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Bud viability in perennial grasses: Water stress and defoliation effects

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Abstract

Effects of the timing and frequency of defoliation under different levels of soil water availability were evaluated on bud metabolic activity and subsequent outgrowth in the desirable (i.e., palatable) *Stipa clarazii* Ball. and *S. tenuis* Phil. in competition with the undesirable (i.e., unpalatable) *S. gynerioides* Phil. Field studies on these native, perennial tussock grasses were conducted from 1995 to 1997 in temperate, semiarid Argentina. Our working hypotheses were 1) axillary bud activation and subsequent tillering are lower under water stress than under higher soil moisture conditions in *S. clarazii*, *S. tenuis*, and *S. gynerioides*, 2) when compared to undefoliated controls, activation, and subsequent outgrowth of axillary buds reach similar or greater values in *S. clarazii* and *S. tenuis* after early (vegetative stage of development), but not late (during internode elongation) defoliations or increased defoliation frequency (vegetative+ during internode elongation) during each growing cycle. Additionally, it was expected that the greatest reduction of axillary bud metabolic activity and outgrowth would ocurr on plants defoliated twice, and 3) axillary bud activation and succeeding tillering are greater in the undefoliated *S. gynerioides* when the desirable species are defoliated than when they remain undefoliated. With a few exceptions, our results led us to reject all 3 hypotheses. Responses of axillary buds were in general specific to the species and treatments, to sampling time, and to the cumulative effects of previous treatments. This makes predictions of plant responses of these species under natural field conditions difficult, where they are often defoliated under water stress.

Key Words: *Stipa clarazii*, *Stipa tenuis*, *Stipa gynerioides*, bud metabolic activity, bud outgrowth, water stress, defoliation, perennial grasses, semiarid Argentina

Succesive tiller production by the development of axillary buds compensates for annual tiller mortality, allowing persistence of perennial grasses (Jewis 1972). Production of new tillers, and of leaf blades, stems, and sheaths from remaining apical and intercalary meristems after defoliation contributes to reestablishment of removed plant tissues (Briske 1991). However, regrowth will depend upon activation and subsequent outgrowth of axillary buds when most, if not all, apical and intercalary meristems are removed by defoliation (Busso et al. 1989). Any factor, such as water stress, which decreases availability, metabolic activity or capacity to grow out of axillary buds would limit reestablishment of photosynthetic canopy of grazed perennial grasses, compromising their persistence in the plant community (Briske and Richards 1995).

Tiller production can be lower on defoliated than on undefoliated plants in perennial grasses exposed to water stress, rainfed or irrigated conditions (Busso et al. 1989, Deregibus and Trlica 1990, Bullock et al. 1994, Hendrickson and Briske 1997). Water stress can also reduce tiller production in defoliated and undefoliated plants; this response has been observed under natural droughts (Bullock et al.

Resumen

Se evaluó el efecto de la época y la frecuencia de defoliación bajo distintos contenidos hídricos del suelo sobre la actividad metabólica de las yemas axilares y rebrote subsiguiente en las especies desables (palatables) *S. clarazii* Ball. y *S. tenuis* Phil. en competencia con la especie indeseable (no palatable) *S. gynerioides* Phil. Los estudios se efectuaron en el campo en estas especies de gramíneas perennes nativas desde 1995 a 1997 en los pastizales templados, semiáridos de Argentina. Nuestras hipótesis de trabajo fueron 1) la activación y rebrote subsiguiente de las yemas axilares son menores bajo condiciones de estrés hídrico que bajo mayores contenidos hídricos del suelo en *S. clarazii*, *S. tenuis* y *S. gynerioides*, 2) en comparación a los controles no defoliados, la activación y rebrote subsiguiente de las yemas axilares alcanzan valores similares o mayores en *S. clarazii* y *S. tenuis* después de defoliaciones tempranas (estadio fenológico vegetativo) pero no luego de defoliaciones tardías (durante la elongación de los entrenudos) o ante una mayor frecuencia de defoliación (vegetativo+elongación de entrenudos) en cada ciclo de crecimiento. Además, se esperó que la mayor reducción en la actividad metabólica de las yemas axilares y rebrote subsiguiente se produjera en las plantas defoliadas con mayor frecuencia, y 3) la activación y subsiguiente rebrote de las yemas axilares son mayores en las plantas no defoliadas de *S. gynerioides* cuando las especies deseables son defoliadas que cuando permanecen sin defoliar. Con unas pocas excepciones, las 3 hipótesis fueron rechazadas con los resultados obtenidos. Las respuestas de las yemas axilares fueron en general específicas a las especies y tratamientos, a la época de muestreo, y a los efectos acumulativos de tratamientos previos. Esto enfatiza la dificultad de predecir la respuesta de estas especies bajo condiciones naturales, en las que normalmente son defoliadas bajo condiciones de estrés hídrico.

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1994, Briske and Hendrickson 1998) or controlled environmental conditions (Busso et al. 1989). Mueller and Richards (1986) and Busso et al. (1989) suggested that the degree of bud metabolic activity would be comparatively more important than bud number or viability in explaining reduced tiller production after defoliation with or without water stress.

Timing of defoliation can also influence tiller production. For example, tiller production was stimulated by defoliation during internode elongation, but not during earlier growth stages in *Agropyron desertorum* (Fisch. ex Link) Schult. (Olson and Richards 1988). This response is partially due to apical meristem removal which stimulates axillary bud activation after eliminating the inhibition source (Murphy and Briske 1992). However, lack of apical meristem removal has also stimulated tiller production on defoliated plants (Deregibus and Trlica 1990). In addition to direct inhibitory effects of the apical meristem on bud outgrowth, both physiological mechanisms and their interaction with environmental variables and resource availability should be considered when studying factors involved in regulating tillering in perennial grasses (Murphy and Briske 1992). For example, bud activation and subsequent outgrowth can be stimulated or suppressed by modifying light quality and quantity at the plant stem bases (Casal et al. 1986, Deregibus and Trlica 1990, Devkota et al. 1997, Gautier et al. 1999).

Knowledge of axillary bud dynamics is essential when considering production and persistence of perennial grasses in the plant community. A few studies have evaluated the effects of various biotic and abiotic factors on this important component of plant growth and development. For example, they include evaluation of defoliation at different phenological stages (*Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack: Becker et al. 1997), water stress with or without defoliation (*Agropyron* species: Busso et al. 1989), and fire (*S. tenuis*: Busso et al. 1993; *S. tenuis, S. gynerioides* Phil. and *P. napostaense*: Peláez et al. 1997). The objective of this study was to evaluate the effects of defoliation at different phenological stages and under different levels of soil water availability on the degree of bud metabolic activity and bud outgrowth in 3 perennial grasses: *Stipa clarazii* Ball., *S. tenuis* and *S. gynerioides*. *Stipa clarazii* and *S. tenuis* are 2 desirable, palatable species which compete with the undesirable, unpalatable *S. gynerioides* in the semiarid, temperate rangelands of Central Argentina. We hypothesized that activation of axillary buds and succeeding tillering 1) would be lower under water stress than under more favorable soil moisture conditions in *S. clarazii*, *S. tenuis*, and *S. gynerioides*, 2) when compared with undefoliated controls, would reach similar or greater values in *S. clarazii* and *S. tenuis* after early (vegetative stage of development), but not late (during internode elongation) defoliations or increased defoliation frequency (vegetative+ during internode elongation) during each growing cycle. Additionally, we expected that the greatest reduction of the studied plant variables would ocurr on plants defoliated twice, and 3) would be greater in the undefoliated *S. gynerioides* when the desirable species are defoliated than when they are not. However, values for these parameters in *S. gynerioides* will be greater after late or more frequent than early defoliations of *Stipa clarazii* and *S. tenuis.* Results of this study are important to gain understanding of the responses of these species to the most common disturbances at the study region: grazing under water stress conditions.

Materials and Methods

Study Site

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, 1996, and early 1997. Soil is a typical Haplustol (Luis Sánchez, Dpto. Agronomía UNSur, pers. comm.) with a petrocalcic horizon at 1.8 m depth. A meteorological station at the experimental site measured rainfall, air temperature, relative humidity, wind speed, solar radiation, and potential evapotranspiration (Fig. 1).

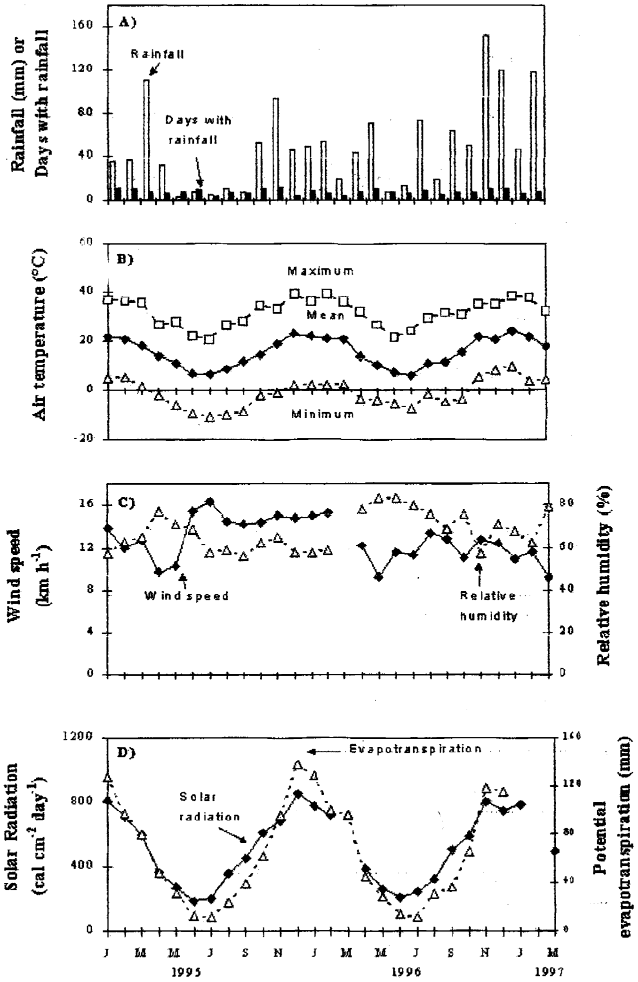

Fig. 1. A) Monthly rainfall (mm) and number of rainy days, B) Absolute minimum and maximum and mean monthly air temperatures (°C) to 0,25 m above the soil surface, C) Mean monthly wind speed (km hour^{-1}) to 2 m above the soil surface and mean monthly relative humidity (%), and D) Mean monthly solar radiation (cal cm^{-2} day^{-1}) and potential evapotranspiration (mm, Thornthwaite) during 1995, 1996 and early 1997. Measurements were taken using a meteorological station located 100 m away from the experimental plots.

Plant material

Studies were conducted on *Stipa clarazii* Ball., *S. tenuis* Phil. and *S. gynerioides* Phil., all C_3 perennial grasses native to the South of the Calden Phytogeographical District, a region of about 4 million hectares in Central Argentina. The first 2 species have a high forage value whereas the latter is an undesirable, unpreferred tussock grass (Cano 1988). Tillering starts with fall rains in all 3 species, although it extends into winter, spring, and even summer if rainfalls are abundant (Giorgetti et al. 2000). Recent studies have shown that *S. clarazii* has a greater competitive ability and tolerance to defoliation than *S. tenuis* (Saint Pierre et al. 2000a, 2000b) and the undesirable species *Stipa trichotoma* Nees, *S. gynerioides*, and *Stipa ambigua* Speg. (Moretto and Distel 1997, Saint Pierre et al. 2000a, 2000b).

Experimental design

During December 1993–April 1994, 28 experimental plots (1.8 x 1.8 m) were established at the field site from transplants on unplowed, weeded soil. Distance among plots was 4 m. Plants were obtained from a 20 year-exclosure to domestic animals located southeast of La Pampa Province (38° 45'S, 63° 45'W) at the South of the Calden Phytogeographical Region. Plants of the 3 species were placed 30 cm from one another in intersecting rows forming a matrix where each plant of *S. clarazii* and *S. tenuis* was surrounded by 4 plants of *S. gynerioides*. Desirable species plants were always present at each plot vertex. This matrix contributed to uniform competitive effects among plants. Plant responses within a plant community are better explained by using plants growing with nearby, competitive neighbors than by utilizing plants growing in isolation (Mueggler 1972, McNaughton 1992). There were 49 plants on each plot (12 of *S. clarazii*, 12 of *S. tenuis* and 25 of *S. gynerioides*) making a total of 1372 transplants for the whole study. At the time of transplanting, plant diameters at crown level were 13.47 ± 0.56 cm ($\bar{X}$ ± 1SE, n = 56) for *S. clarazii*, 10.02 ± 0.51 cm for *S. tenuis*, and 12.27 ± 0.61 cm for *S. gynerioides*. In January 1995, during the plant quiescent period, all tussocks of *S. clarazii* and *S. tenuis* were manually clipped leaving 5 cm stubble height. In this manner, only current year growth was included in subsequent harvests to determine biomass. Two experimental plots (replicates) were randomly assigned to each water level x defoliation treatment combination, giving a total of 14 treatments (see Water levels and Defoliation treatment headings in Fig. 2).

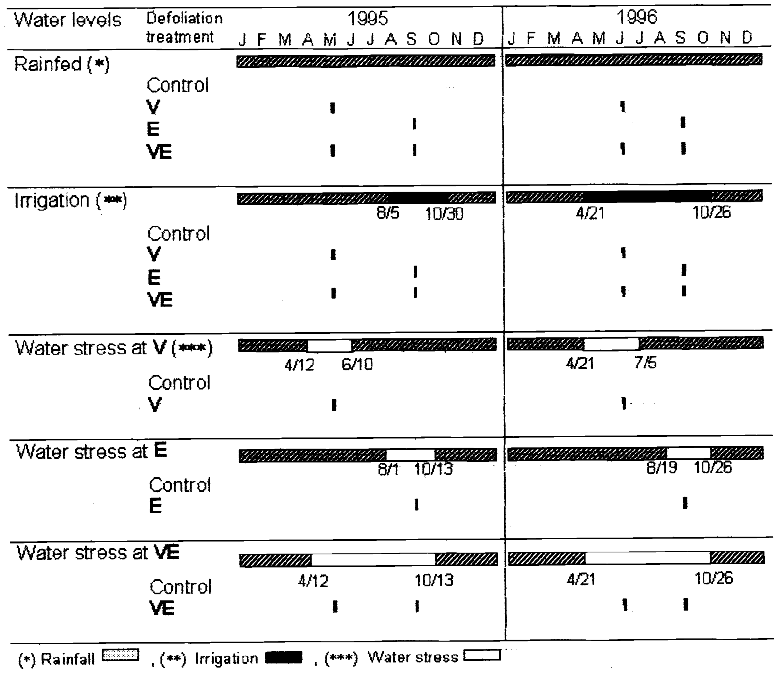

Fig. 2. Periods of imposition of the different water levels and timing of defoliation (indicated as vertical solid bars) at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996.

Measurements during the 3 growing seasons were repeated measures on the same groups of plants. Thus, we report on the cumulative effects of several water and defoliation treatments. Since we worked with an enormous unit of work, labor, and budget constraints made replication of our study in space and time impossible. Despite the fact that we place emphasis on statistical differences, caution is called for extrapolating our results. These should be better viewed under the specific conditions they were obtained. However, our study provided a unique opportunity for a simultaneous comparison of plant responses to various water levels, and to the timing and frequency of defoliation on species having differences in competitive ability.

Treatments

Soil water levels

Timing of application of water level and defoliation treatments during each year is shown in Fig. 2. A set of plots received rainfall all year round (rainfed plots). Irrigated plots received rainfall plus additional water with a drip irrigation system. In the irrigated treatment, plots were watered whenever soil moisture content dropped below 60% of field capacity as determined with soil tensiometers. The amount of water added to these plots was calculated using software (Smith 1992, 1993) which accounted for soil and climate characteristics at the study site, and plant characteristics of species similar to those investigated. Water-stressed plots were covered with transparent plastic sheets (0.2 mm thick) whenever rain fell during the vegetative (V) or early internode elongation (E) or VE phenological stage of development (Fig. 2). Plants are often exposed to water stress conditions during any of these periods in their natural environment (Busso 1997, Fernández and Busso 1999). Plastic sheets were mounted on a specially designed wooden structure that provided an open-sided rain shelter. Lateral movement of water into the water-stressed plots was prevented by surrounding these plots with plastic sheets (0.2 mm thick) up to 1.8 m depth. Plants were exposed to water stress before, during and until 3 weeks after application of the defoliation treatments.

Except for plots exposed to water stress in the VE stage, the amount of water received when the different water levels were imposed (mid-April to mid-October in 1995 and late-April to late-October in 1996) was 373.2 mm in 1995 and 305.4 mm in 1996 in the irrigated plots, 87.2 mm in 1995 and 252.4 mm in 1996 in the rainfed plots, 76.4 mm in 1995 and 172.6 mm in 1996 after alleviation of water stress in the V stage, and 22.0 mm in 1995 and 133.2 mm in 1996 before imposition

Table 1. Midday leaf water potential (MPa) on plants of *S. clarazii, S. gynerioides* and *S. tenuis* during 1995. *Stipa clarazii* and *S. tenuis* were either defoliated or remained undefoliated (Controls: C) at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed, irrigated or water stress conditions. Plants of *S. gynerioides* grew in competition with the other 2 species but remained undefoliated. Each value is the mean (+/-SE) of n=2. Values without SE come from n=1.

	Treatments		1995					
	Water levels	Defoliation	1 Apr	17 May	31 Aug	26 Sep	24 Oct	29 Nov
			(MPa)					
S. clarazii	Irrigation	C	-1.00 -	-2.10 (0.20)	-3.33 (0.28)	-3.33 (0.08)	-3.60 (0.40)	-1.98 (0.78)
		V	-0.88 (0.23)	-2.30 (0.00)	-2.75 (0.25)	-3.05 (0.55)	-3.28 (0.13)	-1.83 (0.83)
		E	-1.30 (0.40)	-2.65 -	-2.78 (0.28)	-3.28 (0.73)	-2.78 (0.38)	-2.00 (0.65)
		VE	-0.85 (0.55)	-2.33 (0.38)	-2.55 (0.10)	-2.95 (0.15)	-2.80 (0.30)	-2.03 (0.88)
	Rainfed	C	-1.75 (0.05)	-2.83 (0.38)	-2.33 (0.18)	-1.40 (0.10)	-1.43 (0.13)	-2.50 (0.55)
		V	-1.58 (0.43)	- -	-1.35 (0.15)	-1.28 (0.58)	-0.65 (0.15)	-1.30 (0.10)
		E	-1.43 (0.38)	-2.60 -	-2.03 (0.03)	-0.85 (0.35)	-1.18 (0.53)	-1.75 (0.15)
		VE	-1.68 (0.03)	-1.30 -	-1.63 (0.28)	-1.38 (0.58)	-1.10 (0.00)	-1.90 (0.10)
	Water stress V	C	-0.65 -	-2.80 (0.10)	-3.13 (0.03)	-3.25 (0.30)	-4.15 (0.80)	-2.28 (0.08)
		V	-1.65 (0.25)	-2.63 (0.43)	-2.93 (0.13)	-3.83 (0.38)	-3.78 (0.13)	-1.85 (0.15)
	Water stress E	C	-0.80 -	-2.60 (0.20)	-2.08 (0.08)	-3.33 (0.08)	-2.35 (0.15)	-2.50 (0.05)
		E	-1.10 (0.10)	-3.00 -	-3.80 (1.60)	-3.35 (1.00)	-2.03 (0.23)	-2.23 (0.23)
	Water stress VE	C	-0.80 -	-2.08 (0.98)	-2.85 (0.05)	-3.85 (0.55)	-1.83 (0.83)	-2.75 (0.25)
		VE	-1.25 (0.55)	-2.35 (0.45)	-2.45 (0.05)	-2.83 (0.18)	-2.13 (0.18)	-3.10 (0.45)
S. gynerioides	Irrigation	C	-0.50 -	-1.95 (0.85)	-3.28 (0.18)	-2.88 (0.18)	-3.60 (0.60)	-1.65 (0.35)
		V	-1.55 (0.75)	-1.70 (0.60)	-3.00 (0.05)	-3.05 (0.25)	-2.95 (0.15)	-2.40 (0.25)
		E	-0.70 (0.10)	-2.60 -	-2.50 (0.00)	-2.38 (0.68)	-3.25 (0.05)	-1.93 (0.23)
		VE	-0.35 (0.15)	-1.50 (0.60)	-2.50 (1.20)	-3.70 (0.70)	-3.15 (0.25)	-1.88 (0.63)
	Rainfed	C	-1.75 (0.75)	-2.88 (0.23)	-2.75 (0.45)	-1.83 (0.58)	-1.58 (0.28)	-1.63 (0.28)
		V	-1.80 (0.80)	- -	-2.10 (0.40)	-1.23 (0.28)	-1.25 (0.05)	-1.55 (0.85)
		E	-1.85 (0.95)	-2.30 -	-2.10 (0.60)	-1.08 (0.63)	-1.35 (0.15)	-1.73 (0.48)
		VE	-1.20 (0.70)	-2.80 -	-1.90 (0.70)	-1.05 (0.20)	-1.50 (0.10)	-1.28 (0.08)
	Water stress V	C	-1.80 -	-1.75 (0.55)	-2.90 (0.50)	-4.53 (0.73)	-2.88 (0.23)	-2.75 (0.25)
		V	-2.60 (0.70)	-2.58 (0.23)	-3.08 (0.63)	-3.45 (0.20)	-3.53 (0.08)	-2.33 (0.03)
	Water stress E	C	-0.30 -	-1.45 (0.95)	-2.10 (1.00)	-2.33 (0.88)	-2.05 (0.30)	-2.13 (0.28)
		E	-1.65 (0.85)	-2.90 -	-2.38 (0.73)	-2.60 (0.60)	-2.08 (0.18)	-2.25 (0.35)
	Water stress VE	C	-2.70 -	-2.08 (1.08)	-4.13 (0.23)	-3.60 (0.10)	-2.90 (0.90)	-1.80 (0.20)
		VE	-1.30 (1.10)	-1.45 (0.95)	-2.08 (0.63)	-2.35 (0.40)	-2.28 (0.03)	-2.38 (0.33)
S. tenuis	Irrigation	C	-1.20 -	-2.60 (0.60)	-2.75 (0.50)	-2.93 (0.18)	-2.90 (0.40)	-1.53 (0.48)
		V	-2.00 (0.30)	-2.35 (0.25)	-2.80 (0.35)	-2.63 (1.03)	-2.53 (0.43)	-2.10 (0.45)
		E	-1.70 (0.10)	-2.40 -	-2.28 (0.28)	-2.65 (0.10)	-2.75 (0.05)	-2.50 (0.15)
		VE	-1.95 (0.05)	-1.78 (0.28)	-3.15 (0.10)	-2.95 (0.45)	-3.00 (0.10)	-2.68 (0.13)
	Rainfed	C	-2.05 (0.05)	-2.45 (0.95)	-1.45 (0.35)	-1.20 (0.25)	-1.15 (0.05)	-1.18 (0.13)
		V	-1.78 (0.68)	- -	-2.68 (0.13)	-1.73 (0.78)	-1.48 (0.38)	-1.65 (0.00)
		E	-1.45 (0.25)	-2.10 -	-2.43 (0.23)	-1.73 (0.38)	-1.60 (0.50)	-1.20 (0.10)
		VE	-1.75 (0.15)	-1.10 -	-1.45 (0.10)	-1.88 (0.38)	-1.70 (0.50)	-1.23 (0.28)
	Water stress V	C	-1.90 -	-2.88 (0.53)	-4.00 (0.80)	-3.65 (0.15)	-3.03 (0.78)	-2.33 (0.48)
		V	-1.65 (0.75)	-2.05 (0.05)	-2.80 (0.30)	-3.05 (0.40)	-2.88 (0.58)	-1.78 (0.93)
	Water stress E	C	-1.60 -	-2.25 (0.15)	-3.13 (0.48)	-3.43 (0.23)	-2.78 (0.93)	-1.65 (0.55)
		E	-1.85 (0.05)	-2.40 -	-2.10 (0.60)	-2.78 (0.23)	-2.20 (0.40)	-1.75 (0.35)
	Water stress VE	C	-1.30 -	-1.65 (0.55)	-4.15 (0.75)	-2.80 (0.10)	-2.30 (0.20)	-2.10 (0.85)
		VE	-1.70 (0.10)	-1.95 (0.85)	-3.58 (0.53)	-3.43 (0.03)	-2.53 (1.53)	-2.23 (0.13)

of water stress at the E stage. Thereafter, 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.

Defoliation treatments

Within each water level, plants of *S. clarazii* and *S. tenuis* remained undefoliated (Controls: C) or were defoliated at either V or E or VE stage of development during 1995 and 1996. Clipping left 5–7 cm stubble height on 23 May (V) or 27 September (E) in 1995, and 12 June (V) or 20 September (E) in 1996 (Fig. 2). *Stipa gynerioides* was not defoliated in 1995 and 1996 since it is not consumed by cattle (Cano 1988, Moretto and Distel 1997). However, all plants of this species were clipped to 5–7 cm stubble height at the end of the study (12 March 1997) to determine biomass production in the different treatments.

Leaf water potential

Determinations of leaf water potential provided a measure of plant water stress. Mid-day leaf water potential was periodically measured in all species using a pressure chamber during 1995, 1996,, and early 1997 (Waring and Cleary 1967). Youngest, fully expanded leaves were taken for these measurements; one tiller was used per species and replicate on each sampling date. Leaves were kept in a plastic bag from excision to end of each determination to reduce water loss (Turner 1987).

Table 2. Midday leaf water potential (MPa) on plants of *S. clarazii, S. gynerioides* and *S. tenuis* during 1996 and early 1997. *Stipa clarazii* and *S. tenuis* were either defoliated or remained undefoliated (Controls: C) at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed, irrigated or water stress conditions during 1996. These plants had been defoliated under these water levels during 1995. Plants of *S. gynerioides* grew in competition with the other 2 species but remained undefoliated. Plants of all 3 species received natural rainfall during early 1997. Each value is the mean (+/-SE) of n=2.

	Treatments		1996						1997
	Water levels	Defoliation	19 Apr	11 Jun	15Aug	22 Sep	14 Nov	21 Dec	22 Feb
						(MPa)			
S. clarazii	Irrigation	C	-1.88 (0.08)	-0.85 (0.45)	-1.80 (0.45)	-2.03 (0.13)	- -	-2.38 (0.18)	-2.55 (0.25)
		V	-1.40 (0.10)	-1.13 (0.13)	-1.15 (0.15)	-2.13 (0.38)	- -	-2.45 (0.10)	-2.40 (0.30)
		E	-1.68 (0.08)	-1.43 (0.73)	-1.68 (0.23)	-2.25 (0.35)	- -	-2.48 (0.38)	-2.45 (0.05)
		VE	-1.30 (0.20)	-1.43 (0.53)	-1.98 (0.28)	-1.95 (0.55)	- -	-2.10 (0.70)	-2.35 (0.05)
	Rainfed	C	-1.53 (0.28)	-0.98 (0.28)	-1.65 (0.65)	-1.70 (0.10)	-3.10 (0.40)	-1.95 (0.45)	-2.95 (0.45)
		V	-1.73 (0.28)	-1.68 (0.43)	-1.85 (0.15)	-1.90 (0.00)	-3.63 (1.03)	-2.65 (0.55)	-2.40 (0.40)
		E	-2.05 (0.25)	-1.25 (0.45)	-0.95 (0.25)	-2.35 (0.05)	-3.10 (0.20)	-2.55 (0.55)	-2.75 (0.75)
		VE	-1.93 (0.23)	-0.88 (0.28)	-1.30 (0.70)	-2.10 (0.10)	-2.40 (0.25)	-2.10 (0.20)	-2.25 (0.05)
	Water stress V	C	-2.38 (0.18)	-3.95 (0.35)	-2.38 (0.28)	-2.60 (0.30)	- -	-2.83 (0.43)	-3.05 (0.25)
		V	-2.15 (0.35)	-4.68 (0.48)	-2.18 (0.33)	-2.40 (0.20)	- -	-2.75 (0.20)	-3.15 (0.45)
	Water stress E	C	-2.00 (0.00)	-1.45 (0.20)	-2.30 (0.10)	-3.65 (0.05)	-6.15 (0.35)	-2.30 (0.30)	-2.90 (0.10)
		E	-1.85 (0.50)	-1.65 (0.15)	-1.73 (0.18)	-4.05 (1.65)	-3.60 (0.80)	-2.15 (0.35)	-2.75 (0.25)
	Water stress VE	C	-2.48 (0.33)	-3.28 (0.03)	-3.50 (0.10)	-3.35 (0.05)	-5.20 (0.50)	-2.88 (0.28)	-2.65 (0.15)
		VE	-1.68 (0.44)	-3.63 (0.38)	-2.73 (0.03)	-2.53 (0.18)	-4.38 (0.23)	-2.75 (0.30)	-2.50 (0.20)
S. gynerioides	Irrigation	C	-1.38 (0.13)	-1.58 (1.18)	-2.80 (0.60)	-2.63 (0.03)	- -	-2.85 (0.15)	-2.60 (0.30)
		V	-1.70 (0.10)	-1.55 (0.05)	-1.65 (0.85)	-2.40 (0.20)	- -	-2.50 (0.05)	-2.15 (0.05)
		E	-1.95 (0.80)	-2.25 (0.55)	-1.43 (0.60)	-2.48 (0.18)	- -	-3.00 (0.15)	-1.85 (0.45)
		VE	-1.25 (0.15)	-2.05 (0.65)	-2.83 (0.68)	-2.33 (0.03)	- -	-2.83 (0.38)	-2.40 (0.40)
	Rainfed	C	-1.48 (0.23)	-3.10 (0.00)	-1.85 (0.45)	-2.00 (0.30)	-3.03 (0.08)	-2.45 (0.45)	-2.90 (0.30)
		V	-1.78 (0.38)	-1.00 (0.10)	-1.00 (0.00)	-2.50 (0.20)	-2.85 (0.65)	-3.10 (0.00)	-2.40 (0.30)
		E	-2.33 (0.13)	-1.08 (0.38)	-1.93 (0.08)	-2.25 (0.15)	-2.55 (0.35)	-2.45 (0.55)	-2.20 (0.80)
		VE	-1.43 (0.43)	-1.08 (0.38)	-2.43 (0.23)	-1.65 (0.05)	-2.15 (0.45)	-2.63 (0.03)	-1.70 (0.20)
	Water stress V	C	-2.25 (0.15)	-4.25 (0.75)	-2.73 (0.23)	-2.83 (0.08)	- -	-2.63 (0.03)	-2.45 (0.65)
		V	-1.43 (0.18)	-4.10 (0.60)	-1.70 (0.50)	-2.93 (0.03)	- -	-2.70 (0.20)	-3.10 (0.40)
	Water stress E	C	-1.45 (0.35)	-1.18 (0.08)	-2.40 (0.30)	-3.70 (0.10)	-4.08 (0.28)	-2.88 (0.13)	-2.75 (0.35)
		E	-1.85 (0.05)	-1.28 (0.13)	-2.60 (0.50)	-4.95 (2.45)	-3.50 (0.60)	-2.73 (0.43)	-2.88 (0.28)
	Water stress VE	C	-1.80 (0.60)	-3.75 (0.15)	-4.05 (0.15)	-3.85 (0.75)	-6.08 (1.33)	-2.38 (0.13)	-2.60 (0.30)
		VE	-2.15 (0.55)	-2.15 (0.85)	-4.65 (0.15)	-4.20 (1.00)	-4.35 (0.35)	-2.65 (0.15)	-1.35 (0.75)
S. tenuis	Irrigation	C	-1.95 (0.05)	-1.30 (0.45)	-2.48 (0.03)	-2.40 (0.10)	- -	-1.88 (0.18)	-2.33 (0.13)
		V	-2.10 (0.05)	-1.80 (0.70)	-2.20 (0.10)	-2.30 (0.30)	- -	-1.85 (0.05)	-1.90 (0.70)
		E	-2.08 (0.18)	-1.63 (0.33)	-1.55 (0.45)	-2.15 (0.05)	- -	-2.38 (0.13)	-1.85 (0.35)
		VE	-1.85 (0.45)	-1.63 (0.78)	-1.75 (0.60)	-1.80 (0.00)	- -	-1.55 (0.30)	-2.10 (0.00)
	Rainfed	C	-2.10 (0.30)	-1.78 (0.83)	-1.35 (0.35)	-1.55 (0.25)	-2.80 (1.20)	-2.00 (0.25)	-2.45 (0.35)
		V	-1.63 (0.28)	-1.43 (0.38)	-1.10 (0.00)	-1.80 (0.00)	-2.50 (0.70)	-1.66 (0.28)	-2.25 (0.15)
		E	-2.00 (0.20)	-2.25 (0.05)	-1.40 (0.45)	-1.90 (0.20)	-2.60 (0.20)	-2.13 (0.13)	-2.40 (0.00)
		VE	-2.40 (0.50)	-1.20 (0.05)	-1.85 (0.35)	-1.90 (0.20)	-1.80 (0.50)	-2.03 (0.33)	-1.98 (0.28)
	Water stress V	C	-2.13 (0.13)	-3.35 (0.10)	-1.38 (0.13)	-1.80 (0.10)	- -	-1.70 (0.30)	-2.48 (0.68)
		V	-1.60 (0.20)	-4.75 (0.45)	-1.93 (0.28)	-1.98 (0.28)	- -	-2.05 (0.20)	-3.35 (1.05)
	Water stress E	C	-2.30 (0.20)	-1.33 (0.03)	-2.28 (0.13)	-4.35 (0.05)	-5.65 (0.65)	-2.10 (0.25)	-3.00 (0.50)
		E	-2.10 (0.35)	-1.73 (0.03)	-1.98 (0.03)	-3.35 (1.25)	-3.93 (0.73)	-1.70 (0.10)	-2.82 (0.29)
	Water stress VE	C	-1.90 (0.10)	-2.70 (0.50)	-2.75 (0.35)	-2.45 (0.15)	-3.75 (1.75)	-2.15 (1.15)	-2.10 (0.00)
		VE	-2.05 (0.55)	-2.40 (0.60)	-3.13 (0.38)	-2.63 (0.63)	-4.38 (0.13)	-2.20 (0.10)	-1.60 (0.30)

Bud metabolic activity and axillary bud outgrowth

These variables were evaluated on parent tillers produced during each growing season. At each observation date, 2 to 4 tillers were harvested per plant of *S. clarazii*, *S. tenuis,* or *S. gynerioides*; one plant was used per replicate in all treatments. Crown samples were maintained at 4°C until dissection. Number, metabolic activity, and outgrowth of axillary buds were determined on each tiller under a binocular microscope. Three bud categories were considered: metabolically active (MAB), dormant or dead (DDB), and buds which grew out originating daughter tillers (DT). Total bud number (TBN) was calculated as MAB+DDB+DT. The potential maximum number of buds per stem base (total node number = TN) was calculated as MAB+DDB+DT+number of foliar scars. Font Quer (1982) reported that this number is equivalent to the number of produced leaves. Foliar scars indicate presence of leaves which do not have buds or daughter tillers in their axilla (Hendrickson and Briske 1997).

Metabolic activity of axillary buds was determined using Triphenyl Tetrazolium Chloride (TTC) following Busso et al. (1989). Each stem base was longitudinally cut leaving entire buds at both sides of the cutting. Both halves were maintained in a solution of 0.6% (weight/volume) TTC-0.05 M Phosphate buffer (pH = 7.38) during 15 hours in darkness at 30°C.

Metabolically active buds were those whose apex stained pink or red indicating enzymatic reduction of colourless tetrazolium salt to red, insoluble formazan. Buds not-stained with TTC were considered dormant or dead.

Statistical analysis

Leaf water potentials were analyzed separately for each date using ANOVA. A split plot design was used with treatments (14 combinations of water x defoliation levels) as main factors and species as secondary factors. One-way ANOVA was used to analyze the bud metabolic activity data; analysis was performed separately for each date and species using a completely randomized design with 14 treatments. Whenever F tests were significant at $p < 0.05$, means were separated using Fisher LSD or Tukey-Kramer test for balanced or unbalanced data, respectively. Values for MAB and DDB were transformed to $\sqrt{x+1}$ to improve normality assumptions (Steel and Torrie 1985). Non-transformed values are presented in Figures.

Results and Discussion

Leaf water potentials

During 1995, 1996, and early 1997, leaf water potentials were similar ($p > 0.25$) among defoliation treatments within each water level in all 3 species (Tables 1 and 2). These results are similar to those of Becker et al. (1997) and Busso and Richards (1993) in these and other perennial grasses. Other studies, however, have reported higher leaf water potentials on defoliated than on undefoliated perennial tussock grasses (Briske and Anderson 1990, Brown 1995, Williams et al. 1998). This positive response to herbivory has been attributed to a reduced transpiratory leaf surface area after defoliation which would conserve soil water (Anderson and Briske 1995, Brown 1995).

At the beginning and end of each growing cycle, leaf water potential was similar ($p > 0.25$) among water levels in *S. clarazii*, *S. tenuis* and *S. gynerioides*. In August, September, and October 1995, however, these species had lower ($p < 0.05$) leaf water potentials under water stress than under irrigated conditions. Similar results were obtained in 1996 during this period, except on plants of the desirable species by the end of September ($p>0.15$). Leaf water potentials were more variable on plants of the 3 species in the rainfed plots. Under these conditions, leaf

Table 3. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. gynerioides* at the different treatments in 1995, 1996 and early 1997. C: Undefoliated controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
23/5/95	Irrigation	C	6.25 (0.75)	3.00 (0.00)	1.25 (0.25)	0.25 (0.25)
		V	5.75 (0.75)	2.00 (0.50)	0.50 (0.00)	1.00 (1.00)
		VE	8.00 (0.00)	5.00 (0.00)	1.00 (0.00)	0.00 (0.00)
	Rainfed	C	7.00 (0.00)	3.50 (0.00)	0.50 (0.00)	0.00 (0.00)
		V	7.75 (1.25)	3.00 (1.00)	0.75 (0.25)	0.50 (0.00)
		VE	7.25 (1.25)	2.25 (0.25)	0.75 (0.25)	1.75 (0.75)
	Water stress V	C	6.75 (0.75)	3.75 (1.25)	0.75 (0.75)	0.75 (0.75)
		V	7.75 (0.25)	3.75 (0.25)	1.00 (0.00)	0.25 (0.25)
	Water stress VE	C	8.25 (0.75)	4.00 (1.00)	0.50 (0.00)	1.00 (1.00)
		VE	6.25 (0.75)	3.25 (0.75)	1.00 (0.00)	0.00 (0.00)
7/9/95	Irrigation	C	7.13 (0.13)	2.63 (0.13)	0.88 (0.13)	2.00 (0.00)
		V	7.25 (2.00)	2.88 (1.13)	0.88 (0.38)	1.00 (0.75)
		VE	6.25 (0.50)	3.13 (0.13)	0.88 (0.38)	0.25 (0.00)
	Rainfed	C	7.25 (0.75)	3.00 (0.25)	0.50 (0.25)	1.75 (1.50)
		V	5.88 (0.63)	2.25 (0.50)	0.75 (0.00)	1.63 (0.38)
		VE	7.13 (1.13)	2.83 (1.17)	0.71 (0.04)	1.25 (0.25)
	Water stress V	C	6.50 (0.00)	2.50 (0.00)	1.50 (0.50)	0.75 (0.50)
		V	8.08 (0.58)	3.38 (0.63)	0.79 (0.46)	1.38 (0.38)
	Water stress VE	C	6.42 (0.08)	2.71 (0.04)	1.09 (0.42)	0.88 (0.13)
		VE	7.75 (0.00)	3.13 (0.13)	0.88 (0.38)	1.00 (0.75)
27/9/95	Irrigation	C	7.38 (0.38)	3.38 (0.38)	0.38 (0.13)	2.00 (0.50)
		E	7.88 (0.13)	3.13 (0.63)	0.88 (0.38)	1.25 (0.00)
		VE	8.88 (0.13)	3.75 (0.50)	1.00 (0.00)	1.50 (0.50)
	Rainfed	C	8.00 (0.75)	2.88 (0.38)	0.50 (0.50)	2.38 (0.63)
		E	9.13 (0.38)	4.00 (0.25)	0.88 (0.13)	2.00 (0.00)
		VE	8.50 (1.00)	3.38 (0.13)	1.25 (0.25)	2.00 (1.00)
	Water stress E	C	7.75 (0.50)	2.88 (0.13)	0.25 (0.00)	1.88 (0.63)
		E	7.88 (0.38)	3.00 (0.75)	0.63 (0.13)	1.00 (0.00)
	Water stress VE	C	7.50 (0.50)	2.75 (0.25)	1.38 (0.13)	1.38 (0.63)
		VE	9.63 (0.13)	4.00 (0.25)	0.63 (0.38)	1.50 (0.25)
14/12/95	Irrigation	C	6.88 (0.13)	2.75 (1.25)	0.00 (0.00)	2.13 (0.63)
		E	7.75 (0.75)	2.38 (0.38)	0.00 (0.00)	3.00 (0.00)
		VE	7.13 (0.38)	2.63 (0.63)	0.00 (0.00)	2.13 (0.38)
	Rainfed	C	7.63 (0.63)	3.00 (0.50)	0.13 (0.13)	2.25 (0.25)
		E	8.63 (1.38)	3.50 (0.25)	0.25 (0.25)	2.63 (1.63)
	Water stress E	C	7.88 (0.63)	3.88 (1.13)	0.00 (0.00)	2.50 (0.50)
		E	7.88 (0.63)	2.88 (0.63)	0.00 (0.00)	2.50 (0.25)
	Water stress VE	C	8.25 (0.50)	4.13 (0.38)	0.00 (0.00)	2.13 (0.63)
		VE	6.88 (0.63)	2.50 (0.75)	0.00 (0.00)	2.63 (0.38)
25/4/96	Irrigation	C	9.00 (0.00)	3.00 (0.50)	1.75 (0.25)	2.00 (0.00)
		V	7.25 (0.25)	0.75 (0.25)	1.75 (0.25)	3.25 (1.25)
		E	6.50 (0.00)	1.50 (0.50)	1.75 (0.25)	2.00 (0.00)
		VE	8.25 (0.25)	1.25 (0.25)	0.75 (0.25)	3.25 (1.25)
	Rainfed	C	6.75 (0.25)	1.50 (0.00)	1.00 (0.00)	2.50 (0.50)
		V	7.00 (0.50)	1.75 (0.25)	2.00 (0.00)	0.75 (0.25)
		E	7.25 (1.25)	1.50 (1.00)	1.25 (0.25)	3.00 (0.50)
		VE	7.75 (0.25)	1.50 (0.00)	1.50 (0.50)	2.25 (0.25)
	Water stress V	C	6.75 (0.25)	2.25 (0.25)	1.00 (0.50)	1.50 (0.50)
		V	7.00 (1.00)	2.50 (0.50)	0.50 (0.50)	2.25 (0.25)
	Water stress VE	C	7.00 (0.00)	2.00 (0.00)	1.75 (0.25)	1.50 (0.50)
		VE	7.50 (1.00)	2.00 (1.00)	1.25 (0.25)	2.75 (0.25)
12/6/96	Irrigation	C	8.13 (0.13)	1.75 (0.75)	2.13 (0.13)	2.63 (0.38)
		V	10.00 (0.25)	2.50 (0.75)	1.50 (0.25)	3.75 (0.50)
		VE	8.63 (0.13)	1.13 (0.13)	1.13 (0.13)	3.25 (0.25)
	Rainfed	C	7.63 (0.50)	1.63 (0.25)	1.50 (0.50)	2.88 (0.13)
		V	8.63 (0.88)	1.88 (0.63)	1.13 (0.63)	3.50 (0.50)
		VE	8.50 (0.00)	2.50 (0.25)	1.38 (0.63)	2.88 (0.63)
	Water stress V	C	8.25 (0.50)	1.13 (0.38)	1.38 (0.13)	3.13 (0.13)
		V	8.50 (1.00)	1.75 (0.25)	1.00 (0.75)	3.63 (1.13)

(Continued on page 156)

Table 3. Continued.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
	Water stress VE	C	7.88 (0.38)	2.00 (0.50)	1.63 (0.13)	2.50 (0.25)
		VE	9.38 (0.88)	3.13 (1.13)	1.00 (0.00)	2.00 (0.50)
30/7/96	Irrigation	C	8.00 (0.00)	1.38 (0.88)	1.75 (0.00)	3.38 (0.63)
		V	8.25 (0.00)	1.75 (0.75)	1.25 (0.00)	3.38 (0.38)
		VE	7.63 (0.38)	2.25 (0.25)	1.13 (0.38)	2.00 (0.25)
	Rainfed	C	8.25 (0.75)	2.50 (0.00)	0.88 (0.13)	2.13 (0.88)
		V	8.88 (0.63)	2.75 (1.00)	1.25 (0.25)	2.50 (1.00)
		VE	8.25 (1.00)	1.88 (0.63)	0.75 (0.50)	4.13 (0.88)
	Water stress V	C	8.00 (0.00)	2.25 (0.00)	0.88 (0.63)	3.13 (0.63)
		V	7.63 (0.13)	1.88 (0.38)	1.13 (0.88)	3.00 (1.25)
	Water stress VE	C	9.25 (1.25)	2.50 (1.00)	1.00 (0.25)	4.25 (0.00)
		VE	8.25 (0.50)	2.63 (0.63)	1.38 (0.13)	2.13 (0.13)
21/9/96	Irrigation	C	8.13 (0.63)	1.50 (0.75)	0.38 (0.13)	3.88 (0.88)
		E	8.13 (0.38)	1.88 (0.88)	0.38 (0.13)	3.63 (1.38)
		VE	8.00 (0.25)	2.88 (0.13)	0.25 (0.25)	2.38 (0.13)
	Rainfed	C	8.75 (0.25)	3.13 (0.13)	0.13 (0.13)	3.25 (0.25)
		E	8.13 (0.13)	1.88 (0.13)	0.25 (0.25)	2.25 (1.25)
		VE	8.88 (0.13)	2.38 (0.13)	0.63 (0.63)	3.63 (0.63)
	Water stress E	C	9.63 (0.63)	3.38 (0.88)	1.13 (0.13)	2.13 (0.38)
		E	8.25 (0.25)	2.38 (0.13)	0.63 (0.63)	2.75 (1.00)
	Water stress VE	C	8.88 (0.13)	2.75 (1.25)	1.13 (0.63)	1.63 (0.63)
		VE	7.88 (0.38)	2.13 (0.63)	0.75 (0.25)	3.13 (0.63)
30/10/96	Irrigation	C	7.88 (0.13)	1.38 (0.13)	0.00 (0.00)	4.50 (0.00)
		V	8.63 (0.63)	2.00 (0.75)	0.38 (0.13)	4.25 (1.00)
		E	–	–	–	–
		VE	7.75 (0.50)	2.25 (0.50)	0.00 (0.00)	3.13 (0.63)
	Rainfed	C	7.88 (0.13)	2.25 (0.25)	0.00 (0.00)	3.75 (0.00)
		V	7.50 (0.25)	2.13 (0.13)	0.13 (0.13)	2.38 (0.63)
		E	8.50 (0.75)	1.63 (0.88)	0.38 (0.38)	4.00 (1.00)
		VE	9.63 (0.38)	2.63 (0.13)	0.13 (0.13)	4.75 (0.00)
	Water stress V	C	7.63 (0.38)	2.00 (0.50)	0.00 (0.00)	3.50 (0.00)
		V	8.63 (0.13)	4.38 (0.38)	0.25 (0.00)	2.00 (0.50)
	Water stress VE	C	8.25 (0.00)	2.13 (0.13)	0.75 (0.25)	4.00 (0.75)
		VE	8.63 (0.38)	2.13 (1.13)	0.13 (0.13)	4.88 (1.38)
7/1/97	Irrigation	C	6.88 (0.13)	2.13 (0.13)	0.00 (0.00)	2.88 (0.13)
		V	6.38 (0.13)	2.13 (0.63)	0.00 (0.00)	2.13 (0.63)
		E	6.50 (0.50)	1.25 (0.25)	0.00 (0.00)	2.25 (0.00)
		VE	6.75 (0.25)	1.50 (0.00)	0.13 (0.13)	2.63 (0.13)
	Rainfed	C	6.75 (0.75)	2.00 (0.25)	0.13 (0.13)	2.50 (0.75)
		V	7.63 (0.63)	2.63 (0.13)	0.00 (0.00)	2.75 (0.75)
		E	6.88 (0.88)	0.88 (0.13)	0.00 (0.00)	4.00 (0.50)
		VE	6.75 (0.75)	1.50 (1.00)	0.13 (0.13)	3.50 (0.25)
	Water stress V	C	6.63 (0.88)	1.63 (0.38)	0.00 (0.00)	3.00 (1.00)
		V	6.25 (0.25)	2.38 (0.13)	0.25 (0.25)	1.63 (0.38)
	Water Stress E	C	7.25 (0.25)	2.00 (0.25)	0.00 (0.00)	2.50 (0.25)
		E	8.13 (1.38)	2.13 (0.63)	0.13 (0.13)	3.25 (1.00)
	Water stress VE	C	9.46 (1.21)	3.04 (0.29)	0.29 (0.04)	1.96 (0.29)
		VE	9.09 (0.58)	2.50 (0.50)	0.00 (0.00)	3.54 (0.21)
12/3/97	Irrigation	C	7.13 (0.38)	3.38 (1.13)	0.00 (0.00)	1.75 (0.25)
		V	6.75 (0.00)	1.88 (0.13)	0.00 (0.00)	2.50 (0.00)
		E	6.96 (0.29)	2.00 (0.00)	0.25 (0.25)	1.71 (0.04)
		VE	6.63 (0.38)	2.25 (0.00)	0.13 (0.13)	1.38 (1.13)
	Rainfed	C	6.13 (0.13)	2.13 (0.63)	0.13 (0.13)	1.50 (1.00)
		V	6.88 (0.63)	1.75 (0.25)	0.63 (0.38)	2.00 (0.25)
		E	7.00 (0.75)	2.13 (0.63)	0.13 (0.13)	2.13 (0.13)
		VE	6.25 (0.25)	1.63 (0.38)	0.25 (0.25)	1.88 (0.13)
	Water stress V	C	6.25 (0.25)	2.63 (0.13)	0.25 (0.25)	1.38 (0.13)
		V	7.38 (0.13)	2.75 (0.25)	0.00 (0.00)	2.25 (0.75)
	Water stress E	C	6.63 (0.13)	2.25 (0.25)	0.00 (0.00)	2.00 (0.50)
		E	7.50 (0.50)	2.00 (0.50)	0.13 (0.13)	3.13 (0.88)
	Water stress VE	C	7.38 (0.38)	3.00 (0.00)	0.13 (0.13)	1.75 (0.25)
		VE	7.50 (0.75)	2.75 (1.25)	0.00 (0.00)	2.25 (0.50)

water potentials were lower ($p < 0 .05$) than those in the irrigated plots in 1995, and higher ($p < 0.05$) than those in the water-stressed plots in 1996 (Tables 1 and 2). This was very likely due to the lower annual rainfall in 1995 (447.2 mm) than in 1996 (621.3 mm) (Fig. 1).

In 1995, leaf water potential on average for all treatments was similar ($p > 0.25$) among species, except in April when this variable was higher ($p < 0.05$) in *S. clarazii* than in *S. tenuis*. Plants of the desirable species had higher ($p < 0.05$) leaf water potentials than *S. gynerioides* in mid-August, September, and December in 1996 (Tables 1 and 2).

Bud metabolic activity and axillary bud outgrowth

On average for each date and species, between 62 and 82% of the total number of nodes had daughter tillers, metabolically active buds or dormant or dead buds on parent tillers. This indicates that not all leaves possess axillary buds which is similar to results of Mueller and Richards (1986) and Hendrickson and Briske (1997) on other perennial grasses.

Numbers of total nodes, daughter tillers, and metabolically active or dormant or dead buds were similar ($p > 0.10$) between defoliation treatments and water levels during 1995, 1996, and early 1997 on parent tillers of *S. gynerioides* (Table 3). This implies that neither axillary bud activation nor initial outgrowth would contribute to explain the observed release from competition of *S. gynerioides* after selective defoliation of *S. clarazii* (Moretto and Distel 1999) and *S. clarazii* and *S. tenuis* (Flemmer 2000). These results also show the lack of sensitivity of axillary buds in *S. gynerioides* to water stress, a common abiotic factor to which plants are exposed in the temperate, central semiarid rangelands of Argentina (Busso 1997, Fernández and Busso 1999). Axillary buds of this species, however, are suceptible to fire (Distel and Bóo 1996, Peláez 2000).

Total node number, and numbers of daughter tillers, and metabolically active or dormant or dead buds were also similar ($p > 0.25$) in all water level and defoliation treatments on parent tillers of *S. tenuis* during 1995 (Table 4). These results indicate that the degree of metabolic activity and outgrowth capacity of axillary buds are maintained on parent tillers of this species after a one-year-exposure to the combined or separate influence of water stress and defoliation. Similar results ($p > 0.25$) were obtained for most sampling dates in 1996 (Table 4).

Table 4. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. tenuis* at the different treatments in 1995, 1996 and early 1997. I: Irrigation, R: Rainfed, WS: Water stress, C: Undefoliated controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2. Values without SE come from n=1.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
23/5/95	Irrigation	C	7.25 (0.25)	2.75 (1.75)	2.25 (1.25)	0.25 (0.25)
		V	7.00 (1.00)	3.00 (0.00)	1.75 (0.25)	0.50 (0.50)
		VE	6.00 (0.00)	2.00 (0.00)	1.50 (0.00)	1.00 (0.00)
	Rainfed	C	7.00 (0.00)	5.00 (0.00)	0.00 (0.00)	0.50 (0.00)
		V	7.00 (0.50)	3.00 (0.50)	1.25 (0.75)	0.75 (0.25)
		VE	5.00 (1.00)	2.50 (0.50)	0.50 (0.50)	1.00 (1.00)
	Water stress V	C	10.00 (1.00)	4.00 (1.00)	3.50 (1.50)	0.00 (0.00)
		V	5.25 (0.25)	3.25 (0.25)	0.50 (0.50)	0.00 (0.00)
	Water stress VE	C	6.75 (0.25)	3.25 (0.75)	0.00 (0.00)	1.00 (1.00)
		VE	7.00 (2.00)	1.50 (0.50)	1.75 (0.25)	0.50 (0.50)
7/9/95	Irrigation	C	9.00 (1.25)	2.88 (1.38)	1.50 (1.00)	2.13 (0.63)
		V	8.71 (1.04)	3.92 (0.58)	1.50 (0.50)	1.75 (0.25)
		VE	8.00 (1.25)	3.25 (0.50)	1.75 (1.50)	1.50 (0.00)
	Rainfed	C	8.00 (2.00)	4.50 (1.50)	1.13 (0.13)	0.38 (0.38)
		V	7.13 (0.88)	3.38 (0.63)	2.25 (0.75)	0.42 (0.08)
		VE	7.46 (0.79)	2.50 (0.50)	2.38 (0.38)	1.29 (0.04)
	Water stress V	C	9.25 (0.25)	3.88 (1.63)	3.25 (1.25)	0.50 (0.00)
		V	7.33 (1.00)	3.17 (1.17)	1.00 (0.67)	1.17 (0.83)
	Water stress VE	C	7.21 (0.54)	2.33 (0.33)	2.21 (1.54)	1.46 (1.21)
		VE	8.04 (1.71)	3.58 (0.08)	1.58 (0.92)	1.04 (0.71)
27/9/95	Irrigation	C	10.13 (0.88)	3.38 (1.38)	1.75 (0.25)	3.38 (0.88)
		E	9.83 (0.83)	3.79 (0.46)	1.58 (1.08)	1.08 (0.42)
		VE	10.00 (1.00)	3.63 (0.13)	2.50 (1.00)	2.25 (0.50)
	Rainfed	C	8.75 (1.25)	2.75 (1.00)	2.88 (0.63)	1.25 (0.50)
		E	9.75 (1.00)	4.50 (0.25)	2.13 (0.38)	1.88 (1.13)
		VE	8.88 (1.63)	3.25 (0.25)	2.50 (1.25)	1.38 (0.38)
	Water stress E	C	9.00 (1.75)	4.25 (0.50)	1.38 (0.63)	2.00 (1.75)
		E	8.88 (0.63)	3.25 (0.25)	3.00 (0.50)	1.25 (0.75)
	Water stress VE	C	8.75 (0.25)	3.88 (0.13)	1.50 (0.00)	1.50 (0.50
		VE	9.75 (1.00)	2.75 (0.50)	3.75 (0.25)	2.00 (0.25)
14/12/95	Irrigation	C	8.75 (0.25)	3.63 (0.88)	1.00 (0.50)	2.63 (0.63)
		E	7.50 (2.50)	1.75 (1.00)	1.00 (0.75)	2.88 (2.13)
		VE	9.00 (1.75)	3.50 (0.25)	0.63 (0.13)	3.63 (1.63)
	Rainfed	C	8.63 (0.88)	3.88 (1.38)	2.00 (0.00)	1.50 (0.50)
		E	8.25 (3.00)	3.88 (2.38)	1.00 (0.25)	2.00 (0.75)
		VE	9.63 (0.88)	4.25 (0.25)	0.75 (0.25)	2.88 (1.38)
	Water Stress E	C	8.75 (0.75)	4.25 (0.50)	0.63 (0.13)	2.38 (0.13)
		E	9.25 (0.75)	4.38 (0.38)	1.25 (1.00)	2.00 (0.75)
	Water stress VE	C	8.25 (1.00)	3.88 (0.13)	1.50 (1.00)	1.25 (0.75)
		VE	9.38 (1.38)	3.63 (0.38)	0.25 (0.25)	4.00 (1.50)
25/4/96	Irrigation	C	6.50 (0.00)	2.75 (0.75)	0.75 (0.75)	1.25 (1.25)
		V	9.50 (0.50)	3.50 (1.50)	1.75 (0.75)	3.00 (0.00)
		E	6.00 (0.50)	1.50 (0.00)	1.75 (0.25)	0.75 (0.75)
		VE	7.00 (0.00)	0.00 (0.00)	3.00 (0.00)	2.00 (0.00)
	Rainfed	C	8.00 (1.00)	3.25 (0.75)	1.00 (0.50)	1.25 (1.25)
		V	7.50 (1.50)	3.25 (0.75)	0.25 (0.25)	1.50 (1.50)
		E	7.00 (0.00)	2.75 (0.75)	1.25 (1.25)	0.50 (0.50)
		VE	7.00 (2.00)	3.75 (0.75)	1.75 (1.75)	0.25 (0.25)
	Water stress V	C	9.25 (1.25)	4.00 (0.00)	1.25 (0.75)	1.25 (1.25)
		V	7.50 (0.00)	3.75 (0.75)	2.00 (0.50)	0.25 (0.25)
	Water stress E	C	7.50 (1.00)	2.25 (0.25)	3.25 (1.25)	0.50 (0.50)
		E	7.25 (2.25)	2.75 (1.25)	2.00 (0.50)	0.25 (0.25)
	Water stress VE	C	8.75 (0.25)	3.00 (2.00)	3.25 (1.25)	0.50 (0.50)
		VE	8.00 (0.00)	2.75 (1.25)	1.50 (1.00)	2.00 (1.50)

(Continued on page 158)

However, defoliation affected bud metabolic activity of *S. tenuis* independently of plant water status in June 1996 (before defoliation at V). While defoliated and undefoliated plants of this species had a similar ($p > 0.25$) total bud number, numbers of metabolically active buds were lower ($p < 0.05$) and those of dormant or dead buds were higher ($p < 0.05$) on plants defoliated at the vegetative and vegetative + early internode elongation stages in the previous year than on undefoliated controls under all water levels (Table 4). Despite this lower degree of metabolic activity, defoliated and undefoliated plants of *S. tenuis* had a similar ($p \geq 0.10$) number of daughter tillers. Busso et al. (1989) also reported a reduction in the number of metabolically active buds on plants of *Agropyron spicatum* (Pursh) Scribn. and Smith (Syn: *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*) under the simultaneous influence of defoliation and water stress during 2 consecutive years. At the same time in June 1996, daughter tiller production (DT) was greater ($p < 0.05$) on plants defoliated twice than on those defoliated at the vegetative stage under rainfed and irrigated conditions in *S. tenuis*; this was associated with a lower ($p < 0.01$) number of metabolically active buds. A greater defoliation frequency has increased daughter tiller production in other perennial grasses by modifying both light quantity and quality at stem bases (Deregibus et al. 1983, Casal et al. 1985, Gautier et al. 1999).

In June 1996, plants of *S. tenuis*, whether defoliated or not during the previous year, had a greater ($p < 0.05$) number of daughter tillers and total nodes after exposure to water stress in the vegetative+early internode elongation than in the vegetative stage. It is likely that accumulation of total nonstructural carbohydrates in the stem bases increased as the period of exposure to water stress also increased. Since this species remains dormant during dry summers (Distel and Fernández 1986), these carbohydrates may be utilized for rapid regrowth during the next growing season. Various studies have reported that accumulation of total nonstructural carbohydrates in the stem bases of perennial grasses during periods of water stress resulted in greater tillering responses (Busso et al. 1990, Fulkerson and Slack 1995, Volaire 1995, Oosthuizen and Snyman 1999). Also by mid-year 1996, numbers of dormant or dead buds were greater ($p < 0.01$) under irrigated than under rainfed or water stress conditions on plants of *S. tenuis* which had been defoliat-

Table 4 Continued.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
12/6/96	Irrigation	C	11.50 (0.25)	4.75 (0.25)	4.38 (0.38)	0.25 (0.25)
		V	11.00 (0.00)	3.25 (0.00)	2.00 (0.00)	4.00 (0.00)
		VE	10.00 (0.00)	5.63 (0.38)	0.50 (0.00)	2.38 (0.13)
	Rainfed	C	8.88 (0.88)	3.88 (0.38)	3.38 (0.63)	0.38 (0.13)
		V	9.75 (1.50)	4.13 (0.13)	1.38 (0.38)	1.38 (0.13)
		VE	10.75 (0.00)	5.25 (1.50)	0.88 (0.88)	2.75 (0.50)
	Water stress V	C	8.25 (0.00)	3.63 (0.63)	2.63 (0.13)	0.25 (0.00)
		V	8.88 (0.38)	4.13 (0.38)	1.00 (0.50)	2.00 (0.50)
	Water stress VE	C	10.50 (0.00)	4.50 (0.00)	4.25 (0.00)	0.25 (0.00)
		VE	10.92 (0.58)	5.96 (0.29)	0.46 (0.21)	2.96 (0.29)
30/7/96	Irrigation	C	9.88 (0.38)	3.25 (0.75)	1.88 (1.38)	2.75 (2.25)
		V	10.63 (1.88)	5.38 (0.63)	2.75 (2.25)	1.25 (0.75)
		VE	12.25 (0.75)	3.50 (0.50)	5.00 (1.00)	2.13 (1.13)
	Rainfed	C	10.00 (1.00)	5.00 (2.25)	1.88 (1.38)	1.25 (0.75)
		V	9.50 (1.00)	3.38 (0.88)	1.50 (1.50)	2.75 (2.25)
		VE	11.00 (0.00)	4.75 (0.25)	2.13 (1.63)	1.63 (1.13)
	Water stress V	C	8.63 (0.13)	4.00 (0.00)	2.00 (0.25)	0.63 (0.13)
		V	9.25 (0.00)	3.38 (0.13)	0.75 (0.75)	2.25 (1.25)
	Water stress VE	C	7.25 (0.00)	3.00 (0.00)	3.25 (0.00)	0.00 (0.00)
		VE	9.25 (0.00)	3.63 (0.13)	2.50 (1.50)	1.63 (1.63)
21/9/96	Irrigation	C	9.88 (0.38)	4.00 (0.75)	2.25 (0.25)	1.88 (1.13)
		E	10.63 (0.13)	5.13 (1.13)	2.50 (1.75)	1.50 (1.25)
		VE	10.50 (1.50)	4.00 (0.25)	1.38 (1.38)	3.38 (0.63)
	Rainfed	C	12.00 (1.50)	5.25 (2.00)	0.63 (0.38)	4.38 (0.38)
		E	10.63 (1.38)	4.38 (0.13)	0.75 (0.75)	3.63 (2.13)
		VE	9.50 (1.00)	4.63 (0.63)	0.00 (0.00)	3.00 (0.50)
	Water stress E	C	10.75 (0.25)	6.00 (0.25)	1.13 (0.63)	2.00 (0.25)
		E	9.88 (0.38)	4.75 (0.50)	2.25 (0.75)	1.13 (1.13)
	Water stress VE	C	10.00 (0.00)	5.75 (0.00)	2.25 (0.00)	0.75 (0.00)
		VE	9.63 (0.88)	4.25 (1.50)	0.38 (0.38)	2.25 (0.00)
30/10/96	Irrigation	C	9.88 (0.13)	5.00 (0.25)	0.88 (0.38)	2.00 (0.00)
		V	8.38 (0.88)	3.13 (0.13)	1.13 (0.88)	2.25 (0.50)
		E	– –	– –	– –	– –
		VE	11.50 (1.50)	5.50 (0.75)	1.00 (1.00)	3.00 (0.25)
	Rainfed	C	8.88 (0.63)	4.25 (1.25)	0.00 (0.00)	2.88 (1.38)
		V	9.63 (0.13)	4.75 (0.75)	0.13 (0.13)	3.13 (0.63)
		E	9.50 (0.25)	4.00 (0.25)	0.50 (0.50)	3.38 (0.13)
		VE	8.75 (1.25)	3.38 (1.63)	0.83 (0.13)	3.50 (0.50)
	Water stress V	C	10.75 (0.25)	5.88 (0.38)	0.38 (0.13)	2.50 (0.00)
		V	10.50 (0.75)	4.88 (0.63)	0.25 (0.25)	3.63 (0.38)
	Water stress E	C	10.50 (0.50)	6.13 (0.38)	0.13 (0.13)	2.25 (0.00)
		E	10.00 (2.00)	3.75 (1.75)	1.63 (0.63)	2.50 (0.00)
	Water stress VE	C	11.67 (0.00)	4.33 (0.00)	0.33 (0.00)	6.00 (0.00)
		VE	10.25 (0.75)	3.75 (0.25)	1.88 (1.88)	3.50 (2.50)
7/1/97	Irrigation	C	9.63 (0.13)	4.25 (1.25)	0.50 (0.50)	2.25 (0.25)
		V	9.25 –	2.75 –	2.00 –	1.25 –
		E	10.00 –	4.50 –	0.00 –	3.00 –
		VE	10.17 (0.83)	2.75 (0.75)	0.83 (0.17)	3.96 (0.29)
	Rainfed	C	10.63 (0.13)	5.75 (0.75)	1.25 (0.75)	2.13 (0.13)
		V	10.50 (0.00)	5.25 (0.50)	1.00 (0.75)	2.63 (0.13)
		E	7.00 –	3.00 –	0.75 –	1.25 –
		VE	11,25 (2.50)	3.88 (2.13)	1.38 (0.88)	3.88 (1.13)
	Water stress V	C	9.50 (0.25)	3.75 (1.00)	0.13 (0.13)	2.63 (0.13)
		V	9.88 (1.63)	3.75 (0.00)	0.13 (0.13)	3.38 (0.88)
	Water stress E	C	8.63 (2.63)	3.25 (1.75)	1.38 (0.88)	0.75 (0.75)
		E	8.00 (1.50)	3.13 (0.38)	0.50 (0.25)	2.25 (0.50)
	Water stress VE	C	11.00 –	6.50 –	0.50 –	2.00 –
		VE	6.50 –	1.25 –	0.00 –	3.25 –

(Continued on page 159)

ed at the vegetative stage the previous year, although numbers of daughter tillers were similar ($p > 0.25$) among water levels.

Axillary bud activation and outgrowth in *S. tenuis* were not affected by any treatment ($p > 0.25$) after defoliation at the vegetative stage in July 1996 (Table 4). Numbers of total nodes in this species, however, were on average lower ($p < 0.01$) under water stress than under better moisture levels. Reduction of leaf production (equal to number of TN) is a common response in plants of perennial grasses exposed to water stress (Brown 1995, Busso and Richards 1995, Volaire 1995).

At the end of the 1996 growing cycle, total bud number was similar ($p>0.15$) among treatments. However, numbers of dormant or dead buds in *S. tenuis* were greater ($p < 0.05$) on plants defoliated twice under rainfed or irrigated conditions, and on those defoliated once or twice under water stress, than on undefoliated controls (Table 4). Defoliation under water stress also lowered metabolic activity on buds of *A. spicatum* (Busso et al. 1989). The observed response resulted in a lower number of daughter tillers on plants defoliated twice than on undefoliated controls under all water levels, although differences were not significant ($p > 0.25$). At the same time, numbers of dormant or dead buds were greater ($p < 0.05$) when defoliated and undefoliated plants of *S. tenuis* were exposed to water stress at the vegetative or vegetative+early internode elongation than at the early internode elongation stage. This indicates that early (i.e., at V) or prolonged (i.e., at VE) water stress can be more detrimental on the degree of bud metabolic activity than late water stress (i.e., at E) in *S. tenuis*.

By early September 1995, responses in *S. clarazii* differed among water levels depending on whether plants were defoliated or not. Numbers of daughter tillers were 50% greater ($p < 0.05$) under rainfed than under irrigated or water stress conditions on undefoliated plants of this species (Table 5). When plants were defoliated, however, numbers of daughter tillers were on average 50% greater ($p < 0.01$) in the water stress than in the other water availability treatments. In comparison to values obtained before defoliation at the vegetative stage, subsequent responses can be explained, at least partially, through a greater bud activation and outgrowth on undefoliated, rainfed plants; a greater suppression of bud activation on defoliated, irrigated plants, and a greater bud outgrowth on plants defoliated at the vegetative stage under water stress.

Table 4 Continued.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
12/3/97	Irrigation	C	7.00 –	3.33 –	0.00 –	1.00 –
		V	9.00 –	4.00 –	0.50 –	2.00 –
		E	0 –	0 –	0 –	0 –
		VE	5.00 –	3.00 –	0.00 –	0.00 –
	Rainfed	C	7.25 –	3.00 –	0.00 –	2.75 –
		V	6.50 (0.00)	3.50 (0.00)	0.00 (0.00)	1.13 (0.38)
		E	6.50 –	3.00 –	0.25 –	0.75 –
		VE	10.13 (3.88)	5.63 (2.38)	0.50 (0.50)	0.63 (0.63)
	Water stress V	C	6.88 (0.63)	3.13 (1.13)	0.25 (0.25)	1.75 (0.75)
		V	6.75 –	3.75 –	0.00 –	0.75 –
	Water stress E	C	6.50 (0.75)	3.50 (0.00)	0.25 (0.25)	0.63 (0.38)
		E	6.88 (0.13)	3.63 (0.38)	0.00 (0.00)	0.75 (0.25)
	Water stress VE	C	9.50 –	6.00 –	0.00 –	1.00 –
		VE	7.63 (1.63)	3.00 (2.00)	0.13 (0.13)	3.00 (1.00)

With a few exceptions, all studied variables showed similar ($p > 0.10$) values in all defoliation and water level treatments at each sampling date in 1996 on parent tillers of *S. clarazii* (Table 5). Early in 1996, variations observed on numbers of daughter tillers in response to treatments were associated with variations on numbers of dormant or dead buds. This means that treatment effects on investigated variables were observed earlier in *S. clarazii* than in *S. tenuis* after the first year of treatment application. Numbers of daughter tillers were greater ($p < 0.05$) and those of dormant or dead buds were lower ($p < 0.05$) on *S. clarazii* plants defoliated twice than on those defoliated at the vegetative stage or nondefoliated during the previous year under rainfed conditions (Table 5). Increases in defoliation frequency have stimulated tillering through changes in light quality and/or quantity reaching stem bases in perennial grasses (Deregibus et al. 1983, Casal et al. 1985, Gautier et al. 1999). However, numbers of dormant or dead buds were greater ($p < 0.05$) on plants defoliated twice than on undefoliated controls under irrigation in *S. clarazii* (Table 5); this contributed to a lower number of daughter tillers, although differences were not significant ($p > 0.10$). At the same time, numbers of daughter tillers were greater ($p < 0.05$) on plants defoliated at the vegetative than at the early internode elongation or vegetative + early internode elongation stage in *S. clarazii* under irrigated conditions. Defoliated plants of this species, however, had a lower ($p < 0.05$) number of daughter tillers than undefoliated controls under water stress; this was associated with a greater number of dormant or dead buds, although differences were not significant ($p > 0.12$). Late or frequent defoliations have reduced daughter tiller production on several perennial grass species exposed to irrigated or water stress conditions (Busso et al. 1989, Simoes and Baruch 1991). This response has been associated with direct effects of defoliation in suppressing bud activation or to a low remaining photosynthetic leaf surface area after defoliation

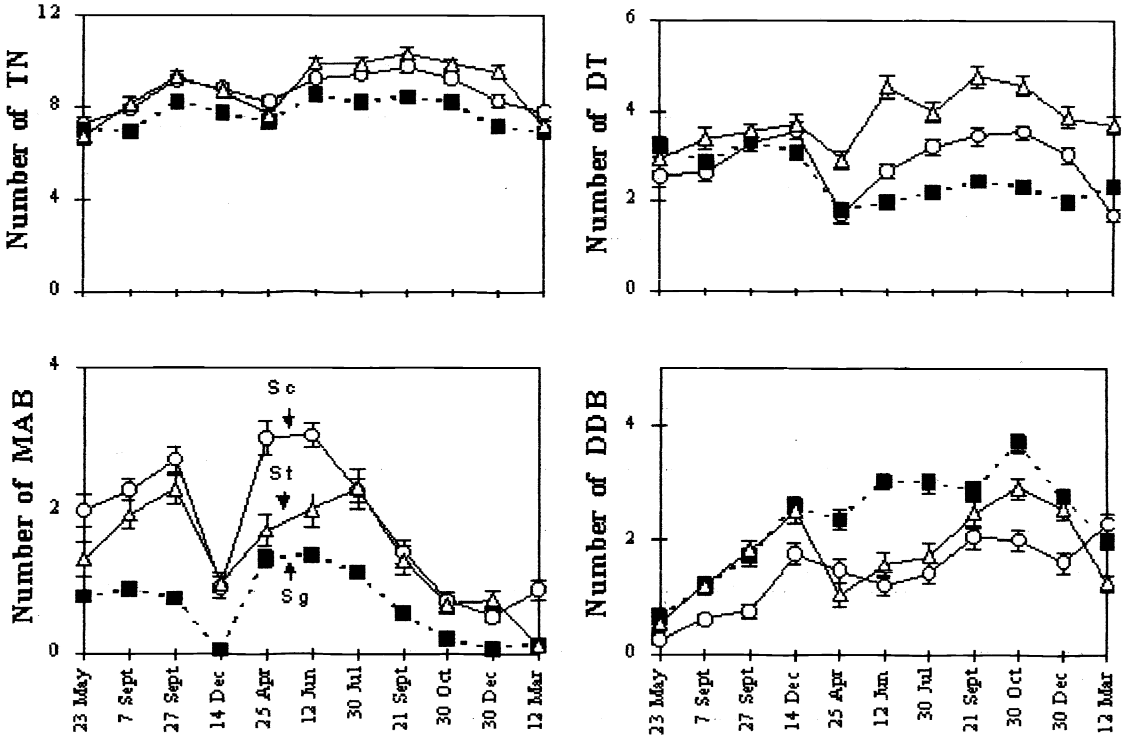

Fig. 3. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on average for all parent tillers of *S. clarazii (Sc), S. gynerioides (Sg),* and *S. tenuis (St)* observed at each date during the study period. Each symbol is an average of n=29-112. Vertical bars represent one S.E.M.

which is insufficient to maintain a high degree of bud metabolic activity under different levels of soil water availability (Busso et al. 1989). As mentioned previously, the opposite response was observed under rainfed conditions. Photosynthetically active radiation at crown level of the desirable grasses under irrigation was 70% of that under rainfed conditions (Flemmer 2000). Greater shading effects by *S. gynerioides* under higher soil water availability levels, and greater leaf water potentials in the rainfed than in the water stress treatment (Tables 1 and 2), may help explain the greater number of daughter tillers and the lower number of dormant or dead buds on defoliated than on undefoliated plants under rainfed than under irrigated or water stress conditions.

At the beginning of 1996, defoliated and undefoliated plants of *S. clarazii* had more daughter tillers ($p < 0.05$) and fewer dormant or dead buds ($p < 0.01$) after exposure to water stress at the vegetative than at the early internode elongation or vegetative + internode elongation stage. Contrary to that found in *S. tenuis*, water stress had a less detrimental impact on the degree of bud metabolic activity and subsequent outgrowth in *S. clarazii* when it occurred early (i.e., at V) than when it was present late (i.e., at E), or was prolonged (i.e., VE) during the growing season. Jamieson et al. (1995) reported a lower leaf senescence associated with a higher light interception on plants exposed to early rather than late water stress.

In October 1996, numbers of total nodes were lower ($p < 0.05$) on plants of *S. clarazii* defoliated at either the early internode elongation stage under water stress, or at the vegetative and vegetative+early internode elongation stages under irrigation than on undefoliated controls (Table 5). At the same time, however, plants of this species showed a greater ($p < 0.01$) number of total nodes under water stress when they were defoliated at the vegetative + early internode elongation stage than when they remained undefoliated. Reduction of transpiratory leaf surface areas after defoliation may have reduced detrimental effects of water stress on plant growth in comparison to undefoliated controls (Mohammad et al. 1982, Simoes and Baruch 1991).

At the end of the 1996 growing cycle, the greatest ($p < 0.05$) number of total nodes in *S. clarazii* was observed on defoliated and undefoliated plants which had been exposed to water stress at the vegetative+early internode elongation stage (Table 5). The amount of rainfall from the

Table 5. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. clarazii* at the different treatments in 1995, 1996 and early 1997. I: Irrigation, R: Rainfed, WS: Water stress, C: Undefoliated controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
			(number)			
23/5/95	Irrigation	C	7.25 (0.25)	2.50 (0.00)	2.00 (0.50)	0.50 (0.50)
		V	7.00 (0.50)	1.25 (0.25)	2.75 (1.75)	0.00 (0.00)
		VE	8.50 (0.00)	2.50 (0.00)	2.50 (0.00)	0.00 (0.00)
	Rainfed	C	8.00 (0.00)	2.00 (0.00)	1.50 (0.00)	1.00 (0.00)
		V	7.25 (0.75)	3.00 (1.50)	1.75 (0.25)	0.25 (0.25)
		VE	6.25 (1.75)	2.25 (0.75)	1.75 (0.25)	0.25 (0.25)
	Water stress V	C	7.25 (0.75)	2.00 (1.00)	1.50 (0.50)	0.25 (0.25)
		V	8.50 (0.50)	3.25 (0.25)	2.75 (0.25)	0.00 (0.00)
	Water stress VE	C	6.25 (0.25)	2.25 (1.25)	2.25 (0.75)	0.25 (0.25)
		VE	7.50 (1.50)	4.00 (2.00)	1.00 (0.00)	0.50 (0.50)
7/9/95	Irrigation	C	9.25 (1.00)	2.75 (0.25)	2.38 (0.13)	0.83 (0.13)
		V	7.67 (0.33)	1.25 (0.75)	3.08 (0.58)	1.00 (1.00)
		VE	7.63 (0.13)	1.63 (0.38)	3.00 (0.25)	0.75 (0.25)
	Rainfed	C	8.50 (0.00)	4.50 (0.00)	2.50 (0.00)	0.00 (0.00)
		V	7.88(1.38)	2.13 (0.13)	2.25 (0.50)	0.50 (0.00)
		VE	7.13 (0.13)	2.13 (1.13)	2.75 (0.25)	0.38 (0.13)
	Water stress V	C	7.25 (0.25)	2.13 (0.38)	2.00 (0.25)	0.88 (0.13)
		V	8.75 (1.00)	4.25 (0.50)	1.38 (0.13)	0.50 (0.50)
	Water stress VE	C	6.83 (0.17)	1.79 (0.54)	2.46 (0.79)	0.33 (0.33)
		VE	8.63 (0.63)	4.38 (0.38)	1.25 (0.25)	0.75 (0.75)
27/9/95	Irrigation	C	9.25 (1.50)	3.75 (0.50)	2.50 (1.50)	0.50 (0.25)
		E	9.42 (1.92)	3.04 (0.71)	3.33 (1.33)	1.25 (0.75)
		VE	8.13 (0.38)	1.88 (0.13)	3.50 (0.25)	0.25 (0.00)
	Rainfed	C	11.25 (1.75)	3.42 (0.08)	2.71 (0.96)	1.88 (0.13)
		E	8.21 (0.46)	1.88 (0.13)	3.46 (0.21)	0.29 (0.04)
		VE	8.63 (0.13)	2.88 (1.13)	2.88 (1.38)	0.38 (0.13)
	Water stress E	C	9.04 (0.29)	4.17 (0.17)	1.54 (0.21)	0.63 (0.38)
		E	10.38 (0.38)	3.13 (0.38)	2.63 (0.38)	1.38 (0.38)
	Water stress VE	C	9.25 (0.75)	4.63 (0.88)	1.88 (0.38)	0.50 (0.50)
		VE	9.25 (0.50)	3.75 (1.00)	3.00 (1.50)	0.75 (0.50)
14/12/95	Irrigation	C	7.38 (2.13)	2.50 (0.25)	0.63 (0.38)	1.25 (1.00)
		E	9.38 (0.38)	4.38 (0.63)	0.25 (0.25)	1.13 (0.13)
		VE	8.63 (0.13)	1.75 (0.25)	2.13 (0.88)	2.50 (0.50)
	Rainfed	C	9.25 (0.75)	3.88 (0.13)	0.63 (0.38)	1.92 (0.58)
		E	8.75 (1.75)	3.13 (0.63)	2.25 (0.75)	0.88 (0.13)
		VE	8.50 (0.75)	3.00 (1.00)	0.75 (0.75)	2.38 (0.88)
	Water stress E	C	8.00 (0.25)	4.38 (1.38)	0.25 (0.00)	0.88 (0.63)
		E	10.25 (1.50)	3.88 (0.63)	1.63 (0.88)	2.13 (1.13)
	Water stress VE	C	8.88 (1.13)	4.25 (0.75)	0.38 (0.13)	2.00 (0.00)
		VE	9.88 (0.13)	4.88 (0.63)	0.25 (0.00)	2.38 (0.63)
25/4/96	Irrigation	C	7.25 (0.25)	1.75 (0.25)	2.50 (0.50)	0.25 (0.25)
		V	7.50 (0.00)	2.25 (0.25)	2.75 (0.75)	1.25 (0.75)
		E	5.75 (1.25)	0.50 (0.50)	2.75 (0.25)	0.50 (0.00)
		VE	8.00 (0.00)	0.75 (0.25)	2.75 (1.25)	2.00 (1.00)
	Rainfed	C	8.75 (2.25)	1.00 (0.50)	2.00 (0.00)	2.75 (0.75)
		V	11.25 (1.75)	1.25 (0.75)	5.25 (2.75)	2.50 (0.50)
		E	8.50 (0.50)	2.00 (0.00)	2.25 (0.25)	1.50 (0.50)
		VE	8.75 (0.25)	2.75 (0.75)	4.25 (0.75)	0.50 (0.00)
	Water stress V	C	7.50 (0.00)	3.50 (0.50)	1.50 (0.00)	0.25 (0.25)
		V	7.75 (0.25)	1.75 (0.25)	4.00 (1.00)	0.50 (0.50)
	Water stress E	C	8.50 (1.00)	1.50 (0.50)	4.00 (1.00)	1.25 (0.75)
		E	8.25 (0.25)	1.25 (0.25)	3.25 (0.25)	2.50 (0.50)
	Water stress VE	C	8.75 (0.75)	2.00 (1.00)	2.75 (0.25)	2.00 (0.00)
		VE	9.00 (1.00)	1.25 (0.25)	2.25 (0.75)	2.75 (0.75)
12/6/96	Irrigation	C	9.13 (0.38)	2.00 (0.75)	4.00 (0.75)	0.25 (0.25)
		V	9.25 (1.25)	2.50 (0.50)	2.38 (0.13)	1.38 (1.13)
		VE	9.00 (1.50)	2.13 (0.63)	3.50 (0.25)	0.63 (0.13)

(Continued on page 161)

Table 5. Continued.

Dates	Treatments Water levels	Defoliation	TN	DT	MAB	DDB
			------------------------------(number)------------------------------			
	Rainfed	C	9.00 (1.00)	2.13 (0.63)	3.50 (0.50)	1.50 (0.00)
		V	9.63 (0.38)	2.75 (0.50)	3.50 (0.25)	1.00 (0.00)
		VE	9.50 (0.25)	2.63 (0.38)	2.88 (0.88)	1.63 (0.13)
	Water stress V	C	9.13 (0.63)	3.75 (0.50)	2.38 (0.38)	1.13 (0.88)
		V	8.75 (0.00)	2.75 (1.00)	1.75 (1.25)	1.38 (1.38)
	Water stress VE	C	9.38 (0.13)	3.50 (0.25)	3.38 (0.13)	0.63 (0.38)
		VE	9.75 (0.00)	2.63 (0.13)	3.25 (0.25)	2.63 (0.13)
30/7/96	Irrigation	C	10.38 (1.38)	4.25 (0.25)	2.13 (0.13)	0.13 (0.13)
		V	9.13 (0.63)	2.88 (0.13)	2.75 (0.50)	1.38 (0.88)
		VE	10.00 (0.25)	3.75 (1.00)	1.13 (0.88)	1.63 (1.38)
	Rainfed	C	8.88 (0.63)	1.50 (0.25)	2.13 (0.63)	2.38 (0.13)
		V	9.88 (0.63)	3.75 (1.00)	3.38 (0.13)	1.13 (1.13)
		VE	9.50 (0.50)	3.75 (0.00)	1.38 (1.13)	1.63 (0.38)
	Water stress V	C	9.00 (0.50)	3.25 (0.50)	2.38 (0.88)	1.13 (0.88)
		V	9.00 (0.75)	3.00 (0.00)	2.50 (0.50)	1.88 (0.63)
	Water stress VE	C	9.13 (1.63)	2.88 (0.13)	2.38 (0.13)	1.50 (1.25)
		VE	9.25 (1.00)	3.00 (0.75)	2.63 (0.38)	1.50 (0.50)
21/9/96	Irrigation	C	9.50 (0.00)	5.13 (1.13)	1.13 (0.38)	0.88 (0.88)
		E	10.25 (1.00)	3.63 (0.38)	1.25 (0.00)	2.00 (0.25)
		VE	9.75 (1.00)	4.00 (1.00)	0.88 (0.13)	2.13 (0.13)
	Rainfed	C	8.38 (0.88)	2.25 (0.50)	1.63 (1.13)	2.00 (1.50)
		E	8.88 (1.63)	3.25 (0.50)	0.25 (0.25)	2.25 (0.50)
		VE	10.75 (0.50)	3.00 (0.75)	0.63 (0.38)	4.25 (1.75)
	Water stress E	C	11.00 (1.25)	4.00 (1.00)	1.25 (1.00)	1.38 (0.38)
		E	8.25 (0.50)	3.00 (0.25)	1.38 (0.63)	1.13 (0.38)
	Water stress VE	C	11.88 (1.38)	4.13 (0.38)	3.38 (1.13)	2.00 (0.75)
		VE	9.25 (1.00)	2.00 (0.00)	2.38 (0.13)	2.50 (0.75)
30/10/96	Irrigation	C	10.50 (1.25)	3.50 (0.00)	0.38 (0.13)	1.75 (0.25)
		V	7.75 (0.25)	3.63 (0.63)	0.75 (0.00)	0.38 (0.13)
		E		– –	– –	– –
		VE	8.00 (0.50)	3.50 (0.25)	0.38 (0.13)	0.88 (0.38)
	Rainfed	C	8.75 (0.50)	3.50 (0.50)	0.13 (0.13)	1.75 (0.25)
		V	8.50 (0.50)	2.25 (0.00)	0.38 (0.38)	3.13 (0.38)
		E	9.13 (0.38)	3.88 (1.88)	1.88 (0.88)	1.00 (0.25)
		VE	9.38 (0.13)	3.25 (0.00)	0.13 (0.13)	3.25 (0.50)
	Water stress V	C	8.50 (0.25)	4.13 (0.88)	0.13 (0.13)	1.50 (0.75)
		V	9.38 (0.63)	4.00 (0.75)	0.63 (0.38)	1.75 (0.25)
	Water stress E	C	10.75 (0.25)	4.25 (0.25)	0.75 (0.75)	2.25 (2.00)
		E	8.88 (0.13)	3.50 (0.50)	0.63 (0.13)	2.38 (0.38)
	Water stress VE	C	8.38 (0.38)	2.63 (0.13)	1.38 (0.38)	1.88 (0.88)
		VE	12.63 (0.13)	3.75 (0.50)	2.13 (1.38)	4.25 (0.50)
7/1/97	Irrigation	C	7.63 (0.88)	2.88 (1.63)	0.13 (0.13)	1.50 (0.25)
		V	7.63 (1.38)	3.13 (0.88)	0.25 (0.00)	0.63 (0.38)
		E	6.75 (0.50)	1.75 (0.25)	0.88 (0.38)	1.00 (0.25)
		VE	7.38 (1.38)	2.38 (0.88)	0.25 (0.25)	1.38 (0.63)
	Rainfed	C	7.13 (1.38)	2.38 (1.13)	0.38 (0.13)	1.13 (0.38)
		V	8.00 (0.50)	2.38 (0.13)	0.63 (0.13)	1.00 (0.75)
		E	10.13 (0.63)	3.88 (1.38)	0.88 (0.63)	2.25 (0.75)
		VE	8.88 (0.88)	3.00 (1.00)	0.13 (0.13)	2.63 (0.13)
	Water stress V	C	7.63 (0.13)	2.63 (0.38)	0.25 (0.25)	0.88 (0.13)
		V	7.00 (0.50)	2.50 (0.25)	0.13 (0.13)	0.63 (0.13)
	Water stress E	C	8.13 (0.13)	3.75 (0.25)	0.25 (0.25)	0.75 (0.25)
		E	7.50 (0.75)	2.63 (1.63)	0.88 (0.63)	1.88 (1.13)
	Water stress VE	C	10.88 (1.13)	5.13 (0.63)	0.50 (0.50)	3.13 (0.13)
		VE	11.38 (1.38)	3.75 (1.00)	1.75 (0.25)	3.63 (0.63)
12/3/97	Irrigation	C	6.13 (0.63)	1.75 (0.25)	0.00 (0.00)	1.75 (0.25)
		V	7.13 (0.38)	2.50 (0.00)	0.50 (0.25)	1.88 (0.63)
		E	7.75 –	1.75 –	0.25 –	2.00 –
		VE	7.63 (0.63)	1.63 (0.63)	0.50 (0.00)	2.63 (0.13)

(Continued on page 162)

end of the water stress treatment at the vegetative + early internode elongation stage to sampling at the end of the growing cycle in 1996 was high (221 mm). This and total nonstructural carbohydrates which may have accumulated during the long water stress period (i.e., VE) may have resulted in such a high number of total nodes at the end of the second year of successive treatments. Numbers of dormant or dead buds, however, were greater ($p < 0.01$) on plants exposed to water stress at the vegetative + early internode elongation than at the vegetative or early internode elongation stage. Similar to that found in other perennial grasses (Busso et al. 1989), prolonged water stress stimulated suppression of bud activation in *S. clarazii.*

At the beginning of 1997, after 2 years of successive treatments, numbers of total nodes and bud metabolic activity and outgrowth were similar ($p > 0.25$) between defoliation treatments or water levels on parent tillers of *S. clarazii* and *S. tenuis* (Tables 4 and 5). A similar response was reported on *S. tenuis* and *P. napostaense*: these species did not modify their potential regrowth capacity after rainfed plants were defoliated at different phenological stages during 2 consecutive years (Becker et al. 1997). The degree of metabolic activity and outgrowth of axillary buds has also been similar on perennial grass plants coming from sites with very different grazing histories (Hendrickson and Briske 1997). Potential regrowth capacity of *S. tenuis*, *P. napostaense* and *S. gynerioides*, however, is reduced by fire (Peláez et al. 1997, Peláez 2000).

Numbers of total nodes, daughter tillers, and metabolically active buds tended to be similar or greater on the desirable than on the undesirable species when averaging values for all parent tillers within each species and sampling date (Fig. 3). Numbers of daughter tillers tended to be greater in *S. tenuis* than in *S. clarazii* during 1996. On the other hand, *S. gynerioides* appeared to have a greater number of dormant or dead buds than *S. clarazii* in 1995, and than both desirable species in 1996 (Fig. 3). Early in 1997, greatest numbers of metabolically active buds and daughter tillers were observed on parent tillers of *S. clarazii* and *S. tenuis*, respectively. Thus, *S. clarazii* showed a greater potential regrowth capacity than *S. tenuis*, whereas *S. tenuis* was able to activate a greater bud number and produce more new tillers than *S. clarazii* after 2 years of treatment. Recent studies have indicated a greater competitive ability and tolerance to defoli-

Table 5. Continued.

	Treatments					
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
			(number)			
	Rainfed	C	7.50 (0.50)	1.75 (0.25)	0.50 (0.25)	1.75 (0.25)
		V	8.88 (1.63)	2.38 (1.13)	1.25 (1.25)	2.25 (1.75)
		E	6.63 (0.13)	1.38 (0.38)	0.63 (0.63)	1.63 (0.13)
		VE	8.21 (1.46)	1.38 (0.63)	2.29 (1.04)	2.13 (0.13)
	Water stress V	C	7.63 (0.88)	1.25 (0.25)	2.25 (1.25)	1.63 (1.38)
		V	8.00 (0.25)	0.75 (0.50)	0.50 (0.00)	3.13 (0.13)
	Water stress E	C	6.88 (1.13)	1.38 (0.38)	0.75 (0.50)	1.13 (0.88)
		E	7.13 (0.13)	0.88 (0.38)	0.88 (0.13)	2.50 (0.00)
	Water stress VE	C	9.13 (1.38)	2.38 (1.13)	0.88 (0.38)	3.38 (0.13)
		VE	11.50 (4.25)	2.75 (1.50)	1.00 (0.50)	4.63 (2.38)

ation in *S. clarazii* than in *S. tenuis* (Saint Pierre et al. 2000a, 2000b). Our results show that plant traits which make *S. clarazii* a superior competitor and more tolerant to defoliation are not linked to producing more daughter tillers.

As the growing season progressed in 1995 and 1996, numbers of metabolically active buds decreased and those of dormant or dead buds increased on parent tillers of the 3 species (Fig. 3). Bud senescence or necrosis may increase suppression of bud activation towards the end of a growing season in perennial grasses (Mitchell 1953). With the advancement of the growing season, however, signs of bud senescence were minor with most buds looking viable in *A. desertorum* and *A. spicatum* (Mueller and Richards 1986). Low percentages of metabolically active buds at the end of 1996 were confirmed early in 1997 indicating a decreased potential regrowth capacity in all 3 species in comparison to previous years, probably because of cumulative treatment effects.

During 1995 in all 3 species and *S. clarazii* and *S. tenuis* in 1996, approximately 50-60% of the entire bud pool (DT+MAB+DDB) was able to grow out and produce new tillers. However, less than 41% of all buds grew out into daughter tillers on parent tillers of *S. gynerioides* in 1996. Percentage of buds which grew out and produced tillers from the entire bud pool is greater than that reported for other perennial grasses of semiarid regions (Mueller and Richards 1986, Busso et al. 1989, Hendrickson and Briske 1997).

Despite some transitory effects of defoliation on axillary bud dynamics, rapid photosynthetic canopy reestablishment after defoliation under all water levels was not limited by availability and/or regrowth capacity of axillary buds in *S. clarazii* and *S. tenuis*. These results do not support hypothesis 2. The only exception, and in agreement with this hypothesis, was observed after defoliation at the vegetative stage in 1995 on parent tillers of *S. clarazii*: these tillers had a greater number of daughter tillers after being defoliated than remaining undefoliated under water stress. At the same time, however, numbers of daughter tillers were lower on defoliated than on undefoliated plants of this species when exposed to rainfed or irrigated conditions. Lack of consistent responses to defoliation have been attributed, at least partially, to the complexity of physiological mechanisms (i.e., see Murphy and Briske 1992) and the great number of potentially intervening factors (i.e., abiotic variables, phenological stage of development, and frequency and intensity of defoliation) which can regulate bud metabolic activity and subsequent regrowth in perennial grasses (Briske and Richards 1995). In our study, responses were specific to the species, imposed treatments, sampling times, and cumulative treatment effects. This makes prediction of plant responses under natural conditions difficult, a conclusion similar to that reported by Haferkamp and Karl (1999) or Allen et al. (1989) after studying the effects of defoliation on plant growth of an annual brome grass or the degree of colonization of perennial grass roots by arbuscular-vesicular mycorrhiza, respectively.

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