The effect of defoliation management on tiller dynamics of prairie grass

Efecto del manejo de la defoliación sobre la dinámica del macollaje de cebadilla criolla

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Summary
An experiment was carried out at Pergamino Experimental Station, Argentina, to study the effects of defoliation management on tiller dynamics of prairie grass swards. There were four defoliation treatments resulting from the factorial combination of two frequencies (5 and 9 cuts a year) and two severities (5 and 10 cm cutting height). Herbage accumulation and plant survival were measured over a two year period and in the second year tiller demography was analysed. Under a regime of 5 cuts a year and 5 cm cutting height, prairie grass swards behaved as annual crop with tiller population recovery in the second year, arising from natural reseeding. By contrast, with 9 cuts a year and 10 cm cutting height, autumn tiller population recovery in the second year was derived mainly from daughter tiller production. In the Humid Pampa region of Argentina, low survival of tillers formed during the second summer prevented this species from persisting beyond 18 months from sowing in plots where seedling recruitment did not occur.
Key words: prairie grass, defoliation, management, tiller dynamics, persistence.

Resumen
Se realizó un experimento en la EEA Pergamino, INTA, para estudiar el efecto del manejo de la defoliación sobre la dinámica del macollaje en pasturas de cebadilla criolla. Hubo cuatro tratamientos resultantes de la combinación factorial de dos frecuencias (5 y 9 cortes por año) y dos severidades (5 y 10 cm de altura de corte) de defoliación. Se midió la acumulación de forraje y la supervivencia de plantas durante dos años y en el segundo, se analizó la demografía de macollos. Con el tratamiento de 5 cortes por año y 5 cm de altura de corte, la pastura de cebadilla criolla se comportó como anual, con la recuperación de la densidad de macollos en el segundo año dependiendo de la resiembra natural. En contraste, con 9 cortes por año y 10 cm de altura de corte, la recuperación de la población de macollos en el segundo año derivó principalmente de la producción de macollos hijos. En la región pampeana, la baja supervivencia de los macollos formados en el segundo verano impidió que esta especie persista más allá de los 18 meses desde la siembra en parcelas donde la resiembra natural no ocurrió.
Palabras clave: cebadilla criolla, defoliación, manejo, dinámica de macollos, persistencia.

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Introduction

Native to the Pampas region of Argentina, prairie grass (*Bromus willdenowii* Kunth*, Syn. B. catharticus* Vahl*, B. unioloides* HBK) is a species capable of producing a high yield of good quality forage. Prairie grass grows year round and has maximum herbage accumulation during spring, with a strong reseeding capability. Hume (1990), reported prairie grass as a true perennial whereas in Argentina, prairie grass commonly does not persist beyond the second year after sowing, except where seeding occurs and the sward is maintained by natural seedling recruitment. Elsewhere, poor persistence of this species has also been reported under various environmental conditions and defoliation managements. There is no consensus as to reasons for non persistence or strategies to improve persistence but undefined environmental sensitivities or grazing management intolerances are often implicated (Belesky and Fedders, 1994; Xia et al., 1994).

Black and Chu (1989) found that prairie grass survived its first summer after sowing much better, where swards were spelled from defoliation during seedhead development, and based on that study Matthew et al. (1999) described prairie grass as having a ‘reproductive’ perennation strategy, with daughter tiller formation from vegetative tillers being comparatively unimportant and persistence relying on formation of replacement tillers from buds at the base of defoliated reproductive tillers. Tillers from defoliated flowering stems appear from mid spring till late summer, and most of them, from October to November (Scheneiter and Rimieri, 2001).

Because prairie grass is widely distributed in the Humid Pampa, and sown in other temperate grasslands worldwide, there is interest in seeking to better define mechanisms involved in its perennation. This paper presents the results of an experiment where variation in frequency and severity of defoliation was imposed in order to evaluate possible changes in tiller dynamics and persistence arising from either change in patterns of daughter tiller formation, or seedling recruitment.

Materials and Methods

Site description

The experiment was carried out at Pergamino Experimental Station (33º52’S, 60º33’W, 68 m a.s.l.) on a Typic Argiudol Soil, Series Pergamino (INTA, 1972) with 2.9% organic matter, 40 ppm phosphorus and pH 6.5 at the beginning of the experiment.

Treatments and experimental procedures

Two defoliation frequencies (infrequent or frequent, I or F, respectively) were combined with two intensities of defoliation (hard or lax, H or L, respectively) giving four treatment combinations.

For I defoliation treatments there were 5 cuts per year (2 in spring, and 1 at the end of the other seasons), and for the F treatments 9 cuts per year (3 in spring, and 2 in each of the other seasons). The defoliation severities were cutting heights of 5 cm (H) and 10 cm (L) from ground level. Seasons were defined as follows: autumn from April to June, winter from July to September, spring from October to December and summer from January to March.

Pasture seeds were drilled into a cultivated seed bed on 7 May 1999 at a seeding rate of 500 viable seeds m^{-2} (47.4 kg ha^{-1}) in rows 20 cm apart and 2.0 cm in depth. Seeds were deawned and treated with fungicide (Tebuconazole 6%). The prairie grass cultivar was an experimental line code 4900, derived from Martín Fierro M.A.G., an old and widely used Argentine population.

Swards were fertilised with calcareous ammonium nitrate (27-28% N) at a rate of 250 kg N ha^{-1} $year^{-1}$ in split dressings in mid spring (30%), late spring (30%) and autumn (40%).

Measurements were made from spring 1999 to summer 2001. The first defoliation to the target heights was carried out on 24 September 1999. Treatments plots were arranged in a complete randomised block design with four replicates. Plots consisted of six rows, 4 m in length, and an area of 4.8 m^2.

Measurements

Herbage accumulation was estimated by cutting a central area of 3 m^2 within each plot using a motorscythe. The fresh herbage was raked up and weighed in a nylon net suspended from a tripod. Then a representative sub-sample was taken to the laboratory and oven-dried for 48 hours at 60 ºC to determine the dry matter percentage. Summer 2001 data were not statistically analyzed due to the presence of summer grass weeds (*Digitaria sanguinalis* L., *Echinochloa cruss-galli* L. and *Eleusine indica* L.).

On 30 October 1999, 35 plants per plot were tagged. Plants were chosen at random, spaced at approximately 10 cm, along two central rows. One tiller of each plant was permanently identified by means of a coloured plastic-coated wire, attached to a nail pushed into the ground. From September 1999, until March 2001, at 3-monthly intervals, surviving tagged plants were recorded, taking care to avoid confusing tagged with untagged plants.

In the last week of March 2000, one fixed frame of 0.06 m^2 (0.2 m wide and 0.3 m long, with longest side along the drill row) was placed in a representative position in each plot. All the tillers inside were counted and tagged with coloured plastic-coated wire. The wire was carefully curled up in each tiller. Every month, until the last week of April 2001, new tillers were recorded and tagged with different colours and dead tillers were counted and their wires removed. New tillers were classified as arising from seedling recruitment (primary tillers) or from existing tillers (daughter tillers).

Data analysis

The majority of measurements in this experiment (herbage accumulation, primary tiller density, relative tiller birth rate, tiller survival probability) were amenable to analysis by normal ANOVA techniques (SAS Institute, 1989), and the approach taken was to carry out a separate ANOVA for each harvest date. Analysis of survival data from this kind of experiment is very difficult. We opted to use analyses conceptually similar to, but computationally simpler than those developed by Bahmani et al. (2003). The analyses adopted focused on identifying rate of disappearance of plants or tillers, and on ensuring that error degrees of freedom were not inflated by treating repeat counts over time as independent observations. Details appear below. Survival diagrams for tiller age cohorts were drawn to depict tiller population density changes throughout the experimental period, and tests developed to evaluate statistical significance of salient features evident from visual inspection of those diagrams.

Plant survival

Treatment differences in plant survival were tested statistically by linear regression of plant density on time. Separate regression analyses were performed for the two summer seasons when mortality was high (December 1999 to March 2000, and December 2000 to March 2001), and for the autumn-winter-spring period when mortality was low (March 2000 to December 2000). This analysis provided estimates ($\beta \pm$ se) of seasonal rates of plant loss.

Tiller dynamics

Primary tillers were counted in all treatments each autumn (April 2000, March and April 2001). Monthly relative tiller birth rate (new tillers per 100 adult tillers per day) was calculated, from June 2000 to April 2001, as the ratio of new tillers to tillers present at the end of the previous measurement period (Bahmani et al., 2003). As an approximation, it was assumed that tillers produced during a given month did not themselves produce daughter tillers within that month. Monthly tiller survival probabilities were calculated as the ratio of tillers at the end of each observation period to tillers present at the start of that observation period (Bahmani et al., 2003). In performing ANOVA of tiller data, no transformation was needed for primary tiller or for relative tiller birth rate data, while survival probability data were either arcsine or square root transformed prior to ANOVA.

To test the time effect and its interactions, monthly relative tiller birth rate and tiller survival probabilities were tested for the Huynh-Feldt condition of Type H covariance matrices through a sphericity test (Montgomery, 1991; SAS Institute, 1989). From these results, it was possible to use the F test of the univariate ANOVA for a repeated measures test of the time effect for relative tiller birth rate. For survival probabilities, a more conservative F test was performed with the use of Greenhouse-Geisser epsilon adjustment in degrees of freedom (Montgomery, 1991; SAS Institute, 1989).

Results

Rainfall (mm month^{-1}) and mean air temperature (ºC) during the experimental period and long term average, are shown in Table 1. From sowing to December 1999 rainfall was 264 mm lower than the average whereas from January 2000 to May 2001 rainfall was 603 mm higher than the average. Mean air temperatures were lightly lower in winter 2000 and lightly warmer in summer 2001 than the average.

Herbage accumulation

In spring 1999, there were no differences among treatments in herbage accumulation (5.6 t DM ha^{-1}). In summer 2000, there was an interaction between frequency and severity of defoliation ($p<0.01$) in that, the infrequently severely cut plots accumulated more herbage than the other combinations (9.3 *vs.* 6.2 t DM ha^{-1}). In autumn, more herbage was harvested with frequent than with infrequent treatments (1.8 *vs.* 1.4 t DM ha^{-1}, $p<0.05$) and with lax treatments, than with hard treatments (2.1 *vs.* 1.2 t DM ha^{-1}, $p<0.001$). That relativity between treatments continued in spring 2000, with corresponding values being, respectively, 3.8 *vs.* 3.2 t DM ha^{-1}, $p<0.001$ (frequent *vs.* infrequent), and 4.0 *vs.* 3.0 t DM ha^{-1}, $p<0.05$ (lax *vs.* hard). In contrast, more herbage was harvested in winter with infrequent than with frequent defoliation treatments (3.3 *vs.* 2.3 t DM ha^{-1}, $p<0.01$) and with hard than with lax defoliation treatments (3.4 *vs.* 2.2 t DM ha^{-1}, $p<0.001$).

Total herbage accumulation during the experimental period was affected by the interaction between frequency and severity of defoliation as the herbage accumulated was higher with the infrequent and severe defoliation treatment than the other treatments (22.7 *vs.* 19.6 t DM ha^{-1}, $p<0.001$).

Plant survival

Plant death was most evident from December 1999 to March 2000, in all treatments (Figure 1 and Table 2) but was more intense with infrequent hard defoliation treatment. Differences in slopes were detected showing this behaviour. Throughout autumn, winter and spring, plant number diminished at a low rate and differences among treatments were statistically significant. In the second summer, plant death was again intense. Differences in slopes showed the convergence of all treatments to a common and low number of living plants in March 2001.

Tiller dynamics

In this experiment, tiller birth and death were recorded at the same time. However, tiller birth was recorded at the population level whereas tiller death was calculated at the cohort level. Therefore, there was no attempt to link these two variables which were analysed and treated separately.

Primary tillers

Although no time effect was tested, visual observation indicated that April was the main month of seedling appearance. In both years, infrequent defoliation treatments had higher tiller population densities than frequent defoliation treatments (Table 3). Hard defoliation had higher values than lax defoliation treatments in the first year, but the reverse was true in the second year. In May 2000, plots of the infrequent hard defoliation treatment averaged 306 primary tillers m^{-2} whereas other treatments had fewer, and there was inconsistency through replicates.

Table 1: Rainfall (mm month^{-1} and mean air temperature (ºC) at the experimental site during the experimental period and the long term average.
Cuadro 1: *Precipitaciones (mm mes^{-1}) y temperatura media del aire (ºC) durante el período experimental y promedio histórico en la EEA Pergamino.*

Month	Rainfall (mm month^{-1})		Mean air temperature (ºC)	
	Experimental period	Long term average (1910/2006)	Experimental period	Long term average (1967/2006)
1999				
May	12,1	59,3	13,1	13,4
June	10,9	38,0	10,3	10,2
July	12,5	36,3	9,1	9,8
August	42,4	40,6	12,4	11,2
September	35,9	54,0	13,9	13,3
October	62,6	104,9	16,7	16,4
November	22,5	100,6	19,9	19,3
December	76,0	106,3	22,4	22,4
2000				
January	71	107,9	24,2	23,4
February	218	101,9	22,3	22,1
March	50	125,5	19,2	20,3
April	172	99,6	17,5	16,6
May	223	59,3	13,1	13,4
June	18	38,0	10,9	10,2
July	2	36,3	7,4	9,8
August	9	40,6	10,3	11,2
September	107	54,0	12,9	13,3
October	156	104,9	16,2	16,4
November	229	100,6	17,9	19,3
December	35	106,3	22,2	22,4
2001				
January	156	107,9	23,9	23,4
February	161	101,9	24,5	22,1
March	353	125,5	21,7	20,3
April	91	99,6	16,7	16,6
May	81	59,3	13,1	13,4

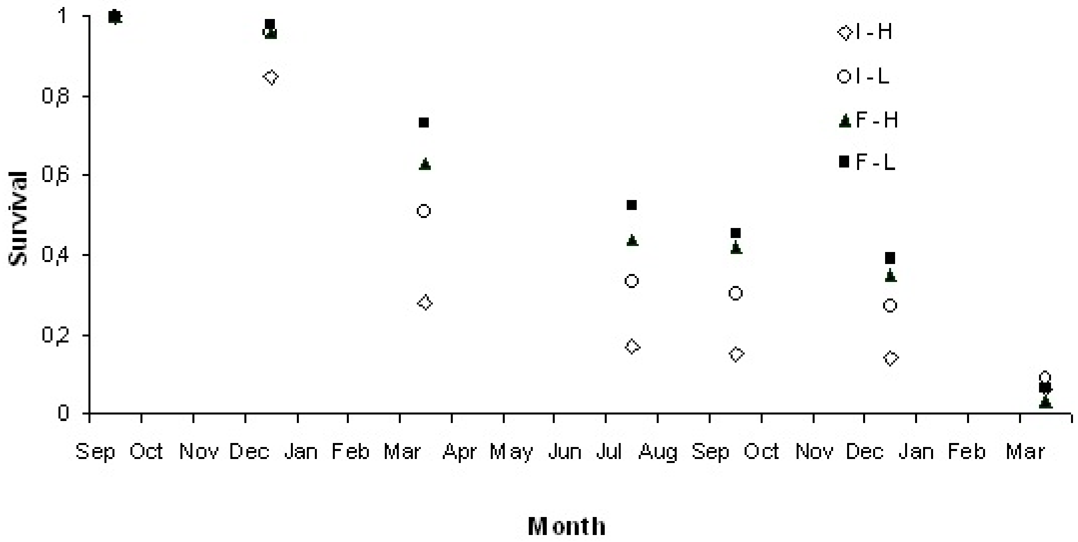

Figure 1: Plant survival in prairie grass swards with different defoliation managements during the experimental period (presented as the ratio live plant number/initial plant number). F, Frequent; I, infrequent; H, hard; L, lax.
Figura 1: *Supervivencia de plantas en pasturas de cebadilla criolla con diferentes manejos de la defoliación durante el período experimental (presentado como la relación entre número de plantas vivas/número inicial de plantas).*

Table 2: Estimates of plant loss during three experimental observation periods under different defoliation management (Number of plants. 90 days^{-1})
Cuadro 2: *Estimadores de pérdida de plantas durante tres períodos de observación con diferentes manejos de la defoliación (Número de plantas. 90 días^{-1})*

Treatment	Period		
	29 Dec '99-Mar'00	Mar'00-Dec'00	Dec'00-Mar'01
	β_1	β_1	β_1
F - H	-8,3	-0,6	-7,8
F - L	-6,3	-1,5	-8,3
I - H	-14,3	-0,3	-2,0
I - L	-12,3	-0,6	-4,5
Significance	p<0,001	p<0,001	p<0,001
S.E.M.	1,91	0,26	0,66

F: frequent; I: infrequent; H: hard; L: lax. S.E.M. standard error of mean.

Table 3: Tiller population density of primary tillers with different defoliation management, in four months (tillers m^{-2}).
Cuadro 3: *Densidad de la población de macollos primarios con diferentes manejos de la defoliación, en cuatro meses (macollos m^{-2}).*

Treatment	April 2000	May 2000	March 2001	April 2001
F - H	491	120	62	91
F - L	71	25	205	261
I - H	976	306	67	277
I - L	691	143	205	305
Significance	Fr p<0,01 S p<0,05 S.E.M. 140,5	Fr p<0,01 S p< 0,01 S.E.M. 38,8	S p<0,01 S.E.M. 32,8	Fr p<0,05 S p<0,05 S.E.M. 43,7

F, frequent; I, infrequent; H, hard; L, lax; Fr, frequency; S, severity; S.E.M. standard error of mean.

Tiller birth

Relative tiller birth rates were lower from June to August 2000 and in February 2001, than in spring-summer (Table 4). However, it should be noted that tiller births from November 2000 onwards arose from lower tiller population densities than in the first months of the experiment (Figure 2). Hence, both sward density and possible seasonal stimuli have to be considered when interpreting tiller density data.

Early in the experiment, tiller birth was higher under H defoliation than L, and higher under I defoliation than F (Table 4). Thereafter, interaction between frequency and severity was a feature of tiller birth data, with the F-H combination having the lowest or second-lowest relative tiller birth rates from August 2000 onwards, and the I-H combination having generally higher tiller birth than other treatments from October 2000 onwards (Table 4).

In March 2001, no daughter tillers were recorded in hard defoliation treatments and very low relative tiller birth rates occurred in lax defoliation treatments (0.20 and 0.11 tillers/100 $tillers^{-1}.day^{-1}$ for frequent lax and infrequent lax defoliation treatments, respectively, $p<0.05$). Again, in April 2001, the frequent hard treatment did not produce daughter tillers.

Tiller survival

Survival probability values were high and without differences among treatments until August 2000 (Figure 2). From November 2000 to January 2001, hard defoliation treatments had lower survival probability values than lax defoliation treatments ($p<0.05$, $p<0.001$ and $p<0.01$ in November, December and January, respectively). Monthly survival probability was irregular with frequent lax defoliation treatment; it had the lowest and the highest values in October and December, respectively. At the end of the measurement period, frequent hard defoliation management had the lowest survival probability value ($p<0.05$).

When tiller survival of each age cohort and tiller birth were plotted in a survival diagram (Figure 3), following the approach of Jewiss (1966), all treatments had in common a comparatively low tiller population at the end of the first summer (typically less than 500 tillers m^{-2} in March 2000), a rapid increase in population in autumn (1300 to 1900 tillers m^{-2} by May 2000), a very high death rate of overwintering tillers during the flowering period in September to November 2000, and a low late-summer population of tillers in February-March 2001 (Figure 3). Variations in this pattern for specific

Table 4: Monthly relative tiller birth rate with different defoliation managements (tillers. 100 tillers^{-1} day^{-1})
Cuadro 4: *Tasa relativa mensual de macollaje con diferentes manejos de la defoliación (macollos.100 macollos^{-1} día^{-1}).*

Month	Treatment				Significance	S.E.M.
	F - H	F - L	I - H	I - L		
June	0,37	0,16	0,41	0,16	S p < 0,001	0,044
July	0,43	0,14	0,75	0,36	Fr p < 0,05 S p < 0,01	0,107
August	0,40	0,36	0,81	1,29	Fr*S p < 0,05	0,110
September	1,14	1,47	0,80	1,52	S p < 0,001	0,106
October	0,64	0,51	1,55	0,70	Fr*S p < 0,05	0,146
November	0,68	1,15	1,29	1,07	Fr*S p < 0,01	0,092
December	0,90	0,81	1,14	1,53	Fr*S p < 0,05	0,103
January	1,07	1,50	1,30	0,94	Fr*S p < 0,1	0,201
February	0,35	0,53	0,66	0,57	Fr*S p < 0,1	0,075
March	0,00	0,11	0,00	0,20	S p < 0,05	0,036
April	0,00	1,96	0,51	2,79	S p < 0,001	0,350

F, frequent; I, infrequent; H, hard; L, lax; Fr, frequency; S, severity; Fr*S, interaction between Fr and S; S.E.M. standard error of mean.

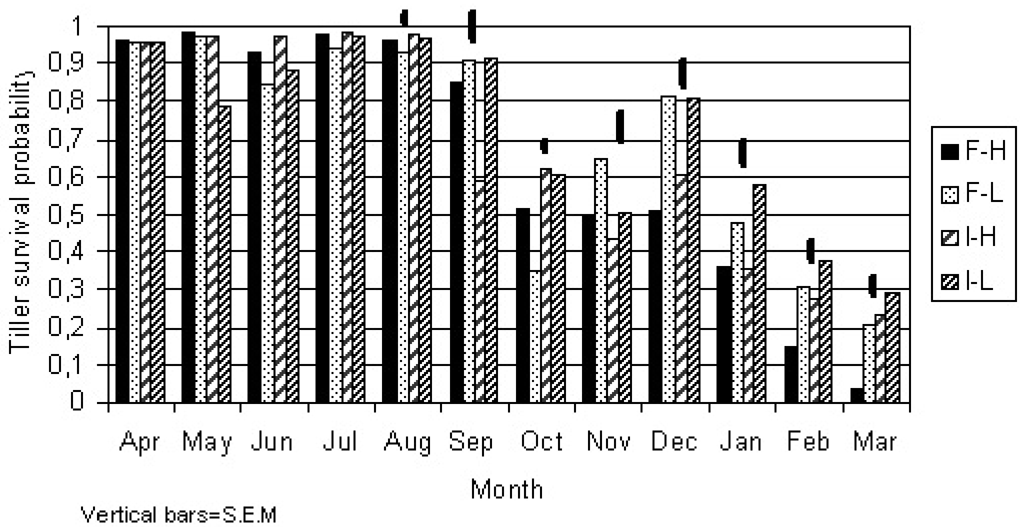

Figure 2: Monthly tiller survival probabilities in prairie grass swards with different defoliation managements during the second year of the experimental period [sqrt(tiller/tiller)]. F: Frequent; I: infrequent; H: hard; L: lax.
Figura 2: *Probabilidades mensuales de supervivencia de macollos en pasturas de cebadilla criolla durante el segundo año del período experimental [√(macollos/macollos)].*

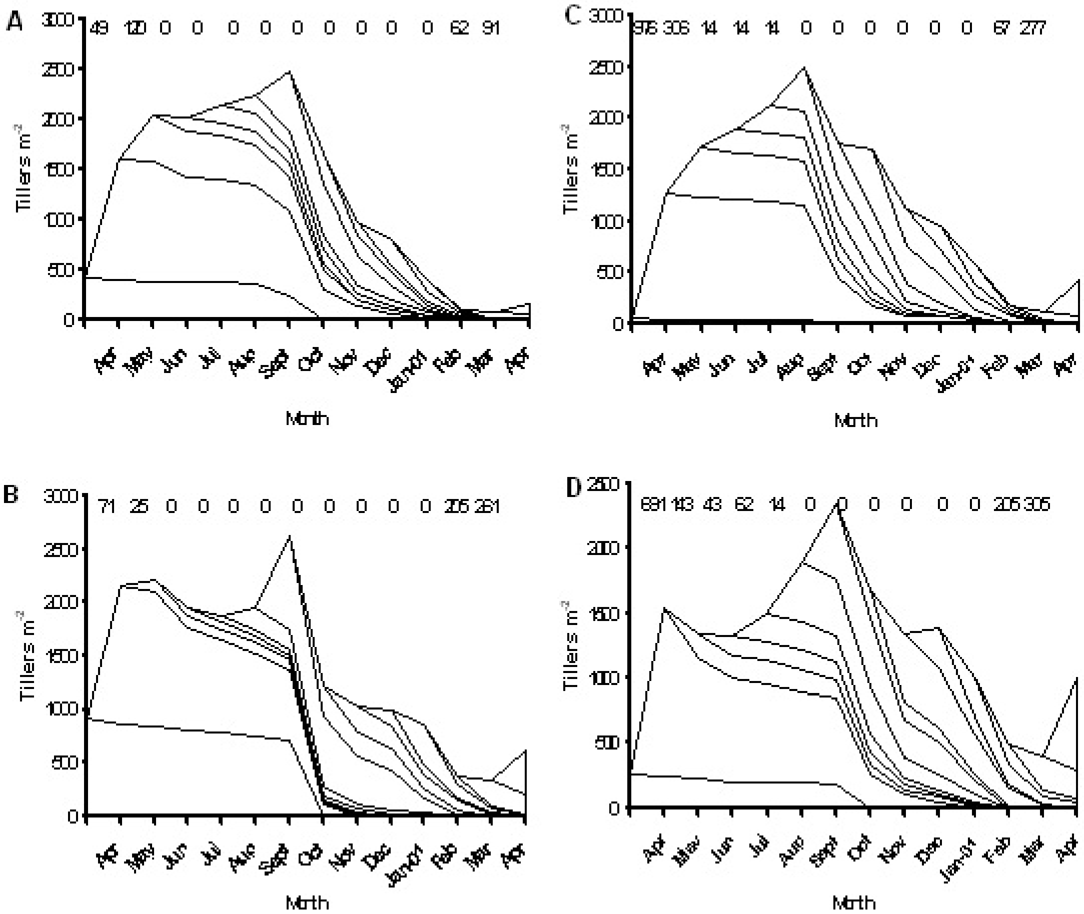

Figure 3: Tiller survival (decrease with time in tillers m^{-2}) of age cohorts in swards under different defoliation managements. (a) Frequent hard, (b) Frequent lax, (c) Infrequent hard, (d) Infrequent lax. Numbers at the top indicate birth of primary tillers in each age cohort.

Figura 3: *Supervivencia de macollos (disminución en el tiempo en macollos m^{-2}) de cohortes por edad en pasturas con diferentes manejos de la defoliación. (a) Frecuente severo, (b) frecuente laxo, (c) infrecuente severo, (d) infrecuente laxo. Los números de arriba indican aparición de macollos primarios en cada cohorte por edad.*

treatments were: (i) the autumn (April to June 2000) increase in tiller density, for which recruitment of new primary tillers was important, was greater with infrequent grazing than frequent grazing, and greater with hard grazing than lax grazing, and (ii) the tiller densities at the end of the summer decline in population (February 2001) ranked in order FH < IH < FL < IL (Figure 3).

Discussion

Herbage accumulation

During spring and summer, the distinctive high proportion of reproductive tillers of prairie grass, determine that the management that allows the expression and accumulation of reproductive tillers will have the higher herbage harvested. For example, in spring the defoliation severity may play an important role if reproductive tillers are not decapitated. Also, as found by Xia et al. (1994) when comparing hard and lax grazing, net production in this season could be higher with lax management, due to higher gross growth and similar senescence early in the season when compared with hard management. In this way, prairie grass appears to differ from perennial ryegrass which performs better with an infrequent hard defoliation regime during the reproductive stage in spring (Parsons, 1988).

In summer, long rest periods could be suited for conservation purposes as found by Bell and Ritchie (1989), also under a cutting regime. However, during summer, care is needed with infrequent hard defoliation; because this management may lead to poor herbage accumulation in the following season arising from interruption of tiller replacement (see below).

Plant survival

Prairie grass is variously described in the literature as having annual, biennial or perennial plants or as a short lived perennial (Cabrera, 1970; Dimitri, 1972; Lowe and Bowdler, 1995). Recent evidence with isolated plants of the local prairie grass population Martín Fierro M.A.G. showed that 85-94% of the plants live for more than one year and 40-45% can reach at least a third year of evaluation (Rosso, 2001; Rimieri, personal observation). In our experiment, summer was the main season in which plant death occurred, especially with infrequent hard defoliation. High herbage mass of reproductive tillers and bare ground post defoliation with infrequent hard management in summer increased the death of smaller plants when compared with frequent lax management. All defoliation treatments failed to sustain a sward stand for more than two years. Intraspecific competition and environmental stresses could be involved or this may be an intrinsic biological trait of the species.

Another approach is to consider that prairie grass, at the sward level, can be considered as perennial provided that seed can be produced and successful reseeding achieved.

Tiller dynamics

High survival in autumn and winter, whatever the defoliation management was, allowed prairie grass to maintain (frequent lax) or increase (infrequent hard) tiller population density at that time. During autumn and winter, population density increased to 2,000-2,500 tillers m^{-2} when an apparent equilibrium was reached.

Conversely, low survival probability during summer, was an important cause of prairie grass failure to persist as a true perennial at Pergamino. Unlike environments with cooler summers than the north of Buenos Aires Province, no tillers born in the second summer remained alive in the following season. For instance, in New Zealand, with a defoliation management that compares well with the infrequent hard defoliation treatment, post flowering age cohorts made an important contribution to tiller appearance in the following year (Matthew et al., 1999).

A key characteristic of prairie grass in the Humid Pampa is its strong reproductive behaviour. In the north of Buenos Aires Province, reproductive tillers appear from early spring to late summer. In September and October, with defoliation frequency as short as 22 to 25 days, reproductive tillers can comprise 39 to 59% of the total tiller population density (Scheneiter and Rimieri, 2001). These figures are important since replacement tillers come from bases of decapitated flowering tillers. For example, at Palmerston North, New Zealand, population recovery begins in early summer and it is extended until early autumn (Black and Chu, 1989). At Pergamino, no tiller population increase was observed during summer months when the high relative birth rates were counterbalanced by low tiller population density and low survival probabilities. Low tiller population densities from December to February were also found in *Festuca arundinacea* Schreb. (Bertín and Rosso, 1988) and in *Thinopyrum ponticum* (Podp.) Barkw. and Dewey (Scheneiter, 2007), the second one with a large proportion of reproductive tillers by early-mid summer. Results of this experiment showed that, whatever the defoliation regime was, April was the month when a sharp increase of tiller population was detected. Two factors may be involved in the between-site differences in the time of population recovery: the proportion of reproductive tillers and the duration of the reproductive period, and environmental constraints limiting tiller appearance from stems bases. At Pergamino, reproductive tillers are present until February-March (approximately: 47% of the population) so it may be that resources are allocated preferentially to reproductive sinks rather than to vegetative perennation. In addition, the death rate of those reproductive tillers may be high. If so, this may at least partially explain why the population density recovery is delayed until early autumn at Pergamino. The second point is that summer temperatures are much lower in the southern portion of the North Island of New Zealand than in the north of Buenos Aires Province (Mean maximun air temperature from December to February is 22.0 ºC at Palmerston North and 29.2 ºC at Pergamino). This has implications in the evaporative water demand and so water deficits from mid December to mid February are common at Pergamino (Rebella and Zeljkovich, 1980). This in turn may result in lower plant/tiller survival when root system is not a strong sink for photoassimilates (Parsons and Robson, 1981; Jatimliansky et al., 1997). During autumn and winter, population density increased to 2,000-2,500 tillers m^{-2} when an apparent equilibrium sward state was reached.

Survival diagrams showed that frequent lax and infrequent hard defoliation managements resulted in two contrasting models of tiller dynamics. Frequent lax management resulted in a short perennial model of persistence. This defoliation management had low seedling recruitment in the first autumn and low relative tiller birth rate between June and August 2000. High survival in autumn and winter allowed tiller population density to be maintained at this time. In September, low herbage mass (1.2 t DM ha^{-1}) and improved light and temperature conditions, allowed a high relative tiller birth rate. Lax management at this time of the year did not decapitate reproductive tillers that flowered, resulting in suppression of tiller birth by apical dominance in October like found by Hume (1991a) in series of glasshouse experiments. In the following months, this treatment had a higher survival probability when compared with other treatments. The studies of Black and Chu (1989) and Matthew et al. (1992) working with ryegrass have both proposed that higher defoliation height can increase carbon export from decapitated reproductive tillers to other attached tillers, and this might explain the better summer survival of tillers in laxly grazed swards.

In contrast, infrequent hard defoliation in the first year allowed seedling establishment and the sward exhibited an annual model of persistence. Previous work, showed that establishment of prairie grass seedlings in autumn was satisfactory provided that sward is spelled from grazing in summer (Hume and Barker, 1991). In the north of Buenos Aires Province, the apical meristem in most tillers begins to elongate from late September to early October (Bertín, 1990); so former reproductive tillers were removed early in spring with this defoliation management. After that, high tiller birth rates can be expected from basal buds of reproductive tillers after flowering (Black and Chu, 1989; Matthew et al., 1999). This mechanism probably, promoted high relative tiller birth rates later in spring.

Frequent hard defoliation management had very low relative tiller birth rates during late spring and summer. This management reduces stubble water-soluble carbohydrate (WSC) levels and more tillers come from axillary than basal buds when defoliation frequency is increased (Hume, 1991b; 1991c).

In addition, root:shoot ratio of prairie grass is reduced during the reproductive state (Jatimliansky et al., 1997) and this may be exacerbated by frequent defoliation (Caldwell et al., 1981). With this treatment, from early November to late December, defoliation interval was as short as 26-27 days, possibly a short time to link basal bud development and high WSC levels in stubble, in order to obtain high tiller birth. Hard defoliation shortened the life of age - cohorts in spring and summer in comparison with lax defoliation and this resulted in the very low population of tillers in February and March (Figures 3a and 3c). Bare ground (and consequently high soil temperatures) and early decapitation of some reproductive tillers with hard defoliation possibly shortened the life of affected cohorts. This was exacerbated by temperatures in summer 2001 which were higher than the historic average.

Infrequent lax defoliation had a high number of reproductive tillers in early spring and this resulted in low relative tiller birth rates at this time. Later, when flowering tillers were decapitated, relative tiller birth rate was increased. In this regard, Black and Chu (1989) found that when hard grazing was delayed in spring until new daughter tillers arose from tiller bases, tillering was encouraged when compared with hard grazing earlier in the season. Bell and Ritchie (1989) recommend long rest intervals between grazing to increase prairie grass production and persistence and pointed out that lax grazing could be beneficial to persistence. This approach may not be strictly different from the Black and Chu approach if the status of the sward at defoliation time is considered (new tillers from stem bases). Age - cohorts with lax defoliation treatments live longer in spring and summer of the second year than cohorts of hard treatments do; even so, survival probabilities were still low. From this point of view, lax defoliation management under cutting does not seem the way to overcome the lack of vegetative persistence in two year old plants in the Humid Pampa.

The reproductive perennation strategy of prairie grass (Matthew et al., 1999) holds under a different environment from that experienced in this study. Differences between sites in tiller population dynamics seem to be linked to the time and extent of reproductive development and the environment experienced by the sward during summer months.

Conclusions

Prairie grass swards can exhibit annual or short-lived perennial modes of persistence in response to defoliation management. When infrequent hard defoliation was imposed over the spring and summer of the first year the sward behaved as an annual crop. On the other hand, when defoliation was frequent and lax, the sward behaved as a short-lived perennial one. At the sward level, low survival probability in late spring and summer at Pergamino drives tiller population density to a very low value, under all defoliation managements tested. Therefore, from the second year on, vegetative persistence has a low possibility of success in the Humid Pampa and natural reseeding is the mechanism of persistence. This behaviour has implications for herbage accumulation in the first and second year. Infrequent, hard defoliation management allows higher herbage accumulation over two years but lower in the second autumn when compared with the frequent lax one.

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