The growth form of dominant grasses regulates the invasibility of Uruguayan grasslands

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Abstract.   In this paper we report the results of a small-scale experiment on patches of natural grasslands in Uruguay. We analyzed whether growth form of C_4 grasses affects invasion success. The experimental plots represented three patch-types arising from short-term grazing effects and were dominated by prostrate C_4 grasses, erect C_4 grasses and codominated by prostrate C_4 grasses and forbs. We seeded the plots with four exotic species: one perennial C_4 grass, one annual C_3 grass, one perennial forb and one annual legume. Contrary to many studies conducted at small spatial scales, our results suggest that in our system, the processes that control invasibility are not directly linked with resident species richness or biomass, but rather are driven by growth form. Emergence of invaders did not differ among patch-types, but seedlings survived less in plots dominated by erect grasses. We suggest that the erect growth form of C_4 grass species is more successful in preventing invasion by mediating seedling competition for light under the canopy for a longer period of time. Grazing management, through its ability to regulate canopy architecture, is a potentially important tool in controlling invasion.

Key words: biotic resistance; erect C_4 grasses; experiment; ligth competition; mesocosm; prostrate C_4 grasses; seed addition.

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INTRODUCTION

Biological invasions by non-native species can cause deep changes in the structure and functioning of natural ecosystems (Mooney and Hobbs 2000). The reason why some communities are less invaded than others is the subject of many studies and debates in ecology. The biotic resistance hypothesis was originally put forward by Elton (1958) and postulates that species-rich communities are less vulnerable to invasion because vacant niches are less common and the intensity of interspecific competition is more severe (Levine and D'Antonio 1999, Tilman 1999, Hector et al. 2001, Dukes 2002, Kennedy et al. 2002, Fargione et al. 2003, Frankow-Lindberg 2012). A decrease in invasibility with increasing species richness could occur by sampling effects, where more diverse communities are more likely to contain strongly competitive species, like the dominant species of a community (Shea and Chesson 2002, Fargione and Tilman 2005, Emery and Gross 2006, 2007) or biotic controls, such as predators, herbivores and pathogens (Levine et al. 2004, Hooper et al. 2005). Also, increasing species richness promotes greater resource use by species that exhibit different spatial and temporal patterns of resource uptake, leaving less resource for invaders and thus reducing invasibility ("resource use

complementarity"; Wardle 2001, Fargione and Tilman 2005). Other factors not related to species number alone, like the diversity of functional types, have been proposed to influence invasibility (Emery 2007, Daneshgar and Jose 2009). It has been postulated that species in a given functional type should most strongly inhibit invasion by functionally similar species with the same resource requirements (Fargione et al. 2003, Emery 2007). Particularly, resident perennial C_4 grasses have been found to strongly inhibit invaders, not only of their own functional type, but also other functionally different ones (Smith and Knapp 1999, Fargione et al. 2003, Fargione and Tilman 2005, Perelman et al. 2007, Bresciano et al. 2014).

Evidence in favor of Elton's (1958) diversity–invasion resistance hypothesis mostly come from small-scale experimental manipulations of diversity conducted in microcosms and other controlled environments (e.g., Naeem et al. 2000, Kennedy et al. 2002, Fargione et al. 2003, Hooper and Dukes 2010, Petermann et al. 2010). Artificially assembled communities have the advantage of isolating the direct effects of diversity on invasion. However, they give no information about the strength of diversity effects compared to other factors that also influence invasions, as most of the variation in these factors is usually eliminated in the relatively homogeneous experimental systems (Levine 2000). Additionally, manipulated experiments may mask the importance of non-random species assemblages and the interspecific interactions found in natural systems (Stohlgren et al. 1999), making it difficult to be certain how well their results might scale to older, larger systems (Naeem et al. 2000). By contrast, studies conducted in natural assembled communities have been less frequent, although this approach provides insights on whether other factors covarying with diversity may be more important than species richness in driving invasion success (Robinson et al. 1995, Stohlgren et al. 1999, Levine 2000). However, confounding factors like disturbance levels, land use or soil resources make it difficult to isolate mechanisms by which diversity affects invasibility (Emery and Gross 2007).

In Uruguay, most of the country is occupied by natural grasslands (ca. 59% Ministerio de Vivienda Ordenamiento Territorial y Medio Am-

biente-FAO 2013). Grazing by domestic herbivores induces changes on community structure and drastically alters plant species composition, increasing species richness (Altesor et al. 2006, Lezama et al. 2014). Vegetation cover of natural grasslands range between 80–100% (Bresciano et al. 2014) and is dominated by perennial C_4 grasses that exhibit two types of growth forms, prostrate and erect. Prostrate grasses are the group with higher cover in grazed communities and spread by means of rhizomes and stolons close to the ground. Erect growth form is represented by bunch grasses that reach 15–30 cm in height (Rodríguez et al. 2003, Altesor et al. 2005, 2006). A recent observational study performed at a large spatial scale showed that exotic species (mostly annual C_3 plants) comprise approximately 10% of the flora. The relationships between native species richness and exotic richness and cover were negative, suggesting that biotic resistance, mainly exerted by the C_4 grasses, may control alien invasion (Bresciano et al. 2014).

Here we report the results of a small-scale experiment on patches of a natural grassland in Uruguay. We analyzed the invasion in patches that differed in the growth form of the C_4 grasses, species richness and biomass. We used plots where, unlike most reported studies, the resident communities were not assembled de novo, but were taken from naturally occurring assemblages. The experimental plots represent patches dominated by (1) prostrate C_4 grasses, (2) erect C_4 grasses and (3) codominated by prostrate C_4 grasses and forbs. We seeded the plots with four exotic species: one perennial C_4 grass, one annual C_3 grass, one perennial forb and one annual legume.

METHODS

The outdoor mesocosm experiment was performed using experimental plots transplanted from a natural grassland belonging to the Southern Campos of the Rio de la Plata grasslands (34°19′ S, 57°02′ W). The average annual precipitations of the site for the last 40 years was 1370 mm, and the mean temperature for the same period was 18.9°C, ranging from 12.6°C in July to 26.3°C in January. In this area, grazing usually leads to a two-strata system: a low and

dense stratum, no more than 5 cm high, dominated by prostrate grasses and rosette forbs, and a higher stratum of bunch erect grasses and small woody plants (Altesor et al. 2005, 2006). C_4 native grasses dominate across the whole region and vegetation cover is around 80% (Altesor et al. 2006).

In August, 2008 we selected three types of vegetation patches which correspond to the most common assemblages in these grasslands. Patches varied in the growth form of the dominant C_4 grasses and forbs and were selected from a small flat area (ca. 1000 m^2) situated on a homogeneous Mollisol. Therefore, we assumed that there were no differences in soil nutrients among patch-types. Vegetation differences result from short-term differences in the grazing regime: prostrate growth dominate in areas continuously grazed, while erect growth is favored in areas that have been under rest during the previous growing season.

From each patch-type, we extracted cylindrical blocks of soil of 30 cm diameter × 10 cm depth with the plant species present. Each block of grassland was placed in a bottomless plastic cylinder, allowing root growth in the place where they settled. The mesocosm consisted of 20 replicates of each patch-type: (1) prostrate C_4 grasses dominance (P), (2) erect C_4 bunch-grasses dominance (E), and (3) codominance of prostrate C_4 grasses and forbs (P + F). We also included 10 equal cylinders with bare soil as control plots (70 plots total).

The experiment was installed on the campus of the Facultad de Agronomía (Universidad de la República, Uruguay), in a fenced field of 300 m^2. The fenced and surrounding area were periodically mowed since the beginning of the experiment. The plots were placed in rows separated by buffer strips of approximately 50 cm. The species composition of each plot was recorded at the beginning and at the end of the experiment, when the resident plants were harvested. No new species was registered at the final date. In order to control for soil moisture as a potential confounding variable, plots were watered weekly to field capacity. Using a soil moisture sensor (ML Theta Probe 2) we corroborated the effectiveness of the treatment as we did not register significant differences among patches (data not shown). Before each sowing date, litter was removed to avoid affecting seed germination and establishment (Facelli and Pickett 1991). Afterward, litter accumulated as in field conditions. The effort to control for confounding variables probably modified the conditions found in nature, but we think it was the only way to isolate the effect of vegetation growth-form on invasion. Canopy height of the plots was measured at the end of the experiment.

We used four exotic species belonging to different functional types that were recorded in natural grassland of Uruguay (Bresciano et al. 2014): a perennial warm-season C_4 grass (*Cynodon dactylon* (L.) Pers.), an annual cool-season C_3 grass (*Lolium multiflorum* Lam), a perennial cool-season forb (*Plantago lanceolata* L) and an annual warm-season legume (*Lotus subbiflorus* Lag.). With the exception of *P. lanceolata*, all species are abundant and broadly distributed in native communities (Bresciano et al. 2014).

We tested seed germination of the four species following standard protocols (ISTA 2009) before installing the experiment. Seeds were placed on moist filter paper in Petri dishes (200 seeds/species) and maintained in the dark at 5°C for seven days. Afterwards, they were placed in a germination chamber under a regime of 8 hours light/30°C and 16 hours darkness/20°C, for a maximum of 21 days. The estimated percentage of germination was 94% for *L. multiflorum*, 80.6% for *P. lanceolata*, 52–56% (March and October, respectively) for *C. dactylon* and 39–62.5% (March and October, respectively) for *L. subbiflorus*. Based on germination rates we adjusted the number of sown seeds of each invader to ensure 50 potentially germinating seeds of each species in each plot. Seeds were sown in early autumn (March 2009) and spring (October 2009) in order to ensure equal opportunities of germination and growth to cool and warm-season species. The seedlings of each species were recorded daily during the first week and monthly throughout six months in each experimental period. Seedlings that germinate and emerged during the spring-summer period were marked with plastic rings in order to estimate their survival until their harvest, six months after they were sown.

At the end of the experiment the resident plants of the plots were harvested. The species were grouped in four plant functional types (prostrate C_4 grasses, erect C_4 grasses, erect C_3
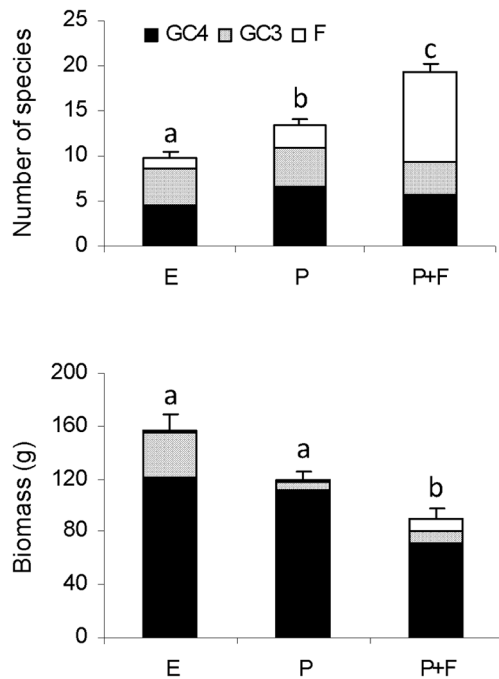
Fig. 1. Richness and biomass of patch-types (E, dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P + F, codominated by prostrate C_4 grasses and forbs; mean + 1 SE). Means with different letters are significantly different from each other ($P < 0.05$). Different colors indicate proportion of functional groups within each patch-type (GC4, C_4 grasses; GC3, C_3 grasses; F, forbs).

grasses and forbs) and aerial and below-ground components were separated and oven-dried (48 h at 70°C) to determine dry biomass. As incident light reaching the soil surface depends on the distribution of the aerial biomass in the space, we estimated the aerial biomass density as $D =$ biomass$/\pi \times r^2 \times h$, where $r =$ plot radius and $h =$ mean canopy height in each patch-type.

We estimated the percent of photosynthetic active radiation (PAR) reaching the bottom of the canopy from measurements of incoming and reflected PAR and estimates of PAR absorption by the canopy derived from normalized difference vegetation index (NDVI) measurements. A 50-cm linear sensor LICOR (Li Quantum Sensor, model Cavadevices) was used to measure incoming and reflected PAR. Taking into account that the canopy of plots was 30 cm wide, we covered 20 cm of the sensor with black polyeth-

ylene. NDVI was calculated from measurements on red (R) and near infrared (NIR) reflectance using a SKYE radiometer. NDVI was calculated as $(IR - R)/(IR + R)$. NDVI is a linear estimate of the fraction of the PAR absorbed by green tissues (fAPAR) (Di Bella et al. 2004). Among the several models that relate NDVI and fPAR we used one locally calibrated (Piñeiro et al. 2006). The percentage of radiation transmitted to the soil surface (%Transmitted PAR) was calculated as (incoming PAR − reflected PAR − absorbed PAR)/incoming PAR. All measurements were performed around noon during 1 hour under completely clear sky conditions in December 2010. Three replicates of PAR were measured at each plot.

Data analyses

Differences in richness, biomass, biomass density and light transmittance among the three patch-types were analyzed using ANOVAs. Biomass data were log10-transformed prior to analysis. Tukey's HSD post-hoc test was used for mean separation. A simple linear regression using the full data set ($n = 60$) was performed to analyze the relationship between resident species richness and resident biomass. The frequency of C_4 grass species was estimated as the proportion of plots of each patch-type where the species was present. To assess if the dominant species identity varied among patch-types, we compared the composition of C_4 grasses using the Jaccard similarity index: $J_{A-B} = c/(a + b + c)$ (Southwood 1978), where $a = C_4$ grasses exclusive to patch-type A, $b = C_4$ grasses exclusive to patch-type B and $c = C_4$ grasses shared by patch-types A and B.

The establishment success of invaders was estimated as the mean number of individuals of each invader species in each vegetated treatment relative to the mean success of the species in the bare plots. We also estimated the relative establishment success of all invaders for each patch-type. This allowed us to ensure that results were due to the presence of vegetation. The proportion data were logit transformed to improve normality. The value 0.01 was added to proportions equal to 0 and subtracted from proportions equal to 1 in order to avoid undefined transformed values (Warton and Hui 2011). We performed ANCOVA analyses to

Table 1. Growth form, life cycle, origin and frequency of occurrence (proportion of plots of each patch-type where the species was recorded) of C_4 grass species at three patch-types: E, dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P + F, codominated by prostrate C_4 grasses and forbs ($n = 20$ for each patch-type).

Species	Growth form	Life cycle	Origin	E	P	P + F
Andropogon ternatus (Spreng.) Wess	Erect	Perennial	Native	45	10	10
Aristida murina Cav.	Erect	Perennial	Native	15	35	25
Aristida venustula Arechav.	Erect	Perennial	Native	0	0	10
Axonopus affinis Chase	Prostrate	Perennial	Native	50	95	90
Bothriochloa laguroides (DC.) Herter	Erect	Perennial	Native	25	85	75
Chloris sp. SW.	Erect	Perennial	Native	0	5	0
Coelorachis selloana (Hack.) A. Camus	Erect	Perennial	Native	80	75	55
Cynodon dactylon (L.) Pers.	Prostrate	Perennial	Exotic	10	60	30
Eragrostis bahiensis Schrad. Ex Schult.	Erect	Perennial	Native	0	30	0
Eragrostis lugens Nees	Erect	Perennial	Native	0	0	40
Eragrostis neesii Trin.	Erect	Perennial	Native	0	15	55
Panicum hians Elliott	Erect	Perennial	Native	0	10	0
Panicum milioides Ness ex Trin.	Erect	Perennial	Native	0	5	0
Panicum sabulorum Lam.	Erect	Perennial	Native	5	10	5
Panicum sp L.	Erect	Perennial	Native	0	0	25
Paspalum notatum Flüggé	Prostrate	Perennial	Native	60	85	90
Paspalum plicatulum Michx.	Erect	Perennial	Native	35	20	30
Schizachyrium microstachyum (Desv. Ex Ham.) Roseng., B.R. Árrill. & Izag.	Erect	Perennial	Native	50	25	0
Schizachyrium spicatum (Spreng.) Herter	Erect	Perennial	Native	15	0	15
Setaria geniculata P. Beauv.	Erect	Perennial	Native	10	40	10
Setaria vaginata Spreng.	Erect	Perennial	Native	5	10	0
Sporobolus indicus (L.) R. Br.	Erect	Perennial	Native	35	25	30
Stenotaphrum secundatum (Walter) Kuntze	Prostrate	Perennial	Native	10	25	10

compare the establishment success of invaders among treatments, using patch-type as a categorical factor and resident species richness or aerial biomass as covariates. Homogeneity of slopes was tested prior to analysis using an F test and showed evidence of compliance ($P > 0.05$).
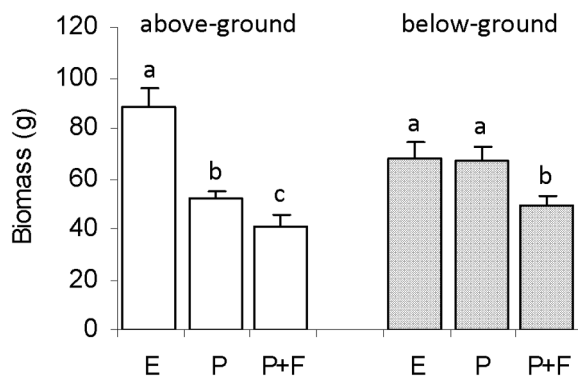

Fig. 2. Aboveground and belowground biomass (mean + 1 SE) of resident plants in each patch-type (E, dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P + F, codominated by prostrate C_4 grasses and forbs). Means with different letters are significantly different from each other ($P < 0.05$).

Hence, the interaction term was removed from the final analysis. Fisher LSD post hoc test was used for mean separation. Absolute values of emerged and established plants in the three patch-types were compared using ANOVA to estimate seedling survival during the second experimental period (spring–summer). All analyses were performed using the statistical software PAST, version 2.09 (Hammer et al. 2001).

RESULTS

Mean richness of resident species was significantly different in the three patch-types analyzed ($F_{2,57} = 41.05$, $P < 0.0001$). The patch-type codominated by prostrate C_4 grasses and forbs (P + F) was the richest in species, mainly due to the contribution of the forbs functional group (55%). The patch-type dominated by erect C_4 grasses (E), where forbs were scarce, presented the lowest species richness (Fig. 1).

The patch-type with greatest species richness (P + F) exhibited the lowest total biomass, differing significantly from the E and P patch-types ($F_{2,57} = 10.53$, $P < 0.001$). The grasses (C_4 grasses in particular) contributed more than 75%
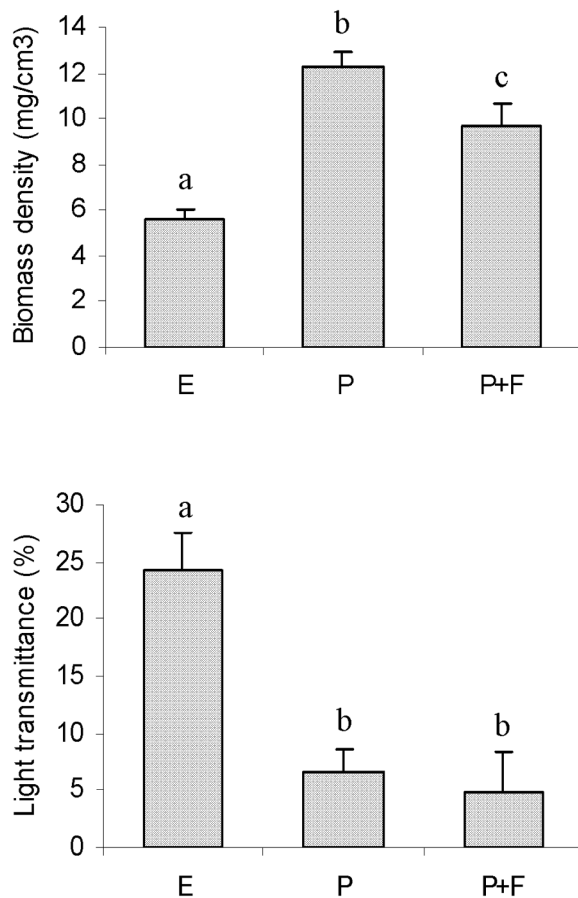
Fig. 3. Aerial biomass density and percentage of full sunlight reaching the soil surface (mean + 1 SE) in each patch-type (E, dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P + F, codominated by prostrate C_4 grasses and forbs). Means with different letters are significantly different from each other ($P < 0.05$).

of the total biomass in all patch-types, whereas the contribution of forbs was low (0.24–11%) (Fig. 1). The composition of C_4 grass species was similar in the three patch-types, with more than 50% of shared species ($J_{E-P} = 0.70$, $J_{E-P+F} = 0.68$, $J_{P-P+F} = 0.57$) although their frequency varied among patches (Table 1). When plots of the three patch-types were pooled together, resident richness was inversely related to biomass of resident species ($r = -0.399$, $P = 0.002$, $n = 60$).

Differences in total biomass among patch-types were explained mainly by differences in aerial biomass. The E patch-type presented the highest aerial biomass, followed by P and P + F

($F_{2,57} = 18.49$, $P < 0.001$). Below-ground biomass in P + F was significantly lower than in E and P ($F_{2,57} = 3.37$, $P = 0.04$) (Fig. 2). The aerial biomass in P and P + F was distributed between 0 and 7 cm, while in E it was distributed between 0 and 30 cm. Therefore, biomass density was higher in the prostrate plots than in E plots ($F_{2,57} = 22.98$, $P < 0.001$), while light transmittance was lower ($F_{2,57} = 12.4$, $P < 0.001$) (Fig. 3).

There was a significant effect of patch-type on invasion success (Table 2). The exotic establishment was significantly greater in plots dominated by prostrate grasses (P and P + F). Patch-type E (dominated by erect grasses) showed values lower than 11% (Fig. 4A). Conversely, resident species richness and aerial biomass, used as covariates, were not related to invasion success (Table 2, Fig. 4B, C). The interaction terms between the covariates and the patch-type were nonsignificant (species richness: autumn-winter, $F_{2,54} = 1.38$, $P = 0.261$; spring-summer, $F_{2,54} = 0.72$, $P = 0.492$), (aerial biomass: autumn-winter, $F_{2,54} = 0.99$, $P = 0.378$; spring-summer, $F_{2,54} = 1.25$, $P = 0.294$) and were excluded from the analyses.

During spring-summer, when seedlings were followed throughout six months, seedling emergence did not differ among patch-types ($F_{2,57} = 2.66$, $P = 0.08$). However, seedlings survived less in E plots, and established plants at the end of the experimental period were lower than in P and P + F ($F_{2,57} = 16.02$, $P < 0.001$) (Fig. 5).

Of the four sowed invaders, only *Lolium multiflorum* showed significant differences on invasion success among patch-types at the two sowing dates. Its success, measured as established individuals relative to bare plot establishment, was lower in E compared to P and P + F patch-types. *Plantago lanceolata* and *Cynodon dactylon* showed very low values of invasion success and *Lotus subbiflorus* never established at all (Table 2, Fig. 6).

DISCUSSION

Our work analyzed the differential invasion success in vegetation patches representative of temperate sub-humid grasslands of Uruguay. Patches resulting from short-term differences in the grazing regime were similar in species composition of the dominant functional type

Table 2. ANCOVA results for invader success (number of established individuals per plot standardized as a percentage of establishment in bare plots) at two sowing dates. Source of variance are patch-type (erect C_4 grasses, prostrate C_4 grasses and prostrate C_4 grasses + forbs) and resident species richness or aerial biomass as covariates. Homogeneity of slopes was tested prior to analyses using an F test and showed evidence of compliance ($P > 0.05$). Hence, the interaction term was removed from the final analyses. Missing values in *Cynodon dactylon* and absence of data for *Lotus subbiflorus* are due to failure in the establishment of the species. Error degrees of freedom 56 for all tests. In bold, significance at $P < 0.05$.

Invader	Source of variance	df	Autumn–winter			Spring–summer		
			MS	F	P	MS	F	P
All invaders	Patch-type	2	7.30	8.30	**0.0007**	2.60	11.14	**<0.0001**
	Richness	1	0.05	0.06	0.8079	0.22	0.92	0.4919
Lolium multiflorum	Patch-type	2	6.54	12.07	**<0.0001**	1.69	3.94	**0.0253**
	Richness	1	0.77	0.59	0.4450	0.42	0.46	0.4983
Plantago lanceolata	Patch-type	2	0.07	0.83	0.4410	2.62	3.56	0.0652
	Richness	1	0.01	0.10	0.7494	3.12	4.80	0.0627
Cynodon dactylon	Patch-type	2	...	...	...	0.65	2.75	0.0730
	Richness	1	...	...	...	0.39	2.37	0.1294
All invaders	Patch-type	2	10.63	12.34	**<0.0001**	1.70	7.28	**0.0015**
	Aerial biomass	1	1.06	1.23	0.2730	0.21	0.92	0.3401
Lolium multiflorum	Patch-type	2	9.95	11.24	**0.0001**	2.16	4.19	**0.0204**
	Aerial biomass	1	0.00	0.001	0.9775	0.03	0.04	0.8447
Plantago lanceolata	Patch-type	2	0.08	0.85	0.4250	2.83	3.20	0.0687
	Aerial biomass	1	0.00	0.02	0.9021	2.46	3.41	0.0703
Cynodon dactylon	Patch-type	2	...	...	...	0.60	2.65	0.080
	Aerial biomass	1	...	...	...	0.32	1.83	0.1815

but differed in species richness, aerial biomass and canopy architecture. Our experiment showed that patches dominated by erect C_4 grasses were less invaded by exotic species compared to those dominated by prostrate C_4 grasses or codominated by prostrate C_4 grasses and forbs.

Several studies conducted at small spatial scales have found an inverse association between resident species richness and invasion success (e.g., Naeem et al. 2000, Symstad 2000, Hector et al. 2001, Lyons and Schwart 2001, Kennedy et al. 2002, Fargione et al. 2003). In these systems, diverse communities occupy more space, generate more biomass, and use more resources, increasing invasion resistance (Fargione and Tilman 2005). In our system, and contrary to these studies, resident richness and biomass were inversely related. Species richness increment was driven by the presence of small forbs, a subordinate group of perennial C_3 species that occupies the spatial interstices left by the dominant grasses (Altesor et al. 1998, Rodríguez et al. 2003). Although abundant, forbs contributed little to biomass (0.24–11%) and are presumably weak competitors, leaving more resources to invaders.

In our system, the ANCOVA results indicated that neither the resident richness, nor the aerial biomass were related to invasion success. Given the same species richness or amount of aerial biomass, the plots dominated by erect C_4 grasses were the less invaded (Fig. 4). By contrast, the categorical variable (patch-type) showed significant effects, suggesting a strong influence of the canopy architecture on invasion success. Invaders establishment may be affected by competition for space, light, nutrients (Naeem et al. 2000) and water (Dukes 2001). Our experimental design attempted to control for water (watering weekly to field capacity), soil resources (extracting the plots from the same soil type), litter (removing the litter before sowing) and dominant species composition (selecting plots with high similarity in C_4 grasses composition). We thus hypothesize that light should be controlling invasion success. Many authors have pointed out that light is one of the most important resources that limit plant production in humid and subhumid grasslands (Semmartin and Oesterheld 1996, Knapp et al. 1998). Canopy architecture could modify light availability and, in turn, the time course of germination, emergence and establishment of invader species.
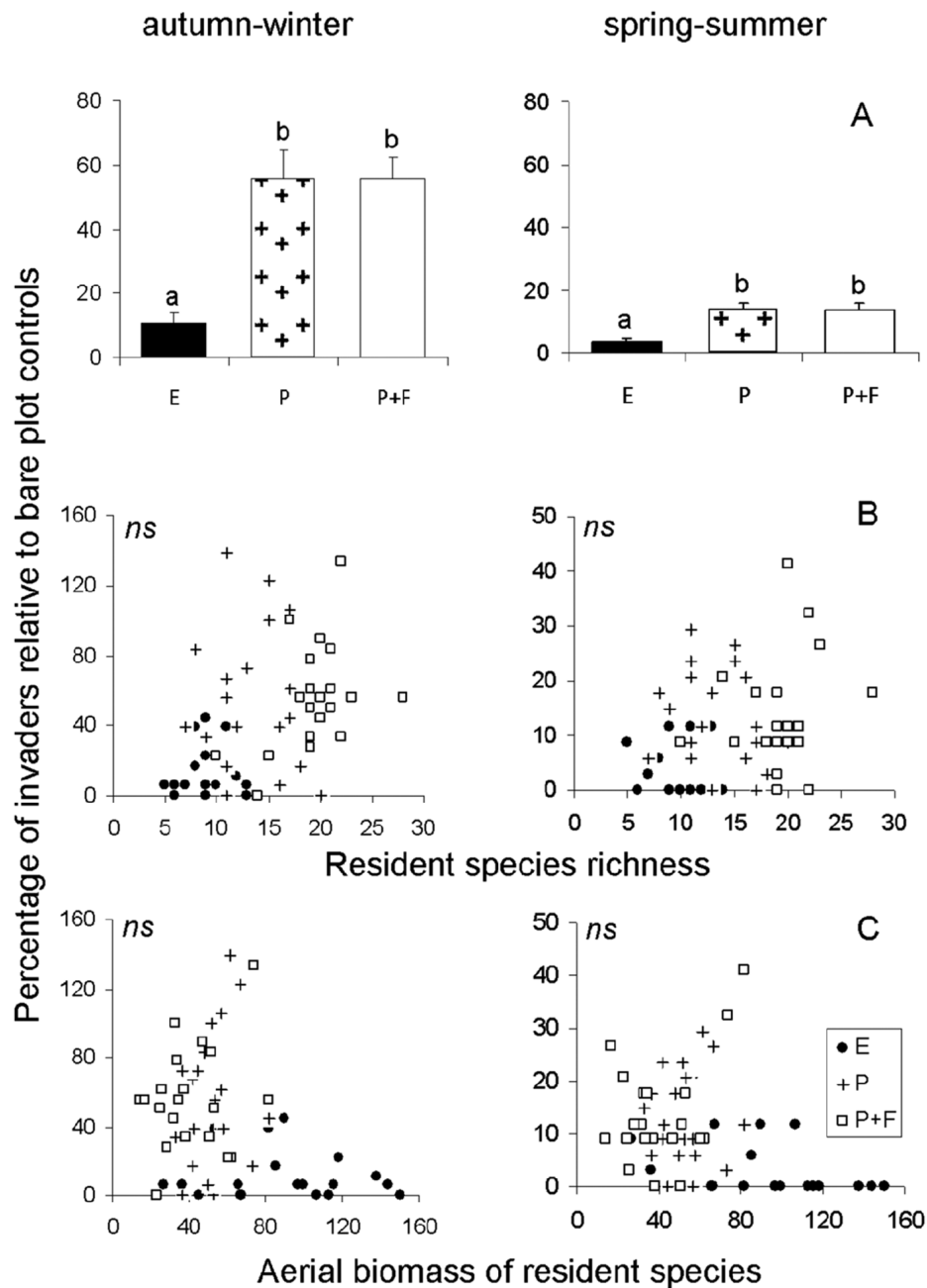
Fig. 4. (A) Success of invaders at two sowing dates expressed as the number of established individuals per plot standardized as a percentage of establishment in bare plots (mean + 1 SE). Lowercase letters represent statistically significant differences ($P < 0.05$) among patch-types: E, dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P + F, codominated by prostrate C_4 grasses and forbs. (B) Relationship between invasion success and resident species richness in each patch-type at two sowing dates. (C) Relationship between invasion success and aerial biomass of resident species in each patch-type at two sowing dates. Invasion success was logit transformed for analyses; here we present raw data. Regression slopes do not differ significantly from 0.
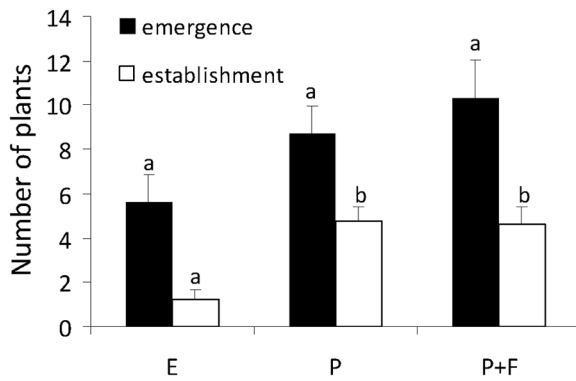
Fig. 5. Emergence and establishment of invaders (mean + 1 SE) in spring-summer. Established plants were those that germinated and emerged during the experimental period and survived until their harvest, six months after they were sown. (E, patch-type dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P+F, codominated by prostrate C_4 grasses and forbs). Means with different letters are significantly different ($P < 0.05$) from each other (within a response variable).

In our study, light transmittance was higher in the patch-type with the highest aerial biomass, dominated by erect C_4 grasses. In the patch-types dominated by prostrate grasses (with and without forbs), most of the above-ground plant biomass was distributed between 0 and 7 cm, while at the patch-type dominated by erect grasses the largest portion of the biomass was between 0 and 30 cm. This unequal aerial biomass distribution affected biomass density and consequently the percentage of light transmitted to the soil: in the plots dominated by erect species light transmitted was higher (24.4% of incident light) than in those plots dominated by prostrate grasses (4.8–6.5%). The thinner (but more compact) plant layer in the plots dominated by prostrate C_4 grasses reduced the light reaching the soil, but this only would affect the initial phase of growth of the invader seedling. However, at this phase, seed reserves may support seedling growth. Promptly, seedlings reach full irradiance and light stops being the limiting factor. On the other hand, the taller canopy of the plots dominated by erect C_4 grasses would keep the invaders in a shadowed environment for a longer period preventing the establishment of exotic species. Our results support this explana-
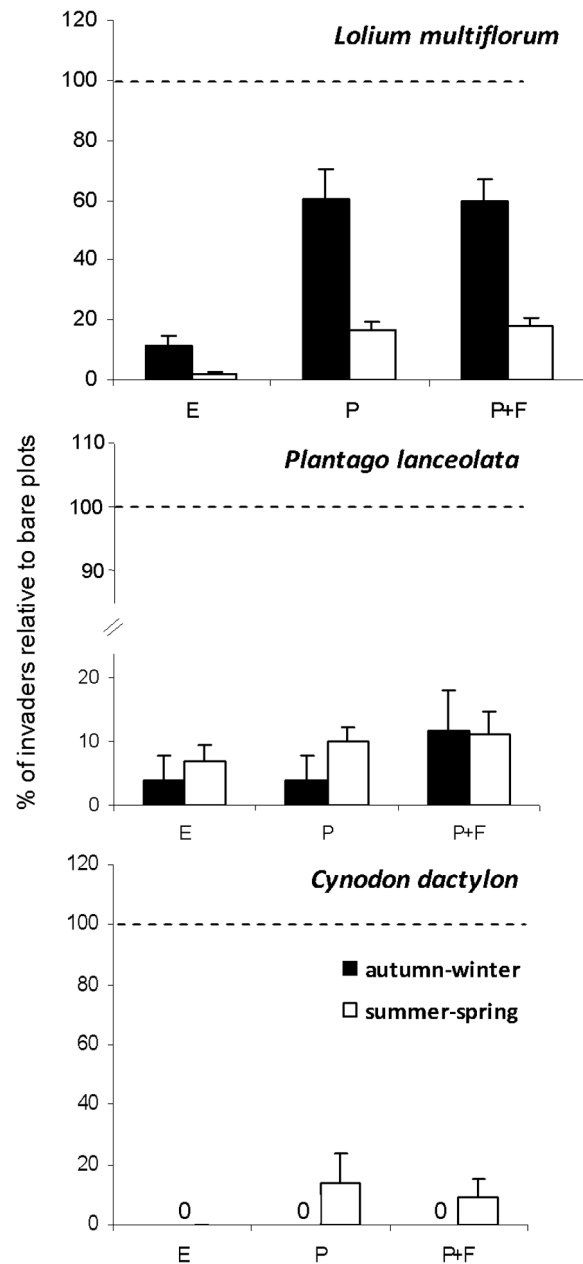

Fig. 6. Success of *Lolium multiflorum*, *Plantago lanceolata* and *Cynodon dactylon* at two sowing dates, expressed as the number of established individuals per plot standardized as a percentage of establishment in bare plots (mean + 1 SE). *Lotus subbiflorus* never established at all. Dashed line at 100% reflects success of invaders in bare plots. Patch-types: E, dominated by erect C_4 grasses; P, dominated by prostrate C_4 grasses; P + F, codominated by prostrate C_4 grasses and forbs (for significant differences see Table 2).

tion: we did not found differences in emergence among patch-types, but seedling survival was between 50% and 60% lower in plots dominated by erect C_4 grasses compared to other plots.

Lolium multiflorum was the most successful invader. *L. multiflorum* is a cool-season annual grass and, as expected, its recruitment occurred mostly during the autumn-winter period, when resident perennial C_4 grasses grow less actively. Therefore, one might assume that invaders and dominant residents have complementary resource-use patterns. The fact that species that belong to a functional group absent in a community invade more easily than species belonging to functional groups already present has been observed in many studies (Fargione et al. 2003, Turnbull et al. 2005, Mwangi et al. 2007). *Cynodon dactylon*, a perennial C_4 grass species, was a weak invader that only established in the summer-spring period, during the peak growing season of the C_4 grasses functional type. Its invasion success could be limited by the overlap in resource requirements with the dominant resident species. Biotic resistance exerted by resident species was even stronger against forbs. *Plantago lanceolata* showed a poor performance at both sowing dates, while *Lotus subbiflorus* did not establish at all. *P. lanceolata* is a flat rosette that grows close to the ground and survives less in relatively dense vegetation (van Tienderen and van der Toorn 1991). The annual legume *L. subbiflorus* probably needs larger gaps for establishment to overcome the resource limitation determined by their small seeds (Rauschert and Shea 2012).

Certain considerations about our experiment need to be mentioned. Our experiment modified some of the conditions found in nature to control for potential confounding variables like soil moisture, soil nutrients, litter and propagule pressure. Further investigations are required to confirm the relative importance of these factors in determining invasibility at a landscape scale. Additionally, as we only examined the initial establishment of invading species, we can not be sure whether the same results would persist in the longer term. However, seedling recruitment is often a key life stage in population growth (Emery and Gross 2007).

Our study shows that growth form of the dominant species affects the success of invaders in Uruguayan grassland communities. Invasion resistance associated with the presence of native perennial C_4 grasses has been documented both in observational large-scale studies (Perelman et al. 2007, Bresciano et al. 2014) as in experimental small-scale ones (Smith and Knapp 1999, Fargione et al. 2003, Fargione and Tilman 2005). Our study suggests that architectural variation of the plant canopy constitutes an important factor that should be considered when trying to understand the mechanisms underlying biotic resistance of C_4 grasses. Grazing management, through its ability to regulate canopy architecture, is a potentially important tool in controlling invasion (Focht and Medeiros 2012).

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