

Effects of Defoliation at Varying Soil Water Regimes on Aboveground Biomass of Perennial Grasses

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*We evaluated the effects of defoliation under varying soil water regimes on above-ground biomass of perennial grasses native to semiarid rangelands of central Argentina. The palatable species *Stipa tenuis* and *S. clarazii* were either defoliated or not for two years within a uniform competitive background of *S. gynerioides*, an unpalatable species which remained nondefoliated until the end of the study in 1997. *Stipa gynerioides* increased biomass when soil water was plentiful compared to water stress conditions. This species showed a greater percentage of medium- to large-size plants under rainfed and irrigated conditions than under water stress conditions. Greater shading of *S. gynerioides* as soil water content increased may have contributed to determine a greater proportion of small-size plants in *S. clarazii* and of dead plants in *S. tenuis* in the irrigated than in the water stress treatment. Results suggested that grazing of perennial forage grasses under high soil water contents speeded rather than slowed their degradation when they were competing within a matrix of ungrazed, unpalatable perennial tussock grasses.*

Keywords Argentina, irrigation, regrowth, semiarid rangelands, water stress, *Stipa* species

Grazing by domestic herbivory has commonly been associated with changes in species composition in rangelands throughout the world (Milchunas & Lauenroth, 1993). Palatable grasses are often replaced by unpalatable grasses or woody perennials or both in grasslands which are grazed both continuously and severely (Archer & Smeins, 1991). Herbivore-induced modification of competitive interactions between palatable and unpalatable vegetation through selective herbivory appears to be the dominant mechanism leading to such species replacement process (Anderson & Briske, 1995).

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Plant productivity of perennial grasses can be reduced because of the detrimental effects of water stress on growth parameters, regardless of the intensity, frequency, or timing of defoliation (Brown, 1995). However, the intensity, frequency, and timing of the defoliation event can influence biomass production (Briske & Richards, 1995). Perennial grasses defoliated during early developmental stages can have a similar or greater biomass compared to nondefoliated plants, but defoliation in late developmental stages generally affects plant biomass negatively (Becker et al., 1997b). Additionally, plant biomass responses to defoliation are influenced by the composition of defoliated and nondefoliated neighbors (Saint Pierre et al., 2000).

In arid and semiarid environments, soil water availability affects plant productivity, and regrowth and development after defoliation (Brown, 1995). Limited soil water availability has been shown to reduce plant biomass and increase plant mortality in several perennial grass species (Busso & Richards, 1995; Volaire, 1995). Plant mortality in *Bouteloua curtipendula* (Michx.) Torr., however, was not affected during a dry year on either ungrazed or moderately grazed areas (Briske & Hendrickson, 1998).

Effects of defoliation and soil water availability on plant biomass generally interact to reduce regrowth in grass species (Busso & Richards, 1995), but this interaction can vary with both the intensity and frequency of such events (Mohammad et al., 1982; Busso & Richards, 1995). Although limited soil water availability or increased defoliation frequency generally reduces plant biomass, detrimental effects of defoliation have been reduced under water stress conditions (Mohammad et al., 1982). These authors reported that removing 40% of above-ground biomass from *Agropyron desertorum* (Fisch. ex Link) Schult. and *Elymus junceus* Fisch. plants experiencing severe soil water stress conditions increased plant biomass compared to nondefoliated plants. This response is partially attributed to reductions in transpiratory surface area after defoliation which conserves soil water and improves plant water status (Briske & Richards, 1995). Higher plant water status has often been associated with greater biomass production in perennial grasses (Williams & Black, 1994). However, prolonged water stress conditions and continued defoliation dramatically reduced plant biomass in both the grazing tolerant *Agropyron desertorum* and the grazing sensitive *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* (Busso & Richards, 1995).

We investigated the effects of defoliation under varying soil water regimes on above-ground biomass production of *Stipa clarazii* Ball., *S. tenuis* Phil., and *S. gynerioides* Phil., all C₃ perennial grasses native to the South of the Calden Phyto-geographical District, a region of about 4 million hectares in Central Argentina (Busso, 1997). The first two species have a high forage value while the third is an undesirable, unpalatable tussock grass (Cano, 1988). Our objective was to evaluate plant productivity under natural (rainfed), plentiful (irrigated), or water stress (temporary rainout shelters) soil water conditions. The two palatable grasses (*S. clarazii* and *S. tenuis*) were defoliated at different phenological stages (vegetative, elongated, or both), whereas the unpalatable perennial tussock grass (*S. gynerioides*) remained nondefoliated.

Materials and Methods

Study Area and Climate Characteristics

This study was conducted at the research field site of the Agronomy Department-CERZOS in Bahía Blanca (38°48' S, 62°13' W) during 1995–1997. Soil is a typical Haplustol (Luis Sánchez, Dpto. Agronomía UNSur, Argentina, personal communication) with a petrocalcic horizon at 1.8 m. During 1971–1990, mean annual precipitation was 662.8 mm; mean air temperature 15°C; absolute minimum and

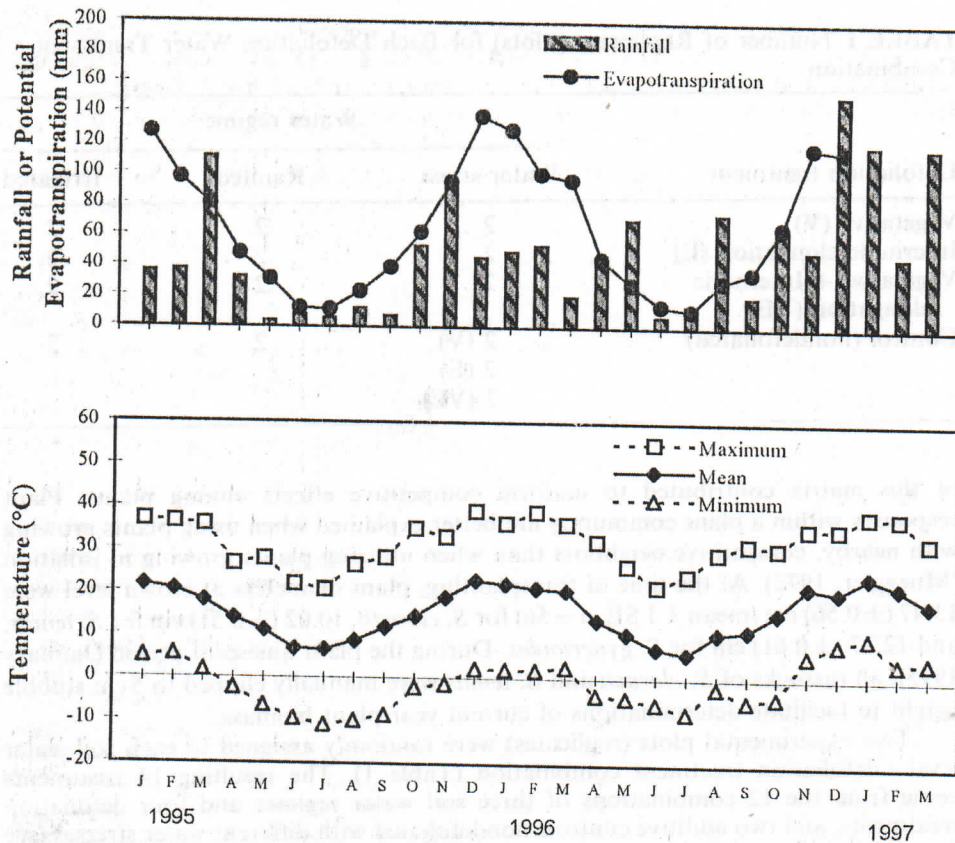


FIGURE 1 (A) Monthly rainfall and mean monthly potential evapotranspiration (Thornthwaite), and (B) absolute minimum and maximum and mean monthly air temperatures at 0.25 m above the soil surface during 1995, 1996, and early 1997. Measurements were taken using a meteorological station located 100 m away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

maximum air temperatures -10.5°C (July) and 42.9°C (January), respectively; mean relative humidity 64.0%; and wind speed 6.44 m sec^{-1} . During the study period, rainfall, air temperature, and potential evapotranspiration were provided by a meteorological station located at the experimental site (Figure 1). Annual rainfall during 1995 and 1996 was 67.4% and 93.7%, respectively, of the long-term mean for the study region.

Plant Material and Experimental Design

Twenty-eight experimental plots ($1.8 \times 1.8\text{ m}$) were established from transplants on unplowed, hand-weeded soil from December 1993 to April 1994. Distance between plots was 4 m. Plants were obtained from a 20-year enclosure to domestic herbivory located southeast of La Pampa Province ($38^{\circ}45'\text{ S}$, $63^{\circ}45'\text{ W}$) at the South of the Calden Phytogeographical Region. Plants of the three species were arranged within each plot in a matrix in which each plant of *S. clarazii* and *S. tenuis* (palatable species) was surrounded by four plants of *S. gynerioides* (unpalatable species), with plant spacing 30 cm. Each plot contained 49 plants (12 of *S. clarazii*, 12 of *S. tenuis* and 25 of *S. gynerioides*) for a total of 1372 transplants used in this study. Formation

TABLE 1 Number of Replicates (Plots) for Each Defoliation-Water Treatment Combination

Defoliation treatment	Water regime		
	Water stress	Rainfed	Irrigated
Vegetative (V)	2	2	2
Internode elongation (E)	2	2	2
Vegetative + Internode elongation (VE)	2	2	2
Control (nondefoliated)	2 (V) 2 (E) 2 (VE)	2	2

of this matrix contributed to uniform competitive effects among plants. Plant responses within a plant community are better explained when using plants growing with nearby, competitive neighbors than when utilizing plants growing in isolation (Mueggler, 1972). At the time of transplanting, plant diameters at crown level were 13.47 (± 0.56) cm (mean ± 1 SE, $n = 56$) for *S. clarazii*, 10.02 (± 0.51) cm for *S. tenuis*, and 12.27 (± 0.61) cm for *S. gynerioides*. During the plant quiescent period (January 1995), all tussocks of *S. clarazii* and *S. tenuis* were manually clipped to 5 cm stubble height to facilitate determinations of current year plant biomass.

Two experimental plots (replicates) were randomly assigned to each soil water level \times defoliation treatment combination (Table 1). The resulting 14 treatments come from the 12 combinations of three soil water regimes and four defoliation treatments, and two additive controls nondefoliated with different water stresses (see Figure 2). Measurements during the three growing seasons were conducted on the same groups of plants. Thus, we report on the cumulative effects of several water and defoliation treatments. Our experiment is another contribution to the understanding of results that are essentially variable in space and time, and our results should be interpreted within the context of the specific conditions under which they were obtained.

Treatments

Defoliation

Plants of *S. clarazii* and *S. tenuis* received one of the four defoliation treatments: vegetative stage (V), elongation stage (E), both the vegetative and elongation stages (VE), or nondefoliated (controls) during 1995 and 1996. Plants were clipped to 5 cm and biomass retained for estimating production. Plants were defoliated on 23 May (V) and 27 September (E) in 1995, and 12 June (V) and 20 September (E) in 1996. Plant biomass produced by nondefoliated plants and regrowth produced by defoliated plants were destructively harvested by clipping to 5 cm in mid-January in 1996 and 1997. Total plant biomass produced by defoliated plants was calculated by adding that removed by defoliation and regrowth. *Stipa gynerioides* remained nondefoliated in 1995 and 1996, since it is not consumed by cattle (Cano, 1988). However, all plants of this species were clipped to 5 cm at the end of the study on 12 March 1997 to estimate biomass production in the different treatments. Plant biomass was oven-dried at 60°C for 72 h prior to weighing.

Soil Water

Soil water treatments imposed were (1) natural (rainfed), (2) plentiful (irrigated), and (3) water stress (temporary rainout shelters). A drip irrigation system was used

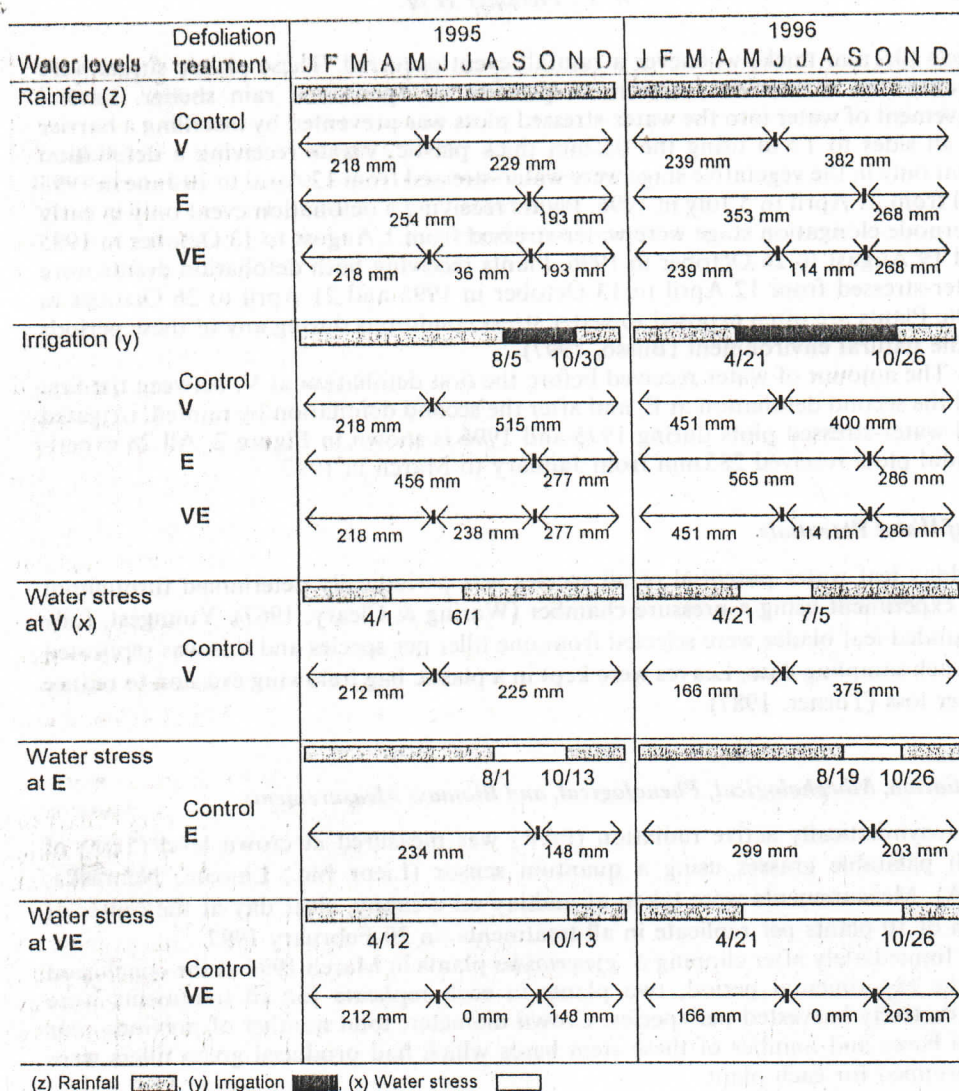


FIGURE 2 Periods of imposition of the different water regimes and timing of defoliation (indicated as vertical, bold bars) at the vegetative (V), internode elongation (E), or both (VE) phenological stages in 1995 and 1996. Numbers above horizontal, bold lines are rainfall before the first defoliation, between the first and second defoliation, and after the second defoliation in 1995 and 1996. No water was received in the water-stressed plots during imposition of this treatment.

to add supplemental water to the plentiful water treatment plots. These plots were irrigated whenever soil moisture content dropped below 60% of its field capacity; this was controlled with soil tensiometers installed in these plots. The amount of water added to reach field capacity was calculated using software (Smith, 1992, 1993) which takes into account soil and climate characteristics, and plant characteristics similar to the investigated species. The period of irrigation equaled that of imposition of water stress in 1996 (21 April to 26 October), although irrigation was initiated later (5 August to 30 October) than the imposition of water stress in 1995 (12 April to 13 October). Water-stressed plots were covered with transparent plastic

sheets (0.2 mm thick) whenever a rainfall event occurred. These plastic sheets were mounted on a wooden structure to provide an open-sided rain shelter. Lateral movement of water into the water-stressed plots was prevented by installing a barrier on all sides to 1.8 m using the 0.2 mm thick plastic. Plants receiving a defoliation event only in the vegetative stage were water-stressed from 12 April to 10 June in 1995 and from 21 April to 5 July in 1996. Plants receiving a defoliation event only in early internode elongation stage were water-stressed from 1 August to 13 October in 1995 and 19 August to 26 October in 1996. Plants receiving both defoliation events were water-stressed from 12 April to 13 October in 1995 and 21 April to 26 October in 1996. Plants are often exposed to water stress conditions during any of these periods in the natural environment (Busso, 1997).

The amount of water received before the first defoliation at V, between the first and the second defoliation at E, and after the second defoliation by rainfed, irrigated and water-stressed plots during 1995 and 1996 is shown in Figure 2. All 28 experimental plots received 285 mm from January to March in 1997.

Leaf Water Potentials

Midday leaf water potential of all species was periodically determined throughout the experiment using a pressure chamber (Waring & Cleary, 1967). Youngest, fully expanded leaf blades were selected from one tiller per species and this was replicated on each sampling date. Leaves were kept in a plastic bag following excision to reduce water loss (Turner, 1987).

Radiation, Morphological, Phenological, and Biomass Measurements

Photosynthetically active radiation (PAR) was measured at crown level (5 cm) of both palatable grasses using a quantum sensor (Licor Inc., Lincoln, Nebraska, USA). Measurements were taken at midday on a sunny, clear day at the center of each of 10 plants per replicate in all treatments on 20 February 1997.

Immediately after clipping *S. gynerioides* plants in March 1997 at the conclusion of the experimental period, two plants in each replicate for all treatments were destructively harvested per species. Crown diameter, total number of previous-year stem bases and number of these stem bases which had produced green tillers were determined for each plant.

Within each water level, total annual biomass obtained in mid-January 1997 for *S. clarazii* and *S. tenuis*, and in March 1997 for *S. gynerioides* were grouped in three size-classes on a per plant basis: small, medium and large. Small-size plants had 0 g, <4 g, and <65 g; medium-size plants had 0–1 g, 4–24 g, and 65–265 g, and large-size plants had >1 g, >24 g, and >265 g in *S. tenuis*, *S. clarazii* and *S. gynerioides*, respectively. In the case of *S. tenuis*, plants that produced 0 g per plant were dead.

Statistical Analysis

A split-plot design using ANOVA where combinations of defoliation and soil water availability were the main factor and species were the secondary factor was used to analyze leaf water potential data for each sampling date. Because the interaction term of treatment combinations and species was not significant ($P \geq 0.09$) on any sampling date, we subsequently performed two-way ANOVA whenever the treatment combination factor was significant ($P < 0.05$). These two-way ANOVA implied two separate analyses. Firstly, defoliation treatments were compared between the rainfed and irrigated plots. Secondly, defoliation treatments were compared between plots which had been water-stressed at the either V or E or VE stages of plant

development. Given that differences between defoliated and nondefoliated plants were not always significant ($P > 0.10$), these data were pooled for each soil water 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.

Plant biomass data was analyzed separately for each date and species using a one-way ANOVA in a completely randomized design with 14 treatments. Photosynthetically active radiation data were analyzed using a completely randomized nested (10 plants per replicate) ANOVA design. Data of proportion of previous-year stem bases which produced green tillers were analyzed using a completely randomized split (species) and nested (two plants per replicate) ANOVA design. Whenever F tests were significant at $P < 0.05$, means were separated using Fisher's LSD or Tukey-Kramer's test for balanced or unbalanced data, respectively. Prior to statistical analyses, data were transformed to improve normality assumptions (Steel & Torrie, 1985) as follows: to $\ln(g/\text{plant} + 1)$ in *S. clarazii* and *S. tenuis*, and to $[(\sqrt{g/\text{plant} + 1}) - 1]$ in *S. gynerioides* for above-ground plant biomass, and to \arcsin of the proportion for percentage of previous-year stems which produced green daughters. Nontransformed values are presented in Figures 3–7.

Results and Discussion

During the study period, leaf water potentials were similar ($P > 0.10$) among defoliation treatments within each species and soil water treatment (data not shown). This agrees with results of Busso and Richards (1993) and Becker et al. (1997a) for *Agropyron*, *Stipa* and *Piptochaetium* species. Higher leaf water potentials on defoliated than on nondefoliated plants for several perennial tussock grasses have been reported, however, and this response has been attributed to conservation of soil water after defoliation (Brown, 1995).

Leaf water potentials were similar among water regimes for all three species at the beginning and end of each growing season (Figure 3). Plants of all three species, however, had lower ($P < 0.05$) leaf water potentials under water stress than plentiful soil water conditions during August–October 1995 (Figure 3). Results were similar in 1996, when leaf water potentials were generally lower on water-stressed than on plentiful soil water treatment plants (Figure 3). Leaf water potentials were more variable on plants in the rainfed plots compared to the other two soil water treatments. Under these conditions, leaf water potentials were lower than those in the irrigated plots in 1995, and higher than those in the water-stressed plots in 1996 (Figure 3). This is likely attributable to the lower annual rainfall in 1995 than in 1996 (Figure 1).

During the study period, leaf water potentials were usually similar between species (data not shown). In mid-August, September, and December of 1996, however, leaf water potentials were 16% greater ($P < 0.05$) for *S. clarazii* and 22% greater ($P < 0.05$) for *S. tenuis* compared to those for *S. gynerioides*.

Total annual plant biomass of *S. clarazii* and *S. tenuis* were similar ($P > 0.15$) among defoliation treatments and among soil water treatments in both years (Figure 4). These results are similar to those obtained for other perennial grasses which were defoliated at different phenological stages or remained nondefoliated (Becker et al., 1997b). However, successive defoliations during late phenological stages of plants for at least two years reduced plant biomass of *Agropyron* species under different levels of soil water availability (Busso & Richards, 1995).

Plant biomass was lower in 1996 than in 1995 for all treatments and for both palatable species (Figure 4). This occurred despite rainfed and water-stressed plots receiving more rainfall in 1996 than in 1995 (Figures 1 and 2). Similar results have

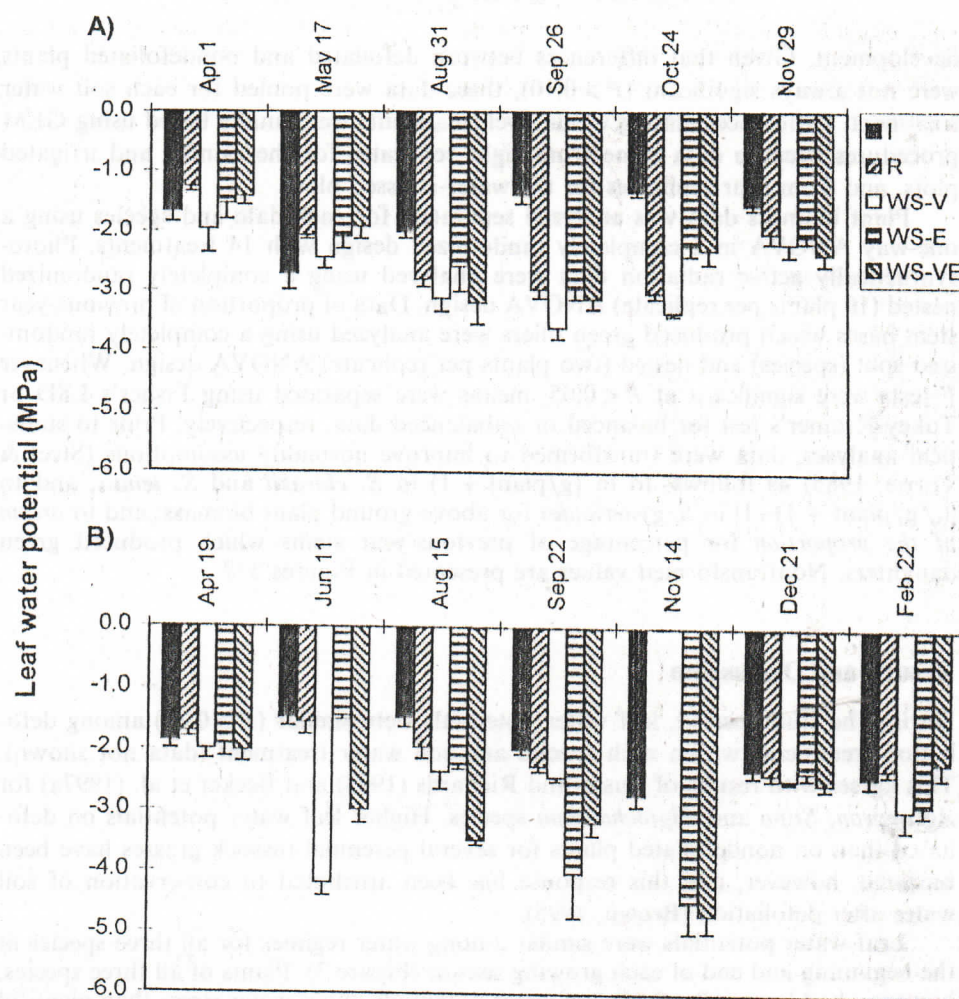


FIGURE 3 Midday leaf water potential on nondefoliated and defoliated plants of *S. clarazii* and *S. tenuis*, and nondefoliated plants of *S. gynerioides* which were exposed to irrigated (I), rainfed (R), or water stress (WS) conditions at the vegetative (V), internode elongation (E), or both (VE) phenological stages in 1995 (A) and 1996 (B). Values presented are averaged over defoliation treatment. Differences between defoliation treatments were not significant, and therefore, data for all defoliated and nondefoliated plants and all three species were averaged per treatment and per date. No data are available for plants which were rainfed or water-stressed at the vegetative phenological stage on 14 Nov 1996. Each histogram is an average of $n = 4-8$. Vertical bars represent 1 SEM.

been obtained for other perennial grass species under various levels of soil water availability where plant biomass was reduced by the cumulative effects of successive, once-a-year defoliations (Busso & Richards, 1995; Becker et al., 1997b). This response has been attributed to a reduction of photosynthetic leaf surface area and reduced numbers and size of replacement tillers (Busso & Richards, 1995; Becker et al., 1997b). In a parallel study, Flemmer et al. (2002) report that the numbers of axillary buds originating daughter tillers on parent tillers of *S. clarazii* were 32% lower at the beginning of 1997 than at the initiation of the study in 1995. Parent

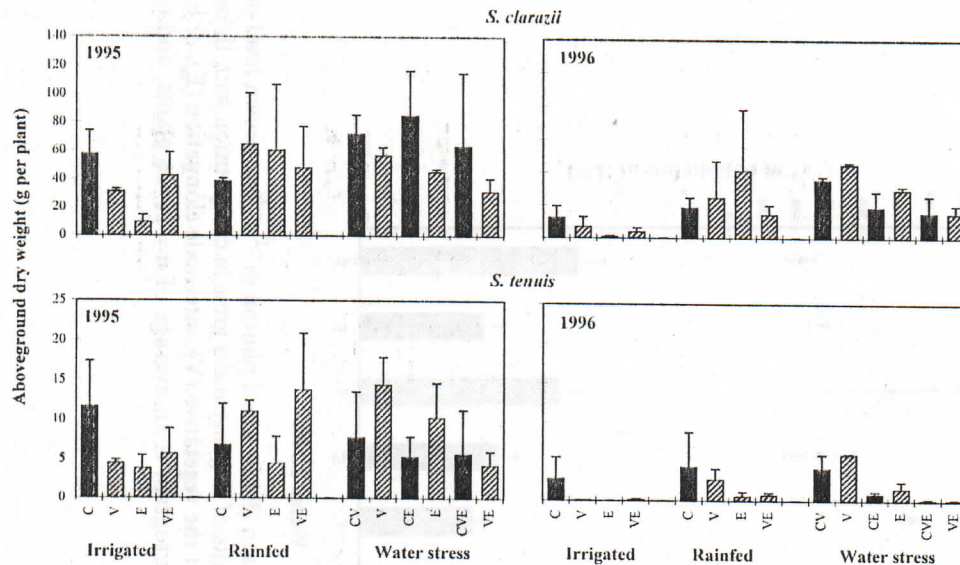


FIGURE 4 Annual plant biomass of *S. clarazii* and *S. tenuis* plants which remained nondefoliated (C: Control) or were defoliated at the vegetative (V), internode elongation (E), or both (VE) phenological stages under irrigated, rainfed, or water-stressed conditions in 1995 and 1996. Each histogram is an average of $n = 12$ plants. Vertical bars represent 1 SEM. Note change of scale between species.

tillers of *S. tenuis*, however, produced a similar amount of green daughters at both times (Flemmer et al., 2002).

Plant biomass of *S. gynerioides* was greater when grown in competition with defoliated than with nondefoliated plants of *S. tenuis* and *S. clarazii* across soil water treatments, although differences were only significant ($P < 0.05$) under water stress conditions (Figure 5). Because of greater plant production in the presence of defoliated than nondefoliated competitors, this unpalatable tussock grass likely gained a competitive advantage over the palatable grasses by obtaining a greater share of soil resources under water stress conditions. In contrast, nondefoliated subordinate perennial grasses did not respond positively to selective defoliation of dominant grass species under rainfed conditions in east-central Texas (Hendon & Briske, 2002).

Plant biomass of *S. gynerioides* was greater ($P < 0.05$) under rainfed and plentiful soil water treatments than under water stress conditions (Figure 5). As a result, photosynthetically active radiation (PAR) at the crown level of palatable grasses was reduced by more than 50% ($P < 0.01$) in the rainfed and plentiful soil water treatments than under water stress conditions at the conclusion of the experiment (Figure 5). This was partially associated with a greater percentage of medium- to large-size plants of *S. gynerioides* under rainfed and plentiful soil water treatments than under water stress conditions (Figure 6). Except on plants of *S. tenuis*, which were water-stressed at VE, greater shading of *S. gynerioides* as soil water content increased very likely contributed toward determining a greater proportion of small-size plants in *S. clarazii* and of dead plants in *S. tenuis* in the plentiful soil water treatment than in the water-stressed treatment (Figure 6). As reported by Flemmer et al. (1999), the smaller size of defoliated plants in the plentiful soil water treatment was partially due to a lower tiller growth under these than lower soil water content conditions.

Plant biomass of *S. clarazii* was >2-fold higher than *S. tenuis* across treatments (Figure 4), which concurs with previously reported values for these species (Saint

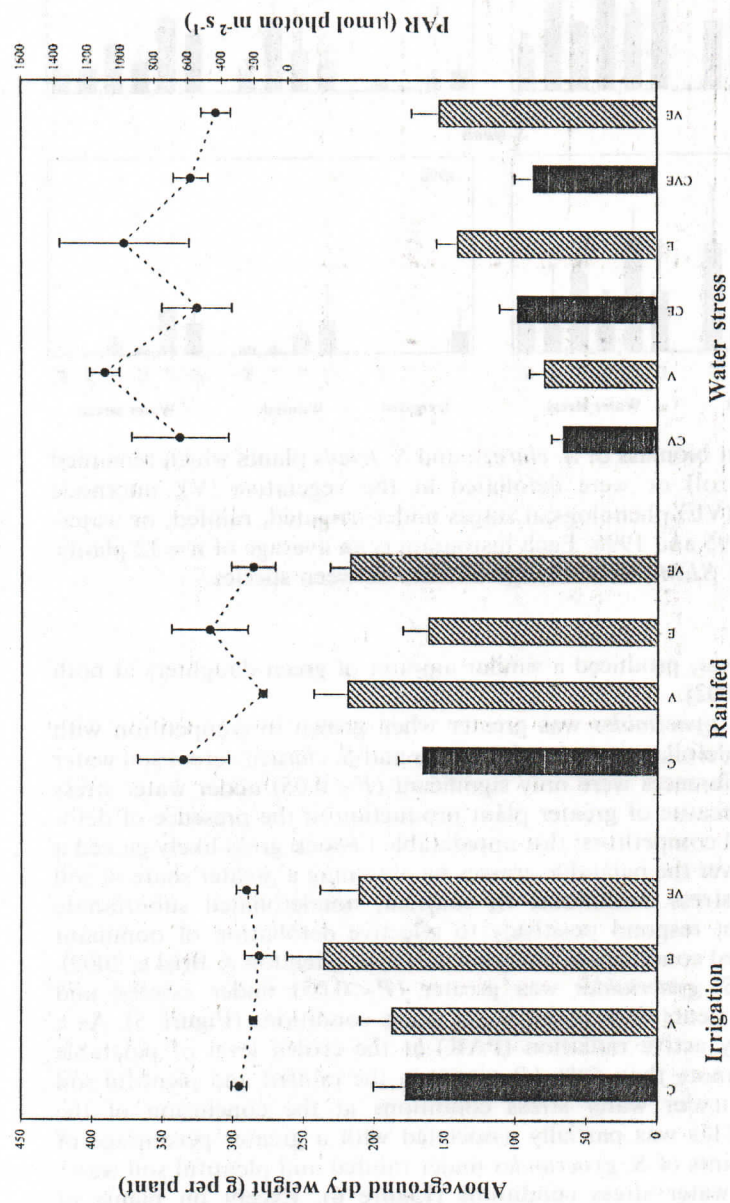


FIGURE 5 Plant biomass of *S. ginerioides* plants, and photosynthetically active radiation (PAR: $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) at crown level of *S. clarazii* and *S. tenius* plants during early 1997. During 1995 and 1996, nondefoliated plants of *S. ginerioides* grew in competition with those of *S. clarazii* and *S. tenius* which remained nondefoliated (C: Control) or were defoliated at the vegetative (V), internode elongation (E), or both (VE) phenological stages under irrigated, rainfed or water-limited conditions. Each histogram is an average of $n = 21-26$ plants, and each symbol is an average of $n = 10$. Vertical bars represent 1 SEM.

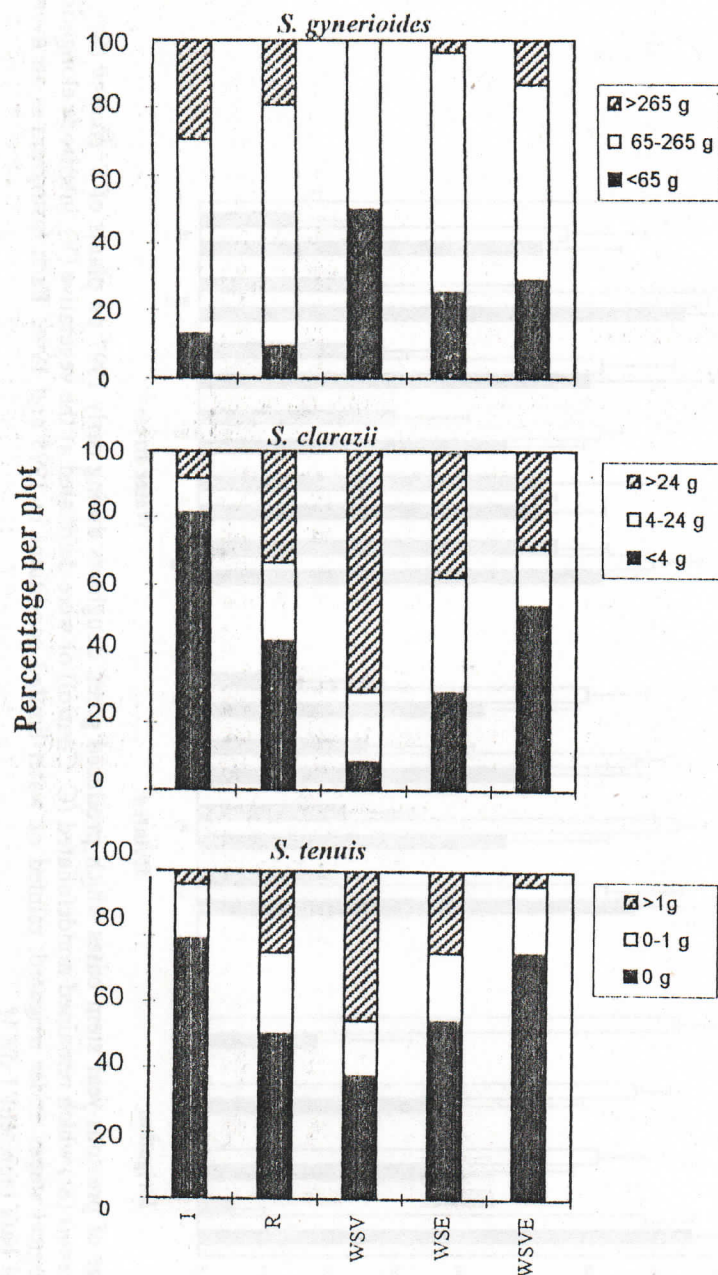


FIGURE 6 Percentage of plants per replicate plot in different size classes (g per plant) for plants of *S. gynerioides*, *S. clarazii*, and *S. tenuis* which were exposed to irrigated (I), rainfed (R), or water-stressed (WS) conditions during the vegetative (V), internode elongation (E), or both (VE) phenological stages of development in 1997. All plants had been exposed to these water treatments since 1995. Plants of *S. tenuis* which produced 0 g/plant were dead. Number of harvested plants within each water regime ranged from 52 to 102 in *S. gynerioides*, and 24 to 48 in *S. clarazii* and *S. tenuis*.

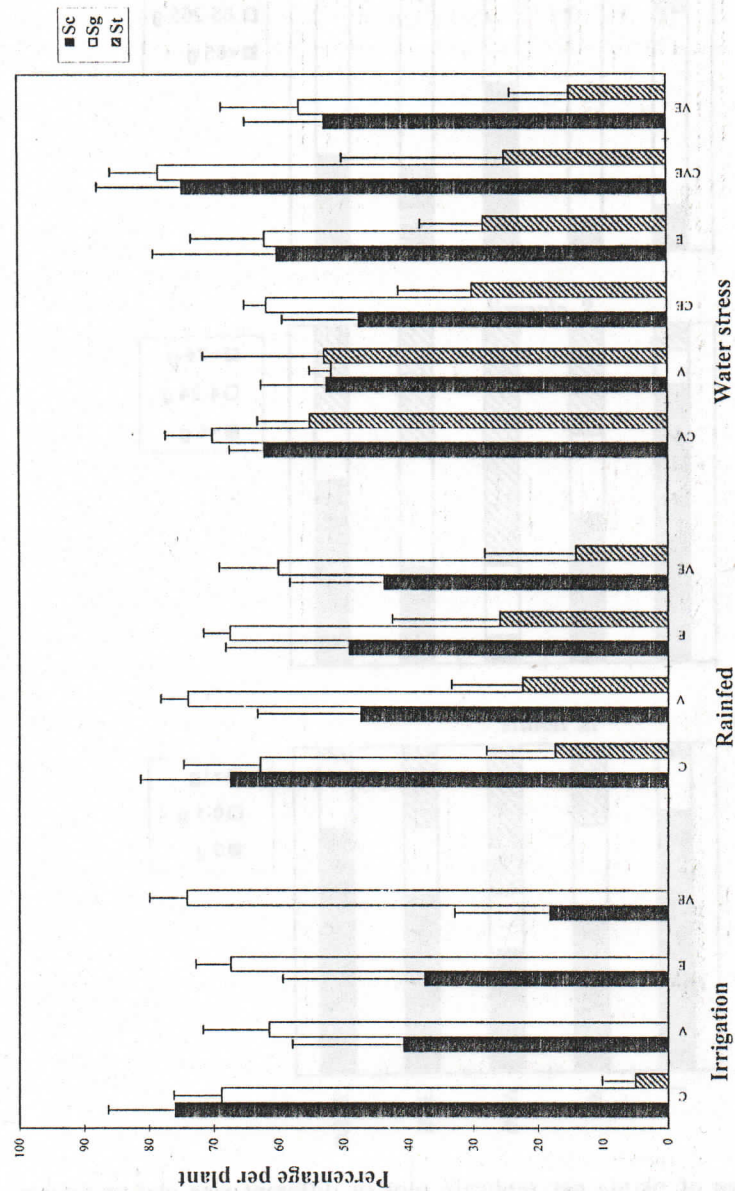


FIGURE 7 Percentage of previous-year stem bases which produced green daughters during early 1997 on plants of *S. clarazii* (Sc), *S. gynerioides* (Sg) and *S. tenuis* (St) which remained nondefoliated (C: Control) or were defoliated at the vegetative (V), internode elongation (E), or both (VE) phenological stages under irrigated, rainfed or water-limited conditions in 1995 and 1996. Each histogram is an average of $n = 56$ plants. Vertical bars represent 1 SEM.

Pierre et al., 2000). For comparative purposes, plant biomass of *S. gynerioides* was more than five times greater than that of the palatable species (Figures 4 and 5). This response can be attributed, at least partially, to differences in plant basal diameter increases for the three species during the experiment. Plant basal diameter of *S. gynerioides* plants increased by 11%, whereas it decreased by 19% in *S. clarazii* and by 48% in *S. tenuis*. This response was associated, at least in part, to a greater ($P < 0.01$) percentage of stem bases which produced green daughters in *S. gynerioides* than in the other two species (Figure 7).

Conclusions

Increasing growth of the nondefoliated, unpalatable *S. gynerioides* with increasing soil moisture overshadowed expected detrimental effects of water stress conditions on growth of the two palatable species. Greater shading of *S. gynerioides* as soil water content increased may have contributed toward determining a greater proportion of small-size plants in *S. clarazii* and of dead plants in *S. tenuis* in the irrigated than in the water stress treatment. These results suggest that grazing of perennial forage grasses under high soil water availability would speed up, rather than slow down, degradation of individual plants when they are competing with ungrazed, unpalatable perennial tussock grasses in a natural setting.

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