The influence of disturbance type on precipitation – use efficiency at functional group and species scales in an arid habitat

Carlos A. BUSSO [1,2]*, Oscar A. MONTENEGRO [3], Yanina A. TORRES [1,4], Hugo D. GIORGETTI [3] and Gustavo D. RODRIGUEZ [3]

[1] Departamento de Agronomía, Universidad Nacional del Sur (UNS), San Andrés, 8000 Bahía Blanca, Pcia. Buenos Aires, Argentina
*e-mail: carlosbusso1@gmail.com (corresponding author)
[2] CERZOS- Consejo Nacional de Investigaciones Científicas y Tecnológicas de la República Argentina (CONICET)
San Andrés, 8000 Bahía Blanca, Pcia. Buenos Aires, Argentina
[3] Chacra Experimental Patagones, Ministerio de Asuntos Agrarios, 8504 Carmen de Patagones, Pcia. Buenos Aires, Argentina
[4] Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (CIC)

ARTICLE INFO

Regular research paper
published in
Pol. J. Ecol. (2016) 64:143–164

received after revision
April 2016

doi
10.3161/15052249PJE2016.64.2.001

key words
precipitation-use efficiency
late- and early-seral plant species
arid zones
burning
old fields
overgrazing
inter-annual variability

ABSTRACT

We used long-term datasets (1984–1992) to contrast precipitation-use efficiency estimates between various disturbance kinds at a functional group and/or a species scale. Effects of varying amounts of precipitation and plant cover on PUE were also examined. Field studies were conducted at northeastern, arid Patagonia, Argentina (40°39′49″S, 62°53′6.4″W). Within each management kind, biomass was sampled in 0.5 × 0.5m permanent plots (n = 30) over 9 years after defoliation at 5 cm stubble at the end of each growing season, and it was separated into species. Biomass sampling allowed determination of annual net primary production. Thereafter, species were grouped into each of three functional groups. Precipitation-use efficiency (PUE) was calculated as the total dry matter produced per unit surface area on any given year divided by the total rainfall in that year. Plant cover on 20 out of those 30 plots was determined to study the relationship between plant cover and PUE. The contribution of cool-season perennial grasses to total PUE was higher (P <0.05) than that found for the other two functional groups in all management kinds and years. PUE was similar (P> 0.05) in wet than dry years, and it was greater (P <0.05) or similar (P> 0.05), but not lower, on the more than less competitive perennial grass species in all management kinds. The relationship between plant cover and PUE was positive, linear (P <0.0000) and management-kind dependent.

INTRODUCTION

Precipitation-use efficiency as calculated (annual aboveground net primary production divided by annual precipitation: Le Houerou 1984, Bhandari *et al.* 2015, Hu *et al.* 2015) by previous and recent research for native grasslands has been observed in the range of 0.5 to 2.0 g dry matter production m^2 per 1 mm of annual precipitation (Epstein *et al.* 1998, O'Connor *et al.* 2001). These studies have shown that precipitation-use efficiencies can vary within and between grasslands because of differences in the amount and temporal distribution of annual precipitation, plant cover, soil texture and water holding capacity, plant species composition, seral stage, and previous year's production. These factors affect PUE through variations in evapotranspiration rate, the major process involved in returning grassland precipitation to the atmosphere (Wilcox *et al.* 2006). Webb *et al.* (1983) and Nielsen *et al.* (2005) also showed that precipitation-use efficiency was related with the above mentioned factors on forests, deserts and agro-ecosystems. However, no studies have yet evaluated the relationship between PUE and the competitive ability of species pertaining to different seral stages. These studies are essential in arid zones where small precipitation events (<5 mm; Sala and Lauenroth 1982) are common. For example, more than 60% of the rainfall events (mean = 1983–2000) have been <5 mm in a previous work at the same study site than ours (Páez *et al.* 2005).

Various management kinds produce different disturbance types, and they can produce dynamic shifts on precipitation-use efficiency (PUE) like burning, control of woody vegetation using herbicides, removal of woody plants, and overgrazing (Vallentine 1990). These management kinds might vary in concert with climatic variations (*e.g.* precipitation: Le Houérou *et al.* 1988) and post-treatment management (Gartner 1988).

Fire, together with grazing and precipitation, are major factors in shaping plant community structure in the Phytogeographical Province of the Caldenal, in semiarid, temperate, central Argentina (Busso 1997). Thousands of hectares of natural grassland are burnt every year at the south of the Caldenal (Bóo 1990). However, the frequency of fire occurrence has decreased notably since the introduction of domestic livestock; the high grazing pressures altered the natural fire regimes because of the reduction of fine combustible material (Peláez *et al.* 2003). As a result, grasslands were transformed to either shrublands or areas of unpalatable grass species for domestic livestock (Pelaez *et al.* 2003). However, Distel and Bóo (1996) proposed that appropriate management of the frequency and intensity of fire could revert the processes of scrub formation and the presence of unpalatable grasses to states with less bushes and a greater cover of palatable perennial grasses. Several studies have reported an increase in palatable, rangeland forage species after the shrub stratum was controlled using various herbicides (Martin and Morton 1980, Jacoby and Meadors 1982). Cramer *et al.* (2008) reported that the abandonment of traditional agricultural lands in some areas can create old fields that require limited or no restoration. Fernández and Paruelo (1993) showed that productivity of the most palatable grass species (*i.e. Poa ligularis* Nees ex Steud) decreases, while that of the non-palatable grass species [*i.e. A. ambigua* (Speg.) Arriaga & Barkworth] increases after grazing in the Occidental District of Patagonia. These changes are triggered by the direct effect of grazing (Sala 1988), which may lead to plant death in extreme cases, or by indirect effects following cover reduction, such as erosion, and losses of soil organic matter, nutrients, and seeds that limit plant establishment (Bertiller 1998). Deflation and deposition processes, and organic matter and nutrient losses, triggered by wind and precipitation after grazing, most often create large areas of bare soil (Mazzarino *et al.* 1998). The increase of the relative or absolute shrub cover, and the decrease of the absolute cover of perennial grasses, occur as an extended process in grazed rangelands of Patagonia (Perelman *et al.* 1997). These studies have determined the benefits of using either fire or shrub control using herbicides or management of abandoned, previously-cultivated lands or proper grazing as management tools to improve rangeland forage production. However, no studies have compared the relative effects of these management kinds occurring at the same time in determining PUE at a functional group scale.

In rangelands of central Argentina, while C_3 cool-season perennial grass species grow during the fall, winter, and spring (and even during summer if water is available; Giorgetti *et al.* 2000), C_4 warm-season perennial grasses grow only in spring and summer (Giorgetti *et al.* 2000). At the study site, C_3 cool-season perennial grasses are relatively exposed to lower saturated water vapour pressure deficits than C_4 warm-season perennial grasses during their growth periods (Giorgetti *et al.* 1997). C_3 cool-season perennial grasses grow mostly during periods of higher air relative humidity and lower air temperatures than C_4 warm-season perennial grasses (Giorgetti *et al.* 1997). This is, the advantage of the grater water-use efficiency in C_4 than C_3 plants (Caldwell *et al.* 1977), that can be overwhelmed by the seasonal distribution of available soil water (Jia *et al.* 2015), might favour more C_3 than C_4 perennial grasses. The seasonal distribution of available soil water, as well as mean annual precipitation, can greatly affect aboveground net primary productivity, a key integrative measure of ecosystem function (Jia *et al.* 2015). Soil water evaporation rates decrease as total plant cover increases (Hu *et al*. 2008). Plant cover was much greater in cool-season- than warm-season-perennial grasses and cool-season annual grasses + Dicots on all study management kinds and years (1984 to 1992) in our study site (Giorgetti *et al.* 1999). Even though plant transpiration rates increase as total plant cover increases (Wang *et al.* 2010), the C_3 cool-season perennial grasses are relatively more exposed to lower vapour pressure deficits than the C_4 warm-season perennial grasses. Since the air is at or near saturation at lower than higher vapour pressure deficits (Prenger and Ling 2015), plant transpiration is expected to be relatively lower in C_3 than C_4 perennial grasses. This suggests that differences in PUE might exist between plant functional groups that (1) have soil water available at different times during any given year (*e.g.* mostly the whole year for C_3 cool-season perennial grasses; Giorgetti *et al.* 1997), (2) differ in basal area percentage cover, and (3) grow during periods with less transpiration rate demands (*e.g.* C_3 species). Then, the advantages of having a greater water-use efficiency can be limited to periods of low demands of evapotranspiration, and might not yield the differences in season-long production expected between C_3 and C_4 species, as a result of the water-use efficiency at any one time. The importance of vegetation composition in determining precipitation-use efficiency was emphasized by Cleland *et al.* in 2013.

The effects of various abiotic and biotic management kinds (*e.g.* drought, fire, soil tillage, pesticide applications, herbivory) on water-use efficiency have been assessed mostly at a plant species scale (Bedunah and Sosebee 1995, Peláez *et al.* 2010, Köhl *et al.* 2014). However, research of the effects of these disturbances on PUE is rather scarce at a plant functional group scale. For example, Tan *et al.* (2009) reported that the difference in water-use efficiency was significant among different plant functional groups. They showed that water-use efficiency followed the order of annual herbs > biennial herbs > perennial herbs, not in accordance with the pattern obtained by previous studies in deserts (Trewin 2006). Tan *et al.* (2009) also suggested that the ranking of water-use efficiency among plant functional groups may be dependent on local water availability. Thus, this information is important to have a more generalized scenario on how various management kinds might affect water-use efficiency of the species within any of those functional groups under local climate conditions.

Hatfield *et al.* (2001) and Nielsen *et al.* (2005) in agro-ecosystems, and Webb *et al.* (1983) in deserts reported that plant cover affects PUE through alterations in evapotranspiration rate: greater plant cover values lead to greater PUE. However, no studies have yet reported how the relationship between plant cover and PUE might change after exposing rangeland vegetation to various management kinds: controlled fire, shrub control using herbicides, long-term abandonment of previously crop-producing lands or overgrazing. Precisely, the novelty of this manuscript was that the stand-scale PUE was partitioned to a functional group and species scales, to allow revealing the mechanisms that control/regulate the relative importance of PUE within management kinds.

Recent studies (Bhandari *et al.* 2015) have indicated that PUE, based on shoot and total (shoots + roots) dry matter, were highest in the meadow steppe and lowest in the desert steppe on grasslands of Inner Mongolia China. Bai *et al.* (2008) reported similar results in the Mongolian Plateau. Other studies also showed that PUE tended to be smaller at drier than wetter sites because of low plant density, and high evaporation and low production potentials (Noy-Meir 1973, Grime 1977). However, some studies have reported that wettest years led to lowest PUE (based on annual shoot dry matter) (Bhanari *et al.* 2015). This is, with a decrease in precipitation there was a decrease in aboveground dry matter but higher PUEs were obtained in dry years. These contrasting results led us to inspect for the variability in the contribution to total PUE between dry *versu*s wet years in various functional groups and management kinds.

Poa ligularis, *Nassella longiglumis* (Phil.) Barkworth [syn. *N. clarazii* (Ball.) (Rúgolo de Agrasar *et al.* 2005)], *N. tenuis* (Phil.) Barkworth, *Pappostipa speciosa* (Trin. & Rupr.) Romasch., *Amelichloa ambigua* and *N. trichotoma* (Nees) Hack. Ex Arech. are abundant C_3 perennial, native grass species in semiarid, temperate rangelands of central Argentina (Rúgolo de Agrasar *et al.* 2005). However, the abundance of any of these species at any one time depends, at least partially, upon grazing and fire management of the vegetation (Busso 1997). Various studies have determined that *N. longiglumis* and *P. ligularis* are more competitive grass species than *N. tenuis*, *N. trichotoma*, *A. ambigua* or *P. speciosa* (Moretto and Distel 1997, 1999, Saint Pierre *et al.* 2004 a, b). Greater competitive ability in various perennial grass species in central Argentina has been attributed to several traits like higher rates of nutrient uptake, root length density, root proliferation, mycorrhizal colonization of the root system, and more often greater relative growth rates of aboveground tissues (Saint Pierre *et al.* 2002, 2004 a, b, Torres *et al.* 2013). However, no studies have yet addressed if PUE is higher in the more than less competitive perennial grasses.

Our objective was to compare the dynamics of PUE during various years between different functional groups and plant species, which had been exposed to various disturbances after the application of different management kinds. We hypothesized that contributions to total PUE are greater (a) in the cool-season perennial grasses than in the warm-season perennial grasses and cool-season annual grasses + dicots in all study management kinds and years, (b) in the more competitive *N. longiglumis* or *P. ligularis* than in the less competitive *N. tenuis*, *N. trichotoma*, *A. ambigua*, or *P. speciosa*.

STUDY SITE

Studies were performed in the Chacra Experimental de Patagones, Buenos Aires, Argentina (40°39′S, 62°54′W, 40 m a.s.l.), within the Phytogeographical Province of the Monte (Cabrera 1976) during 1984 through 1992.

Climate is temperate semiarid, with higher precipitations during the spring and fall seasons (Giorgetti *et al.* 2000). Soil is a typical haplocalcid, with an A horizon having a loamy-clay-sandy texture; 0.20 m deep; 1.69% organic matter; 28.7 ppm available phosphorus, 0.123% total nitrogen. AB_w horizon was found below 0.20 m of soil depth followed by a BC_k horizon between 0.28 and 0.43 m depth. A C_k horizon existed below 0.43 m with very scarce roots. Average pH was 7, and the soil layer depth is not a constraint factor for root growth in the soil profile. Monthly precipitation, air temperature and pan evaporation during the study period are shown in Fig. 1.

The plant community is characterized by an open, shrubby stratum which includes different-quality, herbaceous species for cattle

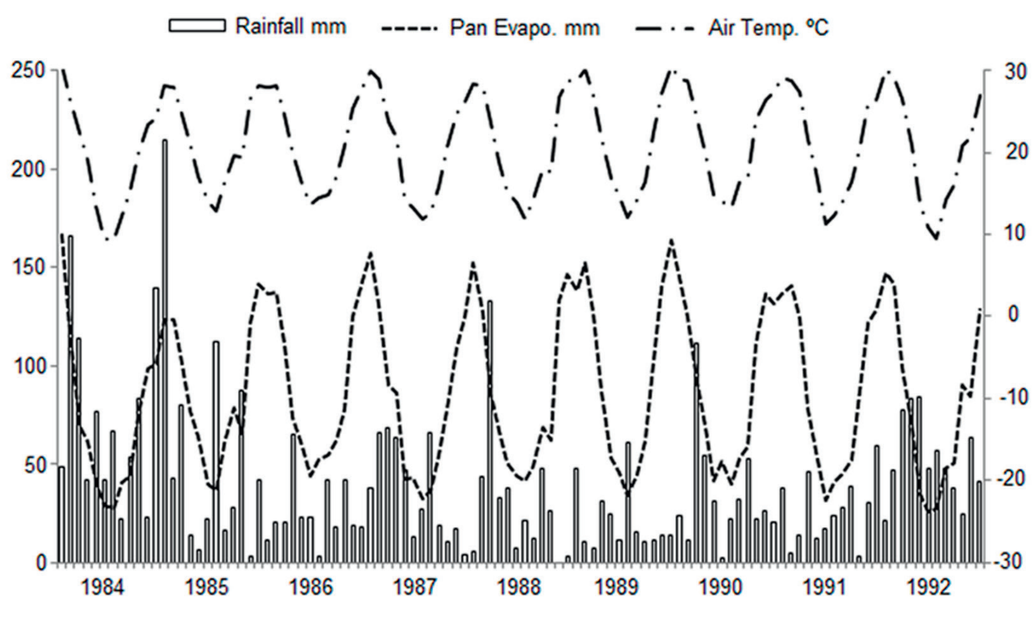

Fig. 1. Monthly precipitation, and mean monthly air temperature and pan evaporation during 1984 to 1992.

production (Busso 1997). The climate and vegetation data during 1984–1992 are similar to those currently occurring at the study region in central-eastern Argentina (Fernández and Busso 1999, Busso *et al.* 2003, Busso and Bolletta 2010, Fernández *et al.* (in press)). Despite current species composition is similar to that present more than two decades ago, dominance of a particular grass or shrubby species at any place within this region is partially dependent on grazing history and fire frequency and intensity (Distel and Bóo 1996).

METHODS

Disturbance as the management kinds

Before management kinds were imposed at the study site, the plant community was characterized (n = 20 stands) by using the abundance-dominance/sociability index of Braun Blanquet (Mueller-Dombois and Ellenberg 1974) on 1 November 1974. *Chuquiraga erinacea* D. Don (mean = 2.3), *Baccharis ulicina* Hook. & Arn. (mean = 1.2) and *Nassella tenuis* (mean = 4.4) were the species with the highest index for the shrubby, forb and grass layers, and the community was then classified as an open shrubland of *Ch. erinacea* and *Condalia microphylla* Cav. within a continuous herbaceous layer of *N. tenuis*. Giorgetti *et al.* (1997) reported on some vegetation characteristics (*e.g.* species composition, percentage contribution of various species to total net primary productivity) during 1984–1992 at the study site. The study was initiated thereafter on areas which had been previously exposed to continuous grazing by cattle and sheep, and then exposed to different managements (*i.e.* disturbance types, see Table 1). At burning time, maximum and mean air temperatures were 23.5 and 14.4°C, respectively, mean relative humidity was 49%, and wind speed and dry weight of fine fuel load

Table 1. Description of the characteristics of the disturbances studied.

History of land previous to imposing the various disturbance types	Name of the disturbance type	Characteristics of the disturbance	Disturbance surface area (ha)
All study, contiguous areas had previously been exposed to continuous grazing by cattle and sheep during several decades.	Control	Uncontrolled grazing by cattle and sheep was allowed in this area, un-cleared from woody and herbaceous vegetation, until 1975. From 1975 to 1993, it was excluded to grazing by domestic herbivores (*i.e.* untreated in comparison to the remaining study areas).	34
	Fire	This area, with a history similar to that in the Control, received a controlled burning in 1978. Details on burning characteristics are given in the text.	37
	Shrub Control	After having a similar land history than the Control until 1975, shrubs were controlled in this area using herbicides. Further details on herbicide application and plant responses are provided in the text.	24
	Old Field 1	This area was first cleared from trees and undergrowth, and then cropped from 1951 until 1975. Previous to cultivation, this area had been exposed to a more severe grazing than the Old Field 2 Disturbance kind as a result of its greater proximity to a water source by animals.	10
	Old Field 2	The history of this area was the same than that described for the Old Field 1. The only exception was that it had been exposed to a less severe grazing than that area because it did not have a nearby water source for cattle and sheep.	10
	Overgrazing	This area was severely, continuously overgrazed until 1981, and then excluded from domestic herbivory until 1993.	40

were 22 km h^{-1} and 438 kg ha^{-1}, respectively. More than or equal to 50% of plants of the shrubs *Geoffroea decorticans* (Gill ex Hook et Arn.) Burkart, *Condalia microphylla*, *Lycium chilensis* Miers ex Bertero, *Chuquiraga erinacea*, *Larrea divaricata* Cav. and *Schinus fasciculatus* (Griseb.) I.M.Johnst. had produced basal regrowth one year after burning. Digiuni (1983) has already reported the chemical shrub control for this study. Briefly, an aerial application of Tordon 213 (2 L ha^{-1}) and 2,4,5,-T (4 L ha^{-1}) was made on 29 December 1977, when mean air temperature and relative humidity were 18.7°C and 58.0%, respectively, rainfall was 108 mm during December, and shrubs were at the reproductive morphological stage of development. Herbicides were very effective in producing death or total defoliation with no basal regrowth in *G. decorticans*, *C. microphylla*, *L. chilensis* and *L. divaricata*, and less than 50% defoliation in *C. erinacea* immediately after their application. Sixteen months later, however, 80–90% of *G. decorticans* and *C. microphylla* plants had not produced any regrowth, but the remaining plants and those of *L. chilensis*, *C. erinacea* and *L. divaricata* were less than 50% defoliated. Lack of enough manpower at the research station, however, prevented us to study how shrubs recovered afterwards.

In 1997, Giorgetti *et al*. reported the major tree and shrub species, the prevailing preferred (*i.e*. palatable), intermediate and non-preferred (*i.e*. unpalatable) perennial grasses, the preferred annual grasses, and the perennial (non-preferred) and annual (preferred) forbs at the research field site. This site is typical of east-central rangelands in Argentina. These authors also reported the percentage contribution of each species within the either preferred or intermediate or non-preferred perennial grass species group to total herbaceous standing crop in the Control, Burning, Shrub Control, Old Field 1, Old Field 2 and Overgrazing treatments during 1984 to 1992.

Procedures

By mid-November 1978, percentage cover was determined per species within each management kind (n = 50) by randomly distributing 20 × 20 cm quadrats following the canopy--cover method of Braun-Blanquet (1979). Maximum aboveground standing crop was also estimated at the Control, Old Field 1, Old Field 2, Burned and Shrub Control management kind sites in 1978 (n = 50), and at these and the Overgrazed site from 1984 to 1992, by hand clipping live + recent dead herbage to 5 cm stubble height. The first clipping was made during late January or late May 1984 on the C_3 cool-season or the C_4 warm-season perennial grasses, respectively, so that only current year's growth would be included in the subsequent harvests. Similar to that reported by Singh *et al.* (1975), aboveground standing crop [*i.e.* live + recent dead tissues (current growth´s production)] was taken as an approximation of ANPP. Annual net productivity data were already reported by Giorgetti *et al.* (1997). Briefly, all harvestings began when major forage species reached maturity, usually late December or early January in the cool-season perennial grasses and cool-season annual grasses + dicots, or late April to early May in the warm-season perennial grasses (Giorgetti *et al.* 2000). This once-a-year harvesting allowed that only current-year growth (*i.e.* live + recent dead) was included in the ANPP estimates made each year. No samplings were conducted during 1979 to 1983 because of economic constraints. At harvesting time during 1984 to 1992, 30 randomly distributed, permanent plots (0.5 × 0.5 m) were clipped to 30 to 50 mm stubble height on each management kind. Herbage was separated by species, except in the 1978 sampling when only total herbaceous standing crop was measured, and dried in a forced draft oven at 70°C until constant weight. Vegetation ANPP was then expressed on a dry weight basis. Within the desirable annual grass or forb group, a species was separated from the remaining total ANPP when its contribution to it was substantial. Previous to clipping from 1984 to 1990, total herbaceous plant cover of the herbaceous vegetation (*i.e.* cool- or warm-season perennial and annual grasses, and dicots) was also determined on 20 out of the 30 randomly distributed, permanent plots following Braun-Blanquet (1979). These total, herbaceous plant cover data were reported by Giorgetti *et al.* (1999).

Aboveground standing crop was measured by species and plant functional groups, which were comprised of cool-season, C_3 perennial grasses; warm-season, C_4 perennial grasses, and cool-season, C_3 annual grasses and dicots. Annual forbs were not included in another, separate functional group because they were just two plant species, and their dry matter contribution to ANPP and plant cover were minimal. Estimates of ANPP were comprised from total standing crop harvests in all species. Table 2 shows the species composition of each functional group and its preference by grazing livestock.

Precipitation-use efficiency (PUE; g dry matter m^{-2} mm^{-1} precipitation) was defined as forage standing crop (g m^{-2}; oven-dry) produced per mm of rainfall received, and is based on the plant growth and rainfall measured between annual harvests. It was calculated similar to reports of past and current research (*e.g.* Wight and Black 1972, Le Houérou 1984, Bhandari *et al.* 2015, Hu *et al.* 2015). Precipitation-use efficiency of individual plant functional groups was converted to its respective percent contribution to total PUE. Similar to reports of Vermeire *et al.* (2009), PUE was reported at a functional group scale. Root biomass was not collected or used in estimates of production. The precipitation year was defined as 1 January through 31 December.

A comparison in PUE was made between wet *versus* dry years. Estimates of forage

Table 2. Species composition and its degree of preference by livestock on each of the study functional groups (*i.e.* CSPG = cool-season perennial grasses; WSPG = warm-season perennial grasses; CSAG+D = cool-season annual grasses + dicots).

Functional Group	Dominant herbaceous vegetation	Preference by livestock
CSPG	*Nassella tenuis* (Phil.) Barkworth	Preferred
	Nassella longiglumis (Phil.) Barkworth	Preferred
	Poa ligularis Nees ex Steud	Preferred
	Jarava plumosa (Spreng.) SLW Jacobs & J. Everett	Preferred
	Piptochaetium napostaense (Speg.) Hackel	Preferred
	Poa lanuginosa Poir	Preferred
	Bromus brevis Nees ex Steud	Preferred
	Koeleria permollis Nees ex Steud	Preferred
	Pappostipa speciosa (Trin. & Rupr.) Peñailillo	Intermediate
	Amelichloa ambigua (Speg.) Arriaga & Barkworth	Not preferred
	Amelichoa brachychaeta (Godr.) Arriaga & Barkworth	Not preferred
	Nassella trichotoma (Nees) Hack. Ex Arech.	Not preferred
	Sporobolus rigens (Trin.) E. Desv.	Not preferred
WSPG	*Pappophorum vaginatum* Buckley	Preferred
	Sporobolus cryptandrus (Torr.) A. Gray	Preferred
	Aristida spegazzinii Arechav.	Intermediate
	Aristida subulata Henrard	Intermediate
	Aristida pallens Cav.	Intermediate
	Aristida trachyantha Henrard	Intermediate
CSAG + Dicots	*Bromus hordeaceus* L.	Preferred
	Schismus barbatus (L.) Thellung	Preferred
	Vulpia megalura (Nutt.) Rydb	Preferred
	Lolium multiflorum Lam.	Preferred
	Hordeum murinum (Link) Arcang	Preferred
	Medicago minima (L.) Grufberg	Preferred
	Erodium cicutarium (L.) L´Herit. ex Ait	Preferred

production during wet years included those years where annual precipitation was higher than the long-term average (*i.e.* 416.7 mm; 1984 = 877.3 mm, 1985 = 667.4 mm, 1987 = 437.6 mm, 1992: 631.2 mm; overall annual mean ± 1 SE, n = 653.4 ± 90.1, 4), while those of forage production during dry years included years where annual precipitation was below the long-term average (*i.e.* 1986 = 303.3 mm, 1988 = 370.4 mm, 1989 = 257.5 mm; 1990 = 408.3 mm; 1991 = 312.2 mm; overall annual mean = 330.3 ± 26.5, 5).

Statistical analysis

At first, a multivariate analysis approach was conducted using the statistic of Wilks (Wilk´s lambda) (Wilks 1932). A repeated measures analysis was made between the study factors (functional groups × management kinds) and years. Since there was an interaction between factors and years (P <0.05), each year was analysed separately. Analyses were limited to annual means because seasonal analyses were not interpretable due to our inability to quantify the intra-seasonal impacts of carry-over soil water on PUE estimates. Precipitation-use efficiency data were analysed using two factorial ANOVA [functional group (or species) × management kinds within each year]. When F tests were significant, means were always compared using the Tukey´s test (P <0.05). The tests of Kolmogorov-Smirnov and Levene were used to evaluate normality and homoscedasticity assumptions, respectively. Data were analysed using the statistical software INFOSTAT (Di Rienzo *et al*. 2013). The relationship between total herbaceous plant cover and precipitation-use-efficiency was analysed using regression analysis following Netter *et al.* (1985). When there were no significant differences among regression lines of the different management kinds for all study years, total herbaceous plant cover and precipitation-use-efficiency data of these management kinds were pooled and just one regression line was obtained after Netter *et al.* (1985). The procedure outlined by these authors was also followed to test for equality of slopes when the regression lines were unequal.

Labour and budget constraints made replication of this study in space (*i.e.* at other study sites in the region) and time (*i.e.* initiating the study in another set of nine, consecutive years) impossible. As stated by Hurlbert (1984), "…when the cost of replication is very great, experiments involving unreplicated treatments may also be the only or best option…". Despite emphasis is placed on statistical differences, caution is called for extrapolating the results of this study. These should be better viewed under the specific conditions they were obtained.

RESULTS

Precipitation

Annual precipitation across years showed a variation coefficient of 27.84% (Fig. 2). Aver-

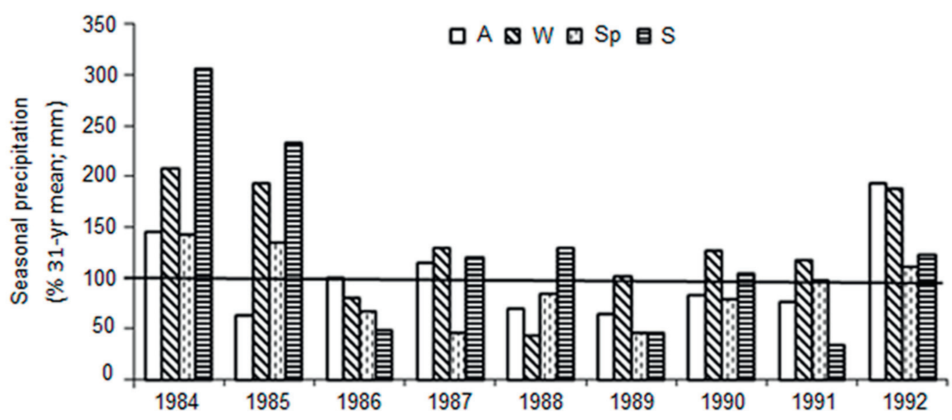

Fig. 2. Seasonal precipitation during each year of the study period (1984–1992). For any given year, each histogram represents the percentage contribution of any season to the long-term average (1981–2011) for that season. The horizontal line (417.6 mm: 100%) indicates the long-term average precipitation. A = Autumn; W = Winter; Sp = Spring; S = Summer.

age precipitation during the 1984–1992 study period (473.91 mm) was 11.9% above the long-term (1981–2011) average (417.6 mm = 100%: Fig. 2). As a percentage of the long-term average, annual precipitation ranged from 61.7 to 210.1% [257.5 (1989) to 877.3 mm (1984)]. In only 2 out of 9-study years (*i.e.* 1984 and 1992; Fig. 2), each season precipitation exceeded the long-term average for that season. Means of long-term (1984–1992) seasonal precipitation were 101.2, 132, 90.4, and 127.8 mm for autumn, winter, spring and summer, respectively (Fig. 2). Other precipitation features included (1) amounts of precipitation received in a single day ranged from 0 mm (no rainfall during November 1988) to 95.5 mm (28 Dec 1984), and (2) numbers of days with more than or equal to 5 mm rainfall fallen in a single day were 211 out of the 609 days with rainfall during the period 1984 to 1992. Monthly pan evaporation was greater than monthly precipitation most of the times during 1984 to 1992 (Fig. 1).

Precipitation-use efficiency

Plant functional groups

Cool-season perennial grasses made the greatest ($P < 0.05$) contribution to total PUE compared with that made by the other two functional groups in all management kinds and years (Fig. 3). The only two exceptions out of 54 comparisons occurred in 1986 on the Old Field 2, and in 1989 in the Overgrazing

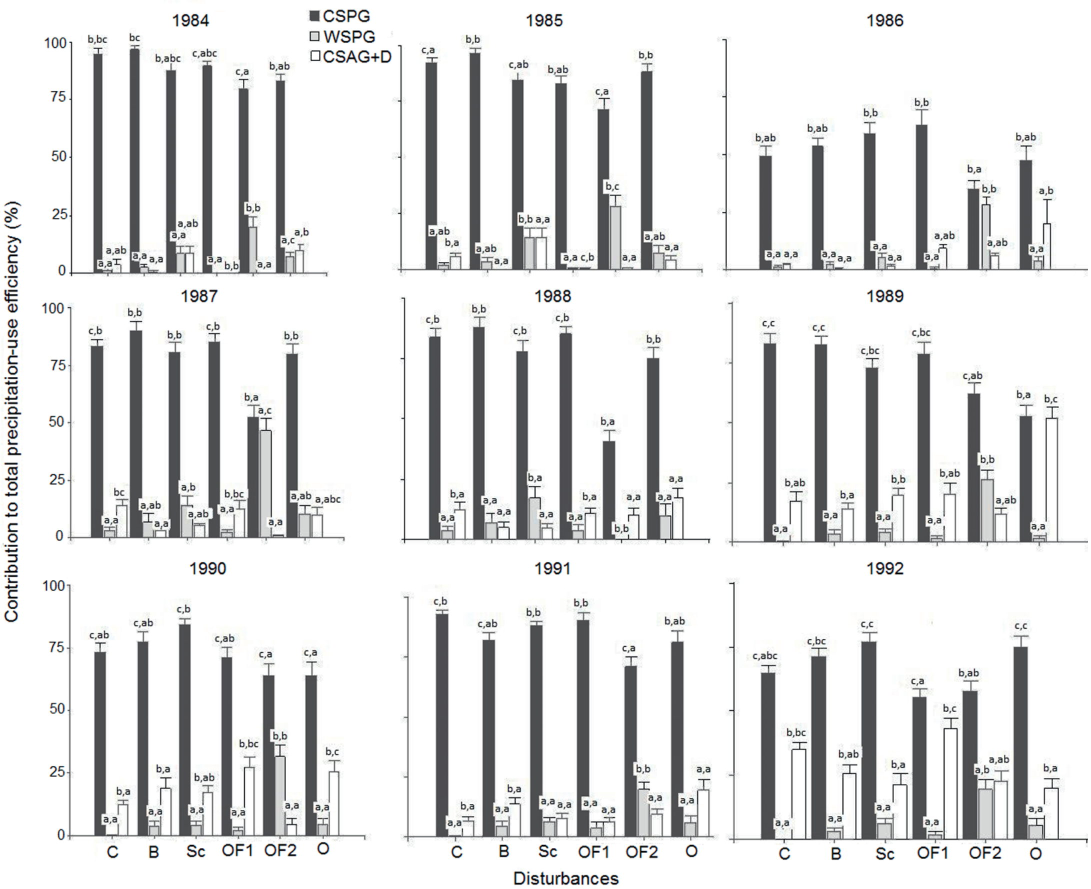

Fig. 3. Contribution (%) to total precipitation-use efficiency (PUE) of the various functional groups (CSPG = cool-season perennial grasses, WSPG = warm-season perennial grasses, CSAG+D = cool-season annual grasses + dicots) in the different management kinds (C = Control, B = Burning; Sc = Shrub Control; OF1 = Old Field 1; OF2 = Old Field 2; O = Overgrazing) during the study years (1984 to 1992). Each histogram is the mean of n = 30. Vertical bars are 1 SE of the means. Different letters to the left of the comma indicate significant differences ($P < 0.05$) among functional groups within each management kind and study year. Different letters to the right of the comma indicate significant differences ($P < 0.05$) within each functional group in the various management kinds on each study year.

management kind (Fig. 3), where the contribution to total PUE was similar ($P> 0.05$) between the cool-season perennial grasses and the warm-season perennial grasses in 1986 in the Old Field 2 management kind, and the cool-season perennial grasses and cool-season annual grasses + dicots in 1989 in the Overgrazing management kind (Fig. 3).

The warm-season perennial grasses made a greater ($P<0.05$) contribution than cool-season annual grasses + dicots to total PUE in the Old Field 2 management kind from 1984 to 1986, and from 1989 to 1991 (Fig. 3).

On the other hand, the contribution of the cool-season annual grasses + dicots to PUE was mostly greater ($P<0.05$) than that of the warm-season perennial grasses in the (1) Control management kind during 1985 and from 1987 to 1992, (2) Old Field 1 management kind in 1985, from 1987 to 1990, and in 1992, and (3) Burning, Shrub Control and Overgrazing management kinds during 1989, 1990 and 1992 (Fig. 3).

The contribution to total PUE tended to decrease with decreases in annual precipitation after wet years on the cool-season perennial grass functional group (Fig. 3). However, it was not necessarily the case for the other two functional groups, which contribution to total PUE in dry years following wet years appeared to be smaller, similar or greater than that in the previous, wet years depending on the management kind (Fig. 3).

The PUE was higher ($P<0.05$) on the cool-season perennial grasses than on the warm-season perennial grasses and cool-season annual grasses + dicots under both wet and dry years (Fig. 4). In addition, the PUE was similar ($P> 0.05$) under wet versus dry years within any of the study functional groups (Fig. 4).

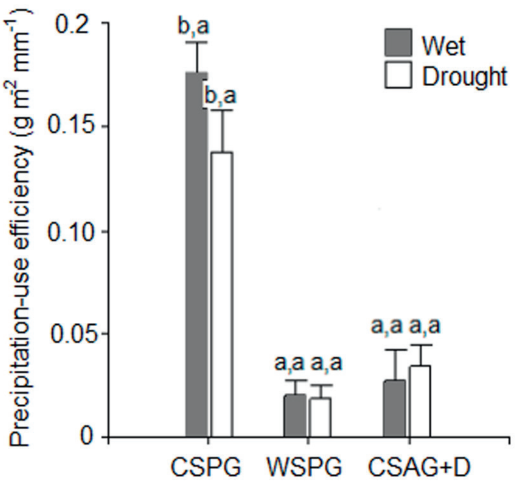

Fig. 4. Precipitation-use efficiency (PUE; kg ha^{-1} mm^{-1}) of each functional group (CSPG = cool-season perennial grasses, WSPG = warm-season perennial grasses, CSAG+D = cool-season annual grasses + dicots) in wet *vs* dry years during 1984 to 1992. Wet or dry years were those which showed an annual precipitation above (n = 4) or below (n = 5), respectively, the long-term (1981–2011) mean annual precipitation. Different letters to the left of the comma indicate significant differences ($P<0.05$) among functional groups within either wet or dry years. Different letters to the right of the comma indicate significant differences ($P<0.05$) between either wet or dry years within each functional group. Vertical bars represent 1 SE of the mean.

Management kinds

The comparison among management kinds within each functional group did not show a very clear pattern throughout the years. However, the cool-season perennial grasses showed a lower ($P<0.05$) contribution to total PUE in the Old Field 2 than in most of the other management kinds during 1984 to 1988, and in 1991 and 1992 (Fig. 3). In addition, the contribution of this functional group to total PUE was lower ($P<0.05$) in the Old Field 2 and Overgrazing management kinds than in the (1) Control and Burning management kinds during 1989, and (2) Shrub Control management kind in 1990 (Fig. 3).

The percentage contribution of the warm-season perennial grasses to total PUE was higher ($P<0.05$) in the Old Field 2 than in the remaining groups of management kind during all study years but 1988 (Fig. 3). At this later time, functional groups showed the opposite response (Fig. 3).

In 5 (*i.e.* 1984, 1987, 1989, 1990 and 1992) out of 9 study years, the contribution of cool-season annual grasses + dicots to total PUE was in general greater ($P<0.05$) in the Overgrazing and/or Old Field 1 management kinds than in the remaining management kinds (Fig. 3).

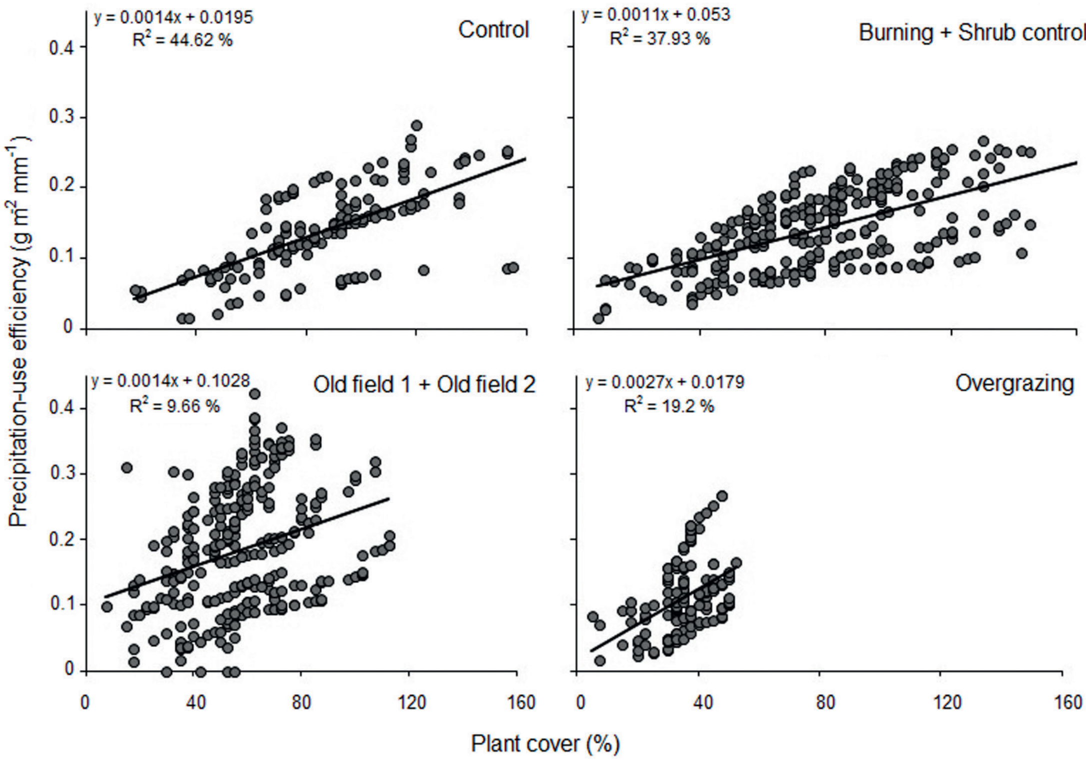

Fig. 5. Single linear regression analysis between % plant cover versus PUE (kg ha^{-1} mm^{-1}) at the various management kinds (Control, Burning, Old field 1, Old field 2, Overgrazing). Equality of regression lines was determined following Neter *et al.* (1985). When any two regression lines were equal (P> 0.05), their data were pooled and just one regression line was obtained (*e.g.* Burning+Shrub control). When regression lines were different (P <0.05), differences (or not) in their slopes were determined following Neter *et al.* (1985, see Table 3). Cover values were obtained from Giorgetti *et al.* (1999). Each symbol is the mean of n = 20. For any management kind, n = 140 (*i.e.* n = 20 × 7 study years: 1984 to 1990). All four regressions in Fig. 5 were significant at P = 0.000.

Plant Species

Nassella longiglumis and/or *P. ligularis* showed a higher (P <0.05) PUE than *N. tenuis*, *P. speciosa*, *A. ambigua* and *N. trichotoma* in the Control, Burning, and Shrub Control management kinds during 1984 to 1992 (Appendix). *Nassella tenuis*, on the other hand, showed the highest (P <0.05) PUE than the other five perennial grasses in 21 out of 27 comparisons in the Old Field 1, Old Field 2 and Overgrazing management kinds from 1984 to 1992 (Appendix). In these latest management kinds, *N. longiglumis* and *P. ligularis* showed a similar (P> 0.05) PUE than *P. speciosa*, *A. ambigua* and *N. trichotoma* in 24 out of 27 comparisons during all 9 study years (Appendix).

Plant cover *versus* precipitation – use efficiency

The regression lines were equal (P = 0.05) between the (1) Burning *versus* Shrub Control ($F^* \leq F_{table}$: 2.33 < 3.00), and (2) Old Fields 1 *versus* Old Field 2 ($F^* \leq F_{table}$: 2.29 < 3.00) management kinds. This allowed pooling of the data and obtainment of a single regression line for (1) or (2) (Fig. 5). Regression lines differed (P = 0.05) between the Control and Overgrazing management kinds ($F^* > F_{table}$: 18.7>3.00; Table 3, Fig. 5). These individual lines were different (P = 0.05) from those for the Burning + Shrub Control ($F^* > F_{table}$: 3.28 > 3.00 for Control, $F^* > F_{table}$: 11.56 > 3.0 for Overgrazing), or for the Old Fields 1 + 2 ($F^* > F_{table}$: 43.20 > 3.00 for Control, $F^* > F_{table}$: 9.90 > 3.00

Table 3. Slope comparison of management kind regression lines. Management kinds were as follows: C = Control; B = Burning; ShC = Shrub Control; OF1 = Old Field 1; OF2 = Old Field 2; O = Overgrazing. Old Field 1 was exposed to a more severe grazing than Old Field 2 by grazing livestock because of its greater proximity to water sources for animals. Following Neter *et al.* (1985), any two slopes were the same when the confidence interval covered $slope_1 - slope_2 = 0$; otherwise the two slopes were different. For calculation of t values, $P = 0.05$.

Slope comparison	Confidence interval
B+ShC *versus* OF1+OF2	-0.00076 ≤ slope difference= -0.00028 ≤ +0.00020
C *versus* B+ShC	-0.00906 ≤ +0.00025 ≤ +0.00956
C *versus* OF1+OF2	-1.97326 ≤ +0.00003 ≤ +1.97332
OF1+OF2 *versus* O	-0.00025 ≤ +0.00124 ≤ +0.00273
O versus C	-0.00218 ≤ -0.00127 ≤ -0.00036
O *versus* B+ShC	+0.00065 ≤ +0.00152 ≤ +0.00238

for Overgrazing) management kinds (Fig. 5).

Whenever two regression lines were different, it meant that they differed either in slope or intercept or both. Slopes were similar ($P > 0.05$) for the (1) Control versus (2) Burning + Shrub Control (Table 3) or *versus* (3) Old Fields 1 + 2 (Table 3). Slopes were also similar ($P > 0.05$) between the Overgrazing *versus* the Old Fields 1+2 management kinds, and between the Burning + Shrub Control *versus* the Old Fields 1+2 management kinds (Table 3). However, the Overgrazing management kind showed a greater ($P < 0.05$) slope than the (1) Control and (2) Burning + Shrub Control management kinds at low plant cover values (Table 3, Fig. 5).

DISCUSSION

Precipitation-use efficiency – Plant Functional Groups

One of the major factors leading to PUE differences within grasslands is plant basal cover (Wilcox *et al.* 2006). Plant cover was most often greater for cool-season perennial grasses [mean under all management kinds and years ± 1 SE (n = 42): 61.15±2.52%) than warm-season perennial grasses (7.12±1.92%) and cool-season annual grasses + dicots (9.28±1.57%). This might be a major reason why PUE was much greater on cool-season perennial grasses than on warm-season perennial grasses and cool-season annual grasses + dicots. Hartfield *et al.* (2001) and Nielsen *et al.* (2005) in agro-ecosystems, and Webb *et al.* (1983) in deserts reported that plant cover affects PUE through alterations in evapotranspiration rate. Anyhow, pastures must be established using cool- and warm-season grasses to maintain soil cover during the year and ensure plant persistence (Hannaway *et al.* 2000). Cool-season grasses could be utilized for fall, winter, and spring grazing and the warm-season grasses would flourish in the summer (Hannaway *et al.* 2000). Also, cool-season perennial grasses made their greatest contribution to total PUE because its total ANPP most often represented at least 50% than that in the warm-season perennial grasses and cool-season annual grasses + dicots in all management kinds and years (Fig. 3).

Burning, conducted in late summer-early fall, most likely favoured growth of the fall-winter-spring C_3 relatively more than that of the spring-summer C_4 perennial grasses. This might be because of various reasons which are as follows. Even though it is possible a decrease in the number of microorganisms immediately after burning, the heat and ashes can modify the soil chemical properties contributing to its recuperation until reaching levels much higher than those found on unburnt soils (Blair 1997). Fire might make soil more favourable to bacteria than fungi, possibly because of the increases of the soil pH and soluble sugars in the soil solution (Raison 1979). DeBano *et al*. (1998) mentioned that after an initial reduction immediately after fire, the number of nitrifying bacteria returned to normality within a week, increased ten times after a month, and reached its maximum level after 18 weeks. However, such number returned to its initial values after 48 weeks (DeBano *et al.* 1998). Additionally, the increase in the amount of ammonium in the soil, together with the alterations in the soil pH, temperature, microbial activity and reduction of allelopathic effects, might contribute to increase nitrification rates of soil nitrogen even more after fire (Kaye and Hart 1998). This is very important in arid and semiarid rangelands, where soil nitrogen is the most limiting factor for plant growth (Krueger-Mangold *et al.* 2004). Picone *et al.* (2006) showed that the increase in the nitrogen concentration after burning can be transitory because, at least in part, it is susceptible of having different losses in the soil. Other authors reported that the high ammonium levels in the soil generally persist during some months and then decline to reach the initial nitrogen levels one year after burning (Kaye 1999). The decline is mostly due to nitrogen losses because of the processes of nitrification, lixiviation, microbial immobilization and plant nitrogen uptake (Kaye 1999). Wan *et al.* (2001) additionally mentioned that it there exist a differential response between the soil ammonium and nitrate. Immediately after burning, the soil ammonium content is twice as much, and then there is a gradual decline up to reaching the initial values after a year. On the other hand, nitrate increase is small immediately after burning, values can be three times as much after six and twelve months, and a nitrate decline can be observed afterwards. Finally, other factors that can control the relative abundance of C_3 and C_4 grasses are the interaction between temperature and precipitation (Hannaway *et al.* 2000).

In agreement with recent studies, the contribution to PUE tended to decrease with decreases in annual precipitation on the cool-season perennial grass functional group in all management kinds (Bhandari *et al.* 2015, Jia *et al*. 2015; Fig. 3). Other authors have reported that ecosystems dominated by mesophytic grasses respond more strongly to precipitation than systems dominated by xerophytic grasses (Yang *et al.* 2010). Our results are also consistent with those of Bai *et al.* (2008) who reported that PUE tended to increase from deserts in the west to meadow steppes in the east on the Mongolia plateau. These authors reported that shoot productivity increases during wet years more than it declines in dry years; this was because soil water storage of the previous year´s precipitation was available in the subsequent dry year. The fact that drier sites tend to have lower PUE because of lower plant densities, lower production potential and high evaporation potentials was emphasized by Noy-Meir in 1973 and Grime in 1977. Our findings for the cool-season perennial grass functional group disagree, however, with those of Bhandari *et al.* (2015) who reported the lowest PUE (based on shoot- and total dry matter) in the wettest years. These authors reported that the general trend is that with a decrease in precipitation, there is a decrease in shoot dry matter, with subsequent increases in PUE during dry years. We found that after the two subsequent wettest years (*i.e.* 1984, 1985), the contribution to total PUE from the warm-season perennial grass or the cool-season annual grass + Dicots functional groups in a drier year (*i.e.* 1986) was management-type dependent (Fig. 3). For example, the contribution to total PUE of the cool-season annual grasses + Dicots appeared to be greater in the dry (1986 = 303.3 mm) than in the two previous wetter years (1984 = 877.3 mm; 1985 = 667.4 mm) only at the Old Fields management-types (Fig. 3).

Management kinds

Cool-season perennial grasses showed the lowest contribution to total PUE at the Old Field 2 than at (a) any management kind during 1984 to 1988, and 1991 and 1992, (b) the Control and Burning management kinds in 1989, and (c) the Shrub Control management kind in 1990. The warm-season perennial grasses showed the greatest contribution to total PUE at the Old Field 2 during 1984 to 1987, and during 1989 to 1992. These C_4, warm-season *Aristida*, un-preferred perennial grass species (Table 2) represented from

14 to 45% of total herbaceous standing crop during 1984-1992 at that management kind (Giorgetti *et al.* 1997). *Aristida* species may indicate rangeland overuse (Rúgolo *et al.* 2005). This indicates that the Old Field 2 management kind may have been exposed to severe grazing previous to cultivation.

Wedin and Tilman (1996) demonstrated that biomass of grasses with the C_4 photosynthetic pathway, as a proportion of aboveground live biomass at mid-growing season, reached 60% with no N addition at old fields in Minnesota grasslands. On the other hand, Reichhardt (1982) determined the successional trends of two old field sites, at least 43 years of age, in the shortgrass prairie of the Pawneee National Grasslands, northeastern Colorado. She reported that the frequency values for the C_4 perennial grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths ranged from 2% in old fields to 40–60% in an adjacent shortgrass prairie. In her work, although a weak trend toward convergence with the unplowed condition was evident, the successional process was slow, and likely to exceed 50 years if the unplowed condition was ever to be reached.

The highest contribution to total PUE for the cool-season annual grasses + dicots was at the Overgrazing and Old Field 1 management kinds in 1984, 1987, 1989, 1990 and 1992. Cool season annual grasses and forbs were also at the end of the grassland degradation gradient as a result of overgrazing in the state-and-transition model of Distel and Bóo (1996).

Contribution to total PUE was most often similar between the Shrub control (with herbicides) and the Old Field 1 management kind in the cool- and warm-season perennial grass groups within each year. It might be that mechanical treatments in the Old Field 1 were more effective in killing shrubs than perennial grasses in our study. Our results disagree with those of Morton *et al.* (1990). These authors showed that low shrub density and high forage production were more consistently achieved after herbicide application (tebuthiuron) than with mechanical treatments, because the most effective mechanical treatments not only destroyed shrubs but also perennial grasses. These authors concluded that forage production on semiarid grasslands (in northern Mexico and southwestern United States with shrub densities greater than 6,000 plants per ha and a remnant of perennial forage grasses) will increase after shrub removal.

The Old Field 2 management kind showed a similar (8 out of 9 comparisons) contribution to total PUE than the control in the cool-season annual grasses + Dicots management kind (Fig. 3). Mechanical treatments might have increased total forage production in rangelands (Griffith *et al.* 1985) because of the release of plant nutrients after soil disturbance (Haferkamp *et al.* 1993).

Contribution to total PUE by the annual grasses + Dicots was most often similar between the Overgrazing and Control management kinds (Fig. 3). However, the contribution to total PUE was greater in the Overgrazing than in the Control management kind during years where precipitation was below the long-term value (416.7 mm) (*i.e.* during 1986, 1989 and 1990). It is possible that during these drier years, greater open, nude spaces among vegetation patches because of overgrazing allowed a greater relative contribution to total PUE in the Overgrazing than in the Control management kind. It is well known that annual cool season and Dicots species might proliferate well in open spaces at the study region (Fresnillo Fedorenko *et al.* 1991).

In a later study at the same site than ours, Giorgetti *et al.* (2006) allowed to increase beef production using a rotational grazing system and other proper management guidelines rather than the overgrazing carried out by private land owners. These people, who do not know much about how to manage their rangelands properly, have a usual, traditional beef production on rangelands of about 8 pounds per acre (Giorgetti *et al.* 2006). This is considering an average stocking rate of 29.6 acres per animal unit, a weaning percentage of about 60%, and an average weight of 375 pounds of a 7–8-month-old weaned calf. In Argentina, an animal unit is defined as the annual average dry forage requirements of an 882-pound cow that goes through gestation and subsequent nursing of a calf, until the 353-pound, 6 month-old calf is weaned, including the forage consumed by the calf. In their study, Giorgetti *et al.* (2006) succeeded in increasing beef production from 7.6 to 20 pounds per acre per year, while at the same time reducing stocking rate from the traditional, abusive 12 to 15 cow equivalent per hectare to 7.8 cow equivalent per hectare. Their report was a good practical guideline for a more appropriate management and recovery of the preferred C_3 and C_4 perennial grasses (Table 2) on rangelands of east-central Argentina.

Plant species

The desirable, late-seral *N. longiglumis* and/or *P. ligularis* showed a greater or similar, but not lower, contribution to total PUE than the less desirable, earlier-seral species to grazing livestock *N. tenuis*, *P. speciosa*, and *A. ambigua* at the (a) Control, Burning and Shrub Control management kinds during 1984 to 1992, and (b) both Old Fields and the Overgrazing management kinds during 1984 to 1992. The greater competitive ability in *N. longiglumis* and *P. ligularis* than in the other species (Saint Pierre *et al.* 2004b, Moretto and Distel 1997, 1999) might contribute to explain this result. Differences in resource acquisition and competitive ability among species within the same plant community have been linked, for example, to the degree of association with arbuscular mycorrhiza, root nutrient uptake rate, and root length density (Caldwell 1994). All of these plant traits have been reported to be greater in *N. longiglumis* and/or *P. ligularis* than in *N. tenuis* and *A. ambigua* (Saint Pierre *et al.* 2004 a, c, Busso *et al*. 2008).

Most of the times, *N. tenuis* had a greater contribution to total PUE than *N. longiglumis*, *P. ligularis*, *P. speciosa*, and *A. ambigua* at both Old Fields and the Overgrazing management kinds during 1984–1992. Distel and Bóo (1996) showed that *N. tenuis* replaced *N. longiglumis* and *P. ligularis* at more advanced stages of grassland degradation as a result of overgrazing in the Phytogeographical Province of the Espinal in central Argentina.

Drought *versus* wet years

The similar precipitation-use efficiency in dry (from 257.5 to 408.8 mm annual precipitation) than wet years (from 437.6 to 877.3 mm annual precipitation) on all functional groups (Fig. 4) suggests that plant shoots most often did not reach a lethal relative water content during dry years. Flowers and Ludlow (1986) suggested that plant tissues die when they reach a lethal relative water content rather than a lethal, low water potential when exposed to water stress conditions.

A higher annual shoot biomass/a higher annual precipitation amount (*i.e*. PUE) during a wet year can equal a lower annual shoot biomass/a lower annual precipitation amount during a dry year. However, plants do need resistance mechanisms to keep growing, even slowly, under drought conditions. Whenever plant tissues die (or stop growing) because of water stress, they do not contribute anymore to ANPP, and thereafter production of annual shoot biomass should be reduced. If so, PUE will also be reduced. To keep growing under water stress conditions, even slower than under wet conditions, the study C_3 and C_4 perennial grass species need to have avoidance and/or tolerance (*i.e*. resistance) mechanisms. Hannaway *et al. (*2000) reported that despite use of water is less in C_4 than C_3 perennial grasses to make dry matter, yield production is lower in C_4 than C_3 perennial grasses; these authors emphasized that the virtue of C_4 perennial grass species is to provide superior midsummer grazing, when cool-season grasses are semi-dormant. Cenzano *et al.* (2013) suggested that *P. ligularis* and *P. speciosa* are able to maintain photosynthetic activity through the increase of photosynthetic pigments under drought conditions in Patagonian rangelands.

Plant cover *versus* PUE

At low percentage plant covers, a same change in percentage cover leaded to greater changes in PUE (*i.e.* greater slopes: Fig. 5) at the Overgrazing management kind. Within the desirable, C_3 perennial grasses, percentage contribution of *Piptochaetium napostaense* (Speg.) Hackel to total standing crop increased from 30.4±3.8% (1984) to 49.0±7.1% (1987), and then it was maintained above 44% in the Overgrazing management kind in this study (1998 to 1990) (Giorgetti *et al.* 1997). Leaf rolling, as a mechanism of water loss avoidance despite determining a decrease in photosynthesis at the same time (Kirkham 2005), appears to occurs earlier, and it appears to be greater, in this than in the other native perennial grasses (Busso C.A., Departamento de Agronomía UNS, personal communication). Turner (1986) reported that an earlier reduction in photosynthesis and water use may enable greater yields by conserving water for later plant developmental stages. Also, Dingkuhn *et al.* (1991) indicated that unrolling decreased instantaneous water-use efficiency on rice leaves.

The greater precipitation-use efficiencies at any percentage plant cover in the Old Field 1 + Old Field 2 management kinds than in any of the other treatments might have been due to the presence of C_4 perennial grass *Aristida* species within the plant community at the Old Field 2 (Giorgetti *et al.* 1997). These species, namely *A. pallens* Cav., *A. spegazzinii* Arechav., *A. subulata* Henrard and *A. trachyantha* Henrard, were exclusively restricted to this treatment (Giorgetti *et al.* 1997). They showed an average contribution from 14 to 45% to total herbaceous ANPP at the Old Field 2 (Giorgetti *et al.* 1997). Way *et al.* (2014) and Pearcy and Ehleringer (1984) reported a greater water-use efficiency and photosynthetic growth rate in C_4 than C_3 species.

PRACTICAL IMPLICATIONS

1. In most study years (1984 to 1992), contribution of each functional-type to total PUE (Fig. 3) was management-kind dependent. This emphasizes the importance of the previous-land history in determining the subsequent values for this study variable.
2. Cool-season perennial grasses made the greatest ($P < 0.05$) contribution to total PUE (Fig. 3) compared with those made by the other two functional groups in all management kinds and years.
3. In more than 44% of the study years, contribution of cool-season annual grasses + dicots to total PUE was greater ($P < 0.05$) at the Old Field 1 or Overgrazing than at any of the other management kinds (Fig. 3). This was most likely because of the creation of nude, un-vegetated patches as a result of abusive over-grazing in those management kinds. Legume production at these excessively overgrazed locations (*e.g. Medicago minima* (L.) Grufberg.) has been particularly high during wet years in similar arid to semiarid zones (see Fresnillo Fedorenko *et al.* 1991).
4. Precipitation-use efficiency was higher ($P < 0.05$) on the cool-season perennial grasses than on the warm-season perennial grasses and cool-season annual grasses + dicots under both wet and dry years. However, PUE was similar ($P > 0.05$) under wet versus dry years on any of the study functional groups. This suggests that plant shoots most often did not reach a lethal relative water content during the dry years (*e.g.* from 257.5 to 408.3 mm), and that plants might have shown resistance mechanisms to deal with water stress in those years.
5. The preferred *N. longiglumis* and *P. ligularis* showed a greater ($P < 0.05$) PUE than the intermediate *P. speciosa* and the non-preferred *A. ambigua* and *N. trichotoma* in 23 out of 27 comparisons among these species in the Control, Burning and Shrub Control management kinds. In the Old Field 1, Old Field 2 and Overgrazing management kinds, however, *N. longiglumis*, *P. ligularis*, *P. speciosa*, *A. ambigua* and *N. trichotoma* showed a similar ($P > 0.05$) PUE during 1984–1992 with only a few exceptions. These results indicate that PUE would most likely be greater in preferred (*e.g. N. longiglumis*, *P. ligularis*) than non-preferred (*e.g. A. ambigua*, *P. speciosa*) perennial grasses under good management conditions.
6. When total herbaceous plant cover from all study years was regressed against PUE values for those years, close, positive relationships were obtained between those variables in all management kinds.

REFERENCES

Bai Y.F., Wu J.G., Xing Q., Huang P.J., Yang D., Han X. 2008 – Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau – Ecology, 89: 2140–2153.

Bedunah D.J., Sosebee R.E. 1995 – Wildland plants. Physiological Ecology and Developmental morphology – Society for Range Management, Denver, USA, 710 pp.
Bertiller M.B. 1998 – Spatial patterns of the germinable soil seed bank in northern Patagonia – Seed Sci. Res. 8: 39–45.
Bhandari J., Pan X., Dhruba Bijaya G.C. 2015 – Spatial and seasonal variation in rain use efficiency in semiari grasslands of Inner Mongolia – Advances in Meteorology (in press), doi: http://dx.doi.org/10.1155/2015/917415.
Blair J.M. 1997 – Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis – Ecology, 78: 2359–2368.
Bóo R.M. 1990 – Algunos aspectos a considerar en el empleo del fuego – Rev. Fac. Agron. UNLPampa, 5: 63–80.
Braun-Blanquet J. 1979 – Fitosociología. Bases para el estudio de las comunidades vegetales – H. Blume Edic., Madrid, España, 820 pp.
Busso C.A. 1997 – Towards an increased and sustainable production in semiarid rangelands of Central Argentina: Two decades of research – J. Arid Environ. 36: 197–210.
Busso C.A., Bolletta A.I. 2010 – Biomass production, arbuscular mycorrhizae and soil plant-available P under water stress in native perennial grasses (In: Mycorrhizal Biotechnology, Eds: D. Thangadurai, C.A. Busso, M. Hijri) – Science Publishers and CRC Press, New York, pp: 56–76.
Busso C.A., Bolletta A.I., Flemmer A.C., Montani T. 2008 – Influence of field soil water status on arbuscular mycorrhiza in three semi-arid perennial grasses of different successional stages in rangelands of central Argentina – Ann. Bot. Fenn. 45: 435–447.
Busso C.A., Brevedan R.E., Flemmer A.C., Bolletta A.I. 2003 – Morphophysiological and demographic responses of perennial grasses to defoliation under water stress (In: Plant Physiology & Plant Molecular Biology in the New Millennium. Advances in Plant Physiology, Ed: A. Hemantaranjan) – Scientific Publishers, Jodhpur, pp: 341–395.
Cabrera A.L. 1976 – Regiones fitogeográficas Argentinas (In: Enciclopedia Argentina de Agricultura y Jardinería, Ed: E.F. Ferreira Sobral) – ACME, Buenos Aires, pp: 1–85.
Caldwell M.M. 1994 – Exploiting nutrients in fertile soil microsites (In: Exploitation of environmental heterogeneity by plants, Eds: M.M. Caldwell, R.W. Pearcy) – Academic Press, San Diego, pp: 325–347.
Caldwell M.M., White R.S., Moore R.T., Camp L.B. 1977 – Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species – Oecologia, 29: 275–300.
Cenzano A.M., Varela M.C., Bertiller M.B., Luna M.V. 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 – Aust. J. Bot. 61: 383–393.
Cleland E.E., Collins S.L., Dickson T.L., Farrer E.C., Gross K.L., Gherardi L.A., Hallett, L.M., Hobbs R.J., Hsu F.S., Turnbull L., Suding K.N. 2013 – Sensitivity of grassland plant community composition to spatial vs temporal variation in precipitation – Ecology, 94: 1687–1696.
Cramer V.A., Hobbs R.J., Standish R.J. 2008 – What´s new about old fields? Land abandonment and ecosystem assembly – Trends Ecol. Evol. 23: 104–112.
DeBano L.F., Neary D., Folliott P.F. 1998 – Fire's effects on ecosystems – John Wiley & Sons, New York, USA. 352 pp.
Digiuni D. 1983 – Métodos de desmonte y su impacto sobre el pastizal natural en el noroeste de Río Negro – Estación Experimental IDEVI, Serie Técnica 11: 1–73.
Dingkuhn M., Farquhar G.D., Datta S.K. De, O'Toole J.C., Datta S.K. 1991 – Discrimination of ^{13}C among upland rices having different water use efficiencies – Aust. J. Agric. Res. 42: 1123–1131.
Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M., Robledo C.W. 2013 – InfoStat. Universidad Nacional de Córdoba, Córdoba, Argentina.
Distel R.A., Bóo R.M. 1996 – Vegetation states and transitions in temperate semi-arid rangeland of Argentina (In: Proceedings of the Fifth International Rangeland Congress, Ed: N. West) – Society for Range Management, Denver, pp: 117–118.
Epstein H.E., Lauenroth W.K., Burke I.C., Coffin D.P. 1998 – Regional productivity patterns of plant species in the Great Plains of the United States – Plant Ecol. 134: 173–195.
Fernández, O.A., Busso C.A. 1999 – Arid and semi-arid rangelands: two thirds of Argentina. (In: Case Studies of Rangeland Desertification, Eds: O. Arnalds, S. Archer) – Agricultural Research Institute, Agricultural Research Institute Report Nro. 200, Reykjavik, Iceland. pp: 41–60.
Fernández O.A., Brevedan R.E., Laborde H., Klich M.G., Busso C.A. (in press) – Los territorios áridos y semiáridos de la Argentina. (In: Colección Lecturas de Cátedra de la Universidad Nacional de Río Negro, Ed: M.G. Klich) – Universidad Nacional de Rio Negro, Río Negro, Argentina. pp. 1–21.

Fernández R.J., Paruelo J.M. 1993 – Estepas arbustivo-graminosas de *Stipa* spp. del centro-oeste del Chubut (In: Secuencias de deterioro en distintos ambientes patagónicos. Su Caracterización mediante el modelo de estados y transiciones, Eds: J.M. Paruelo, M.B. Bertiller, T. Schlichter, F. Coronato) – Convenio Argentino-Alemán de Cooperación Técnica INTA-GTZ. Proyecto LUDEPA-SME, San Carlos de Bariloche, pp: 40–46.

Flowers D.J., Ludlow M.M. 1986 – Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeon pea (*Cajanus cajan* (L.) millsp.) leaves – Plant Cell Environ. 9: 33–40.

Fresnillo Fedorenko D.E., Fernández O.A., Busso C.A. 1991 – Forage production of the annual legume *Medicago minima* in semiarid rangelads of central Argentina – International Rangeland Congress, Montpellier, France, pp: 372–374.

Gartner F.R. 1988 – Improvements practices that increase range efficiency (In: Achieving Efficient use of Rangeland Resources, Eds: R.S. White, R.E. Short) – Montana Agriculture Experiment Station, Montana, pp: 86–91.

Giorgetti H.D., Busso C.A., Montenegro O.A., Rodríguez G.D., Kugler N.M. 2006 – Cattle raising in central, semiarid rangelands of Argentina – Rangelands, 28: 32–36.

Giorgetti H.D., Manuel Z., Montenegro O.A., Rodríguez G.D., Busso C.A. 2000 – Phenology of some herbaceous and woody species in central, semiarid Argentina – ΦYTON, Int. J. Exp. Bot. 69: 91–108.

Giorgetti H., Montenegro O.A., Rodríguez G., Busso C.A., Montani T., Burgos M.A., Flemmer A.C., Toribio M.B., Horvitz S.S. 1997 – The comparative influence of past management and rainfall on range herbaceous standing crop in east-central Argentina: 14 years of observations – J. Arid Environ. 36: 623–637.

Giorgetti H.D., Montenegro O.A., Rodríguez G.D., Busso C.A. 1999 – Influencia de manejos previos en la Provincia Fitogeográfica del Monte: Porcentaje de cobertura – Reunión de la Asociación Argentina de Ecología, 19: 100.

Griffith L.W., Schuman G.E., Rauzi F., Baumgartner R.E. 1985 – Mechanical renovation of shortgrass pairie for increased herbage production – J. Range Manage. 38: 7–10.

Grime J.P. 1977 – Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory – The Amer. Nat. 3: 1169–1194.

Haferkamp M.R., Volesky J.D., Borman M.M., Heitschmidt R.K., Currie P.O. 1993 – Effects of mechanical treatments and climatic factors on the productivity of Northern Great Plains rangelands – J. Range Manage. 46: 346–350.

Hannaway D.B., Teel M., Lane W., Griggs T. 2000 – Grass Growth and Regrowth for Improved Management – http://www.fsl.orst.edu/forages/projects/regrowth/main.cfm?PageID=4. Access date: 22 December 2015.

Hatfield J.L., Sauer T.J., Prueger J.H. 2001 – Managing soils to achieve greater water use efficiency: a review – Agronomy, 93: 271–280.

Hu Z.M., Yu G.R., Fan J.W., Zhong H.P., Wang S.Q., Li S.G. 2015 – Precipitation-use efficiency along a 4500- km grassland transect – Global Ecol. Biogeogr. 19: 842–851.

Hu Z.M., Yu G.R., Fu Y.L., Sun X.M., Li Y.N., Shi P.L., Wang Y.F., Zheng Z.M. 2008 – Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China – Glob. Change Biol. 14: 1609–1619.

Hulbert S.T. 1984 – Pseudo replication and the design of ecological field experiments – Ecol. Monog. 54: 187–211.

Jacoby P.W., Meadors C.H. 1982 – Control of sand shinnery oak (*Quercus havardii*) with pelleted picloram and tebuthiuron – Weed Sci. 30: 594–597.

Jia X., Xie B., Shao M., Zhao C. 2015 – Primary productivity and precipitation-use efficiency in temperate grasslands in the loess Plateau of China – Plos One, doi: 10.1371/journal.pone.o135490, 16 pp.

Kaye J.P. 1999 – Water and nutrient outflow following the ecological restoration of a ponderosa pine-bunchgrass ecosystem – Restor. Ecol. 7: 252–261.

Kaye J.P., Hart S.C. 1998 – Ecological restoration alters N transformations in a ponderosa pine-bunchgrass ecosystem – Ecol. Appl. 8: 1052–1060.

Kirkham M.B. 2005 – Principles of Soil and Plant Water Relations – Elsevier Inc., San Diego, USA. 500 pp.

Köhl L., Oehl F., van der Heijden M.G.A. 2014 – Agricultural practices indirectly influence plant productivity and ecosystem services through effects on soil biota – Ecol. Appl. 24: 1842–1853.

Krueger-Mangold J., Sheley R., Engel R., Jacobsen J., Svejcar T., Zabinski C. 2004 – Identification of the limiting resource within a semi-arid plant association – J. Arid Environ. 58: 309–320.

Le Houérou H.N. 1984 – Rain use efficiency: a unifying concept in arid-land ecology – J. Arid Environ. 7: 213–247.

Le Houérou H.N., Bingham R.L., Skerbek W. 1988 – Relationship between the variability of

primary production and the variability of annual precipitation in world arid lands – J. Arid Enrivon. 15: 1–18.
Martin S.C., Morton H.L. 1980 – Response of falsemesquite, native grass and forbs, and lovegrass after spraying with picloram – J. Range Manage. 35: 219–222.
Mazzarino M.J., Bertiller M.B., Sain C.L., Satti P., Coronato F.R. 1998 – Soil nitrogen dynamics in northern Patagonia steppe under different precipitation regimes – Plant Soil, 202: 125–131.
Moretto A.S., Distel R.A. 1997 – Competitive interactions between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina – Plant Ecol. 130: 155–161.
Moretto A.S., Distel R.A. 1999 – Effects of selective defoliation on the competitive interaction between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina – J. Arid Environ. 42: 167–175.
Morton H.L., Ibarra-F F.A., Martin-R M.H., Cox J.R. 1990 – Creosotebush control and forage production in the Chihuahuan and Sonoran Deserts – J. Range Manage. 43: 43–48.
Mueller-Dombois D., Ellenberg H. 1974 – Aims and Methods of Vegetation Ecology – New York, John Wiley & Sons. 547 pp.
Neter J., Wasserman W., Kutner M.H. 1985 – Applied Linear Statistical Models: regression, analysis of variance, and experimental designs – Homewood, R.D. Irwin, USA, 842 pp.
Nielsen D.C., Unger P.W., Miller P.R. 2005 – Efficient water use in dryland cropping Systems in the Great Plains – Agron. J. 97: 364–372.
Noy-Meir I. 1973 – Desert ecosystems: environment and producers – Ann. Rev. Ecol. Syst. 4: 25–51.
O'Connor T.G., Haines L.M., Snyman H.A. 2001 – Influence of precipitation and species composition on phytomass of a semi-arid African grassland – J. Ecol. 89: 850–860.
Páez A., Busso C.A., Montenegro O.A., Rodríguez G.D., Giorgetti H.D. 2005 – Seed weight variation and its effects on germination in *Stipa* species – ΦYTON, Int. J. Exp. Bot. 74: 1–14.
Pearcy R.W., Ehleringer J. 1984 – Comparative ecophysiology of C_3 and C_4 plants – Plant Cell Environ. 7: 1–13.
Peláez D.V., Bóo R.M., Mayor M.D. 2003 – El Fuego y la Vegetación del Sur del Caldenal. (In: Fuego en los Ecosistemas Argentinos, Eds: C.R. Kunst, S. Bravo, J.L. Panigatti) – Ediciones INTA, Buenos Aires, pp. 71–78.
Peláez D.V., Giorgetti H.D., Montenegro O.A., Elía O.R., Rodríguez G.R., Bóo R.M., Mayor M.D., Busso C.A. 2010 – Vegetation response to a controlled fire in the Phytogeographical Province of the Monte, Argentina – ΦYTON, Int. J. Exp. Bot. 79: 169–176.
Perelman S.B., León R.J.C, Bussacca J.P. 1997 – Floristic changes related to grazing intensity in a Patagonian shrub steppe – Ecography, 20: 400–406.
Picone L.I., Quaglia G, García F.O., Laterra P. 2006 – Biological and chemical response of a grassland soil to burning – J. Range Manage. 56: 291–297.
Prenger J.J., Ling P.P. 2015 – Greenhouse Condensation Control. Understanding and Using Vapor Pressure Deficit (VPD) – The Ohio State University Extension FactSheet Aex-804. Wooster, Ohio. 4 pp. (http://ohioline.osu.edu/aex-fact/pdf/0804.pdf).
Raison R.J. 1979 – Modification of the soil environment by vegetation fires, with particular reference to N transformations: a review – Plant Soil, 51: 73–108.
Reichhardt K.L. 1982 – Succession of abandoned field on the shortgrass prairie, northeastern Colorado – The Southwestern Nat. 27: 299–304.
Rúgolo de Agrasar Z.E., Steibel P.E., Troiani H.O. 2005 – Manual ilustrado de las gramíneas de la Provincia de La Pampa – Universidad Nacional de La Pampa, Universidad Nacional de Rio Cuarto, Santa Rosa. pp: 359.
Saint Pierre C., Busso C.A., Montenegro O.A., Rodríguez G.D., Giorgetti H.D., Montani T., Bravo O.A. 2002 – Root proliferation in perennial grasses of low and high palatability – Plant Ecol. 165: 161–169.
Saint Pierre C., Busso C.A., Montenegro O.A., Rodríguez G.D., Giorgetti H.D., Montani T., Bravo O.A. 2004a – Defoliation tolerance and ammonium uptake rate in perennial tussock grasses – J. Range Manage. 57: 82–88.
Saint Pierre C., Busso C.A., Montenegro O.A., Rodríguez G.D., Giorgetti H.D., Montani T., Bravo O. 2004b – Direct assessment of competitive ability and defoliation tolerance in perennial grasses – Can. J. Plant Sci. 84: 195–204.
Saint Pierre C., Busso C.A., Montenegro O.A., Rodríguez G.D., Giorgetti H.D., Montani T., Bravo O.A. 2004c – Soil resource acquisition mechanisms, nutrient concentrations and growth in perennial grasses – Interciencia, 29: 303–311.
Sala O.E. 1988 – The effect of herbivory on vegetation structure (In: Plant form and vegetation structure, Eds: M.J.A. Werger, P.J.M. van der Aart, H.J. During, J.T.A. Verhoeven) – Academic Publishing, Verboeven, pp: 317–330.
Sala O.E., Lauenroth W.K. 1982 – Small rainfall events: an ecological role in semiarid regions – Oecologia, 53: 301–304.

Singh J.S., Lauenroth W.K., Steinhorst R.K. 1975 – Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data – Bot. Rev. 41: 181–232.

Tan W., Wang G., Han J., Liu M., Zhou L., Luo T., Cao Z., Cheng S. 2009 – δ^{13}C and water-use efficiency indicated by δ^{13}C of different plant functional groups on Changbai Mountains, Northeast China – Chin. Sci. Bull. 54: 1759–1764.

Torres Y.A., Busso C.A., Montenegro O.A., Ithurrart L., Giorgetti H., Rodríguez G., Bentivegna D., Brevedan R., Fernández O., Mujica M.M., Baioni S., Entío J., Fioretti M., Tucat G. 2013 – Plant growth and survival of five perennial grass genotypes exposed to various defoliation managements in arid Argentina – Grass For. Sci. 69: 580–595.

Trewin D. 2006 – Year Book Australia – Australian Bureau of Statistics, Canberra, Australia.

Turner N.C. 1986 – Adaptation to water deficits: a changing perspective – Aust. J. Plant Physiol. 13: 175–190.

Vallentine J.F. 1990 – Grazing management – Academic Press, San Diego, USA. 545 pp.

Vermeire L.T., Heithschmidt R.K., Rinella M.J. 2009 – Primary productivity and precipitation-use efficiency in mixed grass prairie: A comparison of Northern and Southern US sites – Rangeland Ecol. Manage. 62: 230–239.

Wan S., Hui D., Luo Y. 2001 – Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis – Ecol. Appl. 11: 1349–1365.

Wang L., Caylor K.K., Villegas J.C., Barron-Gafford G.A., Breshears D.D., Huxman T.E. 2010 – Partitioning evapotranspiration across gradients of woody plant cover: Assessment of a stable isotope technique – Geophysical Research Letters 37: http://onlinelibrary.wiley.com/doi/10.1029/2010GL043228/full.

Way D.A., Katul G.G., Manzoni S., Vico G. 2014 – Increasing water use efficiency along the C_3 to C_4 evolutionary pathway: a stomatal optimization perspective – J. Exp. Bot. 65: 3683–3693.

Webb W.L., Lauenroth W.K., Szarek S.R., Kinerson R.S. 1983 – Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States – Ecology, 64: 134–151.

Wedin D.A., Tilman D. 1996 – Influence of nitrogen loading and species composition on the carbon balance of grasslands – Science, 274: 1720–1723.

Wight J.R., Black A.L. 1972 – Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains – J. Range Manage. 25: 376–380.

Wilcox B.P., Dowhower S.L., Teague W.R., Thurow T.L. 2006 – Long-term water balance in a semiarid shrubland – Range. Ecol. Manage. 59: 600–606.

Wilks S.S. 1932 – Certain generalizations in the analysis of variance – Biometrika, 24: 471–494.

Winslow J.C., Hunt E.R., Piper S.C. 2003 – The influence of seasonal water availability on global C_3 versus C_4 grassland biomass and its implications for climate change research – Ecol. Model. 163: 153–173.

Yang Y., Fang J., Fay A., Bell J.E., Ji C. 2010 – Rain use efficiency across a precipitation gradient on the Tibetean Plateau – Geophys. Res. Lett. 37, 5 pp. doi: 10.1029/2010GL043920

Appendix. Contribution (%) to total precipitation-use efficiency (PUE; g m^{-2} mm^{-1}) of various perennial grass species on different management kinds from 1984 to 1992. Each value represents the mean±1 S.E. of n = 30. Different letters indicate significant differences ($P < 0.05$) among plant species within each management kind and study year. Plant species are Nt = *Nassella tenuis*; Nl = *Nassella longiglumis*; Pl = *Poa ligularis*; Ps = *Pappostipa speciosa*; Aa = *Amelichloa ambigua*; Ntr = *Nassella trichotoma*. Management kinds are C = Control; B = Burning; Sc = Shrub Control; OF1 = Old Field 1; OF2 = Old Field 2; O = Overgrazing.

	Species	1984	1985	1986	1987	1988	1989	1990	1991	1992
C	Nt	0.03±0.01 b	0.05±0.01 b	0.06±0.01 c	0.06±0.01 c	0.04±0.01 b	0.04±0.01 b	0.05±0.01 b	0.07±0.01 b	0.04±0.01 b
	Nl	0.07±0.01 c	0.08±0.01 c	0.04±0.01 bc	0.04± 0.01 bc	0.08±0.01 c	0.04±0.01 b	0.06±0.01 b	0.07±0.01 b	0.06±0.01 b
	Pl	0.04±0.01 b	0.03±0.01 b	0.03±0.01 b	0.02±0.01 ab	0.04±0.01 b	0.04±0.01 b	0.05±0.01 b	0.04±0.01 b	0.04±0.01 b
	Ps	1.2E-03±0.01 a	3.4E-04±0.01 a	2.2E-04±0.01 a	0.00±0.00 a	9.7E-04±0.01 a	0.00±0.00 a	6.3E-04±0.0 a	4.8E-03±0.01 a	3.2E-04±0.01 a
	Aa	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Ntr	1.5E-04±0.01 a	1.2E-03±0.01 a	3.1E-04±0.01 a	7.0E-04±0.01 a	1.9E-03±0.01 a	2.6E-03±0.01 a	1.6E-03±0.01 a	2.9E-03±0.01 a	9.1E-04±0.01 a
B	Nt	0.03±3.8E-03 b	0.04±4.2E-03 b	0.04±4.8E-03 b	0.02±0.01 ab	0.02±0.01 a	0.01±0.01 ab	0.01±0.01 a	0.02±0.01 a	0.01±0.01 a
	Nl	0.05±3.8E-03 c	0.06±4.2E-03 c	0.05±4.8E-03 b	0.08±0.01 c	0.07±0.01 b	0.03±0.01 bc	0.04±0.01 b	0.06±0.01 b	0.05±0.01 b
	Pl	0.03±3.8E-03 b	0.03±4.2E-03 b	0.04±4.8E-03 b	0.04±0.01 b	0.06±0.01 b	0.04±0.01 c	0.07±0.01 c	0.06±0.01 b	0.06±0.01 b
	Ps	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.01±0.01 a
	Aa	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.01±0.01 a
	Ntr	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.01±0.01 a
Sc	Nt	0.01±4.2E-03 a	0.03±4.9E-03 b	0.03±0.01 b	0.02±0.01 ab	0.01±0.01 ab	0.01±3.7E-03 a	0.01±0.01 a	0.01±0.01 ab	0.01±0.01 ab
	Nl	0.04±4.2E-03 b	0.05±4.9E-03 bc	0.04±0.01 bc	0.04±0.01 bc	0.04±0.01 b	0.01±3.7E-03 a	0.02±0.01 a	0.04±0.01 b	0.03±0.01 b
	Pl	0.05±4.2E-03 b	0.05±4.9E-03 c	0.05±0.01 c	0.07±0.01 c	0.08±0.01 c	0.05±3.7E-03 b	0.11±0.01 b	0.12±0.01 c	0.07±0.01 c
	Ps	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Aa	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Ntr	3.7E-03±4.2E-03 a	0.00±0.00 a	1.4E-03±0.01 a	1.8E-03±0.01 a	3.1E-03±0.01 a	2.5E-03±3.7E-03 a	1.4E-03±0.01 a	3.1E-03±0.01 a	3.1E-03±0.01 a

	Species	1984	1985	1986	1987	1988	1989	1990	1991	1992
OF 1	Nt	0.09±0.01 c	0.16±0.01 b	0.11±0.01 b	0.12±0.01 b	0.10±0.01 b	0.05±0.01 b	0.07±0.01 b	0.14±0.01 b	0.07±0.01 b
	Nl	0.01±0.01 a	0.02±0.01 a	0.02±0.01 a	0.03±0.01 a	0.04±0.01 a	0.01±0.01 a	0.02±0.01 ab	0.04±0.01 a	0.03±0.01 a
	Pl	0.01±0.01 a	0.01±0.01 a	0.02±0.01 a	0.02±0.01 a	0.03±0.01 a	0.01±0.01 a	0.02±0.01 ab	0.06±0.01 a	0.03±0.01 a
	Ps	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Aa	0.05±0.01 b	0.04±0.00 a	0.02±0.01 a	0.04±0.01 a	0.01±0.01 a	0.01±0.01 a	0.05±0.01 ab	0.00±0.00 a	0.00±0.00 a
	Ntr	0.00±0.00 a	0.00±0.00 a	8.8E-04±0.01 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
OF 2	Nt	0.08±4.0E-03 b	0.09±0.01 b	0.06±4.4E-03 b	0.08±0.01 b	0.06±0.01 b	0.09±0.01 b	0.13±0.01 b	0.16±0.01 c	0.06±0.01 b
	Nl	4.6E-03±4.0E-03 a	0.01±0.01 a	0.01±4.4E-03 a	0.01±0.01 a	0.02±0.01 a	0.01±0.01 a	0.02±0.01 a	0.06±0.01 b	0.04±0.01 b
	Pl	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	1.0E-03±0.01 a	4.5E-03±0.01 a	4.7E-03±0.01 a
	Ps	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Aa	2.7E-04±4.0E-03 a	0.00±0.00 a	1.2E-04±4.4E-03 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Ntr	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
O	Nt	0.03±1.9E-03 c	0.04±4.4E-03 b	0.03±3.3E-03 b	0.03±3.4E-03 b	0.01±2.9E-03 a	4.7E-03 ±1.1E-03b b	0.01±4.4E-03 a	0.01±4.0E-03 a	0.03±0.01 b
	Nl	0.01±1.9E-03 b	0.01±4.4E-03 a	0.01±3.3E-03 a	0.01±3.4E-03 a	0.01±2.9E-03 a	3.9E-03±1.1E-03 b ab	0.01±4.4E-03 a	0.01±4.0E-03 a	0.01±0.01 ab
	Pl	1.8E-03±1.9E-03a aab	1.6E-03±4.4E-03 a	4.4E-03±3.3E-03 a	3.2E-03±3.4E-03 a	0.01±2.9E-03 a	1.8E-03±1.1E-03 a ab	0.01±4.4E-03 a	0.01±4.0E-03 a	0.01±0.01 ab
	Ps	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	3.2E-03±3.4E-03 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Aa	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
	Ntr	4.1E-03±1.9E-03 a	0.01±4.4E-03 a	2.0E-03±3.3E-03 a	0.00±0.00 a	1.0E-03±2.9E-03 a	0.00±0.00 a	2.2E-03±4.4E-03 a	0.00±0.00 a	2.7E-03±0.01 ab