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Morphological traits which contribute to the long-term persistence of *Pappophorum vaginatum* in rangelands of Argentina

Características morfológicas que contribuyen a la persistencia a largo plazo de Pappophorum vaginatum en los pastizales naturales de Argentina

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ABSTRACT

Pappophorum vaginatum is the most abundant C₄ perennial grass desirable (i.e., preferred) to livestock in rangelands of northeastern Patagonia, Argentina. Other less abundant, native perennial grasses in the community are *Aristida spegazzinii* and *A. subulata*, and the desirable *Sporobolus cryptandrus*. *Aristida spegazzinii* and *A. subulata* are only grazed when a better forage is not available. The objective of this study was to determine various above- and belowground morphological traits that might help to explain the greater abundance of *P. vaginatum* in relation to the other species, in a community where *P. vaginatum* is the only perennial grass available for livestock grazing since decades ago. Plants of all species were either exposed or not exposed to a severe defoliation twice a year during two growing seasons (i.e., 2007-2008 and 2008-2009). These growing seasons had 42 % (2007-2008) and 30 % (2008-2009) lower precipitation than the annual mean precipitation (i.e., 416.7 mm). This was a desirable water stress to know the response of both species to extreme water levels under field conditions. Plant developmental morphology stages were delayed, on all studied perennial grasses, more in the drier (2008-2009) than in the wetter (2007-2008) study year. Defoliation did reduce the studied morphological characteristics after plants of all species were defoliated twice in 2007-2008 and 2008-2009. The higher values of most of the components of leaf area production in *P. vaginatum* than in the other species in the study could help to explain its higher abundance in the rangelands of Argentina. Knowledge of the mechanisms involved in grazing tolerance of *P. vaginatum* will be useful to:

(1) increasing its grazing tolerance through a genetic improvement plan, and (2) implementing management guidelines that increase its plant production under grazing conditions.

RESUMEN

Pappophorum vaginatum es la gramínea perenne C_4 deseable (preferida) más abundante para el pastoreo por el ganado doméstico en los pastizales naturales del noreste de la Patagonia, Argentina. Otras gramíneas perennes nativas, menos abundantes en la comunidad, son *Aristida spegazzinii* y *A. subulata*, y la deseable *Sporobolus cryptandrus*. *Aristida spegazzinii* y *A. subulata* son solo pastoreadas cuando no hay disponibilidad de un forraje mejor. El objetivo de este estudio fue determinar varias características morfológicas aéreas y subterráneas que podrían ayudar a explicar la mayor abundancia de *P. vaginatum* con respecto a otras especies, en una comunidad donde *P. vaginatum* es la única gramínea perenne preferida por el ganado (disponible para el pastoreo), desde hace varias décadas. Las plantas de todas las especies fueron expuestas o no, dos veces en el año, a una severa defoliación durante dos temporadas de crecimiento (i.e., 2007-2008 y 2008-2009). Estas estaciones de crecimiento tuvieron precipitaciones que fueron un 42 % (2007-2008) y un 30 % (2008-2009) menores que el promedio de precipitación a largo plazo (416.7 mm). Esto determinó un estrés hídrico deseable para conocer la respuesta de ambas especies a niveles extremos de agua bajo condiciones de campo. Los estadios fenológicos fueron más demorados en todas las gramíneas perennes estudiadas en la estación de crecimiento más seca (2008-2009) que en la más húmeda (2007-2008). Las características morfológicas estudiadas fueron reducidas después de que las plantas de todas las especies fueron defoliadas dos veces en 2007/2008 y 2008/2009. Los valores más altos de la mayoría de los componentes de la producción de área foliar en *P. vaginatum* que en las otras especies estudiadas podrían ayudar a explicar su mayor abundancia en las áreas de vegetación natural en el centro de Argentina. El conocimiento de los mecanismos implicados en la tolerancia al pastoreo de *P. vaginatum* serán útiles para: (1) incrementar su tolerancia al pastoreo mediante planes de mejoramiento genético, y (2) implementar guías de manejo que incrementen su producción vegetal bajo condiciones de pastoreo.

Keywords: *Pappophorum vaginatum*, warm season grasses, defoliation, genetic improvement

Palabras clave: *Pappophorum vaginatum*, gramíneas de estación cálida, defoliación, mejora genética

INTRODUCTION

The cattle production industry in 75 % of continental Argentina, characterized by arid and semi-arid areas, is based on grazing of native vegetation (Busso & Fernández, 2018). Unfortunately, most of these areas have been exposed to overgrazing, and fire mismanagement, resulting in shrub encroachment and the local disappearance of acceptable, palatable (desirable) perennial forage grasses

for cattle grazing (Fernandez & Busso, 2018). As a result, rangelands of central Argentina have almost a unique warm-season, native perennial grass that is an acceptable forage to grazing livestock (*Pappophorum vaginatum*, Busso et al., 2004). It is imperative to increase desirable perennial grass species in this region (Anderson, 1980) to address the need for additional forage and subsequent increase in cattle production. Bleak et al. (1966) emphasized that appropriate

management of native vegetation would be the best approach to achieve a good plant cover of forage that is acceptable to grazing livestock in those rangelands. Severe water stress, especially during the warm season, is another constraint the vegetation might be exposed to in rangelands of central Argentina (Giorgetti et al., 1997).

In addition to *P. vaginatum*, other native, warm-season, less abundant, perennial grass species in this region are *Aristida spgazzinii*, *A. subulata*, and *Sporobolus cryptandrus* (Giorgetti et al., 2000a). This last species is a palatable perennial bunchgrass, but it is not only of lower abundance but also of low vigor. The *Aristida* species are less palatable and only eaten if a better forage is not available (Giorgetti et al., 1997). As a result, their basal area keeps expanding in these less grazed tussock perennial grasses. This results in more new shoot biomass production than that in the more palatable grazed *P. vaginatum* (Flemmer et al., 2003). *Pappophorum vaginatum* has resisted continuous grazing for decades, and its abundance in these rangelands is even greater than that of other less preferred perennial grasses (*Aristida* species, Giorgetti et al., 2000c). This suggests an important tolerance to defoliation or competitive ability in this species.

Several studies have been made on the morpho-physiology, demography, plant growth and responses to grazing in *P. vaginatum* (Torres et al., 2011, 2014). However, it is not yet clear which are the mechanisms responsible for its long-term persistence. Rapid reestablishment of a photosynthetic canopy is a distinctive feature of the perennial grasses tolerant to defoliation (Caldwell et al., 1981).

The number of leaves and tiller height are between the growth components that contribute most to photosynthetic canopy reestablishment (Becker et al., 1997b). A high capacity for new tiller formation of rapid growth after forage removal will allow plants to reestablish the photosynthetic tissue lost to herbivores, rapidly recuperate the root-shoot balance, obtain a greater share of soil available resources, and maintain their competitive ability within the plant community (Busso & Richards, 1995). If defoliation has negative effects on one or more of these growth components, plant recuperation to such event can result limited (Busso & Richards, 1995). In general, it has been proposed that the mechanisms of plant response to defoliation will also be affected by suboptimal environmental conditions (Langer, 1963), including drought (Busso et al., 2003).

Tillering in communities of grasses exposed to defoliation is important for its survival. Even more, the exchange rates in tiller density and its weight are important components in the production of dry matter (Wade, 1982). Daughter tiller production not only increases tiller density on plants but also contribute to increase the plant bud bank and immediate carbon gain because they are photosynthetically active at the time parent tillers reach senescence (Olson & Richards, 1988a, b). Species tolerant to defoliation can produce a greater number of daughter tillers of fastest growth than those susceptible to defoliation (Caldwell et al. 1981; Busso & Richards, 1995).

Different studies have reported a variety of responses in the rate of leaf appearance after a severe defoliation of perennial grasses, from increases to no changes (Sáenz & Deregibus, 2001) to

even reductions (Chapman et al., 1983). Possible changes in the environmental conditions (e.g., light intensity and temperature), particularly to a level of the apical meristem, might modify the rate of leaf appearance on defoliated plants (Anslow, 1966). On the other hand, negative responses have been associated with defoliations at late developmental morphology stages, in coincidence with high air temperatures and low soil moisture levels (Chapman et al., 1983).

The speed and magnitude of the photosynthetic canopy reestablishment after defoliation depend on the number, nature and location of the removed meristems (Korner, 1991), which is closely associated to the developmental morphology stage of the plant. Greater total leaf lengths have been produced after active meristems remained on the plant after defoliation (Becker et al., 1997b). Because of this, the timing when the defoliation events occur within the growing season will have a direct effect on the subsequent forage production, survival, and recuperation of the plants (Olson & Richards, 1988a). Several studies observed increases in: (1) the stem + sheath lengths, and (2) total leaf lengths when defoliation occurred earlier during the growing season or when there was no defoliation of perennial grasses and herbaceous species (Paige, 1992). Knowledge of when a plant reaches certain stage of developmental morphology is very important for the synchronization of management guidelines to determine the most appropriate time for grazing, thus minimizing the negative effects of herbivory on the desirable components of vegetation.

Degradation of the plant population induced by grazing would eventual-

ly reduce tiller number and total basal area, potentially reducing productivity and plant competitive ability within the community (Briske & Richards, 1995). However, Giorgetti et al. (2000b, 2006), working on exclosures, reported positive responses in the native perennial grasses *P. vaginatum*, *A. subulata*, *A. spegazzinii* y *S. cryptandrus* under different kinds of management and clipping frequencies. *Sporobolus cryptandrus*, a widely studied species in the United States of America, has shown increases, decreases or absence of considerable changes in relation to its response to grazing (Bragg, 1978; Kleiner, 1983).

Given a competitive situation, a species increases its possibilities of capturing soil mobile and not mobile nutrients by increasing its root length (Ryser & Lambers, 1995). Under soil water stress conditions, which determine that water is absorbed by only a fraction of the root system, the amount of water that enters the plant might be closely related to the root length density (root length per unit soil volume; RLD) where water is available. As a result, a greater RLD might favor water and nutrient uptake, thus contributing to increase competitive abilities. This is especially true in unproductive environments where competition for belowground resources is strong.

Root growth and respiration, and nutrient uptake, depend upon the continuous supply of soluble carbohydrates produced by the plant photosynthetic tissues (White, 1973). Root activity may consume more than half of the available photoassimilates on mature plants (Fogel, 1985). Some authors have reported that carbon availability within the roots is immediately reduced after defoliation in response to a photosynthesis reduc-

tion and to a preferential photosynthetic carbon allocation to meristems and development of new tissues (McNaughton, 1983). However, other authors have reported an increase in carbon allocation to roots, after hours from defoliation, on species adapted to grazing (Holland et al., 1996).

The role of grazing by domestic livestock must be considered when evaluating strategies that contribute to competitive ability of rangeland vegetation. Factors that reduce photosynthetic capacity (e.g., grazing) will also reduce soil resource acquisition mechanisms because these are dependent upon plant carbon fixation (Briske & Richards, 1995). Some grazing tolerant, competitive grass species (like *Agropyron desertorum* (Briske & Richards, 1995) are able to preferentially allocate carbon to regrowing shoot sinks while curtailing root growth after defoliation which allows for rapid photosynthetic canopy re-establishment. In contrast, root growth has remained unabated after defoliation in other grazing sensitive, less competitive grasses (like *Pseudoroegneria spicata*). Differences in carbon partitioning to aboveground or belowground organs after defoliation could help explain species differential responses to defoliation (Caldwell et al., 1981; Chapin & Slack, 1979). Also, timing of defoliation at any particular developmental morphology stage can regulate the magnitude of carbon partitioning between aboveground and belowground sinks in anyone species (Dunn & Frommelt, 1998).

Thereafter, there are various aboveground (e.g., plant green basal area; total green tiller number; number of reproductive tillers; daughter tiller production; tiller height; number and length

of total leaves [blades + sheaths, green + dry]; replacement of new leaves after defoliation) and belowground (RLD) morphophysiological traits that might contribute to herbivory tolerance, nutrient acquisition, and plant biomass production and persistence in a community (Briske & Richards, 1995; Dunn & Frommelt, 1998; Saint Pierre et al., 2004). Since *P. vaginatum* is practically the only perennial grass that has been exposed to grazing by livestock during decades in the warm season, how is it that this species currently persists and is the most abundant in the arid and semi-arid rangelands of central Argentina?

Our objectives were to examine the effect of plant defoliation twice a year, without removing most intercalary and apical meristems, on shoot dry weight production, and shoot and root traits on the native, warm season grasses *P. vaginatum*, *A. spegazzinii*, *A. subulata* and *S. cryptandrus*.

MATERIALS AND METHODS

Study site

The study was performed in the Chacra Experimental Patagones, Buenos Aires, Argentina (40°39'S; 62°53' W; 40 m a.s.l.), within the Phytogeographical Province of the Monte (Cabrera, 1976), during 2 years (2007-2008 and 2008-2009). Climate is temperate arid to semi-arid, with higher precipitations during the summer and autumn. Long term (1981- 2010) annual rainfall is 416.7 mm, with a mean annual temperature of 14.1 °C, absolute minimum temperature of -7.6 °C (August), absolute maximum temperature of 43 °C (January), mean annual relative humidity of 60 %, and mean annual wind speed of 13 km h⁻¹. Annual precipitations

during 2007 and 2008 were 287.5 and 198.0 mm, respectively. Precipitations in 2007-2008 and 2008-2009 were 42 % and 30 % lower, respectively, than the long term annual mean. This provided us a unique opportunity to know the response of both species to water stress under field conditions. High variability in annual precipitation is typical of arid environments (Noy-Meir, 1993). Soil is a typical Haplocalcid. Average pH is 7, and the soil layer depth is not a constraint factor for root growth in the soil profile. The plant community at the Monte study region is characterized by an open, shrubby stratum which includes different quality, herbaceous species for cattle production (Giorgetti et al., 1997). Dominance of a particular grass or shrubby species in the study region is partially dependent on grazing history and fire frequency and intensity (Distel & Bóo, 1996).

Experimental design and defoliation managements

Plants of *P. vaginatum*, *A. spegazzinii*, *A. subulata* and *S. cryptandrus* were marked in the field, in a 1 ha enclosure. In this way, the presence of the *Aristida* species and *S. cryptandrus* were associated to the same community as *P. vaginatum*. A total of 48 plants were marked for sampling in 2007-2008 (4 species x 2 treatments [control versus defoliation] x 6 replicates/treatment). These plants had no neighbors within a radius of more than 0.2 m. This allowed most of RLD measurements to correspond to the marked plants. At the beginning of the second growing cycle (2008-2009), there were not enough plants of *S. cryptandrus* so it had to be discarded during

the second growing season studied. As a result, 36 new plants of *P. vaginatum*, *A. spegazzinii*, and *A. subulata* were marked for studying in 2008-2009, similarly to the previous year cycle. Only undefoliated plants were used in the determinations of plant developmental morphology stage. All plants grew under natural field conditions during the whole study; weed control was not conducted.

During the dormancy winter period, in both growing cycles under study, all plants were clipped to 5 cm stubble height from the soil surface. In grazing management, it is possible to establish a rotational grazing system that includes this type of simulated clipping. Fall-winter-spring and spring-summer pastures, some deferred paddocks, use of natural grasslands, abandoned fields, hay, grains, etc. can be used to cover nutrient deficiencies at given times of the year. There is also the need of planning a forage chain with its corresponding foraging balance. As a result, the deferred paddock where *P. vaginatum* grew can be grazed only during winter time so during the rest of the year the animals graze the other paddocks included in the forage chain. Thus, when the paddock with plants of *P. vaginatum* is deferred, their seeds can be dispersed (by the wind) to the same or to the other paddocks. As a result, only plant growth produced during each growing season was considered for measurements. During the springs of 2007 and 2008, half of the plants were defoliated twice (during the vegetative developmental morphology stage and immediately after the differentiation of the growth apex from vegetative to re-productive) to 5 cm stubble. The other half of the plants remained undefoliated (control). Repeated clipping at 5 cm

stubble can reduce the number, but not the hydration stage of buds under water stress conditions (Busso et al., 1989). Busso et al. (1989) demonstrated this by cutting buds in halves to determine their viability using TTC and Evans's blue. After cutting the buds, they always were normally hydrated (Busso et al., 1989).

Measurements

Height of the apical meristem

In each growing cycle, tillers of each species were dissected every 2 weeks and observed under a binocular microscope to determine both the developmental stage and height of the apical meristem. This permitted to avoid its removal in the majority of plant tillers after applying the defoliation treatments. Defoliation was made by hand using scissors in all cases.

Tiller developmental morphology stages

Plant developmental morphology of undefoliated plants was determined monthly on plants of all the species during both growing cycles. With this purpose, one tiller was marked with a wire cable within each replicate plant. The studied developmental morphology stages were (1) vegetative, (2) boot stage, (3) beginning of exposed inflorescence, (4) exposed inflorescence, (5) anthesis (i.e., flowering stage), (6) immature grain, (7) mature grain, (8) seed dispersal, (9) plant dormancy or death. Determinations were made at a tiller scale (one tiller/plant) and on the same plants used for all the other measurements.

Tiller demography and growth

Plant circumference to determine green basal area was measured in each growing season. Expression of the study variables

on a cm^2 basis was important for comparative purposes because of the inherently differences in basal area among the study species.

On each of the study plants, one current season tiller was permanently marked with wire cables. Tiller number/plant; tiller height; number of reproductive tillers/ cm^2 ; number of daughter tillers/ cm^2 ; number of total blades (green + dry)/ cm^2 and total leaf length (blades + sheaths [green + dry]) / cm^2 were measured periodically on each marked tiller during the growing seasons of 2007-2008 and 2008-2009. Tiller height was measured from the soil surface area to the most distal portion of the longest leaf, maintaining the blade straight and in vertical position. These measurements followed those of Busso et al. (2003).

Root length density

Two destructive harvests were conducted using a soil corer (volume: 181.5 cm^3) at the time of defoliation and three weeks after the second defoliation, during 2007 and 2008. Six plants were harvested per species and defoliation treatment on each of the study years. At these dates, one soil core was taken diagonally from the periphery of each plant up to 0.15 m depth to assure that sampled roots corresponded to the sampled plant. One plant of each species was used per replicate at each sampling date. Roots from each soil core were used for determinations of root length.

Roots were removed from soil cores by manual washing using a 35-mesh sieve. Thereafter, roots from each plant were spread on a 20 x 30 cm glass, and after spreading, roots were covered with another glass of the same size. Then, each glass set was scanned. Obtained images

were processed using the software Root-edge 2.3b (Kaspar & Ewing, 1997) to obtain root length. Since soil core volume was known, RLD (cm roots/cm³ soil) could be calculated.

Aboveground biomass production

Shoot dry weight production was measured at the time of the defoliation treatments (C: clipping). At the end of the growing cycle, the amount of dry weight produced by undefoliated control plants during the whole study period, and that produced by defoliated plants from the time of treatment to the end of the growing cycle (R: regrowth) were measured. Total dry weight produced by defoliated plants was calculated as C+R. All plant tissues obtained above clipping height were oven-dried at 60 °C and then weighed.

Statistical analyses

Data were analyzed using the statistical software INFOSTAT (Di Rienzo et al., 2009). Variables that were periodically evaluated were analyzed using repeated measures ANOVA where factors were the species, the defoliation treatments and sampling dates. The multivariate approximation was utilized using Wilks' statistics (Wilks, 1932). When the interaction between any factor and time was no significant ($p > 0.05$), data from all dates were averaged. When the interaction was significant ($p < 0.05$) each sampling date was analyzed separately. RLD data were analyzed with a two-way ANOVA, where factors were the species and the defoliation treatments. When the interaction was significant, both factors were analyzed separately. Mean separation was conducted using the protected LSD of Fisher, with a significance level

of 0.05. Numbers of daughter tillers/cm² were transformed to $\sqrt[3]{(x+0.5)}$; RLD to $\sqrt[3]{(x)}$; and total dry-matter production/cm² data to $\ln(x + 1)$ to comply with the normality and homoscedasticity assumptions of variance (Sokal & Rohlf, 1984). Untransformed values are shown in illustrations. Combined analysis across the study years was not conducted because they showed similar ($p > 0.05$) monthly precipitation and temperature values during the warm growing seasons in our study.

RESULTS

Height of the apical meristem

Height of the apical meristem from the stem basal area was at the most 7.20 ± 1.41 mm (mean ± 1 E.E.) in 2007 and 7.24 ± 0.84 mm in 2008 on undefoliated tillers ($n = 12$) of all the species at the time of defoliation.

Tiller developmental morphology stages

Plants of the four species were in the vegetative developmental morphology stage in September 2007 (86.5 mm precipitation, **Figure 1**). In the following month (7.5 mm), all species were found at the vegetative stage except for *P. vaginatum* which showed 66.7 % of the sampled tillers at the reproductive developmental morphology state. In November 2007 (29 mm precipitation), the percentage of tillers in that species was greater than 80 % at the reproductive stage. At this time, only 16.7 % of tillers of *A. spagazzinii* were at the boot stage. Tillers of the two remaining species continued at the vegetative stage. During December 2007, 16.7 % of the marked tillers of *P. vaginatum* were at the stage of seed dispersal.

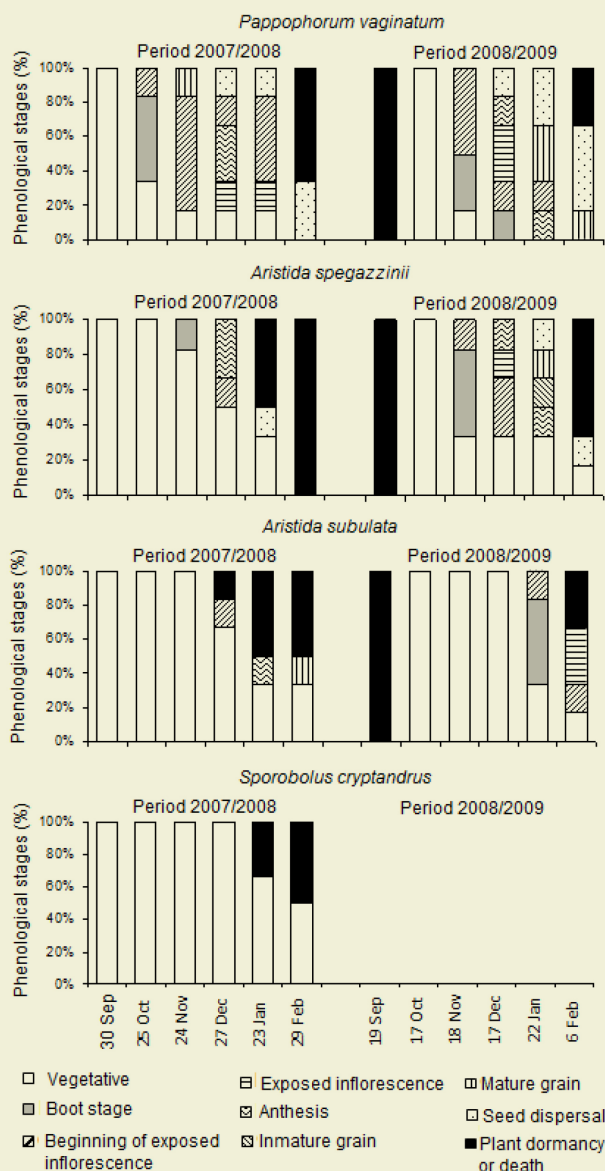


Figure 1. Percentage of the various developmental morphology stages determined on undefoliated plant tillers of four species during two years of study (2007-2008 and 2008-2009). Each histogram corresponds to a sampling date (n=6). 0: Absence of regrowth; n.d.: not determined
 Figura 1: Porcentaje de los distintos estadios de desarrollo morfológico determinados en los brotes no desfoliados de cuatro especies durante dos años de estudio (2007-2008 y 2008-2009). Cada histograma corresponde a una fecha de muestreo (n=6). 0: ausencia de rebrote; n.d.: no determinado

This developmental morphology stage was reached by *A. spegazzinii* in January 2008. The reproductive cycle of *A. subulata* was initiated in December 2007 and no seed dispersal was observed during the study. Even more, in December 2007 (2.5 mm), 16.7 % of their sampled tillers were dead. Fifty percent of marked tillers of *A. spegazzinii* reached this stage a month later, in January 2008 (15 mm). In February 2008, *P. vaginatum* was the only species to reach such dead stage on 66.7 % of its marked tillers (16.5 mm). At this date, it was the only species dispersing seeds. Sampled tillers of *S. cryptandrus* remained at the vegetative stage during most part of the study, until January 2008, when dead tillers started to show.

During the drier second study year (2008-2009), plant regrowth started a month later, in October 2008 (September: 4.5 mm; October: 19 mm, **Figure 1**). The few plants of *S. cryptandrus* found were at a dormancy stage or dead. Because of this, *S. cryptandrus* was not included in the second study year. In November 2008 (6 mm), 83.3 % of *P. vaginatum* tillers were at the reproductive developmental morphology stage. Seed dispersal started in December 2008 (32.5 mm) and continued until February 2009 (January: 26 mm, February: 33.5 mm). *Aristida spegazzinii* presented a greater percentage of tillers at the reproductive stage in November (66.7 %) in relation to the same month during the previous year (16.7 %). This species reached the stage of seed dispersal in January 2009. Once again, tillers of *A. subulata* initiated later its reproductive stage, in January 2009, with 66.7 % of their tillers at the stages of boot and

beginning of exposed inflorescences. All marked tillers in all three species died by February 2009, with a greater percentage in *A. spegazzinii* (66.7 % versus 33.3 % in the other two species).

Tiller demography and growth

Green basal area

In 2007-2008, there were no differences ($p>0.05$) on green basal area between species or treatments (**Figure 2**). During 2008-2009, however, *A. spegazzinii* showed the greatest ($p<0.05$) basal area of all the other species, in both treatments (**Figure 2**).

Tiller number/plant

This variable showed variation during the studied periods. Because of this, results are presented for each sampling date (**Table 1**). There were no differences between defoliation treatments ($p>0.05$) in both studied growing seasons (**Table 1**). During 2007-2008 *A. spegazzinii* showed the greatest ($p<0.05$) number of tillers-plant. The remaining species showed a similar ($p>0.05$) tiller number per plant during September and October (**Table 1**). From November, and until the end of the study, *A. spegazzinii* produced the greatest ($p<0.05$) number of tillers/plant among all species (**Table 1**). Plants of *A. subulata* produced an intermediate ($p<0.05$) tiller number, and those of *P. vaginatum* and *S. cryptandrus* produced the lower ($p<0.05$) number of tillers/plant.

During 2008-2009, the greatest ($p<0.05$) tiller number was shown on plants of *A. spegazzinii* (**Table 1**), and *P. vaginatum* and *A. subulata* produced a similar ($p>0.05$) tiller number.

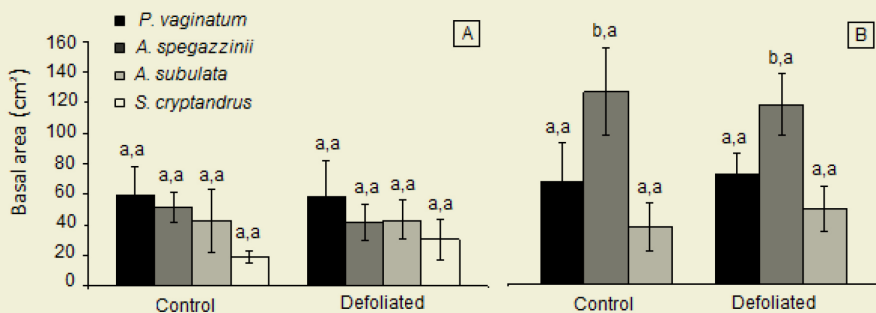


Figure 2. Basal area (cm²) on plants of four (2007-2008) or three warm-season species (2008-2009) exposed to two defoliation treatments (Control, Defoliated) during the periods 2007-2008 (A) and 2008-2009 (B). Each histogram is the mean \pm 1 standard error (S.E.) of $n=36$ (A) or $n=30$ (B). Within each growing season, different letters above histograms indicate significant differences ($p<0.05$) among species (first letter) or between defoliation treatments (second letter)

Figura 2. Área basal (cm²) en plantas de cuatro (2007-2008) o tres especies de estación cálida (2008-2009) expuestas a dos tratamientos de defoliación (Control, Defoliado) durante los periodos 2007-2008 (A) y 2008-2009 (B). Cada histograma es la media \pm 1 error estándar (E.S.) de $n=36$ (A) o $n=30$ (B). Dentro de cada temporada de cultivo, las letras diferentes sobre los histogramas indican diferencias significativas ($p<0,05$) entre especies (primera letra) o entre tratamientos de defoliación (segunda letra)

Tiller height

In September 2007, plants of *P. vaginatum* and both species of *Aristida* showed a greater ($p<0.05$) height than those of *S. cryptandrus* (Table 2). From October to the end of the 2007-2008 growing cycle, plants of *P. vaginatum* showed the greatest height among all study species. In that month, the other species did not show significant differences ($p>0.05$) among themselves. From November onwards (after the first defoliation), and until the end of the growing season, the species showed a different response on each of the treatments (interaction species*treatment: $p<0.05$). Within the control treatment, *Aristida* species showed greater values ($p<0.05$) than *S. crypt-*

andrus in November and December. In January and February, only *A. subulata*, between the *Aristida* species, showed a greater ($p<0.05$) height than *S. cryptandrus*. Within the defoliated treatment, *P. vaginatum* had once again the greatest ($p<0.05$) height, although *A. subulata* showed greater ($p<0.05$) values than *A. spegazzinii* in November and December 2007 and February 2008. Defoliation reduced ($p<0.05$) plant height on all four species between December 2007 and February 2008, except on *S. cryptandrus* in November, and on all four species in September and October ($p>0.05$). From November 2007 to February 2008, control plants of *A. subulata* maintained a similar ($p>0.05$) height to *A. spegazzinii*.

Table 1. Number of tillers per plant
Tabla 1. Número de brotes por planta

		Period 2007/2008					
		30-Sep	25-Oct	24-Nov	27-Dec	23-Jan	29-Feb
<i>P. vaginatum</i>	Control	44.33 ± 10.79 a,a	46.50 ± 11.94 a,a	41.17 ± 11.96 ab,a	66.33 ± 20.30 ab,a	51.83 ± 14.58 ba,a	46.83 ± 13.95 ab,a
	Defoliated	46.50 ± 11.21 a,a	54.00 ± 13.06 a,a	47.50 ± 13.98 ab,a	59.83 ± 17.33 ab,a	51.50 ± 13.09 ba,a	45.67 ± 11.23 ab,a
<i>A. spegazzinii</i>	Control	129.33 ± 25.02 b,a	137.33 ± 24.28 b,a	169.33 ± 26.51 c,a	191.33 ± 24.10 c,a	246.00 ± 37.60 c,a	246.00 ± 37.09 c,a
	Defoliated	138.00 ± 30.84 b,a	168.67 ± 38.16 b,a	138.00 ± 18.38 c,a	183.67 ± 33.78 c,a	187.67 ± 40.39 c,a	184.33 ± 43.47 c,a
<i>A. subulata</i>	Control	56.33 ± 18.34 a,a	63.00 ± 13.20 a,a	61.67 ± 14.93 b,a	83.33 ± 24.32 b,a	89.83 ± 26.25 b,a	79.67 ± 21.39 b,a
	Defoliated	58.67 ± 17.46 a,a	76.67 ± 18.82 a,a	71.17 ± 17.93 b,a	72.67 ± 12.36 b,a	84.00 ± 17.57 b,a	84.50 ± 17.27 b,a
<i>S. cryptandrus</i>	Control	29.33 ± 5.78 a,a	34.00 ± 7.54 a,a	20.00 ± 4.63 a,a	21.83 ± 3.46 a,a	20.67 ± 2.86 a,a	18.00 ± 3.49 a,a
	Defoliated	32.17 ± 9.03 a,a	29.67 ± 6.94 a,a	33.67 ± 8.35 a,a	33.50 ± 9.52 a,a	39.33 ± 17.93 a,a	36.17 ± 18.47 a,a
		Period 2008/2009					
		17-Oct	18-Nov	17-Dec	22-Jan	26-Feb	
<i>P. vaginatum</i>	Control	12.00 ± 3.36 a,a	17.67 ± 7.41 a,a	15.67 ± 5.65 a,a	15.83 ± 5.21 a,a	24.50 ± 4.46 a,a	
	Defoliated	17.67 ± 1.02 a,a	22.50 ± 1.26 a,a	22.33 ± 1.93 a,a	21.83 ± 2.56 a,a	31.50 ± 4.75 a,a	
<i>A. spegazzinii</i>	Control	43.17 ± 15.86 b,a	210.00 ± 59.29 b,a	189.33 ± 57.49 b,a	196.00 ± 44.91 b,a	181.33 ± 42.01 b,a	
	Defoliated	42.33 ± 13.42 b,a	148.00 ± 23.82 b,a	147.33 ± 22.11 b,a	153.33 ± 23.95 b,a	136.00 ± 22.82 b,a	
<i>A. subulata</i>	Control	32.17 ± 10.32 a,a	51.17 ± 19.41 a,a	50.50 ± 21.13 a,a	54.83 ± 20.56 a,a	62.00 ± 23.98 a,a	
	Defoliated	28.00 ± 7.11 a,a	58.83 ± 15.28 a,a	49.67 ± 8.23 a,a	47.50 ± 15.44 a,a	66.00 ± 15.61 a,a	

Note: Data from plants of four (2007-2008) or three warm-season species (2008/2009) exposed to two defoliation treatments (Control, Defoliated) during the periods 2007-2008 and 2008-2009. Each value is the mean ± 1 standard error (S.E.) of n=6. Different letters within the same column indicate significant differences (p<0.05) among species (first letter) or between defoliation treatments (second letter). Differences among species within each treatment (first letter), and defoliation treatments within each genotype (second letter) are reported between parenthesis.

Table 2. Tiller height (cm)
Tabla 2. Altura de brote (cm)

		Period 2007/2008					
		30-Sep	25-Oct	24-Nov (*)	27-Dec (*)	23-Jan (*)	29-Feb (*)
<i>P. vaginatum</i>	Control	15.33 ± 1.65 b,a	27.33 ± 3.24 b,a	31.17 ± 2.93 (c),(b)	32.83 ± 2.33 (c),(b)	32.50 ± 2.74 (c),(b)	33.50 ± 2.64 (c),(b)
	Defoliated	14.58 ± 1.76 b,a	24.42 ± 2.98 b,a	15.83 ± 1.31 (c),(a)	10.00 ± 1.06 (b),(a)	12.08 ± 0.69 (b),(a)	12.33 ± 0.91 (c),(a)
<i>A. spegazzinii</i>	Control	14.00 ± 1.67 b,a	15.00 ± 1.32 a,a	17.50 ± 1.88 (b),(b)	18.00 ± 1.57 (b),(b)	16.00 ± 1.26 (ab),(b)	15.83 ± 1.82 (ab),(b)
	Defoliated	10.98 ± 1.85 b,a	15.25 ± 1.34 a,a	7.75 ± 0.48 (a),(a)	6.83 ± 0.76 (a),(a)	7.33 ± 1.02 (a),(a)	6.17 ± 0.65 (a),(a)
<i>A. subulata</i>	Control	14.58 ± 3.31 b,a	16.58 ± 2.81 a,a	18.00 ± 2.08 (b),(b)	23.25 ± 2.40 (b),(b)	23.17 ± 4.38 (b),(b)	20.50 ± 1.26 (b),(b)
	Defoliated	13.33 ± 2.49 b,a	16.18 ± 2.42 a,a	10.50 ± 0.58 (b),(a)	9.67 ± 0.36 (b),(a)	8.78 ± 0.54 (a),(a)	9.83 ± 0.48 (b),(a)
<i>S. cryptandrus</i>	Control	7.95 ± 2.12 a,a	12.03 ± 2.28 a,a	8.42 ± 1.08 (a),(a)	10.83 ± 0.95 (a),(b)	11.45 ± 1.25 (a),(b)	11.75 ± 0.94 (a),(b)
	Defoliated	6.73 ± 2.15 a,a	11.83 ± 2.48 a,a	8.58 ± 0.51 (ab),(a)	6.88 ± 0.72 (a),(a)	7.25 ± 1.05 (a),(a)	7.17 ± 1.17 (a),(a)
		Period 2008/2009					
		Sep	17-Oct	18-Nov	17-Dec	22-Jan	26-Feb
<i>P. vaginatum</i>	Control		11.50 ± 0.71 a,a	13.50 ± 0.68 b,a	15.00 ± 1.00 b,b	18.33 ± 1.44 b,b	19.33 ± 1.77 a,b
	Defoliated		10.42 ± 0.74 a,a	15.58 ± 0.90 b,a	10.25 ± 1.06 b,a	11.42 ± 0.68 b,a	10.50 ± 0.69 a,a
<i>A. spegazzinii</i>	Control		10.33 ± 0.84 a,a	10.50 ± 0.50 a,a	11.00 ± 1.26 a,b	13.58 ± 1.60 a,b	12.75 ± 1.41 a,b
	Defoliated		9.67 ± 0.80 a,a	10.17 ± 0.87 a,a	9.75 ± 0.84 a,a	8.75 ± 1.56 a,a	9.67 ± 0.79 a,a
<i>A. subulata</i>	Control		10.42 ± 1.00 a,a	11.00 ± 1.00 a,a	11.08 ± 0.92 a,b	16.25 ± 2.06 ab,b	25.17 ± 3.17 b,b
	Defoliated		9.33 ± 0.42 a,a	10.17 ± 0.70 a,a	8.58 ± 1.10 a,a	10.08 ± 1.56 ab,a	16.42 ± 1.93 b,a

Note: Data from plants of four (2007/2008) or three warm-season species (2008/2009) exposed to two defoliation treatments (Control, Defoliated) during the periods 2007/2008 and 2008/2009. Each value is the mean ± 1 S.E. of n=6. Different letters within the same column indicate significant differences (p<0.05) among species (first letter) or between defoliation treatments (second letter). At sampling dates that presented a significant interaction (p<0.05) species*treatment, differences among species within each treatment (first letter), and defoliation treatments within each genotype (second letter) are reported between parenthesis.

Among all study species, *S. cryptandrus* was the species that most often had a lower ($p<0.05$) height during the growing season 2007-2008.

At the beginning of the second growing season, all four species showed a similar ($p>0.05$) height (**Table 2**). Control plants of all four species showed a greater ($p<0.05$) height than the defoliated plants from the time of the first defoliation, differences which were maintained until the end of the study. From November onwards, when *P. vaginatum* initiated its reproductive cycle, a greater ($p<0.05$) height was shown in this one than in the other species. This difference was maintained during December. In January, *A. subulata*, which initiated the production of reproductive structures, showed a similar ($p>0.05$) height to *P. vaginatum*. Height of *A. subulata*, however, was lower ($p<0.05$) than on *A. spagazzinii*. In February, height of *A. subulata* was greater ($p<0.05$) than in the other two species (**Table 2**).

Number of reproductive tillers/cm²

In October 2007-2008, the number of reproductive tillers/cm² was at least 96 % greater ($p<0.05$) on *P. vaginatum* than in the other species on control plants (0.25 ± 0.11 , mean \pm SE), and at least 71.4 % greater ($p<0.05$) in this (0.07 ± 0.03) than in the other species on defoliated plants. Control plants (0.17 ± 0.09) had at least 35.3 % more ($p<0.05$) reproductive tillers than defoliated plants (0.11 ± 0.05) in *Aristida spagazzinii* in comparison to the other species from 24 November onwards in the 2007-2008 growing season.

In the second year (2008-2009), the number of reproductive tillers was at least 34.6 % greater ($p<0.05$) ($0.17 \pm 0.05 = P. vaginatum$; $0.26 \pm 0.08 = A. subulata$; 26

February 2009) on control plants, and at least 12.5% greater ($0.16 \pm 0.05 = P. vaginatum$; $0.14 \pm 0.04 = A. subulata$; $p<0.05$) on defoliated plants in comparison to those in the other species from 18 November 2008 to 22 January 2009. On 26 February, control and defoliated plants of *P. vaginatum* and *A. subulata* showed a similar ($p>0.05$) number of reproductive tillers on control and defoliated plants.

Daughter tiller production/cm²

During 2007-2008, parent tillers of *P. vaginatum* produced a greater ($p<0.05$) amount of daughter tillers than the other species (**Figure 3**). In 2007-2008 and 2008-2009, there were no differences in daughter tiller production between defoliated and undefoliated plants ($p>0.05$; **Figure 3**).

Number of total leaves (green + dry)/cm²

Leaf production was not affected by defoliation ($p>0.05$) in any of the study dates (**Figure 4**). During the first year, *S. cryptandrus* had a greater ($p<0.05$) number of total leaves (green + dry)/cm² than *A. spagazzinii* (**Figure 4**). In 2008-2009, *A. subulata* showed a greater ($p<0.05$) number of total leaves/cm² than *A. spagazzinii* (**Figure 4**), but a similar ($p>0.05$) total leaf number as *P. vaginatum*.

Total leaf (blade + sheath [green + dry]) length/cm²

During 2007-2008, there were no differences ($p>0.05$) neither among species nor among treatments (**Figure 5**). In the following growing season (2008-2009), there were higher ($p<0.05$) values on control than on defoliated plants in *P. vaginatum*, *A. spagazzinii* and *A. subulata* (**Figure 5**). Also, defoliated and undefo-

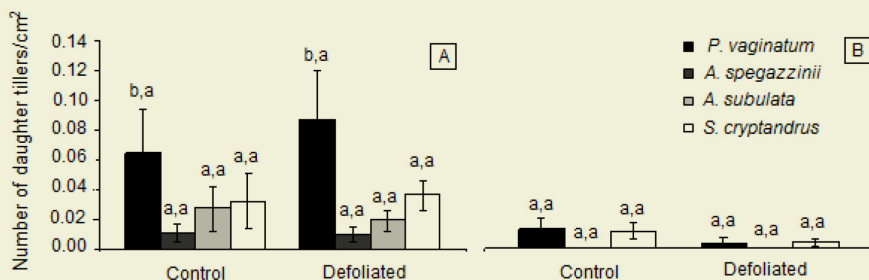


Figure 3. Number of daughter tillers/cm² on plants of four (2007-2008) or three warm-season species (2008-2009) exposed to two defoliation treatments (Control, Defoliated) during the periods 2007-2008 (A) and 2008-2009 (B). Each histogram is the mean \pm 1 S.E. of n=36 (A) or n=30 (B). Within each growing season, different letters on the histograms indicate significant differences (p<0.05) among species (first letter) or between defoliation treatments (second letter)

Figura 3. Número de tallos hijos/cm² en plantas de cuatro (2007-2008) o tres especies de estación cálida (2008-2009) expuestas a dos tratamientos de defoliación (Control, Defoliado) durante los períodos 2007-2008 (A) y 2008-2009 (B). Cada histograma es la media \pm 1 E.S. de n=36 (A) o n=30 (B). Dentro de cada estación de crecimiento, las letras diferentes en los histogramas indican diferencias significativas (p<0,05) entre especies (primera letra) o entre tratamientos de defoliación (segunda letra)

liated plants of *P. vaginatum* and *A. subulata* showed greater (p < 0.05) total leaf (blade + sheath [green + dry]) length/cm² than *A. spegazzinii* (Figure 5).

Root length density

In 2007-2008, there was interaction (p<0.05) between time and the other factors. This is why results are reported separately for each sampling date. There were no significant differences (p>0.05) among treatments during this period (Table 3). However, *P. vaginatum* showed greater values (p<0.05) than the other species at the time of the first defoliation.

During the second year, there were no differences (p>0.05) between time and the other factors. As a result, val-

ues obtained in the two sampling dates were averaged. During this period, no differences (p>0.05) were found neither among species nor among treatments (Table 3).

Aboveground biomass production

At the end of the first year of study, *A. subulata* showed the greatest (p<0.05) aboveground biomass production in comparison to the other species (Figure 6). There were no significant differences (p>0.05) between *P. vaginatum* and *A. spegazzinii*. *Sporobolus cryptandrus* was the lowest (p<0.05) productive species. At this time, aboveground plant biomass was greater (p<0.05) on defoliated than on undefoliated plants of each species (Figure 6).

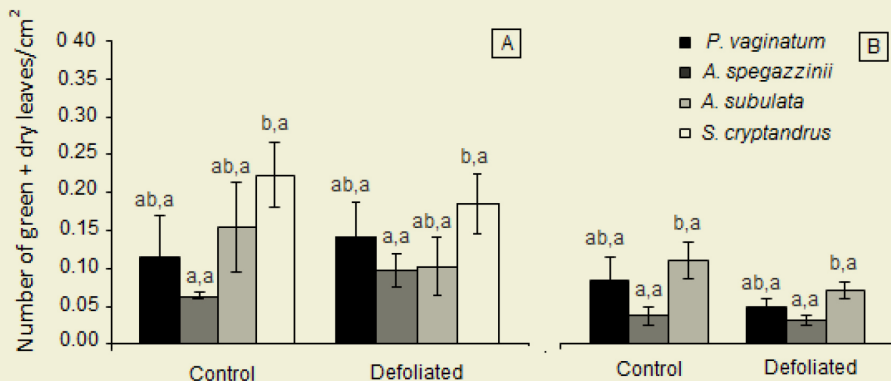


Figure 4. Number of green + dry leaves/cm² on plants of four (2007-2008) or three warm-season species (2008-2009) exposed to two defoliation treatments (Control, Defoliated) during the periods 2007-2008 (A) or 2008-2009 (B). Each histogram is the mean \pm 1 S.E. of $n=36$ (A) and $n=30$ (B). Within each growing season, different letters above histograms indicate significant differences ($p<0.05$) among species (first letter) or between defoliation treatments (second letter)

Figura 4. Número de hojas verdes + secas/cm² en plantas de cuatro (2007-2008) o tres especies de estación cálida (2008-2009) expuestas a dos tratamientos de defoliación (Control, Defoliado) durante los periodos 2007-2008 (A) o 2008-2009 (B). Cada histograma es la media \pm 1 E.S. de $n=36$ (A) y $n=30$ (B). Dentro de cada estación de crecimiento, las letras diferentes sobre los histogramas indican diferencias significativas ($p<0,05$) entre especies (primera letra) o entre tratamientos de defoliación (segunda letra)

In the second year, once again defoliated and undefoliated plants of *A. subulata* showed the greatest ($p<0.05$) production of dry weight in comparison to the other species (Figure 6), and there were no significant differences ($p>0.05$) between defoliated and undefoliated plants on each species (Figure 6). However, while there was a tendency for an increased dry weight production on defoliated than on undefoliated plants on *P. vaginatum*, an inverse tendency was shown on the other *Aristida* species (Figure 6).

DISCUSSION

Stages of developmental morphology

In arid and semiarid ecosystems, plant growth and developmental morphology stages are greatly controlled by precipitation and plant water stress levels (Bertiller et al., 1991; Yuan et al., 2007). Some studies have reported that water stress causes an advance of the plant developmental morphology stages in various herbaceous species (Fresnillo Fedorenko et al., 1996; Giorgetti et al., 2000b). In this study, the long-term average annual precipitation (416.7 mm) was greater than the precipitations during the grow-

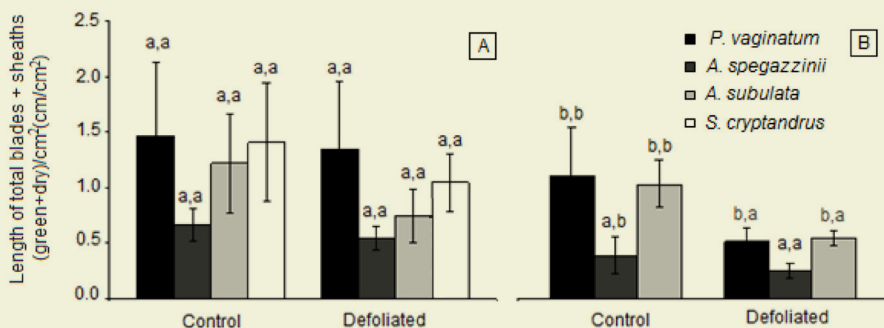


Figure 5. Length of total blade + sheaths (green + dry)/cm² (cm/cm²) on plants of four (2007-2008) or three warm-season species (2008-2009) exposed to two defoliation treatments (undefoliated [control], defoliated) during the periods 2007-2008 (A) and 2008-2009 (B). Each histogram is the mean \pm 1 S.E. of n=36 (A) or n=30 (B). Within each study growing season, different letters over the histograms indicate significant differences (p<0.05) among species (first letter) or between defoliation treatments (p<0.05) (second letter)

Figura 5. Longitud de la hoja total + vainas (verde + seca)/cm² (cm/cm²) en plantas de cuatro (2007-2008) o tres especies de estación cálida (2008-2009) expuestas a dos tratamientos de defoliación (sin desfoliar [control], defoliado) durante los períodos 2007-2008 (A) y 2008-2009 (B). Cada histograma es la media \pm 1 E.S. de n=36 (A) o n=30 (B). Dentro de cada estación de crecimiento del estudio, letras diferentes sobre los histogramas indican diferencias significativas (p<0,05) entre especies (primera letra) o entre tratamientos de defoliación (p<0,05) (segunda letra)

ing seasons in 2007-2008 (September 2007 to April 2008: 178 mm) and 2008-2009 (123 mm). This might have caused an advance on the plant developmental morphology stages in the drier growing season (2008-2009), especially in *P. vaginatum*. For example, regrowth of all species, but *S. cryptandrus*, was delayed about a month in 2008-2009 in comparison with the previous year. However, *P. vaginatum* and *A. spagazzinii* initiated and completed their reproductive cycles despite the water stress conditions.

Knowledge of the advancement of the plant developmental morphology stages during dry periods in the native species is important to adjust manage-

ment guidelines in a way that favors natural reseeding. Giorgetti et al. (2000b) showed that a drier period advanced stem elongation and fructification on *P. vaginatum*, and seed dispersal in this species and on *S. cryptandrus*. These results disagree with those of Jones (1992), who reported that water stress delays blooming on perennial species. In our study, tillers of *S. cryptandrus* did not reach the reproductive plant developmental morphology stage in 2007-2008; during this period, plant mortality was earlier on *S. cryptandrus* than on *P. vaginatum*. In addition, there was no regrowth in this species during 2008-2009. As a result, it was excluded from

Table 3. Root length density (cm root/ cm³ soil)
Tabla 3. Densidad de la longitud de la raíz (cm de raíz/ cm³ de suelo)

		Period 2007/2008		Period 2008/2009
		5-Nov	21-Dec	Average
<i>P. vaginatum</i>	Control	0.67 ± 0.19 b,a	0.57 ± 0.12 a,a	0.59 ± 0.10 a,a
	Defoliated	0.46 ± 0.07 b,a	0.46 ± 0.09 a,a	0.68 ± 0.12 a,a
<i>A. spegazzinii</i>	Control	0.12 ± 0.03 a,a	0.40 ± 0.08 a,a	0.68 ± 0.09 a,a
	Defoliated	0.22 ± 0.03 a,a	0.42 ± 0.06 a,a	0.68 ± 0.10 a,a
<i>A. subulata</i>	Control	0.20 ± 0.03 a,a	0.54 ± 0.06 a,a	0.58 ± 0.09 a,a
	Defoliated	0.33 ± 0.03 a,a	0.56 ± 0.10 a,a	0.61 ± 0.08 a,a
<i>S. cryptandrus</i>	Control	0.21 ± 0.01 a,a	0.41 ± 0.06 a,a	n.d.
	Defoliated	0.28 ± 0.03 a,a	0.64 ± 0.13 a,a	n.d.

Note: Data from plants of four warm-season species exposed to two defoliation treatments (Control, Defoliated) during the periods 2007/2008 and 2008/2009. Each value is the mean ± 1 S.E. of n=6 (2007/2008) or n=12 (2008/2009). Different letters within the same column indicate significant differences (p<0.05) among species (first letter) or between defoliation treatments (second letter).

n.d.:no data.

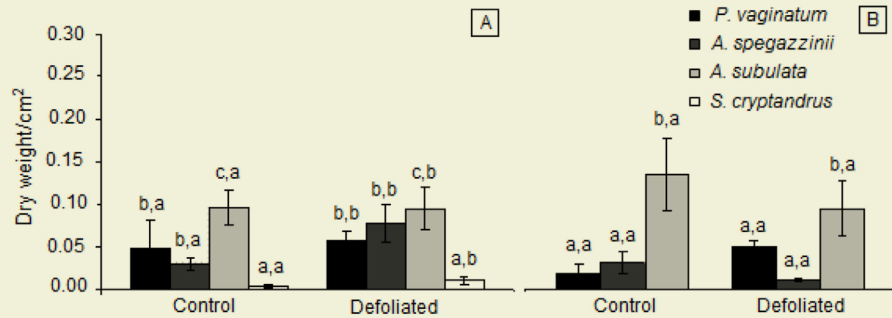


Figure 6. Dry weight/cm² on plants of four (2007-2008) or three warm-season species (2008-2009) exposed to two defoliation treatments (Control, Defoliated) at the end of the growing seasons of 2007-2008 (A) and 2008-2009 (B). Each histogram is the mean ± 1 S.E. of n=6.

Within each study growing season, different letters on histograms indicate significant differences (p<0.05) among species (first letter) or between defoliation treatments (second letter)

Figura 6. Peso seco/cm² en plantas de cuatro (2007-2008) o tres especies de estación cálida (2008-2009) expuestas a dos tratamientos de defoliación (Control, Defoliado) al final de las temporadas de crecimiento de 2007-2008 (A) y 2008-2009 (B). Cada histograma es la media ± 1 E.S. de n=6. Dentro de cada temporada de crecimiento del estudio, las letras diferentes en los histogramas indican diferencias significativas (p<0,05) entre las especies (primera letra) o entre los tratamientos de defoliación (segunda letra)

the study. Cano (1988) reported that although the study species are considered as warm-season grasses, they can stay in a vegetative developmental morphology stage when conditions are not adequate for their growth. Plant dormancy appears to be a mechanism that allows plants to face seasonal droughts and extensive water deficits in semiarid regions. Growth of meristems during adverse conditions is detrimental to meristem survival, and thus perennials often have developed mechanisms for inducing dormancy during or prior to the adverse conditions in order to prevent meristem growth (Sarath et al., 2014). This allows the plant to resume growth with prior stored reserves when conditions are favorable. Seasonal dormancy can occur in the summer months, generally induced by lack of water or high temperature (Sarath et al., 2014), thus reducing leaf exposure to water loss and heat gain during water stress periods (Brown, 1995). Other authors have reported that *S. cryptandrus* has a high dependency on water availability for plant development (Kemp, 1983) and that plant dormancy is induced during drought periods. Dormant organs (rhizomes, crown buds) can survive during long periods (Van Andel & Ernst, 1985).

The beginning of the developmental morphology stages shown on the *Aristida* species agrees with reports by Cano (1988). *Aristida spegazzinii* advanced the reproductive developmental morphology stage in response to a drier spring in 2008. At the same time, *A. subulata* was the only species that delayed their developmental morphology stages in that year. Giorgetti et al.

(2000b) reported an advance in seed dispersal during dry years on *Aristida pallens* at the same study site. This result was not observed in our study on *Aristida subulata*, which was unable to disperse seeds.

Pappophorum vaginatum showed the most extensive seed dispersal developmental morphology stage in both growing seasons among all study species. This species can produce up to 1600 light weight, hairy spikelets per plant (Entío, 2019). It is possible that this response contributes to a possible greater seed germination and seedling establishment in this than in the other species, at a time (late spring-early summer) when precipitations represent more than 25.7 % of the long-term (1981-2010: 416.7 mm) total annual precipitation. Thereafter, future research should investigate if either sexual or asexual reproduction is more important to determine the persistence of this species in the rangelands of central Argentina. Anyhow, and even though the *Aristida* species might differ in their survival strategies, their temporary plasticity in their developmental morphology stages suggests that they are well adapted to the intra- and inter-annual precipitation variability that is common at the Monte.

The advancement in the reproductive developmental morphology stages, a high production of reproductive tillers (even under grazing conditions), and a more extensive period during the seed dispersal developmental morphology stage in *P. vaginatum* might contribute to explain its greater abundance in comparison to the other species in the Monte, grazed rangelands.

Tiller demography and growth

Green basal area

Plants of *A. spagazzinii* showed a green basal area at least 40 % greater than in *P. vaginatum* and *A. subulata* at the end of the 2008-2009 growing cycle, despite the fact that precipitation from September 2008 to May 2009 was more than 24 % lower than in the first study growing season. Undeveloped and defoliated plants of *A. spagazzinii* had at least a 51 % greater tiller number than on defoliated and undeveloped plants of the other species by 26 February 2009 (Table 1). At the initiation of the study on 30 September 2007, undeveloped (129.3 ± 25.0) and defoliated (138 ± 30.8) plants of *A. spagazzinii* had at least a 55 % greater tiller number than the other species. Similarly, at the initiation of the second, drier growing season on 17 October 2008, tiller number of undeveloped (43.2 ± 15.9) and defoliated (42.3 ± 13.4) plants of *A. spagazzinii* was at least 24 % greater than in the other species. This species is only grazed when a better forage is not available (Cano, 1988). As a result, some plants of *A. spagazzinii* with a greater basal area than the other species might have been included in the enclosure by the time it was built. This is because the desirable species within the enclosure (i.e., *Pappophorum vaginatum*) might have been exposed to long-term livestock grazing before the enclosure was made.

Tiller number/plant

The cumulative effects of two successive years of severe defoliations reduced tiller number on plants of all species. These adverse effects of defoliation on tillering of perennial grasses have been reported

by various authors (Briske & Richards, 1995). Defoliation has caused (i) inhibitory effects on activation and viability of axillary buds (Busso et al., 1989); (ii) a reduction in carbon reserve availability which reduce initial regrowth when a photosynthetic surface area is not available after a disturbance (Busso et al., 1990); and (iii) a lower survival of growing tillers (Busso et al., 1989).

The serious reduction in tiller numbers, especially daughter tiller numbers, on defoliated and undeveloped plants across all species from the first to the second year might be in part the result of the dry growing season in 2008-2009. Tiller number is an indication of bud outgrowth (Busso et al., 1989). These authors emphasized that defoliated tillers on drought-treated plants of the bunchgrass *Pseudoroegneria spicata* (Syn: *Agropyron spicatum*) showed a significantly lower number of physiologically active buds than tillers on undeveloped controls in that treatment. Flemmer et al. (2002a) also determined in various perennial grasses that the proportion of stem bases producing tillers per plant was much lower under water stress than under higher levels of soil moisture availability. Additionally, crown and total (crown + roots) pools of total nonstructural carbohydrates were positively associated with early spring tiller regrowth on two perennial bunchgrass species (Busso et al., 1990). Therefore, we suggest that the great reduction in tiller numbers from the first to the second growing season in our study could be a sign of a depleted plant in both axillary bud bank and energy reserves. Additionally, Hodgkinson (2010) reported that the density of live tillers generally declined on plants of the perennial grasses *Austrodanthonia au-*

riculata, *Bothriochloa macra*, *Eragrostis curvula*, *Phalaris aquatica* and *Themeda triandra* as they remained under drought conditions. Furthermore, he showed that the death of plants in the drought treatment began for all species very soon after the foliage of plants had died. Hodgkinson (2010) determined a critical threshold for days in drought beyond which all plants of any of his study species would die, which was species dependent: about 100 days for *A. auriculata*, *P. aquatica* and *T. triandra*, 200 days for *B. macra* and 300 days for *E. curvula*.

Tiller height

During 2007-2008 and 2008-2009, tillers were taller on defoliated and undefoliated *P. vaginatum* plants than on those of the other species on most sampling dates. Since all study plants of all species were defoliated to 5 cm stubble before the start of each growing season, a greater tiller height on *P. vaginatum* was an indication of a fastest growth rate.

The second study year was drier than the first one. This conditioned, at least in part, plant responses to defoliation and interpretation of results. Daughter tiller production and plant growth are very sensitive to water stress (Brown, 1995). For example, water stress can prevent bud outgrowth (Busso et al., 1989) and reduce photosynthetic surface area (Bittman & Simpson, 1987). This can be associated, at least in part, with: (1) reduction in plant height (Turner et al., 1986), (2) smaller number and size of individual leaves (Busso & Richards, 1995), and (3) reduction on tiller longevity (Caldwell et al., 1981). Reestablishment of plant surface area might be severely limited when defoliation occurs under water

stress conditions, as it is usually the case on semiarid rangelands (Ludlow, 1986). In this case, *P. vaginatum* was the species that showed the greatest performance under conditions of defoliation under water stress.

After the second defoliation, by mid-spring 2007-2008 and early summer 2008-2009, overall mean relative growth rates (on a tiller height basis; $\text{cm cm}^{-1} \text{ day}^{-1}$) were greater on *P. vaginatum* than on the other species in 2007-2008 (Defoliated plants: *P. vaginatum*= 0.089, *A. spegazzinii*= 0.034, *A. subulata*= 0.057, *S. cryptandrus*= 0.041; Undefoliated plants: *P. vaginatum*= 0.141, *A. spegazzinii*= 0.096, *A. subulata*= 0.098, *S. cryptandrus*= 0.040) and 2008-2009 (Defoliated plants: *P. vaginatum*= 0.025, *A. spegazzinii*= 0.017, *A. subulata*= 0.021; Undefoliated plants: *P. vaginatum*= 0.039, *A. spegazzinii*= 0.030, *A. subulata*=0.036). Rapid leaf tissue replacement after defoliation is a critical component of defoliation tolerance in various perennial grass species (Briske & Richards, 1995). The number of active meristems and the amount of residual photosynthetic surface area have been reported to be more important than carbon reserves in limiting regrowth rates on defoliated plants (Richards and Caldwell, 1985). Also, changes in environmental conditions, especially at the level of apical meristems, have fostered leaf growth on defoliated plants (Briske & Richards, 1995). Rapid replacement after defoliation in other grasses has been attributed to compensatory photosynthesis on leaf and stem tissues, increase in tissue longevity or increase in the water status of defoliated plants (Briske & Richards, 1995).

Number of reproductive tillers/cm²

Each reproductive tiller in *P. vaginatum* can produce an 11-cm panicle with a mean of up to 70 spikelets of 1 cm each (Entío, 2019). This author also found that plants of *P. vaginatum* could produce a mean of up to 1100 spikelets. These spikelets have a 2-mm antecio and awns of approximately 8 mm. The small size, light weight of these spikelets allow them to be blown away from the mother plant by wind. Results obtained by Entío (2019), taking into account that they are potential reseeding values, would allow to suppose that this mechanism of sexual reproduction might largely contribute to the long term persistence of this species in rangelands of central Argentina. In this way, studies should be conducted to determine which mechanism (sexual, asexual) is relatively more important in contributing to the persistence of *P. vaginatum* to disturbances (grazing with or without drought conditions) in these rangelands.

During the first study year, there was a reduction in the production of reproductive structures because of defoliation. This result agrees with that of N'Guessan (2007) on perennial grasses. This could be the result of a greater photoassimilation demand by the vegetative developmental morphology stage, which must be reestablished after defoliation, with the subsequent reduction in carbon and nutrient partitioning to the reproductive tissues (Culvenor, 1993). It has been reported that the vegetative growth is the major way of reproduction in semiarid rangelands (Belsky, 1992). However, even though new plant establishment as a result of sexual reproduction occurs in a sporadic way (Briske & Richards, 1995), it is necessary for maintaining the genet-

ic diversity of populations. This diversity allows species to adapt to particular environments and overcome changes to greater scales (Briske & Richards, 1995). During the 2008-2009 growing season, production of reproductive structures was highly reduced even on undefoliated plants. This period was characterized by an unusual drought, which caused a general reduction on the leaf area production traits on all study species.

Daughter tiller production/cm²

In both years, daughter-tiller production was similar on defoliated and undefoliated plants in all species. This means that defoliation did not hinder daughter-tiller production, which is known to contribute to defoliation tolerance (Briske & Richards, 1995), even under dry conditions. After clipping to 5 cm stubble under drought conditions, *P. vaginatum* showed in both years not only a high level of daughter tiller production but also plant shoots. These results could explain in great part the persistence of *P. vaginatum* under grazing.

Number of total leaves (green + dry)/cm²

The total number of leaves (green + dry) was not reduced by defoliation in 2007-2008 and 2008-2009, even after plants were exposed to at least 57 % lower precipitation conditions than the long-term mean (416.7 mm). This suggests that defoliated plants, in general, could recover from disturbance. Even though they were unable to overcome the control plants, they were able to reach a similar leaf production, even after being defoliated twice every year. When aboveground tissues are removed, their reestablishment is faster from intercalary meristems, in-

intermediate from the apical meristem, and lower from the activation (and subsequent growth) of axillary crown buds (Hyder, 1972; Briske & Richards, 1995). Our results indicate that permanency of a high proportion of intercalary and apical meristems after defoliations at the beginning and middle of the growing season allowed plants to recuperate the lost tissues. Briske & Richards (1995) reported that the number of active meristems and the residual amount of photosynthetic surface area are more important than the availability of carbon reserves in limiting the regrowth production rate on defoliated plants. In addition, changes in environmental conditions, especially to the level of apical meristems, can favor leaf growth on defoliated plants (Anslow, 1966). Detling et al. (1980) also determined a greater photoassimilate allocation to new leaf production than support structures on plants tolerant to defoliation. A rapid leaf replacement is a critical trait to explain grazing tolerance in various perennial grass species (Caldwell et al., 1981; Briske & Richards, 1995).

Total leaf (blade + sheath [green + dry]) length/cm²

Leaf lengths per unit basal area between both defoliation managements in all species were similar immediately after defoliations in 2008-2009. Rainfall during November and December, when defoliation occurred, was 6 and 32.5 mm, respectively, and potential evapotranspiration was 139.8 and 155.4 mm, respectively. This very likely constrained defoliated plants from growing faster than the undefoliated controls. The effect of water stress in constraining growth of defoliated plants has been

reported in various perennial grasses (Busso et al., 2003).

Height of the growth apex was below 1 cm from the soil surface in the study species during spring. This finding is important because livestock could graze the studied species without removing most active intercalary and apical meristems. This indicates that growth will continue to be rapid after spring grazing, because growth rate is faster from intercalary meristems, intermediate from the leaf primordia in the growth apex, and lower from the activation and subsequent outgrowth of the axillary buds (Briske & Richards, 1995). As active meristems remained on the plants after the defoliation events in 2007 and 2008, they were able to recuperate their tissues lost to defoliation.

At the end of the 2008-2009 growing season, total leaf length produced between the second defoliation in 2008, and the end of the experiment, was similar on defoliated and undefoliated plants in all study species. This indicates that leaves grew faster on defoliated than on undefoliated plants after defoliation to reach equal total leaf lengths at the end of the growing season.

However, leaf replacement per unit surface area was similar ($p>0.05$) on defoliated and undefoliated plants in 2007-2008 and 2008-2009. In 2007-2008, such replacement was enough to reach similar ($p>0.05$) total leaf lengths on defoliated and undefoliated plants of all species. However, it was not great enough in 2008-2009, when defoliated plants showed a lower total leaf length than undefoliated plants on all study species.

Overall, and in relation to the number of total leaves, there were no significant

differences neither between treatments nor among species during the first study year (287.5 mm annual precipitation). However, during the second, drier year (198 mm annual precipitation), control plants of *P. vaginatum*, *A. subulata* and *A. spagazzinii* showed a higher total leaf number than defoliated plants of these species. Also, total leaf length was higher on plants of *P. vaginatum* and *A. subulata* than on those of *A. spagazzinii*. The fact that *P. vaginatum* showed a similar response to other persistent, less palatable species (i.e., *A. subulata* and *A. spagazzinii*) also demonstrates its persistence on grazed environments. This is, *P. vaginatum* was the species which showed the higher yield after defoliation and during the water stress period (2008).

Root length density

Roots of various perennial grasses grew at soil depth deeper than 0-20 cm at the study site (Saint Pierre et al., 2002, 2004; Torres et al., 2014). However, lack of manpower made us to work within the 0-20 cm depth of the soil profile. Distel & Fernández (1986) reported that 67% of the root biomass of the perennial grasses *S. tenuis* and *Piptochaetium napostaense* occurred in the upper 20 cm from the soil surface. Also, there are works that took soil samples from the first 0-15 cm of the soil profile to determine root length density on *S. clarazii*, *S. tenuis* and *S. gynerioides* (Busso & Bolletta, 2007).

Root length density in the first 20 cm of the soil profile was not reduced by defoliation on any species during 2007-2008 and 2008-2009, even though the last growing season was 31% drier than the first one. Other works on perennial grasses native to the Monte demonstrated that root growth was not reduced af-

ter defoliation, neither at different developmental morphology stages (Becker et al., 1997c; Saint Pierre, 2002) nor under water stress conditions (Busso & Bolletta, 2007). This response could be interpreted as a strategy that allows the species a continuous exploration for resources in soils often exposed to water stress (Ludlow, 1986). In *Nassella longiglumis* and *Jarava ichu*, native perennial grasses in the Monte, Flemmer et al. (2002b) found that root growth was not reduced by water stress at the shallower soil horizons (0-20 cm soil depth). In the same way, other species also maintained shallow root systems in response to water stress (Brar & Palazzo, 1995). At our study site, this could be a strategy to make a better utilization of small rainfall events (< 5mm: Sala & Lauenroth, 1982). An analysis of 18 years (1983-2000) of rainfall records at our study site showed that 61% of the rainfall events were <5 mm. Rainfall events of this magnitude were showed to rapidly stimulate ecological processes in rangeland grasses (Sala & Lauenroth, 1982). A continuous root growth during the year, even under conditions of water stress and defoliation, would contribute to a greater survival of the native species at the Monte rangelands.

Our results disagree with those of Richards (1984), who reported that a root growth reduction after defoliation is an effective mechanism that facilitates photosynthetic surface area reestablishment, and the balance between roots and shoots. As such, it contributes to both defoliation tolerance and maintenance of competitive ability.

In *S. cryptandrus* it has been reported that its shallow root system (Canfield, 1948) would limit its capacity of exploring deeper in the soil for resources (Wan

et al., 1993). When plants of *S. cryptandrus* were exposed to water stress, their photosynthetic capacity was progressively reduced at the same time that soil water stress increased at the shallow soil horizons (Wan et al., 1993). Despite of being considered a species adapted to water stress conditions, its survival in the semiarid rangelands would be more related to its capacity of avoiding long-term drought events (through an entrance into a stage of induced dormancy: Canfield, 1948) than to its tolerance capacity.

Belowground biomass presents a greater inertia than that aboveground. This allows that the native species achieve a greater equilibrium with the environment where they develop (Gómez Gutiérrez et al., 1989), offering a sustained production through time. These characteristics highlight the value of *P. vaginatum* as a forage component of the rangelands at the Monte.

Aboveground biomass production

Defoliated and undefoliated plants of *A. subulata* had the greatest dry weight production among all four species at the end of both years of study (**Figure 6**). Plant traits that contribute to explain that response were as follows: (1) Tiller numbers per cm² on defoliated and undefoliated plants of *A. subulata* tended to be greater than those on *P. vaginatum* and *S. cryptandrus*, but not on *A. spegazzinii*, in 2007-2008 (overall means [tillers/cm²]: *P. vaginatum*= 0.9, *A. spegazzinii*= 4.9, *A. subulata*= 2.0, *S. cryptandrus*= 1.1). Also, tiller numbers per cm² tended to be greater on *A. subulata* than on *P. vaginatum* and *A. spegazzinii* in 2008-2009 (overall means [tillers/cm²]: *P. vaginatum*= 0.5, *A. spegazzinii*=

1.1, *A. subulata*= 1.6); (2) in 2007-2008, tiller height of defoliated and undefoliated plants of *A. subulata* was greater than on *A. spegazzinii* and *S. cryptandrus*, but not on *P. vaginatum* (**Table 2**). *Aristida subulata* also had a greater tiller height than *A. spegazzinii* and *P. vaginatum* in 2008-2009 (**Table 2**); (3) Total leaf length of defoliated and undefoliated plants was similar on all species in 2007-2008 (**Figure 5**). However, total leaf length was greater on defoliated and undefoliated plants of *A. subulata* than on *A. spegazzinii*, but not on *P. vaginatum*, in 2008-2009 (**Figure 5**). We have to recognize that standing crop declines have been reported in other perennial grasses towards the end of the growing season, and have been attributed to translocation, leaching, oxidation, leaf dropping and seed dissemination (Pieper, 1978).

We have to highlight that 2008-2009, being drier than 2007-2008, conditioned plant responses to defoliation and increased difficulty in the interpretation of results. In 2008-2009, precipitation was 131.5 mm from September 2008 to May 2009; 29.5 mm from September to November (the most active growing period) 2008; 92 mm from December 2008 to February 2009, and 10 mm from March to May 2009. During 2007-2008, precipitation was 223.1 mm from September 2007 to May 2008; 123 mm from September to November 2007; 34 mm from December 2007 to February 2008, and 65.5 mm from March to May 2008. It is well known that plant growth and tiller formation are very sensitive to water stress (Busso et al., 1989; Briske & Richards, 1995). Mohammad et al. (1982) found that the amount of regrowth in *Agropyron desertorum* and *Elymus junceus* was inversely related to the increased water

stress to which plants had been previously exposed. The low rainfall during the most active growth period (early to mid-spring: September to November) in 2008-2009 and the cumulative effects of two successive years of two severe defoliations annually (which determined substantial reductions in [1] tiller numbers per plant, [2] production of daughter tillers per cm², and [3] total leaf length per cm²) contributed to reductions in plant dry weight per cm² between the first and second years. The negative effects on plant growth of the combined influence of water stress periods and at least one severe defoliation during two or more consecutive years have been demonstrated in various perennial grass species from temperate regions (Busso et al., 1989, 2003). Like in our study, these research works indicated that the difference in plant responses between consecutive years can have a great biological significance.

In 2007-2008, dry weight production per cm² was greater on defoliated than on undefoliated plants of all species. This indicates that defoliated plants overcompensated the tissue lost to defoliation and it is an indication of defoliation tolerance. This response agrees with results in several perennial grasses when the active meristems remained on the plants after defoliation (Becker et al., 1997b). Also, and although it was not significant, defoliated plants of *P. vaginatum* showed three times increase in aboveground dry weight per cm² in comparison to undefoliated plants in 2008-2009. At the same time, however, aboveground dry weight per cm² of defoliated plants did not tend to be greater than on undefoliated plants on *A. spegazzinii* and *A. subulata*. Climate on semi-arid and arid areas has a

great influence on plant populations not only because precipitation is low but also because its distribution during the growing season is unpredictable (Huxman et al., 2004). Plant mortality is correlated with extended low precipitation periods (Turner, 1990).

We observed overcompensation on forage production in 2007-2008, and exact compensation in 2008-2009 on defoliated plants of all species. These results indicate that defoliated plants grew faster than those undefoliated, which allowed defoliated plants to overcompensate or exactly compensate forage production. These responses on defoliated plants have been reported for a great variety of perennial grasses (Noy-Meir, 1993) and other herbaceous species (Paige, 1992). Plants defoliated early or at the middle of the growing season had more time to recuperate their lost tissues to defoliation and most active meristems remained on the plants after defoliation (Becker et al., 1997a). In addition, values of leaf production remained similar on all plants in 2007-2008 and 2008-2009, even after two defoliation events during each growing season.

Cavagnaro & Dalmaso (1983) also studied the response of *Pappophorum caespitosum* to clipping at different heights and frequencies at the Monte in Argentina. They found that clippings at 15 cm stubble height produced the highest values of productivity. Clippings at 5 cm stubble once a year and those made every two months greatly reduced productivity, reducing the alive crown to the 5%. Drought also reduced dry matter production and plant survival. Even though it is a different species of the same genus, *P. caespitosum* always showed a rapid regrowth response to

precipitations, even lower than 10 mm under field exclosures (without grazing conditions) (Dalmasso, 1994).

We have to acknowledge a limitation in this study: the native species are attempted for grazing, but they were assessed under clipping. It is well known that clipping at a given height does not adequately mimic grazing. The primary reasons for this difference are that (i) grazing does not remove uniform amounts of forage from all tillers, hence tiller removal from plants is unrealistically severe, and (ii) grazing animals have substantial indirect effects such as soil compaction and recycling of nutrients via dung and urine (Asner et al., 2004). The greater production or growth on grazed plants than on clipped ones has been partially attributed to the non-uniform nature of herbivory (Parsons et al., 1984).

CONCLUSIONS

In the native species, and because of defoliation, we observed a reduction in the production of reproductive structures during the first study year, in plant height in both growing seasons, and in blade + sheath length during the second growing season. *Aristida subulata* was characterized for having a similar or greater basal area than the other species, with a greater tiller production per plant. *Sporobolus cryptandrus* showed a greater leaf production per unit basal area. However, its plants showed a reduced size and vigor. Besides, this species almost did not produce reproductive structures and had no activity during 2008-2009, possibly because of the scarce precipitations which did not appear to be sufficient to simulate regrowth in *S. cryptandrus*. During this year, the production of inflorescences

was reduced in *P. vaginatum* and in both *Aristida* species. A reduction in the reproductive effort because of the long-term effects of defoliation with or without drought conditions could eventually affect the persistence of these species in the plant community. Defoliated plants were able to have a similar leaf length during the first growing season, and a similar number of parent and daughter tillers and leaf numbers in both growing seasons, as control plants. Hilbert et al. (1981) reported that low growing species may require only a slight increase in their growth rates to replace tissues lost to defoliation. This suggests that the studied grazed species would be adapted to the grazing pressures to which they are exposed continuously. Species with a long herbivory history appeared to have developed certain tolerance to defoliation through evolution of morphological and physiological adaptations (Heady & Child, 1994). *Pappophorum vaginatum* showed a similar or greater daughter tiller production, number of reproductive structures, plant height and total leaf length as compared to the other species. Relative growth rates for tiller height were greater on defoliated and undefoliated plants of *P. vaginatum* than on the other species by mid spring 2007-2008, and early summer 2008-2009. Because greater growth rates are positively related to competitive ability (Grime, 1979), our results suggest that *P. vaginatum* is a superior competitor when compared to the other study species. Rapid growth rates after defoliation also contribute to herbivory tolerance (Briske & Richards, 1995). In addition, at the same study site, *P. vaginatum* showed a greater root proliferation (Torres et al., 2015) and colonization of its root system by fungi

forming arbuscular mycorrhiza (Torres, 2011). These above- and belowground traits in *P. vaginatum* might contribute to the persistence of this species under the effects of grazing and drought in rangelands of central Argentina.

Finally, studies of Entío (2019) on various populations of *P. vaginatum* showed that there was a great variability in the number of spikelets per plant on reproductive tillers between different genotypes within a same population (range=800-1600 spikelets per plant). This highlights the potential that this species has to be improved by genetic programs on the number of spikelets produced per plant. The production of such a high number of light, hairy spikelets per plant during a growing season raises the question of whether sexual reproduction is more or less important than asexual reproduction to determine the long-term persistence of this species on grazed rangelands of central Argentina.

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