium spicatum, Dichondra sericea* var. *holosericea, Hysterionica pinifolia, C. buchtienii, Oxalis refracta, Anemia tomentosa* var. *tomentosa, Z. buphtalmiflora, Mimosa rocae, Blumenbachia insignis, Gomphrena perennis* var. *perennis, Sommerfeltia spinulosa, Crocanthemum brasiliense, Euphorbia portulacoides* var. *portulacoides* and, in contrast, some increasing to the left end like *Eryngium stenophyllum, Koeleria ventanicola,* and *Geranium albicans* (Fig. 2b). The clusters in Figure 2b are only for easy viewing of the location of the species in graph and allow see that some of them, devoid of weight on axes, are clearly linked to a site in particular. In A and B appear species characteristics of R5, in C of R2, in D of R3 and in E, species of sites exposed to S-SW.

a) Sample scores



b) Species scores



c) Mesoclimatic variables scores

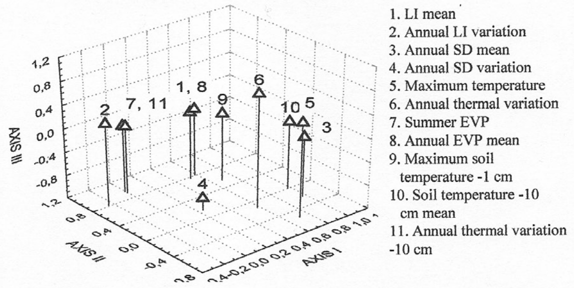


Fig. 2. CCA ordination diagrams of the rock outcrops sites. Circles indicated species location in graph (a)**:** **A=** *Anemia tomentosa*^{7}, *Cheilanthes buchtienii*^{1}, *Oxalis refracta*^{3}, *Schizachyrium spicatum*^{7}, (Axis I+). **B=** *Pavonia cymbalaria*^{4}*, Hybanthus parviflorus*^{7}, *Dichondra sericea* var. *holosericea*^{3}, *Hysterionica pinifolia*^{4}, *Zexmenia buphthalmiflora*^{3}*, Mimosa rocae*^{4}, *Blumembachia insignis*^{7}, *Gomphrena perennis*^{7}*, Sommerfeltia spinulosa*^{4}, *Crocanthemum brasiliense*^{3}*, Euphorbia portulacoides*^{5}, (Axis I+); *Chascolytrum subaristatum*^{7}, *Danthonia cirrata*^{7}, *Jarava juncoides*^{7}, *Aristida spegazzinii*^{5}, *Baccharis articulata*^{7}, *Dichondra sericea* var. *sericea*^{7}, (Axis II+); *Achyrocline satureioides*^{7}, *Cerastium mollissimum*^{7}, *Cuphea glutinosa*^{7}, *Melica rígida*^{7}, *Oxalis articulata*^{7}, *Pellaea ternifolia*^{1}, *Piptochaetium montevidense*^{7}, *Salpichroa origanifolia*^{5}, *Stevia satureiifolia* var. *ventanensis*^{4}. **C=** *Nothoscordum gracile*^{7}, *Acaena ovalifolia*^{2}, *Blechnum cordatum*^{2}, (Axis III+); *Hieracium palezieuxii*^{7}, *Polystichum plicatum*^{2}. **D=** *Hypochaeris variegata*^{7}, *Festuca ventanicola*^{4}, *Cerastium mollisimun*^{4}, *Cardionema ramosissima*^{1}, (Axis II+); *Koeleria ventanicola*^{4}, *Geranium albicans*^{3}, (Axis I-); *Calceolaria parviflora*^{1}, *Conyza sp.*, *Gamochaeta stachydifolia*^{1}, *Grindelia ventanensis*^{4}, *Habranthus gracilifolius*^{6}, *Luzula excelsa*^{1}, *Pseudognaphalium cheiranthifolium*^{1}, *Vulpia bromoides*^{1}. **E=** *Eryngium stenophyllum*^{3}, (Axis I-); *Woodsia montevidensis*^{1}, *Blechnum australe* ssp. *auriculatum*^{2}, *Pleopeltis pinnatifida*^{1}, *Poa iridifolia*^{4}, *Nassella pampeana*^{3}, (Axis II-); *Adiantum thalictroides* f. *bottini*^{3}, *Grindelia buphtalmoides*^{7}, *Senecio ventanensis* ^{4}. Chorology: ^{1}Andean and lower mountains; ^{2}Subantarctic; ^{3} regional endemic; ^{4}local endemic and subendemic; ^{5}extensive distribution in the world, South America or Argentine; ^{6}Pampean and Chaco-Pampean; ^{7}southern-Brazilian.

Among the most important species contributing to the second axis were, increasing to the positive extreme, *Chascolytrum subaristatum, Danthonia cirrata, Jarava juncoides, Aristida spegazzinii, Baccharis articulata, Hypochaeris variegata, Festuca ventanicola, Dichondra sericea* var. *sericea, Cerastium mollissimum* and *Cardionema ramosissima* and, to the negative extreme, *Woodsia montevidensis, Blechnum australe* ssp. *auriculatum, P. pinnatifida, P. iridifolia* and *Nassella pampeana.* The third axis had *Nothoscordum gracile, Acaena ovalifolia* and *Blechnum cordatum* increasing to the positive extreme.

The best positively correlated mesoclimatic variables with the first mesoclimatic axis were the soil mean annual temperature (TEMP) at -10 cm, annual water SD and maximum annual air and soil surface TEMP (Fig. 2c). The best-correlated variables with the second axis were the summer and annual daily evaporation (EVP), soil TEMP annual amplitude at -10 cm, annual light intensity (LI) and its amplitude. The annual variations of SD -and to a lesser extent the annual air thermal amplitude- are the most important variables correlated with the third axis.

The first axis showed that low elevation rock outcrops with N-facing aspect received more energy, as suggested by higher TEMPs, and the atmosphere near the surface had the highest water demanding conditions. The opposite occurred in rock outcrops located in SW-facing slopes at higher altitudes. The second axis indicated that total LI increases from S and SW aspect rock outcrops towards the mountain peaks and on N and NE aspect rock outcrops, independently of elevation; because of high winter cloudiness the LI annual amplitude in the crests was larger than for the also high elevation SW outcrop site. Maximum daily EVP rate increased towards the summit because of higher wind speed, but the annual EVP mean was similar in the crests and N rock outcrops at lowland. Amplitude of the interstitial-soil annual TEMP increased towards the summit mainly because of the decrease in minimum TEMP with the increase in altitude. Comparing the sites receiving low LI (R1, R2), the third axis showed that the SD amplitude was higher at lower altitudes. Comparisons among sunny sites (R3, R4, R5) showed that the SD amplitude was higher at mid-elevations (R4).

DISCUSSION

Some local climate differences observed between rock outcrops must be linked to their responses to solar radiation inputs. Aspect and inclination influence on sun rays reception, and hard rock surface thermal response, explained mainly the observed differences in climatic conditions, floristic composition and traits between southern and northern rock outcrops. Altitude plays a secondary role, so the higher south-facing outcrops were fresh, resembling the summits. In contrast, of the north-facing outcrops, the lowest was the warmest.

North-facing low-elevation site (R5). The high individuality and differentiation of this plant assemblage were highlighted - with the mentioned limitation of method - by the strong contribution of species of this community to the first axis of the CCA. Moreover, the plant adaptive traits of the species allowed us to match them with the correlated climatic variables. Several species restricted to these biotopes have morphological, anatomical and physiological traits frequent in sunny habitats with the highest values and amplitude in TEMP and SD. Those species are xerothermophilous (Rejmánek, 1971) and frequently small- or medium-sized microphyllous plants, in some cases with a dense cover of dead hairs or scales like *Ch. buchtiennii, A. tomentosa* var. *tomentosa, O. refracta, Ch. myriophylla, Tillandsia* spp., and *Gamochaeta* spp. Several are chasmophytes inhabiting small rock fissures with limited retention of water like *Pellaea ternifolia*. *Cheilanthes myriophylla*, and another ferns cited for this habitats, like *Ch. micropteris Sw. and Ch. squamosa* Guilles ex Hook. & Grev. (Frangi y Bottino, 1995), are reviviscent, with a high relative drought index (Ponce, 1982), able to grow under high sun radiation, periodic drought and extremely drained substrates. These environmental conditions are locally specific of the mountainous stations (*sensu* Sota, 1967) inhabited by floristic elements from NW Argentina and S Bolivia, whose geographical distributions include southern Brazil through the migratory route of Andes - Subandean - Pampean - Uruguayan mountain arch; which is also a station for the opposite direction migrant *A. tomentosa* var. *tomentosa*, from southern Brazil.

Northeast-facing mid-elevation site (R4). This location had transitional climatic and floristic characteristics between the drier and warmer site

(R5) and wetter and colder (R1) rock outcrops. This fact has reflected by its location on CCA. They were inhabited by the most eurioic chasmophytes. All these species are often found in several outcrops and shallow soil sites, but prevail in sunny places. Apparently, TEMP values are limiting thermophilous species, and scarcely sun-protected cracks offer reduced opportunities to higrophilous and sciophilous species.

Summits (R3). The high EVP rates all year round in ridge top, probably was favoured by strong winds, despite the high relative humidity and low SD during winter when clouds frequently cover the summits. This site had the lowest specific richness, too often, have scarcity of plants, probably associated with a few ecological residences for vascular plants and showed local endemisms like *F. ventanicola* and truly tolerant chasmophytes that are more frequent in southern sites. The shape and size of rocks, fissures and cracks are important for the presence of plants. Blocky outcrops had protected cracks and fissures with small ferns - some reviviscent - and small herbs associated with cushion mosses. That group included *Elaphoglossum gayanum* and *Luzula excelsa*. In flat rocks there were mesophilous and microthermic plants of sunny environments, located in interstitial-soils, like *H. variegata, D. cirrata, Hieracium palezieuxii, Gamochaeta stachydifolia* and *F. ventanicola*; several are shared with summit grasslands. Cushions of the local endemic *Grindelia ventanensis* were present. R3 was placed at the middle of the 1st CCA axis; the 2nd axis separated it by its higher EVP, and greater annual variation in LI and soil TEMPs.

South-facing sites. These sites (R1 and R2) have a common group of sciophilous species, inhabiting wide cracks among rock blocks, or moss cushions, or small caves. These residences are sun-protected, never hot, and almost constantly humid. Organic substrates located in cracks, are frequently wet by draining water flowing through. Despite this, plants must tolerate a temporarily desiccant atmosphere. Some species are restricted mainly to these outcrops such as the ferns *B. australe* ssp. *auriculatum, P. pinnatifida, E. gayanum, Adiantum thalictroides f. bottini, Melpomene peruviana*, herbs like *Calceolaria parviflora* and *E. stenophyllum* and the grass endemic of Buenos Aires, *P. iridifolia.* The latter prefers shallow humid sedimentary layers on rock surface.

Southwest-facing mid-elevation (R2). Several floristic elements present in these rock outcrops are distributed in high latitude or altitude environments. Among them, distinctive microthermic species, of Subantarctic lineage and those of high subtropical and tropical Andean distribution, converged in these outcrops. These biotopes receive reduced direct solar radiation, about two hours per day within late-fall to early-spring, and around five hours during summer. The mesoclimate is cold and daily isothermic, more pronounced in winter and in the soil, with very low SD and EVP rates. Daytime TEMPs are the coldest, except in winter, when due to a small amplitude, the night-time TEMP is sometimes higher than during day time. Exclusive species of these outcrops, and spatially related to local endemic *Festuca pampeana* grasslands, are *Polystichum plicatum, B. cordatum, A. ovalifolia, Asplenium dareoides*, and another species cited too for this biotopes like *Uncinia phleoides* (Cav.) Pers., *Phlegmariurus saururus* (Lam.) B. Øllg. and *Austrolycopodium magellanicum* (P. Beav.) Holub (Frangi, 1984; Frangi & Bottino, 1995). *A. ovalifolia* and the big-frond ferns, *B. cordatum* and *P. plicatum* are Subantarctic species (Cabrera, 1963-70; Sota, 1967). Shaded habitats are frequently conditioned by biota, and they generally occur in tropical and subtropical climates or during summer in temperate climates, in both cases in coincidence with high TEMPs and humidity. Adaptation to shadow and high TEMPs are associated and the vegetation under the canopies is poor in biomass (Grime, 2001). These shaded habitats are conditioned by high humidity with a summer increasing of solar radiation, and their biomass is moderate to high.

South-facing low-elevation (R1). The climatic differences with R2 site were a consequence of their lower altitude: higher TEMPs and EVP rates. These differences appear to be the cause of the absence of subantarctic microthermal species, whereas the others remain.

As result, Ventania displays contrasting climatic environments with dramatic biotic differences. An example is the extreme opposite abiotic-biotic conditions and species of the north-facing (R5) and south-facing (R1) basal outcrops, located at a straight distance of 50 m. Probably here, like at Mt. Carmel (Israel), the micro and mesoclimatic conditions could play a central role driving the organismal evolution (Nevo, 1995; Pavlíček & Nevo, 1996).

CONCLUSION

The elevation and relief of Ventania generate exclusive biotopes and mesoclimates in the Pampas that are important in supporting species and communities exclusive of the Buenos Aires Province. The differences in plant composition of rock outcrop sites showed the combined result of individual species response to multifactorial mesoclimate that was controlled first by exposure and secondly by the altitude. The community floristics and arrangement of plants in the sierras seem coherent with their lineage.

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