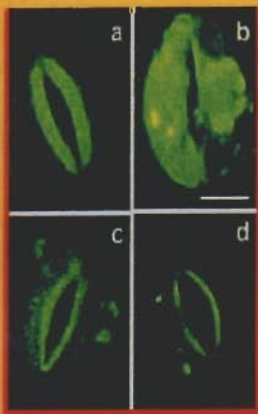


PLANT PHYSIOLOGY & PLANT MOLECULAR BIOLOGY

# ADVANCES IN

# PLANT PHYSIOLOGY

Volume 5



*Editor*

**A. Hemantaranjan**

PLANT PHYSIOLOGY AND PLANT MOLECULAR BIOLOGY

# ADVANCES IN PLANT PHYSIOLOGY

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## **MORPHOPHYSIOLOGICAL AND DEMOGRAPHIC RESPONSES OF PERENNIAL GRASSES TO DEFOLIATION UNDER WATER STRESS**

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### INTRODUCTION

#### **1.1 Importance of Studying the Effects of Defoliation Under Water Stress on Rangeland Vegetation**

Range grasses are commonly defoliated under water stress conditions in arid and semiarid areas (Ludlow, 1986). The interaction of water stress and defoliation may reduce plant survival and lead to more arid conditions (Westoby, 1980; Skarpe, 1986), as soil and

microclimate change. These responses have been observed when pastures have been defoliated during natural droughts (McLean and Ryswyk, 1973; Breman and Cissé, 1977; Ganskopp and Bedell, 1981; Currie and White, 1982). While these studies provide valuable insights into the effect of defoliation during water stress, they are of marginal predictive value because of their anecdotal and often

qualitative nature especially in regard to the degree of water stress experienced by the plants. Thus, most of these studies have limited value for understanding the mechanisms of plant response to the combination of water stress and defoliation since predetermined levels of defoliation or water stress and/or control plants were not measured (Chung and Trlica, 1980; O'Connor, 1995). Most investigations which have addressed the simultaneous imposition of both stresses have been conducted under either greenhouse or growth chamber conditions (Chung and Trlica, 1980). These results cannot be applied directly to rangelands because plant responses differ substantially between the field and controlled environments, especially with regard to water stress (Ludlow and Ng, 1976; Bunce, 1977; Turner and Begg, 1978).

Despite rainfall and grazing are two major determinants of grassland ecosystem structure (McNaughton *et al.*, 1983; Coughenour, 1984; Coughenour *et al.*, 1985 a,b; Busso, 1997; Fernández and Busso, 1999), the effects of these stresses on grass plant responses have often been studied separately (i.e., O'Connor, 1993). Under these conditions, community structure and dynamics in rangelands have been reported to be more dependent upon moisture availability than upon grazing or clipping in some studies (Danckwerts and Nel, 1989; Westoby *et al.*, 1989; O'Connor, 1994; Varnamkhasti *et al.*, 1995; Giorgetti *et al.*, 1997) but not in others (Coughenour *et al.*, 1985b; McNaughton, 1985). In 1994, O'Connor already called attention that these equivocal findings may be resolved if future work considers the frequency, intensity and timing of defoliation with respect to moisture availability.

The great variability of forage production on arid and semi-arid rangelands is a consequence of highly

variable total annual or season amount and timing of precipitation (Stoddart *et al.*, 1975; Wagner, 1976; Ehleringer and Mooney, 1983; Giorgetti *et al.*, 1987; White *et al.*, 1998) and the close correlation of forage production to water availability or use (e.g. Hutchings and Stewart, 1953; Currie and Smith, 1970; Sims and Singh, 1978). Because of this variability, seasons or years of unfavourable forage production are not infrequent events (e.g., Wilhite, 1986; Stafford Smith and McKeon, 1998). Estimates of the frequency of unfavourable production range from 12-40% (Stoddart *et al.*, 1975; Banner, 1981) depending on the definition of 'unfavourable'. Grazing pressure almost inevitably increases during periods of unfavourable production because it is impractical or economically disadvantageous, in the short-term, to reduce the stocking rates of livestock and wildlife to levels that would maintain proper forage utilization. Thus it is important to know to what degree forage species can be utilized during water stress periods without causing degradation of their productive potential or reducing their competitive ability in the range plant community.

Forage producing species of arid and semi-arid rangelands are well adapted to water stress, which develops at the end of each growing season. These same species, however, may be adversely affected, or killed, by low moisture availability during the growing season, even in the absence of grazing (Weaver and Albertson, 1936; Chamrad and Box, 1965; Box, 1967; Herbal *et al.*, 1972; Holmgren and Hutchings, 1972). It is commonly accepted that grazing during water stress accentuates the water stress effects by increasing mortality, reducing plant vigour and changing floristic composition, population size and structure, and basal cover (O'Connor, 1995). However, some studies have shown that certain desirable

species were able to increase following utilization during water stress while others have been unable to show negative effects of grazing during water stress on range plants or range plant communities (e.g., Paulsen and Ares, 1961; Herbal *et al.*, 1972; Smeins *et al.*, 1976; Wright and van Dyne, 1976).

Furthermore, moderate clipping of *Agropyron desertorum* [(Fisch. ex Link) Schult.] and *Elymus junceus* in combination with severe moisture stress allowed increased rather than decreased forage yields (Mohammad *et al.*, 1982). Severe clipping, however, resulted in 100% mortality of both species under severe water stress (Mohammad, 1979). These studies and that of Chambers (1979) suggest that the responses of individual species to grazing during water stress were not predictable from those species' responses to defoliation. Mechanistic studies where levels of water stress and defoliation are quantified are essential to improve our ability to predict species' responses to various levels of defoliation during water stress.

Much research has been completed on water stress effects, adaptation, and tolerance of rangeland and pasture species (see reviews of Brown, 1977; Turner and Begg, 1978; MacMahon and Schimpf, 1981; Brown, 1995). Morphological responses of plants, such as leaf area development, tillering, and root growth have shown more sensitive to water deficits than are physiological responses such as stomatal closure and photosynthesis (Turner and Begg, 1978). Similarly, the importance of the same morphological responses has been demonstrated for plant recovery from defoliation (Caldwell *et al.*, 1981; Mott *et al.*, 1992; Briske and Richards, 1995). This is one of the reasons these morphological parameters will be discussed in this review.

Rapid re-growth following defoliation is important if plants are to tolerate herbivory with minimal damage (Caldwell *et al.*, 1981; Briske and Richards, 1995). High growth rates after defoliation could allow plants to more rapidly re-establish the root/shoot balance and to obtain a greater share of the available space and the resources included in that space thereby better maintaining their competitive position in relation to their neighbours. Following defoliation, rapid production of new leaves on remaining shoots with intact apical meristems and/or activation and growth of axillary buds into tillers could also add to perennation by the addition of axillary buds to the tussock's bud bank (Busso *et al.*, 1989). Immediately after defoliation, grasses can re-establish a photosynthetic canopy by producing both leaf blades and leaf sheaths. These may grow from either undefoliated or defoliated shoots with intact intercalary and apical meristems. They may also be produced from the growth of axillary buds into new shoots. Therefore, any stress, such as water stress, which reduces leaf extension, tiller production and growth, or axillary bud production, activity or viability could impose a limitation on the re-growth potential of a particular species.

Tolerance of perennial grasses to herbivory and water stress may be affected by the degree of root system colonization by vesicular-arbuscular mycorrhizae (VAM; Allen *et al.*, 1989; Allen, 1991). Higher VAM colonization has been associated with greater nutrient acquisition thus improving competitive ability and growth in perennial grasses (Marschner and Dell, 1994; Mohammad *et al.*, 1998; Miller, 2000). However, lack of or even negative responses have been obtained under increased levels of mycorrhizal colonization (). Loss of photosynthetic leaf surface area after defoliation can reduce carbon allocation to

the root system (Richards, 1984). The degree of root system colonization by VAM may thus be reduced because of the plant carbon need by the fungi as an energy source (Andersen and Rygielwics, 1991). Negative effects of defoliation on VAM formation have increased as defoliation intensity and frequency have also increased (Hetrick *et al.*, 1990). Additionally, VAM root colonization may decrease as plant water stress increases (Andersen and Rygielwics, 1991; Auge *et al.*, 1995; Jacobson, 1997). In spite of the importance that defoliation and water stress may have on the degree of root system colonization by VAM, studies which have addressed the interactive effects of both stresses on VAM root colonization and subsequent plant growth are extremely scarce (e.g., Allen *et al.*, 1989).

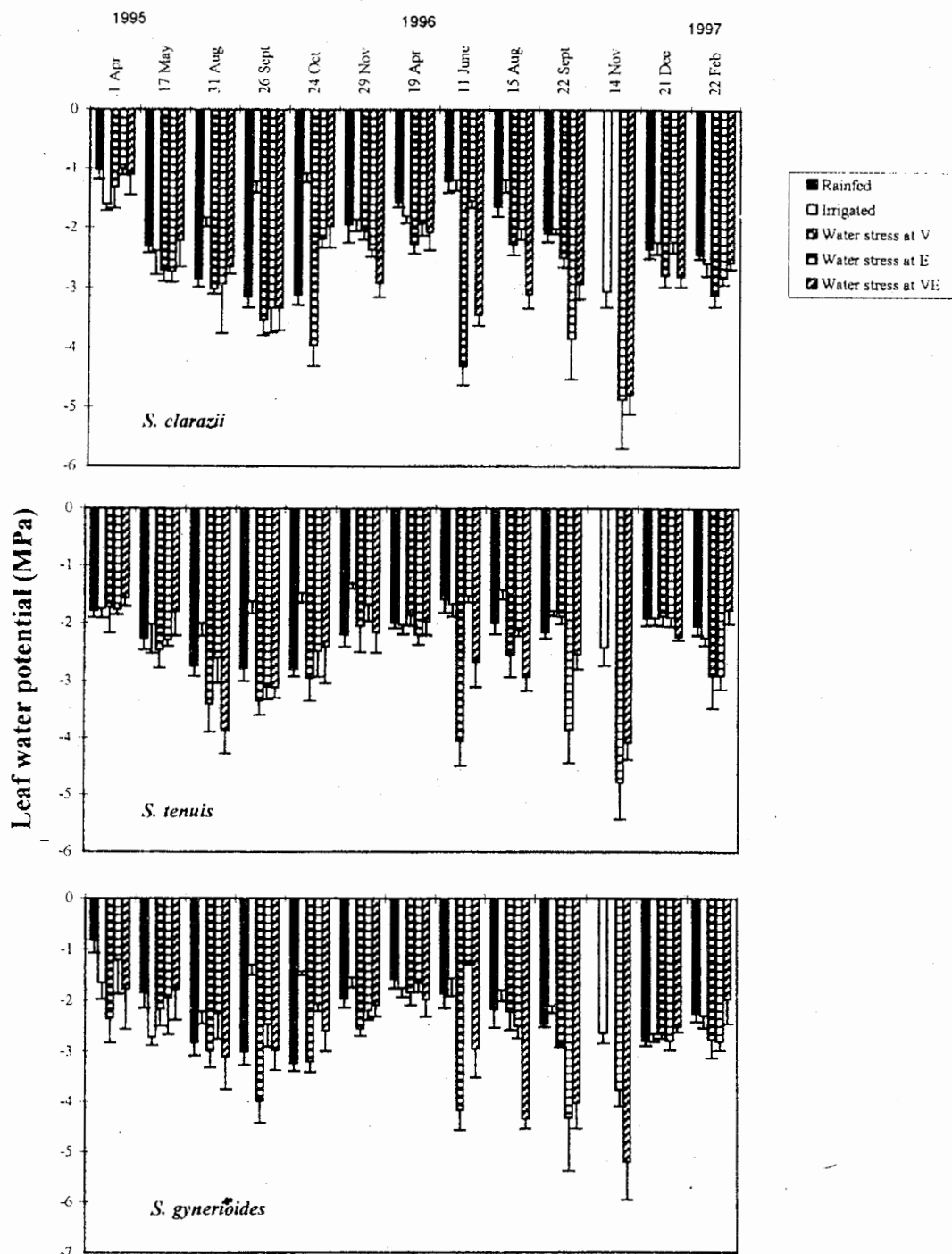
Results obtained from studies on mechanisms of re-growth of perennial grasses following defoliation during water stress will improve the ability of public and private land managers to predict the effects of continued rangeland forage utilization during water stress on plant vigour, productive potential and competitive relationships in rangeland plant communities. In this review, we will report on the effects of defoliation under water stress on several physiological, morphological and demographic factors which may be important in determining plant and community productivities. Within this context, we will discuss previous work with some recent results obtained in our ecophysiology group.

## 1.2 Background Information for our Recent Studies of the Interactive Effects of Water Stress and Defoliation

We conducted a field study during 1995-1997 to determine the effects of water stress, natural rainfall or irrigated

conditions with or without defoliation at various phenological stages on various plant response variables in *Stipa clarazii* Ball, *S. tenuis* Phil. and *S. gynerioides* Phil. These species are abundant, native perennial tussock grasses in temperate, semiarid rangelands of central Argentina (Busso, 1997; Fernández and Busso, 1999). While *S. clarazii* and *S. tenuis* are palatable species, *S. gynerioides* is unpalatable to cattle (Cano, 1988; Moretto and Distel, 1997). Studies were conducted at the research field site nearby the Agronomy Department-CERZOS (CONICET), National University of the South in Bahía Blanca, Argentina (38° 48'S, 62° 13'W). Soil is a typical Haplustol with a petrocalcic horizon at 1.8 m depth. It has a loam-sandy texture; 1.9% organic matter; 7 ppm extractable P; 0.10% total N and a pH of 7.4. During 1995, 1996 and early 1997 (January-March), rainfall was 447.2, 621.3 and 285 mm, respectively. Leaf water potentials were obtained at these times as a measure of plant water status (Fig. 1). Other climatic characteristics during the study period are reported by Flemmer *et al.* (in press).

Between December 1993 and April 1994, 28 experimental plots (1.8 x 1.8 m) were established in the field on unploughed, weeded soil. Plants were obtained from a 20 year-exclosure to domestic animals located southeast of La Pampa Province (38°45'S, 63°45'W). Within each plot, transplants were placed 30 cm apart from one another in seven horizontal and vertical rows such that four plants of *S. gynerioides* surrounded each plant of *S. clarazii* or *S. tenuis*. Disposition of plants within a uniform matrix contributes to reduce potentially confounding effects on plant responses as a result of plant competition. A total of 1372 transplants were used for the whole study. Each plot contained 49 plants: 12 of *S. clarazii*, 12 of *S. tenuis* and 25 of *S. gynerioides*.



**Figure 1.** Mid-day leaf water potential (MPa) on undefoliated and defoliated, palatable plants of *S. clarazii* and *S. tenuis*, and undefoliated, unpalatable plants of *S. gynerioides* which were exposed to irrigated, rainfed or water stress conditions at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996. Data for defoliated and undefoliated plants of the palatable grasses were pooled within each water level after differences were not significant ( $p > 0.10$ ) among defoliation treatments. Each histogram is an average of  $n=2$ . Vertical bars represent one standard error of the mean.

Crown-level plant diameters ( $n=56$ ) were similar among species at time of transplanting:  $13.47 \pm 0.56$  cm (mean  $\pm$  1 SE) for *S. clarazii*,  $10.02 \pm 0.51$  cm for *S. tenuis*, and  $12.27 \pm 0.61$  cm for *S. gynerioides*.

All tussocks of *S. clarazii* and *S. tenuis* were hand-clipped to a 5-cm stubble height in January 1995, during the plant quiescent period. Thus, only current year growth was included in subsequent harvests for biomass determinations. Two experimental plots (replicates) were randomly assigned to each water level  $\times$  defoliation treatment combination, giving a total of 14 treatments (see combination of defoliation  $\times$  water level treatments in Fig. 2). Plants of *S. clarazii* and *S. tenuis* remained undefoliated (Controls : C) or they were clipped either at their vegetative (V), their internode elongation (E) or at both (VE) phenological stages of development within each water level treatment in 1995 and 1996. Clipping was done at a 5-cm stubble height on 23 May (V) or 27 September (E) or both dates (VE) in 1995, and 12 June (V) or 20 September (E) or both dates (VE) in 1996. The unpalatable *Stipa gynerioides* remained undefoliated during the study period since this species is often not consumed by cattle (Cano, 1988).

There were three water level treatments: rainfed, irrigated and water stress. Rainfed plots received rainfall all year round. A drip irrigation system watered the irrigated plots, which were additionally rain-fed. Periods of irrigation were from mid-winter (5 August) to mid-spring (30 October) in 1995, and from mid-autumn (21 April) to mid-spring (26 October) in 1996. Soil tensiometers installed in the irrigated plots allowed watering of these plots back to field capacity whenever they reach 60% of that value.

Transparent plastic sheets (0.2 mm thick) covered the water-stressed plots whenever rain fell at periods when these species are often exposed to water stress in their native environment (Busso, 1997; Fernández and Busso, 1999): vegetative (V; 12 April to 10 June in 1995, 21 April to 5 July in 1996) or early internode elongation (E; 1 August to 13 October in 1995, 19 August to 26 October in 1996) or both phenological periods (VE; 12 April to 13 October in 1995, 21 April to 26 October in 1996). A specially designed wooden structure, which provided an open-sided rain shelter, supported these plastic sheets. Water-stressed plots were surrounded with plastic sheets (0.2 mm thick) up to 1.8 m soil depth to prevent lateral movement of water into these plots.

Except for those plots exposed to water stress in VE, the amount of water received during imposition of the different water levels (mid-April to mid-October in 1995 and late-April to late-October in 1996) was (i) 373.2 mm in 1995 and 305.4 mm in 1996 in the irrigated plots; (ii) 87.2 mm in 1995 and 252.4 mm in 1996 in the rainfed plots; (iii) 76.4 mm in 1995 and 172.6 mm in 1996 after alleviation of water stress at V, and (iv) 22.0 mm in 1995 and 133.2 mm in 1996 before imposition of water stress at E. 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. Water-stressed plots were thus alleviated from water stress during these periods by receiving natural rainfall.

Plant response variables in our study included measurements of physiological [leaf water potential, vesicular-arbuscular mycorrhiza (VAM) and osmotic adjustment] and morphological (root length density; root growth; axillary bud viability, outgrowth and length; tiller growth; dry weight production) variables. We will be referring to this study repeatedly during the subsequent presentation.

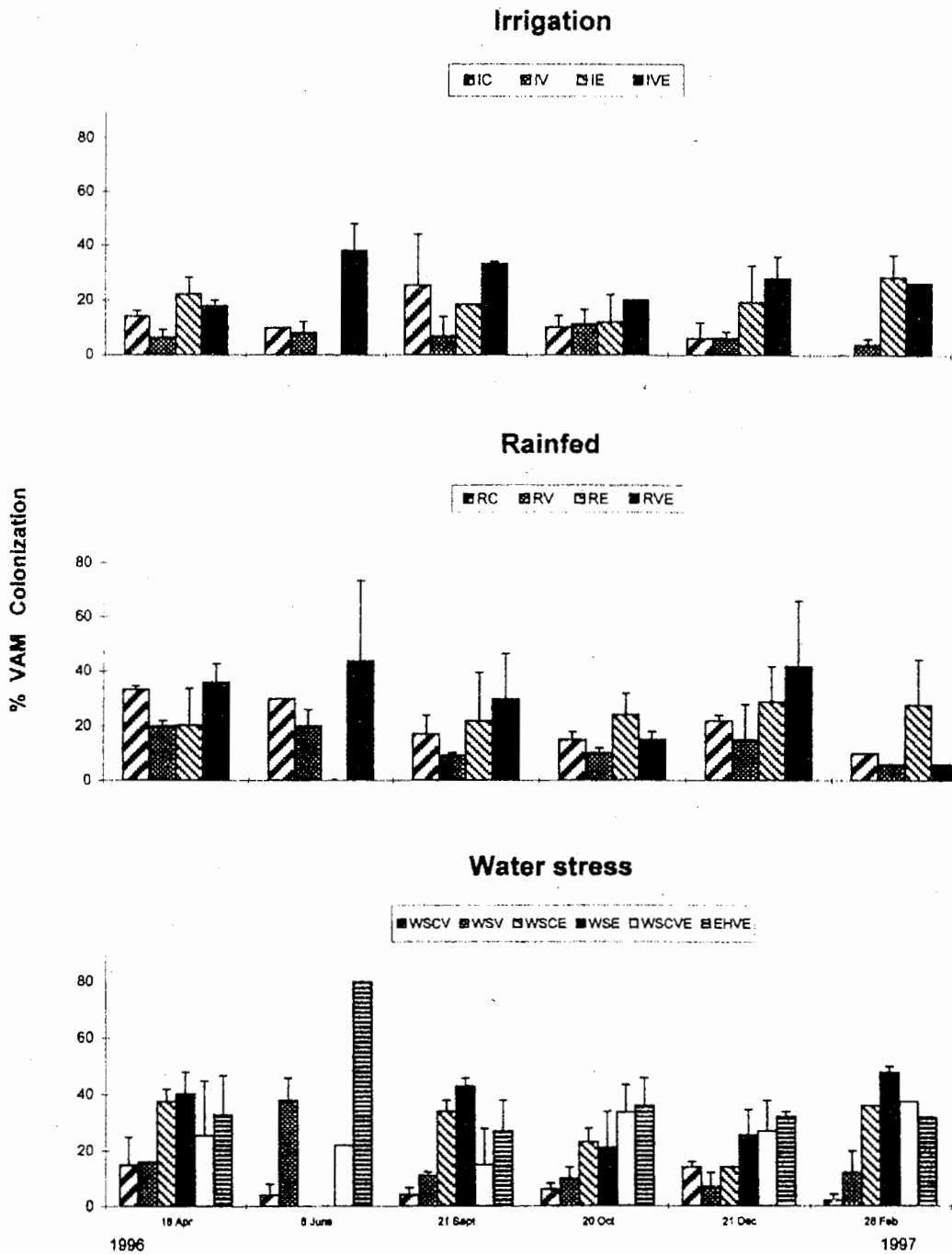


Fig 2

**Figure 2.** Percentage vesicular-arbuscular mycorrhizal (VAM) colonization during 1996 and early 1997 in plants of *Stipa clarazii* which remained undefoliated (Control:C) or were defoliated at the vegetative (V), internode elongation (E) or both phenological stages (VE) under irrigated (I), rainfed (R) or water stress (WS) conditions in 1995 and 1996. Each histogram is a mean of  $n=2$ . Vertical bars represent one standard error of the mean. Lack of vertical bars imply that data come from  $n=1$ .

## 2. PHYSIOLOGY

### 2.1 Leaf Water Potential

We determined leaf water potentials in *S. clarazii*, *S. tenuis* and *S. gynerioides* after plants of these species were either defoliated or not under water stress, rainfed or irrigated conditions during 1995 and 1996. Experimental design and treatments for this study are as described under item 1.2. Measurements were made using a pressure chamber during 1995, 1996 and early 1997 (Waring and Cleary, 1967). Youngest, fully expanded leaf blades were taken for these measurements from one tiller per species and replicate on each sampling date. Leaves were kept in a plastic bag from excision to the end of each determination to reduce water loss (Turner, 1987). Leaf water potentials were similar among defoliation treatments ( $p > 0.05$ , data not shown) within each species and water level during the study period. This agrees with results of Busso and Richards (1993) and Becker *et al.* (1997a) on *Agropyron*, *Stipa* and *Piptochaetium* species. Other studies, however, have reported higher leaf water potentials on defoliated than on undefoliated plants of several perennial tussock grasses, a response which has been attributed to conservation of soil water after defoliation (Brown, 1995).

Leaf water potentials were similar among water levels in *S. clarazii*, *S. tenuis* and *S. gynerioides* at the beginning and end of each growing cycle (Fig. 1). These species, however, had lower ( $p < 0.05$ ) leaf water potentials under water stress than under irrigated conditions during August-October 1995 (Fig. 1). Results were similar in 1996 during this period, except on plants of *S. clarazii* and *S. tenuis* by the end of September ( $p > 0.15$ ). Leaf water potentials were more variable on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* in

the rainfed plots. Under these conditions, leaf 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 (Fig. 1). This was very likely due to the lower annual rainfall in 1995 (447.2 mm) than in 1996 (621.3 mm).

Except in April 1995 when leaf water potential was higher ( $p < 0.05$ ) in *S. clarazii* than in *S. tenuis* (Fig. 1), this variable was similar among species on average for all treatments. By mid-August, September and December in 1996, leaf water potentials were higher ( $p < 0.05$ ) in *S. clarazii* and *S. tenuis* than in *S. gynerioides* (Fig. 1).

### 2.2 Water Use

As available water is relatively limited in arid and semi-arid areas, it is important that water needs and influence of defoliation on range plants be investigated for sustainable animal production in this ecologically sensitive area. Changes in primary productivity of semi-arid rangelands have been shown to accompany changes in the species composition of the vegetation (Snyman, 1999). Rainfall variability has a high effect on annual variation in species abundance (Giorgetti *et al.*, 1997), but unless there is a directional trend, and despite the potential for large annual changes, there is no net change in species composition over the long-term. In contrast, changes as a result of grazing can be small on an annual scale but are cumulative and substantial over the long-term, because the direction of the impact of a certain pattern of grazing is usually consistent for a given species (O'Connor and Roux, 1995).

Snyman (1999) clearly showed that rangeland degradation is not only accompanied by a decrease in productivity, but also reduced in water-use efficiency.

When rangeland is in poor condition, water-use efficiency is low, regardless of soil water content. Consideration of ways to select more drought-tolerant plants usually assumes that greater water use efficiency is the best strategy, *i.e.* greater rates of plant growth per unit of water used. However, pasture plants that are sensitive to water use and stop growth early, may in fact survive dry seasons better than those which have a range of physiological mechanisms to save water, and can then maintain better growth rates. Useful water stress avoidance mechanisms include early wilting, leaf rolling or folding, and leaf shedding (Brown, 1995). This could mean more water retention in the soil that the plant could use to survive the dry season. Reduction of leaf area can reduce the rate of water use and allow roots the opportunity to continue growing into deeper and wetter soil (Kemp and Cuvonor, 1994).

Herbivory may alter both the availability of water and its utilization by plants (Archer and Detling, 1986). Plant water status might be expected to vary as a function of grazing pressure. It has been suggested that grazing may conserve soil moisture through the removal of transpiring leaf tissues (Brown, 1995). This may result in higher water potentials, which in turn may contribute to higher rates of growth in the remaining tissues of grazed plants (Hodgkinson, 1976). Such positive aspects of herbivory on plant water status may partially offset a variety of negative impacts. For example, defoliation during periods of low soil water availability might accentuate plant water stress by reducing the ability of roots to maintain high enough extension rates to keep ahead of the drying front in the soil profile. Herbivores may also affect plant water status indirectly by altering interception of water by the canopy, bulk

density, water infiltration, runoff of precipitation, and bare soil evaporation. Grazing and related activities often reduce litter accumulation, resulting in creation of warmer, drier microclimates. Additionally, soil temperatures, radiant heat loads and ground-level wind speeds can be highest on heavily grazed areas (Whitman, 1971). In drying soils, other factors may mediate to limit growth and any adjustment to water stress. For example, most nutrients are in the surface soil layers and when this layer dries out, plants cannot extract sufficient nutrients. Water may still be available at depth and plants can then sustain a high green leaf area over summer, but the result is that water is used without accompanying growth, which can be considered inefficient (Garwood and Williams, 1967).

The intensity and frequency of defoliation can also influence production and water-use efficiency under normal rainfall conditions (Snyman, 1999). He found that under optimal soil water content, production and water use efficiency increased significantly with higher intensities and frequencies of defoliation.

The interaction between grazing and the physiology of water use is poorly understood, though it is possible that plants with an improved ability to either regulate stomatal conductance or osmotically adjust will be in a better position under grazing for saving water.

In the native tallgrass prairie of North America, *Andropogon gerardii* Vitman is the dominant species. Seasonal differences in stomatal conductance were not detected in *A. gerardii* in grazed relative to ungrazed areas under normal rainfed conditions (Fahnestock and Knapp, 1994). Under increasingly dry conditions, however, leaf water potential and stomatal conductance were higher in grazed than in adjacent, ungrazed areas. Increased

stomatal conductance supports the hypothesis that herbivory can improve water relations, and potentially the recovery and growth rates of grazed plants (McNaughton 1979b, 1983a,b). Data of this author provide additional evidence that the reduction in transpiring grass leaf area indirectly enhances leaf water potential and subsequent growth of intact grasses growing in grazed patches.

In 11 turfgrass species or cultivars, 2 of which were cool season (C3 plants) and 9 were warm season (C4 plants), Biran *et al.* (1981) studied water-consumption and growth rate under different mowing and irrigation regimes during the summer in a warm, semiarid zone. The low-frequency irrigation regime, which caused temporary wilting in most grasses, also caused a significant decrease in growth rate and water consumption. This depression was greater for the C3 species. Increasing the cutting height from 3 to 6 cm changed the growth habit of all the grasses. The amount of chlorophyll per unit weight in the clippings increased with increasing cutting height. In the C3 cultivars there was also a significant and permanent increase in water consumption and growth. Results were different in the warm season grasses: while an increase in water consumption was observed, particularly in the tall growing cultivars, this increase was temporary and after 6 weeks no significant differences were evident. Yield also increased over that of the control treatment during a short time interval, but then decreased to the control level.

With advanced age, *Eragrostis curvula* (Schrad.) Nees leaves were probably less water-use efficient because of a diminished capacity to adjust stomatal openings to control water loss (Masters and Britton, 1990). Clipping influenced two factors that affected plant water-use efficiency: leaf age and leaf surface area.

Reduction in leaf surface area following clipping could have enhanced *E. curvula* water status by reducing transpiring leaf surface. This may have allowed plants to maintain a positive water balance and overcome limitations to growth caused by an inadequate root system or low soil water availability.

### 2.3 Photosynthesis

Fahnestock and Knapp (1994) measured net photosynthesis in *A. gerardii* to evaluate the variation in carbon gain that resulted from changes in leaf water potential. Relatively small reductions in leaf water potential resulted in large decreases in net photosynthesis. Relative to net photosynthesis measured in plants with moderate leaf water potentials (-1.5 to -1.9 MPa), net photosynthesis decreased by 63% when leaf water potentials were slightly reduced (-2.1 to -2.5 MPa). These authors found that enhanced water and light availability in grazed patches would promote carbon gain.

Grazing related changes in the physical structure of grasses can affect their physiological capacities as well, specially their ability to acquire critical resources (Fahnestock and Detling, 2000). For instance, reduction in leaf area through grazing has an immediate effect on whole plant carbon gain by reducing photosynthetic capacity (Detling *et al.*, 1979). Following defoliation, leaf photosynthetic rates of grazed grasses increase, decrease or remain similar to predefoliation rates, depending on the timing of herbivory and its intensity and frequency (Detling, 1987).

The specific physiological responses to changes in the morphological structure of plants induced by herbivory are often difficult to predict and may change over time (Fahnestock and Detling, 2000). For

instance, reduced leaf area in plants from long-term grazed sites can limit their ability to acquire sufficient light, but on the other hand, may have more light available to them (i.e., less shading) than plants from ungrazed sites, enabling them to more effectively use all leaf area in photosynthesis (McNaughton, 1979a,b; Fahnestock and Knapp, 1993). Also plants from grazed areas may have less water available for growth compared to ungrazed sites because of an increase in bare ground evaporation, or by contrast, may have more water available because of a reduction in transpiring leaf area (McNaughton, 1979b; Day and Detling, 1994; Fahnestock and Knapp, 1994).

#### 2.4 Nutrient Allocation

The interactive effects of water stress and defoliation can influence carbon and nitrogen partitioning within the perennial grass plant. Crown and root total nonstructural carbohydrate (TNC) pools in *A. desertorum* and *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* [Syn: *Agropyron spicatum* (Pursh) Scribn. and Smith] were similar for clipped than for unclipped tillers one year after a heavy clipping under drought or irrigated conditions (Busso *et al.*, 1990). Following one or more years of clipping under water stress, rainfed or irrigated conditions, crown and root TNC concentrations were similar between clipped and unclipped plants of both species. The lack of a marked clipping effect on TNC concentrations or pools was attributed to the fact that clipping treatments were applied late during the growing season (Busso *et al.*, 1990). However, when results were expressed on a per plant rather than on a per tiller basis, clipping reduced TNC pools for both species under all water levels in the third successive year of treatment application. This was because tiller number was lower on clipped than on

unclipped plants (Busso *et al.*, 1989). Nevertheless, TNC concentration and pools in spring were less influenced by previous year clipping than by the availability of soil moisture during the previous year (Busso *et al.*, 1990).

Concentration of TNC in crowns or roots was an inadequate indicator of dark re-growth production in early spring (Busso *et al.*, 1990). For example, clipped and unclipped, water-stressed tillers of *P. spicata* showed a similar crown and root TNC concentration, but rates and total production of dark re-growth were greater on clipped than on unclipped tillers (Busso *et al.*, 1990). Previous studies had concluded that TNC concentrations in crown or roots were an important determinant of spring growth (Trlica and Cook, 1972; Daer and Willard, 1981; Menke and Trlica, 1981). These conclusions were based on correlations alone or on comparisons between percentage TNC and re-growth at different times during the growing season. In addition to TNC concentration, other factors such as meristem availability and activity (Richards and Caldwell, 1985; Olson and Richards, 1988; Richards *et al.*, 1988) vary seasonally, thus potentially confounding between-time comparisons of TNC concentration and re-growth. Re-growth in perennial grasses may be more limited by the availability of active intercalary and apical meristems than by TNC availability during a growing cycle (Richards and Caldwell, 1985). At the beginning of a growing season, however, when availability of active meristems and soil moisture are not limiting factors to re-growth production, both crown and total (crown plus root) TNC pools may facilitate rapid plant growth (Busso *et al.*, 1990). For example, Busso *et al.* (1989) showed that when moisture was available in early spring, leaf area was greater for tillers of *A. desertorum* and *P. spicata* that

had been exposed to drought in the previous years, and thus had high TNC contents, than for tillers on plants grown under higher moisture levels: Rapid growth frequently occurs in perennial grasses after water stress is relieved, even when plants have been defoliated while water-stressed (Hodgkinson, 1976; Kigel and Dotan, 1982; Busso *et al.*, 1990). High growth rates of perennial grasses early in the growing season could allow more rapid water and nutrient utilization when they are most freely available. In addition, early production of a photosynthetic surface area may establish an advantage that could remain during vegetative growth and account for higher yields in grasses (Kigel, 1980). However, and in spite of an enhanced early season leaf area growth on clipped, drought-exposed tillers, total production in *A. desertorum* and *P. spicata* plants was reduced in the drought plot because of a reduced tiller production (Busso *et al.*, 1989).

In a Mediterranean climate with regular droughts, summer survival is the main component of persistence of perennial forage plants cultivated without irrigation. Survival of temperate grasses under severe drought has been related to summer dormancy of tillers (Snakary *et al.*, 1969; Biddiscombe *et al.*, 1977) and early flowering (Lorenzetti *et al.*, 1981). In addition to earliness of flowering, the accumulation of water-soluble carbohydrates (WSC) in tiller bases was highly correlated with summer survival and rapid recovery when water stress was relieved in autumn (Volaire, 1995). Dormancy in adapted cultivars can prevent the loss of WSC reserves and subsequently allow fall re-growth. Numerous investigations have shown that plant carbohydrate reserves are reduced following grazing and that the time taken for their replenishment increases under severe defoliation. Water-soluble carbohy-

drates may contribute to regulation of osmotic potential in summer and provide substrate for re-growth in autumn (Booyesen and Nelson, 1975).

In a study with two populations of *Dactylis glomerata* L. subjected to a moderate drought, one a drought-sensitive cultivar and the other a resistant-population, Volaire and Gandoin (1996) showed that the content of WSC, and especially of high-degree of polymerization fructans in live enclosed leaves during drought, seemed to be associated with re-growth after drought independently of sward age. Therefore, any study of the relationship between carbohydrate reserve accumulation and drought survival should focus mainly on the youngest enclosed leaves rather than on whole tiller bases. These main surviving organs reflect better the physiological state of the plants. Their results partly raise the importance of a re-evaluation of the contribution of carbohydrate reserves to shoot re-growth in grasses (Ourry *et al.*, 1989). Onillon *et al.* (1995) proposed that part of the change in the carbon allocation pattern induced by drought is mediated via an effect on nitrogen nutrition. Therefore, pools of proteins, which are associated with foliar re-growth after defoliation in forage plants, should be studied along with carbohydrate pools to better understand the mechanisms of drought survival (Volaire and Gandoin, 1996).

Volaire emphasized the importance of understanding the relationship between phenology, physiology and water stress in 1994. In particular: (1) the contribution of the production and maintenance of leaf area during late summer to maintaining a positive carbon balance; (2) the extent to which summer dormancy contributes to survival, (3) the role of water uptake and control of transpiration in maintaining tissue water status and hence the survival

of tillers and unexpanded tiller buds, 4) the relative contribution of sugars and other solutes to tolerance of low tissue water status, and (5) the role of carbohydrate reserves in maintaining tissues active when no leaf area remains.

Regardless of temperature, reallocation and use of  $^{14}\text{C}$  stored in belowground organs for foliage re-growth was greatest under optimum or moderate than severe soil water stress in plants of *Bouteloua curtipendula* (H.B.K.) Lag. ex Steud., which were defoliated at the reproductive stage of development (Chung and Trlica, 1980). Also, from 30 to 50% of the  $^{14}\text{C}$  was found in the labile fraction of re-growth foliage over a 12-week period following defoliation under all soil water regimes in this species (Chung and Trlica, 1980). However, plants, which were water-stressed more severely, contained a slightly higher proportion of soluble  $^{14}\text{C}$  in foliage during the 12 weeks of re-growth than those exposed to higher soil water levels. The  $^{14}\text{C}$  found in the labile fraction of belowground organs (crowns and roots) was only about 10% or less in the different water and defoliation treatments, and it was mostly lost in respiration during re-growth. A greater proportion of the originally stored labile  $^{14}\text{C}$  was lost via respiration when plants of *B. curtipendula* were water-stressed more severely. The percentage of labile  $^{14}\text{C}$  lost through respiration generally increased from 4 to 8 weeks of re-growth under all water levels, but thereafter, it remained unchanged.

A comparative account of mineral nutrient use (N, P, K) was made by Misra and Singh (1982) in 3 grass species under different soil moisture and clipping regimes. The combined effects of soil moisture and clipping stresses reflected a decrease of shoot P and K concentrations. In some cases, however, soil moisture stress increased shoot N levels and there

was a further increase due to clipping. Despite the increased shoot N level under moisture stress, the net N uptake was lower than under irrigated conditions. This was due to a greater decrease in dry matter production after defoliation under water stress. Both the concentration and net uptake of P and K also declined with increasing soil moisture stress. Differences in nitrogen use efficiency among the 3 grasses were small. The parallel increase in P and K use efficiency with greater soil moisture stress in all species was due to a relatively larger reduction in dry matter production.

Under N-limited growth conditions, drought-induced retranslocation of shoot N to roots and rhizomes can limit loss of N to herbivory during drought, increasing end-of-season whole-plant biomass and N content in *Spartina pectinata* Link (Heckathorn and Delucia, 1996). These authors suggested that the protective benefits of drought-induced shoot N retranslocation in prairie grasses might extend beyond increasing these variables, and affect overwinter survival or early-season growth the following spring. This mesic perennial  $\text{C}_4$  grass species remobilizes 20-30% of shoot N during drought (Heckathorn and Delucia, 1996). Heckathorn and Delucia (1996) also demonstrated that eliminating the opportunity for retranslocation in this species (e.g. by defoliating it before drought) decreased total plant biomass, N content, and tiller production. In contrast to *S. pectinata*, *Schizachyrium scoparium* (Michx.) Nash, a xeric species that retranslocates little shoot N during drought, exhibited decreased biomass, N content, and tiller and seed production in plants defoliated after drought. Defoliating *A. gerardii*, a species of intermediate drought tolerance that retranslocates 10% of shoot N during drought, either before or after drought did

not have a differential effect on these parameters. Undeveloped and well-watered plants of *S. pectinata*, *S. scoparium* and *A. gerardii* always showed greater total end-of-season shoot and seed biomasses, shoot and seed N contents, and tiller number than defoliated and water-stressed plants (Heckathorn and Delucia, 1996). *Schizachyrium scoparium* and *A. gerardii* are frequently subjected to drought (e.g., Weaver and Fitzpatrick, 1932; Knapp, 1984) and probably fix a significant fraction of their seasonal C during and after intermittent drought. Thus, the C costs associated with retranslocation (e.g., decreased post-drought C gain) may be greater in these xeric grasses. *Spartina pectinata*, however, experiences prolonged drought infrequently and does not remain photosynthetically active during drought as do the other two grass species (Heckathorn and DeLucia, 1995). Results of Heckathorn and Delucia (1996) in prairie grasses are thus consistent with the hypothesis that drought-induced shoot N retranslocation to belowground tissues represents a trade-off between N protection and post-drought carbon assimilation.

## 2.5 Vesicular-Arbuscular Mycorrhizae

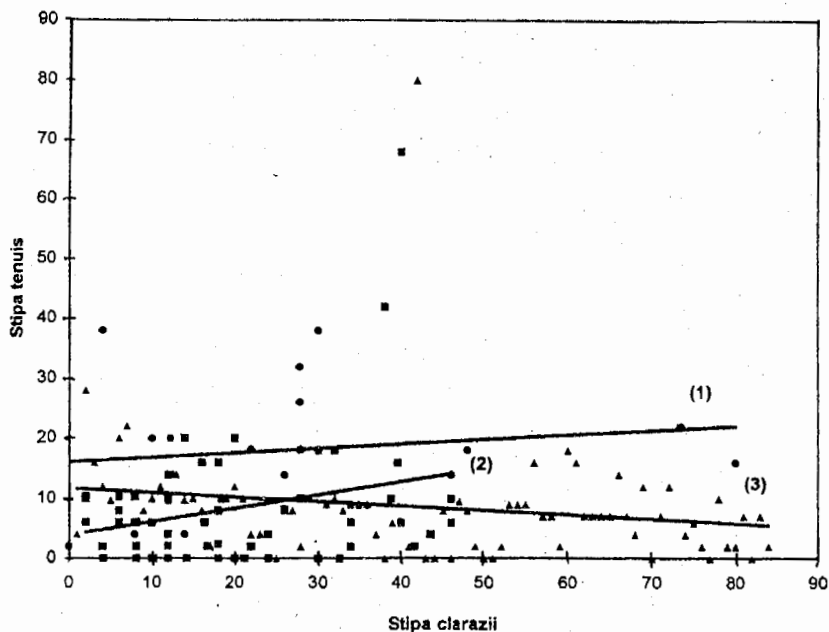
We determined percentage colonization of the root system by vesicular-arbuscular mycorrhizae (VAM) in *S. clarazii*, *S. tenuis* and *S. gynerioides* after plants of these species were either defoliated or not (controls) under water stress, rainfed or irrigated conditions during 1995 and 1996. Experimental design and treatments for this research are explained under item 1.2. A total of 460 soil cores were taken periodically in all three species and treatments (1 plant per species within each replicate plot) during 1996 and early 1997 at the plant periphery. Roots were washed free of soil and mycorrhizal assessment was made

following Phillips and Hayman (1970). Ten root segments were placed on each of three slides per sample. The number of root interceptions containing hyphae, vesicles and arbuscules (C) was determined over a total of 30 root interceptions (T) per slide using a microscope (400X). Vesicular-arbuscular mycorrhizal colonization was obtained thereafter as  $(C/T) \times 100$ . We found that VAM colonization increased in *S. clarazii* as plants were defoliated later or with a higher frequency than earlier during the growing season under irrigated, rainfed or water stress conditions (Fig. 2). Even more, percentage VAM colonization tended to be greater on plants defoliated late or with a higher frequency than on undefoliated controls under irrigated or water stress conditions in this species (Fig. 2). This (see Dry Weight heading) and other studies (Becker *et al.*, 1997b) have demonstrated that late or increased frequency of defoliation is more detrimental to forage production of perennial tussock grasses than defoliations early in the growing season. Forage production of plants defoliated either frequently or late during a growth cycle has also been lower than that on undefoliated controls (Becker *et al.*, 1997b). It is possible that need for soil resource acquisition to sustain re-growth is greater on plants defoliated late or with an increased frequency than on those undefoliated or defoliated earlier during the growing cycle. Fungal hyphae can cross depletion zones and transport nutrients to the roots for a much smaller biomass investment than roots (Bowen and Smith, 1981). In addition, nutrient uptake efficiencies per unit surface area of hyphae are several times higher than those in grass roots (Kothari *et al.*, 1990). Then, a greater degree of VAM colonization seems feasible in the face of increased nutrient demands for reestablishment of a photosynthetic surface area after defoliation. Allen *et al.* (1989) reported that root

length density colonized by VAM was similar on defoliated and undefoliated plants of *A. desertorum* and *P. spicata* under water stress, rainfed and irrigated conditions. Reproduction of the fungus, as indicated by spore counts, was also not consistently different between water and defoliation treatments for these plant species: spore counts were higher under *A. desertorum* than *P. spicata* for two sampling periods, and the reverse was true for another different two sampling dates (Allen *et al.*, 1989). Their data provided no definite answers regarding the effects of water stress with or without defoliation on VAM in *A. desertorum* and *P. spicata*. They found few significant differences, and these were often not consistent between sampling years or

were trivial responses despite the consistent treatments and intensity of sampling. Their reported yearly variation was much greater than any treatment effect and it could not be attributed to moisture. They concluded that simple predictions of VAM responses to reduced host C input and allocation due to defoliation under water stress can not be obtained.

Albeit not consistently significant, VAM colonized root length density tended to be greater under irrigated than water stress conditions on defoliated and undefoliated plants of the grazing-tolerant *A. desertorum* and the grazing-sensitive *P. spicata* (Allen *et al.*, 1989). This was primarily due to increasing total root length under irrigation (Allen *et al.*, 1989).



**Figure 3.** Comparison of the response between species pairs in *Stipa clarazii* and *S. tenuis* when vesicular-arbuscular mycorrhizae is the response variable. These perennial tussock grasses have been either defoliated or not (controls) under water stress, rainfed or irrigated conditions during 1995 and 1996. Comparison among species was effected using linear regression analysis for each of six sampling dates. Regression lines were compared among dates and the data pooled if lines were not significantly different ( $p > 0.05$ ) following Neter *et al.* (1985). Numbers on lines in parenthesis indicate dates the data were either pooled or not as follows: (1) 6 June (filled circles); (2) 21 September + 20 October (filled squares) and (3) 18 April + 21 December + 28 February 1997 (filled triangles). Unless otherwise indicated, all dates correspond to 1996.

Allen *et al.* (1989) reported very high correlations between the grazing-tolerant *A. desertorum* and the grazing-intolerant *P. spicata* for percentage of VAM infection, spore counts and VAM root length density. This indicates that both species responded similarly to their environment and suggests that the VAM of both species appeared to be responding to the same variables (Allen *et al.*, 1989). We also found a positive, significant ( $p < 0.05$ ) relationship for VAM between *S. clarazii* and *S. tenuis* during active plant growth in spring, after exposure of plants of these species to various water and defoliation treatments (Fig. 3; see item 1.2 for a description of experimental design and treatments). However, this response was not consistent throughout the year, and VAM colonization percentages decreased ( $p = 0.015$ ) in *S. tenuis* at the same time that they increased in *S. clarazii* during summer (Fig. 3). Even more, both species did not show a significant relationship ( $p = 0.43$ ) for VAM colonization in winter (Fig. 3).

Plants from variable habitats may show a high degree of plasticity when faced with patchy resources (Crick and Grime, 1987). Effects of VAM on grasses are sensitive to environmental perturbations. For example, some grass species only increased water uptake with VAM during dry periods (Allen and Allen, 1986). VAM has also responded to the patch placement of nutrient resources in other studies (e.g., Anderson and Liberta, 1992). As suggested by Allen *et al.* (1989), and despite the environmental and phenological controls in our sampling protocol, and the severe perturbations imposed, VAM may respond too much smaller resource shifts than has been supposed. Allen *et al.* (1989) indicated that the importance of VAM in natural communities may lie in bursts of activity during 'ecological crunches' (Allen and

Allen, 1986) or at the scale of individual root-fungal infections. This plasticity might be the major reason for the persistence and importance of VAM in native ecosystems, and is not reflected at the large spatial or long temporal scales normally measured.

## 2.6 Osmotic Adjustment

We determined the leaf water relation characteristics on undefoliated plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* exposed to different water treatments during the internode elongation developmental phase (see description of water and defoliation treatments under item 1.2) using a pressure-volume (P/V) technique similar to that described by Turner (1987). Leaves were rehydrated overnight and the fully turgid weight was determined thereafter. Dry weight was determined after drying at 70°C for 48 h. Osmotic potentials at full turgor, water potential and relative water content when zero turgor pressure was first reached, and the proportion of symplastic water were determined using the P/V curve analysis program of Shulte *et al.* (1985). The interaction term (water level x species) was not significant ( $p > 0.05$ ) and there were not significant differences among water levels ( $p > 0.05$ ). The degree of osmotic adjustment was similar in *S. clarazii* and *S. gynerioides* (Table 1). These values are similar to those reported extensively in perennial grass species (e.g. Brown, 1995; Sanderson *et al.*, 1997), and constitute a drought tolerance mechanism which allow these grasses to keep growing in the face of declining leaf water potentials (Turner, 1986). Osmotic potentials at full and zero turgor were significantly lower ( $p < 0.05$ ) in *S. clarazii* than in *S. tenuis* (Table 2). Although relative water contents were similar ( $p > 0.05$ ) among species, symplastic water fraction in *S. clarazii* and *S. tenuis* was significantly greater than in *S. gynerioides* (Table 2).

Table 1. Osmotic potentials at full turgor pressure in leaves of two undefoliated *Stipa* species that were kept adequately watered or were water-stressed during the internode elongation stage of development to a midday leaf water potential of  $-6.15 \pm 0.35$  MPa. The calculated osmotic adjustment is shown. Values in parenthesis are the standard errors (n=2)

Species	Osmotic potential at full turgor (MPa) in:		Osmotic Adjustment (MPa)
	Water-stressed leaves	Watered leaves	
<i>S. clarazii</i>	-3.15 (0.03)	-2.65 (0.33)	0.50
<i>S. gynerioides</i>	-2.51 (0.28)	-2.09 (0.46)	0.42

Table 2. Osmotic potentials at full or zero turgor pressure, relative water content at turgor loss point (RWC<sub>0</sub>) and symplastic water fraction (SWF) on undefoliated plants of *Stipa clarazii*, *S. tenuis* and *S. gynerioides* which were exposed to irrigated, rainfed or water-stress conditions during the internode elongation stage of development in 1996. Plants had been exposed to these treatments in 1995. Two replicate leaves were used per species on each water level treatment to construct pressure-volume curves. Data were analyzed using two-way ANOVA (3 water levels x 3 species) and means were compared using Fisher's LSD when F tests were significant (p<0.05). The interaction term and the main factor water levels were not significant (p>0.05). Different letters in the same column indicate significant differences at p<0.05.

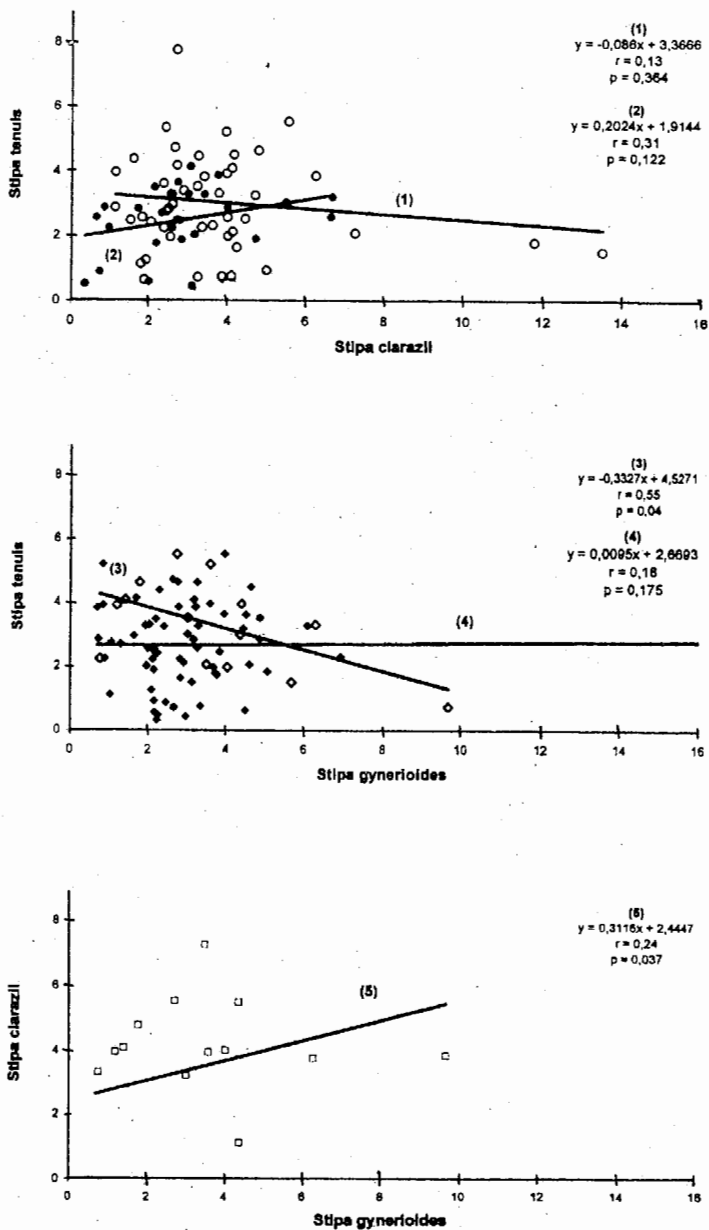
Species	Osmotic potential (MPa) at		RWC <sub>0</sub>	SWF
	full turgor	zero turgor		
<i>S. clarazii</i>	-2.73 a	-3.52 a	0.82 a	0.97 a
<i>S. tenuis</i>	-1.94 b	-2.41 b	0.82 a	0.96 a
<i>S. gynerioides</i>	-2.34 ab	-3.22 a	0.82 a	0.72 b

### 3. MORPHOLOGY

#### 3.1 Root Length Density

We assessed the effects of defoliation under different levels of soil water availability (see item 1.2 for explanation of experimental design and treatments) on root length density (cm root per cm<sup>3</sup> soil) in *S. clarazii*, *S. tenuis* and *S. gynerioides* during 1995 and 1996. Soil cores of known volume (831.3 cm<sup>3</sup>) were taken during 1996 and early 1997 in all treatments at the plant periphery. Roots were washed free of soil, their length was determined using Tennant's (1975) method and root length density was calculated thereafter. Root length density of our native, perennial tussock grasses showed either similar or different responses to their

environment depending on the species pair being compared. For example, changes in root length density with changes in water regimes and defoliation levels were different for *S. clarazii* versus *S. tenuis*, and *S. tenuis* versus *S. gynerioides* (Fig. 4). *Stipa clarazii* and *S. tenuis* are palatable, preferred species while *S. gynerioides* is unpalatable, unpreferred to domestic herbivory (Cano, 1988; Distel and Bóo, 1996). The only exception to the *S. tenuis*-*S. gynerioides* comparison was that root length densities increased in *S. gynerioides* while concurrently they decreased in *S. tenuis* at one harvesting time (Fig. 4). On the other hand, the palatable *S. clarazii* and the unpalatable, undefoliated *S. gynerioides* always showed a similar response to environmental changes (Fig. 4). The



**Figure 4.** Comparison of the response between species pairs in *Stipa clarazii*, *S. tenuis* and *S. gynerioides* when root length density is the response variable. These perennial tussock grasses have been either defoliated or not (controls) under water stress, rainfed or irrigated conditions during 1995 and 1996. Comparison among species was effected using linear regression analysis for each of six sampling dates. Regression lines were compared among dates within each species and the data pooled if lines were not significantly different ( $p > 0.05$ ) following Neter *et al.* (1985). Numbers on lines in parenthesis indicate dates the data were either pooled or not as follows: (1) 18 April+6 June+21 September+28 February (open circles); (2) 20 October+21 December (filled circles); (3) 18 April (open diamonds); (4) 6 June+ 21 September+ 20 October+ 21 December+ 28 February 1997 (filled diamonds); (5) All six dates altogether from 18 April 1996 to 28 February 1997 (open squares). Unless otherwise indicated, all dates correspond to 1996.

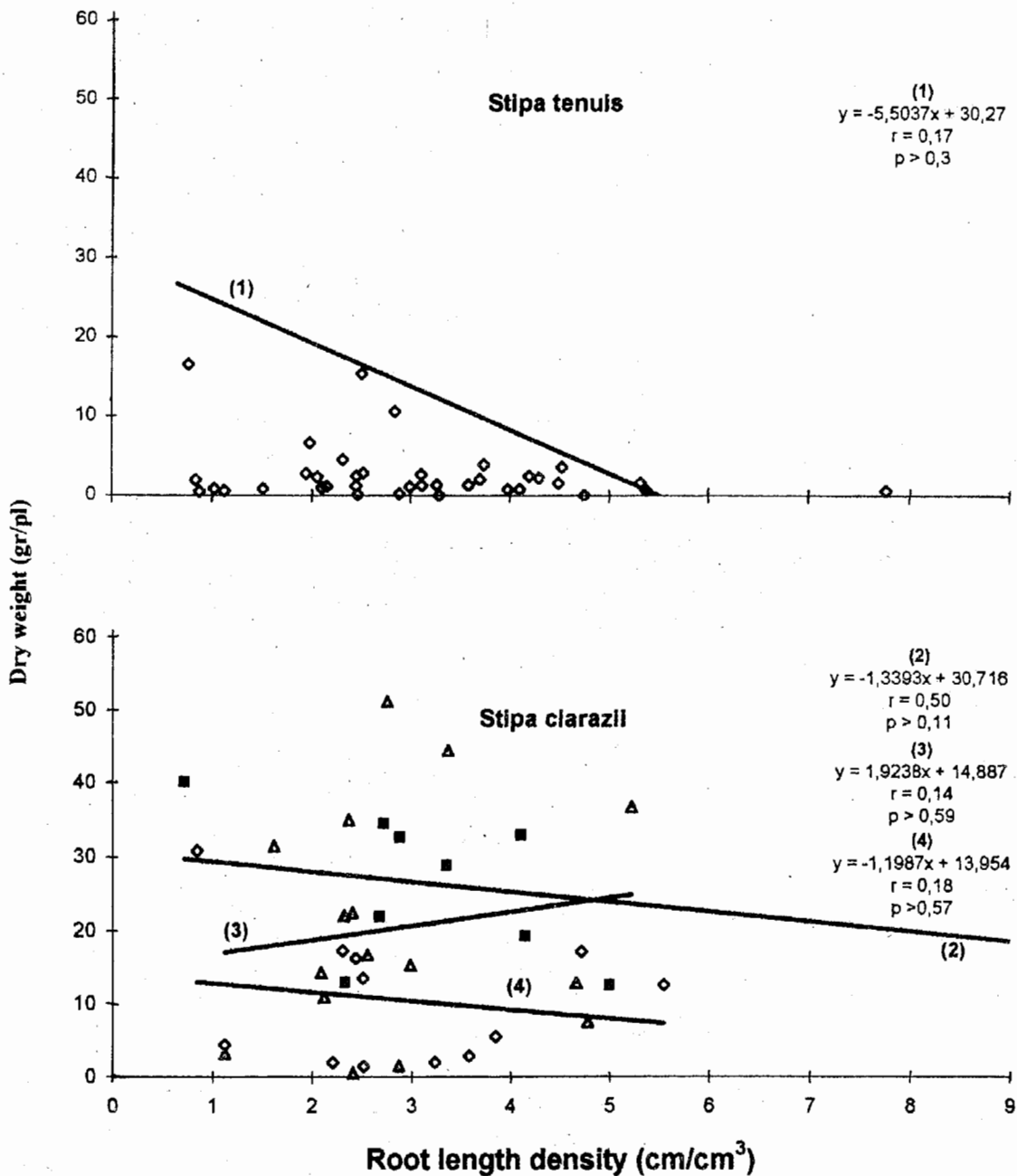
difference in response between *S. tenuis* and *S. clarazii* when compared with *S. gynerioides* may be due to their differences in competitive ability (Saint Pierre *et al.*, 2000 a,b). While the more competitive *S. clarazii* increased its root length density, the less competitive *S. tenuis* had a root length density, which either did not relate or decreased, but never increased, with increases in root length density in *S. gynerioides*.

Root length density and dry weight production were not significantly correlated ( $p > 0.11$ ) in *S. clarazii* and *S. tenuis* when these perennial grass species, which had been either defoliated or not at different phenological stages, were exposed to water stress, rainfed or irrigated conditions (Fig. 5). A similar response was obtained after defoliation in *S. tenuis* on water-stressed, rainfed or irrigated plants of this species ( $p = 0.077$ , Fig. 6). However, increases in root length density led to increased dry weight ( $p = 0.036$ ) production in water-stressed, rainfed or irrigated plants of *S. clarazii* when data coming from plants defoliated once (at the vegetative stage of development) or twice (at the vegetative and internode elongation stages of development) adjusted to just one regression line (Fig. 6).

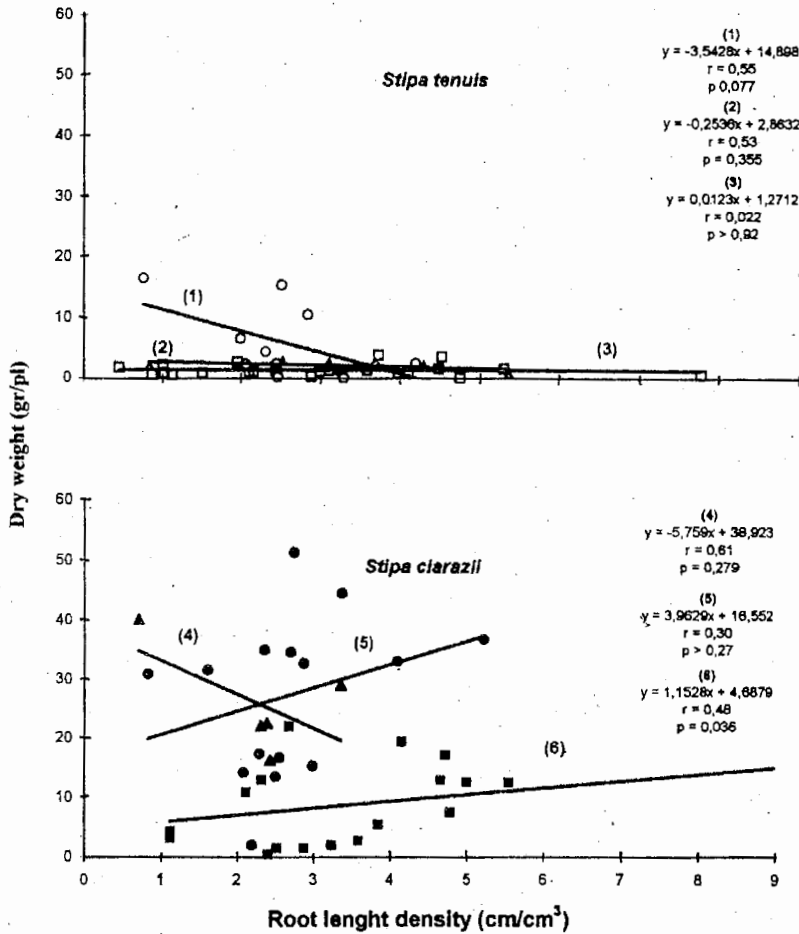
Although differences were not significant, root length density tended to be greater on irrigated than water-stressed defoliated and undefoliated plants of the grazing-tolerant *A. desertorum* and the grazing-sensitive *P. spicata* (Allen *et al.*, 1989). Late and severe once-a-year defoliation during two consecutive years did not affect, however, root length density of these species in comparison to undefoliated controls under water stress, rainfed or irrigated conditions (Allen *et al.*, 1989).

### 3.2 Root Growth

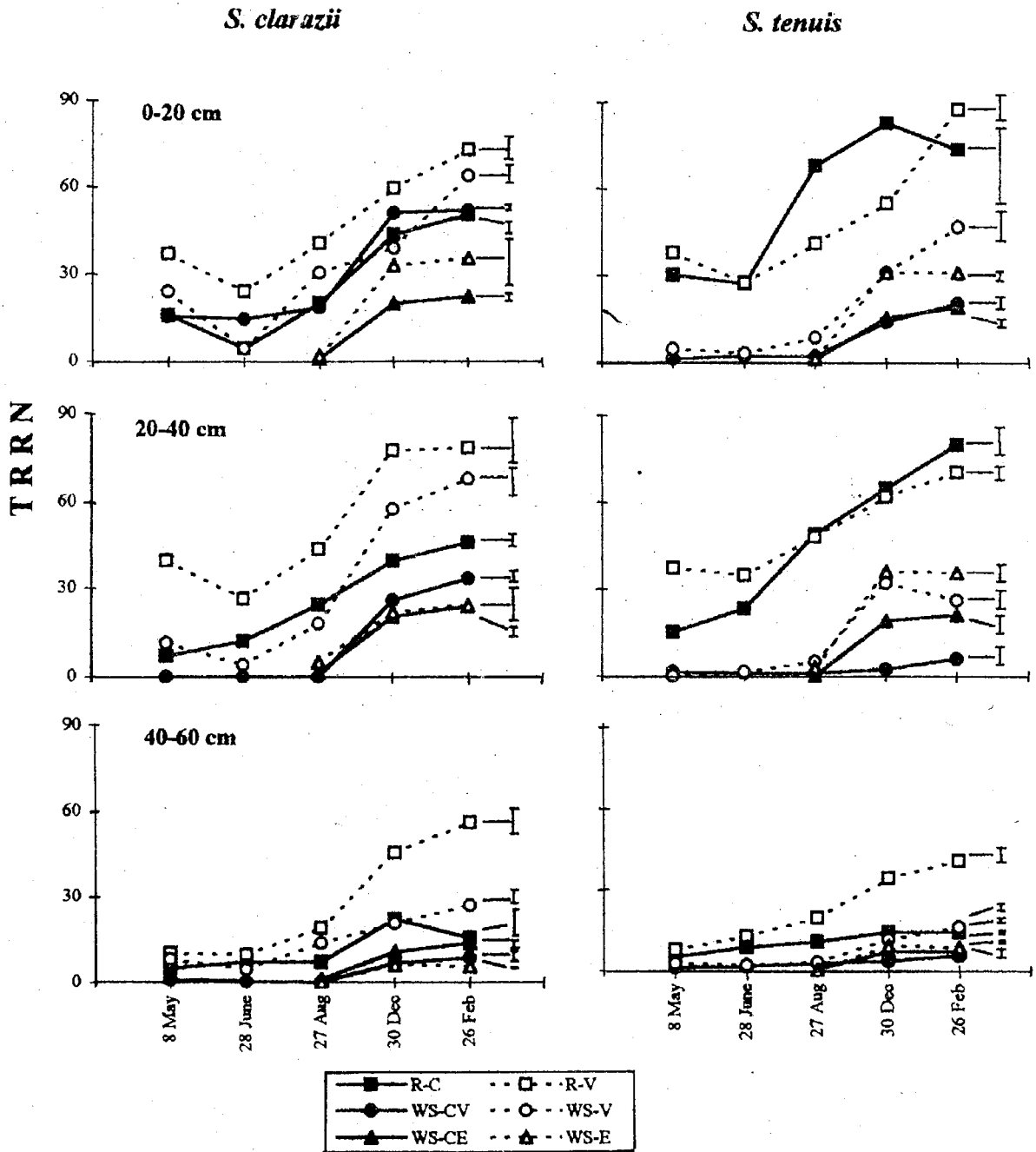
By making use of the root periscope technique (Richards, 1984), we used a relative root number as a measure of root growth by counting the number of roots, which intercepted grid lines, engraved in glass tubes. Experimental design and treatments for this study are reported under item 1.2. Plants of *S. clarazii* defoliated at V under water stress had a greater ( $p < 0.05$ ) total relative root number than undefoliated plants between 40-60 cm depth in August 1996 (Fig. 7). Water recharge of the lower soil horizons (i.e., 40-60 cm) may have been favoured by the 88 mm rainfall fallen between termination of the water stress period at V to that date in August, stimulating a greater root growth on defoliated than on undefoliated plants. Plants of *S. tenuis* defoliated at V or E under water stress also showed a greater ( $p < 0.05$ ) total relative root number than undefoliated controls between 20-40 cm depth by early summer (Fig. 7). Species relatively less tolerant of defoliation, such as *S. tenuis* in comparison to *S. clarazii* (Saint Pierre *et al.*, 2000a,b), can maintain root growth unabated after defoliation even under low soil moisture conditions (Richards, 1984; Dube, 1999). This would contribute to a greater soil exploration and resource finding to sustain re-growth in species native to semiarid rangelands (Distel and Fernández, 1988; Becker *et al.*, 1997c). Defoliation under water stress can contribute to soil water conservation (Brown, 1995) and may then stimulate root growth as observed in early summer (Fig. 7). One mechanism conferring *S. clarazii* a greater competitive ability and defoliation tolerance than that found in other *Stipa* species is a greater proportional carbon allocation to regrowing shoots at the expense of reducing root growth (Moretto and Distel, 1997, 1999). However, grazing tolerance in any given species may not necessarily be



**Figure 5.** Relationship between root length density and dry weight production in *Stipa tenuis* and *S. clarazii* after these species, which have been defoliated at different phenological stages, were exposed to water stress, rainfed or irrigated conditions. Plants had been either defoliated or not (controls) under these water levels at the vegetative, internode elongation or both developmental stages during 1995 and 1996. Regression lines obtained for each water level were compared for equality following Neter *et al.* (1985). Data for all water levels were pooled when regression lines were not statistically different ( $p > 0.05$ ). Numbers on lines in parenthesis indicate whether water levels were combined or not as follows: (1) water stress+rainfed+irrigation; (2) rainfed; (3) water stress; (4) irrigation.



**Figure 6.** Relationship between root length density and dry weight production in *Stipa tenuis* and *S. clarazii* after these species, while being exposed to water stress, rainfed or irrigated conditions, were either defoliated or not (controls, C) at the vegetative, internode elongation or both phenological stages during 1995 and 1996. Meaning for dry weight values obtained at different times during the growing season are as follows: V=aboveground dry weight of plants defoliated at the vegetative stage in 1996; E=aboveground dry weight of plants defoliated at the internode elongation stage in 1996; VE=aboveground dry weight of plants defoliated at the vegetative and internode elongation stages in 1996; RV=plant re-growth after defoliation at the vegetative stage in 1996; RE=plant re-growth after defoliation at the internode elongation stage in 1996; V VE=plant dry weight obtained at clipping time at the vegetative stage in 1996 on plants which had been defoliated at the vegetative and internode elongation stages in 1995; E VE= plant dry weight obtained at clipping time at the internode elongation stage in 1996 on plants which had been defoliated at the vegetative and internode elongation stages in 1995; RE VE=plant re-growth after defoliation at the internode elongation stage in 1996 on plants which had been defoliated at the vegetative and internode elongation stages in 1995. Regression lines obtained for different times during the year were compared for equality following Neter *et al.* (1985). Data were pooled whenever two or more regression lines were not statistically different ( $p > 0.05$ ). Numbers on lines in parenthesis indicate whether dry weights obtained at different times during the year were combined or not as follows: (1) C+RV; (2) RE; (3) V+E+ V VE + E VE + RE VE; (4) E; (5) C+RV+RE; (6) V+V VE + E VE + RE VE.



**Figure 7.** Total relative root number (TRRN) between 0-20, 20-40 and 40-60 cm depth during 1996 and early 1997 on plants of *S. clarazii* and *S. tenuis* which were defoliated at the either vegetative (V) or internode elongation (E) phenological stages or remained undefoliated (controls, C) under rainfed (R) or water stress (WS) conditions in 1995 and 1996. Each symbol is an average of n=2. Vertical lines represent  $\pm$  an average of the standard errors of the means during the study period. Arrows indicate defoliation dates.

explained by just one specific characteristics (Hendon and Briske, 1997). Root length in two *Agropyron* species, for example, showed a similar response to defoliation under water stress in spite of their difference in grazing tolerance (Allen *et al.*, 1989). Results of Flemmer (2000) on *S. clarazii*, *S. tenuis* and *S. gynerioides*, however, are opposite to those reported in other perennial grass species under rainfed conditions (Becker *et al.*, 1997c; Jatimliansky *et al.*, 1997). Young (1956), for example, emphasized that when plants are severely grazed under drought, crowns of desirable perennial grasses can be so severely trampled that few or no new roots can develop. Other studies, however, reported that root biomass of *Themeda triandra* Forsk. was not affected by defoliation either with or without water stress (Dube, 1999). Even more, the concomitant influence of water stress and defoliation has been less detrimental to root biomass in comparison to a situation where the effects of these stresses have been evaluated separately (Mohammad *et al.*, 1982; Simoes and Baruch, 1991), response which has been attributed to a reduction of transpiratory leaf surface area after defoliation.

When water stress was alleviated in early autumn, and after two years of defoliation at different phenological stages under water stress, total relative root number at all depths was similar on defoliated and undefoliated plants of *S. clarazii* and *S. tenuis* (Flemmer, 2000; Fig. 7). Becker *et al.* (1997c) also found that different responses between defoliated plants in the vegetative or internode elongation stage of development and undefoliated controls disappeared in *S. tenuis* and *P. napostaense* in the year following two years of successive defoliations under rainfed conditions. Effects of defoliation on root biomass of perennial grasses, however, may only appear after three or more years of

treatment application (Zhang and Romo, 1994).

In a study of northern North American rangelands, Hild *et al.* (2001) studied the effects of drought and grazing upon pre- and post-drought plant root distribution. Grazing treatment effects on roots appeared only in the A-horizon. The general trend of fewer shallow roots in grazed than in ungrazed plots over the entire study period may be the consequence of a greater C allocation to above-ground growth, removal of annual plant roots by animals, and/or a compensatory shift in root distribution. Shallow roots did not decline immediately after grazing, yet roots in grazed plots did not appear to over-winter well. With the return of the following growing season, ungrazed plants may have had a greater winter root survival than grazed plants (Hild *et al.*, 2001). Other possible explanations for a decrease in shallow roots with grazing included greater C allocation to aboveground production of perennials without subsequent root production (Briske and Richards, 1995; Heitschmidt *et al.*, 1999) or compensatory C shifts to deeper roots. Roots in deeper soil layers (Bw horizon) were fewer during drought, but were not influenced by grazing.

Compensatory root growth in soil layers, which offer more favorable environments for roots, is well documented (Jesko *et al.*, 1997). For example, compensatory root growth can occur at deeper soil depths when surface soils dry out (Fernández and Caldwell, 1975). Thus Bw horizon roots may reflect drought treatments even though drought influences are not apparent in the A horizon roots.

### 3.3 Axillary Buds

The persistence of perennial grasses in pastures depends on maintaining an adequate density of growing tillers or buds

from which to regenerate new tillers (Kemp and Culvenor, 1994). Reinitiation of growth from basal buds after grasses are cut or grazed heavily during stem elongation can interact with increasing moisture stress to affect persistence (Brougham, 1961; Jewiss, 1972; Culvenor, 1994).

In arid and semiarid environments, perennial grasses are often defoliated under water stress conditions (Ludlow, 1986). Most rangeland vegetation has been used abusively worldwide. Overgrazing has led, among other factors, to replacement of desirable by undesirable vegetation for livestock production in most rangelands of the world (i.e., Archer, 1996; Fernández and Busso, 1999). Plants have been grazed at phenological stages which compromise plant recovery after defoliation. When most, if not all, apical and intercalary meristems are removed by defoliation re-growth will depend upon activation and subsequent outgrowth of axillary buds.

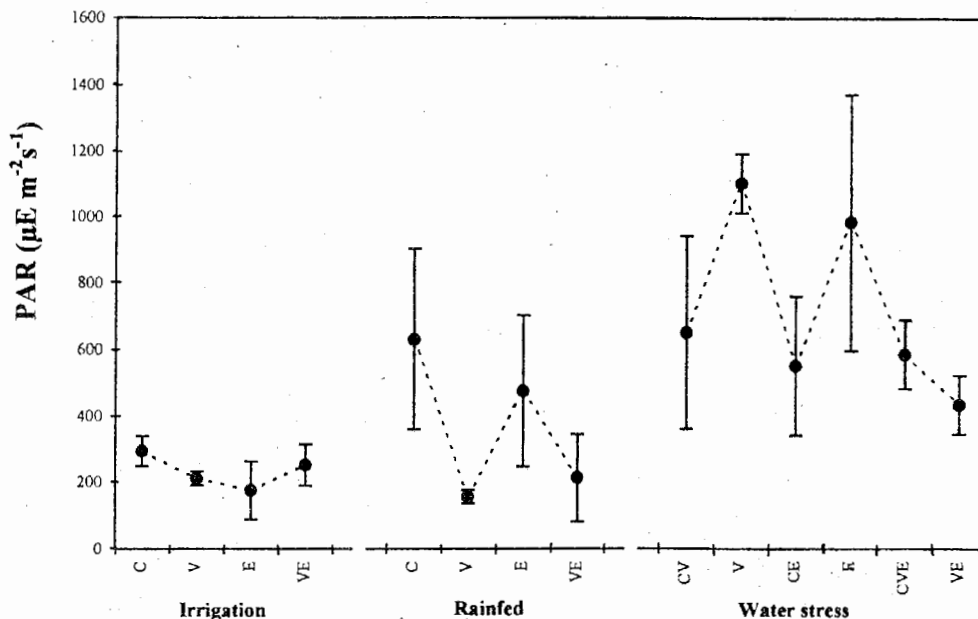
Direct inhibitory effects of the apical meristem on bud outgrowth are well documented in grasses (i.e., Murphy and Briske, 1992). However, in addition to these effects, physiological mechanisms and their interaction with environmental variables and resource availability should be considered when studying factors involved in regulating tillering in perennial grasses (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 (i.e., Busso *et al.*, 1989). Water stress can also reduce tiller production in defoliated and undefoliated plants; this response has been observed under natural droughts (Bullock *et al.*, 1994; Briske and Hendrickson, 1998) or controlled environmental conditions (Busso *et al.*,

1989). Mueller and Richards (1986) and Busso *et al.* (1989) suggested that bud activation would be comparatively more important than bud number or viability in *Agropyron* species to explain the reduced tiller production after defoliation with or without water stress. Despite the importance of a sufficient, active axillary bud bank for plant perennation, very few studies have focused on addressing the effects of the combined influence of defoliation under water stress on axillary bud viability and subsequent outgrowth.

### 3.3.1 Viability

Flemmer *et al.* (in press) determined the effects of water stress, rainfed or irrigated conditions with or without defoliation at the phenological stages vegetative (V), internode elongation (E) or both developmental stages (VE) on the perennial tussock grasses *S. clarazii*, *S. tenuis* and *S. gynerioides* in central, semiarid Argentina. Further details on experimental design and treatments are provided under item 1.2. Studies were conducted at the field during three consecutive years (1995-1997), and measurements were made on individual tillers of total node number, numbers of daughter tillers, total bud number, and numbers of metabolically active or dead and dormant axillary buds. Their results implied that neither axillary bud activation nor initial outgrowth would contribute to explain the observed competition release in the undefoliated *S. gynerioides* after selective defoliation of *S. clarazii* (Moretto and Distel, 1999) and *S. clarazii* and *S. tenuis* (see Tiller growth heading). They also showed 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, semiarid rangelands of central Argentina (Busso, 1997; Fernández and Busso, 1999).



**Figure 8.** Photosynthetically active radiation (PAR) measured to crown height in *Stipa clarazii* and *S. tenuis* during early 1997. Measurements were made using a quantum sensor (LICOR Inc.). Plants of these species, which grew in competition with undefoliated plants of *S. gynerioides*, remained undefoliated (Controls:C) or were defoliated at the vegetative (V), internode elongation (E) or both phenological stages (VE) under irrigated, rainfed or water stress conditions in 1995 and 1996. Each symbol is a mean of  $n=20$ . Vertical bars represent  $\pm 1$  standard error of the mean.

The degree of metabolic activity and outgrowth capacity of axillary buds were maintained on parent tillers of *S. tenuis* after a one-year-exposure to the combined or separate influence of water stress and defoliation (Flemmer *et al.*, in press). Busso *et al.* (1989) and Flemmer *et al.* (in press), however, also reported a reduction in the number of metabolically active buds on plants of various perennial grass species after the simultaneous influence of defoliation and water stress during two consecutive years. Also, and similar to that found in other perennial grasses (Busso *et al.*, 1989), prolonged water stress stimulated a greater bud metabolic inactivity in *S. clarazii* (Flemmer *et al.*, in press).

Flemmer *et al.* (in press) reported that plants of *S. tenuis* either defoliated or not during the previous year had a greater number of daughter tillers and total nodes

after exposure to water stress in VE than in V. They attributed this response to increased accumulation of total nonstructural carbohydrates in the stem bases 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 re-growth 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 determined greater tillering responses (Busso *et al.*, 1990; Fulkerson and Slack, 1995; Volaire, 1995; Oosthuizen and Snyman, 1999).

Defoliation under water stress increased metabolic inactivity on buds of *A. spicatum* and *S. tenuis* (Busso *et al.*, 1989; Flemmer *et al.*, in press). Flemmer

*et al.* (in press) reported that the number of dead and dormant buds were greater when defoliated and undefoliated plants of *S. tenuis* were exposed to water stress at V or VE than at E. Based on these results, these authors suggested 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 this species.

Flemmer *et al.* (in press) found that numbers of daughter tillers were greater on *S. clarazii* plants defoliated twice than on those defoliated at V or left undefoliated during the previous year under rainfed conditions. However, these authors reported that numbers of daughter tillers were greater on plants defoliated at V than at E or VE in *S. clarazii* under irrigated conditions, although defoliated plants of this species had a lower number of daughter tillers than undefoliated controls under water stress. 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 inducing bud inactivation or to a low remaining photosynthetic leaf surface area after defoliation which is insufficient to maintain a high degree of bud metabolic activity under different levels of soil water availability (Busso *et al.*, 1989). In Flemmer *et al.*'s study (in press), photosynthetically active radiation at crown level of the desirable grasses under irrigation was 70% of that under rainfed conditions (Fig. 8). Then, 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 (Fig. 1) may contribute to explain the observed plant responses in the rainfed and irrigated treatments.

Plants of *S. clarazii* showed a greater

number of total nodes under water stress when they were defoliated at VE than when they remained undefoliated (Flemmer *et al.*, in press). 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 beginning of the growing season which followed two years of successive treatments, numbers of total nodes and bud metabolic activity and outgrowth were similar between defoliation treatments or water levels on parent tillers of *S. clarazii* and *S. tenuis* (Flemmer *et al.*, in press). A similar response was reported on *S. tenuis* and *P. napostaense* which did not modify their potential re-growth capacity after plants were defoliated at different phenological stages during two consecutive years under rainfed conditions (Becker *et al.*, 1997a). 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).

Despite some transitory effects of defoliation on axillary bud dynamics, rapid photosynthetic canopy reestablishment after defoliation under irrigated, rainfed or water stress conditions was in general not limited by availability and/or re-growth capacity of axillary buds in *S. clarazii* and *S. tenuis* (Flemmer *et al.*, in press). Lack of consistent responses to defoliation have been attributed, at least partially, to the apparent 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

re-growth in perennial grasses (Briske and Richards, 1995). In the study of Flemmer *et al.* (in press), responses were in general specific to the species, imposed treatments, sampling times and cumulative treatment effects, which makes difficult to predict plant responses under natural conditions.

### 3.3.2 Outgrowth and length

During 1995-1997, we determined bud outgrowth and length on stem bases of plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which had been either defoliated or not (controls) under water stress, rainfed or irrigated conditions in 1995 and 1996 (see item 1.2 for details on experimental design and treatments). Tillers (2-4) were periodically harvested from 1 plant of each species per replicate in all treatments during the study period. The total node number on any stem base was divided in three portions of equal node number. The lowermost, intermediate or uppermost third portion of any stem base included buds, which were called basal, intermediate or distal, respectively. Basal buds were the oldest while distal buds the youngest on any stem base. The percentage of buds, which produced daughter tillers, was determined (i) within each positional category (basal, intermediate or distal) and (ii) for the whole stem base with respect to the total node number on any stem base. Bud length was measured from prophyll tip to the lowest attachment on the tiller, using an ocular micrometer. All statistical analyses were performed separately for each date and species using a completely randomized design. Data of percentage outgrowth from the different bud categories and bud length were analyzed using a two-way ANOVA (water and defoliation treatments x bud categories). Whenever F tests were significant (p), means were separated using Fisher's LSD

(Steel and Torrie, 1981). Percentage data were transformed to arcsin ( $x/100$ ) to homogenize variances.

Within each study variable, the interaction term was not significant ( $p=0.12$ ) at least 27 out of 30 times in all three species during 1995-1997. Then, we will only refer to main effect comparisons. During the study period, there were not significant differences ( $p=0.08$ ) among water and defoliation treatments neither for the percentage of buds which grew out from the total node number nor for bud length on any stem base in 56 out of 60 times in *S. clarazii*, *S. tenuis* and *S. gynerioides*. Under the conditions of our study, these parameters thus showed a high resilience to the various water stress and defoliation regimes during two consecutive years in *S. clarazii*, *S. tenuis* and *S. gynerioides*. It has already been shown that water stress with or without defoliation can reduce daughter tiller production and bud size in perennial grass species (Mitchell, 1953; McIntyre, 1976; Nus and Hodges, 1986; Jennane *et al.*, 1987; Busso *et al.*, 1989). Similar cumulative effects of repeated defoliation on bud length have been observed for *Calamagrostis rubescens* and *Danthonia caespitosa* Gaud. (Hodgkinson, 1976; Stout *et al.*, 1980, 1981). Decreased bud length under water stress than under higher moisture levels in perennial grasses has been attributed to a decreased hydration of tissues, which may limit bud growth (Olmsted, 1941; McIntyre, 1976; Busso *et al.*, 1989). Detrimental effects of water stress and defoliation on either the percentage of buds which grew out from the total node number on any stem base or on bud length, however, were most likely overshadowed in our study because of the shading effects of the undefoliated *S. gynerioides* on *S. clarazii* and *S. tenuis* (Fig. 8) under higher soil moisture levels. Thus, and after two or more years of

successive treatments, re-growth capacity of defoliated or undefoliated *S. clarazii*, *S. tenuis* and *S. gynerioides* appeared similar under various soil moisture levels. A smaller bud size may delay re-growth somehow (Busso *et al.*, 1989). However, it is unlikely that small bud sizes constitute a major constraint to re-growth following defoliation in perennial grasses because in our study, as well as in that of Mueller and Richards (1986), even the basal buds (the smallest within any given stem base : Fig. 9), produced tillers. Mueller and Richards (1986) also found no bud length differences between defoliated and control plants of *A. desertorum* and *A. spicatum* under rainfed conditions.

Similar to results of Mueller and Richards (1986), Busso *et al.* (1989, 1993) and Becker *et al.* (1997a) on *Agropyron*, *Stipa* and *Piptochaetium* species, length was smaller ( $p < 0.05$ ) on basal than distal buds in all three species (Fig. 9). Outgrowth was also lower ( $p < 0.05$ ) from basal than intermediate buds in *S. clarazii*, *S. tenuis* and *S. gynerioides* (Fig. 10), results which agree with those of Busso *et al.* (1989) in *A. desertorum* and *A. spicatum*, Busso *et al.* (1993) in *S. tenuis* and Becker *et al.* (1997a) in *S. tenuis* and *P. napostaense*. However, and in disagreement with results in other perennial grasses (Busso *et al.*, 1989; Busso *et al.*, 1993; Becker *et al.* 1997a), outgrowth was greater ( $p < 0.05$ ) from intermediate than distal buds (Fig. 10).

### 3.4 Tiller Growth

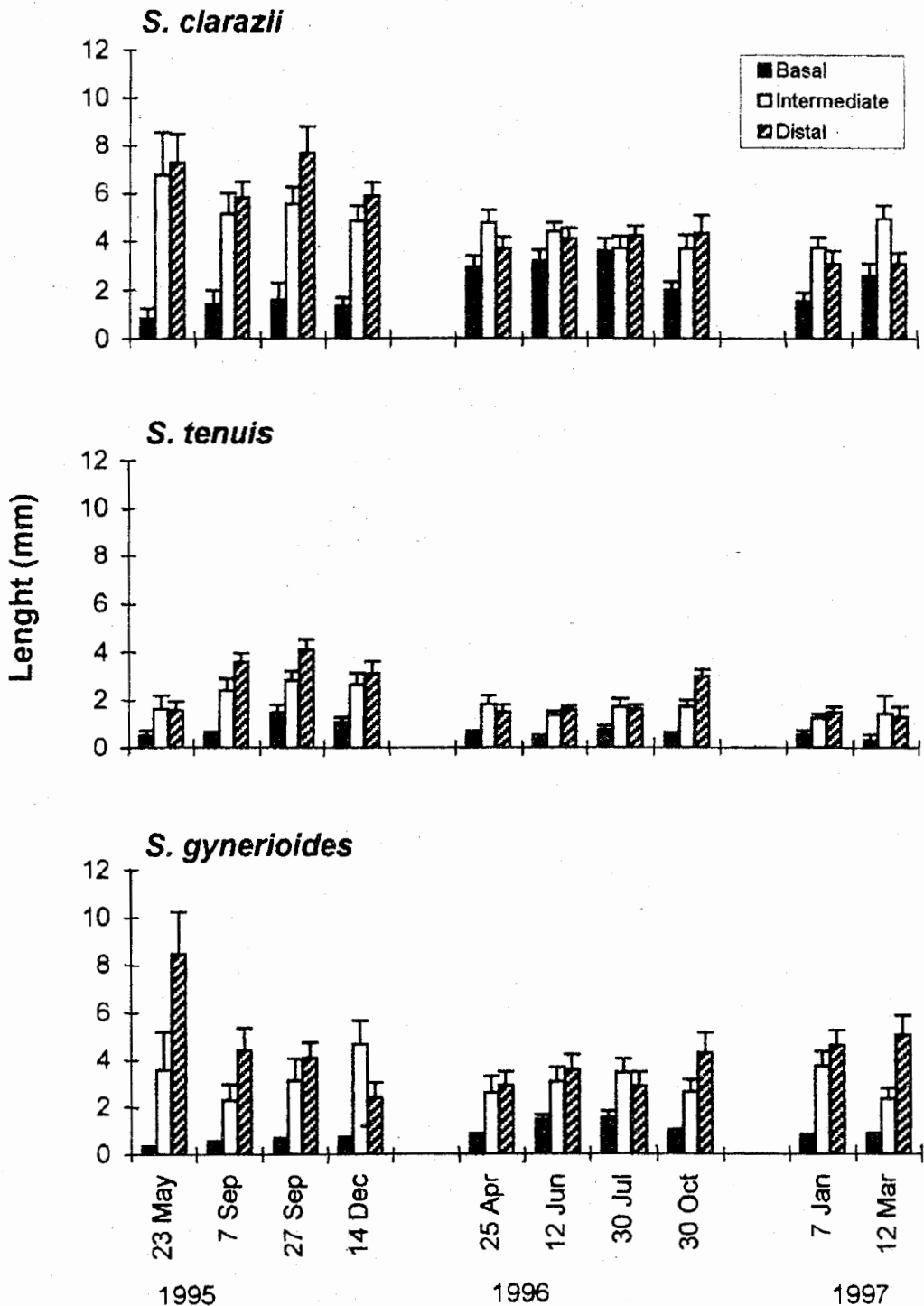
We determined tiller height and total green leaf length on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides*, which were defoliated or remained undefoliated under water, stress, rainfed or irrigated conditions during 1995 and 1996. Experimental design and treatments for this study are reported under item 1.2.

#### 3.4.1 Tiller height

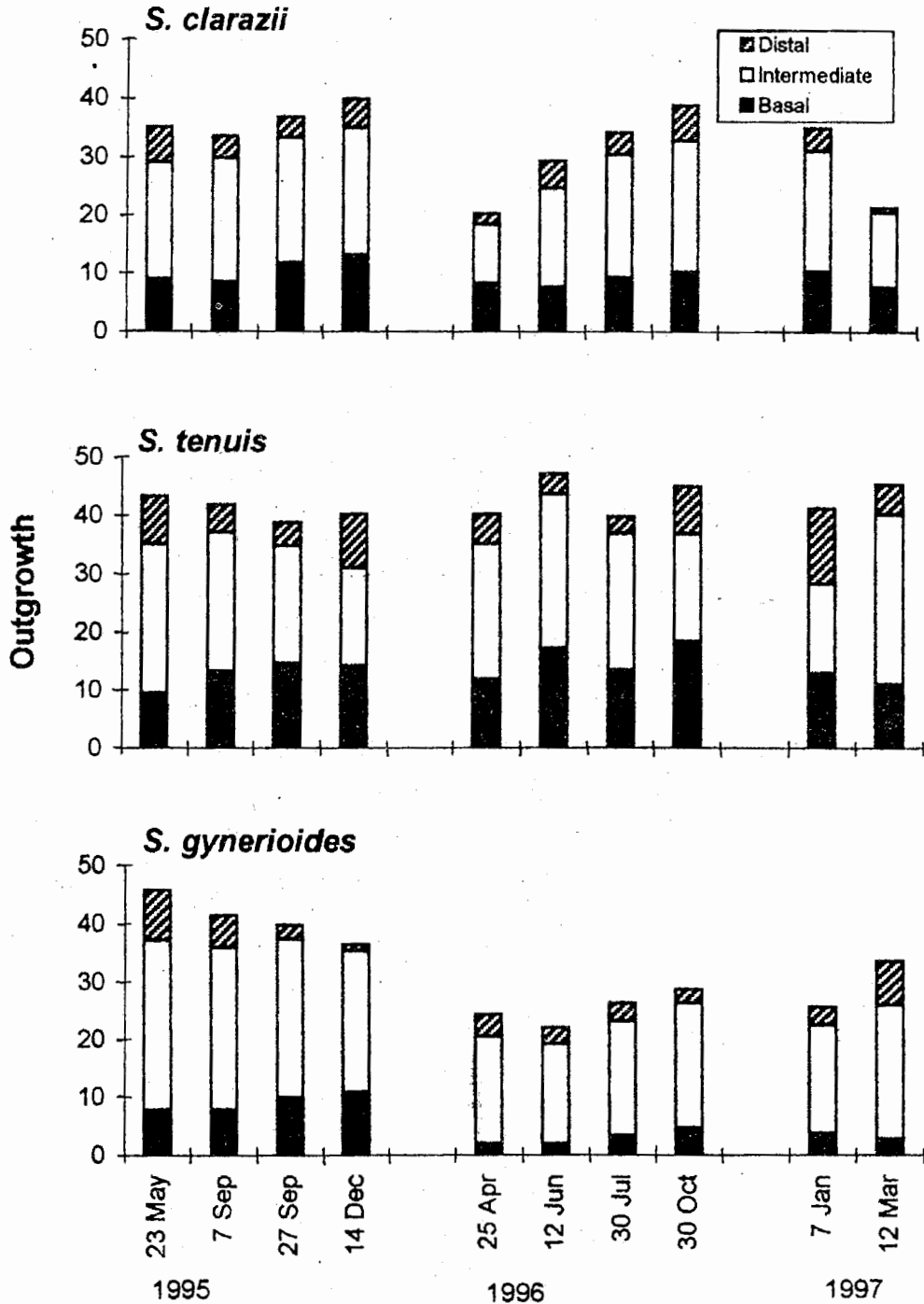
Towards the end of the first year of application of various water and defoliation treatments, tiller height of the undefoliated, unpalatable *S. gynerioides* was greater when in competition with plants of *S. tenuis* and *S. clarazii* which had been defoliated twice during the growing season than when competing with undefoliated controls of these species under rainfed conditions (Fig. 11). Greater growth of *S. gynerioides*, both in terms of tiller height and total green leaf length (see following heading), after defoliation of *S. clarazii* and *S. tenuis* would be an indication that *S. gynerioides* was released from competition with the palatable grasses after these were defoliated. At the end of the first and the second year of treatments, however, tiller height of *S. gynerioides* was similar whether in competition with defoliated or undefoliated plants of *S. tenuis* and *S. clarazii* under water stress (Figs. 11 and 12).

By early spring, and after two years of defoliation at the vegetative and internodes elongation phenological stages of development under various soil water regimes, tiller height was 93 and 60% under conditions of water stress, and 42 and 21% under rainfed and irrigated conditions, of values found on undefoliated controls in *S. clarazii* and *S. tenuis*, respectively (Fig. 12). However, these plants showed a similar tiller height under all soil water regimes by the end of that growing season in early summer whether they had been defoliated or not (Fig. 12). Becker *et al.* (1997b) also reported detrimental effects of late defoliations on tiller height in *S. tenuis* and *Piptochaetium napostaense* under rainfed conditions.

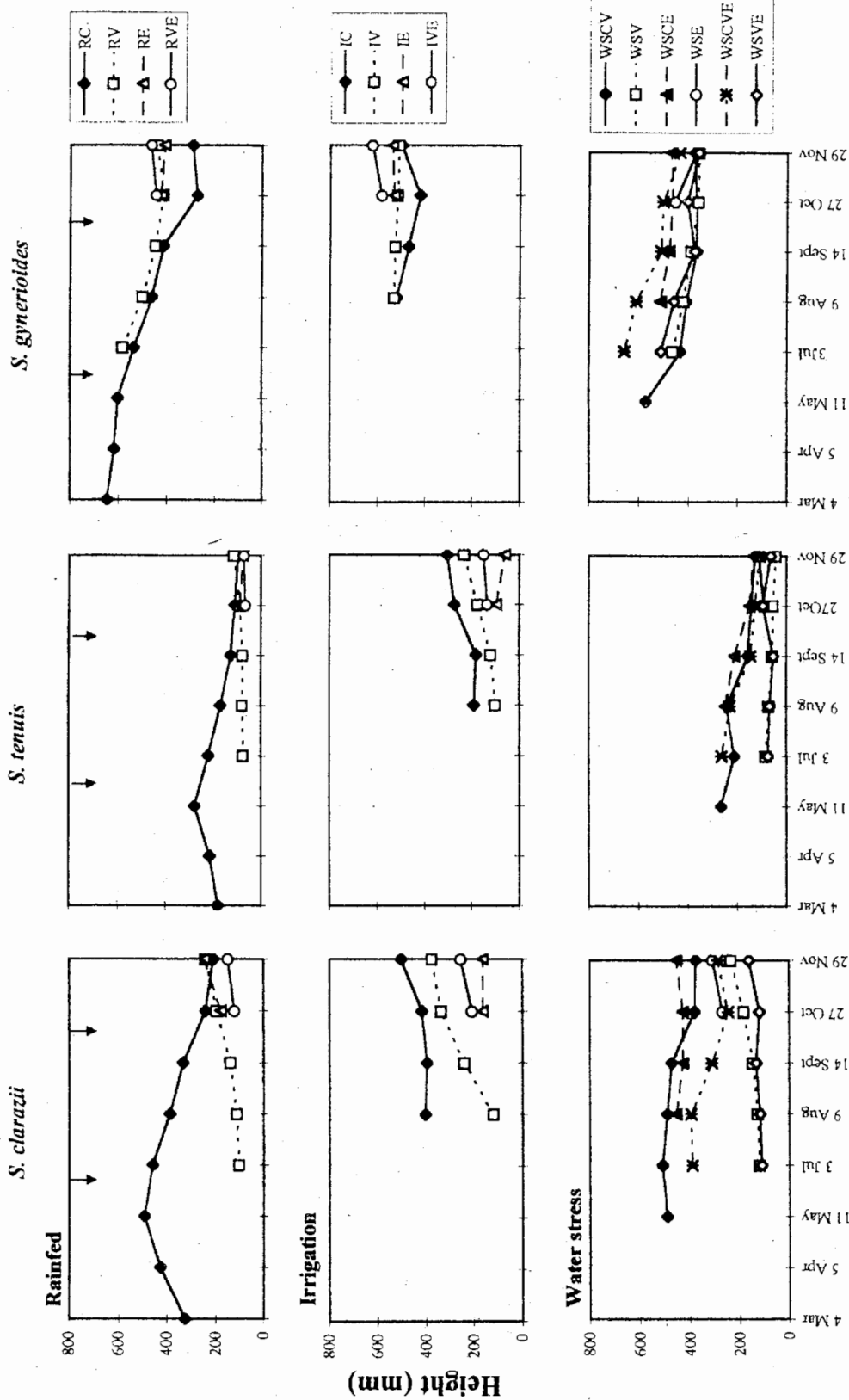
At the initiation of the third consecutive growing season, and after two



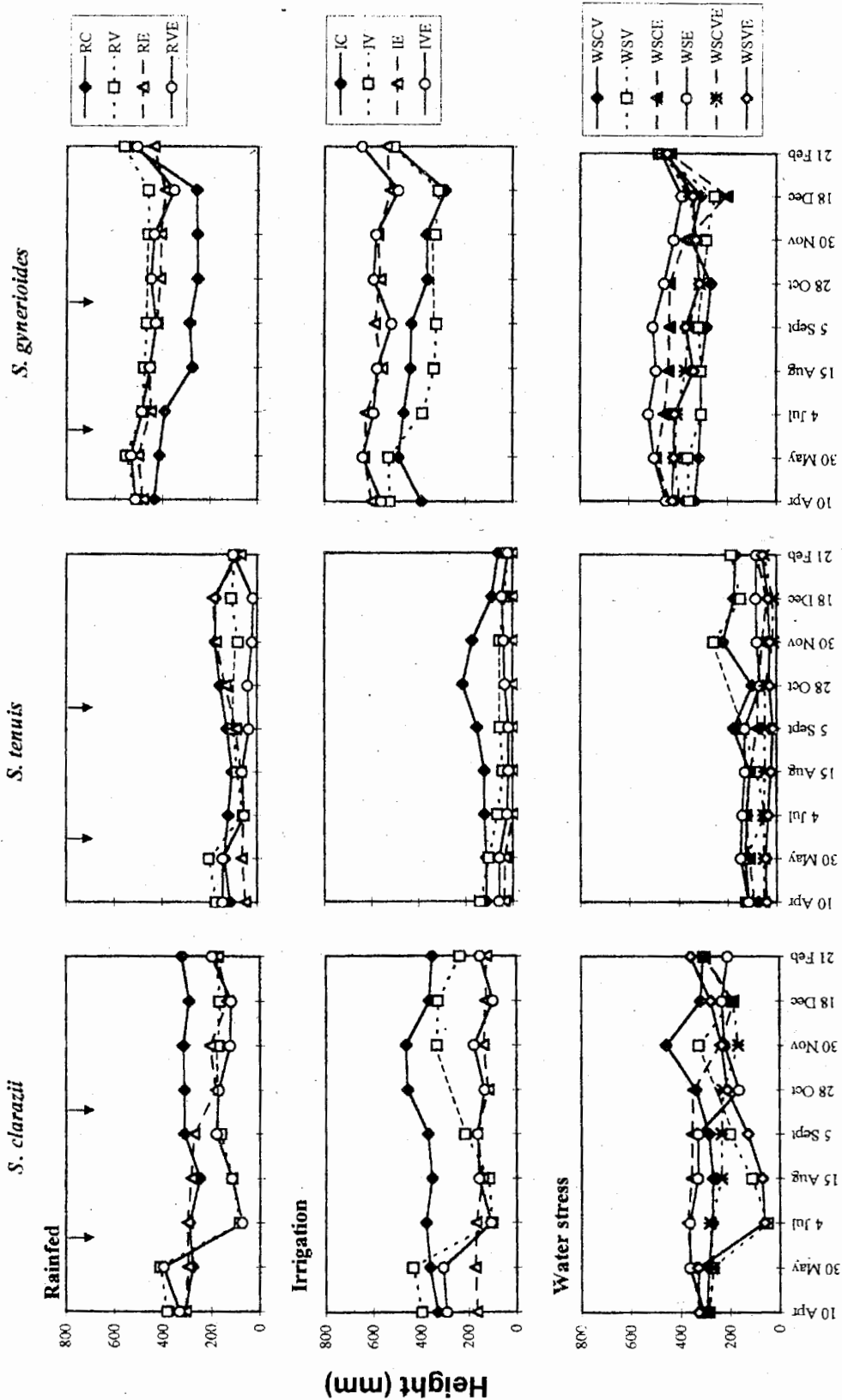
**Figure 9.** Length variation in 1995, 1996 and early 1997 of basal, intermediate or distal buds on stem bases of plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which were either defoliated or undefoliated under water stress, rainfed or irrigated conditions during 1995 and 1996. Each histogram is the mean + 1 standard error on  $n=2$ .



**Figure 10.** Percentage of buds which produced daughter tillers (outgrowth) within any of three bud categories (either basal, intermediate or distal) with respect to the total node number on any stem base. Measurements were effected in 1995, 1996 and early 1997 on stem bases of plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which had been either defoliated or left undefoliated under water stress, rainfed or irrigated conditions during 1995 and 1996. Histograms are the mean of  $n=2$ .



**Figure 11.** Tiller height (green+dry) during 1995 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which either remained undefoliated (Controls:C) or were defoliated at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed (R), irrigated (I) or water stress (WS) conditions in 1995 and 1996. Each symbol is a mean of n=2-28. Arrows indicate defoliation dates.



**Figure 12.** Tiller height (green+dry) during 1996 and early 1997 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which either remained undefoliated (Controls:C) or were defoliated at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed (R), irrigated (I) or water stress (WS) conditions in 1995 and 1996. Each symbol is a mean of n=2. Arrows indicate defoliation dates.

years of treatments, tiller height was similar in all defoliation and water level treatments for all three species (Fig. 12). This agrees with results of Becker *et al.* (1997a) in *S. tenuis* and *P. napostaense* where tiller height of these species was similar at the beginning of the growing season which followed application of various defoliation treatments during two consecutive years under rainfed conditions.

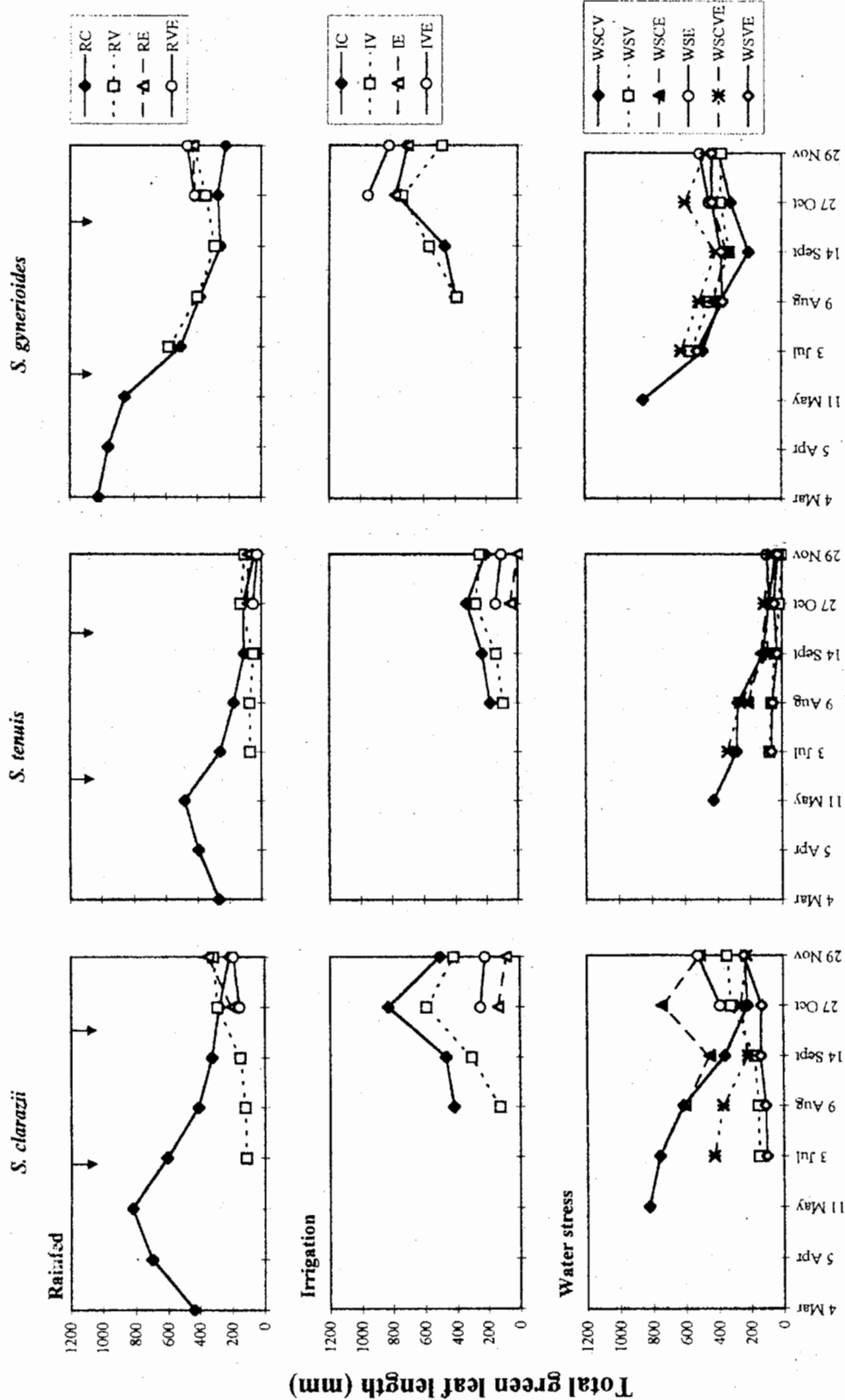
### 3.4.2 Total green leaf length

Relative increases in total green leaf length after defoliation in comparison to undefoliated controls was always similar or greater under water stress than under better soil moisture conditions in *S. clarazii* and *S. tenuis* during both study years (Figs. 13 and 14). For example, total green leaf length on tillers which had been defoliated at the vegetative stage of development in 1995 was 19 or 27% in *S. clarazii* or *S. tenuis*, respectively of values on undefoliated controls under rainfed or water stress conditions (Fig. 13). This response was associated with a greater tiller growth in *S. gynerioides* when in competition with defoliated than with undefoliated *S. clarazii* and *S. tenuis* under rainfed and irrigated conditions, mainly in 1996 (Figs. 13 and 14). After defoliation at the internode elongation developmental stage in 1996, however, total green leaf length in *S. clarazii* and *S. tenuis* was 90% greater on tillers which had been defoliated twice than on those undefoliated during the growing season under conditions of water stress (Fig. 14). At the same time, however, this variable was 32% in *S. clarazii* and 17% in *S. tenuis* on plants defoliated twice of values found on undefoliated controls under rainfed and irrigated conditions (Fig. 14).

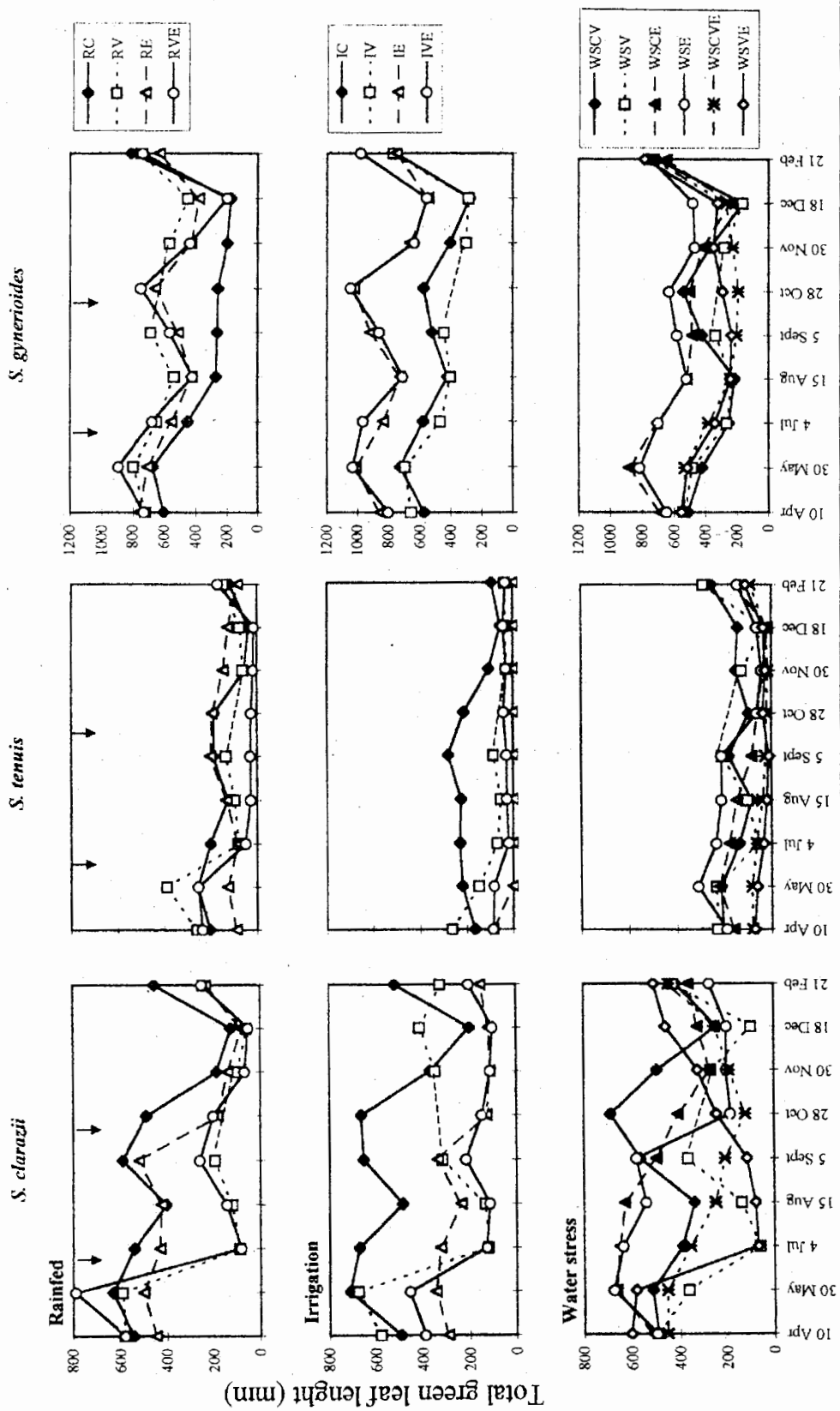
In September 1995, and except under conditions of water stress at the vegetative

and internode elongation developmental stages, tillers on plants of *S. clarazii* did not compensate ( $p < 0.05$ ) total green leaf length on undefoliated controls after being defoliated at the vegetative or vegetative+internode elongation developmental stages under any water level (Fig. 13). Total green leaf length was similar ( $p > 0.05$ ) on defoliated and undefoliated tillers of *S. tenuis* exposed to rainfed, irrigated or water stress conditions in September 1995 and 1996 (Figs. 13 and 14). Except in *S. clarazii* under irrigated conditions, defoliated and undefoliated tillers of both species had a similar ( $p > 0.05$ ) total green leaf length under rainfed, irrigated and water stress conditions towards the end of 1995 (Fig. 13). At this time, tillers of *S. clarazii* defoliated at either the internode elongation or the vegetative+internode elongation developmental stage under irrigated conditions did not compensate ( $p < 0.05$ ) total green leaf length measurements on undefoliated controls (Fig. 13). At the end of 1995, tillers of *S. clarazii* and *S. tenuis* had a similar ( $p > 0.05$ ) total green leaf length after had been defoliated either at V or E or VE stages of plant development under rainfed, irrigated or water stress conditions (Fig. 13). The only exceptions occurred (i) under irrigated conditions where total green leaf length was greater ( $p < 0.05$ ) on plants of both species defoliated at V than at E, and (ii) in the water stress treatment where this variable was greater ( $p < 0.05$ ) in plants of *S. clarazii* defoliated at E than at VE. At the end of two successive years of treatment application, however, total green leaf length in *S. clarazii* and *S. tenuis* was similar ( $p > 0.25$ ) under all defoliation and water level treatments (Fig. 14).

Total green leaf length in *S. gynerioides* was similar ( $p > 0.05$ ) when in competition with either defoliated or



**Figure 13.** Total green leaf length (blade+stem and sheaths) during 1995 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which either remained undefoliated (Controls:C) or were defoliated at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed (R), irrigated (I) or water stress (WS) conditions in 1995 and 1996. Each symbol is a mean of n=2-28. Arrows indicate defoliation dates.



**Figure 14.** Total green leaf length (blade+stem and sheaths) during 1996 and early 1997 on plants of *S. clarazii*, *S. tenuis* and *S. gynerioides* which either remained undefoliated (Controls:C) or were defoliated at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed (R), irrigated (I) or water stress (WS) conditions in 1995 and 1996. Each symbol is a mean of  $n=2$ . Arrows indicate defoliation dates. Note change of scale in *S. gynerioides*.

undefoliated plants of the palatable *S. clarazii* and *S. tenuis* under rainfed and irrigated conditions in 1995, except towards the end of November (Fig. 13). At this time, total green leaf length on tillers of *S. gynerioides* was greater ( $p < 0.05$ ) when *S. clarazii* and *S. tenuis* were defoliated twice than when they remained undefoliated under rainfed conditions (Fig. 13). From July 1996 onwards, and except when the palatable species were defoliated at V under rainfed conditions, total green leaf length on tillers of *S. gynerioides* was on average from 45 to 127% greater when the palatable species were defoliated than when they remained undefoliated under rainfed and irrigated conditions (Fig. 14). Under these water level conditions, however, total green leaf length on tillers of *S. gynerioides* was similar ( $p > 0.25$ ) when competing with either defoliated or undefoliated towards the end of 1996 (Fig. 14). In both years, total green leaf length on *S. gynerioides* tillers was similar when in competition with defoliated or undefoliated plants of the palatable species in the water stress treatment, for example in September and at the end of each growing cycle ( $p < 0.05$ ; Figs. 13 and 14). These results are similar to those observed for tiller height (Figs. 11 and 12) and total leaf blade length (data not shown) in this species.

At the end of each growing cycle, total green leaf length on tillers of *S. gynerioides* was similar ( $p > 0.05$ ) under rainfed, irrigated and water stress conditions when in competition with undefoliated plants of *S. clarazii* and *S. tenuis* (Figs. 13 and 14). The only exception was at the end of 1995, when total green leaf length was greater ( $p < 0.05$ ) under water stress at the vegetative+internode elongation stages and under irrigated conditions than in the rainfed treatment on tillers of *S. gynerioides* (Fig. 13). These results

contrast with growth reductions reported on other perennial grasses under conditions of water stress (Busso and Richards, 1989, 1995; Volaire, 1995; Volaire and Thomas, 1995; Collet *et al.*, 1996). At the same time, total green leaf length in *S. gynerioides* was similar ( $p < 0.05$ ) among water levels when *S. clarazii* and *S. tenuis* were defoliated at the either vegetative or internode elongation or both phenological stages (Fig. 13). The only exception was when the palatable species were defoliated either at the internode elongation or vegetative+internode elongation at the end of 1995 (Fig. 13). At this time, total green leaf length in *S. gynerioides* was greater ( $p < 0.05$ ) when the palatable species were defoliated at the internode elongation stage under irrigated than under rainfed conditions, and when they were defoliated at the vegetative+internode elongation stage under irrigated than under rainfed or water stress conditions.

At the beginning of 1997, total green leaf length in all three species was similar ( $p > 0.05$ ) among water and defoliation treatments (Fig. 14). Similar results were observed for tiller height (Fig. 12) and total green blade length (data not shown). However, total green leaf length was twice as much under water stress in the vegetative developmental stage than under rainfed or irrigated conditions in *S. tenuis* (Fig. 14).

Results obtained in *S. clarazii*, *S. tenuis* and *S. gynerioides* show that variations in aboveground dry matter production (see Dry Weight heading) among water and defoliation treatments in these species can be better explained through tiller growth than bud viability and outgrowth (see Axillary Buds heading) measurements. Greater tiller growth in *S. gynerioides* when in competition with defoliated *S. clarazii* and *S. tenuis* reduced photosynthetically active radiation (PAR)

to crown level of the palatable grasses comparatively more under rainfed and irrigated than under water stress conditions (Fig. 8). This reduced PAR availability contributed to the observed responses on *S. clarazii* and *S. tenuis*. Responses obtained in *S. gynerioides* under water stress may be due to low resistance of this species to scarce levels of soil water availability. Dry years may reduce plant growth and survival comparatively more in unpalatable than palatable grass species (Llorens, 1995; Moretto and Distel, 1999). Growth stimulation on undefoliated *S. gynerioides* under high soil water levels, which increased shading of *S. clarazii* and *S. tenuis*, overshadowed expected growth reductions in the palatable species as a result of water stress and defoliation.

Diurnal patterns in the temperature response of leaf extension, which were described by linear and quadratic regression models, were reported to be consistent under a variety of water stress and defoliation conditions on two bunchgrass species in the field (Busso and Richards, 1992).

### 3.5 Basal Cover

The response to variation in grazing interval on grass persistence over the spring-autumn period in southern New South Wales, Australia was examined on 4 perennial grass species over 2 years. Three introduced perennial grasses and a native one (*Danthonia richardsonii* Cashmore cv. "Taranna") were grazed every 2, 5 or 8 weeks under either rainfed or irrigated conditions (Virgona and Bowcher, 2000). The seasons differed with respect to rainfall: the first season was dry compared to the second one. In the first season, the relative change in basal cover (RCBC, ratio of final to initial basal cover) after 8 months was less than 1 in the three introduced grasses, so there was a decline in basal cover over the period. However,

The relative change in basal cover increased with grazing interval. In the second season, there were interactions between watering, both species and grazing interval. Each of the introduced species increased basal cover when watered whereas it declined in *D. richardsonii*. Differences in RCBC between the grazing treatments depended on the supply of water: RCBC was favored by shorter grazing intervals in the irrigated treatment and longer grazing intervals under rainfed conditions.

### 3.6 Dry Weight

The effects of the simultaneous influence of water stress and defoliation on aboveground dry weight can vary with both the intensity and frequency of such events (Mohammad *et al.*, 1982, Simoes and Baruch, 1991; Busso and Richards, 1995). Dry weight production has been reduced by either water stress or increased defoliation frequency in perennial grasses, although detrimental effects of defoliation have also been reduced under water stress (Simoes and Baruch, 1991). Even more, dry matter production was increased by 40% removal of aboveground biomass in comparison to undefoliated controls under severe water stress in *A. desertorum* and *E. junceus* (Mohammad *et al.*, 1982). These responses have been partially attributed to reductions in transpiratory surface area after defoliation, which would conserve soil water and improve plant water status in comparison with undefoliated controls (Briske and Richards, 1995; Jacobs and Sheley, 1997). Defoliation might enhance reproduction if it conserves soil water (McNaughton *et al.*, 1983). Maximum whole-plant production in *Sporobolus kentrophyllus* (K. Schum) was coincident with optimum conditions for herbivores

(maximum nitrogen concentration in grass leaves) when watering was frequent, and plants were moderately defoliated (Georgiadis *et al.*, 1989). However, these conditions were not the same as those that maximized relative aboveground stimulation of growth (infrequent watering and clipping). Significant overcompensation occurred only when plant growth rates were limited at the time of defoliation, in this case largely by soil water availability. Differences in water potential between clipped and unclipped plants, however, were not a sufficient prerequisite for overcompensation. Severely clipped plants were much less drought stressed than unclipped plants, yet overcompensation was never significant in those plants (Georgiadis *et al.*, 1989). Oesterheld and McNaughton (1991) found that plants growing at low relative growth rates (i.e., plants growing under water stress) can overcompensate in terms of growth rates of live tissue which resulted in overcompensation in the yield to grazers. In their study, however, total productivity of clipped and unclipped plants, which included litter accumulation, was identical for all levels of relative growth rate as a consequence of a larger litter accumulation in unclipped plants. Thus, the difference in relative growth rates between clipped and unclipped plants was in part due to higher rates of biomass fixation per unit of biomass in clipped plants, but it was also due to higher leaf turnover in unclipped plants.

On the other hand, Maschinski and Whitham (1989) reported that plants might have a positive response to defoliation when water and nutrients are not limiting. In this regard, the lowest dry matter production in the grazing tolerant *A. desertorum* and the grazing sensitive *P. spicata*, among various water and

defoliation treatments, was obtained after plants of these species were defoliated under water stress during two consecutive years (Busso and Richards, 1995). The interaction of these stresses has also reduced re-growth in other grass species (Chung and Trlica, 1980; Brown, 1995; Onillon *et al.*, 1995; Donkor *et al.*, 1999). Barker *et al.* (1985) observed that drought reduced leaf expansion and tillering, and that plants in this 'dormant' state were unresponsive to defoliation.

Total seasonal forage production of *A. desertorum* was reduced most markedly by clipping in the wet years, as a result of removal of the apical meristem and subsequent reduction of reproductive stem development and delayed growth (Miller *et al.*, 1990). In the wet years, a larger proportion of tillers were differentiated into reproductive shoots as compared to the drier years. Hyder and Sneva (1963) reported that favourable growth conditions resulted in a higher proportion of apical meristems being differentiated to reproductive status than less favourable growth conditions, and the removal of the apical meristem resulted in 90% of the second tillers being vegetative. The reduction in soil water depletion resulting from clipping was probably attributable to both leaf area removal and reduced root growth (Richards, 1984). Defoliation in the early vegetative stage generally had little effect on soil water content unless soil water potentials were more negative than  $-0.03$  MPa. Reduced soil water depletion after defoliation during early stages of apical meristem elevation was probably caused by reduced leaf area and subsequent delay in leaf initiation from axillary bud growth (Miller *et al.*, 1990). Delayed soil moisture depletion may increase the period of active plant growth for grazing.

Heitschmidt *et al.* (1999) showed that

the combined effects of grazing and late spring to early fall drought were minimal on soil water dynamics and aboveground net primary production, although grazing treatments reduced herbage standing crops. They believed that the primary reason drought had minimal impact on post-drought recovery patterns was most likely related to the timing of drought (i.e., late in the growing season). These grasslands are dominated by cool-season plant species, which complete most of their growth by late spring and early summer (Heitschmidt *et al.*, 1995). Thus, plants only need sufficient amounts of soil water until late spring to complete their "normal" production cycle. In their study (Heitschmidt *et al.*, 1999), there was apparently a sufficient soil water reserve when the drought was initiated which allowed completion of the annual production cycle.

The response of dry matter and nitrogen yields to a lower defoliation frequency was proportional to the amount of moisture available in *Digitaria decumbens* Stent (Blunt and Haydock, 1978). Dry matter yield increased from 3100 to 5200 kg ha<sup>-1</sup> with an increase from 5 to 7 irrigations and a change of average daily available moisture from 78 to 107 mm. Also, dry matter yields increased and N concentrations decreased as defoliation frequency decreased.

A three-year grazing study was carried out on a pasture dominated by *Poa pratensis* L. to estimate the daily quantity of herbage available to cattle in an intensive, rotational grazing system (Kanneganti and Kaffka, 1995). Under adequate soil moisture, herbage available for daily intake was 53 kg ha<sup>-1</sup> d<sup>-1</sup> from April until mid-August. A dry summer, however, reduced herbage availability to 15 kg ha<sup>-1</sup> d<sup>-1</sup>.

Herbage production of perennial pastures can be manipulated by grazing

strategies over a wide range of environmental conditions. For example, Avery *et al.* (2000) found that *Dactylis glomerata* L. pastures in eastern Australia appeared to be relatively stable under moderate grazing pressure (8-10 dry sheep equivalents) despite being subjected to drought conditions. High stocking rates under drought, however, quickly reduced *D. glomerata* herbage mass irrespective of grazing management.

Williamson *et al.* (1989), grazing grasshoppers at various intensities in locations ungrazed for 10-11 years, concluded that grazing optimization of short-grass annual net primary productivity (ANPP) appears most likely to occur during recovery from dry periods. Even more, Varnamkhasti *et al.* (1995) suggested that the potential for increased ANPP with defoliation is greatest after relatively long periods of water stress. Their hypotheses that re-growth following defoliation would decrease with increasing intensity of long-term grazing, but would be proportionally greater under conditions of low water resource availability compared to vegetation receiving supplemental water, was also supported. They also found that long-term grazing would decrease the potential for vegetation to respond to high precipitation with increased production, but the opposite was also true: long-term grazing increased production under conditions of relatively low precipitation.

Flemmer (2000; see item 1.2 for description of experimental design and treatments) found that dry weight production in the undefoliated *S. gynerioides* was significantly greater when in competition with defoliated than with undefoliated plants of *S. tenuis* and *S. clarazii* under water stress. Although not significantly different at *p*, she found that production of dry weight in *S. gynerioides* also tended to be greater after *S. tenuis*

and *S. clarazii* were defoliated later (at E or VE) than earlier (at V) in the irrigated and water stress treatments. The undesirable *S. gynerioides* appeared then to take advantage of late defoliations of both desirable grasses very likely obtaining a greater share of soil resources under those water levels. Moretto and Distel (1999) also reported a competitive advantage in the undefoliated, undesirable *S. trichotoma* after *S. clarazii* was selectively defoliated under field conditions. Aboveground dry weight production in *S. gynerioides* was greater under rainfed and irrigated than under water stress conditions (Flemmer, 2000). After two successive years of defoliating *S. tenuis* and *S. clarazii* in competition with undefoliated *S. gynerioides*, photosynthetically active radiation to crown level of *S. tenuis* and *S. clarazii* was more than 50% lower in the rainfed and irrigated than in the water stress treatment (Fig. 8). Greater shading of *S. gynerioides* as soil water levels increased must have contributed to the lower aboveground dry weight production in *S. tenuis* and *S. clarazii* after defoliation under irrigated than under rainfed or water stress conditions (Flemmer, 2000). A greater proportion of small-size plants in *S. clarazii* and of dead plants in *S. tenuis* was also found in the irrigated than in the water stress treatment (Flemmer, 2000). Greater shading has contributed to reduce aboveground dry weight production in several other perennial grasses (Cruz, 1997; Devkota *et al.*, 1997). The smaller size of defoliated *S. tenuis* plants under irrigation was partially due to a lower tiller growth under these than lower soil water content conditions (Fig. 12). Greater growth of the undefoliated, unpalatable *S. gynerioides* as soil moisture content increased (Figs. 11 and 12) overshadowed expected detrimental effects of water stress on growth of *S. clarazii* and *S. tenuis*. These results suggest that grazing

of perennial forage grasses under high soil water levels would speed up, rather than slowing down, their degradation when they are competing with ungrazed, undesirable perennial tussock grasses in a natural setting (Flemmer, 2000).

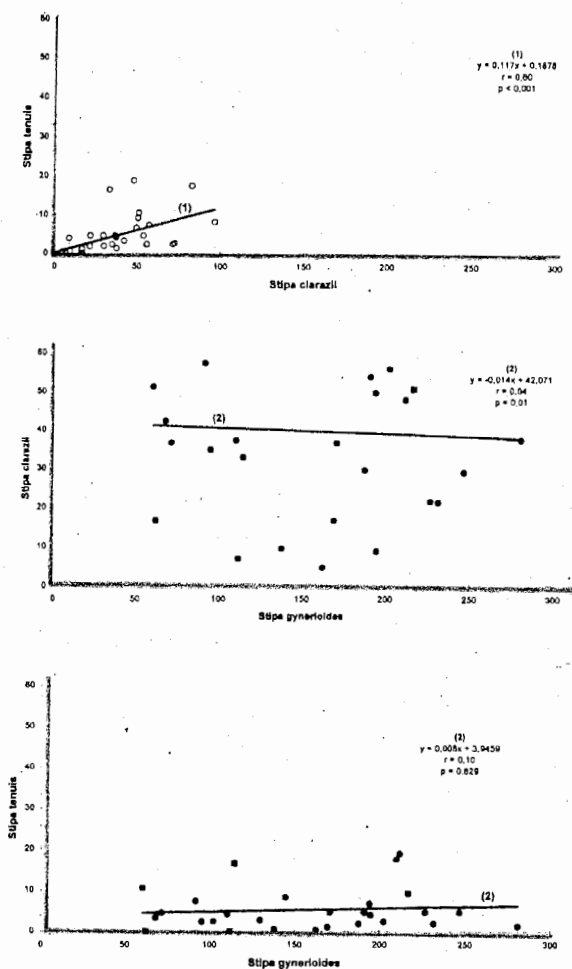
Using Flemmer's (2000) experimental design and treatments (see item 1.2), we evaluated if the perennial tussock grasses *Stipa clarazii*, *S. tenuis* and *S. gynerioides* produced a similar total annual dry weight production after these species were either defoliated or not (controls) under water stress, rainfed or irrigated conditions at the field in temperate, semiarid Argentina (38°48'S, 62°13' W). *Stipa clarazii* and *S. tenuis* responded similarly to the different water levels and defoliation treatments (Fig. 15). However, total annual dry weight production decreased in *S. clarazii*, but not in *S. tenuis*, as dry weight increased in the undefoliated *S. gynerioides* (Fig. 15).

## 4. DEMOGRAPHY

### 4.1 Seed Banks

While drought and herbivory may temporarily reduce vegetative cover, their mutual influence on available seedbanks is unclear (Hild *et al.*, 2001). Cool-season annual grass seeds accumulated after drought. Emerged seedlings of cool-season annual grass (primarily *Bromus japonicus* Thunb. ex Murr and *Vulpia octoflora* Walt. Rydb. were affected little by grazing but were reduced during and increased following drought treatments (Hild *et al.*, 2001).

Annual species can escape drought by setting seeds, and then re-establish quickly when rain falls as they have vigorous seedlings. Most perennials have less vigorous seedlings that limit their ability to establish plants quickly.



**Figure 15.** Comparison of total annual aboveground dry weight production between species pairs in *S. clarazii*, *S. tenuis* and *S. gynerioides* after these perennial tussock grasses were either defoliated or not (controls, C) under water stress, rainfed or irrigated conditions. Defoliation of *Stipa clarazii* and *S. tenuis*, palatable species to domestic livestock, was to 5 cm stubble height during 1995 and 1996 at the phenological stages either vegetative (V) or during internode elongation (E) or both stages (VE). At the same time, the unpalatable *S. gynerioides* remained undefoliated, although aboveground dry weight production was obtained in all three species at the end of the study in 1997. Aboveground biomass was measured at the time of each defoliation in 1995 and 1996 (D). In addition, total amounts of dry weight produced by undefoliated plants during each whole growing season, and that produced by defoliated plants from the time of treatment to the end of each growing cycle (R, re-growth) were measured. Total dry weight produced by defoliated plants was calculated as D+R. It was considered that any pair of species had a similar response to their environment (different water and defoliation treatments) when both of them showed a significant positive relationship to the studied parameter. Comparison among species was effected using linear regression analysis for each biomass harvesting date. Regression lines were compared among harvesting dates within each species and the data pooled if lines were not significantly different ( $p > 0.05$ ) following Neter *et al.* (1985). Numbers on lines in parenthesis indicate defoliation treatments the data were pooled as follows: (1) C+total annual dry weight production of defoliated plants+V+E+VE+R (open circles); (2) C and total annual dry weight production of defoliated plants (filled circles).

However, they can partially escape droughts by reducing leaf area while relying on dormant buds, or underground organs, to enable rapid regeneration after rainfall periods.

Cool-season annual grasses can maintain their prevalence during recovery after drought. Given the flexible composition of seed banks, dominance shifts between cool-season annual grasses, perennial grasses and forbs may be short-lived and greatly influenced by abiotic factors (Hild *et al.*, 2001).

#### 4.2 Plant and Seedling Survival

Plant mortality in *B. curtipendula* remained unaffected during a dry year both on ungrazed and moderately grazed areas, although the proportion of plants producing green tillers was severely reduced (Briske and Hendrickson, 1998). However, perennial grass mortality has been large when grazing under natural, severe droughts has extended during several years (Young, 1956; Brown, 1995). The greater the grazing intensity under drought, the lower the survival of grass plants (Young, 1956). Young (1956) reported that severe defoliation of tall grasses during drought periods would be expected to curtail seed production. In this study, the few grass seedlings which appeared during drought died when grazed or clipped, and surviving grass plants where those protected by dense clumps of brush against close livestock utilization. At the other extreme, plant mortality of defoliated, palatable perennial grasses can also be very high when they are competing with undefoliated, unpalatable vegetation to livestock during subsequent wet years (Flemmer, 2000). This is mainly because plants of the palatable species can be left completely under the shade of unpalatable, undefoliated vegetation (Flemmer *et al.*, 1999).

Chambers and Norton (1993) studied

the natality, mortality and population turnover of the grasses *Sporobolus cryptandrus* (Torr.) Gray (C4 plant) and *Oryzopsis hymenoides* (Roemer & Schultes) Riker (C3 plant) under different timing (winter vs. spring) and intensities (light vs. heavy) of grazing during a drought period in southwestern Utah, USA. Both grasses had highly negative turnover rates in heavily grazed spring pastures due to high mortality and/or very low natality; otherwise, they generally had positive rates of turnover. Spring precipitation during periods of active growth and photosynthesis may have decreased mortality of *O. hymenoides*. These authors concluded that individual species responses to the effects of both grazing and drought were more predictable from life history and physiological characteristics than from past responses to grazing alone. It appeared that negative effects of grazing on natality, mortality, or population turnover could be accentuated for certain species under below average precipitation. Natality of *S. cryptandrus* was high during the drought period for all but heavily grazed plots. In *O. hymenoides* natality was lower in plots grazed heavily in the spring than in ungrazed plots.

Boschma and Scott (2000) conducted an experiment in New South Wales, Australia, to evaluate the productivity and persistence of 6 perennial grasses fewer than 2 defoliation levels and a range of moisture conditions. Plant mortality of over 40% was observed in *D. glomerata* and *Lolium perenne* L. under moderate drought conditions during spring-summer. Plants in this treatment continued to grow, albeit weakly. Under more severe drought conditions, less than 20% of plants died; in this case, plants appeared to become dormant. Boschma and Scott (2000) suggested that plants were using energy reserves to sustain growth under

moderate drought, which could not be replenished due to slow growth and regular cutting.

### 4.3 Plant Demography

O'Connor (1994) reported that *Aristida* species were able to maintain levels of seedling establishment (including both initial recruitment and subsequent seedling survival) under heavy grazing and drought which compensated for the mortality of established tussocks. Transition matrix modelling of population changes of *Aristida* supported this conclusion (O'Connor, 1993). A similar response was recorded for *Aristida ramosa* in Australia (Harradine and Whalley, 1980). However, if grazing is maintained during a sequence of moderate to very poor rainfall conditions there may be relatively small but cumulative changes in the species population dynamics: seedling recruitment can be curtailed and in turn losses to mortality can not be compensated (O'Connor, 1995).

Drought years coupled with domestic and native animal grazing may contribute to increased desirable perennial grass plant mortality, especially if grazing is severe (Scholes, 1985; O'Connor, 1991a; Cliffe and Hoffmann, 1999; Johnson and Hodgkinson, 1999). Unpalatable perennial grass species, which may have not been selectively grazed, may respond irruptively to similar conditions (O'Connor and Pickett, 1992; O'Connor, 1994). Desirable perennial grasses may take a long period to recover from a combination of dry seasons and consistent grazing pressure (Cliffe and Hoffmann, 1999). Despite drought can determine in itself high levels of plant mortality, Danckwerts and Stuart-Hill (1988) reported that the greatest negative impact on the abundance of *Themeda* species in the eastern Cape of Australia was associated

with the grazing history following rather than during a drought period.

It appears that life form and level of grazing may be important determinants of perennial grass plant response to drought and grazing. For example, *Digitaria* species may successfully reproduce by stoloniferous growth, thereby colonizing available space (O'Connor, 1991b), and have maintained positive population growth rates under grazing and drought (O'Connor, 1993). Increases in *Digitaria* during dry years, whereas it decreased in other studies in consecutive dry years (Denny *et al.*, 1977; Donaldson and Rootman, 1983), was possibly facilitated by the light grazing experienced (O'Connor, 1992) relative to the other species in the community. On the other hand, *Setaria* species, whose clonal growth form is more akin to a 'phalanx' type (Carter and O'Connor, 1991; Carter and Robinson, 1993) than the 'guerilla' type of *Digitaria* (sensu Lovett Doust, 1981), has not maintained basal cover during dry years and showed negative population growth rates especially under light grazing (O'Connor, 1993, 1994).

## 5. MANAGEMENT IMPLICATIONS

Heavy grazing under long-term, natural droughts has reduced contribution of palatable perennials within the community and depleted vegetational cover in many areas worldwide leading to the loss of fertile topsoil through wind erosion (Young, 1956; Breman and Cisse, 1977; O'Connor, 1995; Oelofse *et al.*, 1999). In comparison, grazing management following rather than during a drought has most altered grassland communities in semiarid regions (Danckwerts and Stuart-Hill, 1988). Also, when a high percentage of the grasses die because of severe grazing under water stress, weeds of low forage value can make rapid growth

(e.g., Young, 1956). Termites have been among the most destructive agents on many grazed areas during the latter part of drought periods (Young, 1956). In these areas, as severely grazed grasses die during the water stress period, termites can consume roots and parts of root crowns. Ranges subject to this destruction level recover slowly and it may take years of desirable management to restore them to their former productiveness.

Effects of grazing under drought can even be more deleterious to ecological system degradation if other intervening factors, such as fire, are added to the system. For example, after wildlife grazing under a severe drought, perennials were replaced by annual grasses and forbs at the Kruger National Park in South Africa (Oelofse *et al.*, 1999). Despite an increase in rainfall after the drought, the perennial grasses did not recover. The concomitant effects of grazing under drought conditions but also fire occurrence did not only cause this shift. Even though occurrence of desirable perennials has increased more quickly in pastures that started in fair or better conditions, restoration of a productive pasture can still take several years (Bishop *et al.*, 1999). Once perennial grasses are lost, seed banks are rarely adequate for re-vegetation even when grazing pressure is suspended (Oelofse *et al.*, 1999).

Perennial grasses are required to produce forage during drought periods, and dampen oscillations of herbivore biomass. The shift away from perennials results in a reduction in herbivore biomass as populations fail to recover between drought events (Oelofse *et al.*, 1999). Provision of water points during dry periods can reduce system stability and resilience as a result of a reduction in spatial heterogeneity (Noy-Meir, 1995), and the sustainability of the system is

subsequently also reduced (Owen-Smith, 1996).

Brushy ranges in hard land soil areas have supported more healthy grass plants than non-brushy areas during prolonged dry periods because of grass protection from grazing in the former (Young, 1956). This greater survival of grasses, however, does not argue for brush-infested ranges, since other undesirable conditions prevail on such areas. If heavily stocked, few woody plants can die in areas from which desirable grass species had been depleted through intense grazing prior to the drought. However, brush species can suffer heavy mortality in light stocked ranges because of the strong competition for available moisture offered by a high cover of deep-rooted grasses (e.g., Young, 1956).

In areas where severe summer droughts are not uncommon (e.g., eastern Australia), grazing pressure should be regulated before the end of the growing season to allow remnant stem material on plants going into summer, therefore reducing the tendency of plants to break dormancy in summer (Culvenor, 1997). Culvenor (1997) reported that *Phalaris aquatica* L. pastures having low summer dormancy showed a low tiller survival during a severe summer-autumn drought. Popular rotational grazing systems may not be beneficial in reducing mortality of important perennial C<sub>3</sub> grass species if they result in defoliation during drought in arid or semiarid rangelands (i.e., Johnson and Hodgkinson, 1999). Destocking early in drought is critical to the survival of the perennial grass component of those ecosystems (Chambers and Norton, 1993). Such a strategy may require reductions not only in livestock but also large native herbivores. Some authors have recommended tactical resting by agistment as an alternative grazing strategy during drought periods in

the semi-arid, wooded rangelands in Australia (e.g., Hacker and Hodgkinson, 1996; Hodgkinson *et al.*, 1999). Early-warning indicators of perennial grass decline have even been developed such that range managers could decide when rest periods should begin (Hodgkinson, 1993, 1996). Vegetation resting times should be coincident with periods when the species considered are actively growing or involved in activities crucial to the persistence of plants in a sward (i.e. flowering, seedling recruitment) (Westoby, 1980). Management should recognise that a reduction in grazing pressure during and after a severe drought event is required if undesirable vegetation changes for livestock production are to be avoided (Chambers and Norton, 1993). This is because of the negative influence of grazing on mortality of established tufts and on seedling recruitment.

A considerable challenge for the development of a predictive ability of community changes in grazed rangeland vegetation of arid and semiarid regions is to distinguish clearly the influences of rainfall from those of grazing or fire, and to determine if their interactive effects are greater than their summed individual effects on plant responses. Some state and transition models have been proposed which include plant community species composition under different pressures of herbivory, fire or drought (e.g., Llorens, 1995; Distel and Bóo, 1996; Oelofse *et al.*,

1999). However, plant species dynamics in the community should be explored more fully, investigating the interactive effects of drought and fire, with various levels of herbivory grazing. Also, the effects of rainfall may depend not only on the annual amount and its within-year distribution but also on the sequential pattern over years. A clearer understanding of the effects of grazing under water stress will, therefore, only be achieved within the context of long-term field experiments. The minimum length of study should cover the periodicity of climatic influences and, ideally, the plant life span. Failing this, an elaborate experimental procedure would be required to simulate extreme environmental events for both rainfall and grazing (O'Connor, 1994). A long term commitment to monitoring the effects of grazing under drought is necessary at a local, regional and state level to ensure that sites are monitored regularly and that the data collected are analysed and interpreted appropriately to provide ongoing information for responsible rangeland management and administration.

Finally, sustainability of pasture yields under drought can be improved by choosing resistant species yet capable of being productive. It is important to note that the differences between the capacities of various species to support livestock production can be most obvious under drought than under non-stress moisture conditions (Boschma and Scott, 2000).

## REFERENCES

- Allen, M.F. 1991. The ecology of mycorrhizae. Cambridge University Press, Cambridge. pp. 184.
- Allen, E.B. and M.F. Allen. 1986. Water relations of xeric grasses in the field: interactions of mycorrhizae and competition. *New Phytol.*, **104**: 559-571.
- Allen, M.F., J.H. Richards and C.A. Busso. 1989. Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semiarid tussock grasses. *Biol. Fert. Soils*, **8**: 285-289.
- Andersen, C. P. and P.T. Rygielwics. 1991. Stress interactions and mycorrhizal plant response: Understanding carbon allocation priorities. *Environ. Pollut.*, **73**: 217-244.

- Anderson, R.C. and A.E. Liberta. 1992. Influence of supplemental inorganic nutrients on growth, survivorship, and mycorrhizal relationships of *Schizachyrium scoparium* (Poaceae) grown in fumigated and unfumigated soil. *Am. J. Bot.*, **79**: 406-414.
- Archer, S. 1996. Assessing and interpreting grass-woody plant dynamics. In: *The Ecology and Management of Grazing* (eds. J. Hodgson and A.W. Illius), pp. 101-134. CAB International, Wallingford, UK. pp. 466.
- Archer, S. and J.K. Detling. 1986. Evaluation of potential herbivore mediation of plant water status in a North American mixed-grass prairie. *Oikos*, **47**: 287-291.
- Auge, R.M., A.J.W. Stodola, R.C. Ebel and X. Duan. 1995. Leaf elongation and water relations of mycorrhizal sorghum in response to partial soil drying: two *Glomus* species at varying phosphorus fertilization. *J. Exp. Bot.*, **46**: 297-307.
- Avery, A.L., D.L. Michalk, R.P. Thompson, P. Ball, T. Prance, C.A. Harris, D.W. FitzGerald, J.F. Ayres and B.A. Orchard. 2000. Effects of sheep grazing management on cocksfoot herbage mass and persistence in temperate environments. *Aust. J. Exp. Agric.*, **40**: 185-206.
- Banner, R.E. 1981. Economic analysis of long-term management strategies for two sizes of Utah cattle ranches. PhD Dissertation, Utah State University, Logan.
- Barker, D.J., A.C.P. Chu and C.J. Korte. 1985. Some effects of spring defoliation and drought on perennial ryegrass swards. *Proceedings of the New Zealand Grassland Association*, **46**: 57-63.
- Becker, G.F., C.A. Busso, T. Montani. 1997a. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: axillary bud viability and growth. *J. Arid. Environ.*, **35**: 233-250.
- Becker, G.F., C.A. Busso, T. Montani, A.L. Orchansky, R.E. Brevedan, M.A. Burgos and A.C. Flemmer. 1997b. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: tiller demography and growth. *J. Arid. Environ.*, **35**: 251-268.
- Becker, G.F., C.A. Busso, T. Montani, M.A. Burgos, A.C. Flemmer and M.B. Toribio. 1997c. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: root growth. *J. Arid Environ.*, **35**: 269-283.
- Biddiscombe, E.F., A.L. Rogers and R.A. Maller. 1977. Summer dormancy, regeneration and persistence of perennial grasses in South-Western Australia. *Aust. J. Exp. Agric. and Animal Husbandry*, **17**: 795-801.
- Biran, I., B. Bravdo, I. Bushkin-Harav and E. Rawitz. 1981. Water consumption and growth rate of 11 turfgrasses as affected by mowing height, irrigation frequency, and soil moisture. *Agron. J.*, **73**: 85-90.
- Bishop, H.G., T.B. Hilder, G.A. Lambert, R.M. Dodt and G. Bahnisch. 1999. Reclaiming and sustaining the productivity of Queensland bluegrass pastures. In: *Proc. Vith International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 239-240. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Blunt, C.G. and K.P. Haydock. 1978. Effect of irrigation, nitrogen and defoliation on pangola grass in the dry season at the Ord Valley, north-western Australia. *Aust. J. Exp. Agric. Animal Husbandry*, **18**: 825-833.
- Booyesen, P.V. and C.J. Nelson. 1975. Leaf area and carbohydrate reserves in re-growth of tall fescue. *Crop Sci.*, **15**: 262-266.
- Boschma, S.P. and J.M. Scott. 2000. Measuring and predicting the consequences of drought for a range of perennial grasses on the Northern Tablelands of New South Wales. *Aust. J. Exp. Agric.*, **40**: 285-297.
- Bowen, G.D. and S.E. Smith. 1981. The effects of mycorrhizas on nitrogen uptake by plants. *Ecological Bulletins*, **33**: 237-247.
- Box, T.W. 1967. Influence of drought and grazing on mortality of five West Texas grasses. *Ecology*, **48**: 654-656.
- Breman, H. and A.M. Cissé. 1977. Dynamics of sahelian pastures in relation to drought and grazing. *Oecologia*, **28**: 301-315.
- Briske, D.D. and J.H. Richards. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. In: *Wildland plants: Physiological Ecology and Developmental Morphology*

- (eds. D.J. Bedunah and R.E. Sosebee), pp. 635-710. Society for Range Management, Denver.
- Briske, D.D. and J.R. Hendrickson. 1998. Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic evaluation. *J. Veg. Sci.*, **9**: 611-622.
- Brougham, R.W. 1961. Some factors affecting the persistency of short-rotation ryegrass. *N. Z. J. Agr. Res.*, **4**: 516-522.
- Brown, R.W. 1977. Water relations of range plants. In: Rangeland Plant Physiology (ed. R.E. Sosebee), pp. 97-140. Society for Range Management, Denver.
- Brown, R.W. 1995. The water relations of range plants: adaptations to water deficits. In: *Wildland plants: Physiological ecology and developmental morphology* (eds. D.J. Bedunah and R.E. Sosebee), pp. 291-413. Society for Range Management, Denver.
- Bullock, J.M., B. Clear Hill and J. Silvertown. 1994. Tiller dynamics of two grasses - responses to grazing, density and weather. *J. Ecol.*, **82**: 331-340.
- Bunce, J.A. 1977. Leaf elongation in relation to leaf water potential in soybean. *J. Exp. Bot.*, **28**: 156-161.
- Busso, C. A. 1997. Towards an increased and sustainable production in semiarid rangelands of Central Argentina: Two decades of research. *J. Arid Environ.*, **36**: 197-210.
- Busso, C.A., R.J. Mueller and J.H. Richards. 1989. Effects of drought and defoliation on bud viability in two caespitose grasses. *Ann. Bot.*, **63**: 477-485.
- Busso, C.A. and J.H. Richards. 1989. Fenología y crecimiento en dos especies de gramíneas: Efectos del estrés hídrico. *Rev. Fac. Agron.*, **10**: 127-138.
- Busso, C.A. and J.H. Richards. 1992. Diurnal variation in the temperature response of leaf extension of two bunchgrass species in the field. *Plant Cell Environ.*, **15**: 855-859.
- Busso, C. A. and J. H. Richards. 1993. Leaf extension rate in two tussock grasses: Effects of water stress and clipping. *Acta Oecol.*, **14**: 3-15.
- Busso, C. A. and J. H. Richards. 1995. Drought and clipping effect on tiller demography and growth of two tussock grasses in Utah. *J. Arid Environ.*, **29**: 239-251.
- Busso, C. A., J. H. Richards and N. J. Chatterton. 1990. Nonstructural carbohydrates and spring re-growth of two cool-season grasses: Interaction of drought and clipping. *J. Range Manage.*, **43**: 336-343.
- Busso, C.A., R.M. Bóo and D.V. Peláez. 1993. Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. *Ann. Bot.*, **71**: 377-381.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak and R.S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia*, **50**: 14-24.
- Cano, E. 1988. Pastizales naturales de La Pampa. Descripción de las especies más importantes. Convenio AACREA-Pcia. de La Pampa. Buenos Aires. 425 pp.
- Carter, A.J. and T.G. O'Connor. 1991. Investigation of a two-phase mosaic in a savanna grassland. *J. Veg. Sci.*, **2**: 231-236.
- Carter, A.J. and E.R. Robinson. 1993. Genetic structure of a population of the clonal grass *Setaria incrassata*. *Biol. J. Linn. Soc.*, **48**: 55-62.
- Chambers, J.C. 1979. The effects of grazing on salt desert shrub species survival during a period of below-average precipitation. M.Sc. Thesis, Utah State University, Logan.
- Chambers, J.C. and B.E. Norton. 1993. Effects of grazing and drought on population dynamics of salt desert shrub species on the Desert Experimental Range. *Utah. J. Arid Environ.*, **24**: 261-275.
- Chamrad, A.D. and T.W. Box. 1965. Drought associated mortality of range grasses in *South Texas*. *Ecology*, **46**: 780-785.
- Chung, H.H. and M.J. Trlica. 1980. <sup>14</sup>C distribution and utilization in blue gramma as affected by temperature, water potential and defoliation regimes. *Oecologia*, **47**: 190-195.
- Cliffe, N.O. and M.B. Hoffmann. 1999. Monitoring grazing lands in Queensland to identify trends in range condition. In: *Proc. VIth International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 755-756. VI International Rangeland Congress, Inc. Townsville, Queensland.

- Collet, C., H. Frochot and J.M. Guehl. 1996. Growth dynamics and water uptake of two forest grasses differing in their growth strategy and potentially competing with forest seedlings. *Can. J. Bot.*, **74**: 1555-1561.
- Coughenour, M.B. 1984. A mechanistic simulation analysis of water use, leaf angles, and grazing in east African graminoids. *Ecol. Model.*, **26**: 203-220.
- Coughenour, M.B., S.J. McNaughton and L.L. Wallace. 1985a. Responses of an African tall-grass (*Hyparrhenia filipendula* Stapf) to defoliation and limitations of water and nitrogen. *Oecologia*, **68**: 80-86.
- Coughenour, M.B., S.J. McNaughton and L.L. Wallace. 1985b. Responses of an African graminoid (*Themeda triandra* Forsk.) to frequent defoliation, nitrogen, and water: a limit of adaptation to herbivory. *Oecologia*, **68**: 105-110.
- Crick, J.C. and J.P. Grime. 1987. Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *New Phytol.*, **107**: 403-414.
- Cruz, P. 1997. Effect of shade on the carbon and nitrogen allocation in a perennial tropical grass, *Dicanthium aristatum*. *J. Exp. Bot.*, **48**: 15-24.
- Culvenor, R.A. 1994. The persistence of five cultivars of phalaris after cutting during reproductive development in spring. *Aust. J. Agric. Res.*, **45**: 945-962.
- Culvenor, R.A. 1997. Observations on tillering in cultivars of phalaris under rotational grazing in a year with a summer-autumn drought. *Aust. J. Agric. Res.*, **48**: 467-476.
- Currie, P.O. and D.R. Smith. 1970. Response of seeded ranges to different grazing intensities in the Ponderosa pine zone of Colorado. *USDA Production Research Report* **112**.
- Currie, P.O. and R.S. White. 1982. Drought survival of selected forage grasses commonly seeded in the Northern Great Plains. *Can. J. Plant Sci.*, **62**: 949-955.
- Daer, T. and E.E. Willard. 1981. Total nonstructural carbohydrate trends in bluebunch wheatgrass related to growth and phenology. *J. Range Manage.*, **34**: 377-379.
- Danckwerts, J.E. and G.C. Stuart-Hill. 1988. The effect of severe drought and management after drought on the mortality and recovery of semi-arid grassveld. *Journal of the Grassland Society of southern Africa*, **5**: 218-222.
- Danckwerts, J.E. and L.O. Nel. 1989. The effect of frequency of defoliation on *Themeda triandra* in the False Thornveld of the eastern Cape. *Journal of the Grassland Society of southern Africa*, **6**: 32-36.
- Day, T.A. and J.K. Detling. 1994. Water relations of *Andropogon smithii* and *Bouteloua gracilis* and community evapotranspiration following long-term grazing by prairie dogs. *Am. Midl. Nat.*, **132**: 381-392.
- Denny, R.P., D.L. Barnes and T.C.D. Kennan. 1977. Trials of multipaddock grazing systems on veld. 1. An exploratory trial of systems involving 12 paddocks and one herd. *Rhodesian Journal of Agricultural Research*, **15**: 119-127.
- Detling, J.K. 1987. Grass response to herbivory. p. 56-68. In: J.L. Capinera (ed.). *Integrated pest management on rangeland: a shortgrass prairie perspective*. Westview Press, Boulder, Colorado.
- Detling, J.K., M.I. Dyier and D.T. Winn. 1979. Net photosynthesis, root respiration, and re-growth of *Bouteloua gracilis* following simulated grazing. *Oecologia*, **41**: 127-134.
- Devkota, N.R., P.D. Kemp and J. Hodgson. 1997. Screening pasture species for shade tolerance. *Proc. Agronomy Society of New Zealand*, **27**: 119-128.
- Distel, R.A. and Bóo, R.M. 1996. Vegetation States and Transitions in Temperate Semiarid Rangelands of Argentina. In: *Proc. Vth International Rangeland Congress. Rangelands in a Sustainable Biosphere* (ed. N.E. West), pp. 117-118. Society for Range Management. Denver.
- Distel, R.A. and O.A. Fernández. 1986. Productivity of *Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack in semi-arid Argentina. *J. Arid. Environ.*, **11**: 93-96.
- Distel, R.A. and O.A. Fernández. 1988. Dynamics of root growth and decay in two grasses native to semi-arid Argentina. *Aust. J. Ecol.*, **13**: 327-336.
- Donkor, N.T., E.W. Bork and R.J. Hudson. 1999. Defoliation effects on *Bromus-Poa* pasture production in Alberta. In: *Proc. VIth International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 530-531. VI International Rangeland Congress,

- Inc. Townsville, Queensland.
- Donaldson, C.H. and G.T. Rootman. 1983. In: Continuous grazing and fixed seasonal rotational grazing systems. *Final Report T5411/41/1/1*. Department of Agricultural and Technical Services. Pretoria.
- Dube, S. 1999. Effects of moisture and defoliation regime on performance of grass in semiarid rangelands. In: *Proc. Vith International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 273. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Ehleringer, J.A. and H.A. Mooney. 1983. Productivity of Desert and Mediterranean- climate Plants. In: *Physiological Plant Ecology II. Ecosystem processes: Mineral cycling, productivity and man's influence* (eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler), pp. 205-231. Springer-Verlag. Berlin. 644 pp.
- Fahnestock, J.T. and J.K. Detling. 2000. Morphological and physiological responses of perennial grasses to long-term grazing in the Pryor Mountains, Montana. *Am. Midl. Nat.*, **143**: 312-320.
- Fahnestock, J.T. and A.K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective herbivory by bison. *Int. J. Plant Sci.*, **154**: 432-440.
- Fahnestock, J.T. and A.K. Knapp. 1994. Plant responses to selective grazing by bison: interactions between light, herbivory and water stress. *Vegetatio*, **115**: 123-131.
- Fernández, O. A. and C. A. Busso. 1999. Arid and semi-arid rangelands: two thirds of Argentina. In: *Case Studies of Rangeland Desertification* (eds. O. Arnalds and S. Archer), p. 41-60. *Agricultural Research Institute Report Nro. 200*. Reykjavik, Iceland.
- Fernández, O.A. and M.M. Caldwell. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.*, **63**: 703-714.
- Flemmer, A.C. 2000. Influencia simultánea del estrés hídrico y la defoliación en distintos momentos del desarrollo de *Stipa clarazii* y *S. tenuis* en competencia con *Stipa gynerioides*. M.Sc. Thesis, Departamento de Agronomía, Universidad Nacional del Sur. Bahía Blanca, Argentina. 115p.
- Flemmer, A.C., C.A. Busso and O.A. Fernández. Bud viability in perennial grasses: Water stress and defoliation effects. *J. Range Manage.*, (manuscript# 00.88, in press).
- Flemmer, A.C., C.A. Busso, T. Montani, O.A. Fernández, C. Saint Pierre and M.L. García. 1999. Growth of *Stipa gynerioides* in competition with defoliated or undefoliated desirable perennial grasses under different levels of soil water availability. In: *Proc. Vith International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 248-249. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Francis, R.D. and D.J. Read. 1995. Mutualism and antagonism in the mycorrhizal symbiosis with special reference to impacts upon plant community structure. *Can. J. Bot.*, **73**: 1301-1309.
- Fulkerson, W.J. and K. Slack. 1995. Leaf number as a criterion for determining defoliation time for *Lolium perenne*: 2. Effect of defoliation frequency and height. *Grass Forage Sci.*, **50**: 16-20.
- Ganskopp, D.C. and T.E. Bedell. 1981. An assessment of vigor and production of range grasses following drought. *J. Range Manage.*, **34**: 137-141.
- Garwood, E.A. and T.E. Williams. 1967. Growth, water use and nutrient uptake from the subsoil by grass swards. *J. Agr. Sci.*, **69**: 125-130.
- Georgiadis, N.J., R.W. Ruess, S.J. McNaughton and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia*, **81**: 316-322.
- Giorgetti, H., O.A. Montenegro, G. Rodríguez, C. A. Busso, T. Montani, M.A. Burgos, A. C. Flemmer, M.B. Toribio y S.S.Horvitz. 1997. The comparative influence of past management and rainfall on range herbaceous standing crop in east-central Argentina: 14 years of observations. *J. Arid Environ.*, **36**: 623-637.
- Hacker, R.B. and K.C. Hodgkinson. 1996. Implementation of tactical grazing in whole property management. In: *Proc. Vth International Rangeland Congress. Rangelands in a Sustainable Biosphere* (ed. N.E. West), pp. 197-198. Society for Range Management. Denver.
- Harradine, A.R. and R.D.B. Whalley. 1980. Reproductive development and seedling establishment of R. Br. in northern NSW. *Australian Rangeland Journal*, **2**: 124-135.
- Heckarhorn, S.A. and E.H. Delucia. 1996. Retranslocation of shoot nitrogen to rhizomes and roots in prairie grasses may limit loss of N to grazing and fire during drought. *Funct. Ecol.*, **10**: 396-400.

- Heckarhorn, S.A. and E.H. Delucia. 1995. Ammonia volatilization during drought in perennial C<sub>4</sub> grasses of tallgrass prairie. *Oecologia*, **101**: 361-365.
- Heitschmidt, R.K., E.E. Grings, M.R. Haferkamp and M.G. Karl. 1995. Herbage dynamics on 2 Northern Great Plains range sites. *J. Range Manage.*, **48**: 211-217.
- Heitschmidt, R.K., M.R. Haferkamp, M.G. Karl and A.L. Hild. 1999. Drought and grazing: I Effects on quantity of forage produced. *J. Range Manage.*, **52**: 440-446.
- Hendrickson, J.R. and D.D. Briske. 1997. Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. *Oecologia*, **110**: 584-591.
- Hendon, B.C. and D.D. Briske. 1997. Demographic evaluation of a herbivory-sensitive perennial bunchgrass: does it possess an Achilles heel?. *Oikos*, **80**: 8-17.
- Herbal, C.H., F.N. Ares and R.A. Wright. 1972. Drought effects on a semidesert grassland range. *Ecology*, **53**: 1084-1093.
- Hetrick, B.A.D., G.W.T. Wilson and C.E. Owensby. 1990. Mycorrhizal influences on big bluestem rhizome re-growth and clipping tolerance. *J. Range Manage.*, **43**: 286-290.
- Hild, A.L., M.G. Karl, M.R. Haferkamp and R.K. Heithschmidt. 2001. Drought and grazing III: root dynamics and germinable seed bank. *J. Range Manage.*, **54**: 292-298.
- Hodgkinson, K.C. 1976. The effects of frequency and extent of defoliation, summer irrigation, and fertilizer on the production and survival of the grass *Danthonia caespitose* Gaud. *Aust. J. Agr. Res.*, **27**: 755-767.
- Hodgkinson, K.C. 1993. Identification of critical thresholds for opportunistic management of rangeland vegetation. In: *Proc. IVth International Rangeland Congress*, pp. 127-129. Montpellier. France.
- Hodgkinson, K.C. 1996. A model for perennial grass mortality under grazing. In: *Proc. Vth International Rangeland Congress. Rangelands in a Sustainable Biosphere* (ed. N.E. West), pp. 240-241. Society for Range Management. Denver.
- Hodgkinson, K.C., S.G. Marsden and R.B. Hacker. 1999. Simulation of grazing strategies for eastern Australian wooded rangelands. In: *Proc. VIth International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 866-868. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Holmgren, R.C. and S.S. Hutchings. 1972. Salt desert shrub response to grazing use. In: *Wildland shrubs. Their biology and utilization* (eds. C.M. McKell, J.P. Blaisdell and J.R. Goodin), pp. 153-164. USDA-Forest Service Tech. Report INT-1. Intermountain Forest and Range Experiment Station. Ogden, Utah.
- Hutchings, S.S. and G. Stewart. 1953. Increasing forage yields and sheep production on Intermountain winter ranges. *USDA Circ.* **925**.
- Hyder, D.N. and F.A. Sneva. 1963. Morphological and physiological factors affecting the grazing management of crested wheatgrass pastures during May and June, Fort Rock, Oregon. *J. Range Manage.*, **22**: 227-280.
- Jacobs, J.S. and R.L. Sheley. 1997. Relationships among Idaho fescue defoliation, soil water, and spotted knapweed emergence and growth. *J. Range Manage.*, **50**: 258-262.
- Jacobson, K.M. 1997. Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in arid grassland. *J. Arid Environ.*, **35**: 59-75.
- Jatimliansky, J.R., D.O. Gimenez and A. Bujan. 1997. Herbage yield, tiller number and root system activity after defoliation of prairie grass (*Bromus catharticus* Vahl). *Grass Forage Sci.*, **52**: 52-62.
- Jennane, A., P. Landré and A. Nougarede. 1987. Water content and physiological state of the cotyledonary bud of the pea. *J. Plant Physiol.*, **127**: 493-498.
- Jesko, T., J. Navara and K. Dekankova. 1997. Root growth and water uptake by flowering maize plants, under drought conditions. pp. 270-271. In: A. Altman and Y. Waisel (eds.). *Biology of Root Formation. Proc. 2<sup>nd</sup> International Symposium on Biology of Root Formation and Development*. 23-28 June 1996. Jerusalem, Israel. Plenum Press. New York, N.Y.
- Jewiss, O.R. 1972. Tillering in grasses – its significance and control. *Journal of the British Grassland Society*, **27**: 65-82.
- Johnson, P.S. and K.C. Hodgkinson. 1999. Tactical grazing for perennial grass survival – an Australia

- vs. USA comparison. In: *Proc. Vith International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 474-476. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Kanneganti, V.R. and S.R. Kaffka. 1995. Forage availability from a temperate pasture managed with intensive rotational grazing. *Grass Forage Sci.*, **50**: 55-62.
- Kemp, D.R. and R.A. Culvenor. 1994. Improving the grazing and drought tolerance of temperate perennial grasses. *N. Z. J. Agr. Res.*, **37**: 365-378.
- Kigel, J. 1980. Analysis of re-growth patterns and carbohydrate levels in *Lolium multiflorum* Lam. *Ann. Bot.*, **45**: 91-101.
- Kigel, J. and A. Dotan. 1982. Effect of different durations of water withholding on re-growth potential and non-structural carbohydrate content in rhodes grass (*Chloris gayana* Kunth). *Aust. J. Plant Physiol.*, **9**: 113-120.
- Knapp, A.K. 1984. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. *Oecologia*, **65**: 35-43.
- Kothari, S.K., H. Marschner and E. George. 1990. Effect of VA mycorrhizal fungi and rhizosphere microorganisms on root and shoot morphology, growth and water relations in maize. *New Phytol.*, **116**: 303-311.
- LLorens, E.M. 1995. Viewpoint: The state and transition model applied to the herbaceous layer of Argentina's calden forest. *J. Range Manage.*, **48**: 442-447.
- Lorenzetti, F., A. Panella and E. Falistocco. 1981. Summer dormancy in Italian populations of *Dactylis glomerata* L. In: Smith J.A. and Hays V.W. (eds.) *Proceedings of the 14<sup>th</sup> International Grassland Congress, Lexington, Kentucky, USA*. pp. 247-250.
- Lovett Doust, L. 1981. Population dynamics and local specialisation in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *J. Ecol.*, **69**: 743-755.
- Ludlow, M.M. 1986. Simultaneous pressure of water stress and defoliation in rangeland plants. In: *Rangelands: A resource under siege* (eds. P.J. Joss, P.W. Lynch and O.B. Williams), pp. 433-436. Cambridge Univ. Press. Cambridge.
- Ludlow, M.M. and T.T. Ng. 1976. Effect of water deficit on carbon dioxide exchange and leaf elongation rate of *Panicum maximum* var. *trichoglume*. *Aust. J. Plant Physiol.*, **3**: 401-413.
- MacMahon, J.A. and D.J. Schimpf. 1981. Water as a factor in the biology of North American desert plants. In: *Water in desert ecosystems* (eds. D.D. Evans and J.L. Thames), pp. 114-171. Hutchinson and Ross. Stroudsburg.
- Marschner, H. and B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant Soil*, **159**: 89-102.
- Maschinski, J. and T.G. Whitman. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *Am. Nat.*, **134**: 1-19.
- Masters, R.A. and C.M. Britton. 1990. Ermelo weeping lovegrass response to clipping, fertilization, and watering. *J. Range Manage.*, **43**: 461-465.
- McIntyre, G.I. 1976. Apical dominance in the rhizome of *Agropyron repens*: the influence of water stress on bud activity. *Can. J. Bot.*, **54**: 2747-2754.
- McLean, A. and A.L. Van Ryswyk. 1973. Mortality in crested wheatgrass and russian wildrye. *J. Range Manage.*, **26**: 431-433.
- McNaughton, S.J. 1979a. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.*, **113**: 691-703.
- McNaughton, S.J. 1979b. Grassland-herbivore dynamics. Pp. 46-81. In: A.R.E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: studies of ecosystem dynamics in a tropical savanna*. University of Chicago Press, Chicago, Illinois, USA.
- McNaughton, S.J. 1983a. Compensatory plant growth as a response to herbivory. *Oikos*, **40**: 329-336.
- McNaughton, S.J. 1983b. Physiological and ecological implications of herbivory. In: Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H. (eds.) *Physiological Plant Ecology III*. pp. 657-677. Springer-Verlag, New York.
- McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.*, **55**: 259-294.
- McNaughton, S.J., L.L. Wallace and M.B. Coughenour. 1983. Plant adaptation in an ecosystem context:

- effects of defoliation, nitrogen, and water on growth on an african C4 sedge. *Ecology*, **64**: 307-318.
- Menke, J.W. and M.J. Trlica. 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. *J. Range Manage.*, **34**: 269-277.
- Miller, M.H. 2000. Arbuscular mycorrhizae and the phosphorus nutrition of maize: A review of Guelph studies. *Can. J. Plant Sci.*, **80**: 47-52.
- Miller, R.F., Haferkamp, M.R. and Angell, R.F. 1990. Clipping date effects on soil and re-growth in crested wheatgrass. *J. Range Manage.*, **43**: 252-259.
- Misra, G. and K.P. Singh. 1982. Effect of soil moisture and clipping stresses on the nutrient (N, P and K) concentration, uptake and use efficiency in one temperate and two tropical grasses. *Plant Soil*, **69**: 413-421.
- Mitchell, K.J. 1953. Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). II. The control of lateral bud development. *Physiol. Plant.*, **6**: 425-443.
- Mohammad, N. 1979. Effects of water stress on crested wheatgrass and russian wildrye at different levels of defoliation. M.Sc. Thesis, Utah State University, Logan.
- Mohammad, N., D.D. Dwyer and F.E. Busby. 1982. Responses of crested wheatgrass and russian wildrye to water stress and defoliation. *J. Range Manage.*, **35**: 227-230.
- Mohammad, M.J., W.L. Pan and A.C. Kennedy. 1998. Seasonal mycorrhizal colonization of winter wheat and its effect on wheat growth under dryland field conditions. *Mycorrhiza*, **8**: 139-144.
- Moretto, A.S. and R.A. Distel. 1997. Competitive interactions between palatable and unpalatable grasses native to temperate semi-arid grassland of Argentina. *Plant Ecology*, **130**: 155-161.
- Moretto, A.S. and R.A. Distel. 1999. Effects of selective defoliation on the competitive interaction between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *J. Arid Environ.*, **42**: 167-175.
- Mueller, R.J. and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. *Ann. Bot.*, **58**: 911-921.
- Murphy, J.S. and D.D. Briske. 1992. Regulation of tillering by apical dominance: Chronology, interpretive value, and current perspectives. *J. Range Manage.*, **45**: 419-429.
- Neter, J., W. Wasserman and M.H. Kutner. 1985. Applied linear statistical models: regression, analysis of variance, and experimental designs. RD Irwin, Homewood Illinois.
- Noy-Meir, I. 1995. The spatial dimensions of plant-herbivore interactions. In: *Proc. Vth International Rangeland Congress. Rangelands in a Sustainable Biosphere* (ed. N.E. West), pp. 152-154. Society for Range Management. Denver.
- Nus, J.L. and C.F. Hodges. 1986. Differential sensitivity of turfgrass organs to water stress. *Hortscience*, **21**: 1014-1015.
- O'Connor, T.G. 1991a. Local extinction in perennial grasslands: a life history approach. *Amer. Nat.*, **137**: 753-773.
- O'Connor, T.G. 1991b. Patch colonisation in a savanna grassland. *J. Veg. Sci.*, **2**: 245-254.
- O'Connor, T.G. 1992. Patterns of plant selection by grazing cattle in two savanna grasslands: a plant's eye view. *Journal of the Grassland Society of southern Africa*, **9**: 97-104.
- O'Connor, T.G. 1993. The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. *J. Appl. Ecol.*, **30**: 119-132.
- O'Connor, T.G. 1994. Composition and population responses of African savanna grassland to rainfall and grazing. *J. Appl. Ecol.*, **31**: 155-171.
- O'Connor, T.G. 1995. Transformation of a savanna grassland by drought and grazing. *Afr. J. Range For. Sci.*, **12**: 53-60.
- O'Connor, T.G. and G.A. Pickett. 1992. The influence of grazing on seed production and seed banks of some African savanna grasslands. *J. Appl. Ecol.*, **29**: 247-260.
- O'Connor, T.G. and P.W. Roux. 1995. Vegetation changes (1947-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *J. Appl. Ecol.*, **32**: 612-626.
- Oelofse, J., B.H. Brockett, H.C. Biggs and C. Ebersohn. 1999. The effect of drought and post-fire grazing

- on the herbaceous layer of shrub-mopane veld on basalt in the Kruger National Park, South Africa. In: *Proc. VIth International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 505-507. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Oosterheld, M. and S.J. McNaughton. 1991. Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia*, **85**: 305-313.
- Olmsted, C.E. 1941. Growth and development in range grasses. I. Early development of *Bouteloua curtipendula* in relation to water supply. *Bot. Gaz.*, **102**: 499-519.
- Olson, B.E. and J.H. Richards. 1988. Tussock re-growth after grazing: intercalary meristem and axillary bud activity of tillers of *Agropyron desertorum*. *Oikos*, **51**: 374-382.
- Onillon, B., J.L. Durand, F. Gastal and R. Tournebize. 1995. Drought effects on growth and carbon partitioning in a tall fescue sward grown at different rates of nitrogen fertilization. *European Journal of Agronomy*, **4**: 91-99.
- Oosthuizen, I.B. and H.A. Snyman. 1999. The influence of water stress on the growth reserves of *Themeda triandra* Forssk. in the semi-arid grasslands of South Africa. In: *Proc. VIth International Rangeland Congress. People and Rangelands Building the Future* (eds. D. Eldridge and D. Freudenberger), pp. 209. VI International Rangeland Congress, Inc. Townsville, Queensland.
- Ourry, A., J. Bigot and J. Boucaud. 1989. Protein mobilization from stubble an roots, and proteolytic activities during post-clipping re-growth of perennial ryegrass. *J. Plant Physiol.*, **134**: 298-303.
- Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, **26**: 107-112.
- Paulsen, H.A. and F.N. Ares. 1961. Trends in carrying capacity and vegetation on arid southwestern range. *J. Range Manage.*, **14**: 78-83.
- Phillips, J.M. and D.S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Br. Mycol. Soc.*, **55**: 158-162.
- Richards, J.H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia*, **64**: 21-25.
- Richards, J.H. and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in re-growth following defoliation: A field study with *Agropyron* species. *J. Appl. Ecol.*, **22**: 907-920.
- Richards, J.H., R.J. Mueller and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. *Ann. Bot.*, **62**: 173-179.
- Saint Pierre, C., C.A. Busso, O.A. Montenegro, G.D. Rodríguez, H.D. Giorgetti and T. Montani. 2000a. Producción de materia seca en especies de gramíneas perennes nativas del centro de Argentina. *Actas de la XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal*. 28-31 de Marzo, Montevideo (Uruguay). Available in CD-ROM.
- Saint Pierre, C., C.A. Busso, O.A. Montenegro, G.D. Rodríguez, H.D. Giorgetti and T. Montani. 2000b. Demografía y crecimiento en especies de gramíneas nativas del Sur de la Provincia Fitogeográfica del Monte. *Actas de la XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal*. 28-31 de Marzo, Montevideo (Uruguay). Available in CD-ROM.
- Sanderson, M.A., D.W. Stair and M.A. Hussey. 1997. Physiological and morphological responses of perennial forages to stress. *Adv. Agron.*, **59**: 171-224.
- Scholes, R.J. 1985. Drought related grass, tree and herbivore mortality in a southern African savanna. In: *Ecology and Management of the World's Savannas* (eds. J.C. Tothill and J.J. Mott), pp. 350-353. Australian Academy of Science. Canberra.
- Shulte, P.J. and T.M. Hinckley. 1985. A comparison of pressure-volume curve data analysis techniques. *J. Exp. Bot.*, **36**: 1590-1602.
- Sims, P.L. and J.S. Singh. 1978. The structure and function of ten western North American grasslands. II. Intra-seasonal dynamics in primary producer components. *J. Ecol.*, **66**: 547-572.
- Simoes, M. And Z. Baruch. 1991. Responses to simulated herbivory and water stress in two tropical C<sub>4</sub> grasses. *Oecologia*, **88**: 173-180.
- Skarpe, C. 1986. Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Vegetatio*, **68**: 3-18.

- Smeins, F.E., T.W. Taylor and L.B. Merrill. 1976. Vegetation of a 25-year enclosure of the Edwards Plateau, Texas. *J. Range Manage.*, **29**: 24-29.
- Snakary, M.N., H.M. Laude, M. Lover and R.E. Fox. 1969. Variation in summer dormancy among collections of *Phalaris tuberosa* at Davis, California. *J. of British Grass. Soc.*, **24**: 134-137.
- Snyman, H.A. 1999. Short-term effects of soil water, defoliation and rangeland condition on productivity of a semi-arid rangeland in South Africa. *J. Arid Environ.*, **43**: 47-62.
- Stafford Smith, D.M. and G.M. McKeon. 1998. Assessing the historical frequency of drought events on grazing properties in Australian rangelands. *Agr. Syst.*, **57**: 271-299.
- Steel, R.G. and J.H. Torrie. 1981. Principles and procedures of statistics. McGraw-Hill Company, USA.
- Stout, D.G., J. Hall, B. Brooke and A. McLean. 1981. Influence of successive years of simulated grazing (clipping) on pinegrass growth. *Can. J. Plant Sci.*, **61**: 939-943.
- Stout, D.G., A. McLean, B. Brooke and J. Hall. 1980. Influence of simulated grazing (clipping) on pinegrass growth. *J. Range Manage.*, **33**: 286-291.
- Stoddart, L.A., A.D. Smith and T.W. Box. 1975. *Range Management*. McGraw-Hill. New York. 532 pp.
- Tennant, D. 1975. A test of a modified line intersect method of estimating root length. *J. Ecol.*, **63**: 955-1001.
- Trlica, M.J. and C.W. Cook. 1972. Carbohydrate reserves of crested wheatgrass and russian wildrye as influenced by development and defoliation. *J. Range Manage.*, **25**: 430-435.
- Turner, N.C. 1986. Adaptation to water deficits: A changing perspective. *Aust. J. Plant Physiol.*, **13**: 175-190.
- Turner, N.C. 1987. The use of the pressure chamber in studies of plant water status. In: *Proc. of International Conference on Measurements of Soil and Plant Water Status*, pp. 13-24. Utah State University, Logan, Utah, USA.
- Turner, N.C. and J.E. Begg. 1978. Responses of pasture plants to water deficits. In: *Plant Relations in pastures* (ed. J.R. Wilson), pp. 50-66. CSIRO, Melbourne.
- Varnamkhasti, A.S., D.G. Milchunas, W.K. Lauenroth and H. Goetz. 1995. Production and rain use efficiency in short-grass steppe: grazing history, defoliation and water resource. *J. Veg. Sci.*, **6**: 787-796.
- Virgona, J.M. and A. Bowcher. 2000. Effects of grazing interval on basal cover of four perennial grasses in a summer-dry environment. *Aust. J. Exp. Agric.*, **40**: 299-311.
- Volaire, F. 1994. Effects of summer drought and spring defoliation on carbohydrate reserves, persistence and recovery of two populations of cocksfoot (*Dactylis glomerata*) in a Mediterranean environment. *J. Agric. Sci.*, **122**: 207-215.
- Volaire, F. 1995. Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a mediterranean environment. *J. Appl. Ecol.*, **32**: 56-66.
- Volaire, F. and J.M. Gandoin. 1996. The effect of age of the sward on the relationship between water-soluble carbohydrate accumulation and drought survival in two contrasted populations of cocksfoot (*Dactylis glomerata* L.). *Grass Forage Sci.*, **51**: 190-198.
- Volaire, F. and H. Thomas. 1995. Effects of drought on water relations, mineral uptake, water-soluble carbohydrate accumulation and survival of two contrasting populations of cocksfoot (*Dactylis glomerata* L.). *Ann. Bot.*, **75**: 513-524.
- Wagner, F.H. 1976. Integrating and control mechanisms in arid and semi-arid ecosystems: considerations for impact assessment. In: *Proc. Symposium on Biological Evaluation of Environmental Impact. 27th Annual AIBS Meeting, New Orleans*. Council on Environmental Quality, Washington, D.C.
- Waring, R.H. and B.D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. *Science*, **155**: 1248-1254.
- Weaver, J.E. and T.J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of tall-grass prairie. *Bot. Gaz.*, **93**: 113-150.
- Weaver, J.E. and F.W. Albertson. 1936. Effects of the great drought on the prairies of Iowa, Nebraska and Kansas. *Ecology*, **17**: 567-639.
- Westoby, M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. *Isr. J. Bot.*, **28**: 169-194.

- Westoby, M., B. Walker and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *J. Range Manage.*, **42**: 266-274.
- White, D.H., S.M. Howden, J.J. Walcott and R.M. Cannon. 1998. A framework for estimating the extent and severity of drought, based on a grazing system in South-eastern Australia. *Agr. Syst.*, **57**: 259-270.
- Whitman, W.C. 1971. Influence of grazing on the microclimate of mixed-grass prairie. In: Kreitlow, K.M. and Hart, R.H. (eds.). *Plant morphogenesis as the basis for scientific management of range resources*. USDA Misc. Publ. No. 1271. Pp. 207-218.
- Wilhite, D.A. 1986. Drought policy in the U.S. and Australia: A comparative analysis. *Water Resour. Bull.*, **22**: 425-438.
- Williamson, S.C., J.K. Detling, J.L. Dodd and M.I. Dyer. 1989. Experimental evaluation of the grazing optimization hypothesis. *J. Range Manage.*, **42**: 149-152.
- Wright, R.G. and G.M. van Dyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southwest Nat.*, **21**: 259-274.
- Young, V.A. 1956. The effect of the 1949-1954 drought on the ranges of Texas. *J. Range Manage.*, **9**: 139-142.
- Zhang, J. and J.T. Romo. 1994. Defoliation of a northern wheatgrass community: above- and belowground phytomass productivity. *J. Range Manage.*, **47**: 279-284.