Effect of grazing pattern on primary productivity

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Grazing usually increases the relative growth rate (RGR) of plants. However, it is not clear under which conditions this will result in a positive effect on primary productivity. We tested the hypothesis that the effect of grazing on community productivity depends on the level of competition between grazed and neighboring ungrazed plants, and that the level and outcome of that competition depends on the size of the grazed patch. The hypothesis predicts that as the size of a grazed patch increases, the area of influence of the neighboring plants becomes less important in relation to the area of the patch. Thus, grazing will more likely increase the productivity of large patches.

We performed two field experiments in a grassland community of the Flooding Pampa, Argentina under two different weather conditions (non-flooded year and flooded year). We analyzed the productivity of undefoliated patches, defoliated patches of different sizes, and a neighboring area around the defoliated patches. We found that (1) the effect of defoliation on productivity was affected by patch size: defoliation had neutral to positive effects on intermediate and large patches and negative effects on very small patches, and (2) defoliation had no effect on the productivity of the area surrounding the defoliated patches. Our results also suggest that flooding limits the ability of plants to compensate for tissue removal.

Herbivory is one of the major forces that determine the productivity of grasslands and its effects can range from benefit to damage (McNaughton 1979, 1983a). Positive responses of plants to tissue removal by grazing are known as compensatory growth: grazing stimulates the relative growth rate (RGR) of defoliated plants so that the lost tissue may be partially, fully or overly compensated (Belsky 1986, Oesterheld and McNaughton 1991a).

A number of experiments aimed at determining whether grazing has a positive or negative effect on plant growth has been performed (Belsky 1986, McNaughton 1986, Painter and Belsky 1993). The evidence shows that full and overcompensation do occur in a variety of situations, but we still lack a comprehensive model that can predict the result of a single defoliation event in terms of absolute growth, productivity, or fitness.

Analyzing this problem, some authors have pointed out that the response to defoliation may be scale dependent (Belsky 1987, Westoby 1989). They questioned how a single plant or a small group of plants that is grazed could be benefited by the removal of tissue when it is surrounded by competing neighbors that do not lose their biomass. On the other extreme, nobody has questioned the benefits of grazing at the community or ecosystem level through the opening of the canopy or the acceleration of nutrient cycling (Westoby 1989). At the moment, we do not know of any empirical work aimed at specifically testing the role played by the scale of grazing.

The removal of vegetation by herbivory is spatially heterogeneous and generates a pattern of grazed and ungrazed areas or patches (McNaughton 1983b). Competition between grazed and ungrazed plants occurs in the
crease in relation to the size of the grazed surface that contact between grazed and ungrazed neighbors decrease. As the size of grazed patches increases, the perimeter of reduction, and those of them located at the edge of the grazed plants, however, pay a cost in terms of biomass limit plant growth (Knapp and Seastedt 1986). Grazing opens the canopy allowing a greater light penetration (Frank and McNaughton 1993). When grazing occurs, both grazed and their neighboring ungrazed plants receive the benefits from a greater light availability. Grazed plants, however, pay a cost in terms of biomass reduction, and those of them located at the edge of the patch are shaded by the neighboring ungrazed plants. As the size of grazed patches increases, the perimeter of contact between grazed and ungrazed neighbors decreases in relation to the size of the grazed surface that benefits from defoliation. Thus, growth will be most likely increased by grazing if grazing is coarse-grained than if it is fine-grained.

We assume that in grasslands there are 3 different areas: (1) grazed patches, which represent areas where animals recently removed vegetation, (2) ungrazed areas surrounding those patches ("rings"), and (3) ungrazed patches, which represent the areas where animals did not remove vegetation recently and which are not under the influence of a grazed patch. The patch-ring boundary is defined by grazing, whereas the ring-ungrazed patch boundary is not so clearly defined and depends on the extent of the influence of grazing on neighboring plants.

Our specific predictions were (1) grazed patches will show greater productivity as patch size increases, (2) small patches will show lower productivity than the ungrazed patches, and (3) ungrazed rings will show the greatest productivity. In this paper we present data from two similar field experiments carried out under two different weather conditions: an average season and a humid season that resulted in an enduring flooding event. Our approach was to simulate grazing using mechanical defoliation in a grassland community of the Flooding Pampa.

**Methods**

The Flooding Pampa is a region in the province of Buenos Aires, Argentina, which is covered in 80% of its area by native grasslands (León et al. 1984). Mean annual precipitation is 924 mm and mean monthly temperature ranges from 6.8°C in winter to 21.8°C in summer.

Experiments were located on an 8-yr-old exclosure of a native grassland community defined phytosociologically as *Ambrosia tenuifolia*, *Eclipta bellioides* and *Mentha pullegium* (Burkart et al. 1990). We selected this exclosure because it 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 C₃ and C₄ photosynthetic pathways determine the seasonal pattern of aboveground production with a maximum which occurs from late spring to the beginning of summer (Sala et al. 1981). The grassland had a mean canopy height of 40–60 cm and a large accumulation of standing dead tissue (Sala et al. 1986).

Two similar experiments in two years were performed: (1) a defoliation experiment and (2) a defoliation, nitrogen, and water supplementation experiment. The duration of the experiments was 2 months. Weather variation between years determined that the first experiment corresponded to average conditions and the second experiment to flooding conditions. Precipitation during experiment 1 was 256 mm, while the mean for the last 22 yr was 294 mm. Heavy rain during experiment 2 caused a flooding event that started immediately after the application of urea and water and lasted until the end of the experiment.

Experiment 1: the treatments were determined by the different size of circular clipped patches (20, 40, and 80 cm radius) and an unclipped control. Clipping height was 12 cm and resulted in a 53% removal of total standing biomass. The number of samples for each treatment was as follows: unclipped (n = 20), 20-cm patches (n = 16), 40-cm patches (n = 8) and 80-cm patches (n = 6). Biomass of controls was also harvested with a rectangular frame (0.4 m²). Treatment location in the excursion was randomly assigned.

We performed a preliminary experiment to determine the effect of the size and shape of frames on the estimate of aboveground biomass. Treatments were different shapes and sizes: a rectangular frame (80 x 30 cm), and circular frames of 10 and 20 cm radius. Results of harvested biomass showed no significant differences among treatments (P = 0.114).

The experiment started in October and ended in December, a period accounting for approximately 50% of the annual production (Sala et al. 1981). Both initial and final aboveground biomass were determined (October and December). The recovery time of defoliated plants was 65 d. The biomass of a ring (20 cm section) around each patch was harvested in December. Harvested biomass was divided into green biomass of cool season species, green biomass of warm season species, and standing dead biomass.

Mean and variance of initial biomass of patches were calculated on the basis of two independent variables: initial biomass of unclipped controls and clipped biomass. The variance of the natural logarithm of initial biomass (needed to calculate RGR) was estimated from the variance of the natural logarithm of the differences between the biomass of the controls and the replicates of each treatment, respectively. This procedure was repeated for the respective combinations and
a pooled variance was calculated until it reached a fairly constant value (Oesterheld and McNaughton 1988).

Experiment 2: this was a 3-level factorial experiment. Factors were defoliation, urea, and water. On the basis of the results from experiment 1, a smaller patch size was included. Thus, defoliation had 5 levels: unclipped control, and circular clipped patches of 10, 20, 40, and 80 cm radius. The defoliation methodology and the experimental design was the same as in experiment 1. The number of samples for each treatment was as follows: unclipped (n = 16), 10-cm patches (n = 32), 20-cm patches (n = 24), 40-cm patches (n = 16) and 80-cm patches (n = 16). 52% of the total standing biomass was removed. Based on the results from experiment 1, we reduced the section of the ring that was harvested around each patch to a width of 5 cm. This, however, made it difficult to harvest the standing dead material, which was not considered. The recovery time of defoliated plants in this experiment was 74 d.

The urea treatment had 2 levels: control and 10 g N/m². 8 l/m² of urea solution was sprinkled uniformly over the plots. Control plots received the same volume of water. The water treatment had 2 levels: control and 20 l/m² of water. Nitrogen and water were applied once, 15 d after the application of the defoliation treatment.

Likely due to the flood that occurred immediately after the application of treatments and lasted throughout experiment 2, nitrogen and water had no significant effect on any of the response variables. Thus, the subsequent analysis was done after pooling the data and only considering the defoliation treatment.

Data were analyzed using standard ANOVA procedures. Since patches and rings were not independent, they were not compared. Statistical tests were performed to compare either patches of different sizes and controls, or the rings around patches of different size and controls. Unless specified in the text, the level of statistical significance was 0.05.

**Results**

The response of relative growth rate (RGR) to patch size showed a similar pattern for both years (Fig. 1A, B). Compensatory responses (i.e. RGR values above control) were observed in patches of 20 cm radius or larger. Despite the similar pattern, the magnitude of the response was different between years (Fig. 1A, B). In the year with average precipitation, RGR of defoliated patches was larger than the necessary rate to reach full compensation (Fig. 1A). RGR of 40-cm patches was significantly greater than that of 20-cm patches and controls. In the flooded year, RGR of 10-cm patches was lower than the control treatment. RGR of patches of 20-cm radius or greater were close to the values needed to reach full compensation (Fig. 1B). RGR of the rings surrounding the defoliated patches did not differ from controls or among themselves (average: P = 0.8; flooded: P = 0.48).

In the average year, overcompensation determined that green biomass of defoliated patches, which was 47% of control at the beginning of the experiment, was not significantly different from controls at the end of the experiment (Fig. 2A, P = 0.314). In the flooded year, final green biomass was significantly reduced by defoliation only in the smallest patches (Fig. 2B). Final green biomass of rings around the patches was not different from controls in either year (average: P = 0.54; flooded: P = 0.50).

![Fig. 1. Relative growth rate (d⁻¹) of defoliated patches of different size. A) average year; B) flooded year. Two important thresholds are indicated: RGR of control, undefoliated patches and the RGR needed to reach full compensation.](image-url)
Our results showed that the response to defoliation was affected by patch size. Our hypothesis stated that compensatory responses of plants to grazing depend on the outcome of the competition between grazed plants and their neighboring ungrazed plants and that this outcome, in turn, depends on the size of the grazed patch. The results supported this idea and suggest, as the initial model proposed, that there is a decrease in competition between patch and ring as the size of the patch increases. Defoliation had an effect on community productivity that ranged from neutral to positive except for the smallest (10-cm) patches. This indicates that grazing will have a negative impact on productivity only when it is very fine-grained. It was surprising that in patches as small as 20 cm radius, which would be regarded as corresponding to a very selective pattern of defoliation.

Standing dead biomass (final + clipped standing dead biomass) was less responsive to defoliation (Fig. 3A, B). There was no effect in experiment 2 and a slight increase for the 40-cm patches in experiment 1. Standing dead of rings, only considered for the average year, showed no significant differences from controls ($P = 0.83$).

Discussion
These experiments suggested two main conclusions: (1) the effect of defoliation on productivity depended on patch size and (2) defoliation had no effect on the productivity of the ring surrounding the defoliated patch.
grazing, the positive effects of defoliation on productivity overrode the negative effects of the undefoliated neighbors.

Our findings suggest that positive responses in plant growth are more likely to be found if grazing pattern is coarse grained. This agrees with the fact that the best documented cases of productivity stimulation by grazing correspond to grazing lawn systems (McNaughton 1979, Bazely and Jefferies 1985, Dyer et al. 1991, Frank and McNaughton 1993).

The lack of effect of defoliation on the ring of undefoliated neighbors suggests that the beneficial effects of grazing are received by those plants that are effectively grazed, not by their neighbors. Some of the ideas underlying rangeland management are based on the assumption that selective grazing both negatively affects the plants that are grazed and positively affects their ungrazed neighbors (Briske 1991). We found the former to be true only on very small patches, and found no evidence for the latter.

In the average year, the extent of the RGR increment was larger than the necessary to reach full compensation (Hilbert et al. 1981, Oesterheld and McNaughton 1991a), and overcompensation occurred. An intense controversy about the extent of compensatory growth in nature still exists (Belsky 1986, McNaughton 1986, Painter and Belsky 1993). Part of the criticism on the ideas underlying rangeland management is based on the assumption that compensatory growth is focused on the fact that compensatory responses have been observed more frequently under laboratory conditions or in monocultures with high nutrient availability (Belsky 1986, 1987, Verkaar 1988, Briske 1991, Painter and Belsky 1993). This paper provides evidence that shows overcompensation in the field, as shown by McNaughton (1979), Bazely and Jefferies (1985), Williamson et al. (1989), Dyer et al. (1991), and Frank and McNaughton (1993).

We believe that the responses to defoliation that we observed may have been influenced by the particular structure of these Flooding Pampa grasslands and that extrapolation of these results to other systems should be done carefully. The large amount of standing dead material may have played a major role in the large overcompensatory responses to defoliation as it has been shown in pot experiments (Oesterheld and McNaughton 1991a) and has been suggested by other authors (Knapp and Seastedt 1986, Seastedt et al. 1991). The results also showed that the final result of a defoliation event depends on soil conditions: compensatory growth was much lower under flooding. This had been demonstrated in factorial pot experiments which showed that flooding constrains the ability of single plants to compensate for the removal of tissue (Oesterheld and McNaughton 1991b).

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References


