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Effects of livestock exclusion on density, survival and biomass of the perennial sagebrush grass *Hymenachne pernambucense* (Poaceae) from a temperate fluvial wetland

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ABSTRACT

In Argentina, the intensification of soybean production has displaced a substantial proportion of cattle ranching to fluvial wetlands such as those in the Delta of the Paraná River. Cattle grazing affects structure and dynamics of native forage plants but there is little information on this impact in populations from fluvial wetlands. This study addresses the effect of cattle ranching on density, survival, mean life-span and aerial biomass of *Hymenachne pernambucense* (Poaceae), an important forage species in the region. The study was carried out monthly for one year in permanents plots subject to continuous grazing and plots excluded from grazing in the Middle Delta of the Paraná River. In plots excluded from grazing, tillers showed significantly higher population density and survival, and a two-fold increase in mean life-span, while continuous grazing decreased survival of cohorts. The largest contribution to tiller density in ungrazed and grazed populations was made by spring and summer cohorts, respectively. Total and green biomass were significantly higher in the ungrazed population, with highest differences in late spring-early summer. Cattle grazing affected the relationship between tiller density and green biomass suggesting that cattle prefer sprouts because they are more palatable and nutritious than older tissue.

1. Introduction

The knowledge of demographic parameters such as survival, life expectancy and mean life span is of relevance for understanding population dynamics (Harper, 1977; Silvertown and Charlesworth, 2009). There are few studies analysing these parameters for plant species (Lauenroth and Adler, 2008; Roach, 2003; Van Der Maarel, 1996; Wright and Van Dyne, 1976). According to Lauenroth and Adler (2008), this is mainly due to the difficulty of data collection and analysis. The prediction of plant population dynamics is hindered by the lack of demographic data (Silvertown et al., 2001), particularly when vegetation is subject to anthropogenic disturbances (e.g. resulting from its interaction with livestock). Effects of mammal herbivory can lead to decreasing density, production and survival rate of tillers (Bullock et al., 1994; Crawley, 1983; Fetcher and Shaver, 1983; Leiva and Alés, 2000; O'connor, 1994) and changes the biomass-size relationship (Guevara et al., 2002; Nafus et al., 2009). However, there is a lack of information about these topics in fluvial wetlands and there is available data only at community level (e.g., Crosslé and Brock, 2002; Champion et al., 2001; Jutila, 1999; Keddy, 2010; Reeves and Champion, 2004; Tanner, 1992).

A few decades ago, South American wetlands were relatively free of anthropogenic impacts, maintaining their original extension, structure and function. In Argentina, the expansion of the agricultural frontier due to the intensification of soybean production (Paruelo et al., 2006) has displaced a substantial proportion of cattle ranching activity to fluvial wetlands (such as those in the Paraná River Delta region) because of their high natural productivity (Quintana et al., 2014) and a large number of important forage species (González et al., 2008; Rossi et al., 2014).

Hymenachne pernambucense (Spreng.) Zuloaga (Poaceae) is a perennial and mat forming clonal grass, with broad leaves and erect stems of a maximum height of 2.5 m, and is distributed from southern Brazil

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and Paraguay to central-eastern Argentina and central Uruguay (Cabrera and Zardini, 1993). The southernmost limit of its distribution is in the Delta of the Paraná River and along the banks of the De La Plata River, in Argentina (Cabrera and Zardini, 1993). *H. pernambucense* is usually present in highly disturbed areas where it can establish as a pioneer species (Kandus and Malvárez, 2004; Morandeira, 2014). This trait is shared with the South American species *Hymenachne amplexicaulis*, which has been reported as an invader in wetlands of southern USA and Australia (Diaz et al., 2009; Grice et al., 2011).

The aim of this study was to analyse the changes in population dynamics and in the aerial biomass of *H. pernambucense* when this species is excluded to grazing. This grass species was selected because: (i) It is both one of the dominant and most important forage species in the Delta of the Paraná River, (ii) Under grazing situation, its abundance undergoes a significant decrease, and (iii) there is a lack of information about its population dynamics not only in Argentina but also in the remaining of its geographical range. Considering that livestock exhibits forage selection on palatable species including, in the Delta region, species of Genus *Hymenachne* (Quintana et al., 1998), we hypothesized that cattle grazing decreases tiller survival, density and mean life-span as well as aerial biomass of *H. pernambucense*. Thus, we conducted a 1-year study of a freshwater marsh dominated by this species and subject to two different conditions: under continuous grazing and ungrazed. Measurements were made in permanent sample plots on a private ranch located in the Middle Delta of the Paraná River, Argentina.

2. Materials and methods

2.1. Study area

In Argentina, the Paraná Delta Region (with a surface area of about 17,500 km^2) is a complex floodplain located in a strategic position at the lower end of the Paraná River Basin and the mouth of the De La Plata River Estuary, with unique ecological features (Malvárez, 1999). In South America, it is ranked third in importance after the Deltas of the Amazonas and Orinoco Rivers, and is the only of the great deltas that discharges into a freshwater estuary (the De La Plata Estuary) rather than into the sea. This region has been defined by Malvárez (1999) as a vast macro-mosaic of wetlands because it shows distinct climate features, a remarkable landscape diversity resulting from geomorphological processes occurring both in the present and recent past, and a particular hydrological regime. As a result, the biodiversity of the Paraná Delta is higher than that expected at these latitudes (Brinson and Malvárez, 2002). This region is included in a 3400 km wetland corridor along the Paraná and Paraguay Rivers shared by four South American countries. The corridor, which is of primary ecological importance, is inhabited by 20 million people who benefit from wetland goods and services (Benzaquén, 2013). The Paraná Delta is close to the major urban, industrial and agricultural areas of Argentina.

The field study was conducted in a cattle ranch placed on the Lechiguanas Islands (Fig. 1), Entre Ríos province, Argentina (33°27′S, 59°55′W), with a stocking density of about 0.7 livestock units/ha. The ranch is located within a landscape unit that originated from current sedimentation and erosion processes on the alluvial plain of the Paraná River and its main tributaries (Malvárez, 1999). The landscape pattern includes levees, mid-slopes and lowlands along a micro-topographic gradient with different level of flooding. Levees and mid-slopes are characterized by open forest of willows (*Salix humboldtiana*) and grassland dominated by *H. pernambucense*, respectively. Freshwater marshes of *Ludwigia* spp., *Echinochloa polystachya* and *Alternanthera philoxeroides* dominate the lowlands (Malvárez, 1999). The climate is temperate-humid and, for the period 2006–2016, the mean annual temperature was 17.4 °C (mean minimum and maximum temperatures of 10.4 °C and 24.4 °C for July and January, respectively). Mean annual rainfall from last decade was 1093.6 mm, ranging between 28.3 and 170.3 mm in June and February, respectively (INTA, 2017). The water level rises in October, reaches a peak in February–March, upturns in July–August and decreases in the remaining months. This hydrological regime shows remarkable interannual and interdecadal variability leading to severe droughts and to extreme floods (Coronel and Menéndez, 2006).

2.2. Experimental design and data collection

To evaluate the effect of livestock on population parameters of *H. pernambucense*, the study was performed in two contiguous areas, continuously grazed and ungrazed. Both areas, located in the mid-slope of the gradient, placed in a landscape subunit of 1455 ha, with a homogeneous plant community as well as water regime and geomorphology (Borro et al., 2014; Ramonell et al., 2012). Thus, the grazing treatment was considered as the major cause for the eventual differences between areas (Altesor et al., 2005). The experimental plots were settled in the mid-slope because, as was mentioned before, *H. pernambucense* growths only in that part of the topographic gradient.

The selection of *H. pernambucense* for this study was due to the fact that the field observations and the previous nutritional studies (Table 1; Magnano, 2017) show that this grass is an important native forage species both for quality and for the volume of fodder biomass that it produces.

For demographic analysis five and seven mats were randomly chosen from ungrazed (ungrazed population) and continuously grazed area (continuously grazed population), respectively. In each mats a permanent plot of 25 × 25 cm was settled. For the demographic analysis, tillers of *H. pernambucense* were counted within sample plots.

All tillers were tagged at their bases with self-adhesive tape at the beginning of the study period. Newly emergent tillers were tagged on each subsequent sampling date; they were considered a cohort and used to construct survival curves. Tillers present at the beginning of the study period constituted a depletion curve (sensu Harper, 1977), and those that were not recorded on three consecutive dates were considered as dead. Counts were done every 30–45 days for one year, between July 2012 and July 2013. After this date, surveys were suspended due to a flood event occurring at the end of July and beginning of September. Although the field work was performed during a single year, the climatic values for this period (mean annual rainfall of 1100.1 mm and mean annual temperature of 17.5 °C) were similar to the values registered during the last decade (Fig. S1).

Tiller density was expressed as the number of tillers/m^2 and the subsequent multiplication by the average coverage of *H. pernambucense* in both areas. The latter was determined seasonally by measuring the average basal area of all mats (Hayes et al., 1981) present in 10 randomly distributed 5 × 5 m square quadrats, half of which were placed within ungrazed area and the rest outside of it.

The cohort survival curves were based on sampling in different plots and at irregular time intervals. To reduce variation between samples and sampling periods, the number of tillers from each cohort was adjusted by using a regression equation, yielding a monotonically decreasing series of the number of individuals within each age class. We followed one cohort per season, selecting those with a higher number of records. As a result, we only considered the cohorts of winter, spring and summer.

To estimate biomass, an allometric method based on the relationship between tiller total height and biomass (Trilla et al., 2009; Vicari et al., 2002) was used. All tillers present in permanent plots were measured from the base to the tip of the longest upper leaf. To examine the possible influence of seasons on the allometric equations, some tillers were randomly chosen from inside the ungrazed area in each season. They were harvested, submitted to the laboratory and measured as explained above. The green material was then separated from the dry material, oven-dried at 60 °C for 72 h and weighed separately. Weight and height were incorporated into a regression model to establish the

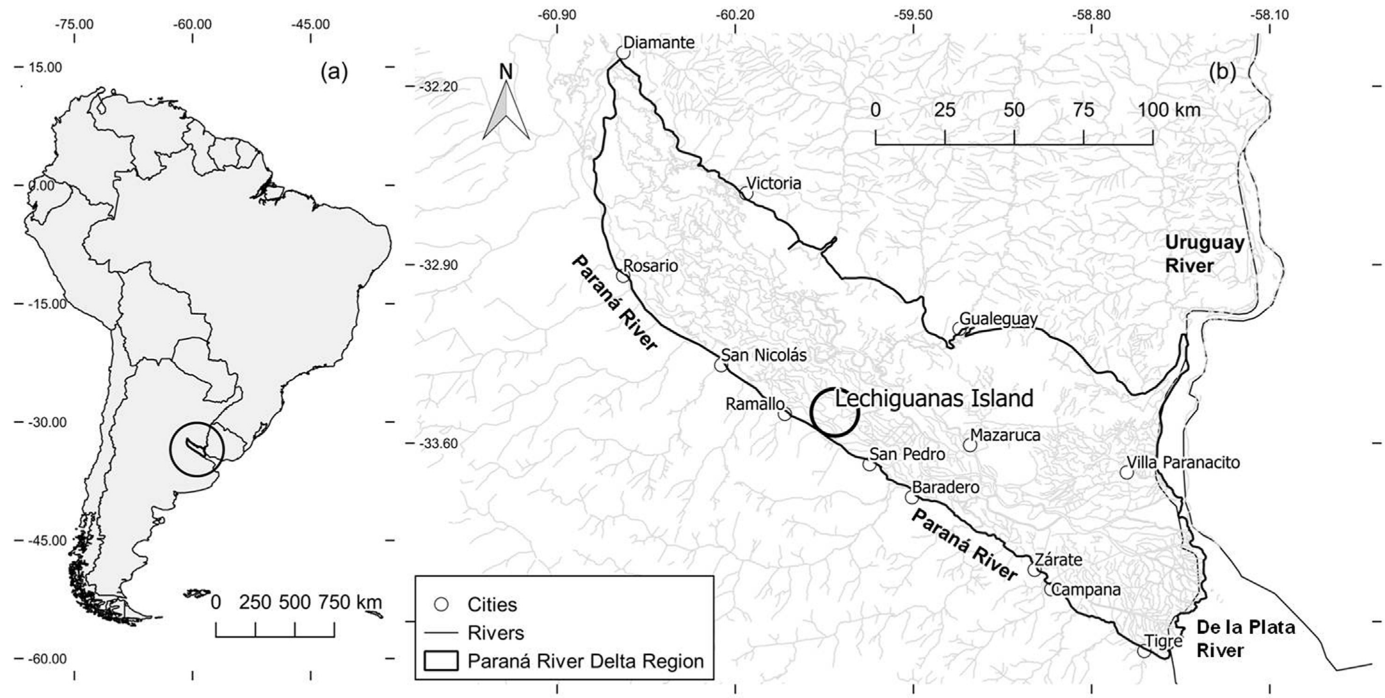

Fig. 1. Location of the study area in (a) South America (encircle area) and (b) the Delta of the Paraná River (Argentina).

Table 1
Forage quality values of *Hymenachne pernambucense* from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). Source: Magnano (2017).

	Acid detergent fiber (%)	Neutral detergent fiber (%)	Digestible dry matter (%)	Crude protein (%)
Mean ± SD	43 ± 4	67.00 ± 2.18	55.40 ± 3.11	16.40 ± 1.26
Min-Max	40–59	63–71	53.40–57.74	14.04–17.85

best allometric equation for each sample. Data were log-transformed because height and weight are growth parameters (Sokal and Rohlf, 1995). We used a general linear model to examine the influence of season on the allometric equations.

The goodness of fit of each regression model was assessed with 25% of field collected data using the χ^2 test. Regressions were only performed for the amount of green and total biomass, since the amount of dry biomass is calculated as the difference between them. Tiller biomass in each plot was calculated as the summation of the biomass of all tillers present in that plot, and total biomass by averaging the biomass from all permanent plots (Vicari et al., 2002). Biomass values were corrected based on *H. pernambucense* cover. Finally, tiller density was regressed on green biomass.

2.3. Statistical analyses

Variation of tiller density along time in ungrazed and grazed areas was analysed using a generalised linear mixed model (GLMM) with a negative binomial error distribution, with the density (number of tillers/m^2) as response variable, herbivore exclusion as fixed factor and time as random factor. Green and total biomass were analysed using general linear models (GLM) with first-order autoregressive correlation structure and variance modelling, with herbivore exclusion as fixed factor and time as random factor. The final models were selected using the parsimonious principle (Crawley, 2007). Data analyses were carried out with softwares Infostat (Di Rienzo et al., 2015) and R (R Core Team, 2014) and the following packages: ade4 (Dray and Dufour, 2007), lme4 (Bates et al., 2014) and glmmADMB (Bolker et al., 2012).

3. Results

3.1. Demographic response to herbivore exclusion

According to the GLMM there were significant differences in tiller density between ungrazed and continuously grazed populations of *H. pernambucense* during the study period ($p < 0.0001$), with the highest difference being observed during early summer (December). Thereafter, differences between treatments remained relatively constant over time (Fig. 2). Although tiller mortality rate for both *H. pernambucense* populations remained more or less constant, the continuously grazed population showed a considerably higher value. Tillers mean life-span from the ungrazed population almost doubled that of the continuously grazed population (9 vs. 4–5 months, respectively) (Fig. 3a).

The depletion curve (Fig. 3b) and the survival curves for the different cohorts (Fig. 3c–e) of the two *H. pernambucense* populations

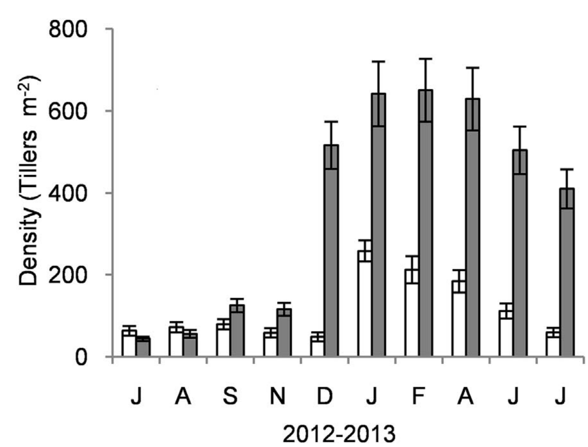

Fig. 2. Variation in tiller density (mean ± SE) between an ungrazed population (grey bars) and a continuously grazed population (white bars) of *Hymenachne pernambucense* from a fluvial wetland in the Middle Delta of the Paraná River (Argentina).

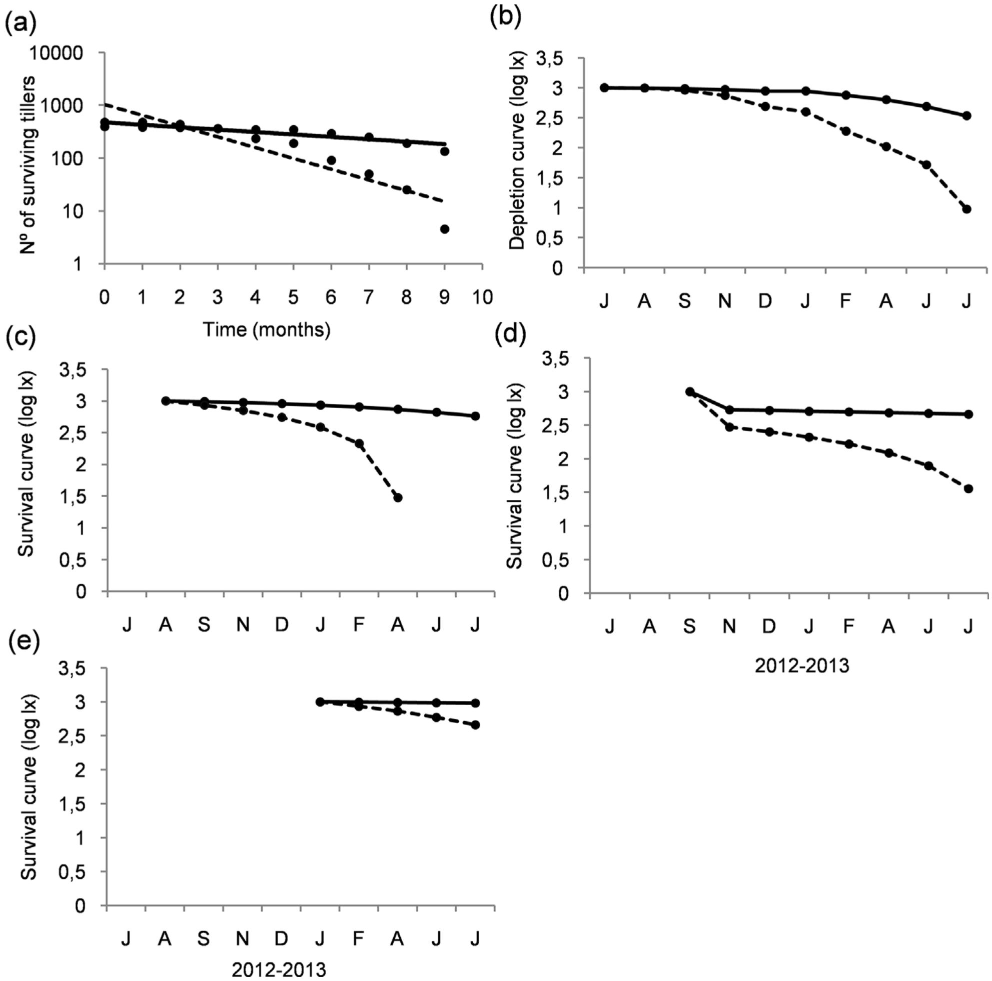

Fig. 3. (a) Number of survival tillers of *Hymenachne pernambucense* from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). (b) Depletion curve of the *Hymenachne pernambucense* populations. (c–d) Survival curves of different cohorts of *Hymenachne pernambucense* tillers from the same population. (c) Winter cohort, (d) spring cohort and (e) summer cohort. The solid line corresponds to the ungrazed population and the dash line to the continuously grazed population.

indicated that mortality risk increased when life expectancy rose to a maximum (Type I, sensu Deevey, 1947). However, mortality risk was higher for the tillers of the continuously grazed population. The cohorts of winter and spring of the continuously grazed population showed a downward trend in survival from the beginning of the study, while those of the ungrazed population survived for more than one year. Likewise, the mortality risk of the summer cohort was higher for the continuously grazed population, even though it included the last sampling months. The initial tiller number varied among the different cohorts depending on the timing of emergence, but it was higher for the ungrazed population (13–3 individuals/m^2 in winter; 70–0.1 individuals/m^2 in spring; and 135–35 individuals/m^2 in summer for the ungrazed vs. continuously grazed populations, respectively).

Fig. 4a shows the contribution of each tiller cohort to the total density of tillers along the seasons for the ungrazed population. The tillers of the depletion curve contributed with 78% of the total tiller density from the beginning of the study to late August. The higher density percentage was shown by the spring cohort and the survivors of the depletion curve till mid-summer, and by the spring and summer cohorts till the end of the study.

The continuously grazed population (Fig. 4b) displayed a different pattern of tiller contribution to density. The tillers of the depletion curve exceeded 75% of density till the end of spring (December) and those of the summer cohort showed the highest density from January to the end of the study.

Regardless of the density, the tillers of the continuously grazed

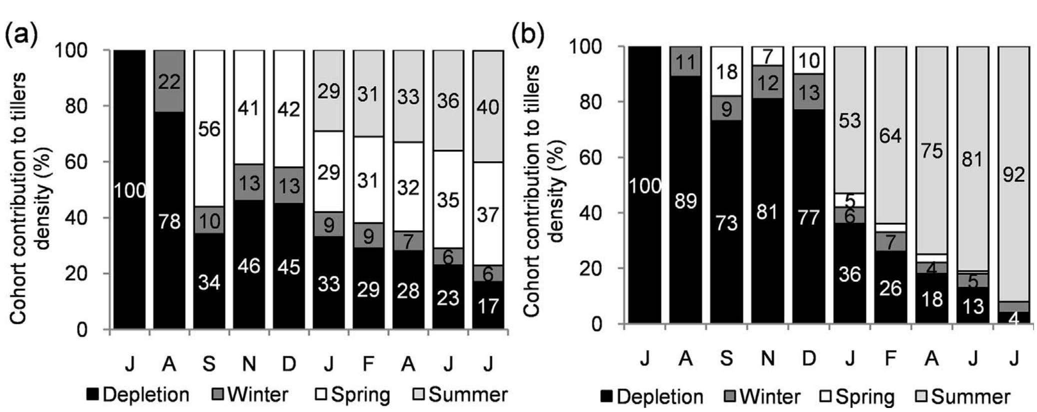

Fig. 4. Cohort contribution (%) to the density of *Hymenachne pernambucense* tillers from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). (a) ungrazed population and (b) continuously grazed population.

Table 2
Seasonal allometric equations for green biomass and total biomass of *Hymenachne pernambucense* tillers from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). *N*: number of tillers used for each allometric equation; R^2: Pearson's correlation coefficient; χ^2: value of the goodness of fit test. DW = dry weight (g) and H = height (cm). ***p < 0.001.

		Allometric Equation	*N*	R^2	χ^2
Total Biomass	Winter	LogDW = 1.21 × LogH – 1.73	97	0.86***	1.16
	Autum	LogDW = 1.59 × LogH – 2.40	76	0.94***	0.24
	Spring	LogDW = 2.02 × LogH – 3.48	76	0.86***	2.81
	Summer	LogDW = 1.87 × LogH – 3.01	81	0.91***	1.68
Green Biomass	Winter	LogDW = 1.19 × LogH – 1.71	97	0.85***	1.16
	Autum	LogDW = 1.48 × LogH – 2.25	76	0.91***	0.32
	Spring	LogDW = 1.98 × LogH – 3.41	76	0.86***	2.78
	Summer	LogDW = 1.83 × LogH – 2.94	81	0.90***	1.86

population survived for about 1 year, whereas tillers of the ungrazed population lived longer (Fig. 4). In the continuously grazed population, the spring cohort was the most affected by cattle grazing and there was an increase in the proportion of the summer cohort from emergence to the end of the study; during this period this cohort replaced the survivors of the depletion curve and the tillers of the spring cohort (Fig. 4b). In contrast, all the cohorts of the ungrazed population survived from their emergence to the end of the study, with the winter cohort being the less represented. In this respect it is of interest to point out that 17% of the tillers present at the beginning of the study survived until the next winter (Fig. 4a).

3.2. Biomass response to herbivore exclusion

We estimated allometric equations of tiller total and green biomass for each season because the slopes of the regression curves were significantly different from each other ($p < 0.01$). The regression model for each allometric equation was significant ($p < 0.001$; Table 2). Model validation using the χ^2 test showed good fit to the data in all cases ($p > 0.05$).

At early summer (December–January), after 6 months of herbivore exclusion, the ungrazed population had a total biomass 4953.07 g/m^2 higher than that of the continuously grazed population (Fig. 5a). The ungrazed population showed an exponential growth in the first months of herbivore exclusion until December–January, when it increased sharply reaching a peak (Fig. 5a). These differences in total biomass between populations remained unchanged to the end of the study. According to the GLM, the ungrazed population showed a significantly higher value of 1304.8 g/m^2 ($p < 0.0001$).

Similarly, there were differences in green biomass between populations until December–January, when the value for the ungrazed population was 4522.12 g/m^2 higher than that of the continuously grazed population. Then, differences in green biomass between populations remained relatively stable to the end of the study, with higher values for the ungrazed population (Fig. 5b). During winter (April, June and July 2013), green biomass reached 82% of total biomass and dry biomass increased in the ungrazed population, whereas green biomass always exceeded 96% in the continuously grazed population. The green biomass of the ungrazed population showed a significant increase (GLM; $p < 0.001$) of 1304.8 g/m^2 with respect to the continuously grazed population.

The relationship between tiller density and green biomass showed a significant exponential fit for the ungrazed population ($t_{\alpha U} = 0.35$, $p_{\alpha U} = 0.36$; $t_{\beta U} = 7.370$, $p_{\beta U} < 0.001$; Fig. 6a), while this relationship showed a non-significant fit for the continuously grazed population ($p_{\beta G} > 0.05$; Fig. 6b).

4. Discussion

Our results show that the ongoing cattle ranching activities in the Middle Delta of the Paraná River have a negative effect on population and functional parameters of *H. pernambucense* tillers, in accordance to previous studies involving other perennial graminoid species (e.g., Bullock et al., 1994; Lauenroth and Adler, 2008; McKenzie, 1997). Although the sampling period was restricted to only one year, the differences observed between treatments were clear enough to evaluate the considered effects of grazing on this species.

The survival curves of type I (sensu Deevey, 1947) obtained for the continuously grazed and ungrazed populations have also been reported for other plant populations (e.g., Bernard, 1976; Noble et al., 1979). This type of survival curve may result from the energetic relationship between the vegetative shoot and the originated unit. Survival of newly emerged shoots strongly depends on reallocation of resources from underground storage organs or ramets through interconnected rhizomes (Lytle and Hull, 1980a, b), and mortality risk increases as they gradually become independent (Marshall and Sagar, 1965, 1968; Mattheis et al., 1976). In our study, the increase in tiller density and biomass observed in both populations in summer could be partly due to the redistribution of nutrients accumulated in the tillers of the winter and spring cohorts.

The differences in the percentage composition of the cohorts observed over the study period may result from herbivore exclusion, as suggested by the fact that the spring and summer cohorts, which provide the bulk of new forage, were the most affected in the continuously grazed population. Biomass experienced an exponential increase from autumn onwards, probably because the forage for grazing is produced in this season, since tiller growth decreases in winter (Ryan et al., 2009). From the point of view of pasture management, however, early herbivore exclusion in autumn may result in large quantities of grass during winter, which leads to an increased rate of senescence, a reduction in stem density and leaf area, and a subsequent decrease in pasture production in spring (Hennessy et al., 2008).

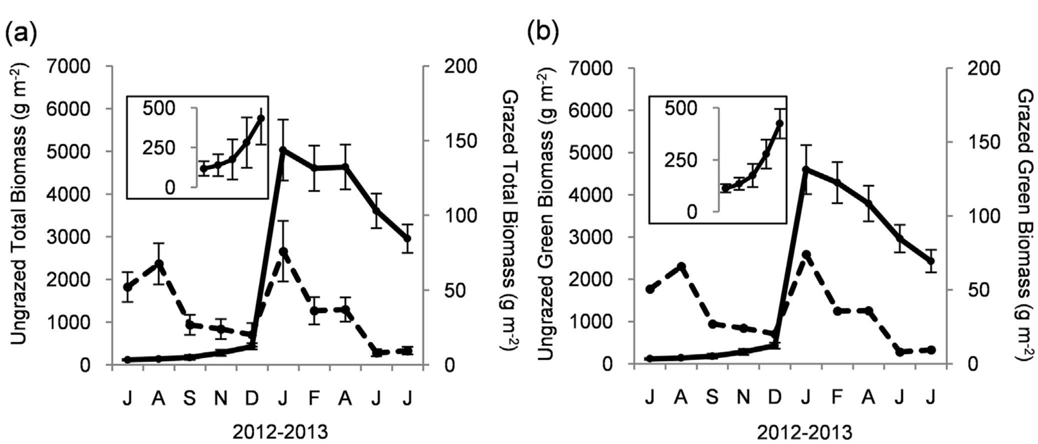

Fig. 5. (a) Aerial total biomass and (b) Aerial green biomass of *Hymenachne pernambucense* tillers from a temperate fluvial wetland in the Middle Delta of the Paraná River (Argentina). The dash line corresponds to the continuously grazed population and the solid line to the ungrazed population. Left and right vertical axes show the biomass values corresponding to the ungrazed and the continuously grazed populations, respectively. The inner squares contain curves at a different scale for the ungrazed population, with values obtained between July and December. Error bar represents mean ± SE.

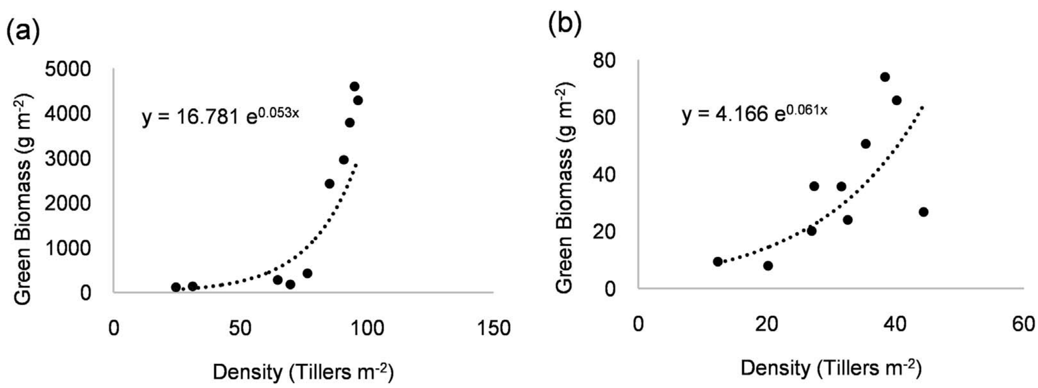

Fig. 6. Relationship between green biomass and density of *Hymenachne pernambucense* tillers from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). (a) ungrazed population and (b) continuously grazed population.

In this study, the good fit of the models to the data indicate that the allometric method is adequate to estimate the biomass of *H. pernambucense*. It is worthy to mention that this method has already been used with success in other Poaceae species (Nafus et al., 2009; Trilla et al., 2009; Vicari et al., 2002). In addition, this method is useful as an indicator of the impact of cattle grazing and trampling, in agreement with other authors (Breceda et al., 2005; Escós et al., 1997; Yang et al., 2008). In our work, the high values of total biomass and green biomass obtained for the ungrazed population are most likely due to an overcompensation of the growth rate in response to herbivore exclusion (Crawley, 1983; Ferraro and Oesterheld, 2002). This would be consistent with the exponential increase in biomass during the first months after herbivore exclusion. Rusch and Oesterheld (1997) found that the biomass of plant communities in humid grasslands was higher for ungrazed than for grazed areas, even when both areas had similar initial biomass levels. However, this exponential growth in biomass values could also be the result of a competitive exclusion process that occurs when livestock are removed. In this regard, erect species such as *H. pernambucense* spend much of their resources in the production of its aboveground biomass, which makes them good competitors by light but highly vulnerable to grazing (Milchunas and Lauenroth, 1993). Considering also *H. pernambucense* is usually a dominant species in natural areas of the Delta region (Morandeira, 2014), biomass could increase exponentially as a consequence of the competitive dominance it exerts over the rest of species when cattle are excluded.

The influence of herbivore exclusion was also evidenced by the differences in tiller density found between populations from spring to the end of the study. The density of *H. pernambucense* tillers exhibited a seasonal dynamics, reaching a peak at the end of summer. Similar results were reported by different authors who studied temperate clonal plant populations (Bullock et al., 1994; Eriksson, 1986; Solbrig et al., 1980; Thorhallsdottir, 1983).

In seasonal environments as the one studied here, tiller production and grass growth are usually higher in spring (Crawley, 1983). The biomass peak in the ungrazed population during summer would have resulted from the combined effect of high temperatures and cattle exclosure, whereas temperature would have played a minor role during the first months of the study period. Although *H. pernambucense* is a perennial grass, it produces a large amount of dry biomass in winter; our results indicate that cattle exclosure had a positive effect on the production of dry material. This implies a higher production of litter and subsequent enrichment of the soil with organic matter, as observed by Magnano et al. (2013), but with the consequent decrease in forage quality. In the continuously grazed population, dry biomass was much lower than green biomass, probably as a response to heavy grazing pressure, as reported elsewhere (Altesor et al., 2005; Casasús et al., 2007).

In most grasslands, forage biomass increases at the expense of its quality if the mean life-span of leaves is longer and the amount of dead or non-nutritive tissues is higher (Crawley, 1983). In this study, cattle grazing affected the relationship between tiller density and green biomass suggesting that cattle prefer sprouts of *H. pernambucense* because they are more palatable and nutritious than older tissue. The impact of grazing is evident from a comparison of this relationship between populations, as it was exponential for the ungrazed population and linear for the continuously grazed population.

Concluding, our results highlight the importance of cattle grazing on population dynamics of *H. pernambucense* tillers. In this regard, George et al. (2011) pointed out that foraging resources of wetlands can be protected by conservation strategies concerning the intensity, timing, and spatial distribution of livestock grazing. In this context and based on our results we propose to implement a grazing system involving rotation of cattle to areas with plant communities composed of palatable species other than *H. pernambucense* during spring. Grazing in *H. pernambucense* freshwater marshes would only be allowed between mid-December and the end of summer. This would favour the resprouting of the spring tiller cohorts, thus enhancing forage quantity and quality with the consequent increase in biomass availability during summer.

Statement of authorship

ALM performed the field work, analysed data and wrote the manuscript; ASN carried out laboratory work; PK performed statistical analysis; EA collaborated with laboratory data; RV designed research; RDQ designed research and wrote the manuscript; all authors contributed to data interpretation and manuscript review.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2017.12.006.

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