

Soil Water Content Dynamics Along a Range Condition Gradient in a Shortgrass Steppe

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Abstract

Evidence is accumulating on the importance of plant cover and plant species composition on the control of ecosystem processes. In this study we examined a gradient considering the proportional contribution of the key species *Bouteloua gracilis* H.B.K. Lag. to assess its influence on the average and dynamic changes in soil water content in the shortgrass steppe from Central Mexico. We chose 4 sites with the following proportions of the key species: < 25%, 25%–50%, 50%–75%, and > 75%, ascribing each proportion to the range condition categories poor, fair, good, and excellent, respectively. Soil water measurements were carried out during 14 months at the 4 sites. Our results showed that range condition had a significant effect on soil water content ($P < 0.01$). The excellent condition was overall 14.5% and 12.5% lower soil moisture content compared to the poor and good range conditions ($P < 0.01$), respectively. Our results indicated a negative correlation between the gradient of soil water content with the range condition classes. Soil water content dynamics also differed among range condition classes, with the excellent condition showing both faster water recharge and extraction patterns than the other 3 range condition categories. Differences in soil water content among the range condition classes appeared to be related to morphological and physiological traits associated with the dominant species cover observed at each site. These results offer insights into the importance of vegetation characteristics as potential indicators of thresholds in grazing ecosystem processes such as soil water dynamics.

Resumen

Existen bastantes evidencias sobre la importancia que tiene la cubierta vegetal y la composición de las especies en el control de los procesos de los ecosistemas. En el presente estudio, examinamos un gradiente definido por la contribución proporcional de la especie clave *Bouteloua gracilis* en la comunidad, para evaluar su influencia en el contenido promedio y la dinámica del agua en suelo de los pastizales semiáridos del Centro de México. Seleccionamos 4 sitios con la siguiente proporción de la especie clave en la comunidad < 25%, 25%–50%, 50%–75%, y > 75%, asignando cada proporción a las siguientes categorías de condición pobre, regular, buena y excelente, respectivamente. Se realizaron mediciones de humedad en suelo en los 4 sitios durante 14 meses. Nuestros resultados muestran que la condición del pastizal tuvo un efecto significativo sobre el contenido de agua en suelo ($P < 0.01$). La condición excelente, por ejemplo, mostró 14.5% y 12.5% menos contenido de agua en suelo comparado a la condición pobre y buena respectivamente. Nuestros resultados exhiben una correlación negativa entre el gradiente del contenido de agua y las clases de condición del pastizal. La dinámica del contenido de agua en suelo, también difirió entre clases de condición, con la condición excelente exhibiendo tanto las tasas de recarga como las tasas de extracción más rápidas. Las diferencias observadas en el contenido de agua en suelo parecen estar relacionadas a los rasgos morfológicos y fisiológicos asociados con la cubierta de la especie dominante. Nuestros resultados ofrecen una perspectiva de la importancia de las características de la vegetación como indicadores potenciales de umbrales en procesos del ecosistema, tal como la dinámica del agua en suelo.

Key Words: ecosystem functioning, semiarid grassland, *Bouteloua gracilis*, soil hydraulics

INTRODUCTION

Water is the principal limiting ecological resource in warm deserts (Smith et al. 1997) and semiarid grasslands (Milchunas et al. 1988; Epstein et al. 1997; Vinton and Burke 1997). Soil water content is a dynamic variable controlled by several biophysical factors that contribute to its spatiotemporal variability (e.g., climate, soil texture, plant cover). Water availability in ecosystems depends on soil characteristics such as texture, depth, and presence of cemented horizons (Smith et al. 1997). Differences in these soil features may affect surface infiltration,

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subsurface percolation, depth of moisture storage, and persistence of plant-available moisture (Schlesinger and Jones 1984; Schlesinger et al. 1989). The spatiotemporal variation of soil water availability is reflected in the distribution, abundance, structure, and functioning of plant communities (McAuliffe 1994; Hamerlynck et al. 2002). Soil horizon development (Holocene vs. Pleistocene), for instance, determines the abundance, size, and function of the widespread shrubs *Larrea tridentata* and *Ambrosia dumosa* in the Mojave and Sonoran deserts (McAuliffe 1994; Hamerlynck et al. 2002).

Plant species also have a large effect on the physical structure and chemical properties of soils (Eviner and Chapin 2003). These physiological, morphological, and chemical properties strongly influence hydrology, biogeochemical cycling, and the activity of soil microorganisms (Angers and Caron 1998). Plant traits that affect soil water content include litter production, root length, water uptake per unit root biomass, root phenology (Gordon and Rice 1993), plant cover, and leaf area (Eviner and Chapin 2003). The effect of changing these traits is reflected in changes in evapotranspiration and infiltration rates at both local and regional scales (Eviner and Chapin 2003).

Grazing can potentially alter ecosystem-level soil moisture dynamics by directly modifying soil physical structure and by altering the composition of plant species and functional groups and associated vegetation traits. Most studies on the effects of herbivores on hydrological aspects in rangeland ecosystems have explored the effects of grazing intensity on soil moisture dynamics. Liacos (1962) and Naeth and Chanasyk (1995) found negative relationships between intensity of grazing and soil moisture content. They attributed the negative relationship to reductions in water infiltration caused by soil compaction and plant cover loss induced by grazing. However, considering the many vegetation assemblages that may result from different grazing regimes, the effect of grazing on plant composition and the subsequent effects on soil water dynamics under relatively homogeneous soil and climatic conditions remain largely unexplored.

The shortgrass steppe of Mexico comprises an area of around 100 000 km². *Bouteloua gracilis* H.B.K. Lag. (blue grama, Poaceae nomenclature follows Beetle 1979) is the key species of this ecosystem (Coffin and Lauenroth 1988). Large areas of this grassland ecosystem have been heavily grazed for decades, inducing substantial changes in species composition and vegetation structure while still maintaining its grassland physiognomy. Among the different vegetation shifts associated with overgrazing that have been observed in Central Mexico is an increase in the abundance of previously subordinate grass species such as *Bouteloua scorpioides* Lag. and *Aristida divaricata* Humb. & Bompl., which have replaced blue grama (Aguado-Santacruz and Garcia-Moya 1998). One apparent change with respect to plant cover is that vegetation patches have become more fragmented (Aguado-Santacruz and Garcia-Moya 1998), apparently influencing soil hydrology by increasing runoff. Continuous records of soil water content in this region have shown that soil underneath *B. scorpioides* tends to be drier than soils beneath *B. gracilis* (Arredondo, unpublished data, 2004–2006). Given the current regional decline in *B. gracilis* and the simultaneous increase in the subordinates *B. scorpioides* and *A. divaricata* as a result of overgrazing, we addressed the following question: how does the

seasonal soil water content dynamics vary along a declining gradient of the key species? We hypothesize that substitution of blue grama by subordinate species should impose dryer soil water conditions year-round. We examined these questions by monitoring a grassland area along a vegetation/condition gradient with a declining proportion of *B. gracilis* while otherwise maintaining relatively homogeneous conditions with respect to plant productivity, soil, and climate conditions.

MATERIAL AND METHODS

Site Study Description

The study was carried out from August 2001 to October 2002 at the “Santo Domingo” ranch, administrated by the National Institute for Forestry, Agricultural, and Animal Research (INIFAP). Santo Domingo is located in the physiographic province of the Mesa Central, subprovince of Llanos de Ojuelos, Jalisco, Mexico (lat 21°49'N, long 101°37'W). The dominant continental climate is classified as temperate semiarid BS1k with mean annual precipitation of 420 mm and mean annual temperature of 17°C (INEGI 1981). The topography includes valleys and rolling hills with slopes between 1% and 12% (COTECOCA 1979). Soils are classified as Xerosols (INEGI 1981), and the vegetation is dominated by *B. gracilis*. In disturbed grasslands *B. gracilis* may be replaced by *B. scorpioides*, *B. hirsuta*, *A. divaricata*, *Lycurus phleoides* H.B.K., and *Muhlehnbergia rigida* (Kunth) Trin.

Monitoring Design Along Vegetation/Condition Gradient

We selected a pure grassland site where shrubby or woody species are very scarce. The site is located midway along an alluvial fan at Santo Domingo within a paddock of around 300 ha; it has a moderate slope (6%–8%) and is facing uniformly N (northward). The site was subjected to heavy grazing for several decades before it was managed by INIFAP in 1984. Drinking water and feeders for cattle have always been located at a lower corner of the paddock, causing a gradient of grazing impact with the upper end of the gradient being the least impacted area. Along this grazing impact gradient, we identified 4 sites; the criteria for site selection were based on a clear decline in the abundance of *B. gracilis* and an increasing dominance of other grass species. At each site 6 monitoring plots were established located within a 1 000-m² area with a maximum distance among sites no greater than 1 km. Since soil characteristics were quite similar along the gradient (Fig. 1), the 4 sites were considered to belong to the same range site (*sensu* Dyksterhuis 1949). Overall, particle size distribution and soil bulk density showed little variation among sites; only soil organic matter (SOM) showed a variation of 0.4% between fair and excellent condition.

Plant cover of *B. gracilis* was visually estimated using the following 4 categories: < 25%, 25%–50%, 50%–75%, and > 75% cover of blue grama per unit area considering total vegetation cover. Afterwards we validated the initial classification using 2 10-m transects within each site (Table 1). Six 1-m² circular plots were randomly established at 8–15 m distances at each site. Plots were used to monitor soil water content, above- and belowground biomass, and plant cover. Previously we had

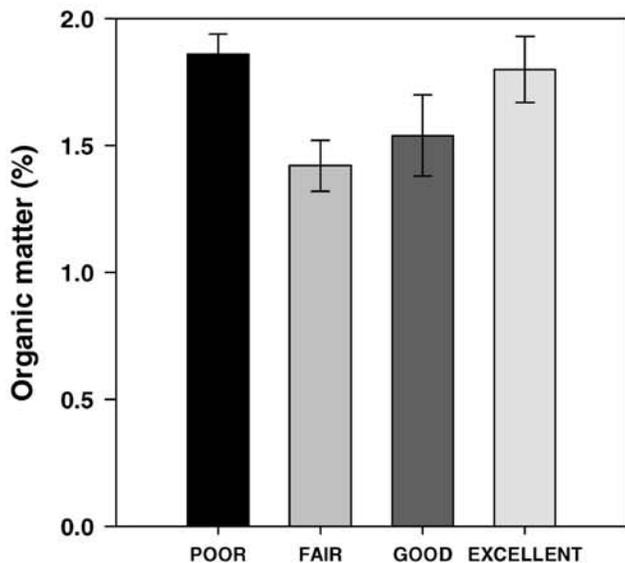
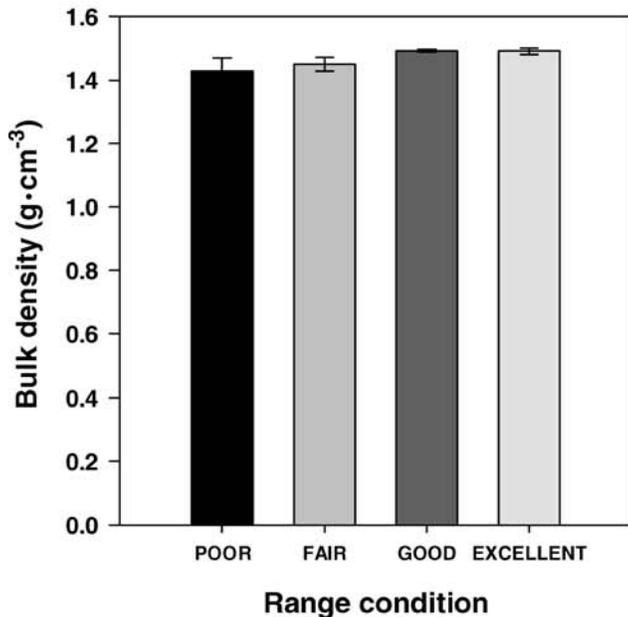
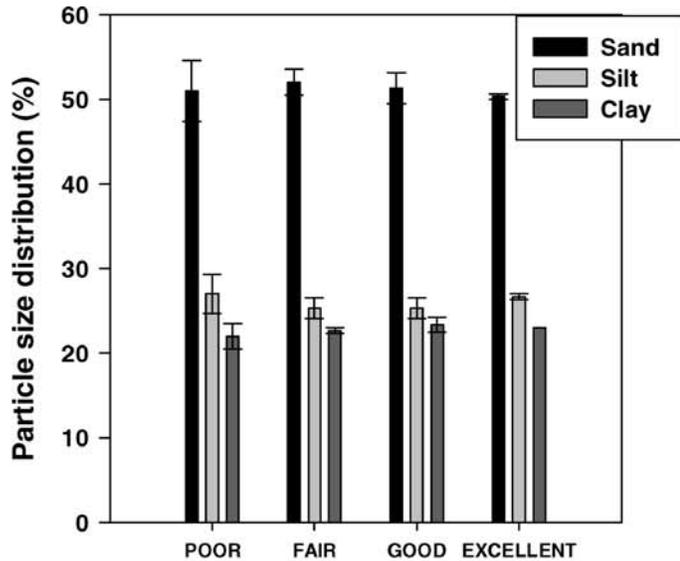


Table 1. Proportional cover of species in 4 sites of the shortgrass steppe in Central Mexico, differing in range condition class. Values in parentheses correspond to ± 1 standard error.

Species	Range condition class			
	Poor	Fair	Good	Excellent
<i>Bouteloua gracilis</i>	4.28 (4.00)	6.82 (3.52)	29.97 (4.60)	80.71 (6.32)
<i>Aristida divaricata</i>	48.20 (5.82)	29.35 (4.14)	18.17 (1.97)	2.36 (1.37)
<i>Bouteloua scorpioides</i>	19.28 (7.94)	39.79 (11.71)	18.90 (3.97)	0.30 (0.30)
<i>Lycurus phleoides</i>	22.61 (6.81)	9.19 (4.17)	6.39 (2.37)	1.57 (1.02)
<i>Sida rzedowski</i>	13.32 (3.56)	8.79 (2.06)	0.32 (0.32)	—
Other species	—	2.22 (2.05)	11.21 (3.60)	8.95 (2.10)
Czekanowski's index	5.82 (2.33)	12.48 (7.27)	39.28 (6.28)	89.6 (3.73)

observed variations in soil water content between 50 and 80 cm distances (Arredondo, unpublished data, 2004–2006), so we consider that each plot represents an independent replicate at the site level. To facilitate the description of treatments we relate the range condition scheme with the cover of *B. gracilis* in which $< 25\%$ cover of *B. gracilis* corresponds to poor, 25% – 50% to fair, 50% – 75% to good, and $> 75\%$ to excellent condition of the grassland (Dyksterhuis 1949) with 6 plots per treatment. While we are aware that our sampling scheme involves pseudoreplication (*sensu* Hurlbert 1984) at the landscape level, the aim of this research was to contrast sites under homogeneous soil conditions.

Data Collection

At the beginning of the study, we characterized soil moisture content for each range condition class by randomly extracting 12 soil cores soil cores at 20 cm depth (blue grama concentrates 90% of its roots at this depth; Coffin and Lauenroth 1991) next to the circular plots. Each soil core was processed conventionally to determine gravimetric soil water content. We measured volumetric soil water content (Topp and Davis 1985) from the fourth sampling date using time domain reflectometry (TDR) at the default depth of the device, 12 and 20 cm depth (HidroSense™, Campbell Scientific, Townsville, Queensland, Australia). To standardized gravimetric and volumetric observations, we transformed gravimetric soil moisture data to volumetric soil water content. We established site-specific relationships between gravimetric and volumetric TDR measurements for a given sampling date (Dasberg and Dalton 1985). All gravimetric soil moisture values are expressed based on this relationship. From 29 August 2001 to 5 October 2002 we sampled soil water content on 7 dates.

Plant cover was determined from digital images of the plots using a digital camera (Digital Mavica Mvc FD7, Sony Corp., New York, NY). The picture was obtained vertically from the center of the plot at 1.50 m height and analyzed with SigmaScan Pro 5 (SPSS, Ashburn, VA). For each picture we

Figure 1. Particle size distribution, soil organic matter, and soil bulk density observed in 4 range-condition grassland sites in a shortgrass steppe ecosystem in Central Mexico. Bars represent the mean values; lines are the respective standard errors ($n = 3$).

used a standard area of 25 cm² for calibration. At the end of the growing season in October 2002, aboveground biomass was determined by clipping all live and dead vegetation at ground level. Aboveground biomass was separated by species and dried at 60°C for 48 hours. Belowground biomass was determined by extracting 2 soil cores (20 cm depth × 5 cm diameter) per plot and range condition ($N = 48$) from plot interspaces, 15–20 cm distant from plot center. Root biomass was determined by the soaking and washing method (Lauenroth and Whitman 1971).

Data Analysis

To analyze differences in species composition among condition classes and relate it to soil water content, we used a quantitative measure of deviation of the excellent condition as the reference. In this way we could directly relate the decline in cover of the key species to functional aspects of the ecosystem. We used a vegetation similarity index suitable for plant cover data (Czekanowski's index, Kent and Coker 1992) and calculated as

$$S_c = \frac{2 \sum_{i=1}^3 \min(X_i, Y_i)}{\sum_{i=1}^3 X_i + \sum_{i=1}^3 Y_i}, \quad [1]$$

where Y_i represents the plot with the maximum *B. gracilis* cover. Given the large variation in floristic composition among sampling plots, we used the abundance of plant groups as described in the traditional range condition scheme, that is, i ranges from 1 to 3 corresponding to decrease, increase, and invader (in this scheme, decrease encompass only *B. gracilis*, increase comprise other perennial grasses, and invader include annual grasses and forbs) to perform the calculations. X_i is the cover of the i th range plant group within a plot. In this way observational plots that deviated in *B. gracilis* plant cover from the excellent condition had values lower than 100% of range condition.

For the analysis of soil moisture we used 2 approaches: 1) a general analysis with range condition as the principal factor for all sampling dates, and 2) an analysis including soil depth as a main factor beginning from the fourth sampling date to the end of the study (depth analysis) when TDR monitoring was implemented. For both analyses, we tested total soil moisture content. All data were tested for normality with the Shapiro-Wilks test (Zar 1996). Soil moisture data were analyzed with a mixed analysis of variance (ANOVA) with repeated measures, with range condition as the main factor for the general analysis and with range condition and depth as main factors for the depth analysis. Time (sampling dates) was used as the repeated measurement factor (repeated factor) for both analyses (Zar 1996).

Above- and belowground biomass and basal cover data were analyzed with a one-way ANOVA with range condition as main factor. The range condition rating obtained with Czekanowski's index was analyzed with the Kruskal-Wallis test given its ordinal nature (Zar 1996). Soil properties were not analyzed statistically because of the small sampling size per site ($n = 3$), but we estimated means and standard errors.

Post hoc mean comparisons were made through the Tukey Honest Significant Differences test and its nonparametric equivalent (Zar 1996). All analyses were run with SAS (SAS Institute, Cary, NC) using a significant level of $P < 0.05$.

RESULTS

Despite the large variation in floristic composition observed along the condition gradient (Table 1) more than 85% of the aboveground biomass was apportioned by 5 species (*B. gracilis*, *A. divaricata*, *B. scorpioides*, *Lycurus phleoides*, and *Sida rzedowski* P.A. Fryxell). The remaining aboveground biomass was made up by the remaining 23 recorded species. The 4 sites showed significant differences in range condition rating as shown by Czekanowski's similarity index ($\chi^2_3 = 17.90$, $P < 0.001$, Table 1), although poor and fair sites turned out to be similar with respect to the cover of *B. gracilis*. However, a remarkable increase in *A. divaricata* and *B. scorpioides* cover was observed for these 2 condition classes.

Plant basal cover and total belowground biomass varied significantly among range condition classes ($F_{3,20} = 16.13$, $P < 0.001$, and $F_{3,20} = 6.66$, $P < 0.01$, respectively), whereas total aboveground biomass did not ($F_{3,20} = 1.21$, $P = 0.3$) (Fig. 2). Plots in the excellent range condition showed twice as much basal cover and belowground biomass compared to the other condition classes.

With the general analysis, we observed a decline in soil water content with increasing improvement in range condition (poor → excellent). The poor and good range condition classes had a significantly (14.5 % and 12.25%, respectively) higher soil water content than the excellent condition class ($F_{3,20} = 6.56$, $P < 0.01$, Fig. 3A). For the depth analysis, a similar pattern was observed for the 12 cm but not for the 20 cm depth ($F_{3,43} = 4.08$, $P < 0.05$). Pooled over the whole sampling period, the excellent condition had the lowest soil water content at both depths.

For the dynamics of soil water content there was a significant interaction between range condition and time ($F_{9,117} = 5.14$, $P < 0.001$). In the excellent condition, greater soil water content was observed at the beginning of summer (6 June 2002), and it was followed by a steep decline in soil moisture by midsummer (13% and 10%, respectively, Fig. 3B). This occurred while all other condition classes still showed soil water recharge. A significant correlation was observed between bare soil and plant cover of different species. There was a significant ($P < 0.01$) reduction of bare soil with increases of *B. gracilis* cover (Fig. 4A), while we observed a significant ($P < 0.01$) proportional increase of bare soil concomitantly with increases of *B. scorpioides* and other species (Figs. 4B and 4C).

Finally, examination of soil water content at 2 depths (12 and 20 cm) indicate significant differences in soil water content between layers in May, but only for the poor and fair conditions (Fig. 5).

DISCUSSION

Our hypothesis that a gradual loss of *B. gracilis* cover should coincide with drier soil conditions was not confirmed by our results. First, we observed that soil water content was negatively related to range condition (Fig. 3A), with the excellent condition showing the overall lowest soil water content when pooled over the sampling period. With respect to soil water dynamics, maximum value of volumetric soil water was similar

among the 4 grassland communities; however, in plots where *B. gracilis* was most abundant, water recharge and utilization rates were highest (Fig. 3B). While the difference in soil water content was significant, the extent was about 10% decline across the condition gradient. We still need to evaluate whether a decline this large is ecologically important for grass species replacement.

Patterns of soil water dynamics may be the result of soil-driven or vegetation-driven influences. Several studies in arid ecosystems have pointed out the coupled nature of vegetation and soil processes and the importance of spatial variation in soil distribution in driving plant responses and vegetation structure (McAuliffe 1994, 1999). Hamerlynck et al. (2002) studying vegetation in the Mohave Desert observed that the size and density of *Larrea tridentata* were associated with the age of alluvial fans. In young alluvial coarse-textured soils greater canopy volume of *Larrea* seemed to be related to deeper water infiltration compared to old alluvial fine-textured soils where a reduced canopy volume precluded water infiltration in the open sites. Although the sites in our study differed with respect to landscape position, with the best range condition in the upper part and the poorest in the lower part of the watershed, soil texture and soil bulk density, as well as other aspects such as slope, soil depth (40, 32, 36, and 42 cm, respectively for poor, fair, good, and excellent conditions), and soil horizon development were quite similar among them. Thus, soil-driven factors did not seem to explain the differences in soil water content in these grassland sites.

For our grazing sites, we suggest that shifts in vegetation characteristics (species abundance, biomass, physiological and morphological traits, etc.) resulting from a decline in the abundance of *B. gracilis* and its subsequent substitution by former subordinate species were the main causes driving the observed soil water dynamics. Each range condition class we monitored included a set of species with a suite of inherent plant physiological, morphological, and chemical traits that have implications for ecosystem functioning (Westoby 1998). The differences in soil water content among the 4 range condition classes may have arisen from direct physiological and morphological effects of species in water extraction or from indirect effects through both the inputs of organic matter and subsequent changes in soil structure and the changes in plant cover and the effects on infiltration and runoff.

The soil water dynamics we examined included the recharge phase as well as the seasonal fluctuations of soil water content associated with the precipitation events (Fig. 3C). Water recharge of the soil was most pronounced in the site of excellent condition; we attribute this pattern to the overall greater plant cover, which enhances soil infiltration rates (Valentin et al. 1999) and the presence of many more roots (Figs. 2A and 2C) and therefore macropores. While it is well known that SOM increases porosity and water-holding capacity of soils (Valentini

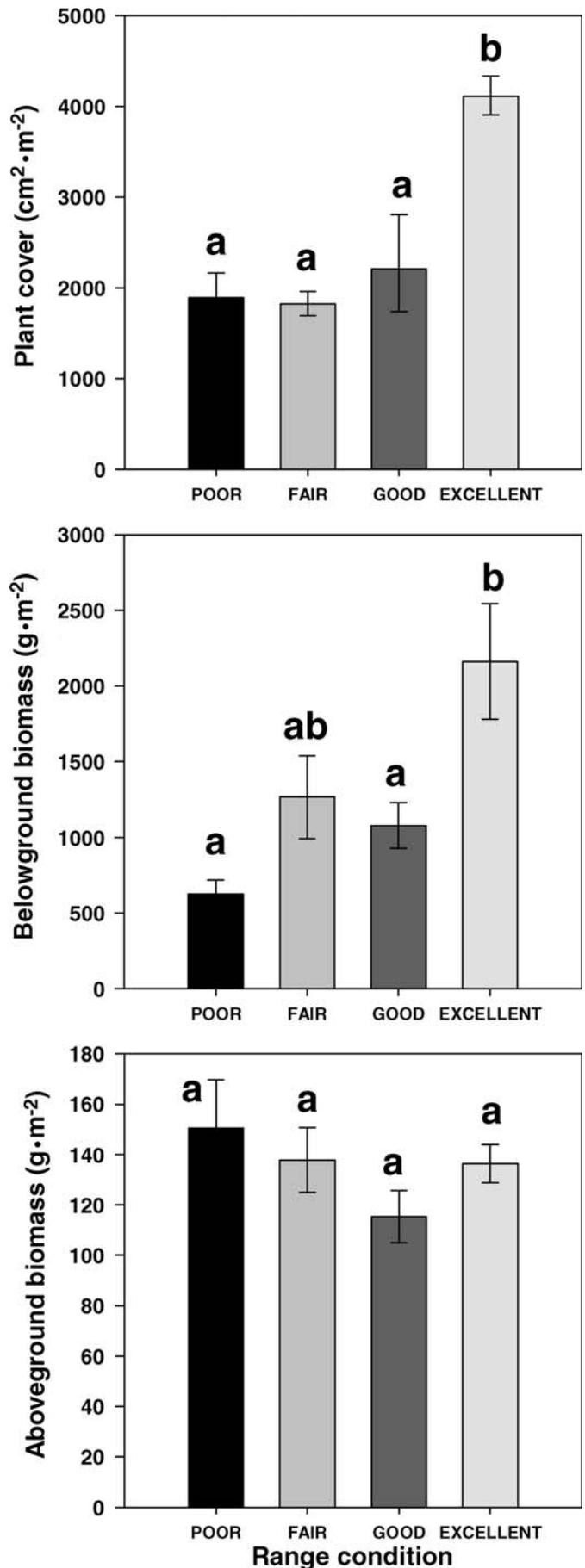


Figure 2. Plant cover, aboveground biomass, and root biomass observed in 4 range-condition grassland sites in the shortgrass steppe in Central Mexico. Bars depict the mean values recorded at peak standing biomass in 2002; lines represent standard errors ($n = 6$). Different letters indicate significant differences among treatments in $P < 0.05$.

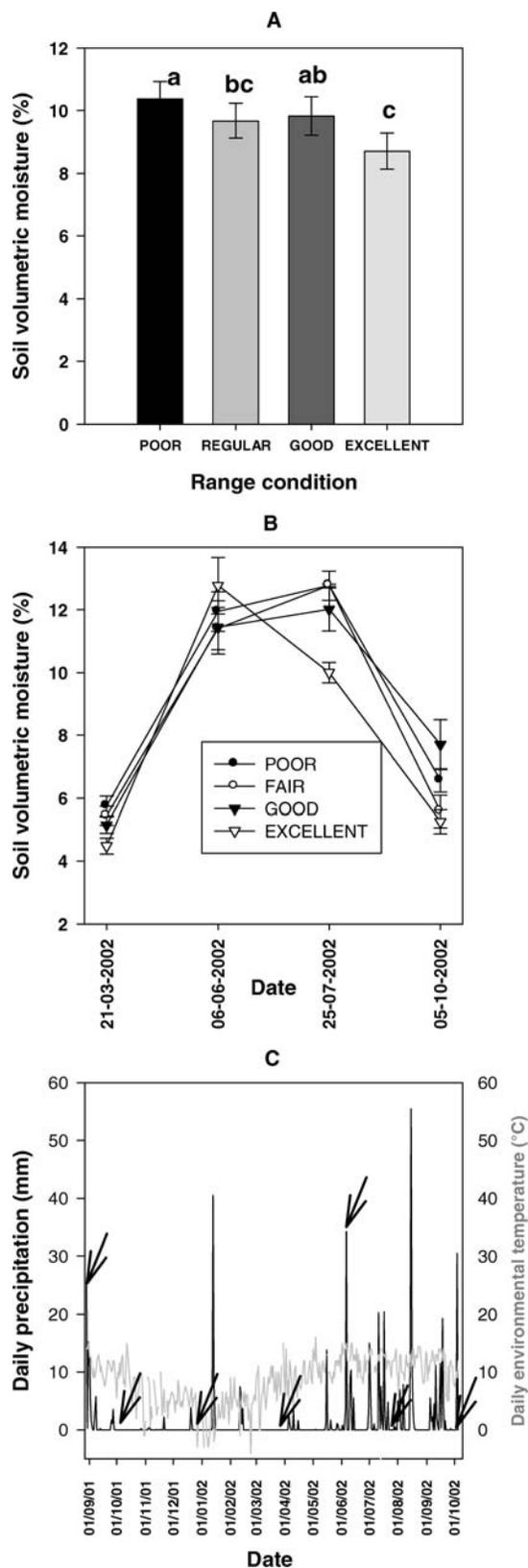


Figure 3. A, Average of soil volumetric water content (including 7 sampling dates) observed in 4 range-condition classes. B, Changes in volumetric soil water for the last 4 sampling dates observed in 4 range-condition classes. Even though data are not a continuous variable, lines are drawn to facilitate visualization. C, Volumetric soil moisture content at 12- and 20-cm depths for the last 4 sampling dates. Daily precipitation

et al. 1991; Troeh and Thompson 1993), the possible role of SOM in controlling differential infiltration was not apparent in our observations. The difference in SOM content between the extreme values was small (0.4%), and we questioned the hydrological significance of this difference (Fig. 1B). This suggests that SOM was not the overriding driver explaining the differences in water recharge in the different sites.

Root biomass in the excellent condition was twice as high as in the other condition sites (Fig. 2C). Additional to the incorporation of organic matter, roots may improve infiltration/percolation by providing root channels that enhance water flow through the profile (Devitt and Smith 2002). This mechanism known as preferential flow may account for increases in vertical water flux from 2.2–7.2 mm·yr⁻¹ to 50–100 mm·yr⁻¹ (Johnston 1987).

Differences in plant cover and plant species composition may also affect runoff speed and runoff patterns. Several authors have documented that vegetation changes can have a significant impact on the amount of intercepted rainfall and ultimately soil recharge (Le Maitre et al. 1999). Also, simulation studies indicate that spatial interactions favoring lateral exchange of water are a function of plant cover and standing biomass (van de Koppel and Rietkerk 2004). Patch connectivity through this mechanism appears to be very important for the resilience of arid ecosystems. Examination of precipitation events in the study site showed that the first large convective storm (Fig. 3C, 5 June 2002) apparently recharged soils faster in the excellent condition. This condition exhibited on average 80% of the total vegetation composed by *B. gracilis* compared to the fair and poor range conditions that were dominated by *B. scorpioides* and *A. divaricata* (68% of total vegetation, Table 1). These communities differed substantially in the diameter of tussocks, in the size of plant interspaces, and in the depth of the wetting front (Fig. 2); that is, with increasing abundance of *B. scorpioides* or *A. divaricata* the area of bare soil increased (Figs. 4B and 4C). Greater abundance of these grass species has been observed to coincide with drier soil conditions (Arredondo, unpublished data, 2003). Hence, superior connectivity among interspaces in the poor and fair range conditions favors runoff and subsequently lowers water recharge capabilities (Davenport et al. 1998).

Differences in soil water recharge among range sites may be better compared when considering soil depth. In June 2002 we observed differences in soil water content between the 12 and 20 cm layers for the poor and fair conditions, while this was not observed for the excellent and good conditions (Fig. 5). Since differences in the wet front in the soil profile occurred after the first large convective storm (Fig. 3C), these patterns suggest important differences in infiltration/percolation rates among sites.

The seasonal fluctuations in soil volumetric water started to diverge from the recharge stage (6 June 2002, Fig. 3B) and became different on 25 July 2002. The lower soil water content in the excellent condition site occurred shortly after 2 important rainfall events in July 2002. This suggests that physiological and morphological traits enhancing plant water uptake were

(black line) and daily temperature (gray line) during the study period. Arrows indicate the sampling dates. Different letters indicate significant differences among treatments in $P < 0.05$.

responsible for the steep decline and dynamics in soil water content. Compared to *B. scorpioides* and *A. divaricata*, *B. gracilis* exhibits a more extensive root system (biomass) and leaf area (data not presented), which explains potentially higher water extraction and transpiration rates. Although root biomass is a poor predictor for plant water extraction (Gordon and Rice 1993), our observations of greater root biomass on the excellent range site coincide with these vegetation characteristics that could contribute to larger water extraction rates (Fig. 2).

Physiological information for *B. scorpioides* and *A. divaricata* is largely missing, but these species possess morphological traits including leaf rolling and short and narrow leaves that are associated with lower transpirational rates (Alcocer-Ruthling et al. 1989; Coughenour 1985 cited in Adler et al. 2004). Also, previous studies (Majerus 1975) showed that *B. gracilis* is able to extract soil water at very low soil water potentials (-8 MPa in shallow layers to -1 MPa at 35 cm depth). In contrast, in a greenhouse study *B. scorpioides* exhibited leaf rolling and chlorosis at -4.0 MPa (Alcocer-Ruthling et al. 1989).

The importance of the combined effects of plant cover, species composition, and morphological and physiological traits of the dominant species on hydrological functioning as shown in this study (Fig. 4) supports the contention that prevalence of the key species is essential in maintaining ecosystem functioning in semiarid grasslands. In particular, the distinctive soil water dynamics observed at the site in excellent range condition suggests that decline of the key species *B. gracilis* beyond a proportional abundance of 75% cover may be a critical threshold in the hydrological functioning of the shortgrass steppe with positive feedbacks with respect to overall drier conditions leading to changes in species composition, lower plant cover, increasing runoff, etc.

Our study highlights how changes in species dominance triggered by different grazing intensities may lead to drastic changes in soil hydrology under practically the same climatic and edaphic conditions. The differences in soil water dynamics were explained by the differences in vegetation and plant traits of the dominant species in each range condition. Our results should be considered with caution, as we did not replicate the study at the landscape level. Nonetheless, the link between plant community traits and a functional process of the ecosystem, such as soil hydraulics, appears to identify an important threshold in the functioning of semiarid grasslands in Central Mexico.

MANAGEMENT IMPLICATIONS

Changes in land use result in a deterioration of the condition of the grassland ecosystem. A key aspect for managers in these threatened ecosystems is to identify vegetation stages that could be used as indicators of thresholds in ecosystem functioning. Our study suggests that monitoring the proportional cover of the key species could be used as a practical tool to identify functional thresholds. The management implications of our results had to do with these tools that managers could implement to monitor grassland integrity. Monitoring the proportional cover of key species in grasslands is relatively simple and could result in a useful tool to alert managers of reaching functional thresholds in grassland function. While a promising approach, there is a strong need to study these links

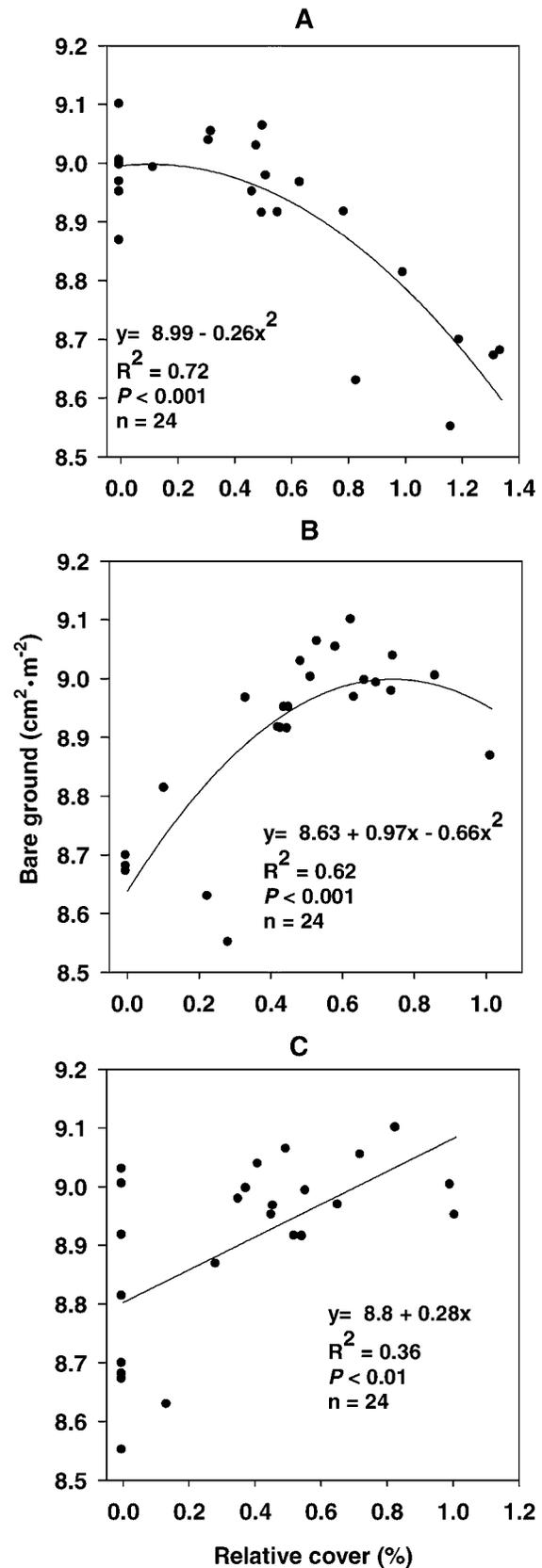


Figure 4. Relationships between the basal relative cover of the main groups of range-condition plants and bare soil surface. **A**, blue grama, **B**, increaser species, and **C**, *B. scorpioides*.

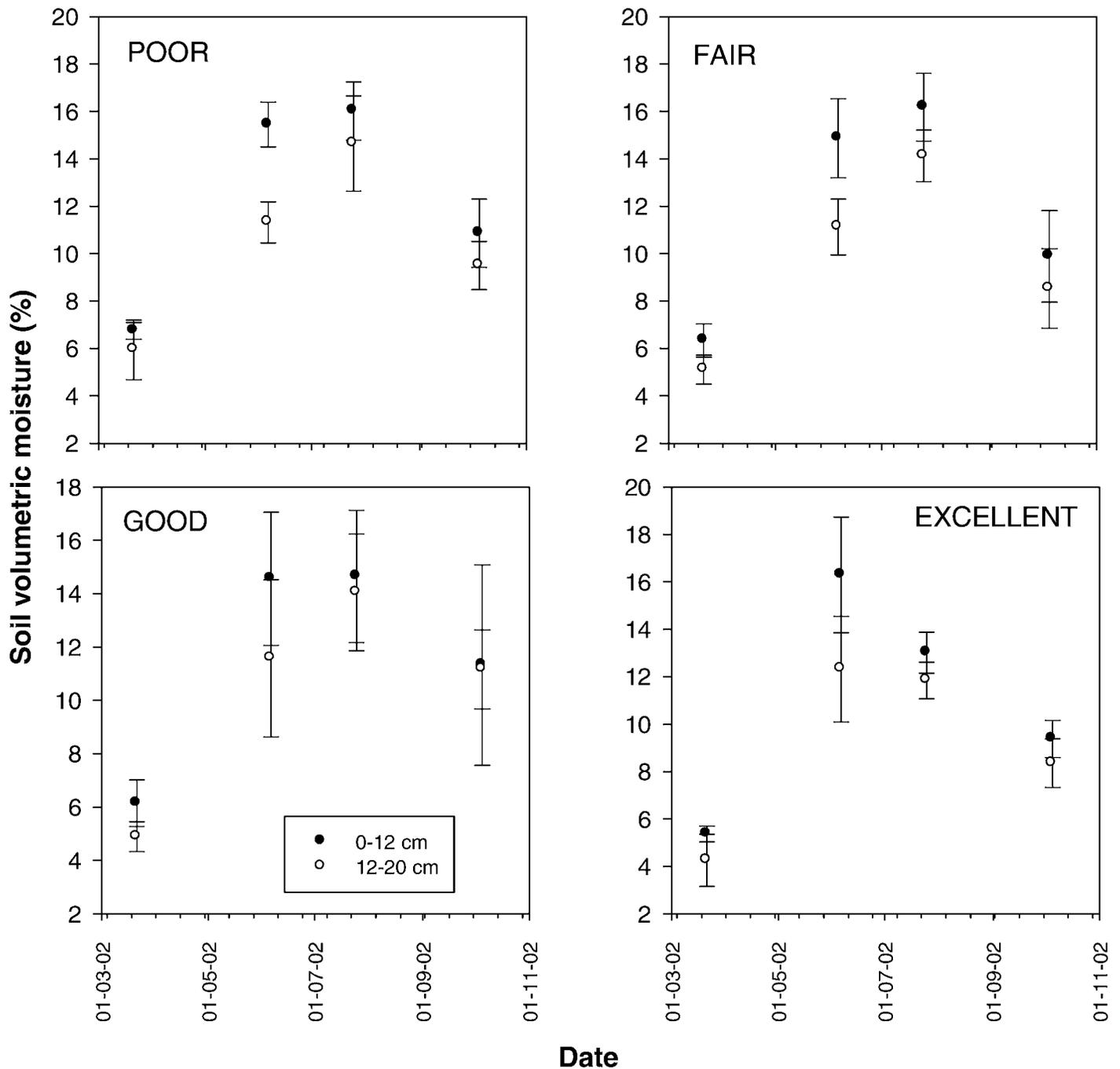


Figure 5. Soil volumetric water in 2 soil depths for the last 4 sampling periods in 2002 observed in 4 range-condition classes in the shortgrass steppe in Central Mexico.

between vegetation attributes and ecosystem functioning at the biome level considering various environmental conditions.

LITERATURE CITED

- ADLER, P. B., D. G. MILCHUNAS, W. K. LAUENROTH, O. E. SALA, AND I. C. BURKE. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653–663.
- AGUADO-SANTACRUZ, G. A., AND E. GARCIA-MOYA. 1998. Environmental factors and community dynamics at the southernmost part of the North American Graminetum—I. On the contribution of climatic factors to temporal variation in species composition. *Plant Ecology* 135:13–29.
- ALCOCER-RUTHLING, M., R. ROBBERECHT, AND D. C. HILL. 1989. The response of *Bouteloua scorpioides* to water stress at two phenological stages. *Botanical Gazette* 150:454–461.
- ANGERS, D. A., AND J. CARON. 1998. Plant-induced changes in soil structure: processes and feedbacks. *Biogeochemistry* 42:55–72.
- BEETLE, A. A. 1979. Las gramíneas de México. Tomo I. Mexico City, Mexico: COTECOCA. 124 p.
- COFFIN, D. P., AND W. K. LAUENROTH. 1988. The effects of disturbance size and frequency on a shortgrass plant community. *Ecology* 69:1609–1617.

- COFFIN, D. P., AND W. K. LAUENROTH. 1991. Effects of competition on spatial distribution of roots of blue grama. *Journal of Range Management* 44:68–71.
- COTECOCA. 1979. Coeficientes de Agostadero de la República Mexicana. Estado de Jalisco. Tomo I. Mexico, City, Mexico: Secretaría de Agricultura y Recursos Hidráulicos. 89 p.
- DASBERG, S., AND F. N. DALTON. 1985. Time domain reflectometry field measurements of soil water content and electrical conductivity. *Soil Science Society of America Journal* 49:293–297.
- DAVENPORT, D. W., D. D. BRESHEARS, B. P. WILCOX, AND C. D. ALLEN. 1998. Viewpoint: sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. *Journal of Range Management* 51:231–240.
- DEVITT, D. A., AND S. D. SMITH. 2002. Root channel macropores enhance downward movement of water in a Mojave Desert ecosystem. *Journal of Arid Environments* 50:99–108.
- DYKSTERHUIS, E. J. 1949. Condition and management of range land based on quantitative ecology. *Journal of Range Management* 2:104–115.
- EPSTEIN, H. E., W. K. LAUENROTH, I. C. BURKE, AND D. P. COFFIN. 1997. Productivity patterns of C3 and C4 functional types in the U.S. Great Plains. *Ecology* 78:722–731.
- EVINER, V. T., AND F. S. CHAPIN III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution and Systematics* 34:455–485.
- GORDON, D. R., AND K. J. RICE. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* 74:68–82.
- HAMERLYNCK, E. P., J. R. McAULIFFE, E. V. McDONALD, AND S. D. SMITH. 2002. Ecological responses of two Mojave desert shrubs to soil horizon development and soil water dynamics. *Ecology* 83:768–779.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Instituto Nacional de Estadística Geografía e Informática (INEGI). 1981. Síntesis geográfica de Jalisco. México, D. F.: Secretaría de Programación y Presupuesto. p 122–128.
- JOHNSTON, C. D. 1987. Preferred water flow and localized recharge in a variable regolith. *Journal of Hydrology* 94:129–142.
- KENT, M., AND P. COKER. 1992. Vegetation description and analysis: a practical approach. Boca Raton, FL: CRC Press. 363 p.
- LAUENROTH, W. K., AND W. C. WHITMAN. 1971. A rapid method for washing roots. *Journal of Range Management* 24:308–309.
- LE MAITRE, D., D. F. SCOTT, AND C. COLVIN. 1999. A review of information on interactions between vegetation and groundwater. *Water S.A.* 25:137–152.
- LIACOS, L. G. 1962. Water yield as influenced by degree of grazing in the California winter grasslands. *Journal of Range Management* 15:34–42.
- MAJERUS, M. E. 1975. Response of root and shoot growth of three grass species to decreases in soil water potential. *Journal of Range Management* 28:473–476.
- McAULIFFE, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs* 64:111–148.
- McAULIFFE, J. R. 1999. The Sonoran Desert: landscape complexity and ecological diversity. In: R. Robichaux [ed.]. Ecology of Sonora Desert plants and plant communities. Tucson, AZ: University of Arizona Press. p 68–114.
- MILCHUNAS, D. G., W. K. LAUENROTH, AND O. E. SALA. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87–106.
- NAETH, M. A., AND D. S. CHANASYK. 1995. Grazing effects on soil water in Alberta foothills fescue grasslands. *Journal of Range Management* 48:528–534.
- SCHLESINGER, W. H., AND C. S. JONES. 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. *Botanical Gazette* 145:116–124.
- SCHLESINGER, W. P., P. J. FONTEYN, AND W. A. REINERS. 1989. Effects of overland flow on plant water relations and soil water percolation on a Mojave Desert landscape. *Soil Science Society of America Journal* 53:1567–1572.
- SMITH, S. D., R. K. MONSON, AND J. E. ANDERSON. 1997. Physiological ecology of North American desert plants. Berlin, Germany: Springer-Verlag. 286 p.
- TOPP, G. C., AND J. L. DAVIS. 1985. Measurement of soil water content using Time-domain reflectometry (TDR): a field evaluation. *Soil Science Society of America Journal* 49:19–24.
- TROEH, F., AND L. THOMPSON. 1993. Soil and soil fertility. New York, NY: Oxford University Press. 489 p.
- VALENTIN, C., J. M. D'HERBES, AND J. POESEN. 1999. Soil and water components of banded vegetation patterns. *Catena* 37:1–24.
- VALENTINI, R., G. E. SCARASCIA, P. DE ANGELIS, AND R. BIMBI. 1991. An experimental test of the eddy correlation technique over a Mediterranean macchia canopy. *Plant, Cell and Environment* 14:987–994.
- VAN DE KOPPEL, J., AND M. RIETKERK. 2004. Spatial interactions and resilience in arid ecosystems. *American Naturalist* 163:113–121.
- VINTON, A. M., AND I. C. BURKE. 1997. Contingent effects of plant species on soil along a regional moisture gradient in the Great Plains. *Oecologia* 110:393–402.
- WESTOBY, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- ZAR, J. H. 1996. Biostatistical Analysis. 3rd ed. Englewood Cliffs, NJ: Prentice Hall. 718 p.