Root growth, appearance and disappearance in perennial grasses: Effects of the timing of water stress with or without defoliation

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Departamento de Agronomia y CERZOS (CONICET), Universidad Nacional del Sur, Altos del Palihue, 8000 Bahía Blanca, Argentina (e-mail:cebusso@criba.edu.ar). *Received 18 December 2000, accepted 24 January 2002.*

Flemmer, A. C., Busso, C. A., Fernández, O. A. and Montani, T. 2002. **Root growth, appearance and disappearance in perennial grasses: Effects of the timing of water stress with or without defoliation.** Can. J. Plant Sci. **82**: 539–547. The effects of early and late defoliations were evaluated under different levels of soil water content on root growth, appearance and disappearance in *Stipa clarazii* Ball, *S. tenuis* Phil., and *S. gynerioides* Phil. Field studies were conducted in 1995, 1996 and early 1997. *Stipa 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. We hypothesized that (1) root growth is reduced after defoliation at any phenological stage in *S. clarazii* and *S. tenuis* in comparison to undefoliated controls, (2) root growth, and root appearance and disappearance in all three species decrease as plant water stress increases, and (3) root growth associated with water stress in *S. clarazii* and *S. tenuis* is reduced comparatively less when plants are water-stressed earlier than later, or for a longer period of time during the growing season. Our results led us to reject hypothesis 1 and accept hypotheses 2 and 3. Maintenance of root growth after defoliation in *S. clarazii* and *S. tenuis* would allow these species a greater soil exploration and resource finding to sustain regrowth in their native, semiarid environments.

Key words: Root growth, appearance and disappearance, perennial grasses, water stress, defoliation, *Stipa* species

Flemmer, A. C., Busso, C. A., Fernández, O. A. et Montani, T. 2002. **Croissance, naissance et mort des racines chez les graminées vivaces : incidence du stress hydrique dans le temps, avec ou sans défoliation.** Can. J. Plant Sci. **82**: 539–547. Les auteurs ont évalué les effets d'une défoliation rapide ou tardive sur la croissance, la naissance et la mort des racines chez *Stipa clarazii* Ball, *S. tenuis* Phil. et *S. gynerioides* Phil. à diverses teneurs en eau du sol. Les études sur le terrain ont eu lieu en 1995, 1996 et au début de 1997. *Stipa clarazii* et *S. tenuis* sont deux importantes graminées vivaces comestibles poussant sur les buttes de gazon dans les grands parcours semi-arides du centre de l'Argentine, où *S. gynerioides* demeure l'une des plus abondantes graminées vivaces impropres à la consommation pour le bétail. Les auteurs ont formulé diverses hypothèses : 1) que les racines de *S. clarazii* et *S. tenuis* croissent plus lentement après la défoliation, peu importe le stade phénologique, comparativement aux plants témoins non défoliés; 2) que la croissance, la naissance et la mort des racines diminuent à mesure que le stress hydrique s'aggrave chez les trois espèces; 3) que le ralentissement de la croissance des racines associé au stress hydrique chez *S. clarazii* et *S. tenuis* est moins grand quand le stress survient au début de la période végétative que quand il survient plus tard ou se prolonge. Les résultats ont amené les auteurs à rejeter la première hypothèse et à retenir les deux autres. En poursuivant leur croissance après la défoliation, les racines de *S. clarazii* et de *S. tenuis* permettraient aux deux espèces d'explorer le sol davantage et de découvrir d'autres ressources qui les aideront à survivre dans leur milieu naturel, semi-aride.

Mots clés: Croissance, naissance et mort des racines; graminées vivaces; stress hydrique; défoliation; genre *Stipa*

Research on root growth and dynamics is an important aspect of the ecology of rangeland perennial grasses. Many of the survival strategies of species from arid and semiarid areas, where water and nutrients are generally limiting, depend on the root system (Brown 1995).

Root growth and distribution in the soil profile are influenced by abiotic and biotic factors such as soil water availability and defoliation (Simoes and Baruch 1991). Total root length has been shown to be reduced under water stress compared with irrigated conditions in several perennial tussock grasses (Mohammad et al. 1982; Simoes and Baruch 1991; Asseng et al. 1998). This response, however, can be associated with reduced root growth in shallower soil layers and simultaneous increases in root growth at depth. This strategy, characteristic of species tolerant to water stress, allows plants to exploit soil horizons with more water (Asseng et al. 1998).

Studies on perennial grasses have demonstrated reductions in root length, increases or even no effect after defoliation, depending on the plant history and the timing,

Abbreviations: **E**, internode elongation phenological stage of development; **TRRN**, total relative root number; **V**, vegetative phenological stage of development; **VE**, vegetative plus internode elongation phenological stage of development

Table 1. Rainfall during 1995, 1996 and early 1997 at the study site

	Rainfall (mm)												
Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
1995	36.0	37.4	110.8	32.4	3.4	7.8	5.6	12.4	7.4	53.2	94.0	45.8	447.2
1996	49.4	53.8	20.3	44.0	71.0	7.4	14.2	74.0	20.2	64.2	50.4	152.4	621.3
1997	119.8	47.0	118.2	–	–	–	–	–	–	–	–	–	285.0

frequency or intensity of the defoliation (Becker et al. 1997b; Engel et al. 1998). Reductions in root growth after defoliation have been associated with grazing tolerance when linked to subsequent increases in the proportion of carbon allocation to regrowing shoots (Briske and Richards 1995).

The concomitant influence of water stress and defoliation has been less detrimental to root biomass in comparison to a situation where the effects of these stresses have been evaluated separately (Mohammad et al 1982; Simoes and Baruch 1991). This response has been attributed to a reduction in transpiratory leaf surface area after defoliation. Root biomass of *Themeda triandra*, however, was not affected by defoliation either with or without water stress (Dube 1999). These studies, however, were conducted under environmentally controlled conditions during either only one or part of one growing cycle.

Rangeland perennial grasses are often defoliated under water stress in the Southern part of the Calden District (Caldenal), a Phytogeographical region of approximately 4 million ha in central Argentina (Busso 1997). Annual rainfall in this area varies between 300 and 500 mm (Busso 1997). Some field studies in these rangelands have determined root growth, and root appearance and disappearance in native perennial grasses defoliated or not at different phenological stages (Distel and Fernández 1988; Becker et al. 1997b). However, no study has yet addressed the cumulative effects of water stress with or without defoliation at various phenological stages on grass root growth, appearance or disappearance under field conditions.

Stipa clarazii Ball, *S. tenuis* Phil. and *S. gynerioides* Phil., three native perennial grass species, have shown different responses to continuous, long-term grazing in rangelands of the south of the Phytogeographical Provinces of the Monte and Espinal (Distel and Bóo 1996). Distel and Bóo (1996) concluded that *Stipa clarazii* is an example of a palatable, dominant, highly competitive grass species under exclosure or light grazing conditions. Under moderate, continuous grazing, this species is replaced by other palatable grasses like *S. tenuis* (Distel and Bóo 1996). Selective grazing of these species, however, has led to their replacement by other unpalatable, early-successional, less competitive grasses such as *S. gynerioides* in semiarid rangelands of central Argentina (Distel and Bóo 1996).

Our objective was to evaluate root growth and root appearance and disappearance in plants of *S. clarazii* and *S. tenuis*, in competition with the undefoliated *S. gynerioides*, when the palatable grasses were either defoliated at different phenological stages under water stress, rainfed or irrigated conditions in the field or remained undefoliated. We hypothesized that (1) root growth is reduced after defoliation at any phenological stage in *S. clarazii* and *S. tenuis* in comparison to undefoliated controls, (2) root growth, and root appearance and disappearance in *S. clarazii, S. tenuis* and *S. gynerioides* are reduced as plant water stress increases, and (3) reductions in root growth as a result of water stress are lower when plants of *S. clarazii* and *S. tenuis* are water-stressed earlier than later or for a longer time period during the growing season.

MATERIALS AND METHODS

Site Description

Studies were conducted at the research field site near the Agronomy Department-CERZOS in Bahía Blanca (38°48′S, 62°13′W). The soil is a typical Haplustol with a petrocalcic horizon at 1.8 m depth. It has a loam-sandy texture, 1.9% organic matter, 7 mg kg^{-1} extractable P (Olsen and Sommers 1982), 0.10% total N and a pH of 7.4. Climate information during the study period (1995, 1996 and early 1997) was provided by a meteorological station located in the research area (Tables 1 and 2).

Experimental Design and Treatments

Between December 1993 and April 1994, 28 experimental plots (1.8 × 1.8 m) were established in the field on unplowed, weeded soil. Plants were obtained from a 20-yr 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 in seven horizontal and vertical rows such that each plant of *S. clarazii* or *S. tenuis* was surrounded by four plants of *S. gynerioides* (Fig. 1). 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 the 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, during the plant quiescent period. Two experimental plots (replicates) were randomly assigned to each water level × defoliation treatment combination, giving a total of 14 treatments (see Defoliation Treatment heading in Fig. 2).

Defoliation Treatments

Plants of *S. clarazii* and *S. tenuis* remained undefoliated (Controls: C) or they were clipped either at their vegetative (V), their internode elongation (E) or at both (VE) phenological stages of development within each water level treatment

Table 2. Range of mean or absolute values for several climate characteristics at the study site during 1995, 1996 and early 1997 (January–March). Time when these values were registered is indicated in parentheses

Climate characteristics		Range
Air Temperature (°C; 0.25 m height)	Monthly mean	6.0 (July 1996) to 24.2 (Jan. 1997)
	Absolute minimum	−11.0 (July 1995) to 10.0 (Jan. 1997)
	Absolute maximum	20.7 (July 1995) to 39.1 (Dec. 1995)
Wind speed (km h^{-1}; 2 m height)	Monthly mean	9.2 (March 1997) to 16.3 (July 1995)
Solar radiation (cal cm^{-2} d^{-1}; 2 m height)	Monthly mean	185 (June 1995) to 851 (Dec. 1995)
Relative air humidity (%; 2 m height)	Monthly mean	56 (Sept. 1995) to 83 (May & Jun. 1996)
Potential evapotranspiration (Thornwaite)[z]	Monthly mean	11 (July 1995 & 1996) to 138 (Dec. 1995)

[z]Villar and Elias (2001).

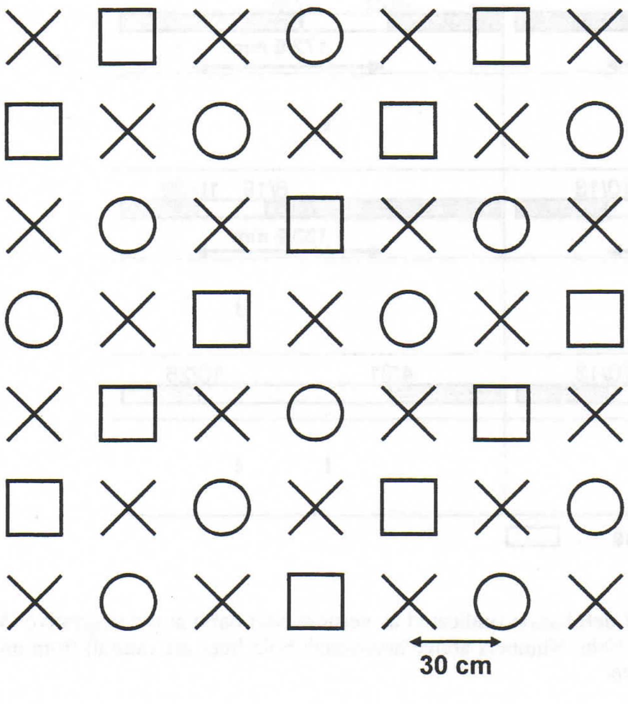

Fig. 1. Disposition of plants of *S. clarazii* (○), *S. tenuis* (□) and *S. gynerioides* (X) within each of 28 experimental field plots.

in 1995 and 1996 (see Fig. 2). Clipping was done at a 5-cm stubble height on 23 May (V) or 27 September (E) or both dates (VE) in 1995, and 12 June (V) or 20 September (E) or both dates (VE) in 1996. The unpalatable *S. gynerioides* remained undefoliated during the study period.

Water Levels

Plants were exposed to rainfed, irrigated or water stress conditions. Rainfed plots received rainfall all year round (Table 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 whenever they reached 60% of field capacity. Periods of irrigation and water stress during 1995 and 1996 are depicted in Fig. 2.

Transparent plastic sheets covered the water-stressed plots whenever rain fell at times when these species are often exposed to water stress in their native environment (Busso 1997): vegetative or early internode elongation or both phenological periods (Fig. 2). Water-stressed plots were surrounded with plastic sheets down to 1.8 m soil depth to prevent lateral movement of water into the plots.

Except for those plots exposed to water stress at VE, the amount of water received in the different treatments from mid-April to mid-October in 1995 and late-April to late-October in 1996 is shown in Fig. 2. All 28 experimental plots received 313.7 mm from mid-October 1995 to late-April 1996, and 487.8 mm from late-October 1996 to March 1997. Water-stress was thus alleviated on the water-stressed plots during these periods by natural rainfall.

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 1200 and 1300h. The youngest, fully expanded leaf blades were taken for these measurements using one tiller per species within each replicated plot and sampling date. From excision to the end of each determination, leaves were cut one at a time and maintained in a plastic bag to reduce water loss (Turner 1981).

A root periscope was used to measure root growth and root appearance and disappearance in plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* (Richards 1984). For this purpose, 57 Pyrex glass tubes (3 cm internal diameter, 100 cm length) were installed in the field at the end of 1994, and in May 1995 and January 1996. Budget constraints allowed installation of glass tubes in only 21 of the 28 experimental plots, and forced us to a stepped placement of these tubes throughout time (see Table 3). One tube was used per species within each plot, except as indicated in Table 3. Two vertical lines, 180° one from another, and horizontal lines

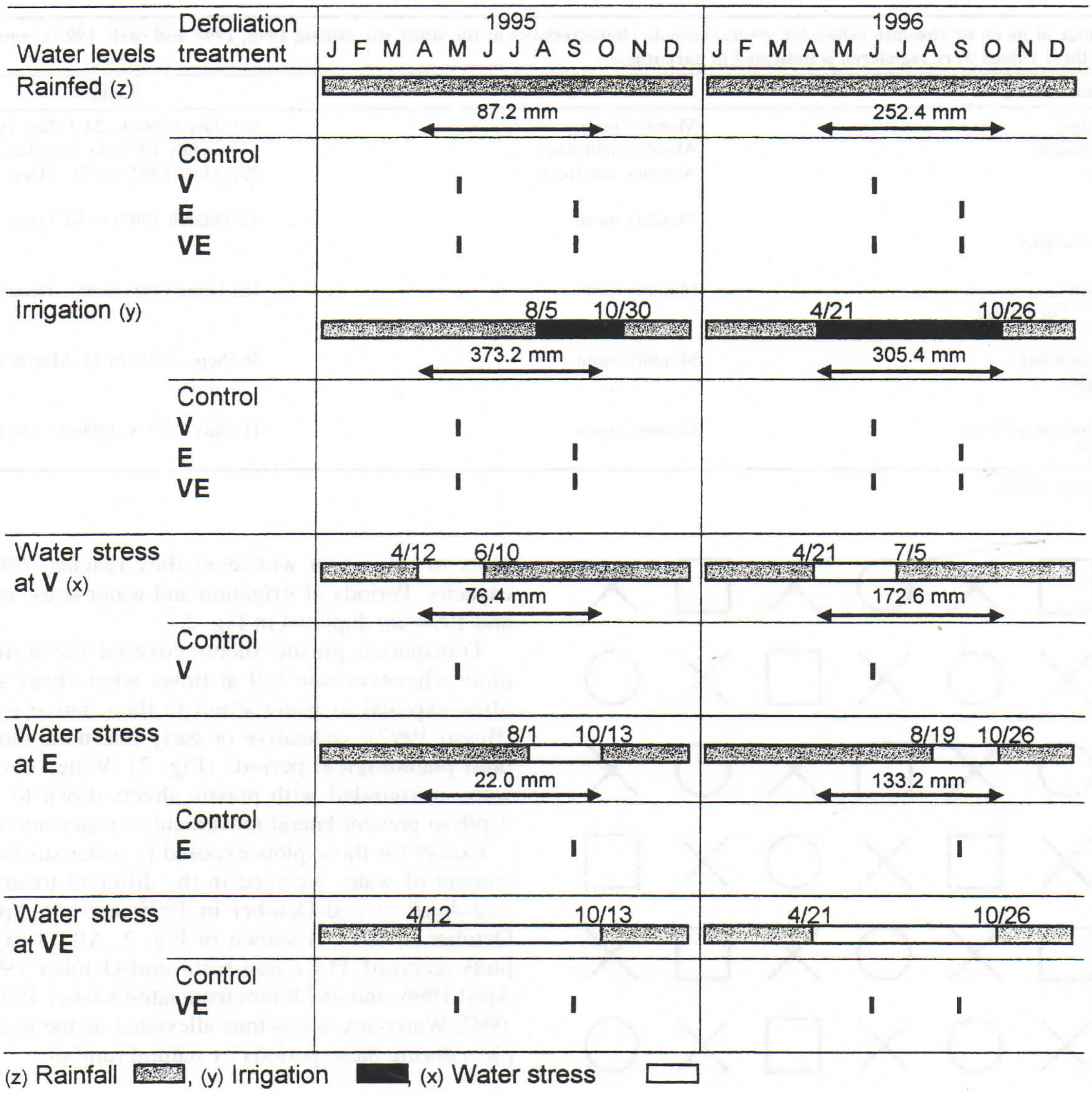

Fig. 2. Periods of imposition of the different water levels and timing of defoliation (indicated as vertical bold bars) at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996. Numbers above horizontal, bold lines are rainfall from mid-April to mid-October in 1995, and from late April to late October in 1996.

spaced at 6.4 cm were engraved on each tube forming 6.4 × 6.4-cm grids. One of these vertical lines was used as a starting point for each set of observations. Further details on installation and use of the root periscope are provided by Becker et al. (1997b).

Root system responses to the different soil water regimes were evaluated in all three species during 1995–1997. However, root system response to defoliation was determined only during 1996 and at the beginning of 1997 in *S. clarazii* and *S. tenuis* under rainfed and water stress conditions. This was caused by delays in tube placement in the corresponding plots during 1995 and 1996 (Table 3). At each sampling date, the number of roots that intercepted any grid line was first counted and then totalled over 0–60 cm of tube length. This provided a total relative root number (TRRN) at these depths. Root appearance and disappearance were also determined for each observation period since the angle of each root interception was registered between successive sampling dates; an average was obtained for these measurements within each water level. Cumulative root appearance or disappearance within each water level was then obtained by summing these average values throughout the study. Thus, root appearance and disappearance between successive samplings can be obtained from cumulative values as changes in these values between any two consecutive sampling periods.

Statistical Analysis

Leaf water potential data were analyzed separately for each date using ANOVA. A split plot design was considered

Table 3. Stepped placement of glass tubes in the different treatments and replicates during 1994–1996

Date	Treatments: Water levels	Treatments: Defoliation	Replicate number[z]
Dec. 1994	Irrigation	Vegetative (V)	1
		Elongation (E)	1 & 2
		Vegetative + elongation (VE)	1
	Rainfed	Control (C)	1
		V	1
		E	1
		VE	1
May 1995	Rainfed	C	2
		V	2
	Water stress at V	C	1[y] & 2
		V	1 & 2
	Water stress at VE	C	1
		VE	1[x]
Jan. 1996	Water stress at E	C	1[y] & 2[y]
		E	1[y] & 2[y]
	Water stress at VE	C	2

[z]Tubes were placed for all three species within each replicate except as indicated.
[y]*S. clarazii* and *S. tenuis*.
[x]*S. clarazii* and *S. gynerioides*.

with this purpose using treatments (14 combinations of water × defoliation levels) as main factor and species as secondary factor. Since the interaction term was not significant ($P \geq 0.09$) on any sampling date, and whenever the treatment factor was significant ($P < 0.05$), two-way ANOVA were subsequently performed. These two-way ANOVA implied two separate analysis. First, defoliation treatments were compared in the rainfed and irrigated plots. Second, defoliation treatments were compared in the plots that had been water-stressed at either V, E or VE stages of plant development. Given that differences between defoliated and undefoliated plants were always not significant ($P > 0.10$), these data were pooled within each water level treatment. Differences among water level treatments were finally tested using GLM procedures because data came from eight replicates for the rainfed and irrigated plots, and from four replicates for the water-stressed plots.

Data analysis for TRRN, and numbers of roots that either appeared or disappeared compared treatments within each date and species using ANOVA; a completely randomized design was considered for this purpose. Treatments with only one replicate were excluded from the analysis. Species needed to be analyzed separately because the number of tubes available for root measurements was different between species.

Counts of the number of root interceptions were transformed to $\log_e$(root counts +1) before statistical analysis to improve normality assumptions. Fisher's LDS test was used for balance data to separate means (Steel and Torrie 1985). Tukey-Kramer's test was used for unbalanced data utilizing a software developed by Salomón, Camina and Winzer (Mathematics Department, National University of the South, Bahía Blanca, Argentina). Non-transformed values are presented in text and figures.

RESULTS AND DISCUSSION

Leaf Water Potentials

Leaf water potentials were similar among defoliation treatments during the study period (data not shown). This agrees with results for Becker et al. (1997a) on *Stipa* and *Piptochaetium* species. Other studies, however, have reported higher leaf water potentials on defoliated than on undefoliated plants of several perennial tussock grasses, a response that has been attributed to conservation of soil water after defoliation (Brown 1995).

Leaf water potentials were similar among water levels in all three species at the beginning and end of each growing cycle (Table 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 (Table 4). Results were similar in 1996, when leaf water potentials were generally lower on water-stressed than on irrigated plants (Table 4). 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 (Table 4). This was likely due to the lower annual rainfall in 1995 than in 1996 (Table 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*.

Root Numbers

In May 1996, TRRN between 0 and 60 cm depth was greater ($P < 0.05$) on plants defoliated at V than on undefoliated controls under rainfed and water stress conditions in *S. clarazii* (Table 5). In August 1996, plants of *S. clarazii* defoliated at V under water stress again had a greater ($P < 0.01$) TRRN than undefoliated plants. These root system responses to defoliation are opposite to results reported in other perennial grass species under rainfed conditions (Becker et al. 1997b; Engel et al. 1998). A greater proportional carbon allocation to regrowing shoot sinks, to the expense for reducing root growth, has been reported as one mechanism conferring a greater competitive ability and defoliation tolerance to many perennial grasses (Briske and Richards 1995) Grazing tolerance in any given species, however, may not necessarily be explained by just one specific characteristic (Hendon and Briske 1997). For example, root length showed a similar response to defoliation on plants of two *Agropyron* species that differ in grazing tolerance (Allen et al. 1989).

Plants of *S. tenuis* that had been defoliated at V or E under water stress had a greater ($P < 0.05$) TRRN than those undefoliated at 0–60 cm depth (Table 5) by the end of December. Lack of root growth reduction after defoliation during 1996 agrees with the results of Becker et al. (1997b) in this species after it was either defoliated at V or E, or remained undefoliated under rainfed conditions. Species relatively less tolerant of defoliation, such as *S. tenuis* when compared with *S. clarazii* (Saint Pierre et al. 2000), can maintain root

Table 4. Midday leaf water potential (MPa) on undefoliated and defoliated plants of *S. clarazii* and *S. tenuis*, and undefoliated plants of *S. gynerioides* which were exposed to irrigated, rainfed or water stress conditions at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996. Each value is an average of *n* = 4–8

	Date											
	1995						1996					
Water level	4/1	5/17	8/31	9/26	10/24	11/29	4/19	6/11	8/15	9/22	11/14	12/21
	(MPa)											
Irrigation	−1.67*a*	−2.72*a*	−2.02*a*	−1.39*a*	−1.33*a*	−1.57*a*	−1.86*a*	−1.47*a*	−1.47*a*	−1.97*a*	−2.11*a*	−2.28*a*
Rainfed	−1.25*a*	−2.07*a*	−2.80*b*	−2.98*b*	−3.05*c*	−2.04*a*	−1.71*a*	−1.55*a*	−1.94*ab*	−2.24*ab*	ND[z]	−2.35*a*
Water stress at V	−1.97*a*	−2.45*a*	−3.14*b*	−3.63*b*	−3.37*c*	−2.22*a*	−1.99*a*	−4.18*c*	−2.35*b*	−2.42*ab*	ND	−2.44*a*
Water stress at E	−1.53*a*	−2.10*a*	−2.59*ab*	−2.98*b*	−2.25*b*	−2.08*a*	−1.93*a*	−1.43*a*	−2.21*ab*	−4.01*c*	−4.49*ab*	−2.31*a*
Water stress at VE	−1.42*a*	−1.89*a*	−3.21*b*	−3.14*b*	−2.32*b*	−2.39*a*	−2.01*a*	−3.10*b*	−3.47*c*	−3.17*bc*	−4.69*b*	−2.50*a*

[z]ND, not determined

[y]Difference between defoliation treatments were not significant and therefore data for all defoliated and undefoliated plants and all three species were averaged per treatment and per date (see text under statistical anlysis in the Materials and Methods section).

a–c Within each date, values followed by different letters are significantly different ($P < 0.05$).

Table 5. Total relative root number between 0 and 60 cm depth during 1996 and early 1997 on plants of *S. clarazii* and *S. tenuis* which were defoliated at either vegetative (V) or internode elongation (E) phenological stage or remained undefoliated (controls, C) under rainfed (R) or water stress (WS) conditions in 1995 and 1996. Each value is an average of *n* = 2 ± the standard error of the mean

	1996				1997
	8 may	28 June	27 Aug.	30 Dec.	26 Feb.
			S. clarazii		
R-C	28.00 ± 15.0	23.50 ± 7.5	51.50 ± 12.5	105.00 ± 29.0	112.00 ± 26.0
R-V	86.50 ± 2.5	60.00 ± 30.0	103.00 ± 23.0	182.50 ± 50.5	207.50 ± 75.5
WS-C-V[z]	16.50 ± 1.5	15.00 ± 3.0	18.50 ± 3.5	83.50 ± 10.5	94.00 ± 12.0
WS-V[z]	43.50 ± 8.5	13.00 ± 0.0	62.00 ± 25.00	117.00 ± 16.0	159.00 ± 28.0
WS-C-E	NR[y]	NR	3.50 ± 3.5	51.00 ± 12.0	59.50 ± 12.5
WS-E	NR	NR	7.00 ± 5.0	61.00 ± 33.0	65.50 ± 44.5
			S. tenuis		
R-C	50.50 ± 27.5	58.50 ± 34.5	127.50 ± 49.5	162.00[x]	168.00[x]
R-V	82.00 ± 19.0	74.50 ± 12.5	108.50 ± 5.5	151.00[x]	199.00[x]
WS-C-V	3.50 ± 0.5	4.50 ± 0.5	5.50 ± 0.5	20.00 ± 6.0	32.00 ± 14.0
WS-V	7.00 ± 5.0	6.50 ± 2.5	16.50 ± 0.5	74.50 ± 36.5	89.00 ± 58.0
WS-C-E	NR	NR	1.50 ± 1.5	41.50 ± 3.5	47.00 ± 12.0
WS-E	NR	NR	4.50 ± 1.5	76.00 ± 16.0	75.00 ± 3.0

[z]Plants remained undefoliated (WS-C-V) or were defoliated (WS-V) at the vegetative stage of development while they were exposed to water stress conditions at this phenological stage.

[y]NR, no roots were registered because tubes were placed during early 1996.

[x]$n = 1$.

growth unabated after defoliation even under low soil moisture conditions (Richards 1984; Dube 1999). This latter strategy, which was true not only for *S. tenuis* but also for *S. clarazii* in our study, contributes to greater soil exploration and access to resources to sustain regrowth in species native to semiarid rangelands (Distel and Fernández 1988; Becker et al. 1997b). Defoliation under water stress can contribute to conservation of soil water (Brown 1995), and may then stimulate root growth, as we observed in early summer.

In February 1997, after alleviation of all treatments TRRN at 0–60 cm depth was similar on defoliated and undefoliated plants of *S. clarazii* and *S. tenuis* in the rainfed and water stress treatments (Table 5). Similar results were obtained by Becker et al. (1997b) in *S. tenuis* and *Piptochaetium napostaense* in the year following defoliation of these species in the field at the vegetative or internode elongation stage of development during 2 consecutive years. Some studies have even reported effects of defoliation on root biomass of perennial grasses only after 3 yr of treatment application (Zhang and Romo 1994).

On average, for defoliated and undefoliated plants within each water level and date, TRRN between 0 and 60 cm depth was similar on plants exposed to rainfed and irrigated conditions in all three species during 1995, and in *S. clarazii* and *S. gynerioides* during 1996 and early 1997 (Table 6). However, water stress at E or VE reduced ($P < 0.05$) TRRN between 0 and 60 cm depth in *S. clarazii* when compared to values obtained under rainfed or irrigated conditions in 1996 and early 1997 (Table 6). In June 1996, plants of this species also showed a lower ($P < 0.05$) TRRN between 0 and 60 cm depth under water stress at V than under better soil moisture levels (Table 6). In plants of *S. tenuis*, TRRN between 0 and 60 cm depth was always lower ($P < 0.05$) under water stress at V or E than under rainfed conditions during 1996 and early 1997 (Table 6). Plants of other grass species have also shown reductions in root length after being exposed

Table 6. Total relative root number between 0 and 60 cm depth during 1995, 1996 and early 1997 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which were exposed to irrigated (I), rainfed (R) or water stress (WS) conditions at the vegetative (V), internode elongation (E) or both stages (VE) of phenological development in 1995 and 1996. Each value is an average of n = 2–6 ± the standard error of the mean

	1995				1996				1997
Water levels	14 Mar.	28 Aug.	1 Nov.	8 Dec.	8 May	28 June	27 Aug.	30 Dec.	26 Feb.
					S. clarazii				
I	49.3 ± 11.0	79.5 ± 32.5	97.8 ± 30.8	125.8 ± 37.3	93.0 ± 0.0	80.5 ± 12.5	131.5 ± 36.5	198.5 ± 25.5	235.5 ± 33.5
R	50.0 ± 8.6	42.8 ± 14.4	50.0 ± 14.7	63.5 ± 19.2	66.8 ± 13.4	49.7 ± 13.0	83.5 ± 13.8	148.0 ± 21.6	165.7 ± 27.5
WS-V		ND[z]	ND	ND	30.0 ± 8.6	14.0 ± 1.4	40.3 ± 16.2	100.3 ± 12.4	126.5 ± 22.5
WS-E	NT[y]	NT	NT	NT	NR[x]	NR	5.3 ± 2.7	56.0 ± 14.6	62.5 ± 19.0
WS-VE		ND	ND	ND	14.0 ± 5.0	14.0[w]	13.0 ± 13.0	36.0 ± 17.5	55.3 ± 5.6
					S. tenuis				
I	54.7 ± 20.9	40.7 ± 9.8	79.0[w]	62.0[w]	PD[v]	PD	PD	PD	PD
R	32.0 ± 2.9	47.0 ± 2.4	40.8 ± 4.1	60.5 ± 12.0	59.8 ± 14.3	59.6 ± 14.0	104.4 ± 21.2	156.5 ± 5.5	165.3 ± 24.6
WS-V		ND	ND	ND	5.3 ± 2.3	5.5 ± 1.2	11.0 ± 3.2	47.3 ± 21.8	60.5 ± 29.4
WS-E	NT	NT	NT	NT	NR	NR	3.0 ± 1.2	58.8 ± 12.0	61.0 ± 9.5
WS-VE		ND	ND	ND	ND	ND	3.0[w]	ND	30.0[w]
					S. gynerioides				
I	27.8 ± 6.5	51.3 ± 14.2	68.8 ± 10.8	98.0 ± 18.2	63.3 ± 4.8	47.3 ± 11.4	94.8 ± 8.2	139.8 ± 10.4	171.8 ± 10.1
R	43.0 ± 11.6	45.3 ± 10.2	53.0 ± 15.2	80.0 ± 13.7	51.2 ± 7.7	42.2 ± 8.4	64.5 ± 8.5	138.0 ± 8.2	153.5 ± 9.8
WS-V		ND	ND	ND	28.7 ± 11.3	9.7 ± 5.2	37.7 ± 6.6	87.3 ± 18.0	93.3 ± 3.0
WS-VE		ND	ND	ND	19.00 ± 5.0	0.5 ± 0.5	12.0 ± 5.0	54.0 ± 3.0	92.5 ± 39.5

[z]ND, not determined
[y]NT, no tubes were available in this treatment during 1995.
[x]NR, no roots were observed becuse tubes were placed during early 1996.
[w]n = 1
[v]PD, no data available during 1996 and 1997 because of plant death.

Table 7. Cumulative root appearence during 1995, 1996 and early 1997 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which were exposed to irrigated (I), rainfed (R) or water stress (WS) conditions at the vegetative (V), internode elongation (E) or both stages (VE) of phenological development in 1995 and 1996. Each value is an average of n = 2–6

	1995				1996					1997
Water levels	9 Apr.	28 Aug.	1 Nov.	8 Dec.	8 May	28 June	27 Aug.	12 Nov.	30 Dec.	26 Feb.
					S. clarazii					
I	27.33	46.83	65.50	94.16	103.16	115.66	144.66	161.16	188.16	217.16
R	16.00	20.00	24.50	34.10	48.60	55.27	77.07	96.07	117.07	135.52
WS-V		ND[z]	ND	ND	ND	1.75	15.50	31.50	52.50	73.75
WS-E		NT[y]	NT	NT	NR[x]	NR	ND	15.50	36.00	46.25
WS-VE		ND	ND	ND	ND	2.00	8.00	ND	ND	21.67
					S. tenuis					
I	23.50	38.50	63.50[w]	79.50[w]	PD[v]	PD	PD	PD	PD	PD
R	11.50	11.50	18.50	34.83	44.83	55.33	73.58	89.08	111.08	138.58
WS-V		ND	ND	ND	ND	2.00	6.33	16.33	22.33	33.08
WS-E		NT	NT	NT	NR	NR	ND	8.50	22.00	31.50
					S. gynerioides					
I	17.67	17.67	31.92	59.92	73.92	76.92	95.42	111.75	136.42	167.42
R	24.00	27.00	32.83	44.23	61.57	69.23	84.90	104.40	134.07	156.87
WS-V		ND	ND	ND	ND	0.00	16.50	ND	ND	28.50
WS-VE		ND	ND	ND	5.00	5.50	11.00	ND	ND	40.00

[z]ND, not determined
[y]NT, no tubes were available in this treatment during 1995.
[x]NR, no roots were observed becuse tubes were placed during early 1996.
[w]n = 1
[v]PD, no data available during 1996 and 1997 because of plant death.

to water stress than to irrigated conditions (Mohammad et al. 1982; Simoes and Baruch 1991; Asseng et al. 1998).

Similar to results in *S. clarazii* and *S. tenuis*, root growth was also lower under water stress than under higher soil water levels in the unpalatable *S. gynerioides*. Early in 1996 (8 May), *S. gynerioides* had a lower (P < 0.05) TRRN between 0 and 60 cm depth under water stress at VE than in the irrigated treatment (Table 6). In subsequent sampling dates during this year, this species continued to show a lower (P < 0.05) TRRN between 0 and 60 cm under water stress at V or VE than under rainfed and irrigated conditions (Table 6).

Table 8. Cumulative root appearence during 1995, 1996 and early 1997 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which were exposed to irrigated (I), rainfed (R) or water stress (WS) conditions at the vegetative (V), internode elongation (E) or both stages (VE) of phenological development in 1995 and 1996. Each value is an average of n = 2–6

	1995				1996					1997
Water levels	9 Apr.	28 Aug.	1 Nov.	8 Dec.	8 May	28 June	27 Aug.	12 Nov.	30 Dec.	26 Feb.
					S. clarazii					
I	11.00	30.00	39.33	50.67	87.17	101.67	108.67	134.17	140.17	148.17
R	9.00	25.00	29.25	32.05	37.55	51.22	55.82	67.15	73.65	87.65
WS-V		ND[z]	ND	ND	ND	8.50	10.75	13.75	21.75	35.75
WS-E		NT[y]	NT	NT	NR[x]	NR	ND	1.00	7.50	15.25
WS-VE		ND	ND	ND	ND	5.00	7.00	ND	ND	13.00
					S. tenuis					
I	12.50	41.50	43.50[w]	65.50[w]	PD[v]	PD	PD	PD	PD	PD
R	5.00	ND	12.00	17.33	25.83	35.33	40.33	55.33	68.33	86.33
WS-V		ND	ND	ND	ND	1.00	2.67	2.67	6.67	12.67
WS-E		NT	NT	NT	NR	NR	ND	0.50	3.50	9.25
					S. gynerioides					
I	4.00	24.00	32.25	42.75	50.42	63.17	65.17	77.83	85.83	96.83
R	5.00	30.00	34.17	36.77	37.77	47.10	52.27	61.27	68.60	82.60
WS-V		ND	ND	ND	ND	15.00	16.50	ND	ND	31.17
WS-VE		ND	ND	ND	2.00	9.00	9.50	ND	ND	14.50

[z]ND, not determined
[y]NT, no tubes were available in this treatment during 1995.
[x]NR, no roots were observed becuse tubes were placed during early 1996.
[w]n = 1
[v]PD, no data available during 1996 and 1997 because of plant death.

The effects of imposing water stress at different phenological stages on root growth were observed in August (before defoliation at E) and December 1996. In August, TRRN between 0 and 60 cm depth was lower ($P < 0.05$) on plants of *S. clarazii* and *S. tenuis* being exposed to water stress at E than on those that had previously been subjected to water stress at V (Table 6). By the end of 1996, plants of *S. clarazii* showed a lower ($P < 0.05$) TRRN between 0 and 60 cm depth after being water-stressed at VE compared to V (Table 6).

Root Appearance and Disappearance

On average, for each water level, cumulative root appearance was always greater ($P = 0.08$) under irrigated than under rainfed conditions in *S. clarazii* during 1995 (Table 7). On 28 June 1996, this variable was also greater ($P < 0.05$) in the irrigated treatment than under conditions of water stress at V in *S. clarazii* (Table 7). Cumulative root disappearance in this species was also greater ($P < 0.05$) in the irrigated than in the rainfed treatment by early December 1995, and greater in the irrigated than in the water stress treatment by November 1996 (Table 8). Although plants of *S. tenuis* showed a greater root appearance and disappearance under rainfed than under water stress conditions in 1996, differences were only significant ($P < 0.05$) by the end of August for root appearance (Table 7) and in June and November for root disappearance (Table 8). Finally, root appearance and disappearance in *S. gynerioides* were greater ($P < 0.05$) under irrigated than rainfed conditions at the end of 1995 (Tables 7 and 8). Similar to our results, root growth and root appearance and disappearance were decreased by soil moisture reductions in other herbaceous species (e.g., Brown 1995; Fresnillo Fedorenko et al. 1995).

Cumulative root appearance was similar to or greater than, but not lower than cumulative root disappearance in all three species and water levels. This would help explain the continued root growth in these species during the period of study (Table 6), which agrees with results of Distel and Fernández 1988) and Becker et al. (1997b) in field-grown plants of *S. tenuis* and *P. napostaense*. Similar to reports of Hansson et al. (1994) and Majdi (1996), most roots observed in the glass tubes had a diameter ″ 1 mm. An uninterrupted fine root turnover, such as the one observed in our study, would contribute to a continued supply of soil resources (i.e., water), which is so important for plant growth in arid and semiarid regions (Brown 1995).

CONCLUSIONS

Defoliation of *S. clarazii* and *S. tenuis*, did not reduce root growth under any water level or defoliation treatment in our study. On the contrary, root growth on defoliated plants was similar to or higher than on undefoliated plants of these species. Maintenance of root growth after defoliation in *S. clarazii* and *S. tenuis* would allow greater soil exploration and access to resource to sustain regrowth in their native, semiarid environments. Total relative root number and root appearance and disappearance in *S. clarazii*, *S. tenuis* and *S. gynerioides* were similar to or lower, but not higher, under water stress than under better soil moisture levels. Albeit to a lower rate, maintenance of root growth under water stress in all three species would contribute to a continued exploration for soil resources. Effects of water stress on root growth of *S. clarazii* and *S. tenuis* were more detrimental when the stress occurred later or for a longer period of time than earlier during the growing season.

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