Segregation of patches by patterns of soil attributes in a native grassland in central Argentina

Separación de parches vía patrones de atributos de suelos en un pastizal de Argentina central

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Abstract. Demand for greater cattle production at the El Caldenal area in central Argentina has resulted in overgrazing in a patchy grassland structure. Patches are clearly identified on the basis of dominant plant species resulting from their grazing history. Our primary objective was to examine the influence of individual plants at each patch on the local multivariate pattern of soil nutrients, assessing the magnitude of the association between the concentration of nutrients in the plant and its underlying soil. Canonical discriminant analysis highlighted the important role of soil organic matter, available P, and Zn content of soils to segregate among patches. The canonical correlation analysis between soil and plant variables revealed a significant association (R^2 0.97). Patches with a different grazing history may be identified not only by the dominant plant species but also by the underneath pattern of soil attributes. This information can help to device managerial tools to reclaim degraded patches.

Keywords: Canonical correlation; Overgrazing; Discriminant analysis; Plant chemistry; Soil chemistry; Soil-plant interactions.

Resumen. La demanda de una mayor producción bovina en la región del Caldenal en la zona centro de Argentina ha resultado en un sobrepastoreo continuo determinante de una estructura de la vegetación en parches. Estos parches son claramente identificados en base a las especies dominantes resultantes de la historia de pastoreo. El objetivo principal del presente trabajo fue examinar la influencia de las plantas individuales sobre el patrón multivariado de nutrientes del suelo en cada parche, evaluando asimismo la magnitud de la asociación entre la concentración de nutrientes en planta y suelo. El análisis discriminante canónico señaló a los contenidos de materia orgánica, fósforo disponible y zinc en el suelo como las variables de mayor impacto en la segregación de los parches de vegetación. El análisis de correlación canónica entre las variables de suelo y planta indicó una asociación significativa entre ambos grupos (R^2 0,97). Los parches con diferente historia de pastoreo pueden ser identificados no sólo por las especies vegetales dominantes, sino también a través del patrón de atributos del suelo. Esta información puede contribuir al desarrollo de prácticas de manejo orientadas a la recuperación de los parches degradados por sobrepastoreo.

Palabras clave: Sobrepastoreo; Química vegetal; Química de suelos; Interacciones suelo-planta; Correlación canónica; Análisis discriminante.

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INTRODUCTION

Overgrazing by livestock is one of the leading causes of desertification in arid and semiarid areas worldwide (Schlesinger et al., 1990; 1996). The semi-arid region of El Caldenal in central Argentina is currently in an advanced state of ecological degradation and desertification (Busso, 1997). The pristine vegetation structure is that of a grassland with isolated woody plants, where perennial C3 cool-season bunchgrasses dominate the grass layer. After more than 100 years of grazing by sheep and cattle, selective defoliation of palatable grasses has led to species replacement in a patchy grassland structure. Distel and Bóo (1996) depicted the vegetation dynamics for the area in terms of a state and transition model with grazing history and fire frequency as the main agents responsible for the transition between states. The authors reported that *Nasella clarazii* and *Poa ligularis* are the dominant palatable species under exclosure or light grazing conditions, also shown to be part of the pristine vegetation (Gallego et al., 2004). Under moderate and continuous grazing these species are replaced by palatable shortgrasses like *Nassella tenuis*. Selective grazing of these species leads to their replacement by unpalatable grasses such as *Stipa ichu*. Yet in highly disturbed areas, invasion by exotic annual forbs such as *Medicago mínima* accompanies shrub encroachment, triggered by the combined action of overgrazing and the absence of fire.

Species replacement in the area indicates a reduction in the productive potential of the affected rangelands (Moretto & Distel, 1997) yet the reversibility of these changes by relaxing or even removing grazing is limited (Distel et al., 2005; 2008). The probabilities of deteriorated patches to recover their previous qualities strongly diminish beyond a given disturbance threshold determined to a certain extent by grazing, but to a greater extent by soil-plant interactions (Rietkerk & van de Koppel, 1997). Distel et al. (2008) pointed out that transitions to more desirable states are limited by low availability of propagules of palatable grass species and safe sites for seedling establishment; strongly depleted soil seed banks of palatable species in overgrazed areas (Mayor et al., 2003); limited fire mortality of unpalatable grasses; and high regrowth capacity after defoliation. Although these features relate to competitive abilities of the dominant plants after grazing, they may also relate to an ability to alter site conditions in such a way that over time the substrate becomes more favorable for their own growth and survival (van Breemen, 1993; Berendse, 1998).

As stated by Hook et al. (1991), description of soil heterogeneity associated with patchiness is important for analyzing the influence of plant cover on soil fertility and seedling dynamics in semiarid grasslands, and for understanding changes in productivity that may result from changes in plant life forms and cover patterns. In this regard, Villamil et al. (2001) showed that deterioration of soil physical properties accompanies changes in botanical composition of the Caldenal area.

The impact of grazing animals resulted in significant losses of topsoil depth seriously impairing land's future productivity and compromising the possibility of reverting to more desirable states. Degradation of soil structure was homogeneous among grazed patches, and the lack of a plant species effect on soil physical properties can both be ascribed to the homogenizing impact of hoof action, formation of uniform grazing lawns, and wind erosion in grazed areas, also observed by Steffens et al. (2009). Preliminary work at El Caldenal area (Villamil, 2000) found no differences on soil chemical attributes of the bulk soil related to grazing intensity due to a substantial variability in those attributes. Increased heterogeneity of soil nutrients has been proposed as a common feature of ecosystems undergoing desertification (Schlesinger et al., 1990; 1996).

Burke et al. (1998) pointed out that one of the strongest sources of variation of soil chemical properties in arid and semiarid grasslands is the presence of individual plants. Changes in plant functional type (life span, growth form, biomass distribution, etc.) resulting from increasing grazing pressures may strongly differ in the quantity and quality of litterfall affecting soil organic matter input, decomposition, N mineralization rates, soil fertility, and nutrient cycling (Moretto & Distel 2001, 2002; Semmartin et al., 2004; Bertiller et al., 2005; Carrera et al., 2009).

In dry grasslands, plant functional type also affects the amount and quality of material that accumulates beneath individual plants forming resource islands (Vinton & Burke 1995) that generate feedbacks to plant establishment and affect the outcome of competition between species as a result of changes in water and nutrient supply (Burke et al., 1998; van Breemen & Finzi, 1998). Thus, soil chemical attributes associated with patterns of plant cover can significantly control ecosystem and plant population dynamics (Hook et al., 1991) and may greatly influence state transition and reversibility in the semiarid rangelands of El Caldenal. Increased knowledge should increase our ability to manage these grasslands both to avoid patch formation and to reclaim degraded patches. Our primary objective in this study was to examine the influence of dominant plants at each patch on the local multivariate pattern of soil nutrients and determine the magnitude of the association between the concentration of nutrients in the plant and its underlying soil.

MATERIALS AND METHODS

Study area. The research area is located in Caleu-Caleu (38° 45′ S, 63° 45′ W), in the SE of La Pampa Province, Argentina. The climate is temperate semiarid with a mean annual temperature of 15.3 °C. Mean annual precipitation varies from 300-500 mm. Selected patches stand for different states of the vegetation (Distel & Bóo, 1996) where the ungrazed site (U) resembles the pristine situation of the grassland and

the sites G1, G2, and G3 show increasing levels of pasture deterioration related to grazing intensity. All the studied patches lie on the same soil belonging to the Vizcachera series (coarse-loamy, thermic, Petrocalcic Calciustolls; Soil Survey Staff, 2010) with a horizon sequence of: A - C - Ck - 2Ckm.

Plant and soil sampling and analysis. Each patch or site is clearly identified on the basis of its dominant plant species, which is the result of grazing intensity. Four plants representative of each state of the vegetation were randomly chosen and collected with their attached soil. Selected species were *Nassella clarazii*, *N. tenuis*, *Stipa ichu*, and *Medicago minima* as dominant species of the U, G1, G2, and G3 patches, respectively. Soil samples were taken at increasing depths from the soil beneath selected plants within each particular patch. Above and belowground plant biomass and soil samples were analyzed for nutrient content. N, P, S, and the micronutrients Cu and Zn were selected for the analysis after the work of Peinemann et al. (1978) who identified these nutrients as the most limiting for plant and animal production in soils of the region.

Plant parts were washed in distilled water containing 0.3% detergent (phosphate free) and then in 0.01M Na EDTA and later dried in a convection oven set at 70° C for 36 hours. Prior to chemical analysis, plant tissues were ground to pass a 40-mesh sieve. Total N was determined in unextracted material using the semimicro-Kjeldhal method and we used a Shimadzu (ICPS-1000 III model) inductively coupled plasma-atomic emission spectrometer (ICP-AES) to determine P, S, Cu, and Zn after digestion of tissue samples with a concentrated mixture of nitric and perchloric acids. Soil samples were gently separated from the roots at 0-2, 2-4, and 4-6 cm of depth. Air-dried soil samples (< 0.5 mm) were used to determine soil organic matter (SOM, Walkley-Black), pH (1:2.5, soil:water), total N (TN, semimicro-Kjeldhal) and available P (Bray-Kurtz 1). Soil samples were extracted with DTPA for determination of Cu and Zn, and with LiCl for extractable S, and subsequently measured by atomic emission spectrometry.

Statistical analysis. All statistical analyses were done with R (R Development Core Team, 2009). The soil dataset included the variables pH, SOM, TN, P, S, Cu, and Zn measured at three depths at each site (Table 1). The complete statistical model considered factors site and depth and the interaction site x depth. A multivariate analysis of variance was performed in R to assess the effect of these factors on soil chemical properties (Table 2). Since the interaction factor was not significant (p<0.075), we proceeded with model simplification and tested both models on their explanatory power using the directive 'anova' in R. Results show that the simpler model (without the interaction term site x depth) was not different in its explanatory power than

the complex model, and therefore, model simplification was justified (Crawley, 2005). Canonical discriminant analysis (CDA) was performed to obtain new linear discriminant variables (LD) for data reduction and to determine which of the original variables were mainly responsible for the mean differences between sites (Johnson & Wichern, 2002). The probabilities of correct classification were estimated by re-substitution. Furthermore, associations between average soil chemical characteristics and dominant plant chemical composition at each site were investigated with canonical correlation analysis (CCA).

RESULTS

Table 1 shows mean values and standard errors of the variables measured at increasing depths in the soil attached to dominant plants in patches representative of the different states of the vegetation. In all cases we are dealing with nutrient-poor soil systems; yet since we are working with soil in contact with roots, the values of SOM and nutrients may be higher than expected for soils of this semiarid region.

Comparing with the nutrient levels provided by Mayland & Wilkinson (1996) macronutrient supply for plant growth is adequate in the upper soil layer yet levels of P become critical with increasing depth. There are adequate supplies of Cu in all sites yet Zn deficiencies are generalized except for the surface soil layer from G3 patches. The bioavailability of Zn may be lowered due to interactions with Cu and/or S but more reliable measures of mineral element availability depend on plant tissue analysis.

Table 1 shows that there is a general rise in pH and Cu with increasing soil depth and a parallel decrease in SOM, TN, P, and Zn while the content of S remains about constant. There is significant variability in the data set at all studied depths for pH and the contents of SOM, P, and S but not for TN, Cu and Zn. On average, U and G3 patches show lower pH values with higher variability than the other sites. G2 patches show the highest content and variability of SOM and S, the latter variability also shared by G3 sites. On the other hand, G1 patches show the lowest amount of variability for most of the variables at all studied depths.

A multivariate approach aids to identify patterns and trends therefore Table 2 shows the results from the multivariate analysis of variance. A significant effect of factor depth reflects the stratification of nutrients within the soil profile that occurs in undisturbed soils. More importantly, lack of a significant site ´ depth interaction (p<0.075) implies that the studied variables behaved similarly among patches within the top 6-cm of the soil.

Discriminant analysis indicated that the first two LD account for 90.5% of the total variance among sites. Each LD is a linear combination of the independently measured soil

Table 1. Mean values and standard errors (in brackets) of the variables in the soil data set at three depths (0-2, 2-4 and 4-6 cm) for: U, ungrazed sites; and G1, G2, G3, sites with increasing grazing levels of herbivory.

Tabla 1. Valores promedio y errores estándar (entre paréntesis) de las variables de suelo a tres profundidades (0-2, 2-4 and 4-6 cm) para: U sitios sin pastoreo; y G1, G2, G3, sitios con niveles crecientes de pastoreo.

Site	pH	SOM	TN	P	S	Cu	Zn
		-----(%)-----		------------(mg/kg)-----------			
0-2 cm							
U	7.2	3.8	0.2	11.2	13.4	0.8	0.5
	(0.21)	(0.35)	(0.02)	(2.81)	(0.68)	(0.08)	(0.07)
G1	7.7	4.2	0.2	5.4	13.8	0.7	0.5
	(0.04)	(0.34)	(0.01)	(0.44)	(0.41)	(0.02)	(0.06)
G2	7.6	5.8	0.3	4.2	17.6	0.8	0.6
	(0.07)	(0.49)	(0.02)	(0.74)	(1.85)	(0.12)	(0.03)
G3	7.7	4.7	0.3	13.2	10.6	0.8	0.9
	(0.17)	(0.38)	(0.03)	(0.97)	(1.20)	(0.03)	(0.12)
2-4 cm							
U	7.6	3.2	0.2	5.0	11.8	1.1	0.2
	(0.11)	(0.12)	(0.01)	(1.09)	(0.94)	(0.14)	(0.04)
G1	7.9	3.3	0.2	2.1	14.1	1.1	0.3
	(0.02)	(0.16)	(0.01)	(0.21)	(1.10)	(0.12)	(0.07)
G2	7.9	4.4	0.2	2.2	17.1	1.2	0.5
	(0.04)	(0.56)	(0.02)	(0.41)	(3.18)	(0.16)	(0.05)
G3	7.6	2.7	0.2	7.2	10.0	0.8	0.4
	(0.16)	(0.20)	(0.01)	(0.80)	(0.81)	(0.11)	(0.06)
4-6 cm							
U	7.8	2.8	0.1	3.1	12.5	1.3	0.2
	(0.11)	(0.16)	(0.01)	(0.70)	(1.03)	(0.14)	(0.04)
G1	8.0	2.8	0.1	1.3	12.9	1.2	0.3
	(0.03)	(0.13)	(0.01)	(0.14)	(1.08)	(0.09)	(0.04)
G2	7.9	3.0	0.2	0.8	13.4	1.5	0.3
	(0.03)	(0.34)	(0.02)	(0.25)	(1.06)	(0.47)	(0.13)
G3	7.7	2.4	0.2	3.1	11.8	1.3	0.4
	(0.13)	(0.19)	(0.02)	(0.23)	(2.58)	(0.31)	(0.07)

Table 2. MANOVA of the factors site, depth, and the interaction term site x depth on the studied soil variables. Statistical significance is indicated by ns (not significant) and asterisks (***) when the results are statistically significant (p<0.0001).

Tabla 2. MANOVA para los factores sitio (site), profundidad (depth) y el término de interacción sitio x profundidad (site x depth) para las variables de suelo estudiadas. La significancia estadística es indicada con ns (no significativa) y con asteriscos (***) cuando los resultados son estadísticamente significativos (p<0,0001).

Factors	Pillai's trace	F value	num Df	den Df	Pr (>F)
Site	1.47	4.41	21	96	< 0.0001 ***
Depth	0.98	4.22	14	62	< 0.0001 ***
Site x depth	1.30	1.38	42	210	< 0.0750 ns
Residuals	36				

Fig. 1. Scatterplot of the coefficients of the linear discriminant functions LD1 and LD2 aim to show the relative contribution of the combined soil parameters to the segregation among sites with different grazing histories: U, ungrazed sites; and G1, G2, G3, sites with increasing grazing levels of herbivory.

Fig. 1. Diagrama de dispersión de los coeficientes de las funciones lineales discriminantes LD1 y LD2 mostrando la contribución relativa de los parámetros de suelo combinados en la segregación entre sitios con diferente historia de pastoreo: U, sin pastoreo; y G1, G2, G3, sitios con niveles crecientes de pastoreo.

A scatterplot of LD1 against LD2 values is displayed in Fig. 1. This graph shows that U and G3 sites shared lower LD1 scores compared with G1 and G2 sites due to higher P content and lower pH, SOM, and S content in the first two sites. Fig. 1 also shows that we need LD2 to be able to segregate all the patches; LD1 alone cannot differentiate between U and G3 or between G1 and G2 sites. LD2 explains an additional 31% of the total variance and showed the dominant role of Zn (with very high loading), followed by SOM, and

attributes and is orthogonal to the others. Table 3 shows the loadings of the soil attributes on the first two LDs and the variables that most contributed to the discriminant power of each LD function. The first LD (LD1) explained 59.5% of the variance and was dominated by high loadings from SOM and available P, with pH, Zn, and S contributing to the discrimination power of the function to a lesser degree.
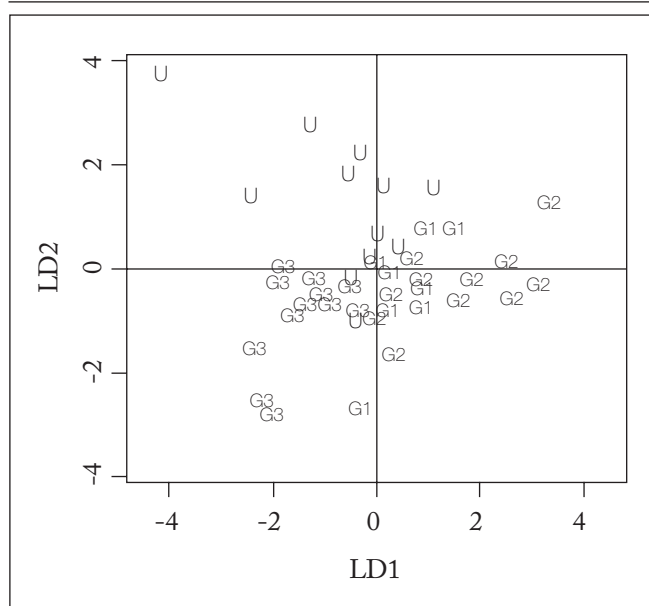
Table 3. Coefficients of linear discriminant functions, LD1 and LD2 (coefficients greater than 0.30 in bold) that show the relative contribution of each soil variable to the discriminant power of each linear function.
Tabla 3. Coeficientes de las funciones lineales discriminantes, LD1 y LD2 (coeficientes iguales o mayores que 0.30 en negrita) que muestran la contribución relativa de cada variable de suelo al poder discriminatorio de cada función lineal.

Soil Variable	LD1	LD2
pH	**0.30**	-0.14
SOM	**1.14**	**1.26**
TN	-0.08	**-0.46**
P	**-0.83**	**1.26**
S	0.24	-0.06
Cu	-0.08	**0.67**
Zn	**-0.40**	**-1.93**

Table 4. Confusion matrix with the number of sites with true class *I* classified as of class *j* (predicted vegetation site) and error rates of these discrimination results. U: ungrazed sites; and G1, G2, G3: sites with increasing grazing levels of herbivory.
Tabla 4. Matriz de confusión indicando el número de sitios con clase real *I* clasificados como clase *j* (sitio predicho) y las tasas de error de los resultados de discriminación. U: sin pastoreo; y G1, G2, G3: sitios con niveles crecientes de pastoreo.

Site	Predicted				Classification	
TRUE	U	G1	G2	G3	% Success	Error rate
U	8	3	0	1	67	0.33
G1	0	10	1	1	83	0.17
G2	0	5	7	0	58	0.42
G3	0	1	0	11	92	0.08
				Overall	75	0.25

P (with high loadings), and Cu and TN in sorting out the sites. Higher contents of Zn clearly separate the G3 patches from the other sites while higher loadings of SOM and Zn and lower available P than the rest does the same for the G2 patches. The U patches seem to be characterized by low pH values, low SOM and TN and extractable S yet higher available P than the other patches. A measure of accuracy is of primary importance when dealing with classification procedures though the presentation of error rates is generally absent in the soil literature. Table 4 shows the confusion matrix (Venables & Ripley, 2002) which gives the number of cases with true class *I* (True vegetation site) classified as of class *j* (Predicted vegetation site) by the resubstitution procedure on our CDA results.

We can see that ~ 67, 83, 58, and 92% of the observations in U, G1, G2, and G3 sites respectively, were correctly classified by the discriminant rule for an overall error rate of 25%.

The error rates associated to each site shows the high variability found in the U patches along with the transitional character of the G1 and G2 patches, yet the discriminant rule clearly segregates soils from the extreme situation of G3 where most of the grassland community had been replaced by shrubs and opportunistic annual species.

Figure 2 shows the nutrient content in the above- and below-ground biomass of the dominant plants collected at each site. As we can see, the opportunistic species present at G3 site at the time of sampling were characterized by the highest levels and variability in the contents of TN, P, and S in both the above and belowground biomass. *Nassela clarazii*, the dominant plant at the U sites reveals high contents and variability of P and S in aboveground biomass. *N. tenuis* the dominant species at G1 sites, show higher TN in both above and belowground compared to U or G2 dominant species. Tissue contents of P and S seems to be similar for *N. clarazii, N. tenuis,* and *S. ichu*, dominant of the U, G1, and G2 sites respectively, yet the variability is higher in the first species. The presence of Cu and Zn in plant tissues seems to differentiate sites G1 and G3 from the U and G2 patches. Comparing with the nutrient ranges required for plant growth in whole plant tissue provided by Mayland & Wilkinson (1996), the levels obtained in our results indicate adequate to high supply of macronutrients and adequate levels of Cu and Zn only for G1 and G3 sites.

The associations between soil chemical attributes at each site and mineral elements found in dominant plants were studied using canonical correlation analysis. One canonical variate pair (Soil 1-Plant 1) was significantly correlated and dependent on one another (p<0.007, Wilk's lambda) with an adjusted canonical R^2 of 0.97. This R^2 is the proportion of the variance in the soil canonical variate explained by the canonical variate of the plant variables. To interpret each component we looked at the correlations between the original variables and the corresponding canonical variate in Table 5.

The canonical variable Soil 1 explained 20% of the variability of the original soil variables and the largest correlations were with Zn, available P, and TN. The significant plant canonical variable Plant 1 explained 34% of plant variation and showed the largest correlations with the average tissue contents of S, TN, and P. Putting this together we can see that plant contents of S, TN, and P were the best predictors of soil TN, P, and Zn status as these indicators stand out most. Only about 2 and 3% of the variability in SOM and soil Cu contents may be explained by plant attributes.

DISCUSSION

This study provided evidence that plant species affected local soil properties of El Caldenal grassland. Nutrient concentrations in soil and plant tissues are interrelated. Nutrient availability in soil is primarily regulated by the geochemistry

Fig. 2. Nutrient content (TN, P, S, Cu, and Zn) in the above- (ABG) and below-ground (BGB) biomass tissue of the dominant plants at the ungrazed sites (U) and at the sites with increasing grazing levels of herbivory (G1, G2, G3).
Fig. 2. Contenido de nutrientes (TN, P, S, Cu, y Zn) en los tejidos de biomasa superficial (ABG) y subsuperficial (BGB) de las especies vegetales dominantes en los sitios sin pastoreo (U) y en los sitios con niveles crecientes de pastoreo (G1, G2, G3).
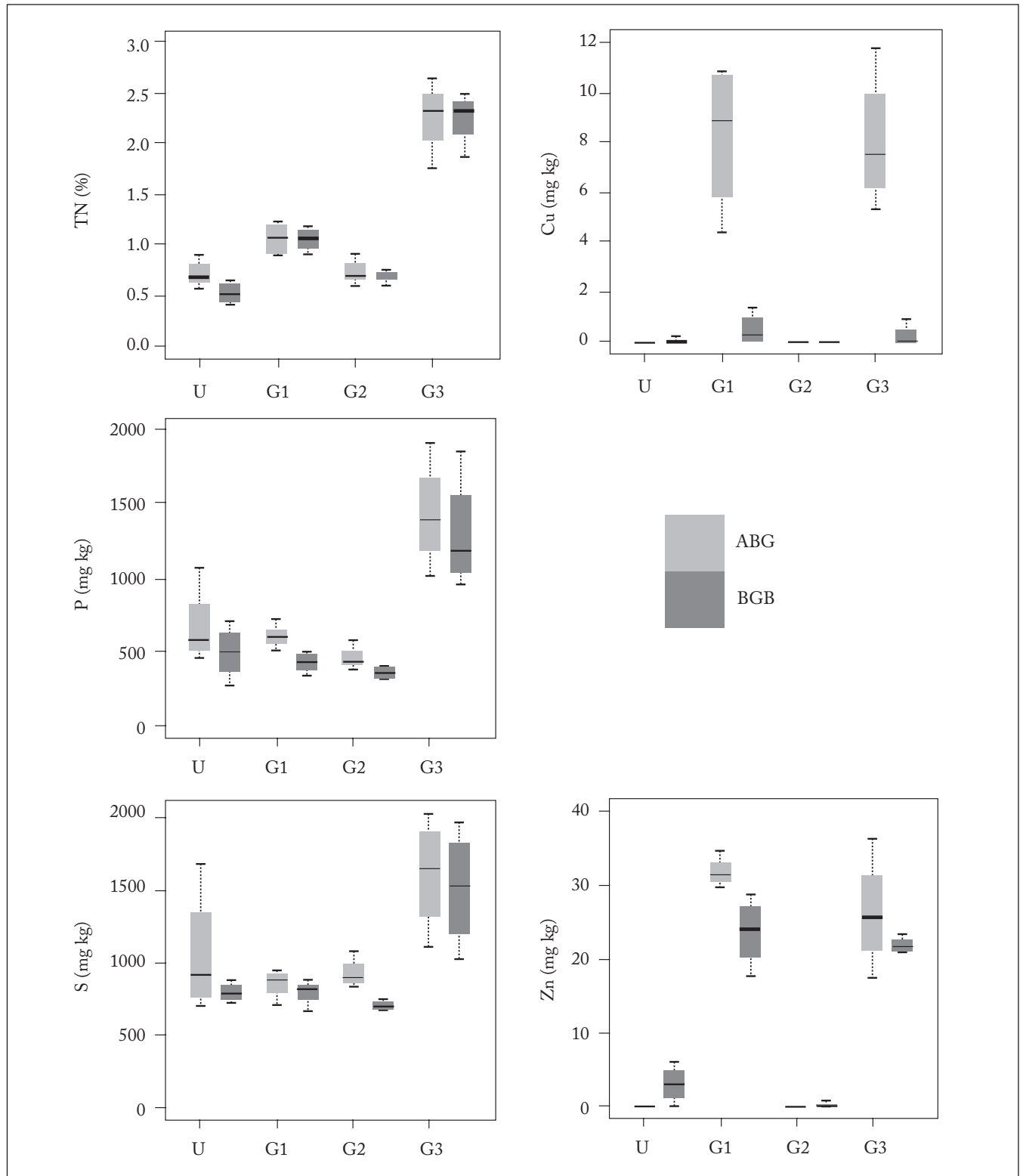
Table 5. Correlations between the original soil and plant variables and the canonical variates Soil 1 and Plant 1 obtained by CCA (coefficients greater than 0.30 in bold).
Tabla 5. Correlaciones entre las variables de suelo y planta originales y las variables canónicas Suelo 1 (Soil 1) y Planta 1 (Plant 1) obtenidas por CCA (coeficientes mayores que 0,30 en negrita).

Soil variables	Soil 1	Plant variables	Plant 1
pH	-0.26	TN	**0.75**
SOM	0.02	P	**0.70**
TN	**0.56**	S	**0.77**
P	**0.60**	Cu	0.21
S	-0.15	Zn	0.08
Cu	0.03		
Zn	**0.79**		

of the parent material and also by the quantity and quality of the plant litter entering the soil. In turn, nutrient concentration in plant tissue depends on innate plant physiological treats and soil nutrient availability. *Nassella clarazii* is a highly productive palatable mid-grass present under exclosure or light grazing conditions which is replaced by *N. tenuis*, a preferred short-grass, under moderate and continuous grazing. Both species are replaced by an unpalatable tall grass *S. ichu* under selective grazing (Saint Pierre et al., 2004). Selective grazing is due to a different expression of avoidance mechanisms in plant species resulting in a reduction in defoliation frequency and/or intensity due to lowered tissue palatability and/or accessibility (Briske & Richards, 1995). Thus, unpalatable grasses such as *S. ichu* are less productive and have higher C:N ratio and lignin content than palatable grasses (Moretto & Distel, 1997).

The low forage quality of *S. ichu* translates into a marked avoidance by livestock despite accounting for more than 50% of the plant biomass in grazed areas (Pisani et al., 2000). Villamil et al. (2001) showed the adaptive characteristics of *S. ichu* extend to their root system with a greater proportion of thicker roots (>2 mm diam) than the root systems of palatable grasses. Thicker roots are less susceptible to damage by grazing and have greater resistance to mechanical damage than fine roots (Boot, 1989). It's a common observation that once unpalatable species attain dominance it can be difficult to reverse the change by relaxing or even removing grazing (Distel et al., 2005, 2008). This observation is consistent with the model of Aerts & van der Peijl (1993) that states nutrient-poor habitats will be dominated by slow growing species with low nutrient loss rates.

Reduced nutrient losses are achieved by prolonging the longevity of plant organs with the side effects of lower potential growth, and lower litter decomposability (Berendse, 1998). With increasing life span the amount of soil organic matter that accumulates under an individual plant is likely to increase (Vinton & Burke, 1995). This is confirmed by our results that show an important SOM accumulation under unpalatable grasses with concomitant increases in TN and Zn availability in these patches. The increased SOM under G2 patches may be the result of many interacting factors. Reduced vegetation height and cover in grazed areas along with the negative effect of animal trampling on soil structure (Villamil et al., 2001) dramatically increases the effect of wind and water erosion in the system, detaching silt-sized sediments enriched in SOM and nutrients (Burke et al., 1995; Adema et al., 2001). Individual tussocks of *S. ichu* grow tall, have a wide canopy cover, are long-lived, and seem to occupy preferably lowlands (Cano 1975 cited by Moretto & Distel, 1997). Therefore, G2 patches may be acting as natural barriers to the movement of sediments, increasing the proportion of silt and clay under their canopies (van Breemen, 1993). Villamil et al. (2001) determined an average three percent increase in both silt and clay size particles in soils of the G2 patches compared with the other vegetation states at El Caldenal. Higher contents of SOM and fine materials generally increase the water- and nutrient-holding capacity of the soil. In addition, the attenuation of climatic conditions under plant canopy enhance microbial activity resulting in higher decomposition rates and increased nutrient availability than in the surrounding areas with low cover (G1 patches) or bare soil.

All these interacting factors generate islands of fertility of an important magnitude in G2 patches given the fundamental role that SOM plays for plant growth in coarse-textured soils. This situation cannot develop in the valuable G1 patches whose conservation is critical for grassland production strategies. Since dominant plants at G1 patches are actively seek out by grazers, small mounds around plants are removed and soil is compressed by the physical impact of animal hooves. In addition, herbivory removes plant biomass and therefore the input of litter, limiting SOM formation and nutrient cycling even further. In the present conditions of grazing management, or lack thereof, the G2 patches act as nutrient reservoirs, conserving resources that otherwise may be lost from the system by wind or water erosion (Burke et al., 1998). Yet from a productive standpoint it becomes important to develop strategies to revert the transition state defined by G2 patches. Adding on to the already harmful effect of selective grazing, our results suggest that the chemical status associated with tussocks of *S. ichu* may promote their persistence in the grassland potentially realizing a positive plant-soil feedback.

Exotic annuals are leguminous N-fixers that may greatly impact nutrient cycling yet further reduce the production potential of the grassland due to the large variability and limited duration of the growth period (Busso & Lobartini, 2004). The chemical imprint of *Medicago minima* in the G3 sites is pronounced although the impact on patch recovery may be less significant than that of the G2 sites due to their

very short life span and high ground cover variability. As expected, we found that the opportunistic annual species that accompany shrub encroachment in the G3 patches have higher mineral content of TN, P and S, and micronutrients Cu and Zn in both above and belowground biomass than the perennial bunchgrasses. Despite the significant islands of fertility that develop under the crowns of medics, these species are shown to generate auto-toxicity (Bonanomi et al. 2008). There is little evidence that the presence of resource islands has relevance to plant establishment (Burke, 1995) but further research will be appropriate. In this regard, the considerable Zn availability that characterizes the G3 patches may be of great importance for the colonization by biological soil crusts (Bowker et al., 2005) which are frequent in these ecosystems performing key ecological functions, potentially acting as bioindicators of rangeland conservation and degradation (Scutari et al., 2004).

CONCLUSIONS

The dominant plant life forms in patches representative of different states of the vegetation at El Caldenal area, *Nassella clarazii, N. tenuis, Stipa ichu,* and *Medicago minima*, were segregated with respect to the measured soil properties. Species substitution resulting from selective grazing generated a particular imprint on the underlying soil strongly related to the tissue chemistry of the dominant plant at each patch. Thus, the different vegetation states can be identified not only by the dominant plant species but also by the underneath pattern of soil attributes. This information can help to elucidate management tools to revert patch formation though our results also suggest that reversibility of the transition state represented by G2 patches may be seriously impaired by the soil imprints of the dominant plant in those sites.

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