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Limits to recruitment of tall fescue plants in poplar silvopastoral systems of the Pampas, Argentina

M. P. Clavijo · P. S. Cornaglia · P. E. Gundel · M. Nordenstahl · E. G. Jobbagy

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Abstract Forage production in silvopastoral systems of the Flooding Pampa is based on cool season grasses with a relatively asynchronous phenology regarding their accompanying deciduous trees. However, the productivity of cool season grasses in these systems is usually low. The hypothesis of this work is that the low productivity of cool season grasses is caused by tree litter constraining plant recruitment. Emergence and establishment (reproductive propagation), and tillering (vegetative propagation) patterns of tall fescue, a cool season grass in the region, were studied in two pairs of adjacent non-afforested and afforested poplar stands (tree age 26–28 years, tree density 453–797 plants ha^{-1}). Observational and manipulative (i.e. addition of seeds, leaf litter removal) experiments indicated that the recruitment of tall fescue plants is strongly limited by the fall of poplar leaves over emerged seedlings, during autumn. Results suggest that any management practice capable of removing poplar litter, either through grazing or machinery, could neutralize this limitation enhancing the herbaceous primary production of the system.

Keywords Cottonwood · Establishment · Litter · Recruitment · Understory vegetation

M. P. Clavijo (✉) · P. S. Cornaglia
Cátedra de Forrajicultura, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín, 4453 (1417) Buenos Aires, Argentina
e-mail: mclavijo@agro.uba.ar

P. E. Gundel
Cátedra de Ecología-IFEVA (CONICET), Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín, 4453 (1417) Buenos Aires, Argentina

M. Nordenstahl · E. G. Jobbagy
Grupo de Estudios Ambientales-IMASL, Universidad Nacional de San Luis and CONICET, San Luis, Argentina

M. Nordenstahl
Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia

Introduction

Grassland afforestation is an attractive production option to diversify farm outputs and reduce risks in cattle production systems (Pearson and Ison 1997). As part of a global trend, afforested areas are increasing in the Pampean grasslands, Argentina (Wright et al. 2000). Silvopastoral systems that combine cattle production and forestry represent a valuable alternative for this region traditionally dedicated to cattle breeding (Marlats et al. 1995).

The combination of winter-deciduous trees and cool season grasses minimizes competition and enhances ecological complementarity, especially for resources that can not be transferred in time (i.e. radiation; Ong and Leakey 1999; Roupsard et al. 1999). Evergreen trees do not leave any window for development of C_3 grasses, and C_4 grasses can not either develop under deciduous trees because their phenologies overlap.

In the Flooding Pampa, differences in seasonality of forage production are found between open grasslands and those planted with deciduous trees (Clavijo et al. 2005). While open grasslands are dominated by warm season species (C_4 grasses) with high spring–summer–autumn production (Perelman et al. 2001), the understory vegetation of poplar plantations is dominated by cool season species (C_3 grasses) that concentrate their activity in autumn–winter–spring. Although the presence of trees has a negative impact on the overall annual aboveground primary production of the understory (50% decline), it favors cool season species and winter forage availability (Monlezun et al. 2008).

Structure and function of the understory vegetation is mainly determined by light quantity and quality below the tree canopy. In the case of deciduous trees, leaves phenology explains seasonality of radiation (Chen 1997; Coates 2002; Arrieta and Suárez 2005). The highest understory radiation levels occur in autumn and winter (Pincemin et al. 2007) accounting for most of grassland productivity dynamics. Cover of cool season grasses is promoted but total cover is poor. Grass tillering is usually reduced because the tree canopy decreases the ratio of red/far red light (R:FR) reaching the understory (Casal et al. 1987). C_3 grasses' tillering is reduced under pines, poplars or oaks when compared with open pastures (Burner and Belesky 2008; Pincemin et al. 2007).

On the other hand, Devkota et al. (2001) found that in deciduous tree silvopastoral system with canopy closure of the 40–50%, tillering was two-thirds of that of open pastures.

While the effects of tree foliage on the understory are clear and predictable, the effects of leaf litter covering soil surface and exerting a possible physical or chemical barrier to understory plants is less understood (Carroll 1994; Larrea-Alcázar and Simonetti 2007). The timing of litterfall may be a key factor regulating plant tillering throughout temporal changes in light quality (Pincemin et al. 2007; Burner and Belesky 2008); but it could also be a barrier to grass seedlings recruitment. Accumulated tree litter limits the recruitment of small-seeded tree species (Dupuy and Chazdon 2008).

This work presents the case of study of two plantations in Flooding Pampa grasslands where tall fescue dominates the understory vegetation, but total cover is limited (Clavijo et al. 2005). Low herbaceous cover suggests restrictions for plant growth and recruitment. Tall fescue recruitment results from vegetative propagation or sexual reproduction (Maddaloni and Ferrari 2001). In this study tiller production, seedling emergence and establishment were evaluated in order to investigate how poplar leaf dynamics impact on tall fescue plant recruitment in Flooding Pampa silvopastoral systems. For this purpose, the presence of tree litter on natural and artificial soil seed bank was manipulated.

Materials and methods

Study site

The study site was located in Castelli (lat: 36°06′S, long: 57°48′W 10 m a.s.l.; Buenos Aires Province, Argentina), where mean annual temperature and precipitation are 15.4°C and 980 mm, respectively (Jobbágy and Jackson 2003). Upland soils are generally Mollisols of silty–loam texture in the surface and clay–loam texture in the B horizon. Organic carbon of the A horizon is 2.5–2.9% in grasslands while under plantations reach to 3.9% (*Eucalyptus* sp. plantations, Jobbágy and Jackson 2003). Native grasslands have been deteriorated by continuous grazing or replaced by crops in the most suitable areas. In addition, many grasslands are naturalized old pastures (>30 years), which conserve a small proportion of exotic species and have been re-invaded by native ones (Oesterheld and León 1987; León and Burkart 1998; Chaneton et al. 2002). In general, the dynamics of forage production follows a clear seasonal pattern with a peak in spring–summer since the productivity of C_4 species is threefold greater than that of C_3 species (Sala et al. 1981).

The present study covered two sites within a cattle production farm. Both were located in upland areas and included a pair of adjacent afforested (poplar plantation) and non-afforested stands (open grassland). The afforested ($F1 = 3.5$ ha, $F2 = 4.5$ ha) stands were planted with eastern cottonwood poplar (*Populus deltoides Bartr. ex Marsh. ssp. deltoides*) in 1979 (Table 1).

Four years before tree planting (1976) the stands were sown with tall fescue (*Schedonorus arundinaceus*

Table 1 Description of each plantation and it adjacent grasslands

Component	Variable	Plantation	
		*F*1	*F*2
Soil	Bt horizon depth (cm)	45	40–75
Plantation	Actual density (trees ha^{-1})	453	797
	Basal Area (m^2)	36.4	39.1
	Tree litter (kg ha $year^{-1}$)	2,698	2,818
	Wood Yield (kg ha $year^{-1}$)	7,550	9,420
Grassland	Non-afforested grassland plant cover (%)	74	63
	Afforested grassland plant cover (%)	33	19
	Non-afforested grassland yield (kg dry matter ha $year^{-1}$)	8,328	11,530
	Afforested grassland yield (kg dry matter ha $year^{-1}$)	4,505	5,857
Cattle management	Grazing management*	Intermittent	Intermittent
	Stocking rate (cows ha^{-1})	0.7	0.7

Density, basal area, Bt horizon depth, stocking rate and grazing management data correspond to Clavijo et al. 2005. Pasture and wood production as well as tree litter data correspond to Nordenstahl unpublished

* Without specifically intensities and frequencies of grazing

Schreb., Dumort (= *Festuca arundinacea* Schreb.; Soreng and Terrell 2003). It is assumed here that the pasture was naturalized at the moment of the afforestation and that the value of tall fescue cover was similar to the present one although invader C_4 natives' grasses disappeared as a consequence of the plantation (Clavijo et al. 2005). Hole-digging for individual plants was the only disturbance associated with tree establishment. No plowing fertilization, or irrigation was ever applied, and plantations were never thinned or pruned. At the moment of this work the pasture under plantations had preserved 95% of tall fescue (C_3), while outside the plantation communities were more diverse and dominated by C_4 species (Clavijo et al. 2005). Main C_4 species outside plantations (14, 3% cover each one) were: *F*1: *Paspalum dilatatum* and *Stenotaphrum secundatum*; and *F*2: *Paspalum dilatatum* and *Paspalum vaginatum.*

Measurements

Tillering of individual tall fescue plants was characterized in open grasslands and plantations. Focus was set on seasonal differences of number and size of tall fescue tillers (plant scale) between afforested and non-afforested stands. The trial was carried out between June 2004 and June 2005, at five dates (winter, spring and summer 2004, and autumn and winter 2005). In plantations (*F*1 and *F*2) and their adjacent open grasslands, four 2 m^2-cages were randomly placed. The cages were built of iron and net wire to prevent biomass removal by domestic and wild grazers but leaf litter was available to pass through the net. Before the first sward and after each evaluation, artificial clipping at 10–15 cm height was applied in all cages to simulate biomass removal by cattle grazing observed outside the cages. Within each cage, seven tall fescue plants were identified and permanently marked with wire rings. For each plant, the number of live tillers, flowered tillers (panicles), and dead tillers were counted at each date (each date corresponds to 1 day only). The clipped biomass of spring 2005 was weighed in order to estimate dry mass for each tiller. The harvested biomass was oven-dried at 60°C during 48 h and then weighted.

Since non-afforested grasslands presented high cover, the seedling recruitment experiments were carried out only under plantations. First, soil seed bank was assessed through soil seed samples and transects. Second, seed addition experiments were performed in order to control seed amount and quality. Seedlings that naturally emerged along transect and in the seed addition experiments were marked and observed for 120 days to assess final establishment.

The seed bank was randomly sampled at each study site in 2005. We took four samples, of 400 cm^2

and 2 cm depth, around each cage. Samples were incubated in a greenhouse with 15–25°C of alternating temperature, natural photoperiod and no water limitations. Emerged grass seedlings were weekly recorded until there was no more emergence. After counting, each seedling was removed from the soil sample.

Two seed addition experiments were carried out in two consecutive autumns. In autumn (before tree litter fall) 2005, 10 micro-plots of 64 cm^2 were settled in each cage inside the plantations and sown with 50 seeds from a tall fescue commercial variety. Seed viability was 95%. Before sowing, superficial soil was removed and seeds were slightly covered with the same soil. The number of seedlings as well as their growth stage (number of leaves and tillers) and poplar litter cover were recorded every 15 days. Leaf litter cover was assessed using a visual scale of 25, 50, 75 and 100%. In autumn 2006, this experiment was repeated with an additional treatment of tree litter exclusion. The micro-plots were subject to two treatments: half of them remained as controls with no tree litter exclusion (NLE) and the other half was subject to the full exclusion of tree litter (LE). The complete exclusion of tree litter was achieved by means of wire cones covering the micro-plots. The remaining micro-plots were uncovered (NLE). For the LE-NLE experiment results from 2005 are not presented as they were identical to those of NLE from 2006.

Simultaneously to the seedling addition experiment, in each study site four 3-m-long transects were randomly located to study natural establishment of soil bank seeds. The natural seed bank has a different sensitivity to environmental factors (e.g. light conditions), than artificial ones (Scopel et al. 1991). Transects were visited every 15 days and in each visit, tree litter cover was estimated in terms of the percentage of transect covered by leaves and seedlings of tall fescue were marked recording their specific positions along transect (tape measure). Based on the number of leaves and tillers, the growth stage of the seedlings was characterized. Final seedling establishment was determined for both experimental settings (transects and seed addition experiments) at the end of autumn. Seedlings with $\geq$4 expanded leaves were considered as established. In both experiments, establishment was defined as the proportion of emerged seedlings that reached the established stage.

Additionally, dynamics of incident radiation and R:FR ratio were measured as components of plant tillering capacity and seedlings establishment. Four samples of incident ration were measured in the understory with a Li-118B radiometer (Li-Cor Inc., Lincoln, NE, USA) during tree litter fall (1 April, 15 April and 15 May 2006). R:FR ratio was measured with a Skye SDL 2520 sensor (Skye Instruments Ltd, Llandridrod Wells, UK) under and outside the plantations taking four samples per season, respectively. All samples were taken on sunny days at midday, in order to avoid tree shading in any direction, with sensors placed on the ground. Shade produced by litter on the ground is not considered assuming that for established plants is low and that in case of seedlings mechanical effect is stronger.

Statistical analyses

Comparisons of tillering dynamics between non-afforested and afforested stands were performed independently for each site using repeated measures analysis (Morris 1999). No statistical comparison has been performed between sites. In the model, the effects of plantation (afforested and non-afforested), time (seasons) and their interaction were evaluated on tillers per plant. The number of tillers per plant in each cage was estimated by averaging seven marked plants. Differences in emergence and establishment patterns between poplar litter exclusion and no exclusion treatments ($F1$ and $F2$) were tested with ANOVA ($p = 0.05$). Pertinent data transformations were done to accomplish with ANOVA assumptions.

Results

The amount of solar radiation that reached the ground was lower in the afforested stands compared with the non-afforested ones. Measured ratios were 89, 64.5 and 15.5% in March, April and May, respectively. Towards the autumn, as leaves fell, we observed a positive correlation between tree litter cover and incident radiation on the herbaceous layer (Fig. 1).

The effect of tree plantations on the quality of light varied across seasons. In autumn (trees without leaves), the R:FR ratio was similar in afforested and non-afforested stands while in spring (trees with high

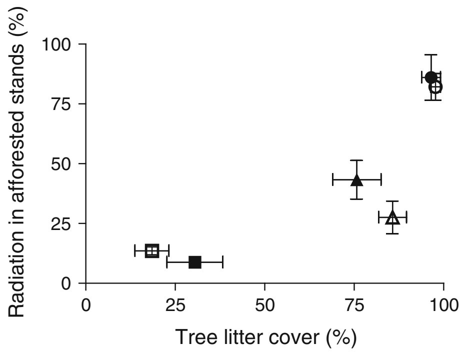

Fig. 1 Relative radiation reaching the ground in afforested stands (incident radiation in adjacent stands: afforested/non-afforested) related to tree litter cover under plantations (*white* symbols site *F*1, *black* symbols site *F*2, *squares* April 1, *triangles* April 15, *circles* May 20). *Standard error bars* are indicated for both variables

Table 2 Red to far red ratios: in afforested and adjacent non-afforested stands in autumn–winter (trees without leaves) and spring–summer (trees full of leaves)

Plantation	Stand	R:FR	
		Autumn–winter	Spring–summer
*F*1	Afforested	1.04 (0.02)	0.76 (0.31)
	Non-afforested	1.06 (0.01)	1.15 (0.04)
*F*2	Afforested	1.02 (0.01)	0.59 (0.26)
	Non-afforested	1.05 (0.02)	1.12 (0.01)

Values are average of four samples in each stand with corresponding standard deviations in brackets

leaf coverage) non-afforested stands showed 34 and 47% higher values of R:FR in *F*1 and *F*2, respectively (Table 2).

The number of tillers of tall fescue plants did not show significant differences between afforested and non-afforested stands (*F*1 $p = 0.75$ and *F*2 $p = 0.43$). In both sites, we found a typical autumn–winter–spring production curve. The number of live tillers peaked in spring and had its minimum at autumn–winter (Fig. 2). In October (beginning of spring), the proportion of flowering tillers of tall fescue was higher in the plantations than in the open grasslands (*F*1 $p = 0.032$ and *F*2 $p = 0.054$), suggesting they flowered earlier.

The dry mass of tillers harvested in spring was not significantly different in afforested and non-afforested stands ($p = 0.65$). In afforested stands, dry mass of tillers was 0.76 ± 0.28 g tiller^{-1} and 0.95 ± 0.25 g tiller^{-1}, while it was 0.73 ± 0.41 g tiller^{-1} and 0.81 ± 0.47 g tiller^{-1} for non-afforested stands, in *F*1 and *F*2, respectively.

Seedling emergence of tall fescue was reduced in afforested stands as the levels of poplar litter cover increased (Fig. 3). The dynamics of poplar litter finally reached a plateau by autumn covering 75 and 100% of the soil surface in transects and micro-plots, respectively. The dynamics of seedling emergence and poplar litter cover followed the same pattern in both seed addition experiments (2005 and NLE in 2006). Under NLE (2006), the number of emerged seedlings observed in the micro-plots started from 55% and decreased to 0% of the total seed sown. Finally, both years (autumn 2005 and autumn 2006) no seedlings became established at the end of the experiment. The dynamics of seedling emergence were slightly different in transects experiment. The maximum number of seedlings over transects was counted 45 days after the beginning of the experiment. This value declined to 5% of total live seedlings around day 60 (Fig. 3).

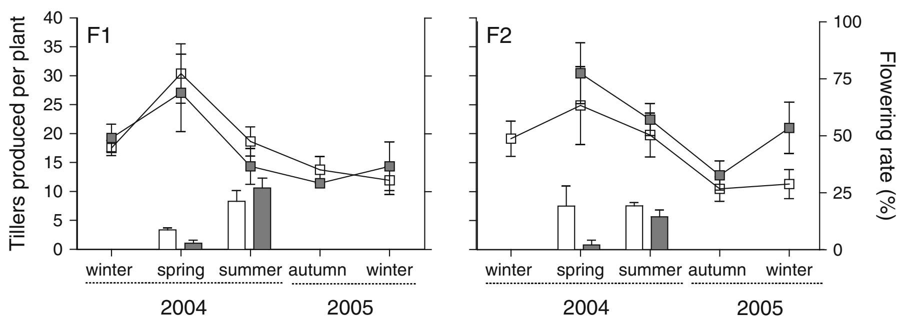

Fig. 2 Dynamics of tillers production (stock) per plant (*square* symbols and *left* axis) and flowering rate (*bars* and *right* axis) of tall fescue in afforested (*open square*) and non-afforested (*filled square*) stands of sites *F*1 and *F*2. Values are average of four samples within stand, and *vertical bars* show standard error. Seven plants were measured within each stand

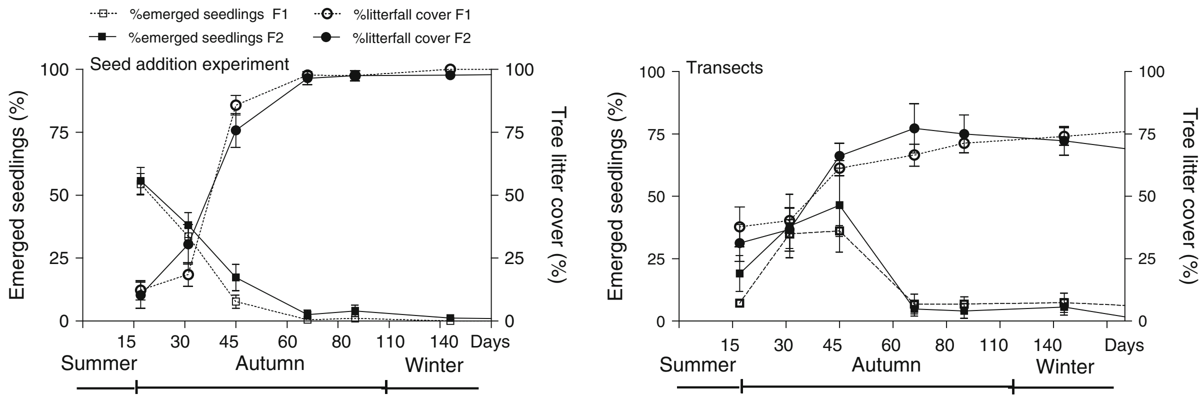

Fig. 3 *Seed addition experiment* emerged seedlings of tall fescue (left *y* axis, percentage of 50 seeds sown in each micro-plot) and tree litter cover (right *y* axis, area percentage) in relation to days elapsed since the beginning of the addition experiment. *Transects* same variables of the seed addition experiment were measured. *Vertical bars* show standard errors

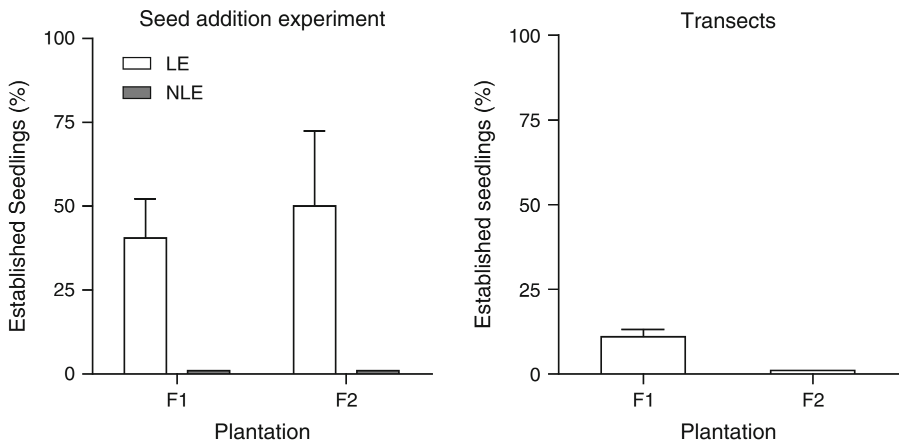

Fig. 4 *Seed addition experiment* proportion of tall fescue seedlings found in March 2006 that became established by the end of the experiment in the micro-plots of plantations *F*1 and *F*2. *NLE* no litter exclusion, *LE* litter exclusion. Total seedlings emerged per micro-plot *F*1: NLE 27, LE 28 and *F*2: NLE 28, LE 30. *Transects* proportion of tall fescue seedlings that became established (mean emerged seedlings was 35 in *F*1 and 17 in *F*2) in four fixed transects of three lineal meters in the grassland underlying plantation *F*1 and *F*2. *Vertical bars* show standard errors

In soil bank samples taken to greenhouse 188 ± 21 and 291 ± 40 emerged seedlings m^{-2} (average and SE $n = 4$) were counted in *F*1 and *F*2, respectively. But seedling survival under poplar litter was very limited (Fig. 4). At the beginning of the experiment in the micro-plots with no litter exclusion (NLE) and litter exclusion (LE) both treatments showed a very similar pattern of seedlings emergence. However, none of the seedlings at the NLE treatment reached the stage of four leaves (establishment) whereas in the LE treatments establishment reached 41 and 50% (*F*1 and *F*2, respectively) of the emergence (Fig. 4). In transects establishment rates of natural emerged seedlings was also poor: 11 and 1% at *F*1 and *F*2, respectively (Fig. 4).

Discussion and conclusions

Plant cover under poplar plantations is limited by restrictions to the establishment of cool season grasses. Although constrictions to seed production of plants were not found, tree leaves acted as a physical barrier preventing colonization of bare soil through seedling establishment. Tall fescue tillering was similar in plantations and open grasslands, suggesting that poplars and summer grasses exert similar competitive effects on cool season grasses. Germination and emergence under plantations was high (Fig. 3) and potentially enough to develop a population similar to open cultivated pastures of the region (target 100–400 plants m^{-2}) (Maddaloni and Ferrari 2001). Probably this high emergence was associated with the abundance of "gaps" without herbaceous competition and likely protected from direct evaporation by the presence of old tree litter (Xiong and Nilsson 1997). However, new litterfall interrupted the establishment of seedlings supporting the notion that it exerts a physical barrier to small non-shade tolerant species (Dupuy and Chazdon 2008), particularly when their initial growth is very slow like tall fescue (Lodge 2004). In fact, in the "gaps" where tree litter was removed (LE) establishment of tall fescue reached 25% of sown seeds (emerged seedlings were 56% of sown seeds), compared to 0% without removal in the seed addition experiment (NLE) and in *F*1 transect, and 11% in *F*2 transect (Fig. 4). Differences between *F*1 and *F*2 were not tested but the tendency can be explained by a higher frequency of gaps in *F*2 because of higher density of trees and less herbaceous cover (>50% bare soil), despite litter production was similar (Table 1).

Number, size and seasonal production of tall fescue tillers were not different between plantation and open grassland in both sites (*F*1 and *F*2) (Fig. 2). Tall fescue tiller production may be constrained in open grasslands exerted by summer native grasses that account for the 50% of the total basal cover (Clavijo et al. 2005). Dominant C_4 grasses in open grasslands were all perennial species, which develops big tufts between swards interfering with tillering of C_3 grasses. Despite radiation being the only resource analyzed in the present work competition for water and nutrients could also be significant between C_3 and C_4 perennial species at the expense of tillering capacity of C_3. Competition under plantations is almost absent (bare soil 30%), suggesting that some restrictions are imposed on tall fescue tillering by trees or by intraspecific-competition (Kays and Harper 1974). Size of tillers was also similar but structure of plants is expected to differ under and outside plantations. Under shade, grasses can produce longer stems and leaves (Benavides et al. 2009) with the same dry weight that in open pastures. Guevara-Escobar et al. (2007) and Lin et al. (1999) observed as under plantations tall fescue conserved the same shoot dry weight that in open pastures. Tillering dynamics followed the same pattern in both physiognomies (plantation and open grassland) and in both sites with a pick of production with a minimum in winter and a maximum in spring. The high number of panicles observed in spring under plantations suggests an anticipated flowering. The appearance of panicles involves development and growth processes. Proportion of induced buds from vegetative to reproductive stages depends on vernalization and photoperiod. Once induced, the growth is mainly controlled by thermal units (Maddaloni and Ferrari 2001). Considering that in open grassland minimal temperatures are lower in late-winter and early spring (Benavides et al. 2009), the results suggest that requirements for floral induction could be complied in both physiognomies but the accumulation of thermal units would be higher under plantations. Besides that effect, the availability of seeds in the soil did not show any constraints. In contrast with tall fescue plants showing declining flowering under evergreen pines (Burner and Belesky 2008), tall fescue plants under deciduous poplars may not compromise the reposition of seeds in the soil bank.

Finally, the main limit to recruitment of tall fescue under poplars was the influence of litter fall during autumn on the survival of seedlings. The variables: tillering, seed production and seedling emergence were not affected by poplars.

Winter productivity (at the critical season in Pampean grazing systems of the Pampas), is similar or even higher in afforested grasslands than in non-afforested grasslands. However, it could be improved by developing some tree litter removal techniques to favor herbaceous cover through seedling recruitment (Xiong and Nilsson 1999). That would reinforce the role of silvopastoral systems as an interesting alternative to classic forestry agroecosystems.

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