2007
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Interciencia, marzo, año/vol. 32, número 003
Asociación Interciencia
Caracas, Venezuela
pp. 206-212

PERENNIAL GRASSES OF DIFFERENT SUCCESSIONAL STAGES UNDER VARIOUS SOIL WATER INPUTS: DO THEY DIFFER IN ROOT LENGTH DENSITY?

Carlos Alberto Busso and Andrea Ivana Bolletta

SUMMARY

Information about root length density (RLD) on perennial grasses of different successional stages exposed to various soil water inputs is limited. The effects on RLD of different soil water inputs were evaluated in the late-seral Stipa clarazii Ball, the comparatively earlier-seral S. tenuis Phil, and the early-seral S. gynerioides Phil. Field studies were conducted in 1996 and early 1997, although treatments were imposed since 1995. S. clarazii and S. tenuis are two important palatable perennial tussock grasses in temperate, semiarid rangelands of central Argentina, where S. gynerioides is one of the most abundant, unpalatable perennial grass species. It was hypothesized that 1) S. clarazii and S. tenuis have a lower RLD under irrigated than under rainfed or water stress conditions, 2) S. clarazii has a greater RLD than S. gynerioides and S. tenuis under all water inputs and sampling dates, and 3) the RLD of the three species will vary with sampling date, within each species and soil water level. Results led to reject hypothesis 1 and accept hypotheses 2 and 3. Maintenance of root growth under all water inputs would allow these species a greater soil exploration and resource finding to sustain regrowth in their native, semi-arid environments. Also, the study demonstrated that late-seral perennial grasses (S. clarazii) should have a superior competitive ability than earlier seral grasses (S. tenuis and S. gynerioides) because of, at least in part, their greater average RLD under water stress, rainfed and irrigated conditions.*

RESUMEN

La información sobre densidad de longitud de raíces (DLR) es escasa en gramíneas perennes de diferentes estados sucesionales expuestas a varios niveles hídricos del suelo. Los efectos de distintos niveles hídricos sobre la DLR fueron evaluados en gramíneas perennes de etapas sucesionales tardías (Stipa clarazii Ball.), intermedias (S. tenuis Phil.), y tempranas (S. gynerioides Phil.). Se condujeron estudios de campo en 1996 y principios de 1997, aunque los tratamientos fueron impuestos desde 1995. S. clarazii y S. tenuis son importantes gramíneas perennes cespitosas palatables en pastizales templados semiáridos del centro de Argentina, donde S. gynerioides es una de las especies de gramíneas perennes no palatables más abundantes. Se probaron las siguientes hipótesis: 1) S. clarazii y S. tenuis tienen menor DLR bajo condiciones de riego que bajo condiciones naturales o estrés hídrico, 2) S. cla-razii tiene mayor DLR que S. gynerioides y S. tenuis bajo todos los niveles hídricos y fechas de muestreo, y 3) la DLR de las tres especies varía con la fecha de muestreo, dentro de cada especie y nivel hídrico del suelo. Los resultados condujeron a rechazar la hipótesis 1 y aceptar las hipótesis 2 y 3. El mantenimiento del crecimiento radical en todos los niveles hídricos les permitiría a estas especies una mayor exploración del volumen del suelo y adquisición de recursos que mantengan el rebrote en sus ambientes nativos, semiáridos. El estudio también demostró que las gramíneas perennes de estados sucesionales tardíos (S. clarazii) deberían tener mayor capacidad competitiva que especies más tempranas en la sucesión vegetal (S. tenuis y S. gynerioides) debido, al menos en parte, a su mayor DLR promedio bajo condiciones de estrés hídrico, naturales y de riego.

Introduction

Root growth and dynamics are an important aspect in rangeland ecology. Many of the survival strategies of rangeland species, where water and nutrients are often limiting, depend on the root system (Brown, 1995). Soil occupation, of primary importance for nutrient competition processes, depends upon root characteristics such as root length (Casper and Jackson, 1997). Inspite of the potential importance of root length density (root length per unit soil volume), information of this primary variable is limited for native species in rangelands, particularly for those which grow under competition in the field (Schulze *et al.*, 1996). Root length density is a very precise parameter to estimate the spatial pattern of nutrient and water uptake (Yoder *et al.*, 1995). Caldwell and Richards (1986) demonstrated that grasslands with greater root length densities absorb soil water more rapidly, especially from deep layers in the soil profile, and are more effective competitors with neighboring shrubs.

Root growth is influenced by water availability in the soil profile (Asseng *et al.*, 1998). Total length and elongation rates of roots can be reduced under water stress in various perennial grasses (Mohammad *et al.*, 1982; Simões and Baruch, 1991; Asseng *et al.*, 1998). This response, however, can be associated with a root growth reduction in shallow soil layers and a simultaneous increase of such growth in deeper soil

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RESUMO

A informação sobre densidade de longitude de raízes (DLR) é escassa em gramíneas perenes de diferentes estados sucessionais expostas a vários níveis hídricos do solo. Os efeitos de distintos níveis hídricos sobre a DLR foram avaliados em gramíneas perenes de etapas sucessionais tardias (Stipa clarazii Ball.), intermediárias (S. tenuis Phil.), e precoces (S. gynerioides Phil.). Conduziram-se estudos de campo em 1996 e começo de 1997, ainda que os tratamentos fossem impostos desde 1995. S. clarazii e S. tenuis são importantes gramíneas perenes cespitosas palatáveis em pastagens temperados semi-áridos do centro de Argentina, onde S. gynerioides é uma das espécies de gramíneas perenes não palatáveis mais abundantes. Provaram-se as seguintes hipóteses: 1) S. clarazii e S. tenuis têm menor DLR sob condições de irrigação que sob condições naturais ou estresse hídrico, 2) S. clarazii têm maior DLR que S. gynerioides e S. tenuis sob todos os níveis hídricos e datas de amostragem, e 3) a DLR das três espécies variam com a data de amostragem, dentro de cada espécie e nível hídrico do solo. Os resultados conduziram a rejeitar a hipótese 1 e aceitar as hipóteses 2 e 3. A manutenção do crescimento radical em todos os níveis hídricos, permitiria a estas espécies uma maior exploração do volume do solo e aquisição de recursos que mantenham o rebrote em seus ambientes nativos, semi-áridos. O estudo também demonstrou que as gramíneas perenes de estados sucessionais tardios (S. clarazii) deveriam ter maior capacidade competitiva que espécies mais precoces na sucessão vegetal (S. tenuis e S. gynerioides) devido, pelo menos em parte, a seu maior DLR médio sob condições de estresse hídrico, naturais e de irrigação.

horizons. This strategy, characteristic of water stress tolerant species, allows plants to explore soil horizons with greater water availability (Asseng *et al*., 1998). Root length density of thin roots was greater in soils often exposed to water stress than in those with a more continuous water supply (Babel, 1981; Kottke and Agerer, 1983).

However, when palatable species like *Stipa clarazii*, a late-seral species, and *S. tenuis*, an earlier-seral species than the previous one, have been watered in competition with unpalatable ones, such like *S. gynerioides*, an early-seral species, the latter took advantage of the greater soil water supply (Flemmer *et al*., 2003). Under these conditions, biomass production of *S. gynerioides* was so great that it left *S. clarazii* and *S. tenuis* under the shade and their aboveground biomass was reduced 70% under irrigation, in comparison to water stress conditions (Flemmer *et al*., 2003). As a result, it is expected that root length density of *S. clarazii* and *S. tenuis* is lower under irrigated than under rainfed or water stress conditions.

In addition, differences in root proliferation have been observed between these species. *S. clarazii* showed a greater root proliferation than *S. tenuis* in a field study (Saint Pierre *et al*., 2002), a fact that contributes to the greater competitive ability of the first one.

Patterns of accumulated root appearance and disappearance can vary during the growing season in these C_3 perennial grasses. Flemmer *et al*. (2002) showed that in June (late auttum), accumulated root appearance in *S. clarazii* was always greater under irrigation than under water stress in the vegetative phenological stage; in November (mid spring), accumulated root disappearance was greater under irrigation than under water stress in this species. These authors noted that the root system was comparatively less sensitive to soil water in *S. gynerioides*, as accumulated root appearance and disappearance in this species were similar under irrigated and rainfed conditions. At the end of August, and in June and November, accumulated root appearance and disappearance were greater under rainfed than water stress conditions in *S. tenuis* (Flemmer *et al*., 2002).

Despite differences in shoot growth, and root growth and turnover under various soil water contents, the study species (*S. clarazii*, *S. tenuis* and *S. gynerioides*) have a similar phenology under rainfed conditions (Distel and Fernández, 1988; Becker *et al*., 1997; Giorgetti *et al*., 2000; Busso *et al*., 2003). All three perennial grasses are C_3 species which vegetate during autumn and winter. If water

is available all year round, tilling will extend to spring and summer. At the beginning of spring (late September), the vegetative apex differentiates into reproductive, internode elongation occurs, and by early October 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 plant remains in a dormant stage during summer (late December-late February), unless soil water content is high at this time. Root growth under rainfed conditions remains unabated during the whole year (Distel and Fernández, 1988; Becker *et al*., 1997; Busso *et al*., 2003).

Working hypotheses in this study were 1) *S. clarazii* and *S. tenuis* have a lower root length density under irrigated than under rainfed or water stress conditions, because of the increase in root length density in *S. gynerioides* under more favorable water conditions; 2) *S. clarazii* has a greater root length density than *S. gynerioides* and *S. tenuis* under all water inputs and sampling dates, and 3) root length density of the three species will vary with sampling date, within each species and soil water level.

The overall purpose of this study was to evaluate root length density on plants of *S. clarazii*, *S. gynerioides* and *S. tenuis* exposed to water stress, rainfed or irrigated conditions

in the field. The results will contribute to a better interpretation of aboveground and belowground differences in growth, as well as differences in competitive ability and persistence in the community, when plants of these grass species of different successional stages are exposed to various soil water inputs in the field.

Study area

Studies were conducted at the research field site nearby the Agronomy Department, Center of Renewable Natural Resources of the Semiarid Region (CERZOS), Bahía Blanca, Argentina (38º48'S, 62º13'W). Soil is a typical Haplustol with a petrocalcic horizon at 1.8m depth. It has a loam-sandy texture; 1.9% organic matter; 7mg·kg⁻¹ extractable P (Olsen and Sommers, 1982); 0.10% total N; and a pH of 7.4. Climate information during the study period (1996 and early 1997) was obtained from a meteorological station located at the research area (Figure 1). The year 1995 is also shown because a parallel research on the experimental plots used in this study was initiated this year.

Materials and Methods

Experimental design

Between December 1993 and April 1994, 28 experi-

mental plots (1.8×1.8m) were established in the field on un-plowed, weeded 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 30cm apart from one another in 7 horizontal and vertical rows such that each plant of *S. clarazii* or *S. tenuis* was surrounded by 4 plants of *S. gynerioides* (Figure 2). Nomenclature follows Cano (1988). Disposition of plants within a uniform ma-trix contributes to reduce po-tentially 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 ±0.56cm (mean ±SE) for *S. clarazii*, 10.02 ±0.51cm for *S. tenuis*, and 12.27 ±0.61cm for *S. gynerioides.*

All tussocks of *S. clara-zii* and *S. tenuis* were hand-clipped to a 5cm stubble height in January 1995, dur-ing the plant quiescent pe-riod. Eight experimental plots (replicates) were randomly assigned to the irrigated and rainfed treatments, and 4 rep-licates to each of the water stress treatments (vegetative, internode elongation, and vegetative+internode elonga-tion).

Water inputs

Plants were exposed to rainfed, irrigated or water stress conditions. Rainfed plots received rainfall all year round (Figure 3). A drip ir-rigation system watered the irrigated plots, which were additionally rainfed. Soil ten-siometers installed in the ir-rigated plots allowed watering of these plots to saturation whenever they reach 60% of field capacity. Periods of ir-rigation and imposition of water stress during 1995 and 1996 are depicted in Figure 3. Transparent plastic sheets cov-ered the water-stressed plots whenever rain fell at periods
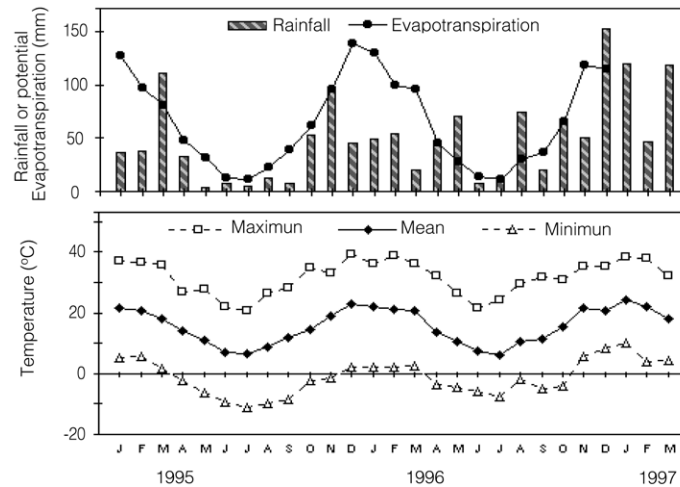

Figure 1. a: Monthly rainfall and mean monthly potential evapotranspiration (Thornthwaite), and b: absolute minimum and maximum and mean monthly air temperatures to 0.25m above the soil surface during 1995, 1996 and early 1997. Measurements were taken using a meteorological station located 100m away from the experimental plots.
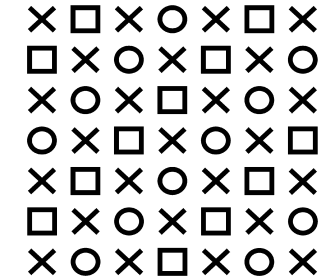

Figure 2. Disposition of plants of *S. clarazii* (O), *S. tenuis* (□) and *S. gynerioides* (×) within each of 28 experimental field plots. Distance among plants on horizontal and vertical rows is 30cm.

when these species are of-ten exposed to water stress in their native environment (Bus-so, 1997): vegetative or early internode elongation or both phenological periods (Fig-ure 3). Water-stressed plots were surrounded with plastic sheets up to 1.8m soil depth to prevent later-al movement of water into these plots.

All 28 experi-mental plots re-ceived 313.7mm from mid-Octo-ber 1995 to late-April 1996, and 487.8mm from late-October 1996 to March 1997. Water-stressed plots were thus alle-viated from wa-ter stress during these periods by receiving natu-ral rainfall.

Sampling procedures

Leaf water potentials were periodically determined at mid-day in all treatments to provide a meas-ure of plant wa-ter status dur-

ing the study period. Meas-urements were done using a pressure-chamber on sunny days only between noon and 1pm. Youngest, fully expand-ed 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, 1981).

A total of 460 soil plus root samples were obtained between 0-15cm soil depth using a soil corer of 8.4cm diameter, 15cm height (831.3cm³ volume) during April, June, September and October in 1996, and Feb-ruary in 1997. Parallel, la-
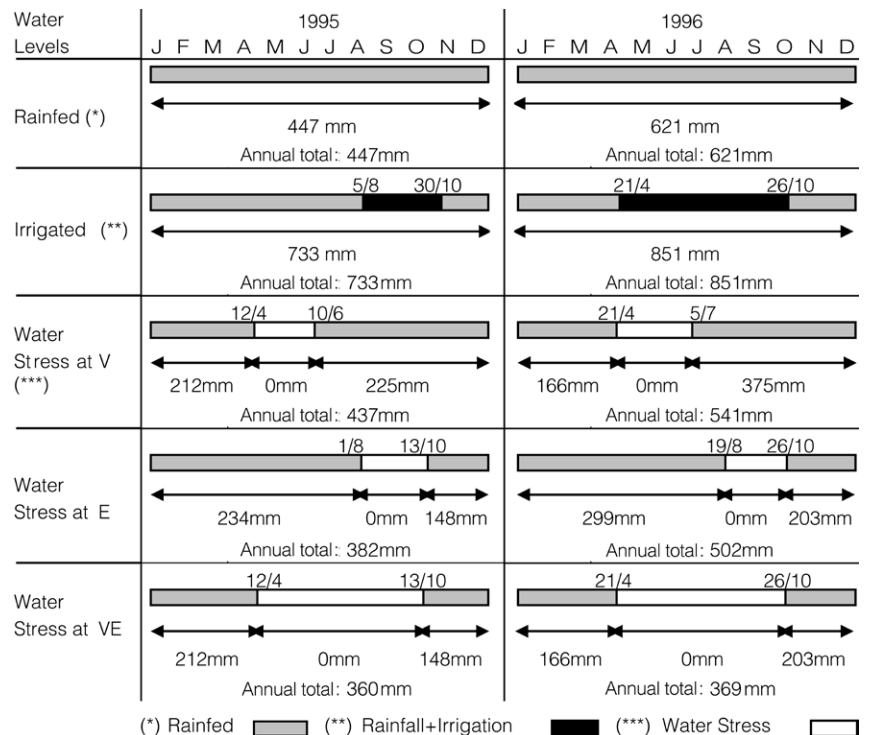

Figure 3. Periods of imposition of the different water inputs at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996. Numbers below horizontal, bold lines are rainfall fallen in the rainfed, and water stress treatments, or rainfall+irrigation in the irrigated treatment. Total annual precipitation is indicated for each year and water level within rectangles. Numbers immediately above horizontal bars represent the beginning and end, respectively, of imposition of any given water level. Black, grey or white horizontal bars represent irrigated, rainfed or water stress conditions, respectively.
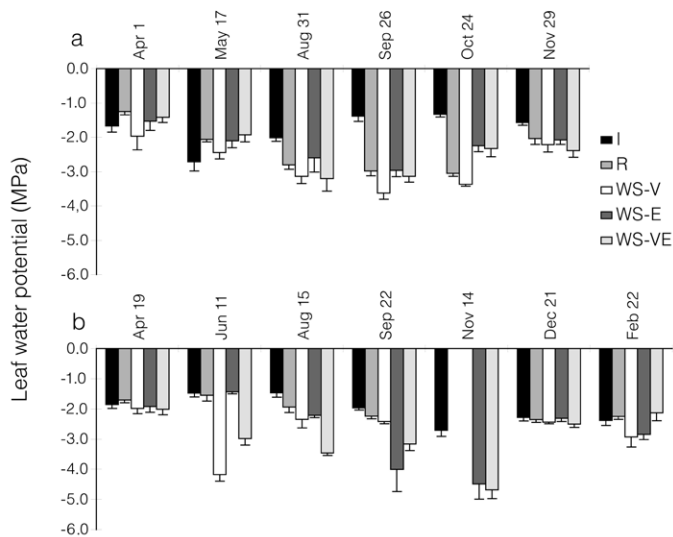
Figure 4. Mid-day leaf water potential on plants of *S. clarazii*, *S. tenuis*, and *S. gynerioides* exposed to irrigated (I), rainfed (R) or water stress (WS) conditions at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 (a) and 1996 (b). No data are available for plants which were rainfed or water-stressed at the vegetative phenological stage on 14 Nov 1996. Since leaf water potentials were usually similar (p>0.05) among species, values were pooled for *S. clarazii*, *S. gynerioides* and *S. tenuis*. Each histogram is an average of n=4-8. Vertical bars=1SEM.

bor-intensive studies on these plots prevented taking soil plus root samples during 1995. Samples were obtained diagonally from the plant periphery to the plant center to assure that sampled roots corresponded to the sampled plant. One plant of each species was used per replicate at each sampling date. Roots were obtained after washing soil samples through a 60 mesh screen (Williams and Baker, 1957), and they were maintained at 4°C in a solution of formaldehyde, glacial acetic acid and ethanol (Phillips and Hayman, 1970). Roots from each soil sample were evenly distributed on glass where root length was estimated using the Tennant´s method (1975): an acetate sheet (30×20cm) divided in quadrants of 3cm side was utilized. Numbers of root interceptions on horizontal and vertical lines of this sheet were counted. Root length was estimated as number of interceptions (N) times a conversion factor (2.3571) for a reticulate of 3×3cm. With known root length and soil volume, root length density (cm root/cm^3 soil) was calculated.

Statistical analysis

Leaf water potential data were analyzed separately for each date using ANOVA. A split plot design was considered with this purpose using treatments (water input) as main factor and species as secondary factor. Since the interaction term was not significant (p≥0.09) on any sampling date, and whenever the treatment factor was significant (p<0.05), two-way ANOVA were subsequently performed. Differences among water level treatments were tested using 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, root length density data were analyzed using a three way split plot ANOVA (5 water inputs ×3 species ×5 sampling dates: April, June, September and October 1996, and February 1997). Soil water input 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 4 replicates were

utilized for each of the water stress treatments (vegetative, internode elongation, vegetative+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 to be sampled previous to the sampling dates. This allowed to avoid measurements of root parameters on nearby plants previously sampled. However, this rigid scheme did not allow replacement of lost plants (plants which died as a result of treatment application) during the study. Because of this, it was necessary to adapt the statistical analysis when the loss of sampling units resulted in an unbalance not proportional among the species within each plot. This phenomenon was mainly presented in June and September.

In this way, a 'Design 1' was applied 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 a 'Design 2: a split-plot two-way ANOVA with the same main factor (soil water input) 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 decomposed to evaluate the effects of water input, dates and species. 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). The statistical package used for all data analysis was BMDP New System for Windows (Dixon, 1994).

Results

Leaf water potentials

Leaf water potentials were similar among water inputs in all three species at the begin-

ning and end of each growing cycle (Figure 4). 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. Results were similar in 1996, when leaf water potentials were generally lower on water-stressed than on irrigated plants. Leaf water potentials were more variable on plants in the rainfed plots. Under these conditions, leaf water potentials appeared lower than those in the irrigated plots in 1995, and higher than those in the water-stressed plots in 1996 (Figure 4). This was very likely due to the lower annual rainfall in 1995 than in 1996 (Figure 1).

During the study period, leaf water potentials were usually similar among species (data not shown). 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 4).

Root length density

Soil water inputs showed a similar (p>0.05) root length density at all sampling dates in 1996 and 1997 (Tables I and II). Except in June, all three species showed a similar root length density (p>0.05; Table II). In June, plants of *S. clarazii* showed a greater (p<0.05) root length density than those of *S. gynerioides* and *S. tenuis* on average for all soil water input treatments (Figure 5). Root length density, on average for all three species and the five soil water inputs, was greater (p>0.05) in April (3.84cm roots/cm^3 soil) than in October and February (2.60 and 2.90cm roots/cm^3 soil, respectively; Table III).

Discussion

Water stress conditions were successfully imposed at the field in the water stress treatment. Other studies used a methodology similar to the

TABLE I

ROOT LENGTH DENSITY (cm root/cm^3 soil) ON PLANTS OF *S. clarazii* (Sc), *S. gynerioides* (Sg) AND *S. tenuis* (St) EXPOSED TO IRRIGATED (I), RAINFED (R) AND WATER STRESS (WS) CONDITIONS DURING THE VEGETATIVE (WS-V), INTERNODE ELONGATION (WS-E) OR VEGETATIVE+INTERNODE ELONGATION (WS-VE) PHONOLOGICAL STAGE

	April 1996			October 1996			February 1997		
	Sc	Sg	St	Sc	Sg	St	Sc	Sg	St
I	3.23 ±0.53 aab	4.08 ±0.70 aab	3.56 ±0.58 aab	2.69 ±0.53 aaa	2.05 ±0.20 aaa	2.03 ±0.44 aaa	2.42 ±0.42 aaa	2.35 ±0.34 aaa	2.55 ±0.66 aaa
R	6.52 ±1.17 aab	3.27 ±0.73 aab	3.27 ±0.70 aab	1.31 ±0.51 aaa	1.92 ±0.53 aaa	2.64 ±0.25 aaa	2.99 ±0.60 aaa	2.83 ±0.37 aaa	3.40 ±0.30 aaa
WS-V	3.65 ±0.65 aab	1.70 ±0.54 aab	3.19 ±0.91 aab	3.02 ±0.40 aaa	3.95 ±1.26 aaa	3.73 ±0.37 aaa	3.05 ±0.62 aaa	3.24 ±0.57 aaa	2.85 ±0.21 aaa
WS-E	3.49 ±0.49 aab	4.64 ±1.57 aab	3.44 ±0.64 aab	3.29 ±0.88 aaa	3.07 ±0.97 aaa	2.88 ±0.73 aaa	3.32 ±1.41 aaa	2.88 ±1.01 aaa	2.68 ±0.19 aaa
WS-VE	4.32 ±0.39 aab	5.72 ±3.26 aab	2.71 ±1.31 aab	3.94 ±0.50 aaa	3.56 ±1.38 aaa	1.97 ±0.62 aaa	2.58 ±0.32 aaa	4.34 ±1.17 aaa	2.86 ±0.16 aaa

Each value is the mean ±SEM, n=4-8. Different 1st, 2nd and 3rd letters indicate significant differences (p<0.05) between water inputs, species, and sampling dates, respectively.

present one to impose water stress and obtained similar results (Fresnillo Fedorenko *et al.*, 1995; Busso *et al.*, 1998). These field studies also prevented horizontal soil water movement into the water-stressed plots, but using plants grown in PVC pots which were buried into the soil. They also used plastic sheets to cover the water-stressed plots whenever rainfall fell during the study period. These plastic sheets were mounted on a specially designed wood structure that provided an open-sided rain shelter.

Root length density in all three species was similar in the irrigated, rainfed and water stress treatments, in disagreement with the first hypothesis tested. Continued root growth under water stress in *S. clarazii*, *S. tenuis* and *S. gynerioides* may be interpreted as a strategy of these species for a continued exploration of soil resources. This strategy would contribute to sustain shoot growth under water stress, which is common in arid and semiarid regions (Ludlow, 1986; Flemmer *et al.*, 2002). Results similar to the present ones were found by Dube (1999) and Flemmer *et al.* (2002) in *S. tenuis*; a species that can maintain an unabated root growth under low soil water input. In *S. clarazii* and *S. gynerioides*, Flemmer *et al.* (2002) found that root growth was reduced by water stress in deeper (20-40 and 40-60cm soil depth) but not shallower horizons (0-20cm soil depth). Similarly, other species either did

TABLE II

ROOT LENGTH DENSITY (cm root/cm^3 soil) ON PLANTS OF *S. clarazii* (Sc), *S. gynerioides* (Sg) AND *S. tenuis* (St) EXPOSED TO IRRIGATED (I), RAINFED (R) AND WATER STRESS (WS) CONDITIONS DURING THE VEGETATIVE (WS-V), INTERNODE ELONGATION (WS-E) OR VEGETATIVE+INTERNODE ELONGATION (WS-VE) PHENOLOGICAL STAGE

	June 1996			September 1996		
	Sc	Sg	St	Sc	Sg	St
I	5.03 ±0.78 ab	3.50 ±0.71 aa	3.89 ±0.26 aa	2.00 ±0.32 aa	3.35 ±0.57 aa	1.94 ±0.39 aa
R	6.50 ±1.70 ab	2.34 ±0.94 aa	1.69 ±0.38 aa	2.27 ±0.62 aa	3.25 ±0.61 aa	2.23 ±0.90 aa
WS-V	3.81 ±0.69 ab	3.54 ±0.45 aa	2.75 ±0.64 aa	3.96 ±0.83 aa	2.30 ±0.46 aa	2.23 ±1.05 aa
WS-E	nd	nd	nd	2.47 ±0.10 aa	3.28 ±0.93 aa	3.31 ±0.71 aa
WS-VE	4.16 aa	2.80 aa	3.99 aa	2.26 ±0.39 aa	1.96 ±0.79 aa	2.70 ±2.06 aa

Values are the mean ±SEM, n=1-7. Values in parentheses represent one standard error of the mean. When there are no parentheses, values come from n=1. Different 1st and 2nd letters indicate significant differences (p<0.05) between water inputs and species, respectively. nd= not determined.

not increase root growth in deep soil layers (Onillon *et al.*, 1995) or maintained shallower root systems in response to water stress (Brar and Palazzo, 1995). A shallower root system would allow to take advantage of small (<5mm) rainfall events (Sala and Lauenroth, 1982; Singh *et al.*, 1998) which are common in rangelands of central Argentina (Fresnillo Fedorenko *et al.*, 1992; Busso, 1997). For example, more than 60% of the rainfall events were <5mm at the Chacra Experimental of Patagones, in southern Buenos Aires Province, Argentina, during the period 1983-2000 (Páez *et al.*, 2005). Precipitations of this magnitude can rapidly stimulate various physiological processes in grass species (Bartos and Sims, 1974; Sala and Lauenroth, 1982). Other authors have found root growth decrease as the soil water also decreased in other perennial grass species (Mohammad *et al.*, 1982; Simões and Baruch, 1991; Williams and Black, 1994; Asseng *et al.*, 1998). Changes in both soil water content

TABLE III

ROOT LENGTH DENSITY (cm root/cm^3 soil) ON PLANTS OF *S. clarazii*, *S. gynerioides* AND *S. tenuis* EXPOSED TO VARIOUS SOIL WATER INPUTS DURING 1995 AND 1996*

April 1996	October 1996	February 1997
3.85 ±0.18 b	2.62 ±0.17 a	2.90 ±0.20 a

* Data were pooled for species and water input as they were not statistically significant (P>0.05; see Table I). Values are the mean ±SEM, n=84. Different letters indicate significant (p<0.05) differences among sampling dates.

and potential can change root growth patterns and activities in relation to apical shoot growth, and have a significant impact on plant productivity (Asseng *et al.*, 1998).

Saint Pierre *et al.* (2002, 2004a, b, c) demonstrated a greater competitive ability in the late-seral *S. clarazii* than in the earlier-
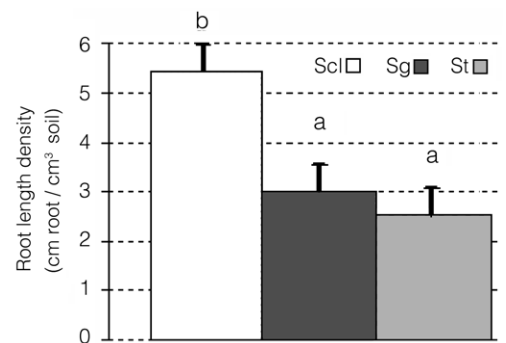

Figure 5. Root length density (cm root/cm^3 soil) on plants of *S. clarazii* (Sc), *S. gynerioides* (Sg) and *S. tenuis* (St) exposed to irrigated, rainfed and water stress conditions during the vegetative, internode elongation or vegetative+internode elongation phenological stage during 1995 and 1996. Data shown are for June 1996, and were pooled for all water inputs within each species because they were not statistically significant (p>0.05; see Table II). Each histogram is the mean of n=124-127. Vertical bars= 1SEM. Different letters indicate significant (p<0.05) differences among species.

seral *S. tenuis*. A greater root proliferation in terms of both, root length and weight, in the first than in the second species contributed to explain those plant responses. These results are similar to those obtained in June 1996: *S. clarazii* showed greater root length densities than *S. gynerioides* and *S. tenuis* on average for all soil water inputs. This is in agreement with the second hyphotesis tested. The fact that a greater root length density can contribute to a greater competitive ability has already been reported in several perennial grasses (Caldwell *et al.*, 1981, 1991a, b; Crick and Grime, 1987; Eissenstat and Caldwell, 1989). Species which are more competitive have a high plasticity to rapidly modify their root growth (Crick and Grime, 1987). Additionally, a greater root growth allows occupying a greater soil volume and exploring nutrient-rich areas (Caldwell, 1979; Silberbush and Barber, 1983; Caldwell and Richards, 1986). However, it does not necessarily imply an immediate greater soil resource acquisition (Eissenstat and Caldwell, 1989).

Root length densities found in the last sampling dates were similar to those reported by Saint Pierre *et al.* (2002). These authors demonstrated that root length densities were similar in *S. clarazii*, *S. ambigua* and *S. tenuis* in December, under rainfed conditions.

Becker *et al.* (1997) and Flemmer *et al.* (2002) found a continuous root appearance and disappearance in *S. clarazii*, *S. gynerioides* or *S. tenuis* during the growing season under rainfed conditions in the temperate, semiarid rangelands of central Argentina. These authors reported that root growth of these species showed a pulse pattern in response to rapid changes of soil water availability. A continued root growth during the year, even under conditions of water stress, would contribute to an unabated soil exploration for resources such as water and nutrients (Flemmer *et al.*, 2002). In this study, increases of root length density in the three species under all water inputs at different sampling dates suggest that root appearance was greater than root disappearance at those times. In such situations, and depending on the species and soil water level (i.e., *S. tenuis* from June 1996 to February 1997 under rainfed conditions), it is possible that a greater root appearance than disappearance, and then a continued root growth, occurred throughout the year. These results are in agreement with the third hypothesis.

In this study, all plots were rainfed from the end of October 1995 to April 1996. The high precipitation during this period (313.7mm; Figure 1) may explain the greater root length density in April than in October 1996, and February 1997. Normal seasonal changes in precipitation can have direct effects on root growth and development (Brown, 1995).

This study demonstrated that late-seral perennial grasses (*S. clarazii*) should have a superior competitive ability than earlier seral grasses (*S. tenuis* and *S. gynerioides*) because of, at least in part, their greater root length density on average under water stress, rainfed and irrigated conditions.

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