Plant growth and survival of five perennial grass genotypes exposed to various defoliation managements in arid Argentina

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Abstract

The field performance of the native *Pappophorum vaginatum*, the naturalized *Eragrostis curvula*, and various cultivars of the introduced *Achnatherum hymenoides* and *Leymus cinereus* were evaluated as potential forage resources in rangelands of arid Argentina during the warm-seasons of 2007/2008 and 2008/2009. Plants of these grass species, obtained from seeds, were transplanted to the field in 2006, when they were one-year-old. During the study years, there were two defoliation managements: plants of all study genotypes either remained undefoliated (controls) or were defoliated twice a year during spring at 5 cm stubble height. Despite tiller number being lower ($p<0.05$) on defoliated than on undefoliated plants, and total leaf length per unit basal area being similar ($p>0.05$) between defoliation managements by mid-spring, there were no differences ($p>0.05$) in dry weight production between defoliated and undefoliated plants in all genotypes at the end of the second growing season. Plants of one or more of the introduced genotypes showed a similar ($p>0.05$) or greater ($p<0.05$), but not lower, tiller number per plant and per cm^2, daughter tiller production, total leaf length, and dry weight production per unit basal area than the native species at the end of the first and/or second growing seasons. These morphological variables were similar ($p>0.05$) or greater ($p<0.05$) in the native than in the naturalized genotype. Plant survival, however, was lower ($p<0.05$, overall mean= 20%) in the introduced than in the native (> 70%) or naturalized (> 39%) genotypes at the end of the first or second growing seasons.

Keywords

Achnatherum hymenoides, Eragrostis curvula, *Leymus cinereus, Pappophorum vaginatum*, plant demography, plant growth

Introduction

The cattle production industry in 75% of continental Argentina, characterized by arid and semiarid areas, is based upon grazing of native vegetation (Fernández and Busso, 1999). Unfortunately, most of these areas have been exposed to grazing and fire mismanagement, resulting in shrub enchroachment and the local disappearance of acceptable perennial forage grasses for cattle grazing (Fernández and Busso, 1999). As a result, rangelands of central Argentina have few warm-season, native perennial grasses that are acceptable forages to grazing livestock (i.e., *Pappophorum vaginatum*; Busso *et al,* 2004a). Therefore, there is an imperative need to increase perennial grass species in this region (Anderson, 1980) to address the increasing cattle production and need for additional forage. Severe water stress, especially during the warm-season, is another constraint the vegetation might eventually be exposed to (Giorgetti *et al*., 1997). The need to develop more appropriate forage resources for semiarid grasslands and rangelands was emphasized by various researchers worldwide (Torres, 2010).

Various C_3 perennial grass genotypes were worthy of consideration to complement use of the native/naturalized genotypes in our region. Those genotypes, coming from the western arid and semiarid U.S.A. rangelands, included (1) *Leymus cinereus* cvs 'Magnar' and 'Trailhead', and (2) *Achnatherum hymenoides* (Roemer & J.A. Schultes.) Barkworth cvs. 'Paloma', 'Nezpar' and 'Rimrock'. These genotypes grew during the warm, but not the cool, season in our region. An additional, warm-season, perennial grass tested in the region was *Eragrostis curvula* cv. 'Tanganyika'.

Results on productive performance and plant survival in native versus introduced species are scarce (Wilsey and Polley, 2006) and contradictory (Vilá and Weiner, 2004). There are examples where the introduced species have responded very flexible and optimally to the colonized environment either growing more vigorously or distributing

more resources to reproduction (Maron *et al*., 2004). However, it needs also be considered that native species of any given environment are adapted to the local conditions of such environment. Therefore, greater plant establishment and persistence should often be expected for native than for introduced species. Insufficient water availability has been mostly the responsible of failures in the attempts of introducing plant species in arid rangelands (e.g., Bleak *et al*., 1966). These authors 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.

There are several examples, however, where introduced species have contributed to increase forage supply in cultivated and rangeland areas of Argentina and other countries: (1) *Agropyron desertorum* (Fischer ex Link) Shultes from Eurasia into the Western U.S. rangelands; (2) *Eragrostis curvula* (Schrader) Nees and *Tetrachne dregei* Nees, from South Africa into the cultivated area of the semiarid Pampas region, and into the central rangelands of La Pampa Province, Argentina, respectively, and (3) *Cenchrus ciliaris* L. from Africa into the Catamarca Province, Argentina (Briske and Richards, 1995; Fernández *et al*. 1991; Ruiz and Terenti, 2012). Among the reasons for these successes are (a) a greater competitive ability than the native forage grasses, and (b) a high plasticity to various habitat conditions (i.e., extreme pHs, water stress, soil types) (Fernández *et al*., 1991; Briske and Richards, 1995; Ruiz and Terenti, 2012). Therefore, we can expect that traits related with high competive ability to various habitat conditions might be useful characteristics that could make plant introductions successful.

Several studies have been made on the morphophysiology, demography, plant growth and responses to grazing in *P. vaginatum*, *L. cinereus, A. hymenoides and E. curvula* (Fernández *et al*., 1991; Ogle *et al*., 2002; Torres *et al.*, 2011). Although there

are many studies, it is not clear yet which are the mechanisms responsible for grazing tolerance in these species. In addition, performance of the introduced genotypes might be different in Argentina than in other locations where previous work has been done. This is because climate and soil physico-chemical characteristics influence species introductions into degraded areas (De Graaf *et al*., 1998).

Tolerance to defoliation is given by the speed of photosynthetic surface reestablishment after such disturbance is produced (Briske and Richards, 1995). Rapid daughter tiller production is a major factor contributing to defoliation tolerance (Briske and Richards, 1995). Timing of defoliation has direct effects on subsequent shoot growth rates, and plant dry matter production and survival (Briske and Richards, 1995). Greater total leaf lengths have been produced after active meristems remain on the plant after defoliation (Becker *et al*., 1997). Therefore, we hypothesize that a greater daughter tiller production in the native and naturalized than in the introduced grasses determine a greater dry matter production in *P. vaginatum* and *E. curvula* than in the other introduced genotypes.

Objectives of this work were: to compare productivity, survival, and some morphological traits that might contribute to determine grazing tolerance of seven perennial grass genotypes (one native, one naturalized, and five introduced) under two defoliation managements (undefoliated controls versus early and midseason defoliations) during each study growing cycle. These objectives would contribute to develop a better understanding of grass growth response to aid management.

Materials and methods

Study site

We conducted one study spanning two years (2007/2008 and 2008/2009), involving genotype and defoliation treatments, and multiple measurements. Studies were performed in the Chacra Experimental de Patagones, Buenos Aires, Argentina (40º 39' 49.7" S; 62º 53' 6.4" W; 40 m.a.s.l.), within the Phytogeographical Province of the Monte (Cabrera, 1976).

Climate is temperate arid to semiarid, with higher precipitations during the spring and fall seasons (Giorgetti *et al*., 2000). Long-term (1981-2009) annual rainfall is 412.9 ± 159 mm (mean ± 1 S.D.), with a mean annual temperature of 14.6 ^{o}C, absolute minimum temperature of -7.6 ^{o}C (August), absolute maximum temperature of 43 ^{o}C (January), mean annual relative humidity of 60%, and mean annual wind speed of 13 km h^{-1}. Mean rainfall values from September to May (the warm-season growing period) were 178 and 135 mm during 2007/2008 and 2008/2009, respectively. These values were lower than the long-term average (1981-2010; 336 mm) during that growing period. Within the region, fertilization and irrigation are not an option: 55% of the years within the long-term mean (1981-2009: 412.9 mm; range=195.5 to 877.3 mm) have showed an annual precipitation equal to or lower than 390 mm. High variability in annual precipitation is typical of arid environments (Noy-Meir, 1973). Climate conditions were registered by a meteorological station located at the study site and are depicted in Figure 1.

Soil is a typical Haplocalcid. Average pH is 7, and depth is not a constraint 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 and Bóo, 1996). A description of the study species is provided in Table 1.

Experimental design and defoliation managements

Plants used in this study were obtained from seeds in the laboratory during spring 2005. Pre-germinated seeds were put on plastic pots (10 cm diameter, 15 cm height) which remained under natural, rainfed conditions until transplanting time in 2006. Thereafter, this study was conducted on a natural grassland excluded from grazing; one exclosure (30 x 40 m) to domestic livestock was established on this grassland. The natural vegetation within the exclosure was taken out from the soil by hand, trying to make the least amount of soil disturbance.The soil had not been cropped during at least the last 30 years. The experiment was initiatied on November 2006, by establishing 98 single-genotype plots from one-year-old transplant [7 genotypes (*P. vaginatum; L. cinereus* cvs. 'Magnar'and 'Trailhead'; *A. hymenoides* cvs. 'Paloma', 'Nezpar' and 'Rimrock'; *E. curvula* cv. Tanganyika) x 2 defoliation managements (unclipped controls or plots clipped twice during the growing period) x 7 replicate]. A completely randomized design was used during plot establishment. Each plot constituted an experimental unit. Defoliation managements were applied at random within each set of single-genotype plots. Plants on these plots were irrigated during spring 2006 and allowed to establish during a year previous to the study initiation in 2007/2008 and 2008/2009. We used vigorous transplants, instead of obtaining plants directly from sowing at the field, to better ensure successful plant establishment. Within each plot, plant distance among plants in horizontal and vertical lines was 30 cm (from center to center on each plant crown; 3 x 4 = 12 plants). In this way, competitive relationships among plants were most likely similar. Similar approaches for transplant disposition within plots have been

reported in other studies (Flemmer *et al*., 2002). During the study, plants were exposed to natural rainfall.

The first defoliation (i.e., clipping) was made using scissors during winter (the plant dormancy period) across all plants (i.e., across all plots) of the seven genotypes to remove aftermath in 2007. The purpose was that only aerial plant growth produced above 5 cm stubble during the following warm growing season was used for sampling. This defoliation did not count as a treatment since plant were dormant at this time (i.e., aerial tissues were dead at this removal time, and then it was not the commencement of the defoliation managements). Defoliating plants while they are in a dormant stage, with minimal physiological function, does not influence future plant performance (Schacht *et al*., 1998). Thereafter, plants in half of the plots were defoliated twice within each of the study growing cycles (i.e., the defoliation treatment was repeated for all plants on both dates each growing cycle). During 2007/2008, defoliations were made on 5 and 11 November (mid-spring) 2007, and during 2008/2009, they were done on 19 November and 20 December 2008 (late-spring). In the other half of the plots, the control plants were defoliated in winter 2007 and 2008 (i.e, during the dormancy developmental morphology stage), and in fall 2008 and 2009, respectively, so their biomass was the forage accumulated during each growing season. Defoliation treatments were delayed in the second growing cycle because of a lower rainfall during September to December in 2008/2009 (see Fig. 1: 62 mm; i.e., a smaller plant growth) than in 2007/2008 (125.5 mm). This defoliation management mimics the short duration – high intensity, rotational grazing system applied at the ‘’Monte’’ vegetation in the Chacra Experimental of Patagones (see Giorgetti *et al*., 2006 for details; mean= 29.2 animal unit/ha). Within this system, some acceptable forage can be grazed twice by grazing livestock during their at least 30-day-stay in the paddocks (Giorgetti, 1995). In Argentina, an animal unit is

defined as the annual average dry forage requirement of a 400-kg cow that goes through gestation and subsequent nursing of a calf, until the 160-kg, 6-month-old calf is weaned, including the forage consumed by the calf (Giorgetti *et al*., 2006). Defoliations were applied to the same plants in each year. In all cases, plants were defoliated leaving 5 cm stubble height. Defoliations were made during the vegetative stage and immediately after differentiation of the growth apex from vegetative to reproductive. It means that actively growing meristems (intercalary and leaf primordia in the gowth apex) remained on the plants after the defoliation events.

We have to acknowledge the fact that there were not any plants that remained undefoliated throughout the entire study. Table 2 shows a detail of all defoliations made in this study, including an explanation as why they were conducted.

Measurements

A summary of measurements made, measurements dates and why they were taken is provided in Table 3. A more detailed description follows:

Height of the apical meristem Tillers of all seven genotypes were dissected every two weeks (Table 3) and observed under a binocular microscope to determine both the developmental stage and height of the apical meristem.

Components of leaf area production Tiller growth and demography were periodically determined. Ninety eight randomly chosen plant were marked for this purpose (one per plot) in 2007/2008; we used 70 plants during 2008/2009 because *A. hymenoides* cvs. 'Nezpar' and 'Rimrock' were unable to persist after the drought years and defoliation managements. On each one of these plants, one current-season tiller was

permanently marked with wire cables. Plant circumference of green basal areas (it was used to calculate total green basal area), number of total tillers, and number of daughter tillers produced by each marked tiller were determined on each plant. Total tiller number per plant was divided by total green basal area to obtain tiller number/cm^2. In addition, total leaf length [blades + sheaths (green + dry)] was measured on each marked tiller. These measurements followed Busso *et al*. (2003). Total leaf length data were used to calculate growth rates following Larcher (2003). The timing for the measurement of each variable is indicated in Table 3.

Aboveground biomass production Aboveground biomass was harvested using scissors at the time of defoliation (springs 2007 and 2008) on defoliated plants, and at the end of the growing seasons (autumns 2008 and 2009) in all study plants. This allowed to obtain the total aboveground biomass productions of defoliated plants and undefoliated controls during 2007/2008 and 2008/2009. All plant materials were dried to 70ºC for 72 h and weighed.

Plant survival At the end of fall 2008 and 2009, number of surviving plants (SP; plants which regrow and continue growing) was counted in each of the 98 experimental plots. This allowed obtaining percentage plant survival (PS) at a plot scale as:

$$PS = SP / IN \times 100 ,$$

where IN = initial plant number/plot (=12).

Statistical analyses

Our treatments were combinations of genotype x defoliation management. Therefore, we used a factorial treatment design (7 genotypes x 2 clipping

managements) with 7 replications/treatment. Data were analyzed using the statistical software INFOSTAT (Di Rienzo *et al*., 2009). Variabes that were periodically evaluated were analyzed using repeated-measures two-way ANOVA. A mixed model ANOVA was used were genotype, defoliation management, and genotype x defoliation management were considered fixed effects, and sampling date, replication, and three-way-interactions with sampling dates were considered random effects. The multivariate approximation was used using the statistics of Wilks (Wilks, 1932). Whenever an average for all sampling dates (within each of the study years) is provided for any given variable within each defoliation management and genotype, it indicates that the multivariate analysis conducted using the Wilks' statistics was not significant ($p>0.05$). Otherwise, data are reported for each sampling date because of the interaction ($p<0.05$) between the factors (defoliation managements, genotypes) and the sampling dates. Numbers of daughter tillers/parent tiller were transformed to $\sqrt{(x+0.5)}$, and total dry matter production data were transformed to ln (x+1) to comply with the normality and homoscedasticity assumptions of variance (Sokal and Rohlf, 1984). Untransformed values are shown in illustrations. In all two-way ANOVA where the interaction genotype x defoliation management was significant, both factors were analyzed separately. Plant survival was analyzed using two-way ANOVA. Mean separation was conducted using protected LSD, with $p\leq0.05$. Some results were expressed on a per cm^2 basis for comparative purposes, because of plant size differences among the study genotypes. Combined analysis across the study years was not conducted since they showed similar ($p>0.5$) monthly precipitation and temperature values during the study warm-growing-seasons.

Results

Height of the apical meristem Mean height of the apical meristem at the time of the defoliation managements in 2008 and 2009 was less than or equal to 9.43 ± 0.90 mm (mean ± 1 SE, n=14) in all seven genotypes.

Green plant basal area Green plant basal areas were at least 40% greater in the native (mean ± SD: 77.1 ± 16.3 cm^2, n=22) than in the introduced genotypes (34.0 ± 13.0 cm^2, n=90) on average for 2007/08 and 2008/09. The only exception was *E. curvula* cv Tanganyika that showed at least a 47% greater green basal area than the other six genotypes on average for both years (data not shown). Because of differences in green plant basal areas among genotypes, most of the traits will be presented on a per cm^2 basis for comparative purposes.

Tiller growth and demography

Tiller number per plant Before defoliation in 2007/2008, tiller numbers of defoliated and undefoliated plants in the native species were similar ($p>0.05$) to those in *L. cinereus* cv. 'Magnar', and *A. hymenoides* cvs. 'Paloma' and 'Rimrock' (Figure 2). A similar ($p>0.05$) result was obtained immediately after defoliation on 24 November. (data not shown). During early summer (27 December), *A. hymenoides* 'Paloma' showed a 56% greater ($p<0.05$) tiller number than the native species and the remaining introduced genotypes. At the end of the growing season (29 February), tiller numbers of defoliated and undefoliated plants were similar ($p>0.05$) in the native species, and in *A. hymenoides* cvs. 'Paloma' and 'Rimrock' (Figure 2). At this time, tiller numbers on defoliated and undefoliated plants of the native species were similar ($p>0.05$) to those on undefoliated plants of *L. cinereus* cv. 'Magnar'; defoliation increased ($p<0.05$) tiller

numbers in *A. hymenoides* cv. 'Rimrock', and decreased ($p<0.05$) them in *L. cinereus* cv. 'Trailhead' (Figure 2). Other than these cases, defoliated and undefoliated plants showed a similar ($p>0.05$) tiller number in the native and introduced genotypes. Defoliated and undefoliated plants of *E. curvula* cv. 'Tanganyika' showed the greatest ($p<0.05$) tiller numbers among all genotypes, but on undefoliated *A. hymenoides* cv. 'Paloma', during the all growing season. By early (23 January) and late (29 February) summer, tiller numbers were greater (<0.05) on defoliated than on undefoliated plants of *E. curvula* cv. 'Tanganyika' (Figure 2).

At the beginning of the 2008/2009 growing season (17 October), tiller numbers were similar ($p>0.05$) in the native species and in *L. cinereus* cvs. 'Magnar' and 'Trailhead' (Figure 2). However, after the first and second defoliations towards the end of the growing season, tiller numbers were greater ($p<0.05$) in the native genotype than in *L. cinereus* cvs. 'Magnar' and 'Trailhead', and *A. hymenoides* cv. 'Paloma' (Figure 2). From mid-spring (18 November) onwards, tiller numbers were similar ($p>0.05$; overall mean undefoliated plants: 51.4 ± 3.0, defoliated plants: 38.1 ± 1.6) in the native and naturalized genotypes (Figure 2). Also, from mid-spring to the end of the growing season, defoliated plants showed at least a 12.4% lower ($p<0.05$) tiller number than the undefoliated controls in the native and naturalized genotypes, and in *L. cinereus* cvs. 'Magnar' and 'Trailhead', and *A. hymenoides* cv. 'Paloma' (Figure 2).

Tiller number per plant across all genotypes increased by more than 19% on undefoliated and 88% on defoliated plants from early spring to late summer in 2007/2008 (Figure 2). However, during early spring and late summer of the next year, tiller number per plant across all genotypes had decreased at least 54% on defoliated and undefoliated plants (Figure 2).

Tiller number per cm² Defoliation management and genotype interacted with time in 2007/2008 and 2008/2009. This is because data were analysed within each date. During most of the sampling dates during the first and second year, defoliated and undefoliated plants showed a similar ($p>0.05$) tiller number/cm^2 (30 Sept.: 1.46 ± 0.18, 25 Oct.: 1.45 ± 0.15 and 24 Nov. 2007: 1.38 ± 0.15; 29 Feb: 1.85 ± 0.19, 17 Oct.: 0.50 ± 0.08, 18 Nov.: 0.52 ± 0.10, and 17 Dec. 2008: 0.53 ± 0.11; 22 Jan.: 0.47 ± 0.11, and 26 Feb. 2009: 0.35 ± 0.10). The only exceptions were on 27 December 2007 and 23 January 2008, when tiller number/cm^2 was lower ($p<0.05$) on undefoliated (2007: 1.43 ± 0.24; 2008: 1.71 ± 0.30) than defoliated (2007: 1.88 ± 0.21; 2008: 2.35 ± 0.30) plants.

During the first and second years, tiller number/cm^2 was similar ($p>0.05$) between the native and naturalized genotypes (Figure 3). In both years, this variable was similar ($p>0.05$) or greater ($p<0.05$), but not lower, in the introduced than in the native or naturalized genotype (Figure 3). Plants of *A. hymenoides* cvs. 'Rimrock' and 'Nezpar', however, were dead by the initiation of the second year.

The reduction in tiller number/cm^2 across all genotypes between the first and second years was greater than 78% (Figure 3).

Daughter tiller production per unit surface area Defoliated and undefoliated plants of *A. hymenoides* cvs. 'Paloma' and 'Rimrock' showed a greater ($p<0.05$) daughter tiller production than the native and the remaining genotypes in 2007/2008 (Figure 4). In this year, production of daughter tillers by the native species was similar ($p>0.05$) to that of *L. cinereus* cv. 'Trailhead', *A. hymenoides* cv. 'Nezpar' and *E. curvula* cv. 'Tanganyika', and greater ($p<0.05$) to that in *L. cinereus* cv. 'Magnar' (Figure 4). During the following growing season (2008/2009), however, the greatest ($p<0.05$) daughter tiller production was determined in the native genotype, and

production of daughter tillers was similar ($p>0.05$) in the remaining six genotypes (Figure 4). In 2007/2008 and 2008/2009, daughter tiller production was similar ($p>0.05$) on defoliated versus undefoliated plants in all genotypes (Figure 4).

Between the first and second year, the reduction in the production of daughter tillers across all, but the native, genotypes was greater than 90% on defoliated or undefoliated plants (Figure 4). The only exception were the defoliated and undefoliated plants of *P. vaginatum*, which maintained an overall daughter tiller production of 0.0100 ± 0.0004 tillers/cm^2 between both years (Figure 4).

Total leaf length Before defoliation in 2007/08, total leaf length per unit surface area was similar ($p>0.05$) (1) among genotypes, and (2) between defoliated and control plants (Figure 5). The only exception was *A. hymenoides* cv. 'Nezpar' that showed greater ($p<0.05$) total leaf length than that in the other genotypes (Figure 5). After the two defoliations events in 2007, defoliated and undefoliated plants of (1) *Leymus cinereus* cv. 'Trailhead', and *A. hymenoides* cvs. 'Rimrock' and 'Nezpar' on 24 November 2007; (2) *A. hymenoides* cv. 'Nezpar' on 27 December 2007; (3) *L. cinereus* cvs. 'Magnar' and 'Trailhead', and *A. hymenoides* cvs. 'Paloma' and 'Nezpar' on 23 January 2008, and (4) *L. cinereus* cvs. 'Magnar' and 'Trailhead' and *A. hymenoides* cv. 'Nezpar'on 29 February 2008 showed at least 150% greater ($p<0.05$) total leaf lengths than those on the native species (Figure 5).

After defoliation, total leaf length was at least 15% lower ($p<0.05$) on defoliated than on undefoliated plants in all genotypes from 24 November 2007 to 29 February 2008 (Figure 5). The only exception was on *L. cinereus* cv. 'Magnar' where total leaf length was similar ($p>0.05$) on defoliated than on undefoliated plants on 29 February 2008 (Figure 5).

In the next growing cycle (2008/09), defoliated and undefoliated plants of (1) *L. cinereus* cvs. 'Magnar' and 'Trailhead' and *A. hymenoides* cv. 'Paloma' on 17 October, and (2) *L. cinereus* cvs. 'Magnar' and 'Trailhead' on 18 November showed greater ($p<0.05$) total leaf length than the native species (Figure 5). On 17 October and 18 November 2008/2009, defoliated and undefoliated plants showed similar ($p>0.05$) total leaf lengths in all genotypes (Figure 5). From 17 December 2008 to 26 February 2009, total leaf length was on average more than 70% greater ($p<0.05$) in *L. cinereus* cv. 'Trailhead' than in the native genotype, *L. cinereus* cv. 'Magnar', *A. hymenoides* cv. 'Paloma', and *E. curvula* cv. 'Tanganyika' (data not shown). Once again, defoliated and undefoliated plants showed a similar ($p>0.05$) total leaf length in *P. vaginatum*, *L. cinereus* cvs. 'Magnar' and 'Trailhead', *A. hymenoides* cv. 'Paloma' and *E. curvula* cv. 'Tanganyika' (data not shown).

In early spring, the total leaf length reduction across all genotypes from 2007 to 2008 was 80.9% on control plants, and 78.3% on defoliated plants (Figure 5). By late summer, the reduction of total leaf length across all genotypes between the first and second year was more than 66% on defoliated and undefoliated plants (data not shown).

Total dry weight production No significant differences ($p>0.05$) in production of total dry weight were found among genotypes during 2007/2008 (Figure 6). At the same time, however, total dry weight production was greater ($p<0.05$) on defoliated than on undefoliated plants of all genotypes (Figure 6). During 2008/2009, *L. cinereus* cv. 'Magnar' showed a greater ($p<0.05$) total dry weight production than the native genotype, while production of total dry weight was similar ($p>0.05$) in *P. vaginatum* than in *L. cinereus* cv.'Trailhead', *A. hymenoides* cv. 'Paloma' and *E. curvula* cv.

'Tanganyika' (Figure 6). Total dry weight production was similar ($p>0.05$) on defoliated versus undefoliated plants in all study genotypes in 2008/2009 (Figure 6).

There was a substantial reduction in total dry weight production across the genotypes on defoliated (76.1%) and undefoliated (59.7%) plants between the first and second year (Figure 6).

Plant Survival Greatest ($p<0.05$) percentage survival at the end of the 2007/2008 growing season was found on defoliated and undefoliated plants of the native (mean= 83.3%) and naturalized (mean=74.4%) genotypes (Figure 7). These values approximately double those found in the introduced genotypes (overall mean=36.9%), but *A. hymenoides* cv. 'Nezpar' that presented the lowest ($p<0.05$) plant survival (Figure 7). During the second growing season (2008/2009), defoliated and undefoliated plants of the native species showed the greatest ($p<0.05$) plant survival (mean=71.4%, Figure 7). Percentage survival was on average 35% lower ($p<0.05$) in the naturalized genotype, that presented greater ($p<0.05$) values than on those introduced (Figure 7). Defoliated and undefoliated plants of *A. hymenoides* cvs. 'Nezpar' and 'Rimrock' were dead at the end of the 2008/2009 growing cycle (Figure 7). Plant survival was greater on undefoliated than defoliated plants across all genotypes during both growing seasons (Figure 7).

Discussion

At least during the first three years of growth and development in this species, height of the growth apex was below 1 cm from the soil surface during spring in the northwestern region of arid Patagonia, Argentina. This finding is important since livestock could graze *L. cinereus* genotypes during spring without removing most active intercalary and

apical meristems, at least during the first two years after plant establishment. This means that growth will keep fast after spring grazing, since growth rate is fastest from intercalary meristems, intermediate from the leaf primordial in the growth apex, and lowest from the activation and subsequent outgrowth of the axilary buds (Briske and Richards, 1995). Since active meristems remained on the plant after the defoliation events, they might be able to recuperate their tissues lost to defoliation. However, the fact that active meristems measured in this study were at 1 cm did not guarantee persistence of *L. cinereus* in our study. This was the result that *Leymus* genotypes defoliated at 5 cm, in a spaced plant situation, loss 60% of the plants in the first season and more than 80 % in the second. Other studies in the western rangelands of the U.S.A. have reported that this genotype needs to be clipped to no less than 30 cm height for reducing grazing damage (USDA, NRCS, 2000).

Plants of *Eragrostis curvula* cv 'Tanganyika' showed the greatest basal area during the first and second years, and the greatest tiller number per plant during the first growing season among all genotypes. Fernández *et al*. (1991) reported that vegetative tillers in *E.curvula* cv. 'Tanganyika' multiply rapidly during the growing season such as hundred of thems can be originated on a plant basis during the plant establishment year under favorable biotic and abiotic conditions. During the first year, defoliation increased tillering in *E. curvula*. Tillers at the periphery are often exposed to a greater radiation intensity than those at the plant center, where shading might be high (Briske and Richards, 1995). Defoliation might have reduced shading, and increased the quantity and quality of light reaching the crown at the plant center. The positive effects of defoliation on tillering of *E. curvula* were only shown during the first year. During the second year, tiller numbers per plant in December on plants of all genotypes, and those

of *E. curvula* were similar to those in the native species from before the first defoliation to the end of the growing season.

The cumulative effects of two successive years of severe defoliations reduced tiller number on plants of all genotypes. These adverse effects of defoliation on tillering of perennial grasses have been reported by various authors (Briske and Richards, 1995). Defoliation has caused (1) inhibitory effects on activation and viability of axillary buds (Busso *et al*., 1989); (2) a reduction in carbon reserve availability, that allows initial re-growth when a photosynthetic surface area is not available after a disturbance (Busso *et al*., 1990), and (3) a lower survival of growing tillers (Busso *et al*., 1989).

Plants of the native species showed a greater basal area, and have a similar or lower tiller number, than those of the introduced genotypes, especially with respect to *L. cinereus*, after the first-year defoliations. At this time (i.e., end of the first growing season), tiller number on defoliated plants was similar or greater, but not lower, than that on undefoliated controls in all genotypes (but *L. cinereus* cv. 'Trailhead'), which is an indication of defoliation tolerance. *Pappophorum vaginatum* was affected by defoliation during the second study year, which produced a reduction in the basal area of their plants. The only genotype that showed an equal or greater tiller number per plant than *P. vaginatum* in the first growing season was *A. hymenoides* cv. 'Paloma'. This introduced species was unable to have a greater basal area, but its tillers were thinner (Torres, 2010), than those in the native genotype.

At the beginning of the growing season, regrowth from axillary meristems was about 3 weeks earlier in *L. cinereus* cv. 'Magnar' than in *P. vaginatum*. This response in cv. 'Magnar' would contribute to an earlier occupancy of the more favorable soil parcels, which in turn should improve competitive effectiveness. Favorable soil microsites may be important areas of root competition (e.g., Jackson and Caldwell, 1989). This could

help explain the earlier shoot regrowth in early spring in *L. cinereus* than in *P. vaginatum*. The fact that the C_3 genotype started growth earlier than the C_4 one agrees with the report of Niu *et al*. (2008). These authors stated that the C_3 species begin growth in early spring as soon as the soil is above freezing, while C_4 species grow during warmer periods.

In the two study growing seasons, total leaf length was most often greater in the introduced *Achanatherum* or *Leymus* species than in the native genotype. Even more, total leaf length in 2007/2008 was greater on defoliated than on undefoliated plants of *L. cinereus* cv. 'Magnar', thus showing tolerance 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 than on undefoliated plants in all study genotypes. 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.

Except for *L. cinereus* cv. 'Magnar', where daughter tiller production was greater in the native than in the introduced genotype, daughter tiller production was similar or greater in the introduced genotypes than in the native species in the first growing season (2007/08: 222.5 mm from September 2007 to May 2008; 123 mm from September to November 2007). The dry 2008/2009 growing season (September 2008 to May 2009: 131.5 mm; 29.5 mm from September to November 2008), might have contributed to determine a lower daughter tiller production in the introduced and naturalized than in the native genotype. In both years, daughter tiller production was similar on defoliated than on undefoliated plants in all genotypes. It means that defoliation did not hinder daughter tiller production, which we know contributes to defoliation tolerance (Briske and Richards, 1995), even under dry conditions.

The serius reduction in tiller numbers, especially daughter tiller numbers, on defoliated and undefoliated plants across all genotypes 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 undefoliated controls in that treatment. Flemmer *et al.* (2002) 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 non-structural carbohydrates were positively associated with early spring tiller regrowth on two perennial bunchgrass species (Busso *et al*., 1990). Thereafter, we suggest that the great reduction in tiller numbers from one year to the next in our study could be a sign of a depleted plant both axillary bud bank and energy reserves. These two factors might have contributed to the high plant mortality at the end of the study in the introduced genotypes. Additionally, Hodgkinson (2010) reported that the density of live tillers generally declined on plants of the perennial grasses *Ausrodanthonia auriculata*, *Bothriochloa macra*, *E. curvula*, *Phalaris aquatica* and *Themeda triandra* as they remained under drought conditions. Even more, 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*.

After the second defoliation in 2007/2008, by mid spring, growth rates (on a total leaf length basis) were between 0.009 ± 0.001 and 0.205 ± 0.081 cm/cm^2/d on defoliated and 0 cm/cm^2/d on undefoliated plants of all genotypes. Rapid leaf replacement after defoliation is a critical component of defoliation tolerance in various perennial grass species (Briske and 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 and Richards, 1995). Rapid leaf replacement after defoliation in other grasses have been attributed to compensatory photosynthesis on leaf and stem tissues, increases in tissue longevity, or increases in the water status of defoliated plants (Briske and Richards, 1995). Leaf replacement was rapid immediately after defoliation. However, it was not great enough as to allow leaf lengths to be either similar or greater on defoliated than on undefoliated plants in all genotypes during the first year (but in *L. cinereus* cv. 'Magnar').

Leaf lengths per unit basal area between both defoliation managements in all genotypes were similar immediately after defoliation in 2008/2009. Water stress conditions at this time (during November and December, when defoliation occurred, rainfall was 0.5 and 32.5 mm, respectively, and potential evapotranspiration was 139.8 and 155.4 mm, respectively) 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 observed in various perennial grasses (Busso *et al*., 1989; Busso *et al*., 2003).

Dry matter production was similar in the native than in most of the introduced genotypes during both study years. During the second growing season, dry matter production was similar in the native and naturalized species, but greater in *L. cinereus* cv. 'Magnar' than in the native species. Defoliated plants of all genotypes showed a greater dry matter production than the undefoliated ones during the first study year. This is an indication that defoliated plants tolerated defoliation. However, the dry 2008/2009 may have constrained defoliated plants from reaching a greater dry matter production than their undefoliated counterparts. 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 scarce rainfall (29.5 mm, Figure 1) 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 tiller numbers per plant, production of daughter tillers/cm^2, total leaf length/cm^2, and plant survival) contributed to determine important reductions in plant dry weight/cm^2 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 range perennial grass species from temperate regions (Busso *et al.* 1989; Busso *et al*. 2003). Like in our study, these research works indicated that the difference in plant responses between consecutive years can be of a very biological significance.

We have to highlight that the drier 2008/2009 than 2007/2008 conditioned plant responses to defoliation, and increased difficulty in result interpretation. It is well known that plant growth and survival, and tiller formation are very sensitive to water stress (Busso *et al*., 1989; Briske and Richards, 1995). The native and naturalized

species and *L. cinereus* showed a better performance than the remaining genotypes after defoliation under water stress in the growing season of 2008/2009. Blades of *L. cinereus* cv. 'Trailhead' which grew at the study site, for example, showed osmotic adjustment (Torres *et al*., 2010). This physiological mechanism allows plants to sustain leaf growth under severe water stress conditions (Kirkham, 2005). *Achanatherum hymenoides* cvs. 'Nezpar' and 'Rimrock' showed an important leaf production (Torres, 2010), but they did not survive beyond the first study year.

Plant survival was greater in the native species than in the introduced genotypes. Similar results have been reported for other species in *Pappophorum* under grazing conditions (Privitello *et al*. 1998). Survival values shown by *L. cinereus* and *A. hymenoides* after two years of study were lower than those reported by other authors on different environmental conditions and defoliation managements (Tilley, 2005). However, several authors reported difficulties for plant establishment of *L. cinereus* and *A. hymenoides* in various semiarid regions of the U.S.A. (Vogel and Jensen, 2001). In this study, plants were grown from seeds at the greenhouse, and seedlings were transplanted to plots on single rows of space-transplanted plants on 1.1m centers. Fernández *et al*. (1991) reported that failure of *E. curvula* introduction in the study region is due to its reduced seed size, and low growth rates when precipitations are low.

Climate on semiarid 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 establishment is often related to high precipitations during certain times, while plant mortality is correlated with extended low precipitation periods (Turner, 1990). Bleak *et al*. (1966) and Roundy (1985) already emphasized the high sensitivity of plant establishment to water stress of *L. cinereus* and *A. hymenoides* in areas receiving less than 200 mm annually. In

2008/2009, precipitations were 29.5 mm from September to November (the most active growing period); 92 mm from December to February, and 10 mm from March to May.

We have to acknowledge a limitation in this study: the introduced genotypes are intended 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 (a) grazing does not remove uniform amounts of forage from all tillers, hence tiller removal from plants is unrealistically severe, and (b) 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 than clipped plants has been partially attributed to the nonuniform nature of herbivory (Parsons *et al*., 1984).

We have to reject our hypothesis since daughter tiller production, and the subsequent dry matter production were most often similar or greater on the introduced than on the native genotype during the two study years. Plant survival at the end of the study, however, was greater in the native than in the introduced genotypes. Plant of these introduced genotypes showed a weakened stage into the second, dry year, leading to reduced growth variables, and a high plant mortality at the end of the study. As a result, further studies should focus on improving plant persistence of the study, introduced genotpes. There is a worldwide need for developing more appropriate forage resources for arid and semiarid grasslands and rangelands (Torres, 2010).

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Table 1. Some major characteristics of the perennial grass genotypes used in this study.

Genotype	Origin	Description	Reference
Pappophorum vaginatum	North and Central, up to northern Patagonia, Argentina	- Warm season, C_4 native bunchgrass acceptable to grazing livestock. - Mean biomass production (1984-1992)=560.9±130.8 kg/ha/yr (mean± 1 S.E.); reduced by overgrazing. - Tolerant to frost while dormant. - High seed production. - Seeds can not be seeded by conventional drilling because of diseminule morphology (hairy anthecia + long awn).	Cano, 1988; Giorgetti *et al*., 1997; Allen *et al*., 2011
Leymus cinereus cv. 'Magnar'	Saskatchewan, Canada	- Very drought tolerant, long-lived and productive. It withstands flooding. - Cool season, C_3, rhizomatous genotype acceptable to grazing livestock. - Excellent for enhancing soil structure. - Seeds can be seeded by conventional drilling.	Majerus, 1992; Johnson *et al*., 2003; Allen *et al*., 2011.
Leymus cinereus cv. 'Trailhead'	Roundup, MT, USA	- Same as 'Magnar', but also it can survive in areas with 150 mm annual precipitation.	Majerus, 1992; Johnson *et al*., 2003; Chambers and Miller, 2004; Allen *et al*., 2011.

Achanatherum hymenoides cv. 'Paloma', 'Nezpar' and 'Rimrock'	- 'Paloma': Pueblo, CO, USA - 'Nezpar': Whitebird, ID, USA - 'Rimrock': Billings, MO, USA	- Excellent for rangeland improvement and land reclamation. - Densely tufted, very drought tolerant, nutritious C_3 bunchgrasses acceptable to grazing livestock. - Seeds can be seeded by conventional drilling.	Jones, 1990; Allen *et al*., 2011.
Eragrostis curvula cv. 'Tanganyika'	South Africa	- Warm season, C_4 naturalized bunchgrass acceptable to grazing livestock. - Biomass production without fertilization of a seeded forage crop was between 4000 or 5000 kg/ha/yr depending on vegetation management (without or with fall resting from livestock grazing, respectively). - Tolerant to frost while dormant. - Drought tolerant. - Its establishment and subsequent performance is limited to a series of successive wet years. - Seeds can be seeded by conventional drilling.	Fernández *et al*., 1991.

Table 2. Summary of applied treatments, and treatment dates and purposes. Plant used during the second growing cycle (2008/2009) received the same treatments than those on the first growing cycle (2007/2008).

Treatment	Date of treatment (season; plant developmental morphology stage)	Purpose of treatment
Removal of aftermath at a 5 cm stubble height on all study plant (it was not the commencement of the defoliation treatments).	1 August 2007 (mid-winter; dormancy)	To determine aerial plant growth produced above 5 cm stubble during the following warm growing season, and various traits related with plant growth (see Table 3), as affected by two defoliation managements (clipping; unclipped controls)
Defoliated (clipped) plant		
1st year of treatment during the 2007/2008 growing cycle.	5 + 11 November 2007 (mid-spring; actively growing tissues) + 30 May 2008 (late autumn; dormancy)	To evaluate the cumulative effects of the first year of two defoliations on the same plant within the growing cycle on total plant production and various traits related with it (see Table 3 for measurements).
2nd year of treatment during the 2008/2009 growing cycle.	19 November + 20 December 2008 (late spring; actively growing tissues) + 3 June 2009 (late autumn; dormancy)	To evaluate the cumulative effects of a second year of two defoliations on the same plant within the growing cycle on total plant production and various traits related with it (see Table 3 for measurements).
Undefoliated plant		
1st year of treatment	30 May 2008 (late autumn; dormancy)	To evaluate total plant production, and various traits related with it (see Table 3 for measurements), during the first study growing cycle.
2nd year of treatment	3 June 2009 (late autumn; dormancy)	To evaluate total plant production, and various traits related with it (see Table 3 for measurements), during the second study growing cycle.

Table 3. A summary of measurements (unit) taken, and date and purpose of measurements. Results were expressed on a per unit surface area basis (i.e., per cm^2) because of inherent differences in tiller density (tiller number per cm^2) and plant basal area among genotypes.

Measurements	Date of measurements	Purpose of measurements
Apical meristem height (cm)	2007/2008: 10, 24 Sept.; 8, 22 Oct.; 9 Nov. 2008/2009: 9, 23 Set.; 7, 21 Oct.; 1, 18 Nov.; 2, 16 Dec.	To determine height of the tiller apical meristem as to leave it on the plant after the defoliation managements.
Plant circumference (cm)	2007/2008: 30 Sept.; 25 Oct.; 24 Nov.; 27 Dec.; 23 Jan.; 29 Feb. 2008/2009: 17 Oct.; 18 Nov.; 17 Dec.; 22 Jan.; 26 Feb.	To calculate plant basal area, and thereafter express results on a per unit surface area basis (i.e., cm^2), on all study genotypes.
Total (live + dry) plant tiller number	Same as for plant circumference in both years.	To determine the cumulative effects of defoliation on total plant tiller number, as a measure of plant size on the study genotypes.
Number of daughter tillers/parent tiller	Same as for plant circumference in both years.	To determine if, immediately after defoliation, any of the study genotypes showed higher production of daughter tillers than the undefoliated controls as a measure of defoliation tolerance.
Total tiller leaf length [blades + sheaths (green + dry); cm]	Same as for plant circumference in both years.	To determine the effects of the defoliation managements on leaf growth of the study genotypes at a tiller scale.
Total dry weight production (gr)	2007/2008: 25 April 2008. 2008/2009: 5 May 2009.	To evaluate the effects of the defoliation managements on total dry weight production of the study genotypes at the end of the growing cycles, after studying some major factors (see measurements above) that determine it.
Plant survival	2007/2008: 25 April 2008. 2008/2009: 5 May 2009.	To evaluate the effects of the defoliation managements on plant survival of the study genotypes at the end of each of the study growing cycles.

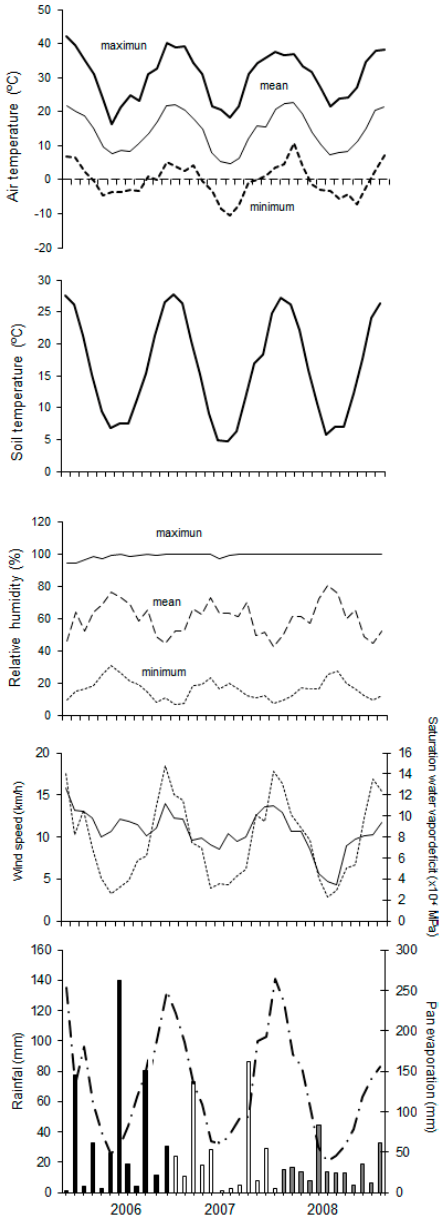

Figure 1. Absolute monthly maximum and minimum, and mean monthly air temperatures; mean monthly soil temperatures at 0-20 cm soil depth; absolute monthly maximum and minimum, and mean monthly relative humidities, mean monthly wind speed and saturation water vapour deficit, and mean monthly pan evaporation and monthly rainfall during 2006, 2007 and 2008 at a meteorological station located at the study site. Annual precipitations during 2006, 2007, and 2008 were 428.1; 287.5 and 198.0 mm, respectively.

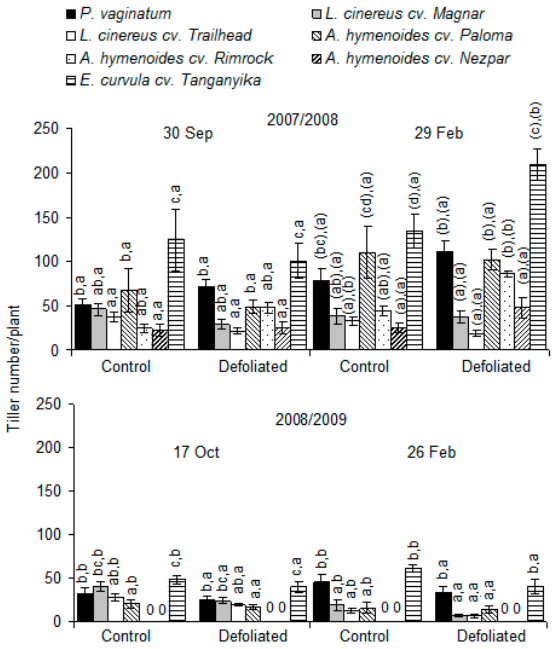

Figure 2. Tiller numbers on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. All plants were obtained from seeds. Each histogram is the mean ± 1 SE of n=7. Different letters above histograms indicate significant differences ($p<0.05$) among genotypes (first letter) or between defoliation managements (second letter). Letters in parenthesis indicate that there was an interaction ($p<0.05$) between genotype and defoliation management. In these cases, differences ($p<0.05$) among genotypes within each defoliation management (first letter), and between defoliation management within each genotype (second letter) are indicated in parenthesis. Presence of zero values indicates dead plants.

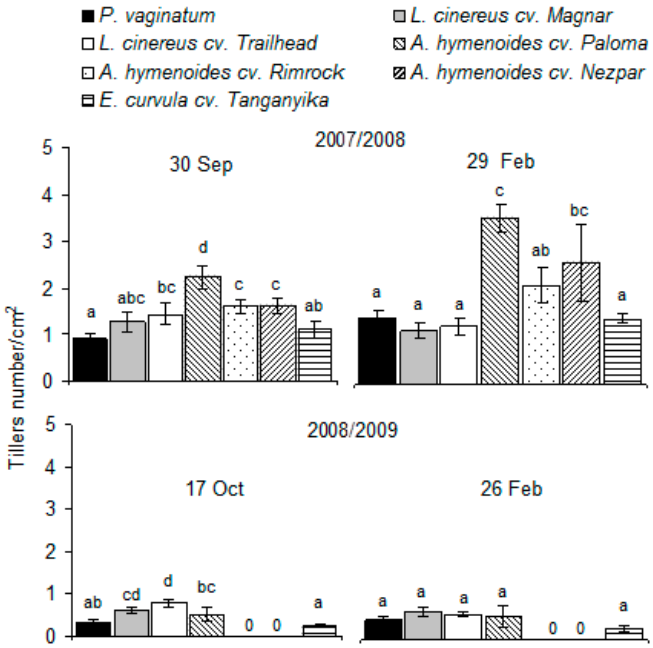

Figure 3. Tiller numbers per cm^2 of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. All plants were obtained from seeds. Data for Control and Defoliated plants were pooled after there were no significant differences ($p>0.05$) among them. Each histogram is the mean ± 1 SE of n=14. Within each date, different letters above histograms indicate significant differences ($p<0.05$) among genotypes. Presence of zero values indicates dead plants.

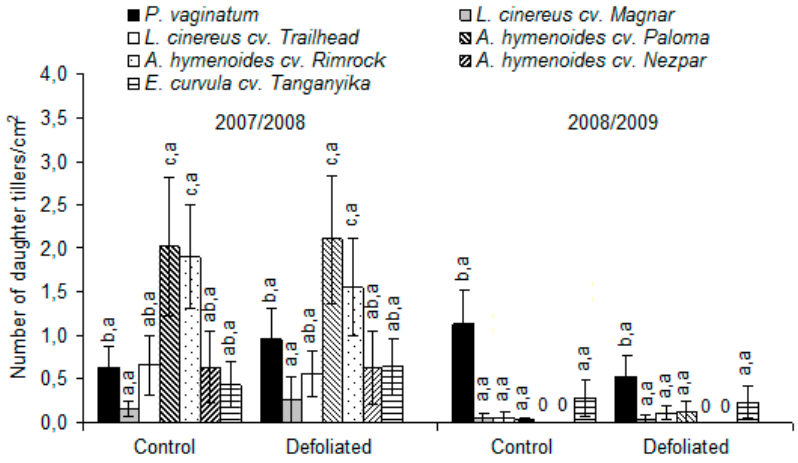

Figure 4. Number of daughter tillers/cm^2 on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. Each histogram is the mean ± 1SE of n=42 (2007/2008) or n=35 (2008/2009). Within each growing cycle, different letters above histograms indicate significant differences ($p<0.05$) among genotypes (first letter) or between defoliation managements (second letter). Presence of zero values indicates dead plants.

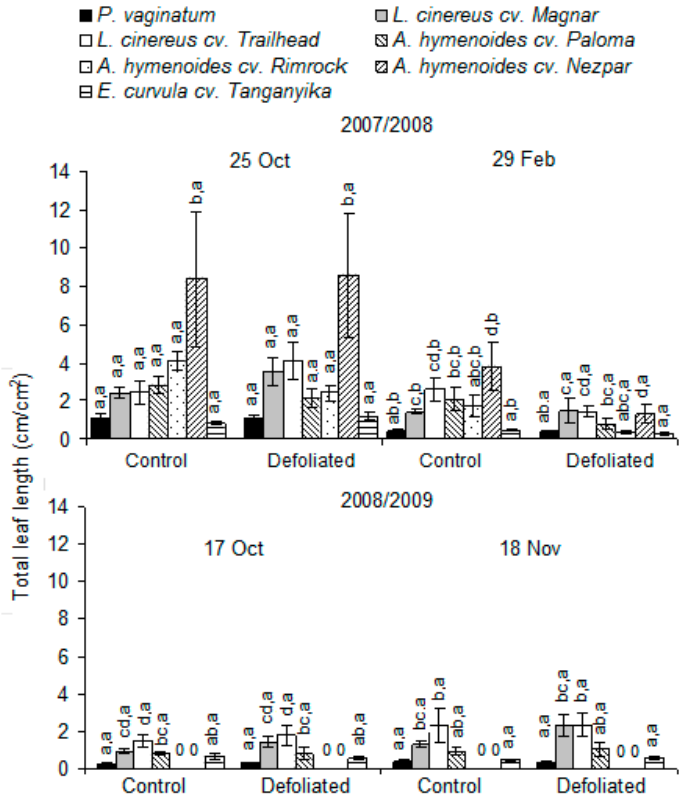

Figure 5. Total leaf length [length of total blades + sheaths (green + dry)/cm^2; cm/cm^2] on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. Each histogram is the mean ± 1 SE of n=7. Within each growing cycle, different letters above histograms indicate significant differences ($p<0.05$) among genotypes (first letter) or between defoliation managements (second letter). Presence of zero values indicates dead plants.

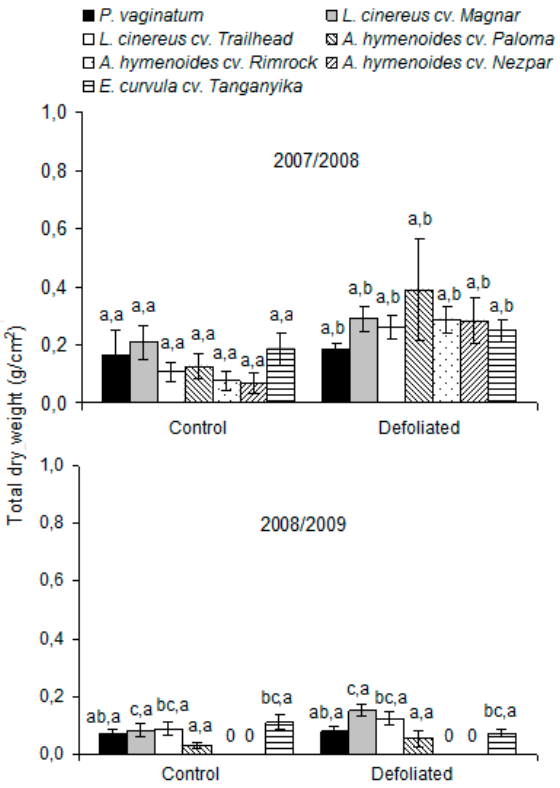

Figure 6. Total dry weight production/cm^2 in 2007/2008 or 2008/2009 on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated). Each histogram is the mean ± 1 SE of n=7. Within each growing cycle, different letters above histograms indicate significant differences ($p<0.05$) among genotypes (first letter) or between defoliation managements (second letter). Presence of zero values indicates dead plants.

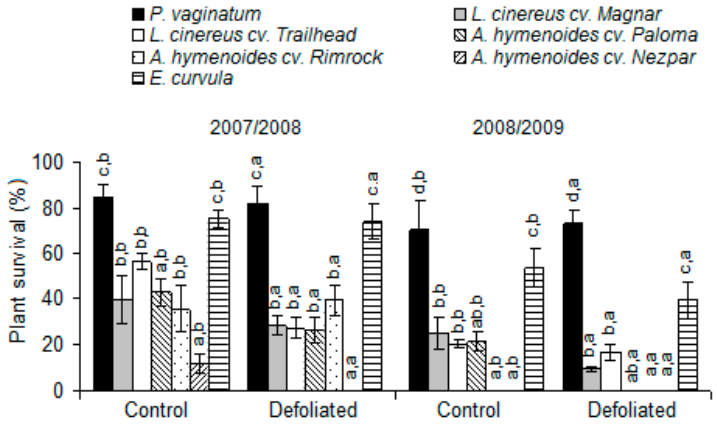

Figure 7. Percentage suvival of seven genotypes exposed to two defoliation managements (Control, Defoliated) at the end of the growing seasons of 2007/2008 or 2008/2009. Each histogram is the mean ± 1 SE of n=7. Absence of histograms indicates zero values (i.e., dead plants). Within each growing cycle, different letters above histograms indicate significant differences ($p<0.05$) among genotypes (first letter) or between defoliation managements (second letter).