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Effects of grazing pattern and nitrogen availability on primary productivity

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Abstract A major part of the impact of grazing on primary productivity results from the joint action of tissue removal and nutrient return to the soil via dung and urine. Grazing, however, is not uniformly distributed in space: grazed grasslands show a matrix of grazed and ungrazed patches, which in turn, may or may not be affected by faecal or urine deposition. This paper investigates the effects of grazing spatial pattern and nitrogen availability on primary productivity. We propose that grazed plants located at the edge of a grazed patch are more shaded by their taller ungrazed neighbours than plants at the center. Since the border effect is less important as patch size increases, the effects of grazing will be more positive, or less negative, when grazing pattern is coarse-grained than when it is fine-grained. We also propose that nitrogen availability will affect this response to grazing through its effects on the intensity of competition for light and on the amount of compensatory growth. We performed a field experiment in a grassland community of the Flooding Pampa, Argentina, in which we compared the productivity of undefoliated controls and defoliated patches of different size, with and without nitrogen application. Defoliation reduced primary productivity and this effect was greater in the smallest, fertilized patches. Productivity was highest at patches of intermediate and large sizes. Nitrogen addition increased productivity by two-fold. The integrated photon flux density reaching the base of the canopy was affected by defoliation and by patch size: it was lower in controls than in defoliated patches and increased with patch size. Our results showed that (a) the size of the defoliated patch modified the response of this grassland to defoliation, (b) this response was correlated with light availability, and (c) nitrogen addition, simulating urine depositions, increased primary productivity and affected the response to defoliation of the smallest patches.

Keywords Flooding Pampa · Herbivory · Relative growth rate · Spatial pattern · Nitrogen

Introduction

A major part of the impact of grazing on primary productivity results from the joint action of tissue removal and nutrient return through dung and urine deposition (McNaughton et al. 1997). The effect of tissue removal on plant growth can range from damage to benefit depending on the changes in the relative growth rate (RGR) suffered by grazed plants in response to defoliation (Belsky 1986; Oesterheld and McNaughton 1991). Negative impacts on RGR are known as damage, whereas positive responses, that may include partial, full, and over compensation for the tissue lost to grazers, are known as compensatory responses (Hilbert et al. 1981; Belsky 1986; Oesterheld and McNaughton 1991).

Herbivores also affect primary productivity through accelerating nitrogen mineralization rate. Herbivores recycle about 75–85% of the nitrogen that they remove from vegetation (Afzal and Adams 1992; Russelle 1992). Nitrogen returned to the soil as dung and urine is more readily available for microbes, thereby bypassing the rate-limiting step of the release of nitrogen from litter (Day and Detling 1990; Seagle et al. 1992). This nutrient recycling becomes essential for the regrowth of grazed plants, particularly in those habitats that are nutrient-limited.

These two components of grazing, tissue removal and nutrient return, are not uniformly distributed across the landscape: grasslands are composed of a heterogeneous matrix of grazed and ungrazed patches, affected and unaffected by depositions. Previous work has studied separately the properties of patches created by either defoliation or urine deposition (Day and Detling 1990; Afzal and Adams 1992; Jaramillo and Detling 1992; Semmartin

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and Oesterheld 1996), but to our knowledge the properties of patches affected by combinations of the two effects have not been studied. In this paper, we investigate the effects of grazing spatial pattern, represented by grazed patches differing in size and nitrogen deposition level, on primary productivity. We also explore whether shifts in light availability account for those effects.

We propose that the effects of the spatial pattern of tissue removal on primary productivity will be mediated by shifts in light availability. Within a dense canopy, biomass removal by grazing changes the light environment (Deregibus et al. 1983, 1985; Casal et al. 1987; McNaughton 1992; Frank and McNaughton 1993), increasing the light availability per unit of biomass in both grazed and neighbouring ungrazed plants. However, only the grazed plants suffer biomass reduction, and those located at the edge of the patch are shaded by their taller, ungrazed neighbours. Thus, within the grazed patch, light intensity at canopy base is expected to be lower at the edge than at the center. As the size of the grazed patch increases, the perimeter of contact between grazed plants and their ungrazed neighbours, where shading would be more intense, decreases in relation to the total size of the grazed patch. Therefore, light intensity at the entire grazed patch will be greater and plant growth will be more likely increased, or less reduced, by grazing if it is coarse-grained than if it is fine-grained (Semmartin and Oesterheld 1996).

How will nitrogen availability modify the effect of the spatial pattern of tissue removal on primary productivity? The addition of soil nitrogen by animal depositions increases primary productivity in many grasslands (Day and Detling 1990; Seagle et al. 1992). However, the experimental evidence on the interaction between defoliation and nitrogen availability is controversial and allows the co-existence of two opposite models. On the one hand, high nutrient availability is expected to depress compensatory growth because ungrazed plants would be growing at maximum intrinsic rates (Hilbert et al. 1981). On the other hand, an alternative model proposes that compensatory growth will only be possible when the nutrients required to generate new tissue are readily available (Maschinski and Whitham 1989). Thus, although our hypothesis proposes that the response of plants to tissue removal will depend on nutrient availability (Georgiadis et al. 1989), the direction of this interaction is not clear. We propose that nitrogen availability will affect the response to the spatial pattern of defoliation. We predict that a greater nitrogen availability will increase the effect of patch size because as nitrogen availability increases shoot competition, light becomes more critical for productivity (Wilson and Tilman 1995).

This paper presents data from a field experiment carried out in a grassland community of the Flooding Pampa (Argentina). The experimental approach was to simulate the different field situations mentioned above using mechanical defoliation and urea application to simulate grazing and urine patches, respectively.

Methods

The Flooding Pampa is a region in the province of Buenos Aires, Argentina, which is 80% native grasslands (León et al. 1984). Annual mean precipitation is around 900 mm and mean monthly temperature ranges from approximately 7°C in winter to 22°C in summer.

The experiment was located on a 12-year-old, 4-ha exclosure of a native grassland community defined phytosociologically as *Ambrosia tenuifolia, Eclipta bellidioides*, and *Mentha pullegium* (Burkart et al. 1990). This exclosure provides a developed, ungrazed canopy and is one of the few sites in the region resembling the natural grassland as it likely was in pre-settlement times (Sala et al. 1986; Sala 1988). Species with C_3 and C_4 photosynthetic pathways determine the seasonal pattern of aboveground productivity with a maximum that occurs from late spring to the beginning of summer (Sala et al. 1981). The grassland within the exclosure had a mean canopy height of 40–60 cm and a large accumulation of standing dead tissue; 75% of the aboveground biomass was dead. The annual primary production of this grassland is approximately 4,000 kg ha^{-1} (Sala et al. 1981; J. Loreti, G. Marino, M. Oesterheld, M. Oyarzábal and M. Semmartin, unpublished work) and total aboveground biomass ranges between 600 and 700 g m^{-2} at the beginning of the spring (Semmartin 1998). A two-way factorial experiment was performed. Factors were defoliation and urea application. The defoliation treatment had five levels determined by the different size of circular clipped patches (10, 20, 40, and 80 cm radius) and an unclipped control. These patch sizes were selected to represent a wide range of sizes commonly observed in field situations. Clipping height was 12 cm and resulted in 50% removal of total standing biomass. Initial biomass of patches was estimated from the difference between the aboveground biomass of unclipped plots and the clipped biomass of the patches. There were five replicates for each defoliation-nitrogen combination. Biomass of controls was harvested with a rectangular frame (0.4 m^{-2}). Possible differences due to different frame shape were discarded based on the results of a previous experiment where total standing biomass, harvested with frames of different sizes and shapes, was compared (Semmartin and Oesterheld 1996). Treatment location in the exclosure was randomly assigned. The urea treatment had two levels, control and 10 g N m^{-2} sprinkled uniformly over the plots in the form of 8 l m^{-2} of urea solution (Day and Detling 1990). Control plots received the same volume of water. Urea was applied once, 15 days after the application of the defoliation treatment.

The experiment started in November and ended in January, a period accounting for approximately 50% of annual production (Sala et al. 1981). Both initial and final aboveground biomass were determined. The recovery time of defoliated plants was 60 days. Harvested biomass was divided into green biomass and standing dead biomass. Primary productivity was estimated as the difference between final and initial biomass divided by the length of the recovery period. Thus, primary productivity of the defoliated patches represents the rate of production after defoliation and does not include the biomass removed by clipping. Nitrogen content in aboveground biomass was determined by the Kjehldahl procedure.

The photosynthetically active radiation (PAR) at canopy base, in both the center and the edge of patches, was assessed half way through the experiment (day 30), a time which most likely represented average conditions experienced by the different treatments. PPFD was measured using a quantum sensor (LI-190SZ, LiCor, Lincoln, NE, USA) in a horizontal position, at noon, when light was perpendicular to the canopy. PPFD was measured in two locations within the patch: at the center and in the western edge. Before taking each reading, PPFD on the canopy surface was recorded, as reference. An integrated PPFD value for each patch was calculated as follows: since PPFD at the center of patches was the same for all patch sizes (including the smallest, 10-cm-radius patches) but was different in the borders, a linear decrease of light intensity beginning at 10 cm from the edge was assumed. Therefore, every patch had a variable central area, depending on its size,
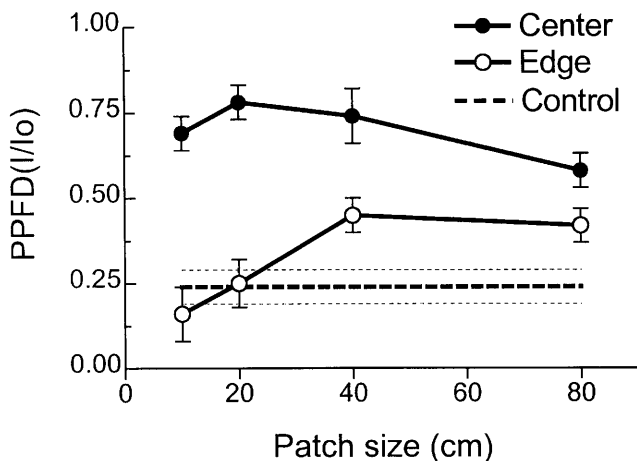
in which light was considered constant, and a border stripe 10 cm wide in which light intensity linearly decreased until reaching the corresponding value measured at its edge. Data were analyzed by a two-way ANOVA, followed by Tukey's tests. Unless otherwise specified in the text, the level of statistical significance was 0.05.
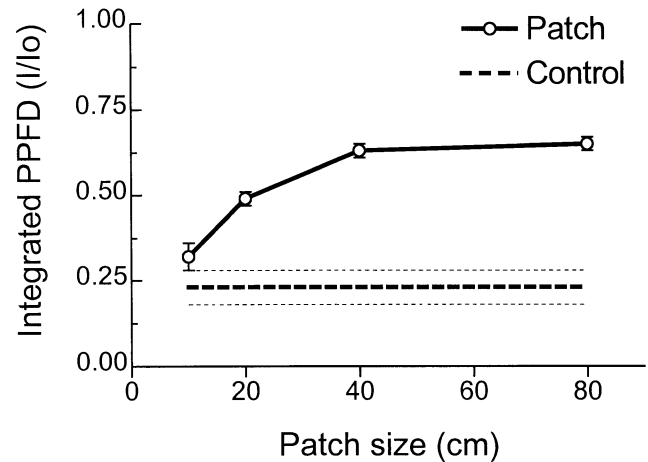
Results

Photosynthetic photon flux density data showed three important results. First, light at the center of the defoliated patches was independent of patch size and N availability and it was higher than at controls (Fig. 1). Second, PPFD recorded at the edge of patches was similar to control in small patches and greater in large patches. Thus, smallest patches not only had a larger proportion of edge but they also had a more shaded edge (Fig. 1). Finally, integrated PPFD of the whole patch area (see Methods), increased with patch size and reached a plateau in patches of 40 cm (Fig. 2). This result suggests that, as stated by the hypothesis, the negative influence of neighbours decreases as patch size increases.

Defoliation significantly reduced primary productivity, and fertilization increased it (Fig. 3, $F_{defol}=4.5$; $F_{fertil}=17.7$). The effect of defoliation was more negative on the smallest, fertilized patches, which were the only ones that did not respond to fertilization. Thus, as we had proposed, the effect of the spatial pattern of tissue removal was more evident under high nutrient availability. Our determination of initial biomass allowed us to calculate RGRs and, thus, to evaluate the amount of compensatory growth. Both fertilized and unfertilized treatments showed either no compensatory growth or slight damage (Fig. 4).

Nitrogen content in green biomass was not affected by defoliation nor by fertilization ($P_{defol}=0.78$; $P_{fertil}=0.11$). Nitrogen content was 1.8% and 1.2% in green biomass and standing dead biomass respectively

Fig. 2 Integrated PPFD of control and defoliated patches of different size (see detailed explanation in Methods), 30 days after treatment. *Vertical bars* indicate the SE. *Dotted lines* over and under *control line* indicate SE of control
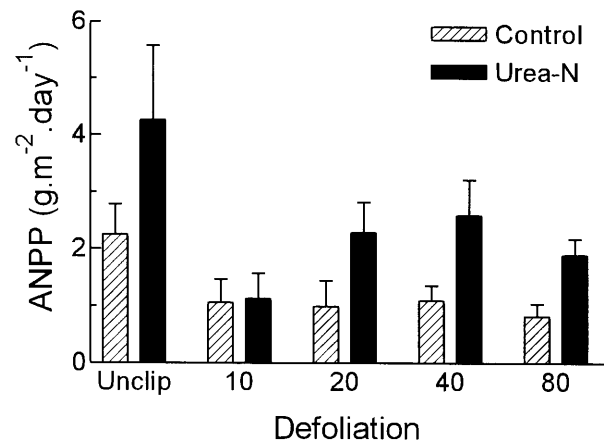
Fig. 3 Aerial net primary productivity (ANPP) of control and defoliated patches of different size (radius in cm) under two levels of urea-N application. *Vertical bars* indicate SE
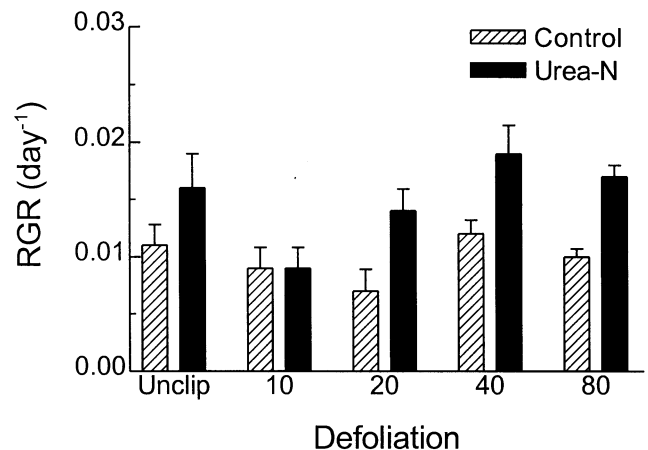

Fig. 1 Photosynthetic photon flux density (PPFD) of defoliated patches of different size recorded at the center and the edge of the patches, 30 days after treatment. *Vertical bars* indicate the SE. *Dotted lines* over and under *control line* indicate SE of control

Fig. 4 Relative growth rate (RGR) of control and defoliated patches of different size (radius in cm) under two levels of urea-N application. *Vertical bars* indicate SE

and these values were similar at both the beginning and the end of the experiment.

Discussion

In agreement with our predictions, plant growth was affected by patch size only in fertilized patches, which suggests that a greater N availability increased the competitive interactions between grazed and ungrazed neighbouring plants. We found that the pattern of productivity of fertilized patches matched the irradiance pattern (greater productivity in larger and intermediate patches). This suggests that shifts in productivity along a patch size gradient might be governed by shifts in light availability, provided that N is not limiting. Therefore, under high N availability, the negative effects of the ungrazed neighbours decreased as patch size increased beyond 20 cm radius. The spatial pattern of defoliation affected the amount of light available to defoliated plants. The removal of 50% of aboveground biomass increased the irradiance at the base of plants, but the magnitude of this effect depended on the spatial pattern of defoliation: irradiance increased with patch size and reached a constant value at intermediate patch sizes. This was a combined result of the decreasing importance of edge effects and edges being more luminous as patch size increased. Thus, in a defoliated patch, there is a perimetral interface where defoliated plants suffer a more constrained light environment; as patch size increases, the importance of that interface decreases and the constraint is less intense. McNaughton (1992) found, under laboratory conditions, that the effect of defoliation was more negative when canopy closure was simulated by placing a piece of cardboard around individual pots. In this paper, the smallest, urea-N patches, which could be considered similar to those pots, also showed a negative response to defoliation.

The effect of defoliation on relative growth rates ranged between no compensation for the removed tissue and damage (Hilbert et al. 1981; Oesterheld and McNaughton 1991). It translated into a significantly lower total production of forage to herbivores because defoliated patches had part of their biomass removed without any possitive effect (and negative in some cases) on their growth rate per unit of biomass. However, the type of response of these Flooding Pampa grasslands is not consistent among years, since we have shown overcompensatory responses in growing seasons with high initial green biomass and low RGR (Semmartin and Oesterheld 1996; Semmartin 1998).

The size of grazed patches varies in actual range situations according to various factors (Edwards et al. 1994, 1995). Different stocking rates (Milchunas and Lauenroth 1989; Guevara et al. 1996), the type of herbivore (McNaughton et al. 1991) and its level of selectivity (Edwards et al. 1994, 1995), and the spatial distribution of the most palatable species may account for different grazing grain. A fine-grained pattern frequently results from systems with low stocking rates, whereas coarse-grained systems result from higher stocking rates. These different patterns may be accompanied by different levels of nitrogen input via animal depositions, with higher N levels at higher stock rates. The magnitude of the interface between grazed and ungrazed plants of these two extreme patterns is different and is translated, provided that N is not limiting, into a different response to grazing. The proportion of the area affected by urea depositions has not been determined in this grassland, but stocking rates in this region are much higher than in natural ecosystems in which that proportion has been considered significant for overall nutrient cycling (Oesterheld et al. 1992).

Our results showed that nitrogen fertilization increased primary productivity twofold. Positive effects of nitrogen fertilization are frequently found in natural grasslands (Clark and Woodmansee 1992). However, in the Flooding Pampa phosphorus is considered as the most limiting nutrient (Ginzo et al. 1982, 1986; Marchegiani et al. 1982; Pruess et al. 1992). This work shows that nitrogen is also a limiting factor. However, when the grazing spatial pattern is very fine-grained, the positive effects of fertilization on the defoliated patch is counteracted by the undefoliated neighbours. Our results also showed that fertilized, defoliated patches had the same productivity as unfertilized, undefoliated controls, except when the defoliation pattern was very fine-grained. Then, grazed patches that receive urine deposition would transfer energy to a higher trophic level without a detrimental effect on primary productivity. Nitrogen content in biomass was not affected by fertilization, which suggests that the additional nitrogen was diluted as a consequence of the greater productivity of the fertilized patches. These findings agree with those of Aerts et al. (1995) who showed that in nitrogen-limited sites, primary productivity increases with nitrogen application while the nitrogen concentration in tissues remains constant.

Experimental evidence showing plant responses to defoliation along nutrient gradients suggests two possible models with different outcomes (Oesterheld and McNaughton 1991). The first model proposes a positive interaction between defoliation and nutrient availability (Maschinski and Whitham 1989; Whitham et al. 1991). This model predicts that plants will more likely compensate for grazing when soil nutrient availability is high because there will be more nutrients in soil for the replacement of lost tissue. At low nutrient availability, compensatory growth would be limited because grazing removes nutrients that plants have to replenish from a nutrient-poor environment and because grazing may reduce root volume to take up nutrients (Ingham and Detling 1984). The second model proposes a negative interaction between defoliation and nutrient availability (Hilbert et al. 1981; Georgiadis et al. 1989). This model predicts that plants will more likely compensate for grazing when soil nutrient availability is low rather than high because plants in a poor environment grow at lower rates, far below their potential maximum RGR. Any increase in their

RGR as a consequence of grazing will generate a greater relative response that can result in the compensation of lost tissue. In nutrient-rich sites, plants grow faster, close to their potential maximum RGR. Then, increases in the RGR of defoliated plants as a consequence of grazing are less likely to be found. There is a third model that complements the other two: it proposes that the response is curvilinear with minimum compensation at both ends of the gradient and a maximum at an intermediate point, and that it is possible that the opposing evidence regarding this interaction comes from studies carried out at both extremes of the gradient (Oesterheld and McNaughton 1991). Our work showed that competition for light may modify the interaction between grazing and N availability: in small patches, the effect of defoliation was more negative under high N availability, whereas in intermediate and large patches the effect of defoliation was independent of N availability. The grassland studied in this work is located at the high end of the productivity gradient of grasslands and savannas (Milchunas and Lauenroth 1993; Oesterheld et al. 1999), where the interaction between light and nutrients is expected to be relevant. This pattern of response is less likely in drier sites where water explains most of the variation in productivity (Milchunas and Lauenroth 1993).

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