

Explaining patterns of primary production from individual level traits

Leoni, E.^{1,2}; Altesor, A.^{1*} & Paruelo, J.M.^{1,3,4}

¹Departamento de Ecología, Facultad de Ciencias, Universidad de la República, Iguá 4225 Montevideo, C.P.11400, Uruguay; ²E-mail elsa@fcien.edu.uy;

³Laboratorio de Análisis Regional y Teledetección, IFEVA, Facultad de Agronomía, Universidad de Buenos Aires y CONICET, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina; ⁴E-mail paruelo@agro.uba.ar;

*Corresponding author; Fax +59825258616; E-mail aaltesor@fcien.edu.uy

Abstract

Question: Do species traits explain differences in productivity in grazed and ungrazed plots?

Location: Río de la Plata grasslands, Uruguay (31°54'S, 58°15'W).

Methods: In a greenhouse experiment, we measured the relative growth rate (RGR) of grasses with contrasting responses to grazing (increasers and decreaseers). We performed six harvests at weekly intervals in order to calculate the RGR and assess 12 plant traits. We compared the RGR between increaser and decreaseer species after 2 and 5 weeks using *t*-tests. Linear and potential regression models were fitted to time versus natural logarithm of total dry biomass relationships. The RGR temporal trajectories of increaser and decreaseer species were obtained from the derivatives of the best-fit functions. Principal component analysis (PCA) was used to sort species according to their traits.

Results: The RGR of decreaseer grasses was higher than that of increasers at the second week, while at the fifth week the opposite was observed. The RGR of decreaseers dropped through time, while the RGR of increaser species was constant. The PCA separated increaser from decreaseer species. The attributes related to increaser species were: high specific leaf area, tillering rate, green leaf rate, total leaf number, root weight ratio and leaf weight ratio; while those associated with decreaseer species were: high dead biomass, senescence rate, reproductive biomass, leaf elongation rate and total biomass.

Conclusions: Traits possessed by decreaseers reduce light availability and increase the reproductive investment, explaining the drop in RGR. Specific differences in RGR seem to scale up to the ecosystem level and would explain the pattern in aboveground net primary production observed in the field under contrasting grazing regimes.

Keywords: grasslands; grazing response; growth rate.

Nomenclature: Cabrera & Zardini (1978).

Introduction

Grazing is a key disturbance that shapes the structure and function of grassland communities (McNaughton 1983a, 1985). Functionally, grazing alters the flow of energy and the cycling of materials, both directly through defoliation, trampling and dung and urine deposition, and indirectly through modification of species composition and species interactions (Schlesinger et al. 1990; Aguiar et al. 1996; Hobbs et al. 1996). Changes in plant species composition and in aboveground net primary production (ANPP) have been identified as two major alterations associated with grazing, particularly in mesic grasslands (Milchunas & Lauenroth 1993; Oesterheld et al. 1999). Many studies have reported grazing-induced changes in floristic composition and community structure (Facelli 1988; Díaz et al. 1992; Rodríguez et al. 2003; Cingolani et al. 2005; Altesor et al. 2006), ecosystem functioning (Oesterheld et al. 1999; Altesor et al. 2005) and biogeochemical and physical properties of soils (Taboada & Lavado 1988; Milchunas & Lauenroth 1993; Lavado et al. 1995; Altesor et al. 2006).

In the Uruguayan campos, an extensive subunit of the Río de la Plata grasslands (Soriano 1991), many comparative studies between adjacent grazed and ungrazed areas reported significant differences in both structural and functional attributes of the vegetation. Species richness and diversity were higher in grazed than in ungrazed areas (Rodríguez et al. 2003; Altesor et al. 2006). Floristic composition changed in response to grazing regime; species tolerant to herbivory increased their abundance in grazed areas (increaser species) and others became scarce (decreaseers) and were common in ungrazed

conditions. Prostrate grasses behave as increasers and dominate under grazed conditions, generating a low and dense stratum, no more than 5-cm high that defines the matrix of the grassland (Altesor et al. 1999). There is a second stratum scattered in this matrix that is dominated by bunch grasses and small shrubs. In ungrazed areas, where domestic herbivores were excluded for more than 3 years, the vegetation turns into a tall canopy dominated by erect grasses and shrubs (Altesor et al. 1999, 2005, 2006; Rodríguez et al. 2003).

Altesor et al. (2005) provided evidence that in the Uruguayan grasslands, ANPP also changed between grazed and ungrazed areas. ANPP was 51% higher under grazing than in areas where large herbivores were excluded. However, grazing-simulated plots inside exclosures were the most productive treatment (29% more ANPP than grazed plots). Several mechanisms may explain the observed differences in ANPP among plots. At the ecosystem level, the mechanisms should be related to resource availability. Light may become limiting in ungrazed plots due to self-shading resulting from the lack of biomass removal. At the community level, several studies showed that species richness was positively associated with ANPP (Vitousek & Hooper 1994; Sala et al. 1996). The results of Altesor et al. (2005) did not support this hypothesis because richness was lower inside exclosures than in grazed areas. Rusch & Oesterheld (1997) suggested that the identity of the dominant species, rather than the number *per se*, could account for the differences in ANPP. In an attempt to explain changes in ANPP associated with herbivory, we focused our analysis on differences in plant traits between grazed and ungrazed areas. Lavorel & Garnier (2002), analysing plant responses to environmental factors, proposed the relative growth rate (RGR) as one of the “hard” traits with a direct functional role. RGR, the dry weight increase per unit biomass and per unit time, is an essential quantitative trait that differs among plant species (Grime & Hunt 1975; Poorter 1989; Poorter & Remkes 1990). Often, differences in RGR among plants are habitat-related (Poorter 1989). Plants occurring in fertile habitats usually have a higher RGR than plants from nutrient-poor environments (Grime & Hunt 1975; Lambers & Poorter 1992). It has been postulated that differences in RGR are a consequence of selection for traits that, in turn, determine RGR (Poorter 1989). Such traits include, among others, leaf elongation rate (LER), tillering rate (TR), green leaf rate (GLR), senescence rate (SR), green leaf weight ratio (LWR) and specific leaf area (SLA). Grazing is a key selective pressure

operating upon such plant traits (Díaz et al. 2001; Vesik & Westoby 2001; Vesik et al. 2004).

Our objective in this article was to evaluate differences in RGR and related traits in species that increase their abundance under grazing (increasers) or become scarce as a consequence of herbivory (decreasers). Evidence suggests that, once light limitation is removed (clipped treatments inside exclosures, Altesor et al. 2005), areas dominated by decreaser species have higher ANPP. We expected, consequently, that the RGR of decreaser grasses would be higher than the RGR of increaser grasses.

Methods

We collected several individuals of grass species in two contiguous areas, one of them grazed and the other excluded from domestic herbivory for 11 years. The area corresponded to a natural prairie of the Campos subregion of the Rio de la Plata grasslands (Soriano 1991) in south-central Uruguay (34°19'S, 57°02'W) on a homogeneous and typical prairie soil (Argiudol).

Increaser grasses were collected in the grazed area. All of them were perennial C₄ species (*Stenotaphrum secundatum*, *Axonopus affinis*, *Paspalum notatum*). Decreaser species, collected in the ungrazed area, included two C₃ grasses (*Stipa neesiana* and *Bromus auleticus*) and two C₄ grasses (*Coelorachis selloana* and *Paspalum plicatulum*). Species selection was based on previous studies on the effect of grazing on species composition and abundance in paired grazed and ungrazed plots (Rodríguez et al. 2003; Altesor et al. 2005, 2006). Although the number of species was limited (Wright et al. 2005), we sought to focus on species with clearly contrasting responses to grazing.

We collected tillers of each species from five different places separated by at least 5 m. In June, tillers were extracted with their roots, brought to the greenhouse and planted in pots containing 2300 g of river sand. Pots were watered periodically with distilled water to field capacity and weekly fertilized with 50 mL of modified Hoagland nutrient solution. After 2 months, the plants were carefully divided in order to generate approximately 50 individuals of each species. One month later, in September, we eliminated the extreme individuals, selecting 24 plants of similar size of each species: the number needed to complete six harvests of four individuals each. The first harvest corresponded to the start of the experiment and the remaining harvests were carried out at weekly intervals. Every week, four

plants were randomly selected and harvested. The plants were separated into roots, stolons or rhizomes, green leaves, dead leaves and inflorescences. At each harvest, dry weight of each fraction was determined on oven-dried (36 h at 70°C) material. The RGR of the species was calculated as the slope of the linear regression through the ln-transformed total dry mass versus time (Hoffmann & Poorter 1992; Poorter & Garnier 1996) (milligrams of new biomass produced per gram of pre-existing biomass per day, $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$). The RGR of each species was calculated at two times: (1) after 14 days from the start of the experiment, RGR was calculated from the first three harvests and (2) after 35 days, RGR was estimated from biomass data of six harvests.

Before oven drying the material, the number of tillers, dead leaves and young and total green leaves was counted. SLA was estimated only in the third harvest (in the middle of the experiment), on fully expanded leaves of the four plants harvested. In the middle of leaf blades, a 4-cm piece was cut and the width measured with a caliper. LER was also calculated at the middle of the experiment, in marked leaves with a lamina shorter than 2 cm. Three times every other day we measured the length of the leaf blade with a ruler. The other plant traits (summarized in Table 1) were calculated twice during the experiment, at the third and sixth harvest. Table 1 includes the trait code, units and a description of the methods.

Statistical analysis

We compared the RGR of increaser and decreaser grasses after 2 and 5 weeks of growth using a *t*-test. Linear ($y = a + bx$) and potential ($y = ax^b$) regression models were fitted to the time versus

natural logarithm of total dry biomass relationship. We calculated RGR temporal trajectories for each group of species (increasers and decreasers) from the derivatives of the best function adjusted (linear or potential) to each species dataset.

We used multivariate ordination to explore if the plant traits would sort species according to grazing regime. We performed two principal component analyses (PCA), one using data from the third harvest, in the second week, and the other with data from the sixth harvest, after the fifth week of the experiment. The analyses were performed using PCOrd (McCune & Mefford 1999) and Statistica (1999).

Results

The RGR of decreaser species was higher than the RGR of increasers at the first harvest date, although the difference was not significant ($t = -1.09$, $df = 5$, $P = 0.3$). At the second date, the opposite was observed: RGR of the increases was higher than RGR of decreaser species ($t = 3.4$, $df = 5$, $P = 0.02$) (Fig. 1). For increaser species the linear model was the best descriptor of the relationship between ln biomass and time, indicating that RGR (the slope of the model) remains constant through time (Table 2, Fig. 1, inset). The potential function was the best descriptor of the ln biomass versus time relationship for most of the decreaser grasses (Table 2). Only one species (*Bromus auleticus*) did not show an increase in r^2 with the potential model. Decreasers species, therefore, presented a decreasing RGR (the derivative of the potential model $y' = abx^{b-1}$) through time (Table 2, Fig. 1, inset). The RGR temporal trajectory of decreaser species

Table 1. Plant traits, abbreviations, units and method description.

Plant trait	Code	Unit	Method description
Relative growth rate	RGR	($\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)	Linear and/or potential regression between time and natural logarithm of total dry biomass
Senescence rate	SR	($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)	Increment of senescent leaf biomass relative to the biomass of green leaves per unit time
Green leaf rate	GLR	($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)	Increment of green leaf biomass relative to total biomass per unit time
Tillering rate	TR	($\text{tills} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)	Increment of tillers relative to total biomass per unit time
Leaf elongation ratio	LER	($\text{cm} \cdot \text{d}^{-1}$)	Increment in leaf length per unit time
Specific leaf area	SLA	($\text{m}^2 \cdot \text{kg}^{-1}$)	Leaf area over leaf biomass
Total biomass	TB	(g)	Whole plant biomass
Green leaf weight ratio	LWR	($\text{g} \cdot \text{g}^{-1}$)	Green leaf biomass over total biomass
Root weight ratio	RWR	($\text{g} \cdot \text{g}^{-1}$)	Root biomass over total biomass
Stolon biomass/total biomass	SB/TB	($\text{g} \cdot \text{g}^{-1}$)	Stolon biomass over total biomass
Dead biomass/total biomass	DB/TB	($\text{g} \cdot \text{g}^{-1}$)	Dead leaf biomass over total biomass
Reproductive biomass/total biomass	RB/TB	($\text{g} \cdot \text{g}^{-1}$)	Inflorescence biomass over total biomass
Total leaf number	TLN	(n° leaves)	Number of leaves

showed a marked drop through time, crossing the RGR value of increasers after approximately 2 weeks (inset Fig. 1).

A PCA of the species by traits matrix based on data recorded in the third harvest showed that the first two components accounted for 78.9% of the variance (Fig. 2a and b). The first axis (explaining 54.4% of the variance) separated the increaser from the decreaser species. The increaser species, with

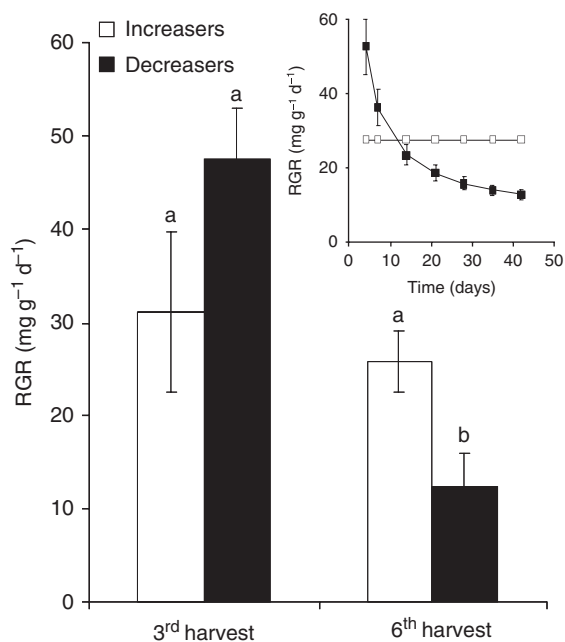


Fig. 1. Mean relative growth rate (RGR) of increaser and decreaser grasses calculated from biomass data of three (2 weeks of experiment) and six harvests (5 weeks of experiment). Bars correspond to ± 1 standard error. Different letters indicate statistical differences between increasers and decreasers within dates. The inset shows the RGR temporal trajectories of increaser and decreaser grasses calculated from the derivatives of the best function (linear or potential) fitted to the time versus \ln biomass relationship for each species (see Table 2). Bars correspond to ± 1 standard deviation.

negative values in axis 1 (*P. notatum*, *A. affinis* and *S. secundatum*) were associated with high tillering rate (TR), total leaf number (TLn), specific leaf area (SLA), leaf weight ratio (LWR), green leaf rate (GLR) and root weight ratio (RWR). The decreaser species with positive values in axis 1 (*C. selloana*, *P. plicatum*, *B. auleticus* and *S. neesiana*) were associated with high values of dead biomass/total biomass (DB/TB), leaf elongation ratio (LER), reproductive biomass/total biomass (RB/TB), senescence rate (SR) and TB. A second PCA, based on the traits recorded at the sixth harvest showed a similar pattern (Fig. 2c and d). The first two axes explained 81.8% of the variance and PC 1, which accounted for 57.0% of the variation, also separated out decreaser from increaser species and was associated with the same attributes as the first PCA.

Discussion

Our results show that decreaser species had a higher RGR than increasers for only a short period of time: the RGR of decreaser species dropped through time. The RGR of increasers, however, remained constant during the whole period of the experiment. A decline in RGR through time is common in herbaceous plants cultivated from seedlings (Poorter 2002). In this analysis, we used adult plants generated from tillers, and the decline was not associated with ontogeny. Moreover, our results showed significant differences in the temporal trend of this trait for species with contrasting responses to herbivory. Functional and morphological traits associated with decreasers would explain the RGR reduction through time. Decreaser species had a high DB/TB ratio. DB is not only photosynthetically inactive material but also reduces the light intercepted by green leaves due to self-shading (Poorter et al. 1988; Di Bella et al. 2004). In addition, biomass

Table 2. Coefficients, r^2 and P value for the linear ($y = a + bx$) and potential ($y = ab^x$) regressions between time and natural logarithm of total dry biomass of increaser and decreaser grasses ($n = 24$).

	Linear model				Potential model			
	a	b	r^2	$P <$	a	b	r^2	$P <$
Increaser grasses								
<i>Paspalum notatum</i> (<i>P.no</i>)	0.9782	0.1770	0.56	0.01	0.7731	0.5540	0.41	0.01
<i>Axonopus affinis</i> (<i>A.af</i>)	0.2044	0.2105	0.51	0.01	0.3811	0.6216	0.22	0.05
<i>Stenotaphrum secundatum</i> (<i>S.se</i>)	0.3324	0.1946	0.52	0.01	0.5081	0.5342	0.40	0.01
Decreaser grasses								
<i>Stipa neesiana</i> (<i>S.ne</i>)	1.6032	0.0247	0.02	ns	1.5308	0.0720	0.05	ns
<i>Bromus auleticus</i> (<i>B.au</i>)	1.4591	0.1176	0.19	0.05	1.4718	0.1878	0.18	0.05
<i>Coelorachis selloana</i> (<i>C.se</i>)	1.4665	0.1568	0.31	0.01	1.3965	0.3029	0.44	0.01
<i>Paspalum plicatum</i> (<i>P.pl</i>)	1.4554	0.1084	0.17	0.05	1.2982	0.2814	0.30	0.01

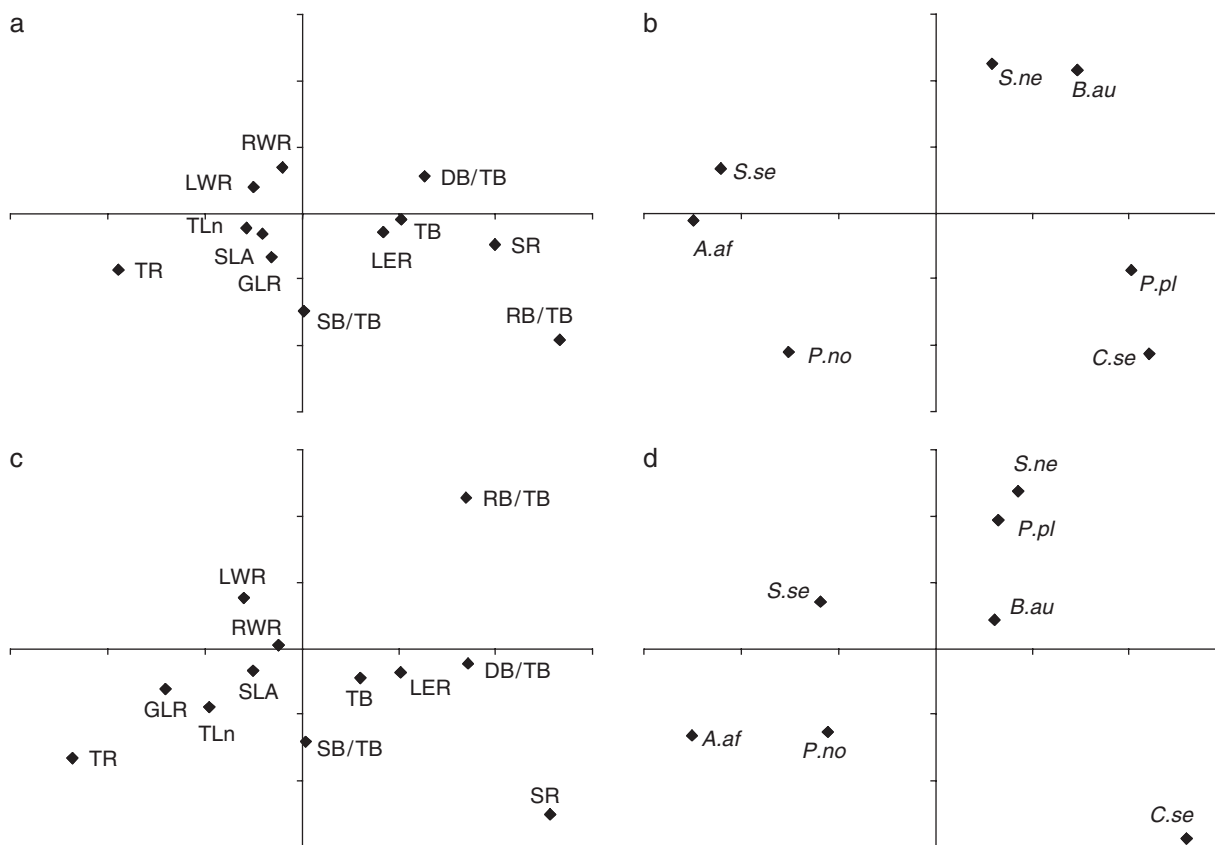


Fig. 2. Principal component analysis (PCA) of the species by traits matrix based on the data recorded at the third (a, b) and sixth harvest (c, d). See Tables 1 and 2 for trait codes and species, respectively.

accumulation in tall plants might reduce RGR by increasing maintenance costs (Konings 1989). The high values for LER and the low SLA of erect species are associated with a large investment in supporting structures (Konings 1989) in response to a light-limited environment (ungrazed areas). In ungrazed areas, shrub encroachment (Altesor et al. 2006) and standing DB accumulation (Altesor et al. 2005) generate a marked reduction in light availability for grasses.

While decreaser plants started to produce culms in the second week of the experiment, increasers did not produce any reproductive structures throughout the whole experimental period. The trade-off between allocation to reproduction and allocation to growth has been reported in many studies (Grime & Hunt 1975; Jurado & Westoby 1992; Swanborough & Westoby 1996). The investment in reproductive structures observed in decreaser species might also contribute to the drop of RGR through time.

The RGR of increaser species did not change through time. High SLA, TLn, GLR and TR would maximize regeneration of photosynthetically active surfaces that would further allow a constant growth rate through time. The production of leaf area

would result from high meristematic activity and from physiological processes, including compensatory growth and increased carbon allocation to leaves (McNaughton 1983b; Briske 1991; Briske & Richards 1995). All of these mechanisms are strategies to maximize photosynthetic surfaces that allow persistence despite trampling and defoliation by herbivores. In prostrate species, high TRs generate many growth points that allow the plants to spread horizontally (Coughenour 1985). This would reflect an adaptive response to defoliation. Many authors have reported that vegetative spread, by means of rhizomes and stolons, is the main form of reproduction under grazed conditions (Abrahamson 1980; Rodríguez et al. 2003).

The observed RGR values supported our prediction only during a short time window. The effects of DB accumulation, high senescence and LERs, and culm production led to a reduction in the RGR of decreaser species. Specific differences in RGR seem to scale up to the ecosystem level and could explain the patterns of ANPP change under contrasting grazing regimes observed by Altesor et al. (2005). Our results agree with previous studies that suggest

relationships between nonadjacent levels of organisation (Lavorel & Garnier 2002; Suding et al. 2003; Garnier et al. 2004; McGill et al. 2006; Westoby & Wright 2006). The highest values of ANPP reported in Altesor et al. (2005) were observed in a grazing-simulation treatment inside an enclosure that was dominated by increasers. Under this simulation, both green tissue and standing DB was removed. Two possible effects related to the grazing simulation may explain this pattern. First, removal of standing DB increases light interception by green leaves, thus enhancing productivity. ANPP in ungrazed areas would be limited by self-shading, given the amount of standing DB accumulated in the absence of herbivores. Second, clipping may have altered plant allocation patterns from maintenance towards production of new leaves (Caldwell et al. 1981). In the greenhouse experiment, the cumulative effects of the attributes that reduced the RGR of decreaser species seem to be the same as those that limited the ANPP in the enclosure. Therefore, the decreaser species of the Uruguayan campos are potentially more productive.

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