Effect of defoliation on grass growth. A quantitative review

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The diversity of responses of individual grasses to defoliation created a controversy about 15 years ago, which still needs clarification. We quantitatively assessed the evidence of defoliation effects on individual grass growth, addressing two main questions: 1) what is the average and variability of the effect of defoliation on plant growth? and 2) what are the associated conditions accounting for the diversity of effects? Regarding the first question, the results showed a negative overall effect of defoliation on plant growth and substantial variability in the defoliation responses of different plant components. There was an intermediate negative effect on total production (which included clipped-off biomass), a large negative effect on final live biomass at harvest, and a minimal effect on root biomass. Regarding the second question (conditions accounting for the diversity of effects), defoliation intensity had no effect on the response to defoliation, but both time for recovery from the last defoliation and the period of time between defoliation events significantly decreased the negative effect of defoliation. Nitrogen availability also altered the effect of defoliation, as plants grown at highest nitrogen levels were more negatively affected by clipping than plants with no supplementary addition of nitrogen. These results indicate that the magnitude of defoliation response by an individual plant differs among plant compartments and this response is modulated by other factors, such as time for recovery after defoliation, and nutrient availability. In general, the effect of defoliation on individual plant production was more negative than reported effects of grazing on ecosystem primary production.

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At the individual plant level, defoliation by herbivores has manifold consequences on plant growth and allocation (McNaughton et al. 1983). Aboveground biomass of grasses directly experiences the effects of defoliation, loosing photosynthetic tissue and resulting in loss of carbon and nutrients. A decrease in the final vegetative biomass of defoliated plants, caused by the lost of functional tissue, has been observed in many pot and field experiments, some of them reviewed in Belsky (1986), Verkaar (1986) and Painter and Belsky (1993). However, the negative effect of defoliation on growth rate or final biomass is usually less than proportional to the removal of live biomass. Occasionally, it is even positive (McNaughton et al. 1983). This response is known as compensatory regrowth because the defoli-ated plants partially or fully compensate for the removal of biomass. The magnitude of the compensatory response has been associated with nutrient levels (Georgiadis et al. 1989, Alward and Joern 1993, Hicks and Reader 1995), flexible carbon allocation (Briske et al. 1996), evolutionary mechanisms (Crawley 1987, Vail 1992), light environment (McNaughton 1992), and recovery conditions (Oesterheld and McNaughton 1988). Defoliation may also affect root growth and belowground carbohydrate reserves, decreasing root biomass (Holland et al. 1996, Thornton and Millard 1996, Morón Rios et al. 1997) and belowground relative growth rate (Oesterheld 1992).

These potentially opposing effects of defoliation result in a continuum of potential plant responses in

terms of growth, from increase through reduction (Belsky 1986, Oesterheld and McNaughton 1991a). When defoliation increases growth rates, the response is known as overcompensation (Belsky 1986), whereas when defoliation decreases growth rates the response may be either partial compensation (the reduction of growth is less than expected from the proportion of biomass removed), or damage (the reduction is more severe than expected from the proportion of biomass removed). Finally, when defoliated plants grow as fast as undefoliated plants the response is known as full compensation. If the proportion of biomass removed is unknown, compensatory growth may still be inferred from a comparison of relative growth rates (RGR) of defoliated and undefoliated plants: any increase in RGR as a result of defoliation indicates a compensatory response. Compensation may be analyzed for other response variables, such as seed production, final biomass, or yield to grazers, but plant growth is the most common and integrative variable.

Although the effect of defoliation on growth of individual grass plants has been studied extensively, the magnitude and generality of compensatory growth responses has been under a great deal of discussion (McNaughton et al. 1983, Belsky 1986, Crawley 1987, Bergelson 1992, McNaughton 1993, Painter and Belsky 1993). The analyses of the evidence have so far been of a qualitative nature. Quantitative techniques are needed to obtain a more objective conclusion and reveal the conditions leading to different types of responses. In this paper, we quantitatively synthesize the evidence on the effects of defoliation on growth of individual grasses. We address two main questions: 1) what is the average and variability of the effect of defoliation on plant growth? and 2) what are the associated conditions accounting for the diversity of effects? Our approach was to review the literature on the effects of defoliation on individual grass growth.

Materials and methods

In order to assess the average and variability of the effect of defoliation on plant growth, we analyzed responses in the literature on defoliation effects using two complementary approaches: linear regressions and meta-analysis. The criteria for selection of a study for inclusion in the analysis were that (1) defoliated grasses were compared with undefoliated controls, (2) the study focused on individual plant responses, (3) growth was measured in terms of total biomass (including clip-off), final biomass (live biomass harvested at the end of the experiment), root biomass or relative growth rate of aboveground biomass, and (4) direct growth measures were reported, instead of test statistics, ANOVA tables, and regression or correlation coefficients. In addition to these criteria, meta-analysis required that standard deviation and sample size were reported. Other restrictions such as independence of measures between plant components and normal distribution were analyzed in order to comply with the assumptions of meta-analysis (Cooper and Hedges 1994). Based on their titles and keywords, approximately 300 potential articles dated since 1980 were inspected and no more than 28 met our criteria. Only 16 of these 28 studies met the meta-analysis additional requirements. All data sources are shown in Table 1. An important number of studies were left out mainly because of the absence of an undefoliated treatment, reporting patch or stand measures of biomass instead of individual plant output, lacking of values of biomass, and omitting some measure of variance (standard deviation/error value). The inclusion of some basic data, such as measures of variance, number of replications, and biomass values, instead of probability or test statistic tables, would make defoliation studies more useful for comparative purposes in the future.

Simple regression analyses were performed between response variables measured in defoliated plants and undefoliated plants. Each point of these regressions represented a defoliated-undefoliated comparison of the chosen variable. In the case of using studies that had different levels of additional treatments (competition, water, light), a control undefoliated must have been included at each additional treatment level. Each level of treatment was treated as a separate comparison. To quantify defoliation effects, the regressions were compared with an equality line (no effect of defoliation) by testing if the slope (b) was different from 1, and the intercept (a) was different from 0. The response variables were: (1) total production, (2) final biomass, (3) root biomass, and (4) relative growth rate of aboveground biomass.

The meta-analysis technique estimates the magnitude of a general effect from a number of studies (Cooper and Hedges 1994, Arnqvist and Wooster 1995, Gurevitch and Hedges 1999). In our case, we used this approach to evaluate the general effect of defoliation on several plant growth parameters as reported in several individual papers. For each response variable, the unbiased effect size, d_i, of an individual experiment is the standardized difference between the means of the defoliated and undefoliated groups (Rosenthal 1991, Rosenberg et al. 1997):

$$d_i = \frac{\overline{Yd} - \overline{Yu}}{s}$$

where $\overline{Yd}$ is the mean of defoliated plants, $\overline{Yu}$ is the mean of undefoliated plants, and s is the pooled standard deviation of both treatments (Hedges and Olkin 1985, Gurevitch et al. 1992), such that

$$s = \sqrt{((Nd - 1)(s_d)^2 + (Nu - 1)(s_u)^2/Nd + Nu - 2}$$

where Nd and Nu are the sample sizes of the defoliated and undefoliated groups, respectively; s_d is the standard deviation of the plants in the defoliated group, and s_u is the standard deviation of the plants in the undefoliated group.

The individual effect sizes, d_i, are combined into a mean effect size, $\overline{d_{ij}}$, calculated as a weighted mean with samples weighted by their variances:

$$\overline{d_{ij}} = \frac{\sum w_i \times d_i}{\sum w_i}$$

The weights w_i are the reciprocal of the sampling variances, $w_i = 1/v_i$

$$v_i = \frac{Nd + Nu}{NdNu} + \frac{(d_i)^2}{2(Nd + Nu)}$$

We tested a null hypothesis ($\overline{d_{ij}} = 0$), which was rejected if the $\overline{d_{ij}}$ values were significantly greater than zero (at $P < 0.05$). We used the effect size categories suggested by Cohen (1969): small (0.2), medium (0.5), large (0.8) and very large (more than 1.0).

The mean effect size, $\overline{d_{ij}}$, measures the magnitude of the defoliation effect on a response variable. Thus, we compared the $\overline{d_{ij}}$ values of our four response variables

Table 1. Characteristics of selected data.

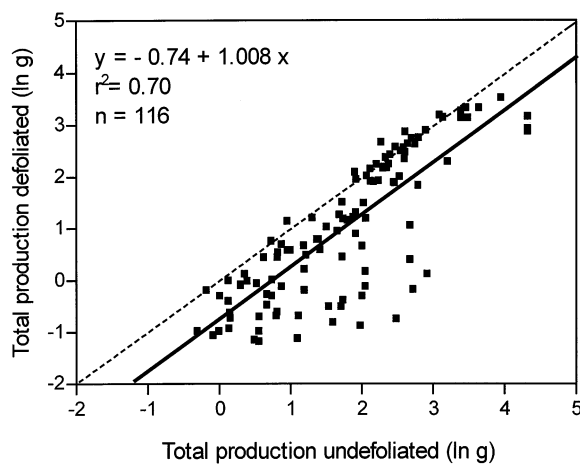| Citation	Species	Location: Species origin
Alward and Joern 1993	*Bouteloua gracilis*	USA: Nebraska, Sandhills mixed grass praire
	Bouteloua hirsuta	
Banyikwa 1988	*Digitaria macroblephara*	Tanzania: Serengeti, heavy grazed, short grasslands
	Sporobolus ioclados	
Briske et al. 1996	*Andropogon gerardii*	USA: Texas
	Schizachyrium scoparium	
	Aristida purpurea	
	Bouteloua rigidiseta	
Caldwell et al. 1981	*Agropyron spicatum*	USA: North Utah
	Agropyron desertorum	
Chapin and McNaughton 1989	*Sporobolus ioclados*	Tanzania: Serengeti, heavy grazed, short grasslands.
	Pennisetum mezianum	
	Eustachys paspaloides	
Detling and Painter 1983	*Agropyron smithii*	USA: North Dakota, mixed grass praire
Detling et al. 1980	*Bouteloua gracilis*	USA: Colorado, short grass praire
Hartnett 1989	*Andropogon gerardii*	USA: Kansas, Flint Hills tall grass praire
	Panicum virgatum	
Hicks and Reader 1995	*Poa pratensis*	Canada: Guelph.
	Poa compressa	
	Dactylis glomerata	
Gold and Caldwell 1989	*Agropyron desertorum*	USA: Logan, Utah.
Jaramillo and Detling 1988	*Bouteloua gracilis*	USA: North Dakota, mixed grass praire
McNaughton 1985	*Sporobolus pyramidalis*	Tanzania: Serengeti, heavy grazed, short grasslands
	Sporobolus ioclados	
McNaughton 1992	*Themeda triandra*	Tanzania: Serengeti, heavy grazed, short grasslands
	Eustachys paspaloides	
McNaughton et al. 1983	*Kyllinga nervosa*	Tanzania: Serengeti, heavy grazed, short grasslands
McNaughton and Chapin 1985	*Kyllinga nervosa*	Tanzania: Serengeti, heavy grazed, short grasslands
	Digitaria macroblephara	
Morón Ríos et al. 1997	*Muhlenbergia quadridentata*	México: Neovolcanic belt of central Mexico
Oesterheld and McNaughton 1988	*Themeda triandra*	Tanzania: Serengeti
Oesterheld and McNaughton 1991a	*Briza subaristata*	Argentina: Flooding Pampa
Oesterheld and McNaughton 1991b	*Hyperthelia dissoluta*	Tanzania: Serengeti plains
	Echinochloa haploclada	Tanzania: Serengeti floodplains
	Panicum coloratum	Tanzania: Serengeti plains
Oesterheld 1992	*Briza subaristata*	Argentina: Flooding Pampa
	Stipa bavioensis	
Painter and Detling 1981	*Agropyron smithii*	USA: Colorado, North American short grass praire
Painter et al. 1989	*Agropyron smithii*	USA: North Dakota, mixed grass praire
	Bouteloua gracilis	
Polley and Detling 1988	*Agropyron smithii*	USA: South Dakota
Polley and Detling 1989	*Agropyron smithii*	USA: South Dakota
Ruess et al. 1997	*Carex ramenskii*	USA: Alaska
Ruess et al. 1983	*Kyllinga nervosa*	Tanzania: Serengeti grassland
Simoes and Baruch 1991	*Hyparrhenia rufa*	Venezuela: Llanos
	Trachypogon plumosus	
Wilsey 1996	*Stipa occidentalis*	USA: Wyoming, Yellowstone National Park

Fig. 1. Relationship between total production of defoliated and undefoliated plants. Total production includes final live biomass plus clipped-off biomass. Each point represents the mean biomass of defoliated plants and their respective controls undefoliated. The solid line is the least square best fit; the dashed diagonal (equality line $y = x$) was included as a reference. Data were transformed in logarithmic values.

Table 2. Effects of defoliation over four plant components

Variable	$\bar{d}_{ij}$	d_{ij} inf.	d_{ij} sup.	n
Total production	−0.24	−0.48	−0.01	29
Final biomass	−1.55	−1.73	−1.37	35
Root	−0.18	−0.41	0.04	29
RGR	0.25	0.13	0.37	36

Values reported are mean effect size (d_{ij}), 95% confidence interval (d_{ij} inf. − d_{ij} sup.), number of comparisons (n).

by computing the between-class heterogeneity between response variables. This test of homogeneity was based on the Qb statistic, with chi-square distribution (Hedges and Olkin 1985, Cooper and Hedges 1994) and, as one can partition variance in an ANOVA, is a measure of the variation between response variables in the mean effect size $\bar{d}_{ij}$. The hypotheses tested were: H0: All effect sizes $\bar{d}_{ij}$ are equal; H1: Effect sizes $\bar{d}_{ij}$ are not equal (i.e. the defoliation effect depends on the response variable being considered). All calculations of $\bar{d}_{ij}$ and the combination of effect sizes $\bar{d}_{ij}$ across comparisons were based on a fixed-effect model (Gurevitch et al. 1992).

In order to answer our second question (what are the associated conditions accounting for the diversity of defoliation effects?), we related the response to defoliation with different experimental conditions: (1) defoliation intensity, (2) time for recovery since the last defoliation, (3) time between defoliations, and (4) nitrogen level. Defoliation intensity is measured as percent of clipped biomass from initial aerial biomass. Time for recovery since the last defoliation, and time between defoliations are both measures of the amount of time allowed for regrowth. The former applies to

experiments with a single defoliation and represents the time between that defoliation and final harvest, whereas the latter corresponds to experiments with more than one defoliation (it is the inverse of defoliation frequency).

To test for an overall relationship between the associated conditions and the defoliation effect, we performed standard least-square regression analysis of the relative effect of defoliation on experimental conditions. The variable describing the magnitude of defoliation effect on total production was:

RCT: $(TP_{defoliated} - TP_{undefoliated}/TP_{undefoliated})$

where RCT is the relative change of total biomass production of defoliated plants respect to undefoliated plants, and TP is the total production. This regression approach on standardized difference values is also, like the measured of the weighted mean effect size $\bar{d}_{ij}$, a formal application of a method to summarize evidence across studies.

RCT has a simple, intuitive interpretation: the proportional reduction in biomass due to defoliation. RCT = 0 indicates full compensation in terms of biomass production, RCT > 0 indicates overcompensation, and RCT < 0 indicates either partial compensation or damage. A similar index (relative competitive intensity) has been used to assess the influence of competition from neighboring plants on the growth of target plants (Paine 1992, Wilson and Tilman 1993, Goldberg et al. 1999). These relative indexes eliminate any direct effects of the environment on the response variable because the measured effect is relative to the target's intrinsic capacity in that particular environment (Goldberg et al. 1999). For the analysis of the effect of nitrogen availability on RCT, we selected papers that compared the effect of defoliation on plants growing at either high or low nitrogen level. As a reference, we also compared the RCT of these two extreme treatments with the RCT of the rest of the data set.

Results

Both analyses (regression and meta-analysis) showed a negative overall effect of defoliation on plant growth, with a substantial variability in the defoliation responses between plant components, as evidenced by the different regression equations and a Qb value of 278.5, $P < 0.001$, in the meta-analysis. Total production, which includes final live and clipped-off biomass, was reduced by defoliation (Fig. 1), showing a medium and significantly negative effect size (Table 2). In agreement with this, the intercept of the regres-

sion line was significantly lower than zero ($P < 0.0001$) and the slope was not significantly different from 1 ($P = 0.89$) (Fig. 1). A slope close to 1 and an intercept of -0.74 in a log-log relationship indicates that the effect of defoliation was a nearly constant proportion (52%) of the total production of undefoliated plants: $1 - \exp(-0.74) = 0.52$. Final live biomass at harvest was the most affected plant component. The mean effect size was very large and significantly lower than zero (Table 2). The intercept of the regression line was significantly lower than 0 ($P < 0.001$) and the slope was marginally lower than 1 ($P < 0.10$) (Fig. 2). This indi-

Fig. 4. Relationship between relative growth rates of above-ground tissue (RGR) of defoliated and undefoliated plants. Each point represents the mean RGR of defoliated plants and their respective controls undefoliated. The solid line is the least square best fit; the dashed diagonal (equality line $y = x$) was included as a reference.
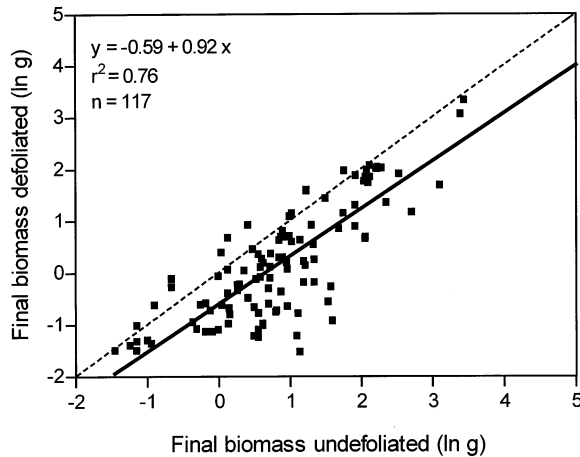

Fig. 2. Relationship between final biomass of defoliated and undefoliated plants. Each point represents the mean biomass of defoliated plants and their respective controls undefoliated. The solid line is the least square best fit; the dashed diagonal (equality line $y = x$) was included as a reference. Data were transformed in logarithmic values.
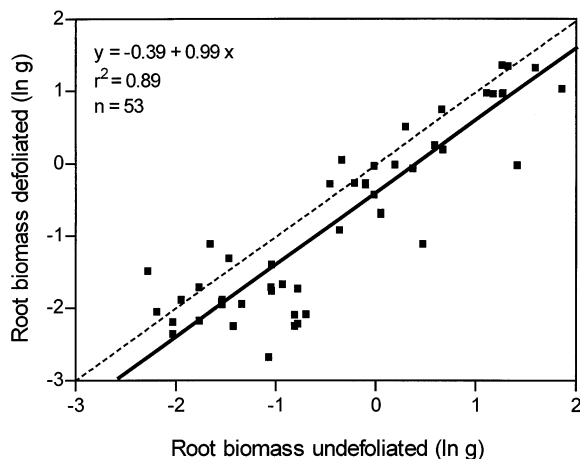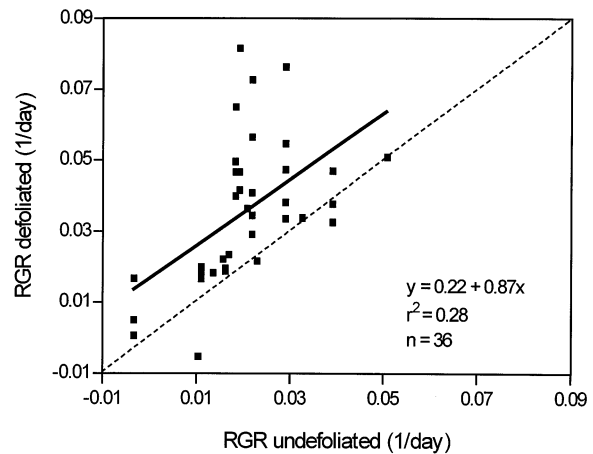

Fig. 3. Relationship between root biomass of defoliated and undefoliated plants. Each point represents the mean biomass of defoliated plants and their respective controls undefoliated. The solid line is the least square best fit; the dashed diagonal (equality line $y = x$) was included as a reference. Data were transformed in logarithmic values.

cates a 44% reduction for small plants and 57% for larger plants. According to the meta-analysis, root biomass was not significantly affected by defoliation (Table 2). However, the regression analysis showed an intercept statistically lower than zero ($P < 0.001$), and a slope similar to 1 ($P = 0.46$) (Fig. 3). This represented a constant 32% reduction of root biomass across plant sizes. In contrast to the former responses, the relative growth rate was larger in clipped plants than in un-clipped ones. The effect size was medium, significantly greater than zero (Table 2). The intercept of the regression line was significantly larger than zero ($P < 0.001$) and the slope was marginally lower than 1 ($P < 0.10$) (Fig. 4).

The experimental conditions during clipping treatments differentially accounted for the total biomass outcome of defoliated plants related to undefoliated plants (Fig. 5). Defoliation intensity had no effect on the response to defoliation (slope not different from 0, $P = 0.12$, Fig. 5a). In contrast, the time for recovery from the last defoliation significantly decreased the negative effect of defoliation (slope greater than 0, $P < 0.001$, Fig. 5b). Time between defoliations also decreased the negative effect of defoliation (slope greater than 0, $P < 0.001$, Fig. 5c). Nitrogen availability also altered the magnitude of the defoliation effect on total biomass production. Plants grown at high nitrogen levels were more negatively affected by clipping than plants growing at standard level of nutrient availability (Fig. 6). Plants growing under lower than normal levels of nitrogen showed an intermediate reduction of total biomass production by defoliation, but this reduction was not statically significant ($P < 0.13$, Fig. 6).

Discussion

Defoliation differentially affected various growth parameters. Defoliation had a greater negative effect on final aboveground biomass, and affected belowground biomass the least. The effects on total production were intermediate. The ubiquitous compensatory responses to tissue removal (i.e. increases in RGR) mitigated the negative effects of defoliation on growth. The effects of

Fig. 6. Relative change in total production (RCT) in defoliated plants respect to their controls, undefoliated under different nitrogen availability. Low and high nitrogen correspond to experiments that compared the effect of defoliation with low and high nitrogen availability. Rest of data set column represents the RCT average value of comparisons between defoliated and undefoliated plants growing at non-manipulated nitrogen levels. Bars with different letters show significant differences ($P < 0.05$). N provides the number of cases.
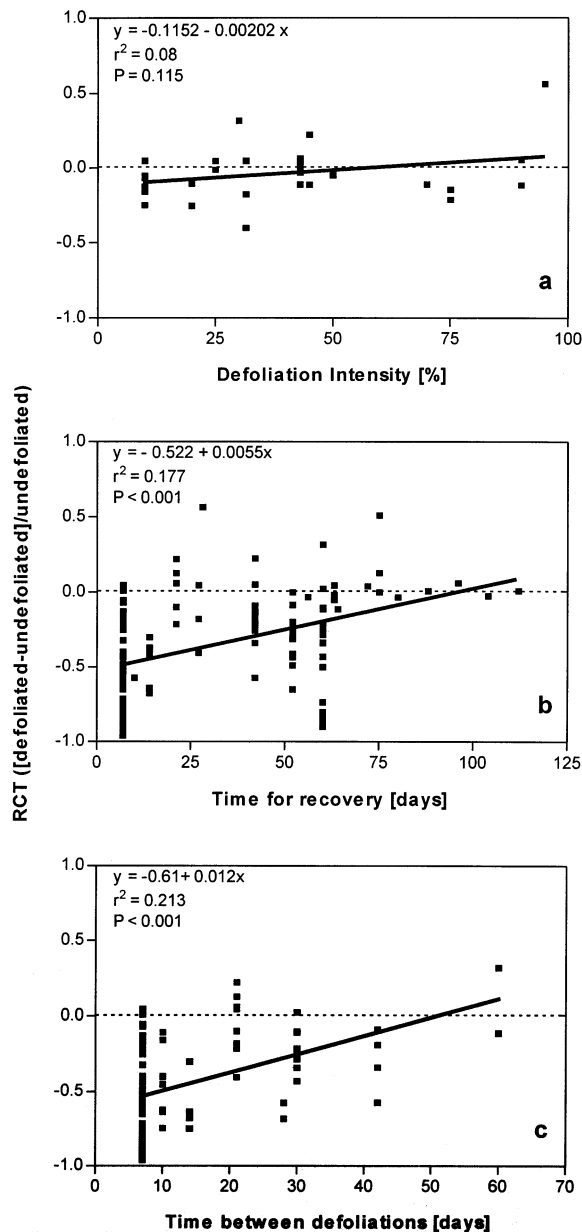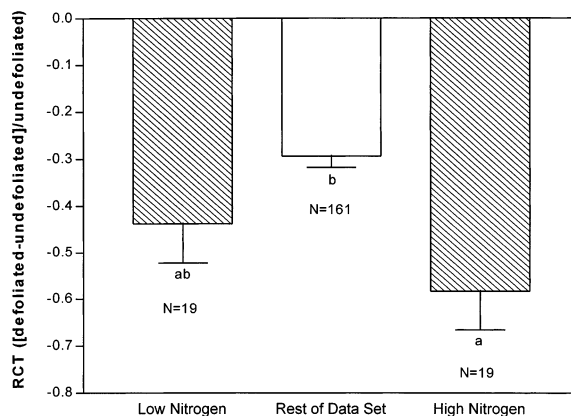

Fig. 5. Relationships between the relative changes in total production (RCT) in defoliated plants respect to undefoliated controls, and three variables that describe the defoliation regimes. The solid line is the least-square best fit. The dashed line represents RCT = 0 (no defoliation effect).

defoliation on growth tended to be, on average, proportional to the performance of undefoliated plants across a wide range of plant biomass (10-fold or wider). Underlying this average trend, there was a strong variability of response within each response variable (shown by the wide dispersion of points in the regression analyses and the confidence intervals of the meta-analyses).

Our results showed that defoliation frequency and time for recovery explained part of that variability: experiments with high frequency of defoliation or short time for recovery showed more negative effects. In contrast, the proportion of tissue removed by defoliation had little impact on the response to defoliation. High soil-N fertility also accounted for the more negative effects.

The patterns of individual plant growth responses to defoliation revealed here show both similarities and differences with the patterns of ecosystem production responses to grazing (reviewed by Oesterheld et al. 1999). Among the similarities, both individual and ecosystem effects are more frequently negative. In our study, 85% of the data points of total production corresponded to negative effects of defoliation, and in a comparison of 105 grazed and ungrazed grasslands and savannas, 72% of the sites had their aboveground net primary production (ANPP) reduced by grazing. Also, both individual plants and entire ecosystems showed an overall constant, proportional effect of both defoliation and grazing across steep gradients of plant biomass or productivity. However, the magnitude of these proportional effects differed between the two data sets: at the individual plant level, defoliation reduced production

by 52%, whereas at the ecosystem level grazing reduced ANPP by 10–20% (Oesterheld et al. 1999). Defoliation experiments on individual plants tend to mimic only one of the manifold influences of grazing: the removal of leaf biomass. Other concomitant, more positive effects, such as nutrient returns or competition release, are usually absent from these controlled experiments. The synergetic effects of the components of grazing may be important in the field. For example, a defoliation experiment in the Flooding Pampa grasslands showed a negative effect at any level of urea addition, but patches that were both defoliated and fertilized with urea, which would resemble a grazed condition, produced the same amount of biomass as undefoliated, unfertilized patches, which would resemble an ungrazed condition (Semmartin and Oesterheld 2001). Some of the variability between defoliation studies and grazing in the field may also be explained by artificial defoliation frequencies in pot experiments that may exceed what any plant really experiences in grazing systems. Defoliation experiments usually also fail to reproduce the often limiting growth conditions of ungrazed plants (McNaughton 1992). When the conditions of canopy closure common to ungrazed situations in humid or subhumid grasslands are recreated experimentally, neutral or positive effects of defoliation are commonly observed (Oesterheld and McNaughton 1991a, McNaughton 1992).

Our results show that compensatory responses to defoliation are the norm. Virtually all data points with simultaneous measurement of RGR of clipped and unclipped plants showed a positive effect. The "damage" response, a negative effect of defoliation on RGR (Belsky 1986, Oesterheld and McNaughton 1991a) was hardly observed. A number of mechanisms for these frequent compensatory responses have been identified. The photosynthesis rate increase (Senock et al. 1991), the decreasing of self-shading (Oesterheld and McNaughton 1991a, McNaughton 1992), the reallocation of growth from elsewhere in the plant (Briske et al. 1996, Holland et al. 1996), the activation and proliferation of meristems (Wandera et al. 1992, Hay and Newton 1996), reduction of the rate of leaf senescence, and greater rain-use efficiency (Varnamkhasti et al. 1995) are among them.

Although compensatory responses were common, they encompassed a continuous range of values, which could be partially explained by experimental conditions directly related with the defoliation regime. By means of simple calculations, Hilbert et al. (1981) showed that high intensity of defoliation (the percentage of biomass removal) and short time for recovery require higher increases of RGR in defoliated plants for a given result in terms of biomass production. Our results showed that the relative effect of defoliation on biomass production was not related to the intensity of defoliation, which, according to Hilbert et al. (1981), indicates that compensation increases exponentially with defoliation intensity. In contrast, time for recovery was significantly and positively related with the relative effect of defoliation on biomass production.

Nutritional growing conditions also accounted for some of the patterns. Plants growing under high levels of nitrogen availability were more negatively affected by defoliation than plants growing under standard conditions. Based on the similar, but marginal ($P < 0.13$) difference observed in plants growing under poor nitrogen availability, we speculate that there seems to be an optimal response, with a trend to more severe reductions in growth by defoliation at high and low nutrient availability. At high levels of nitrogen, plants are growing at their highest growth rate and defoliation would not promote any compensatory growth (Georgiadis et al. 1989). Oppositely, at low level of nitrogen, the ability of plants to tolerate defoliation would be affected by the removal of stored nutrients and the reduction of the capacity to take up nutrients when they are in low supply (McNaughton and Chapin 1985).

Summarizing, our study indicated that the magnitude of defoliation response by an individual plant is different for the various plant components. The magnitude of defoliation impact is modulated by a number of factors. Longer time for recuperation after defoliation favors the occurrence of compensatory responses. Nutrient availability also showed an influence on defoliation responses.

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