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Substitution of *Lotus glaber* for the dicots of a natural grassland in the flooding Pampa of Argentina.

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Introduction

Gap opening and colonization are considered substantial mechanisms of community dynamics (Grubb, 1977). They represent opportunities for new trade-off between the species already present or for newcomers to be established. Every new gap represents an available volume of resources (light, water and nutrients) for the encircling plants and for new individuals naturally dispersed or purposely introduced in it (Tilman, 1982).

The objective of this work was to assess the ability of *Lotus glaber* to colonize gaps opened as a result of dicots death and to appraise the degree to which an individual species is able to fill the niche of a whole guild (dicots) and even to enlarge another guild (graminoids). Under the effect of livestock grazing, the grasslands of the Pampa lowlands, currently dominated by a rich array of grass species, modify their structure leaving way to an increase in cover of dicots (Sala *et al.*, 1986), most of them introduced species of low forage value. Flooding, a frequent but aleatoric disturbance in this area, has the opposite effect, namely, the removal of most of the introduced dicots and also of some native herbs (Insausti *et al.*, 1999), resulting in the opening of a high number of gaps.

The hypothesis was that *L. glaber* introduced immediately after gap opening, would outcompete the dicots (Tilman, 1982) associated to its ability to fix atmospheric N. Also, this ability would enlarge the graminoids niche, more than compensating for the elimination of dicots competition. Thus, the hypothesis embodies the assumption that *L. glaber* would fill the role of a keystone or an engineer species in the modified system (Lawton and Jones, 1995; Power *et al*., 1996).

Materials and Methods

The experiment was carried out in a natural grassland located in flooding Pampa (Argentina). Two kinds of manipulations were generated inside an exclosure: 1) removal of dicots with herbicide application and 2) introduction of *L. glaber*, resulting in a combination of four treatments: (a) grassland without dicots, (b) grassland without dicots in which *L. glaber* was introduced, (c) *L. glaber* intersown controls (with dicots) and (d) undisturbed controls, arranged in a 2 x 2 factorial randomized blocks design. Six 3 x 6 m experimental plots were assigned at random to each treatment. Seeds of *L. glaber* were intersown one month after herbicide application.

Seedling density of *L. glaber* was recorded 10 days after sowing; plant density and the number of shoots per plant was recorded three times: 2, 6 and 28 months after sowing. Aboveground living biomass was sampled in each plot 12 months after sowing (autumn); the clipped material was sorted to dicots, graminoids and *L. glaber* and was dried at 70 ºC for 72 hours and weighed. Dried aboveground biomass from each guild was analyzed for total tissue N. The measure of total nitrogen content of plant material was determined with the Kjeldahl-method. Data were analyzed by means of the single classification analysis of variance. The density data were transformed by the factor $\sqrt{(x+0.5)}$, to attain the ANOVA assumptions.

Results and Discussion

Seedling density of *L. glaber* 10 days after sowing was similar in plots with dicots or without them, but differences in the number of established plants between those two treatments progressively increased up to 28 months (Table 1). The number of shoots per plant was larger ($P<0.01$) six months after sowing in plots in which dicots had been killed, but this difference was not apparent 28 months after.

Table 1. Plant density and number of shoots per plant of *Lotus glaber*, 2, 6 and 28 months after sowing in plots with dicots or without them. Values followed by different letters are significantly different ($P<0.05$).

Time	Plants/m^2		Shoots/Plant	
	With Dicots	Without Dicots	With Dicots	Without Dicots
2 months	210a	306b	1h	1h
6 months	173c	225d	1.1h	1.7i
28 months	4f	48g	30j	29j

Twelve months after sowing (autumn), aboveground biomass of *L. glaber* in plots previously treated with herbicides was 25 times higher than in plots with dicots (Table 2). At this time, dicots biomass was significantly lower in intersown plots, with herbicides applied treatment, than all the others ($P<0.01$; Table 2). The biomass of grasses was larger in plots in which dicots had been killed than in those in which they were not (Table 2). However, grasses biomass in plots in which herbicides had been applied as the only treatment (no *L. glaber* sowing), differ from those with *L. glaber* sown after herbicides application ($P<0.05$). Total aboveground biomass in this last treatment was also larger than all the others ($P<0.01$; Table 2). Content of N expressed as the amount of the element per unit area was higher in graminoids when dicots were killed by herbicides application (Table 3). Moreover, N content in total biomass and in graminoids biomass was higher in plots with *L. glaber*, previously treated with herbicides than in the other three treatments (Table 3).

Table 2. Aboveground biomass ($g.m^{-2}$) twelve months after sowing (autumn). Values are means of six replicates with standard errors in brackets.

	Herbicide +*L.glaber*	Control +*L.glaber*	Herbicide	Control
Graminoids	71 (2.2)	39.1 (2.1)	60.7 (1.9)	38 (1.3)
Lotus glaber	32.4 (1.8)	1.3 (0.2)	---	---
Dicots	1.6 (0.3)	24.5 (2.5)	5.6 (0.6)	26.3 (0.9)
Total	105 (5.3)	64.9 (3.3)	66.3 (3.8)	64.3 (2.7)

Table 3. Total nitrogen expressed as the amount of the element content per unit area ($mg.m^{-2}$). Values followed by different letters are significantly different ($P<0.05$).

	Herbicide +*L.glaber*	Control +*L.glaber*	Herbicide	Control
Graminoids	1.95a	0.86b	1.54c	0.84b
Lotus glaber	0.81b	0.03d	---	---
Dicots	0.12e	1.02b	0.36f	1.12b
Total	2.88	1.91	1.90	1.96

In these grasslands, *L. glaber* introduced after gap opening outcompeted the dicots guild. Moreover, biomass enhancement of graminoids is interpreted as the result of interaction of the facilitation mediated by *L. glaber* (Quinos *et al.,* 1998) and the release of competition exerted by the dicots guild. *L. glaber* reduces the shortages in N supply and enhances vegetative growth of graminoids, resulting in an increase in the competitive ability of this guild. It is on these grounds that *L. glaber* might be considered as a keystone species in the managed grassland.

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