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Persistence of tall fescue in a subtropical environment: tiller survival over summer in response to flowering control and nitrogen supply

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Abstract

Enhancing pasture persistence is crucial to achieve more sustainable grass-based animal production systems. Although it is known that persistence of perennial ryegrass is based on a high turnover of tillers during late spring and summer, little is known about other forage species, particularly in subtropical climates. To address this question, this study evaluated survival of grazed tall fescue tillers growing in a subtropical climate. We hypothesized that hard tactical grazing during winter to remove reproductive stems (designated as ‘flowering control’), and nitrogen fertilization in spring, would both improve tiller survival over summer, and thus enhance tiller density. This was assessed in two experiments. In both experiments, few tillers appeared during late spring and summer and so tiller density depended on the dynamics of vegetative tillers present in the sward in spring. In Experiment 2, flowering control and nitrogen fertilization both enhanced the survival of that critical tiller cohort, but the effects were not additive. Responses were similar but not statistically significant in Experiment 1, which had a warmer, drier summer and lower overall survival rates. Unlike grasses in temperate environments, persistence of tall fescue in this subtropical site appeared to follow a ‘vegetative pathway’; i.e., new tillers were produced largely in autumn, from vegetative tillers that survived the summer.

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Introduction

Pasture persistence is a major concern in grass-based animal production systems. Perennial pastures generally have a lower cost per unit dry matter than other forage resources (Chapman *et al.*, 2014). Further, they improve soil fertility and may help control nutrient leaching and erosion (McCallum *et al.*, 2004), thus contributing to agroecosystem sustainability. These benefits become less evident if pasture swards are not persistent.

Lack of persistence – defined as a decrease in the physical presence of plants of the sown species in the pasture (Parsons *et al.*, 2011) – is associated with either failure of the sown species to survive or with reduced growth due to adverse climate or inappropriate management (Chapman *et al.*, 2011). In perennial grasses, persistence strongly depends on vegetative tiller establishment and survival. Therefore, achieving adequate tiller densities is crucial in late spring and early summer (Valentine and Matthew, 1999), when tiller death rates tend to peak, at least in perennial ryegrass in temperate environments.

Grazing management is an effective way to manipulate tiller density. Lax spring grazing usually results in the development of a high proportion of flowering tillers and delays tiller appearance to mid-spring, a situation that can compromise vegetative tiller survival (Thom *et al.*, 1998; Matthew, 2002). Compared with lax grazing, short-term intense grazing during spring has been shown to promote higher tiller densities in

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temperate pastures (Korte *et al.*, 1984; Sheath and Boom, 1985; L'Huillier, 1987). This tactical hard defoliation aims to reduce the proportion of reproductive tillers in the sward, which has been associated with better pasture longevity (Davies, 1988).

In perennial ryegrass (*Lolium perenne* L.) growing in temperate climates, the pathway of perennation has been described as 'reproductive' (Matthew *et al.*, 1993), which means that persistence relies on the production of daughter tillers from decapitated flowering tillers. The window of opportunity to remove flowering tillers – a management hereby referred to as 'flowering control' – ranges from the start of floral induction until anthesis (Korte *et al.*, 1984; L'Huillier, 1987; Da Silva *et al.*, 2004). A study conducted at the single tiller level by Matthew *et al.* (1991) showed that the most favourable option is to delay the moment of elimination of reproductive stems until anthesis, a management referred to as 'late control'. These results were also confirmed at the paddock scale (Da Silva *et al.*, 1994; Hernández-Garay *et al.*, 1997). Enhanced tiller survival and new tiller formation observed under 'late-flowering control' have been suggested to be caused by the preferential partitioning of assimilates to flowering stems during reproductive development and subsequent translocation of those assimilates to daughter tillers when those stems are removed at the heading stage (Matthew, 2002). In tall fescue, Lafarge (2006) found an increase in the density of vegetative tillers in close proximity to reproductive tillers cut at anthesis; a mother-tiller effect similar to that observed for ryegrass.

Compared with ryegrass, information on tall fescue (*Festuca arundinacea* Schreb = *Lolium. arundinaceum* (Schreb) Darbysh) is scarcer. In this species, reproductive tillers appear during a narrower window of time in early spring (Hare, 1992) and constitute a lower proportion of the tiller population than in ryegrass (Matthew *et al.*, 1993). In a recent review, Edwards and Chapman (2011) concluded that literature referring to defoliation and its impact on pasture persistence is considerably old, and mainly focused on perennial ryegrass. In agreement, we are aware of no study on the survival of tillers of temperate grasses in subtropical climates.

Tall fescue is one of the most sown species in perennial pastures in the world, from humid to subhumid areas, and from cool temperate to subtropical regions. Its persistence is rarely an issue in temperate and humid climates (Easton *et al.*, 1994; Lattanzi *et al.*, 2007) although in warmer and drier environments this can be a problem (Lowe *et al.*, 1999) though to a lesser extent than in perennial ryegrass (Hannaway *et al.*, 2009). Optimum temperatures for growth of tall fescue range between 20 and 25°C; at 30°C, it is 80% of maximal; at 35%, it is <10% (see Figure S1). In subtropical climates, summers are hot and evapotranspiration rates are typically higher than precipitation. This creates water deficits, which can be detrimental to tall fescue's persistence (Easton *et al.*, 1994; Milne, 2009). Experimental evidence shows that under frequent and intensive grazing, summer productivity and persistence of tall fescue can be severely affected (Mattiauda *et al.*, 2009; Claramunt *et al.*, 2011) a situation that can give place to the rapid appearance of C4 weeds (Lowe and Bowdler, 1995; Formoso, 2010).

Fertilization may also be a key factor affecting tiller survival, as improvement in the nitrogen supply has been demonstrated to induce a higher 'site filling' and higher tiller appearance rates (Harris *et al.*, 1996; Cruz and Boval, 2000b). In tall fescue, the positive effects of autumn nitrogen dressings are well known (Mazzanti *et al.*, 1994; Scheneiter and Améndola, 2012), but little is known about the effect of nitrogen applied during spring. During this season, nitrogen could enhance daughter tiller survival, by increasing their size and nutrition (Olson and Richards, 1989) and alleviating negative effects of competition by flowering tillers.

The aim of this study was to assess, in a subtropical region, the effects of both tactical hard grazing in winter to remove flowering stems ('flowering control') and nitrogen fertilization during spring on tiller dynamics of tall fescue swards.

Materials and methods

Experimental site

Two experiments were carried out, Experiment 1 during 2011–2012 and Experiment 2 in 2012–2013, both at the Estación Experimental 'Mario A. Cassinoni' (EEMAC) of the Faculty of Agronomy of the Universidad de la República, in Paysandú, Uruguay (32° 22′ S, 58° 02′ W). Experiment 1 was carried out on a pasture of tall fescue cv. La Sorpresa established in 2009 and Experiment 2 on a pasture of tall fescue cv. INIA Tacuabé established in 2011. Both cultivars begin reproductive differentiation in mid-July and flower in September in temperate Uruguay (Carámbula and Elizondo, 1969; Formoso, 1995). Both swards were amply dominated by tall fescue.

The climate is humid subtropical, Cfa in Köppen classification (McKnight and Hess, 2002). The average rainfall is 1200 mm, fairly well distributed throughout the year. Summers are warm, with a long-term average temperature of 24°C between December and February (1961–2011). Water deficits usually occur during summer, even when rainfall is high, because of high evapotranspiration. January has the highest deficit, with more than 100 mm (Cruz *et al.*, 2000a). Soils are mainly Eutric Brunisols from the San Manuel Series (Altamirano *et al.*, 1976), equivalent to Vertic Argiudolls according to the USDA Soil Taxonomy (Durán *et al.*, 1999). Soils had an average organic matter content of 7·9% (0–20 cm), 18 mg kg^{-1} of P (0–10 cm) and average pH of 7·1. Soil water balance was calculated based on Thornthwaite and Mather (1957), assuming a maximum water holding capacity of 117 mm up to 80 cm depth.

Previous management

Pastures used in Experiment 1 had received a total of 122 kg N ha^{-1} (15% at sowing, 12% in March 2010, 20% in May 2010, 20% in June 2010, 10% in August 2010 and 23% in April 2011) and 48 kg P ha^{-1} (38% at sowing, 31% in March 2010 and 31% in August 2010).

Pastures used in Experiment 2 received a total of 78 kg N ha^{-1} equally split between November 2011, March 2012 and April 2012, and 55 kg P ha^{-1}, applied in April 2012. Both pastures were rotationally stocked with dairy cattle. Grazing started with mean biomass of between 1·5 and 2·0 t of dry matter per hectare (DM ha^{-1}), and left residuals of approximately 1 t DM ha^{-1}.

Experimental design

Experiment 1 was run in swards grazed at the 2-leaf stage, i.e. with a grazing frequency of approximately 400 degree-days (base temperature = 4°C). In September 2011, two grazing treatments were imposed to generate swards with contrasting proportions of flowering tillers: eight paddocks of 0·2 ha each were grazed down to target residual heights of either 6 or 12 cm, measured with a rising plate meter (Ashgrove Co., Palmerston North, New Zealand) in three successive occasions: from 1 September–3 September 2011; from 23 September to 24 September and from 16 October to 17 October.

In November, each of the eight paddocks subjected to hard and lax grazing were divided into halves that received either nil or 48 kg N ha^{-1}. Thus, a complete randomized block design was set up in 16 plots accommodating the four treatments resulting from the 2 × 2 factorial arrangement of grazing intensity in late winter and early spring, and nitrogen fertilizer applied in spring, replicated four times. These are referred as Lax-N0, Lax-N50, Hard-N0 and Hard-N50.

From November 2011 and until the end of the trial in June 2012, grazing intensity was the same in all plots, approximately 10 cm of residual height. There was no grazing from mid-December until February, and in March, all plots were cut to 10 cm residual height using a mower. Afterwards, grazing frequency continued unaltered at the 2-leaf stage.

Experiment 2 was conducted on swards that were also grazed at the 2-leaf stage. At the end of winter of 2012, two grazing treatments were imposed to generate swards with contrasting proportions of flowering tillers: six paddocks of 0·4 ha each were grazed down to target residual heights of either 9 or 12 cm, measured with a rising plate meter, in two successive occasions, from 28 August to 1 September 2012 and again from 20 to 22 September 2012. These treatments are referred to as hard and lax grazing respectively.

Each of the six paddocks subjected to hard and lax grazing were then divided into halves that received either nil or 92 kg N ha^{-1}, equally split between 26 September and 1 November 2012. Thus, a complete randomized block design was set up in 12 plots, accommodating the four treatments that resulted from the 2 × 2 factorial arrangement of grazing intensity in late winter and early spring, and nitrogen fertilization rate at the beginning of spring, replicated three times. These are referred to as Lax-N0, Lax-N100, Hard-N0 and Hard-N100. From 23 September 2012 and until the end of the trial in July 2013, grazing intensity was the same in all plots, approximately 10 cm of residual height, and grazing frequency continued unaltered at the 2-leaf stage.

Sward state measurements

Sward herbage mass was measured before and after each grazing event using a double sampling technique adapted from Haydock and Shaw (1975). Briefly, five sampling places per paddock were selected representing the range of sward heights. At each sampling place, sward height was measured using a rising plate meter, and 0·3 × 0·3 m quadrats were cut to ground level with scissors. This was repeated three times per paddock. Cut herbage was weighed, dried for 48 h at 65°C and weighed again. The data were used to derive linear regression equations relating sward herbage mass to sward height. Before and after each grazing event, sward height was measured at 200 points in each paddock, and herbage mass estimated applying the previously determined equation.

Tiller dynamics measurements

In Experiment 1, three random sites per paddock (i.e. nine per treatment) were selected and supervised throughout the duration of the experiment. Tiller population demography was monitored in one 0·30 m line (coinciding with the sowing line) located inside the randomly selected sites. On 15 November 2011, all tillers present in each line were marked with coloured plastic wires. Lines were monitored on March and July. Tiller death and production rates were determined for November–March. Flowering stems were counted on 16 November 2011 in nine randomly allocated 0·5 m × 0·5 m quadrats per paddock.

In Experiment 2, five 2-m long transects were established per paddock (i.e. fifteen per treatment). Transects were placed perpendicular to the sowing lines, marked with wooden stakes and georeferenced (Etrex 20, Garmin Instruments Inc., Olathe, KS, USA). During the two periods of differential grazing – 28 August to 1 September and 20 to 22 September 2012 (see above) – ten vegetative tillers were marked in each transect using plastic coloured wires. Post-grazing extended tiller height (ETH), and grazed/ungrazed status were recorded. Flowering stems were counted on 29 September 2012.

Tiller population demography was monitored in one 0·15 m line per transect. On 13 November 2012, all tillers present in each line were marked with coloured plastic wires. The authors are aware that this marking procedure would promote bud release and tiller population in the marked line as shown by Hernández-Garay *et al.* (1993), but relativity between treatments would likely be conserved. Lines were monitored on 12 December 2012, 13 February 2013, 10 April 2013 and 3 July 2013. Each time, dead tillers were recorded and newly produced tillers marked with a different colour. From these measurements, absolute (tiller m^{-2}) and relative (tiller tiller $^{-1}m^{-2}$) tiller death and production rates were determined for four different periods: November–December, December–February, February–April, and April–July.

In November 2012, independent sets of tillers were harvested from 0·15 m lines near each transect. Tillers were cut to ground level with razor blades, placed in plastic bags previously wetted to reduce plant dehydration, taken to the laboratory and frozen. Tillers were then counted, dried and weighed.

Statistical analysis

Experiment 1

Grazing intensity effects on pre- and post-grazing herbage mass were tested using a general linear model (GLM, SAS, 9.1.3, SAS Institute, Cary, NC, USA). The percentage of flowering stems, tiller density and tiller survival were analysed using a mixed model that included the fixed effects of grazing intensity and nitrogen fertilization, and their interaction, and the random effect of block (PROC MIXED, SAS). Treatment means were compared using Tukey's test (α = 5%).

Experiment 2

Grazing intensity effects on pre- and post-grazing herbage mass and ETH, and on the percentage of grazed tillers, and the percentage of flowering stems were tested using a general linear model (GLM, SAS). Tiller density, and production and death rates were analysed using a mixed model that included the fixed effects of grazing intensity and nitrogen fertilization, and their interaction, and the random effect of block (PROC MIXED, SAS). Treatment means were compared using Tukey's test (α = 5%).

Results

Weather

Air temperatures were well above the optimal range for tall fescue during extended periods of time in both experiments, and particularly during summer of Experiment 1 (2011–2012). In both experiments, air temperature between November and February was above 25°C, on average, at least 7 h every day, and between 30 and 35°C at least 2 h every day (Table 1). In January 2012, on average, air temperature was above 35°C for more than one and a half hour every day.

Estimated soil water balances showed that deficits occurred in both experiments, but were of lesser magnitude and duration in Experiment 2 (Figure 1). Indeed, in Experiment 2 the ratio of ET to ET0 never decreased below 0·4 and water stress was relatively mild and short-lived. The summer 2011–2012, on the other hand, was significantly drier, with values of ET/ET0 generally lower than those of Experiment 2.

Sward state

Experiment 1

The proportion of flowering stems was mostly affected by grazing (65% more flowering stems for L treatments) and little affected by nitrogen. The highest number of flowering stems was found for L-N0 treatments (18%). During the experimental grazing, pre-grazing HM was similar for both H and L treatments. Although numerical differences were encountered in post-grazing HM (more HM in lax), no statistical differences were found either. However, post-grazing height measured with the rising plate meter differed significantly (11 cm for lax and 8 cm for hard; Table 2).

Experiment 2

Compared with lax grazing, the hard grazing treatment resulted in lower post-grazing herbage mass,

Table 1 Hours/day during which air temperature was between 25 and 30°C, between 30 and 35°C, and above 35°C, in both experiments.

Range (°C)	Year	October	November	December	January	February	March	Average
25–30	2011–2012	0·8	5·0	5·1	6·8	5·9	3·8	4·6
	2012–2013	1·8	5·5	5·9	6·4	5·0	3·3	4·6
30–35	2011–2012	0·0	2·0	2·4	4·6	2·1	1·4	2·1
	2012–2013	0·1	2·1	3·0	2·1	2·1	0·3	1·6
+35	2011–2012	0·0	0·0	0·4	1·6	0·5	0·0	0·4
	2012–2013	0·0	0·0	0·1	0·2	0·2	0·0	0·1

more grazed tillers, and a lower number and proportion of flowering stems at the end of winter. Pre-grazing herbage mass did not differ between treatments (Table 2). Once the grazing treatments were finished in early spring, the percentage of grazed tillers was similar in all treatments, and ETH decreased by 25–35% during grazing in all treatments (October 2012). However, in the plots that had been hard-grazed at the end of winter there were 50% fewer flowering stems.

Tiller density

In both experiments, there was a similar tillering pattern, with a decrease in total tiller density during late spring and summer (a maximum of 50% and a minimum of 10%) and a recovery of tiller density during autumn and winter (between 75% and 12% compared with summer). In Experiment 1, nitrogen increased vegetative tillers in autumn and winter. Hard grazing also increased the number of vegetative tillers in autumn (40%), but the effects on tiller density faded out as winter progressed and no effect was observed in June. Similarly, in Experiment 2, hard grazing resulted in an increase in total tiller density prior to summer (20% more tillers in December), but the effects disappeared in the autumn. Nitrogen increased mean tiller population in February, and these differences remained throughout the experimental period, confirming a similar tendency to that of year 1.

In Experiment 2, nitrogen fertilization affected tiller death rates in December. Thus, 32% of the total tiller population died in the non-fertilized treatments, while 17% died in N100 ($P < 0{\cdot}05$). A similar trend was found for grazing treatments, with 30 and 20% of tiller death for lax and hard treatments respectively ($P < 0{\cdot}05$).

In both experiments, the contribution of flowering tillers to total tiller population density was always relatively small (<15% in all treatments; Figure 2). Yet, differences between paddocks that had been lax- or hard-grazed at the end of winter were statistically significant: 349 vs. 227 in Experiment 1, and 347 vs. 64 flowering tillers m^{-2} in Experiment 2 respectively ($P < 0{\cdot}05$).

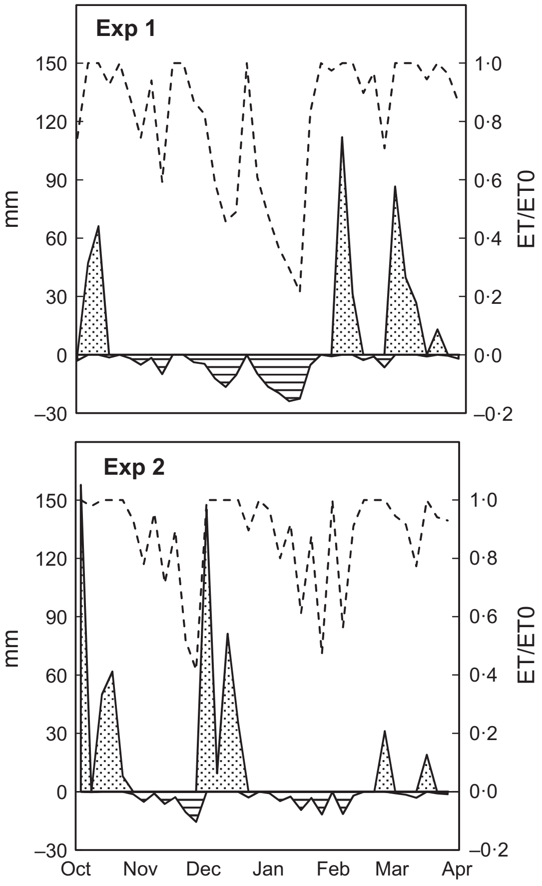

Figure 1 Ratio of evapotranspiration to reference evapotranspiration (dotted line, ET/ET0) and water surplus and deficits (continuous line, mm) from October to March. All values were estimated from a water balance that considers measured precipitation, soil water retention potential, and potential evapotranspiration measured from a grass 5 cm tall.

Vegetative tillers present in November, i.e. cohort 1 (Figure 2), made the greater contribution to total tiller

Table 2 Mean pre- and post-grazing herbage mass (HM) and mean pre- and post-height, % of grazed tillers and % of flowering stems (s.e. in parentheses).

		Treatment	Pre-grazing HM (kg DM/ha)	Post-grazing HM (kg DM/ha)	Pre-grazing height* (cm)	Post-grazing height* (cm)	Grazed tillers (%)	Flowering stems (%)
Experiment 1	July 2011	L	4159 (609) a	3027 (374) a	18·0 (1·8) a	11·1 (1·0) a	– –	– –
		H	4523 (609) a	2133 (374) a	19·7 (1·8) a	7·9 (1·0) b	– –	– –
	November-2011	L-N0	–	–	–	–	–	18·0 (2·7) a
		L-N50	–	–	–	–	–	9·3 (2·3) ab
		H-N0	–	–	–	–	–	6·3 (2·3) b
		H-N50	–	–	–	–	–	10·3 (2·3) ab
Experiment 2	August-2012	L	1879 (142) a	1546 (118) a	–	10·2 (0·3) a	56·0 (2) a	–
		H	1967 (146) a	1307 (118) b	–	9·2 (0·3) b	91·0 (2) b	–
	September-2012	L	1924 (89) a	1618 (58) a	–	12·3 (0·3) a	60·0 (2·0) a	29·0 (2·0) a
		H	1828 (89) a	1400 (58) b	–	9·8 (0·3) b	82·0 (2·0) b	12 (2·0) b
Post-experimental period (1)	October-2012	L	1829 (173) b	1121 (77) b	21 (1·3) b	16·8 (1·2) b	34·5 (2·1) a	28·0 (3·2) a
		H	1066 (173) a	634 (77) a	17·7 (1·3) a	12·4 (1·2) a	37·2 (2·1) a	11·7 (3·2) b
		N0	1389 (173) a	866 (77) a	17·9 (1·2) a	13·5 (1·2) a	35·1 (1·8) a	21·6 (3·1) a
		N100	1507 (173) a	889 (77) a	20·8 (1·3) b	15·7 (1·3) b	36·5 (2·3) a	19·1 (3·2) a

*In Experiment 1, this height corresponds to compressed height measured with the rising plate meter. In Experiment 2, this height corresponds to extended tiller height.

L and H indicate lax and hard grazing treatments respectively. Different letters indicate significant differences between treatments at $P < 0{\cdot}05$. (1) No interaction Grazing × Nitrogen for none of the measured variables.

density throughout the summer in both experiments. Depending on the experiment and treatment, that cohort of tillers represented at least 74 and up to 91% of all tillers present in the swards at the end of summer. Clearly, tiller production during late spring and summer – the warmest period of the year – was always low (Figure 5a) even though the degree of water stress was relatively mild in Experiment 2.

Conversely, towards the end of autumn there was a substantial and consistent contribution of newly produced tillers to total tiller density, in both experiments. In consequence, the relative importance of the cohort of vegetative tillers that survived through the summer decreased to <64%, and as little as 48%, of the tiller population.

Tiller survival

Nitrogen fertilization and grazing management at the end of winter were both important factors affecting the survival of vegetative tillers over summer. In both experiments, survival rates of tillers of the cohort 1 were lowest in L-N0 and similar in all other treatments (Figure 3a and b). However, this response was detected as statistically significant only in Experiment 2 (interaction $P < 0{\cdot}1$).

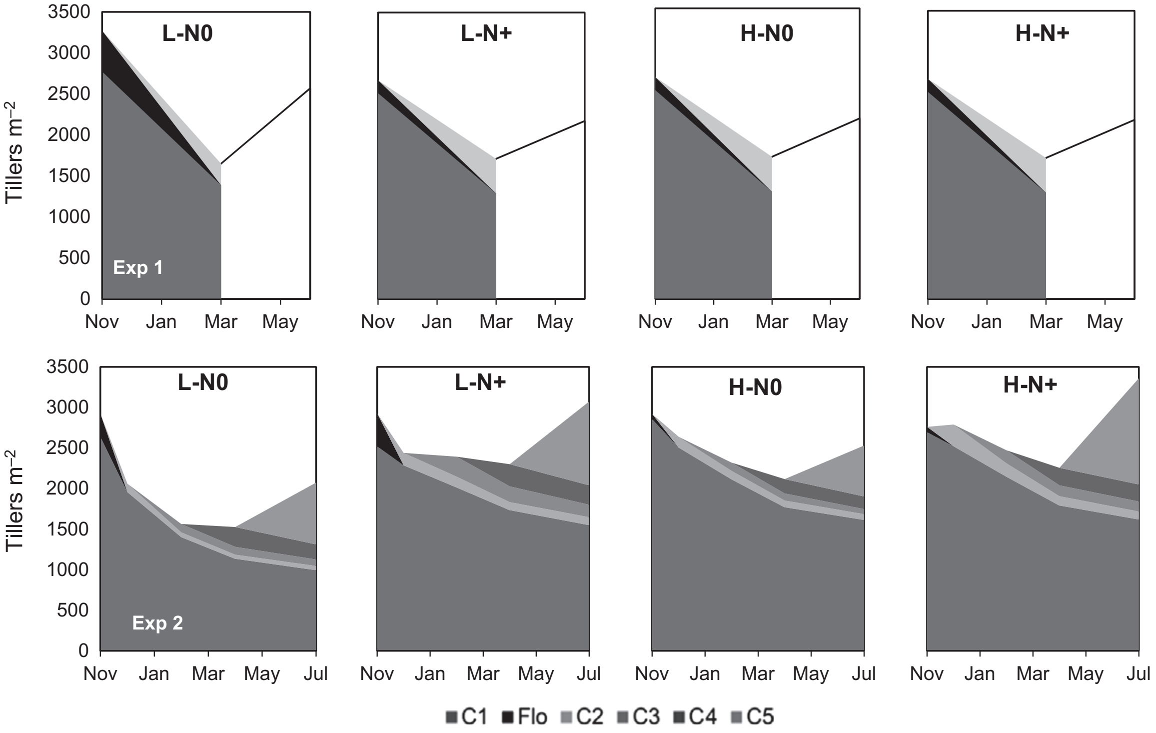

Figure 2 Survival diagrams of tiller age cohorts in tall fescue pastures subjected to hard (H) or lax (L) grazing to remove flowering tillers, and fertilized (N+) or not (N0) with nitrogen during spring, for Experiment 1 and Experiment 2. C1–C5: successive tiller age cohorts. Flo: flowering stems.

Results from Experiment 2, where sampling frequency allowed to estimate tiller death rates, indicate that differences between treatments were largely concentrated in early summer. Tiller death rates were maximal in L-N0 during December, almost doubling that of all other treatments (Figure 5b). In this period, a positive correlation was evident between tiller survival rate and tiller size. In general, heavier tillers survived better ($r^2 = 0{\cdot}69$ and $r^2 = 0{\cdot}54$ for L and H, respectively, $P < 0{\cdot}05$; Figure 4). Nitrogen increased tiller size and survival, while lax grazing increased tiller size but decreased survival. (Figure 4). Tiller survival of all other cohorts was generally higher than for cohort 1, but quite variable due to very low tiller production during the measurement dates (Figure 5a).

Tiller production

Tillers formed during spring–summer were few and had little influence on the balance of tillers present after summer. In Experiment 1, tiller appearance rates were positively influenced by hard grazing and nitrogen fertilization, although there was no interaction between factors. However, there were no statistical differences in relative tillering rates. Similar results were observed in Experiment 2, where sampling frequency allowed to estimate tiller appearance rates in shorter intervals. In this experiment, tiller appearance rates were increased by N fertilization, particularly in autumn, but similar to Experiment 1, there were differences between N in relative tillering rates only in December, and no differences from then onwards. Thus, the greater total production of tillers in fertilized and hard-grazed plots was due to higher tiller densities caused by increased tiller survival and not greater tillering per individuals in both experiments.

Discussion

Perennation strategy of tall fescue in a subtropical environment

How does perennation of grasses actually occur? Despite its obvious relevance for the function and performance of many forage production systems, this question has received little attention in agronomic studies (Matthew *et al.*, 2000). Matthew *et al.* (1993) proposed two possible perennation strategies for

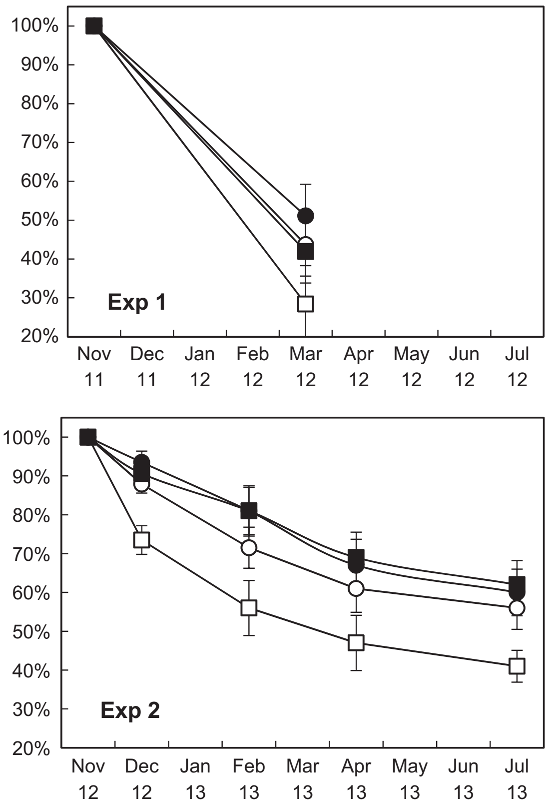

Figure 3 Survival (expressed as % of live tillers) of the cohort of vegetative tillers present in spring (i.e. cohort 1) in tall fescue pastures subjected to hard (circles) or lax (squares) grazing to remove flowering tillers, and fertilized (closed symbols) or not (open symbols) with nitrogen during spring. Vertical bars are SE of mean.

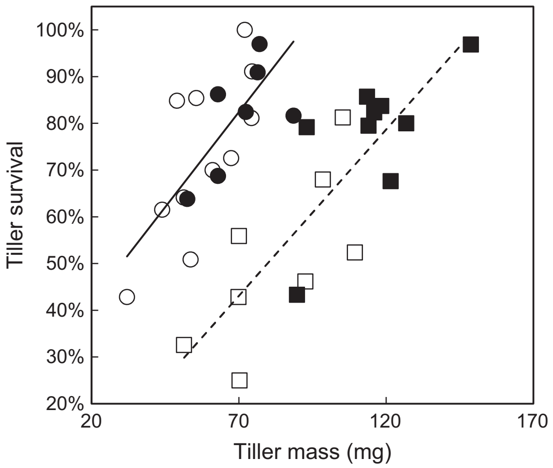

Figure 4 Tiller survival (%) and tiller mass of the cohort of vegetative tillers present in spring (i.e. cohort 1) in tall fescue pastures subjected to hard (circles) or lax (squares) grazing to remove flowering tillers, and fertilized (closed symbols) or not (open symbols) with nitrogen during spring. Continuous and dotted lines represent linear equations for hard and lax grazing, respectively.

temperate forage grasses: a 'reproductive pathway' involving daughter tiller production by flowering tillers, and a 'vegetative pathway' in which perennation relies on tillering from surviving non-flowering tillers. These pathways are not mutually exclusive and both contribute to perennation (Matthew *et al.*, 2013). In the present study, carried out in tall fescue in a subtropical environment, perennation appeared to be based on the cohort of vegetative tillers present in spring, which constituted more than 60% of the population of tillers present in the following autumn in both years and for all treatments. Indeed, tiller appearance rates during late spring and summer were low (Experiment 2) or very low (Experiment 1; Figure 5a).

Unfortunately, few studies have reported tiller survival and production in temperate grasses – almost none in subtropical environments – which restricts the possibilities for comparisons. In temperate NZ, perennial ryegrass swards showed a high proportion of reproductive tillers (from 25% to 70%), a marked tiller population turnover at flowering, and an overall increase in total tiller density (Matthew *et al.*, 1993; Hernández-Garay *et al.*, 1997; Bahmani *et al.*, 2000; Da Silva *et al.*, 2004), which is consistent with the reproductive perennation pathway being dominant. Although there is evidence that this may differ among cultivars (Bahmani *et al.*, 2000) and that tiller density can be manipulated through grazing (Thom, 1991; Hernández-Garay *et al.*, 1997; Da Silva *et al.*, 2004), management appears to have little influence on the persistence strategy of perennial ryegrass (Korte, 1986; Matthew *et al.*, 1993). Likewise, data from Langer *et al.* (1964) for timothy (*Phleum pratense* L.) compiled by Jewiss (1966) show an almost complete turnover of tillers in spring, in both frequently and infrequently cut swards, indicating a prevalent reproductive perennation pathway. The same dynamics were observed in infrequently cut swards of meadow fescue (*Festuca pratensis* L.), but in this species grazing regime did affect the perennation strategy: in monthly cut swards about two-thirds of the tillers present during summer were formed in the previous season (Jewiss, 1966).

An analysis of unpublished data made by Matthew *et al.* (1993) suggests that in temperate climates tall fescue seems to follow a tillering pattern similar to that of meadow fescue: up to 60% of tillers present in December were daughters of reproductive tillers when

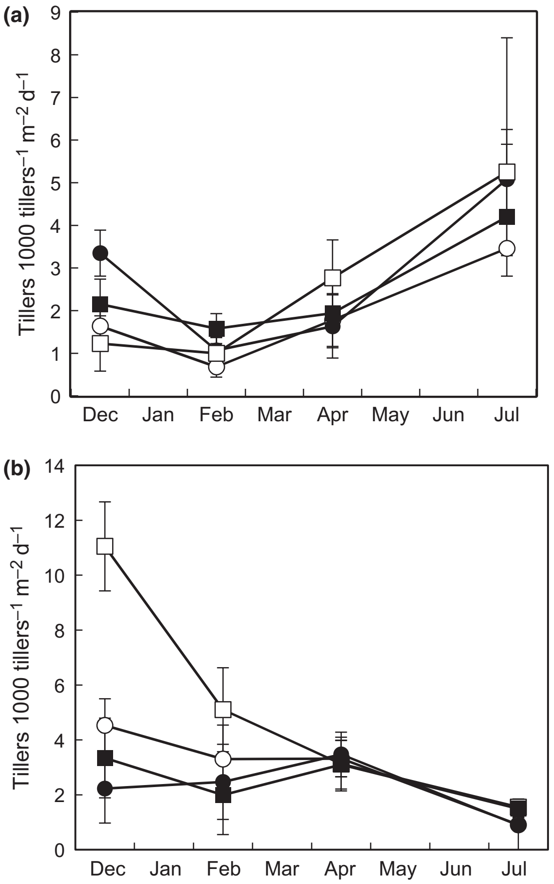

Figure 5 Tiller appearance rate (tillers 1·000 tillers^{-1} m^{-2} d^{-1}) and (b) tiller death rate (tillers 1·000 tillers^{-1} m^{-2} d^{-1}) of tall fescue pastures subjected to hard (circles) or lax (squares) grazing to remove flowering tillers, and fertilized (closed symbols) or not (open symbols) with nitrogen during spring. Vertical bars are SE of mean.

swards were grazed to a residual height of 10 cm, but this decreased to 30% when residual height was 4 cm. Thus, there appears to be environmental- and management-related factors that define the persistence of tall fescue. In temperate climates, under lax grazing, the reproductive pathway predominates and tiller production increases during the reproductive phase, most new tillers arising from reproductive tillers. Under harder grazing regimes, the vegetative pathway becomes more important (Matthew *et al.*, 1993). In subtropical climates (present study), the vegetative pathway seems prevalent in both lax and hard grazing regimes: tiller production was low to non-existent during spring and summer (Figure 5a), in years with either little or moderate water stress (Figure 1). Tillers seem to be produced in autumn and winter, from vegetative tillers that survived the summer. This would explain why tall fescue pastures growing in subtropical Australia show decreases in tiller density (and size) between spring and autumn even with no water stress (Lowe *et al.*, 1999). Low tiller appearance rates during spring and summer have also been reported for tall fescue in subtropical Argentina (Pergamino), regardless of grazing frequency (Scheneiter and Améndola, 2012). In temperate areas of Argentina, however, summer tiller density is not an issue (Lattanzi *et al.*, 2007).

Causes of tiller death during summer

The relevance of the cohort of vegetative tillers present in spring (cohort 1) to sustain tiller density over summer makes it crucial to comprehend the determinants of the survival of those tillers if we are to understand tall fescue's persistence in subtropical climates.

Swards that received no fertilizer and had a highest proportion of flowering stems showed the highest tiller death rates on both years. In Experiment 2, differences in relative tiller death rates were most clear from mid-November to mid-December; afterwards survival rates became similar in all treatments. In Experiment 1, tiller survival rates also tended to be higher in swards grazed so as to remove flowering stems and fertilized with N (51%) than in swards with no fertilizer and more flowering stems (28%), but these differences were not detected as statistically significant. Overall tiller survival rates were lower in Experiment 1 than in Experiment 2. We suspect this might be due to higher air temperatures recorded during Experiment 1, as temperatures above 30°C reduce tall fescue's growth rates to less than 50% of its potential (see Figure S1). High temperatures can also increase respiration thus reducing net carbon fixation, a situation that can have negative impacts on tillering rates (Assuero and Tognetti, 2010). Water deficits observed during Experiment 1 (Figure 1) could also be responsible for reduced tiller survival.

Tillers of similar weight had higher survival in intense grazing than in lax grazing. However, this effect was not observed for fertilized treatments, where survival of tillers of similar weight did not appear to be influenced by fertilization. Although there is evidence that tiller size might explain tiller survival during summer (Hoen, 1968; Ong *et al.*, 1978), our results indicate that this apparent association would depend on the presence of reproductive stems.

Elongating stems are strong sinks for carbohydrates (Colvill and Marshall, 1984), and also for nitrogen (Power and Alessi, 1978). Therefore, small vegetative tillers formed during spring that compete poorly for assimilates would be most likely to die, as observed in temperate cereals (Davidson and Chevalier, 1990). An analysis of tiller age-cohort data from Hernández-Garay *et al.* (1993, 1997) reveals that the increased density in perennial ryegrass swards under late-flowering management was purely due to changes in tiller production during summer: survival rate of tillers present in mid-spring was similar in hard and lax grazing (40% and 30%, respectively, values not unlike those observed in the present study; Figure 3). Matthew (2002) linked this increased tiller production under 'late control' to translocation of assimilates from decapitated reproductive stems to daughter tillers. Thus, the main difference in tiller dynamics between tall fescue in a subtropical environment and perennial ryegrass in a temperate one appears to be very low summer tiller production in tall fescue, summer survival of spring tillers apparently being similar in both species.

Nitrogen fertilization has been proven to increase tiller survival in cereals (Power and Alessi, 1978; Ramos *et al.*, 1995). Also, nitrogen dressings can increase tiller size of grasses and therefore positively affect survival of spring-initiated tillers that would otherwise be too immature to survive summer droughts (Davies, 1988). In the present study, this was observed in Experiment 2. Lack of effects of nitrogen on tiller survival for Experiment 1 could be due to lower nitrogen fertilizer rates and/or more severe summer conditions. Nitrogen compounds may be used as carbon substrates for regrowth (Lattanzi *et al.*, 2005). This role may become more important when water-soluble carbohydrates are depleted due to high rates of respiration and/or low rates of photosynthesis (Fulkerson *et al.*, 1993). However, we did not observe an intrinsic effect of nitrogen: when compared at similar size, fertilized and non-fertilized tillers survived similarly.

Production of new tillers in autumn is affected by nitrogen

In both experiments, tiller appearance rates were low during spring and summer and highest in autumn. This finding is consistent with previous results for tall fescue in subtropical regions showing low tiller appearance rates during summer (Lowe *et al.*, 1999; Scheneiter and Améndola, 2012). These responses were unlikely to be related to the effects of sward mass on tillering (Simon and Lemaire, 1987): standing mass was generally low and was highest in the treatments with the highest tillering rates (Figure S2). More likely, temperatures that were less stressful for tall fescue (Figures 1 and S1), and probably also better plant water status, could explain increased tillering in autumn. Several studies have shown the positive effects of nitrogen fertilization on tillering (Simon and Lemaire, 1987; Lemaire and Culleton, 1989; Mazzanti *et al.*, 1994; Scheneiter and Améndola, 2012). In the present study, relative tiller appearance rate (i.e. the number of tillers produced by each tiller present in the sward) was increased by nitrogen fertilization only during November–December. However, as a result of differences in total population density, absolute tiller appearance rates (i.e. the number of tillers produced per square meter of sward) were higher on fertilized plots in late spring, summer and autumn. Grazing treatments did not modify either relative or absolute tiller appearance rates.

Conclusions

This study indicates that perennation of tall fescue in a subtropical environment relies heavily on the survival of tillers present in spring, as these tillers represented the most abundant cohort during summer. Removal of flowering stems by short-term intense grazing at the end of winter, and nitrogen dressings in early spring, can both reduce tiller mortality rates in late spring and increase tiller survival over summer. Subsequent higher tiller densities at the end of summer allow greater absolute tiller production in autumn (relative tillering rates are unaffected). In a harsher summer, the beneficial effects of these treatments became less evident. More information on the ecophysiological mechanisms underlying tiller demography during summer is needed if persistence of temperate grasses in subtropical climates is to be understood.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Potential growth rate of tall fescue plants (as % of maximum) as a function of air temperature.
Figure S2. Evolution of pre- (a) and post-grazing (b) biomass (kg ha^{-1}) of tall fescue pastures subjected to hard (circles) or lax (squares) grazing to remove flowering tillers, and fertilized (closed symbols) or not (open symbols) with nitrogen during spring.