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Soil Phosphorus Concentration under the Canopy of Perennial Grasses of Different Successional Stages Exposed to Water Stress

Carlos A. Busso[1] **and Andrea I. Bolletta**[2]

[1]Agronomy Department and Center for Renewable Resources of the Semiarid
Region (CER205-CONICET), National University of the South,
Bahía Blanca, Argentina
[2]National Institute of Agropecuarian Technology (INTA), Agropecuarian
Experimental Station (EEA), Bordenave, Argentina

Abstract: In this field study, the effects of water-stress, rainfed, or irrigated conditions on soil phosphorus (P) concentration under the canopy of the native grasses of semi-arid Argentina (late seral *Stipa clarazii* Ball., early serals *S. tenuis* Phil., and *S. gynerioides* Wild. Ex Steud) at different developmental stages and sampling dates during 1996 and 1997 were determined. Plants grew in a uniform matrix such that each plant of *S. clarazii* and *S. tenuis* was surrounded by four plants of *S. gynerioides*. In September 1996, Bray and Kurtz extracted soil P concentrations were greater under plants of *S. clarazii* if water stress was imposed during the vegetative stage than under rainfed conditions. Bray and Kurtz extracted soil P concentrations were either similar or between 8.7 to 31% greater under plants of *S. clarazii* than under those of the other two species. The higher nutrient concentration under *S. clarazii* than under *S. gynerioides* and *S. tenuis* may explain previously measured increases in density, frequency, and cover throughout a long-term span (years) in the late over the earlier seral perennial grasses under field exclosures to domestic livestock or appropriate grazing management conditions.

Keywords: Developmental stages, perennial grasses, semi-arid Argentina, soil water regimes, successional stages, temperate

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Address correspondence to Carlos A. Busso, Departamento de Agronomía-CERZOS, UNSur, 8000 Bahía Blanca, Argentina. E-mail: cebusso@criba.edu.ar

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INTRODUCTION

The effect of soil water has been studied on soil phosphorus (P) availability and its uptake by plants (Jupp and Newman 1987). Soil P uptake and transport have been reduced in plants if soil water content decreased (Fawcett and Quirk 1962; Mouat and Nes 1986). A reduction in plant growth rate and root length density under water-stress conditions suppressed plant P uptake (Barber et al. 1988). As a result, soil P concentration will increase as its soil water content decreases (Holdford 1979). Soil water content directly influences soil nutrient availability for plants and in turn ultimately will affect plant growth (Millar 1955; Hsiao 1973).

Decomposition of dead plant material is a fundamental process in ecosystem functioning, because it is a major determinant of nutrient cycling. This process is regulated by abiotic (water, temperature) and biotic (composition of soil detritus communities, plant matter quality) factors (Swift, Heal, and Anderson 1979). Chemical composition of organic matter, in particular, exerts a high degree of control in the decomposition process. The greater the carbon (C)–nitrogen (N) ratio and lignin concentration, the lower the decomposition and mineralization rates of the young organic matter (Hobbie 1992; Van Vuuren, Berendse, and De Visser 1993; Berendse 1994; Couteaux, Bottner, and Berg 1995; Grime et al. 1996). The high persistence of low-palatability grasses in rangelands throughout the world also is related with their low-quality litter. This action is because poor quality of litter delays nutrient cycling and soil nutrient availability (Archer and Smeins 1991; Berendse 1994; Jones, Lawton, and Shachak 1994; Aerts 1995; Wedin 1995). Litter and root decomposition were faster in the late seral, palatable perennial grasses *Poa ligularis* and *Stipa clarazii* (low C:N ratio) than in the early seral, unpalatable perennial grasses *S. gynerioides* and *S. tenuissima* (high C:N ratio) under rainfed, semi-arid conditions (Moretto and Distel 2000, 2003; Moretto, Distel, and Didoné 2001). Root decomposition, a major input of organic matter in the soil system, was faster in *Stipa clarazii* than in *Poa ligularis* Nees ap. Steud. (Moretto, Distel, and Didoné 2001). Furthermore, nutrient net mineralization was higher in late than early seral perennial grasses (Moretto and Distel 2003).

Rangeland perennial grasses often are exposed to water stress in the southern part of the Monte district (Monte), a phytogeographical region of approximately 50 million ha in Argentina (Fernández and Busso 1999). Cattle raising on natural vegetation is the most important economical activity in this region (Busso 1997). *Stipa clarazii*, *S. tenuis*, and *S. gynerioides* were chosen for this study because they are abundant in the semi-arid rangelands of the Monte under different management regimes and because they are representative of different successional stages. All three perennial grasses are C_3 species, which vegetate during autumn and winter (Cano 1988). If water is available all year around, tillering will extend to spring and summer (Giorgetti et al. 2000). At the beginning of spring (late September), the vegetative apex differentiates into reproductive and internode elongation occurs, and by early October (early spring) plants can be in the boot stage. Flowering can occur by mid- to late October, and seeds are formed in November and dispersed in December. Aboveground shoots die, and the plants remain in a dormant stage during summer (late December–late February), unless soil water content is high at this time (Giorgetti et al. 2000). Root growth remains unabated during the whole year under rainfed conditions (Busso et al. 2003). *Stipa clarazii* is a late seral, palatable, dominant, and highly competitive species under exclosure or light grazing conditions (Saint Pierre et al. 2004). Under moderate grazing, this species is replaced by the palatable, comparatively earlier seral *S. tenuis*. Selective grazing of both species produce their replacement by another less competitive, unpalatable, early seral species: *S. gynerioides* (Saint Pierre et al. 2004).

Two hypotheses were tested in this study: 1) Bray and Kurtz extracted soil P increases when soil moisture content decreases (Bray and Kurtz 1945), and 2) Bray and Kurtz extracted soil P is greater under the canopy of the late seral, palatable *S. clarazii* than under that of *S. gynerioides* or *S. tenuis* under all soil water levels. The objective of this research was to determine the effects of various soil water contents (water stress, rainfed, or irrigated conditions) on Bray and Kurtz extracted soil P under the canopies of *S. clarazii* and *S. tenuis*, in competition with plants of *S. gynerioides*.

MATERIALS AND METHODS

Study Area

Studies were conducted at the research site nearby the Departamento de Agronomía–CERZOS in Bahía Blanca (38° 48′ S, 62° 13′ W). Soil is a typical Haplustoll with a petrocalcic horizon at 1.8 m deep. It has a sandy loam texture, 1.9% organic matter, 7 mg extractable P kg^{-1} (Olsen and Sommers 1982), and 0.10% total N and has a pH of 7.4. Climate information during the study period was provided through a meteorological station located at the research site. Rainfall levels in the different water levels are presented in Figure 1.

Experimental Design

Between December 1993 (summer) and April 1994 (fall), 28 experimental plots (1.8 × 1.8 m) were established in the field on unplowed, weeded extend to spring and summer (Giorgetti et al. 2000). At the beginning of spring (late September), the vegetative apex differentiates into reproductive and internode elongation occurs, and by early October (early spring) plants can be in the boot stage. Flowering can occur by mid- to late October, and seeds are formed in November and dispersed in December. Aboveground shoots die, and the plants remain in a dormant stage during summer (late December–late February), unless soil water content is high at this time (Giorgetti et al. 2000). Root growth remains unabated during the whole year under rainfed conditions (Busso et al. 2003). *Stipa clarazii* is a late seral, palatable, dominant, and highly competitive species under exclosure or light grazing conditions (Saint Pierre et al. 2004). Under moderate grazing, this species is replaced by the palatable, comparatively earlier seral *S. tenuis*. Selective grazing of both species produce their replacement by another less competitive, unpalatable, early seral species: *S. gynerioides* (Saint Pierre et al. 2004).

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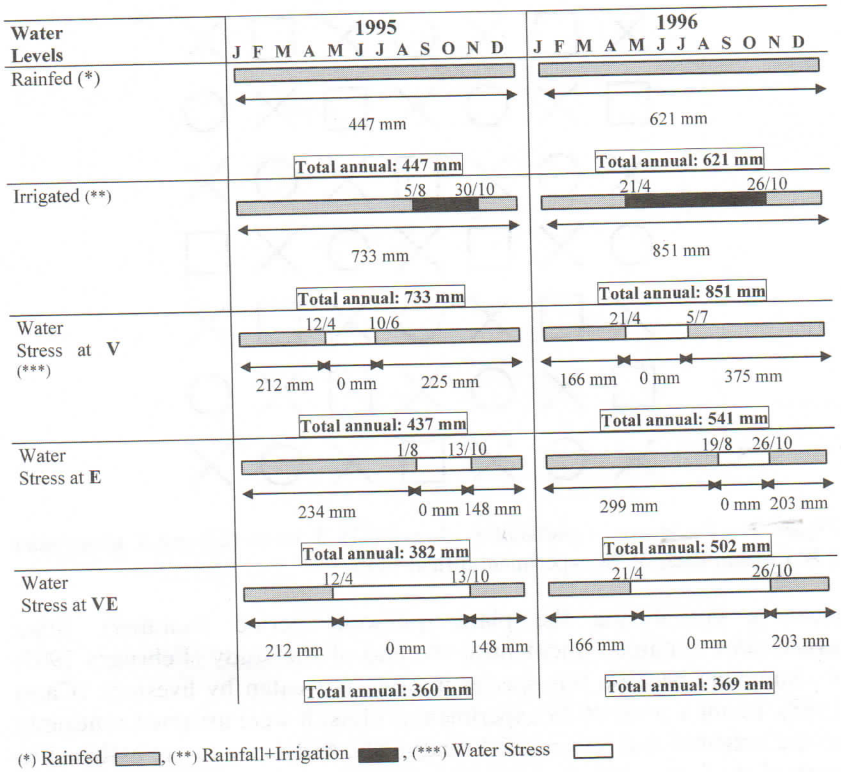

Figure 1. Periods of imposition of the different water levels (Rainfed, Irrigated or Water-stressed) at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996. Numbers below horizontal, bold lines are water fallen during each water level treatment. Numbers above horizontal histograms (day/month) indicate initiation and finalization of a specific water level treatment.

soil. Plants were obtained from a 20-year exclosure to domestic animals located southeast of La Pampa Province (38° 45′ S, 63° 45′ W). Within each plot, transplants were placed 30 cm apart from one another in seven horizontal and vertical rows such that each plant of *S. clarazii* or *S. tenuis* was surrounded by four plants of *S. gynerioides* (Figure 2). Disposition of plants within a uniform matrix contributes to reduce potentially confounding effects on plant responses as a result of plant competition. A total of 1372 transplants were used for the whole study. Crown-level plant diameters ($n = 56$) were similar among species at time of transplanting: 13.47 ± 0.56 cm (mean ± 1 SE) for *S. clarazii*, 10.02 ± 0.51 cm for *S. tenuis*, and 12.27 ± 0.61 cm for *S. gynerioides*.

All tussocks of *S. clarazii* and *S. tenuis* were hand-clipped to a 5-cm stubble height in January 1995 and 28 December 1996 to produce a

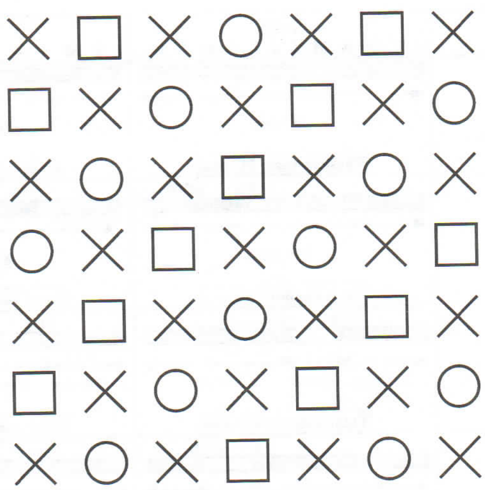

Figure 2. Placement of plants of *S. clarazii* (○), *S. tenuis* (□) and *S. gynerioides* (✕) within each of 28 experimental field plots.

cleaning cut during the plant quiescent period (summer). *Stipa gynerioides* remained uncut until the end of the study (February 1997; midsummer) because this species is often not eaten by livestock (Cano 1988). From a total of 28 experimental plots, 8 were assigned randomly to the irrigated and 8 to rainfed treatments, and 4 plots were assigned to each of the water-stress treatments (vegetative, internode elongation, and vegetative plus internode elongation).

Water Levels

Plants were exposed to rainfed, irrigated, or water-stress conditions. Rainfed plots received rainfall all year around (Figure 1). A drip-irrigation system watered the irrigated plots, which were additionally rainfed. Soil tensiometers installed in the irrigated plots allowed watering of these plots to saturation to 50 cm deep whenever they reach 60% of field capacity. Periods of irrigation and imposition of water stress during 1995 and 1996 are depicted in Figure 1. Transparent plastic sheets covered the water-stressed plots whenever rain fell (Busso 1997) during vegetative or early internode elongation or both phenological periods (Figure 1). Water-stressed plots were surrounded with plastic sheets up to the 1.8-m soil depth to prevent lateral movement of water into these plots.

All 28 experimental plots received natural rainfall (313.7 mm from mid-October 1995 to late April 1996, and 487.8 mm from late October 1996 to March 1997) when water treatments were not imposed. Water stress was thus alleviated from water-stressed plots during these periods.

Sampling Procedures

Leaf water potentials were periodically determined at midday in all treatments to provide a measure of plant water status during the study period. Measurements were done using a pressure chamber on sunny days only between noon and 1 PM. Youngest, fully expanded leaf blades were taken for these measurements using one tiller per species within each replicate plot and sampling date. From excision to end of each determination, leaves were cut one at a time and maintained in a plastic bag to reduce water loss (Turner 1987).

A total of 460 soil samples were obtained between 0–15 cm deep using a soil corer (8.4 cm in diameter, 15 cm high; 831.3 cm^3 volume) during 1996 and early 1997. Soil P concentrations at the outset of the experiment (1995) were not determined because of financial constraints at that time. We recognize that this limits use of measured soil P data. However, during the study period (1996–early 1997), samplings for soil Bray and Kurtz extracted P determinations were not only conducted under water stress and irrigated but also rainfed conditions, which provided an untreated control.

Samples were obtained diagonally from the plant periphery to the plant center to assure that sampled soil corresponded to the sampled plant. One plant of each species was used per replicate at each sampling date. Bray and Kurtz extracted soil P was determined following Olsen and Sommers (1982). Soil was air dried and then screened through a mesh of 0.5 mm, and 2.5-g soil samples were weighed. This sample was placed within a tube, which contained 20 mL of Bray and Kurtz extractant. The tube was agitated for 5 min at 190 agitations per minute. Contents of the tube were filtered, and P was determined by colorimetry (UV-visible recording spectrophotometer, UV-2100, Shimadzu Corporation, Tokyo, Japan; Bray and Kurtz 1945).

Statistical Analysis

Leaf water potential data were analyzed separately for each date using analysis of variance (ANOVA). A split-plot design was considered with this purpose using treatments (water levels) as main factor and species as secondary factor. When the interaction term was not significant ($P \geqslant 0.09$) on any sampling date and whenever the treatment factor was significant ($P < 0.05$), two-way ANOVAs were subsequently performed. Differences among water-level treatments were tested using general linear model (GLM) procedures because data came from 8 replicates for the rainfed and irrigated plots and from 4 replicates for the water-stressed plots.

At first, soil P concentration data were analyzed using a three-way split plot ANOVA [5 water levels × 3 species × 5 sampling dates: April (fall), June (winter), September (early spring), October (spring) 1996, and February (summer) 1997]. Soil water levels acted as main factors, applied to randomly distributed plots, in a proportional but unbalanced manner. Eight replicates were used for the irrigation and rainfed treatments, and four replicates were utilized for each of the water-stress treatments (vegetative, internode elongation, vegetative plus internode elongation). Plants of the three species were within each plot, assigning one plant of each species for analysis at each sampling date. Secondary factors were sampling dates and species. Within each plot, plants were assigned for sampling previous to the sampling dates. This procedure allowed avoiding measurements of soil Bray and Kurtz extracted P corresponding to nearby plants previously sampled. However, this rigid scheme did not allow replacement of lost plants (i.e., plants that died as a result of treatment application) during the study. Because of this (cf. Flemmer et al. 2003), it was necessary to adapt the statistical analysis when the loss of sampling units resulted in an unbalanced not proportional distribution among the species within each plot. This phenomenon mainly occurred in June and September.

In this way, we have design 1 using a three-way ANOVA for those months where information was complete: April, October, and February. Months with missing data (June and September) were analyzed with design 2: a split-plot two-way ANOVA with the same main factor (soil water levels) and a unique secondary factor (the species). Uncompleted plots, which lack information on the three species, were eliminated to apply this analysis, leaving an unbalanced, proportional design. Interactions were analyzed to evaluate the effects of water levels, dates, and species. Means were compared with Fisher's protected least significant difference (LSD) at 5% when the F test indicated that the variables differed at that significance level (Steel and Torrie 1981).

RESULTS

Leaf Water Potentials

Leaf water potentials were similar among water levels in all three species at the beginning and end of each growing cycle (Figure 3). Plants of all three species, however, had lower ($P < 0.05$) leaf water potentials under water stress than under irrigated conditions during August–October 1995 (Figure 3). Results were similar in 1996, when leaf water potentials were generally lower on water-stressed than on irrigated plants (Figure 3). Leaf water potentials were more variable on plants in the rainfed plots. Under these conditions, leaf water potentials appeared lower than those in the

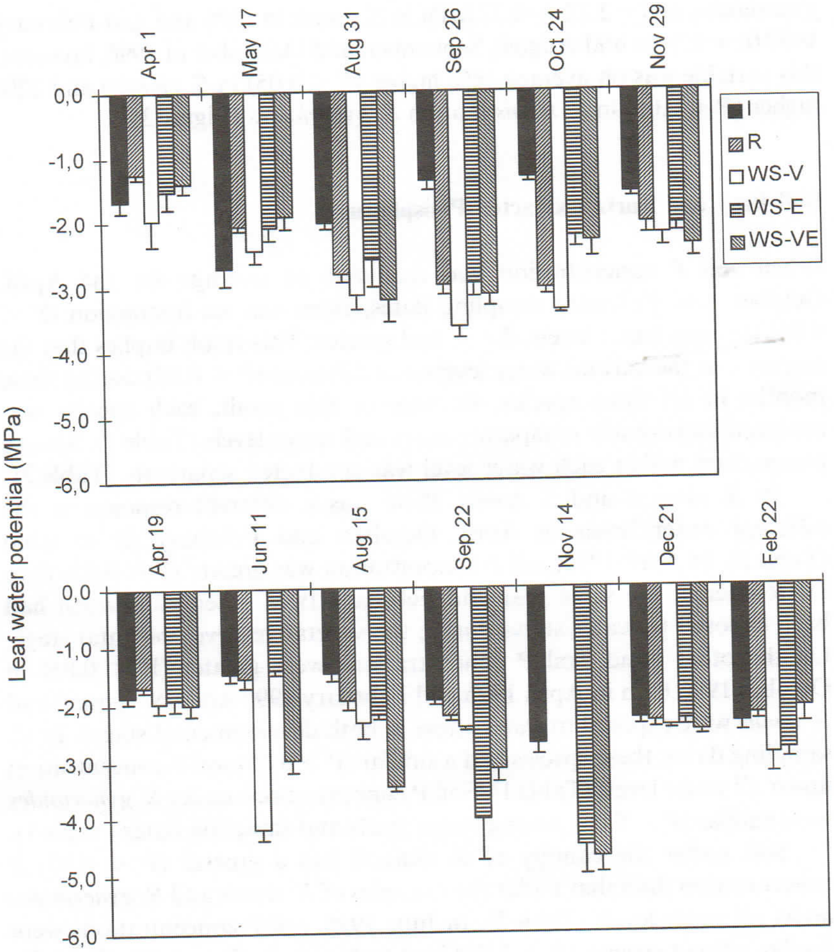

Figure 3. Mid-day leaf water potential of plants of *S. clarazii* and *S. tenuis*, and *S. gynerioides* that were exposed to irrigated (I), rainfed (R) or water stress (WS) conditions at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 (A) and 1996 (B). Difference between all three species were not significant, and therefore for species data were averaged into water level treatments and into dates. There were not date x water level treatment x species and water level treatment x species interactions. Each histogram is an average of n=4 to 8. Vertical bars represent 1 S.E. of the means.

irrigated plots in 1995 and higher than those in the water-stressed plots in 1996 (Figure 3).

During the study period, overall leaf water potentials were similar among species. They were (mean ± 1 SD) −2.23 ± 0.87 MPa in *S. clarazii*, −2.20 ± 0.83 MPa in *S. gynerioides*, and −2.24 ± 0.69 MPa in *S. tenuis* in 1995 ($n = 83$) and −2.38 ± 0.92 MPa in *S. clarazii*, −2.49 ± 0.94 MPa in *S.*

gynerioides, and -2.22 ± 0.77 MPa in *S. tenuis* in 1996 and mid-February 1997 ($n = 92$). In mid-August, September, and December of 1996, however, this variable was on average 16% higher ($P < 0.05$) in *S. clarazii* and 22% higher ($P < 0.05$) in *S. tenuis* than in *S. gynerioides* (Figure 3).

Soil Bray and Kurtz Extracted Phosphorus

When soil P concentration was analyzed on average for the April, October, and February sampling dates, there was an interaction ($P < 0.05$) between water levels, dates, and species. This result implies that the response in the various water levels was different ($P < 0.05$) during these months in all three species. Because of this result, each species was analyzed individually comparing dates and water levels (Table 1). Species comparison within each water level was conducted separately (Table 2).

In *S. clarazii* and *S. tenuis*, there was a different response in the different water levels in April, October, and February ($P < 0.05$) (Table 1). In April 1996, soil P concentration was greater ($P < 0.05$) than in October of the same year and February 1997, where *S. clarazii* had been exposed to water stress during the vegetative developmental stage. On the other hand, soil P concentrations were greater ($P < 0.05$) in October 1996 than in April 1996 and February 1997 when *S. clarazii* and *S. tenuis* were exposed to water stress in both developmental stages. In all sampling dates, these species had a similar ($P > 0.05$) soil P concentration under all water levels (Table 1). Soil P concentrations under *S. gynerioides* were similar ($P > 0.05$) among water levels and sampling dates (Table 1).

Soil under the canopy of *S. clarazii* has a greater ($P < 0.05$) P concentration than that under the canopies of *S. tenuis* and *S. gynerioides* under all water levels (Table 2). In June 1996, soil P concentrations were similar among species ($P > 0.05$) and water levels ($P > 0.05$) (Table 3). However, in September, soil where *S. clarazii* grew had a greater ($P < 0.05$) P concentration if plants were exposed to water stress at the internode elongation developmental stage than under irrigation (Table 3). With *S. gynerioides*, soil P concentrations were lower ($P < 0.05$) under water stress in the vegetative stage than under irrigated, rainfed, or water-stress conditions in the vegetative plus internode elongation developmental stages (Table 3). There were no differences ($P > 0.05$) in soil P concentrations among water levels in *S. tenuis*.

In September 1996, soil under the canopies of *S. clarazii* and *S. gynerioides* had a greater ($P < 0.05$) P concentration than that under the canopy of *S. tenuis* under rainfed conditions (Table 3). However, soil P concentrations were greater ($P < 0.05$) under plants of *S. clarazii* than under those of the other two species under water-stress conditions in the vegetative or internode elongation developmental stage in September 1996 (Table 3).

Table 1. Soil phosphorus concentration (ppm) under the canopy of three perennial grass species of different successional stages exposed to various soil water regimes

Regime	April 1996			October 1996			February 1997		
	Scl	Sg	St	Scl	Sg	St	Scl	Sg	St
I	44.2 a,ab	36.8 a,a	30.8 a,a	43.9 a,a	43.7 a,a	33.2 a,a	42.6 a,a	38.8 a,a	39.5 a,a
R	40.3 a,a	36.9 a,a	30.8 a,a	48.2 a,ab	43.3 a,a	32.7 a,a	40.8 a,a	39.0 a,a	40.1 a,a
WS-V	49.6 a,b	34.3 a,a	34.5 a,a	40.9 a,a	36.3 a,a	29.0 a,a	41.4 a,a	28.2 a,a	34.0 a,a
WS-E	43.1 a,ab	26.5 a,a	34.7 a,a	45.9 a,a	32.0 a,a	32.5 a,a	38.9 a,a	31.7 a,a	31.8 a,a
WS-VE	37.7 a,a	47.3 a,a	33.7 a,a	55.0 a,b	36.3 a,a	46.8 a,b	44.5 a,a	35.1 a,a	34.8 a,a

Notes. Soil extractable P was determined by the method of Bray and Kurtz following Olsen and Sommers (1982). Determinations were made on samplings conducted during April and October 1996 and February 1997. Scl = *S. clarazii*, Sg = *S. gynerioides*; St = *S. tenuis*; I = irrigated plants; R = rainfed plants; WS-V = plants exposed to water stress during the vegetative developmental stage; WS-E = plants exposed to water stress during the early elongation developmental stage; and WS-VE = plants exposed to water stress during the vegetative and early internode elongation stages. Each value is the mean of n = 2–8. Different letters to the left of the comma indicate significant differences ($P < 0.05$) among soil water levels within each species and sampling date. Different letters to the right of the comma indicate significant differences ($P < 0.05$) among sampling dates within each species and soil water regime. Means were compared with Fisher's protected LSD at 5% when the F test indicated that the variables differed at that significance level (Steel and Torrie 1981).

Table 2. Soil phosphorus concentration (ppm) under the canopy of three perennial grass species of different successional stages exposed to various soil water regimes

Regime	*S. clarazii*	*S. gynerioides*	*S. tenuis*
I	43.56 b	39.78 a	34.48 a
R	43.09 b	39.72 a	34.52 a
WS-V	43.93 b	32.92 a	32.48 a
WS-E	42.65 b	30.07 a	32.99 a
WS-VE	45.72 b	39.55 a	38.42 a

Notes. Soil extractable P was determined by the method of Bray and Kurtz following Olsen and Sommers (1982). Determinations were made on samplings conducted during April and October 1996 and February 1997. Scl = *S. clarazii*; Sg = *S. gynerioides*; St = *S. tenuis*; I = irrigated plants; R = rainfed plants; WS-V = plants exposed to water stress during the vegetative developmental stage; WS-E = plants exposed to water stress during the early elongation developmental stage; and WS-VE = plants exposed to water stress during the vegetative and early internode elongation stages. Each value is the mean of n = 28. Different letters indicate significant differences ($P < 0.05$) among species within each soil water level. Means were compared with Fisher's protected LSD at 5% when the F test indicated that the variables differed at that significance level (Steel and Torrie 1981).

Table 3. Soil phosphorus concentration (ppm) under the canopy of three perennial grass species of different successional stages exposed to various soil water regimes

Regime	June 1996			September 1996		
	Scl	Sg	St	Scl	Sg	St
I	38.4 a,a	42.0 a,a	34.7 a,a	37.8 a,a	35.0 b,a	35.1 a,a
R	40.2 a,a	39.6 a,a	35.7 a,a	41.2 ab,b	38.2 b,b	32.1 a,a
WS-V	42.1 a,a	40.4 a,a	35.1 a,a	43.6 ab,b	23.9 a,a	30.1 a,a
WS-E	ND	ND	ND	46.8 b,b	30.7 ab,a	31.7 a,a
WS-VE	48.7 a,a	50.3 a,a	36.1 a,a	47.7 ab,a	44.6 b,a	34.9 a,a

Notes. Soil extractable P was determined by the method of Bray and Kurtz following Olsen and Sommers (1982). Determinations were made on samplings conducted during June or September 1996. Scl = *S. clarazii*; Sg = *S. gynerioides*; St = *S. tenuis*; I = irrigated plants; R = rainfed plants; WS-V = plants exposed to water stress during the vegetative developmental stage; WS-E = plants exposed to water stress during the early elongation developmental stage; and WS-VE = plants exposed to water stress during the vegetative and early internode elongation stages. Each value is the mean of n = 2–8. Different letters to the left of the comma indicate significant differences ($P < 0.05$) among soil water levels within each species and sampling date. Different letters to the right of the comma indicate significant differences ($P < 0.05$) among species within each soil water level and sampling date. Means were compared with Fisher's protected LSD at 5% when the F test indicated that the variables differed at that significance level (Steel and Torrie 1981).

DISCUSSION

Leaf Water Potentials

The methodology to impose water stress under field conditions was successful in this study. Leaf water potentials were similar among water levels in all three species at the beginning and end of each growing cycle. Plants of all three species, however, had lower ($P < 0.05$) leaf water potentials under water stress than under irrigated conditions during August–October 1995 and 1996 (Figure 3). The increased water levels in 1996 than in 1995 (Figure 1) imparted higher leaf water potentials during June–September 1996 in the rainfed than in the water-stressed plots.

Soil Bray and Kurtz Extracted Phosphorus

Stipa clarazii showed similar or greater, but not lower, soil P concentration under water stress than in the other soil water regimes. These findings agree with hypothesis 2 for this species only under water-stress conditions. Also, soil P concentrations under *S. gynerioides* plants were almost doubled if plants were exposed to long-term (vegetative + internode elongation) rather than short-term (vegetative) water stress. Phosphorus mineralization from organic matter depends on soil moisture and temperature (Ferguson 1964). Under conditions of high soil moisture contents, a deficiency in P diffusion and a possible loss of this nutrient through lixiviation can be produced (Ferguson 1964). It is possible that the results of this research are a consequence of lower P uptake as the soil water content decreased (i.e., Eck and Fanning 1961; Olsen, Watanabe, and Danielson 1961). Our results are similar to those reported by Gutiérrez-Boem and Thomas (1998) with a wheat crop under water stress. In addition, and even though it was not always detected in this study probably as a result of a small replicate number, the greater soil P concentration under water stress than under irrigated conditions was also likely due to a greater aboveground biomass in *S. clarazii* and *S. tenuis*, in competition with *S. gynerioides*, in the water stress than in the irrigated treatment (Flemmer et al. 2003). This result would lead to a greater litter amount to be decomposed under water stress. A continued root turnover in *S. clarazii* and *S. tenuis* under rainfed conditions would also contribute to maintain high levels of soil Bray and Kurtz extracted phosphorus (Becker et al. 1997; Flemmer et al. 2002).

In April and October 1996 and February 1997, soil Bray and Kurtz extracted P levels were greater under the canopy of the late seral, palatable perennial grass *S. clarazii* than under the canopy of the earlier seral, palatable *S. tenuis* and unpalatable *S. gynerioides* under all water levels. In

September 1996, *S. clarazii* again showed a higher soil P concentration than *S. gynerioides* and *S. tenuis* under its canopy under conditions of water stress in the vegetative or internode elongation developmental stage. A similar response was reported by Moretto and Distel (2000, 2003) for grasses under rainfed conditions. In their study, total nitrogen (N), Bray and Kurtz extracted P, organic carbon (C), and soil organic matter were greater at sites dominated by *P. ligularis*, a late seral, palatable perennial grass, than at sites dominated by *S. gynerioides*, the early seral, unpalatable tussock grass. This (Moretto and Distel 2000, 2003) would be the result, at least in part, of differences in litter and root chemical composition between species; litter and root decomposition were faster in *P. ligularis* (low C:N ratio) than in *S. gynerioides* (high C:N ratio) (Moretto and Distel 2000, 2003).

The high degree of persistence of low-palatability grasses in rangelands of central Argentina might be related to their low litter quality, which delays nutrient cycling and soil nutrient availability (Archer and Smeins 1991; Berendse 1994; Jones, Lawton, and Shachak 1994; Aerts 1995; Wedin 1995). These species would be favored under low-nutrient availability conditions, because they reach, in an equilibrium situation, a greater biomass than the most productive and competitive species (Aerts and Van der Peijl 1993). However, if colonization of these sites by late seral and more productive and competitive perennial grasses is favored, early seral grasses might be slowly, but eventually replaced, by late seral grasses. Giorgetti et al. (1998, 1999, 2000) demonstrated that during a 10-year period, density, frequency, and cover of *S. clarazii* substantially increased, and at the same time these parameters decreased in the early seral, unpalatable perennial grass *Stipa ambigua* in a site initially dominated by this species under exclosure with rainfed conditions. This result is consistent with findings of Moretto and Distel (2002), who suggested that C_3 unpalatable grasses from the temperate semi-arid grasslands of central Argentina have a relatively low potential to immobilize soil nutrients; they demonstrated that *in situ* net N mineralization in the soil under the unpalatable *S. tennuisima* was higher than or similar to net N mineralization in the soil under the palatable *P. ligularis*. If so, pulses of high nutrient availability (caused by fire, drought, fertilizer applications) may create opportunities for plant species with high resource requirements (palatable species) to realize a competitive advantage and maintain or gain dominance within natural grassland communities (Wedin 1999).

CONCLUSIONS

Various abiotic and biotic factors may be contributing to obtain similar or greater, but not lower, soil Bray and Kurtz extracted P concentrations under water stress than under higher soil water contents. Most of the times, soil Bray and Kurtz extracted P levels were greater under the canopy of the late seral, palatable perennial grass *S. clarazii* than under the canopy of the earlier seral, palatable *S. tenuis* and unpalatable *S. gynerioides* under all water levels. This higher nutrient content under *S. clarazii* than under *S. tenuis* and *S. gynerioides* may contribute to determine a greater density, frequency, and cover throughout a long-term span (years) in the late seral than in the earlier seral perennial grasses under good grazing management conditions.

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