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Interacting effects of soil degradation and precipitation on plant productivity in NE Patagonia, Argentina

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ABSTRACT

Our objective was to examine the effects of inter-annual variation of precipitation on productivity of two dominant species (*Chuquiraga avellanedae*, an evergreen shrub, and *Nassella tenuis*, a perennial grass) in two communities of contrasting soil degradation: a herbaceous steppe with shrubs (HSS) and a degraded shrub steppe (SS). Data were collected during two consecutive years with different annual precipitation. Aboveground productivity was determined nondestructively using a double sampling approach. The number of inflorescences per plant was recorded too. Perennial grass productivity was lower in SS than in HSS in both years, while shrub productivity was lower in SS only during the year of below average precipitation. With rising precipitation the perennial grass increased the number of inflorescences while the evergreen shrub augmented vegetative biomass. In summary, the effects of precipitation on plant productivity are community dependent; abiotic factors, such as superficial and sub-superficial soil characteristics, and biotic factors, such as leaf area index (LAI) or tussock sizes, may interact to influence the responses of species to precipitation. Our results suggest that if precipitation increased, this would favor the dominance of shrubs over grasses.

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Arid ecosystems; desertification; evergreen shrubs; infiltration; meristem limitation; perennial grasses

Introduction

Quantifying aboveground annual net primary production (ANPP) is essential to understand the carbon cycle and the impact of different environmental factors and management schemes on ecosystem functioning (Robinson et al. 2013). Ecologists generally agree that the seasonality of precipitation, the timing between precipitation events, the quantity of rainfall per event, and the previous-year precipitation describe variation in ANPP as well as annual precipitation (Oesterheld et al. 2001; Knapp et al. 2002; Fay 2009). The distinctive contribution of individual plant species or functional groups to the overall community needs to be understood when we study community ANPP responses to precipitation (Robertson et al. 2009). In that sense, Jobbágy and Sala (2000) found, for western Patagonian steppes, that shrub ANPP was correlated to annual precipitation but it was not the case for perennial grasses. Some authors suggest that "stress-tolerant" species such as

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woody plants may be less responsive to precipitation variability than grasses since shrubs tend to have low specific leaf area and foliar N, making them less efficient at acquiring and using water (Köchy and Wilson 2004; Fernandez-Going, Anacker, and Harrison 2012).

Recent studies have suggested that in addition to species, soil types can influence community responses to changes in precipitation (Dameschen, Harrison, and Grace 2010; Friedley et al. 2011; Fernandez-Going and Harrison 2013). Soil conditions affect surface and subsurface infiltration and the depth of moisture storage (Noy-Meir 1973). In consequence, the effectiveness of precipitation is not exclusively a function of precipitation, but it is also deeply linked to the edaphic properties that influence the temporal persistence of plant-available moisture (McAuliffe 1994; Hamerlynck, McAuliffe, and Smith 2000). Thus, plant performance is related to ecohydrological behaviors of soils. When soil is eroded, the amount of water runoff significantly increases, and with less water entering the soil, less is available to support the growing vegetation. When erosion occurs, basic plant nutrients are also lost (Pimentel et al. 1995; Chartier, Rostagno, and Videla 2013). Although these studies have demonstrated the effects of soil erosion on soil attributes, more information is needed on the effects of soil erosion on the productivity of natural and managed ecosystems (Pimentel and Kounang 1998).

Previous studies in northeastern Patagonia found that herbaceous steppes were replaced by shrub steppes, mainly as a consequence of overgrazing by sheep (Beeskow, Elissalde, and Rostagno 1995; Chartier and Rostagno 2006). This change is accompanied by superficial soil erosion (Rostagno 1989; Chartier and Rostagno 2006), which modifies its hydrological properties. Eroded soils, dominated by shrub steppes, present lower infiltration rates than un-eroded ones (Parizek, Rostagno, and Sottini 2002; Chartier, Rostagno, and Pazos 2011). Moreover, shrub steppes present high rates of fine particles, litter, and nutrients loss through overland-flow (Chartier, Rostagno, and Videla 2013). However, the effects of these changes in soil characteristics on species productivity are still unknown. The aim of this study was to evaluate the effects of inter-annual variation of precipitation on productivity of the dominant species (*Chuquiraga avellanedae*, an evergreen shrub and *Nassella tenuis*, a perennial grass) in two communities of contrasting soil degradation: a herbaceous steppe with shrubs (HSS) and a degraded shrub steppe (SS).

Material and methods

Site, community, and species description

The study was undertaken in Punta Ninfas (42°57′S, 64°33′W), in northeastern Patagonia where sheep grazing has been practiced since the beginning of the last century. Continuous grazing is practiced in paddocks greater than 2500 ha. The mean stocking rate is 0.25 sheep ha^{-1} (Parizek, Rostagno, and Sottini 2002). Considering a thirteen-year period, mean air temperature is 12.7°C and mean annual precipitation is 259.32 mm (1995–2004, Chartier and Rostagno 2006 and 2011–14, own data). The characteristic vegetation is a mosaic of herbaceous and shrub steppes where *Chuquiraga avellanedae* Lorentz (known as quilembai) is the main shrub and *Nassella tenuis* (Phil.) Barkworth (flechilla) the dominant grass (Beeskow, Elissalde, and Rostagno 1995). Xeric Calciargid is the prevailing soil in the study area with Xeric Haplocalcid as the subdominant soil (Soil Surface Staff 1999).

We chose two communities that differ in their degree of soil degradation: an herbaceous steppe with shrubs (HSS) and a degraded shrub steppe (SS) (Beeskow, Elissalde, and

Rostagno 1995; Chartier and Rostagno 2006; Chartier, Rostagno, and Pazos 2011). At landscape scale, the abovementioned steppes form stands not exceeding a few hectares in area. These communities differ in superficial and sub-superficial soil characteristics. Shrub steppe soil has a finer texture, presents a shallow A horizon and the Bt horizon is locally exposed (Table 1; Chartier and Rostagno 2006; Chartier, Rostagno, and Pazos 2011). The loss of the A horizon and the formation of desert pavements are good indicators of the erosion process in the study area (Rostagno and Degorgue 2011). The relief is plain, slope does not exceed 1% (Palacio, Bisigato, and Bouza 2014).

This study focused on two dominant species representing different functional groups (evergreen shrubs and perennial grasses). *C. avellanedae* is an evergreen shrub with a peak of biomass in spring, when new leaves are produced in a short period (September). This species exhibits a period of inactivity during winter, matching with the lowest temperatures. The reproductive period extends from mid-spring (October) to summer (February) (Campanella and Bertiller 2008, 2009). *C. avellanedae* has a root system that extended up to 1.7 m compared to *N. tenuis* that concentrates its roots in the first 0.3 m of soil (Bertiller, Beeskow, and Coronato 1991). *N. tenuis* is a perennial grass with vegetative activity from mid-fall (April) to late spring (December) and, depending on the year, it can present a second peak from late summer to the beginning of autumn (March). This species presents a period of inactivity during extremely dry summers (January–February). The reproductive period lasts from spring (September) to early summer (December) (Campanella and Bertiller 2008).

Precipitation measurements and soil surface characteristics

Daily precipitation was recorded with an automatic weather station at the study site. Ground (perennial grasses, litter, and gravel) and bare soil cover was visually estimated in 1.5×1 m plots (eighty plots, forty in different stands of each community).

Plant productivity and number of reproductive structures

Plant productivity, that is, vegetative, was determined nondestructively using a double sampling approach for each species, based on Fernández-A, Sala, and Golluscio (1991) and Guevara, Gonnet, and Estévez (2002). We developed allometric regressions between field growth measurements (length of new shoots for shrub and basal diameter for grasses) and biomass (see supplemental material). Data were collected during two consecutive years

Table 1. Soil characteristics (mean ± SE) for herbaceous steppe with shrubs (HSS) and shrub steppe (SS).

	HSS	SS
Sand (%)[a]	71.9 ± 0.7	66.1 ± 1.2
Silt (%)[a]	19.2 ± 0.5	18.4 ± 0.9
Clay (%)[a]	8.8 ± 0.7	15.5 ± 2.4
Organic carbon (g kg^{-1})[b]	6.4 ± 0.5	6.5 ± 0.6
Total N (g kg^{-1})[b]	0.6 ± 0.03	0.5 ± 0.03
A horizon thickness (cm)[a]	15.7 ± 2.0	4.2 ± 0.8

Note: [a]Data from Chartier, Rostagno, and Pazos (2011).
[b]Data from Chartier, Rostagno, and Videla (2013).

(2012 and 2013) in eighty research plots (1.5 × 1 m) containing one adult of *C. avellanedae* in its center and many individuals of *N. tenuis* (i.e., 2 species × 2 communities × 40 replicates = 160 individuals).

At mid-December, after plant growth, we measured the lengths of new shoots for *C. avellanedae*, in 15 × 15 cm quadrats. One to three quadrats were used depending on plant size. When more than one quadrat was used, we averaged lengths from all quadrats. Plant productivity of *C. avellandae* was estimated using the equation mentioned in the supplemental material (see Equation (1), supplemental material). The number of inflorescences per plant was also recorded. Individuals of *N. tenuis* were enclosed to avoid its consumption by large herbivores (sheep). Basal diameters were measured in each season (December, March, June, and October) and biomass was estimated using allometric regressions (see Table S2, supplemental material). Plant productivity was determined as the - positive increment of biomass. At the beginning of December, the number of inflorescences per plant was counted.

Statistical analysis

We assessed the significance of the differences in productivity and the number of inflorescences among species, communities and years by ANOVA of repeated measures. In this analysis, we included species and communities as fixed factors, and years as repeated measures within each plant. Significant effects were further analyzed using Tukey post hoc tests. All statistical analyses were performed with the SPSS package and the level of significance was $\alpha = 0.05$ throughout the study.

Results

Precipitation measurements and soil surface characteristics

Total rainfall differed between years. During the first year, total rainfall (221.8 mm) was scarcely below the long-term average (259.32 mm). In contrast, during the second year the precipitation (354.6 mm) was well above the long-term average. During the first year the largest precipitation events occurred in summer (Figure 1) when most water is lost

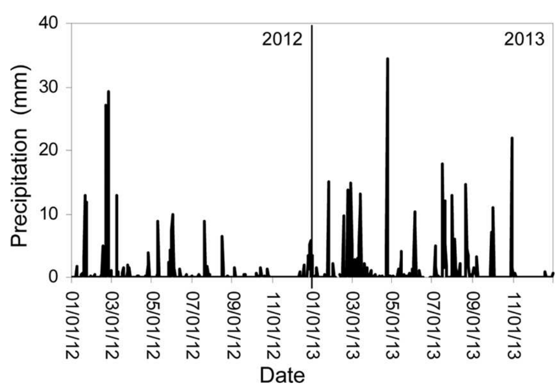

Figure 1. Daily precipitation during the study period.

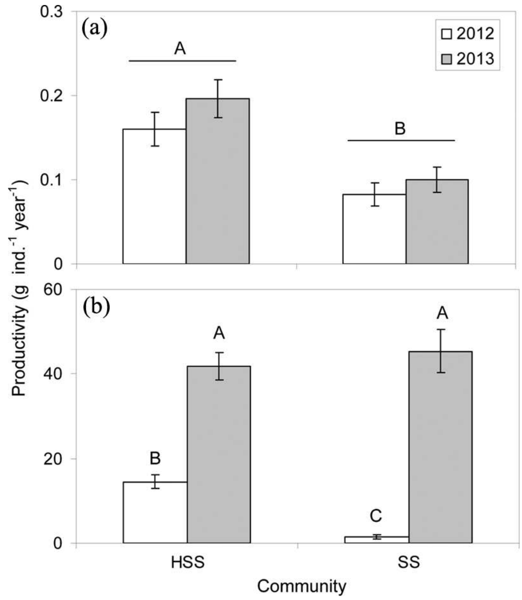

Figure 2. Productivity (mean ± 1SE) of *N. tenuis* (a) and *C. avellanedae* (b) of the two communities (HSS and SS) and years (2012 = white bars and 2013 = grey bars). Capital letters indicate differences in years and communities within species.

by evaporation. In the second year there were more events of high precipitation, especially throughout the winter and spring seasons (Figure 1), favoring deep water recharge.

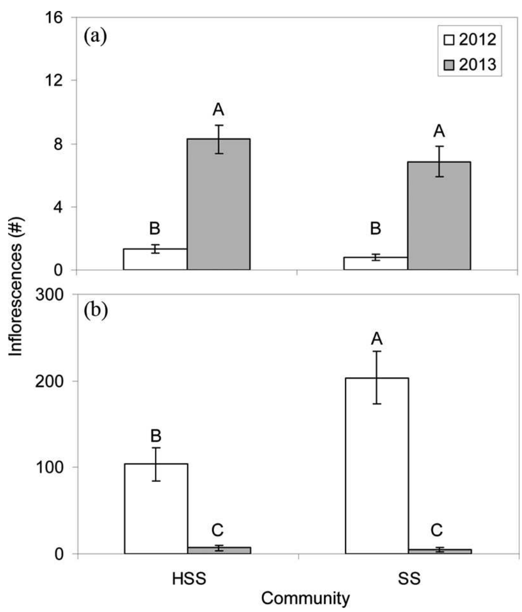

Figure 3. Number of inflorescences (mean ± 1SE) per bunch of *N. tenuis* (a) and per shrub of *C. avellanedae* (b) of the two communities (HSS and SS) and years (2012 = white bars and 2013 = grey bars). Capital letters indicate differences in years and communities within species.

Soil surface characteristics differed between communities; HSS presented a higher grass (23.87% vs. 3.17%) and litter cover (17.77% vs. 9.55%), and a lower bare soil (47.35% vs. 68.40%) and gravel cover (0.35% vs. 9.67%) than SS.

Plant productivity and number of reproductive structures

There was a significant community × species × year interaction ($F_{1,156} = 8.46$, $P = 0.004$). *C. avellanedae* showed a significantly higher productivity in the wet year while *N. tenuis*, the perennial grass, did not present changes between years (Figure 2). The perennial grass exhibited higher productivity in the HSS than in the SS (Figure 2a) while *C. avellanedae*, the evergreen shrub, presented less productivity in SS than HSS only during the dry year (Figure 2b).

The number of inflorescences was affected by the inter-annual variation in precipitation, although the effect differed between species. *N. tenuis* presented more inflorescences in the wet year in both communities ($F_{1,78} = 100$, $P < 0.001$) (Figure 3a). In contrast, *C. avellanedae* showed less inflorescences in the wet year in both communities (Figure 3b), but during the dry year the number of inflorescences in *C. avellanedae* was higher in SS than HSS (year × community interaction; $F_{1,78} = 8.74$, $P = 0.004$).

Discussion

The effects of precipitation on species' productivity were clearly community-specific and depended on the conditions of each year. Perennial grass productivity was lower in SS than HSS in both years, while shrub productivity was lower in SS only during the year of below average precipitation. This difference was possibly caused by lower infiltration in SS than HSS (see Figure S3, supplemental material). The differences between communities might be vanished in years of high precipitation and benefit shrubs because of their deep root systems (Schenk 2006). In contrast, grasses show shallow root systems so they are not favored if deep soil layers are recharged (Schenk 2006). Surface and subsurface soil physical characteristics played an important role in determining the hydrological soil properties in both communities (Chartier, Rostagno, and Pazos 2011). Coarser texture in the upper soil layer in HSS, added to the high herbaceous plant density that delays the runoff (Rostagno 1989; Davenport et al. 1998; Chartier and Rostagno 2006) increases infiltration rates of that community compared to the exposed argillic horizon of the SS (Súnico, Bouza, and Del Valle 1996; Rostagno and Degorgue 2011). These results are in agreement with the findings that arid land degradation, generally referred to as desertification, diminishes the proportion of precipitation conducted to infiltration and transpiration and increases the proportion derived from runoff and evaporation (Verón, Paruelo, and Oesterheld 2006; Chartier, Rostagno, and Videla 2013). Other studies have found that differences in soil properties can affect water availability and plant performance (Hamerlynck, McAuliffe, and Smith 2000).

Shrub species productivity increased with precipitation, while grass productivity did not change between years. One reason for these results might be that in wetter years more water reaches deeper soil layers, enhancing shrub production instead of grass production. In that sense, field measurements (Coronato and Bertiller, 1997) and modeling approaches (Paruelo and Sala 1995; Bisigato and Lopez Laphitz 2009) have shown that in other Patagonian ecosystems superficial soil layers are refilled all years, while deep layers are refilled only during above average precipitation years. Moreover, productivity of *N. tenuis* could be nitrogen limited in years of high precipitation. A long-term study conducted in the Chihuahuan Desert showed that the shrub *Dasylirion leiophyllum* (Engelm.) exhibited its highest productivity during the wetter years, while the grass species Bouteloua curtipendula (Michx.) Torr. was primarily limited by water availability during dry years and became *N*-limited in wet years (Robertson et al. 2009). Likewise, an experiment conducted in a southern Mongolian desert-steppe showed that increasing water input had no positive effect on the productivity of *Stipa* species but the fertilization had a significant impact (Ronnenberg and Wesche 2011). However, it should be mentioned here that although an increase in *N. tenuis* productivity in response to above average precipitation was not observed, plant density could be augmented after one or more years of above-average precipitation conducting to a higher productivity at a community scale.

It is possible that the increase in shoot production of *C. avellanedae* would be associated with their leaf area index (LAI) as *C. avellanedae* shows higher LAI compared to *N. tenuis* (1.05 ± 0.14 *vs.* 0.38 ± 0.02, respectively; Campanella and Bertiller 2008). The branching architecture of shrubs allows the deployment of more meristems and leaves (Knapp et al. 2008). At site and biome scales, precipitation, temperature, and nitrogen have been raised as controls of productivity (Webb et al. 1983; Knapp and Smith 2001). Moreover, biotic constraints such as meristem limitation (Knapp and Smith 2001) may reduce productivity below the climatic and/or edaphic site potential (Knapp et al. 2008). Differences in grass productivity between communities may be due to differences in tussock sizes. *N. tenuis* plants were in general smaller in the SS ($3.57 \pm 0.21\,cm^2$) than in the HSS ($6.76 \pm 0.50\,cm^2$). Similarly, when comparing individual biomass of annual species in grasslands and shrublands, Xia et al. (2010) found that the species that occurred in both communities had a lower individual biomass in shrublands than in grasslands. This was attributed to slightly lower nitrogen availability in shrub-compared to grass-dominated areas.

The two species presented different allocation patterns in response to contrasting annual precipitation. While *N. tenuis*, the grass species, had more inflorescences in wet years, the opposite pattern was found for *C. avellanedae*, the shrub species. A similar result was found in a greenhouse experiment, in which reproductive output (i.e., number of flowering tillers and inflorescence dry weight) of perennial grass species tended to decrease with lower water availability (Cenzano et al. 2013). On the other hand, in the shrub *Larrea tridentata* (Sessé & Moc. ex DC) Coville, vegetative growth occurred when resources were not limited, but under stress conditions this species changed the allocation of resources toward the production of reproductive structures (Bazzaz et al. 1987; Cunningham et al. 1979). This response fits the trade-off hypothesis that assumes competition for limiting resources between reproduction and growth (Obeso 2002).

In conclusion, our results show that abiotic factors, such as superficial and subsuperficial soil characteristics, and biotic factors, such as LAI or tussock sizes, may interact to influence the responses of species to precipitation. Thus, the effects of precipitation on plant productivity are community dependent. All these differences probably modify species interactions whose final community consequences may be more complex than previously predicted.

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References

Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. *BioScience* 37: 58–67. doi:10.2307/1310178

Beeskow, A. M., N. O. Elissalde, and C. M. Rostagno. 1995. Ecosystem changes associated with grazing intensity on the Punta Ninfas rangelands of Patagonia, Argentina. *Journal of Range Management* 48: 517–22. doi:10.2307/4003063

Bertiller, M. B., A. M. Beeskow, and F. Coronato. 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). *Journal of Arid Environments* 21: 1–11.

Bisigato, A. J., and R. M. Lopez Laphitz. 2009. Ecohydrological effects of grazing-induced degradation in the Patagonian Monte, Argentina. *Austral Ecology* 34: 545–57. doi:10.1111/j.1442-9993.2009.01958.x

Campanella, M. V., and M. B. Bertiller. 2008. Plant phenology, leaf traits and leaf litterfall of contrasting life forms in the arid Patagonian Monte, Argentina. *Journal of Vegetation Science* 19: 75–85. doi:10.3170/2007-8-18333

Campanella, M. V., and M. B. Bertiller. 2009. Leafing patterns and leaf traits of four evergreen shrubs in the Patagonian Monte, Argentina. *Acta Oecologica* 35: 831–37. doi:10.1016/j.actao.2009.08.007

Cenzano, A. M., M. C. Varela, M. B. Bertiller, and M. V. Luna. 2013. Effect of drought on morphological and functional traits of *Poa ligularis* and *Pappostipa speciosa*, native perennial grasses with wide distribution in Patagonian rangelands, Argentina. *Australian Journal of Botany* 61: 383–93. doi:10.1071/bt12298

Chartier, M. P., and C. M. Rostagno. 2006. Soil erosion thresholds and alternative states in northeastern Patagonian Rangelands. *Rangeland Ecology & Management* 59: 616–24. doi:10.2111/06-009r.1

Chartier, M. P., M. C. Rostagno, and G. E. Pazos. 2011. Effects of soil degradation on infiltration rates in grazed semiarid rangelands of northeastern Patagonia, Argentina. *Journal of Arid Environments* 75: 656–61. doi:10.1016/j.jaridenv.2011.02.007

Chartier, M. P., C. M. Rostagno, and L. S. Videla. 2013. Selective erosion of clay, organic carbon and total nitrogen in grazed semiarid rangelands of northeastern Patagonia, Argentina. *Journal of Arid Environments* 88: 43–49. doi:10.1016/j.jaridenv.2012.08.011

Coronato, F. R., and M. B. Bertiller. 1997. Climatic controls of soil moisture in an arid steppe of northern Patagonia, Argentina. *Arid Soil Research & Rehabilitation* 11: 277–88. doi:10.1080/15324989709381479

Cunningham, G. L., J. P. Syvertsen, J. F. Reynolds, and J. M. Wilson. 1979. Some effects of soil-moisture availability on above-ground production and reproductive allocation in *Larrea tridentata* (DC) Cav. *Oecologia* 40: 113–23. doi:10.1007/bf00347929

Dameschen, E. I., S. Harrison, and J. B. Grace. 2010. Climate change effects on an endemic-rich edaphic flora: Resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). *Ecology* 91: 3609–19. doi:10.1890/09-1057.1

Davenport, D. W., D. D. Breshears, B. P. Wicox, and C. D. Allen. 1998. Viewpoint: Sustainability of piñon-juniper ecosystems – A unifying perspective of soil erosion threshold. *Journal of Range Management* 51: 231–40. doi:10.2307/4003212

Fay, P. A. 2009. Precipitation variability and primary productivity in water-limited ecosystems: How plants "leverage" precipitation to "finance" growth. *New Phytologist* 181: 5–8. doi:10.1111/j.1469–8137.2008.02695.x

Fernández-A, R. J., O. E. Sala, and R. A. Golluscio. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. *Journal of Range Management* 44: 434–37. doi:10.2307/4002739

Fernandez-Going, B. M., B. L. Anacker, and S. Harrison. 2012. Temporal variability in California grasslands: Soil type and species functional traits mediate response to precipitation. *Ecology* 93: 2104–114.

Fernandez-Going, B. M., and S. Harrison. 2013. Effects of experimental water addition depend on grassland community characteristics. *Plant Ecology* 214: 777–86. doi:10.1007/s11258-013-0207-9

Friedley, J. D., J. P. Grime, A. P. Askew, B. Moser, and C. J. Stevens. 2011. Soil heterogeneity buffers community response to climate change in species-rich grassland. *Global Change Biology* 17: 2002–11. doi:10.1111/j.1365-2486.2010.02347.x

Guevara, J. C., J. M. Gonnet, and O. R. Estévez. 2002. Biomass estimation for native perennial grasses in the plain of Mendoza, Argentina. *Journal of Arid Environments* 50: 613–19. doi:10.1006/jare.2001.0915

Hamerlynck, E. P., J. P. McAuliffe, and S. D. Smith. 2000. Effects of surface and sub-surface soil horizons on the seasonal performance of Larrea tridentata (creosotebush). *Functional Ecology* 14: 596–06. doi:10.1046/j.1365-2435.2000.00469.x

Jobbágy, E. G., and O. E. Sala. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications* 10: 541–49. doi:10.1890/1051-0761(2000)010[0541:cogasa]2.0.co;2

Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. Syndonia Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, E. Pendall, and M. B. Cleary. 2008. Shrub encroachment in North American grasslands: Shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* 14: 615–623. doi:10.1111/j.1365-2486.2007.01512.x

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Charlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298: 2202–05. doi:10.1126/science.1076347

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291: 481–84. doi:10.1126/science.291.5503.481

Köchy, M., and S. D. Wilson. 2004. Semiarid grassland responses to short-term variation in water availability. *Plant Ecology* 174: 197–203. doi:10.1023/b:vege.0000049098.74147.57

McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs*. 64: 111–48. doi:10.2307/2937038

Noy-Meir, I. 1973. Desert Ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4: 25–52. doi:10.1146/annurev.es.04.110173.000325

Obeso, J. R. 2002. The cost of reproduction in plants. *New Phytologist* 155: 321–48.

Oesterheld, M., J. Loreti, M. Semmartin, and O. E. Sala. 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science* 12: 137–42. doi:10.1111/j.1654-1103.2001.tb02624.x

Palacio, R. G., A. J. Bisigato, and P. J. Bouza. 2014. Soil erosion in three grazed plant communities in northeastern Patagonia. *Land Degradation & Development* 25: 594–603. doi:10.1002/ldr.2289

Parizek, B., C. M. Rostagno, and R. Sottini. 2002. Soil erosion as affected by shrub encroachment in northeastern Patagonia. *Journal of Range Management* 55: 43–48. doi:10.1007/s00267-012-9810-0

Paruelo, J. M., and O. E. Sala. 1995. Water losses in the Patagonian steppe: A modelling approach. *Ecology* 76: 510–20. doi:10.2307/1941209

Pimentel, D., C. Harvey, P. Resosudarmo, K. Sinclair, D. Kurz, M. McNair, S. Crist, L. Sphpritz, L. Fitton, R. Saffouri, and R. Blair. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science* 267: 1117–23. doi:10.1126/science.267.5201.1117

Pimentel, D., and N. Kounang. 1998. Ecology of soil erosion in ecosystems. *Ecosystems* 1: 416–26. doi:10.1007/s100219900035

Robertson, T. R., C. W. Bell, J. C. Zak, and D. T. Tissue. 2009. Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland. *New Phytologist* 181: 230–42. doi:10.1111/j.1469-8137.2008.02643.x

Robinson, T. M., K. J. La Pierre, M. A. Vadeboncoeur, K. M. Byrne, M. L. Thomey, and S. E. Colby. 2013. Seasonal, not annual precipitation drives community productivity across ecosystems. *Oikos* 122: 727–38. doi:10.1111/j.1600-0706.2012.20655.x

Ronnenberg, K., and K. Wesche. 2011. Effects of fertilization and irrigation on productivity, plant nutrient contents and soil nutrients in southern Mongolia. *Plant and Soil* 340: 239–51. doi:10.1007/s11104-010-0409-z

Rostagno, C. M. 1989. Infiltration and sediment production as affected by soil surface conditions in a shrubland of Patagonia, Argentina. *Journal of Range Management* 42: 382–85. doi:10.2307/3899544

Rostagno, C. M., and G. Degorgue. 2011. Desert pavements as indicators of soil erosion on aridic soils in north-east Patagonia (Argentina). *Geomorphology* 134: 224–31. doi:10.1016/j.geomorph.2011.06.031

Schenk, H. J. 2006. Root competition: Beyond resource depletion. *Journal of Ecology* 94: 725–39. doi:10.1111/j.1365-2745.2006.01124.x

Soil Surface Staff. 1999. *Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. Agricultural Handbook 436, USDA Soil Conservation Service*. Washington, DC: U.S. Government Printing Office.

Súnico, A., P. Bouza, and H. Del Valle. 1996. Erosion of subsurface horizons in northeastern Patagonia, Argentina. *Arid Soil Research and Rehabilitation* 10: 359–78. doi:10.1080/15324989609381450

Verón, S. R., J. M. Paruelo, and M. Oesterheld. 2006. Assessing desertification. *Journal of Arid Environments* 66: 751–63.

Webb, W. L., W. K. Lauenroth, S. R. Szarek, and R. S. Kinerson. 1983. Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. *Ecology* 64: 134–51. doi:10.2307/1937336

Xia, Y., D. I. Moore, S. L. Collins, and E. H. Muldavin. 2010. Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities. *Journal of Arid Environments* 74: 378–85. doi:10.1016/j.jaridenv.2009.08.016