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DEFOLIATION SYNCHRONIZES ABOVEGROUND GROWTH OF CO-OCCURRING C_4 GRASS SPECIES

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Abstract. The aboveground net primary productivity (ANPP) of grass communities in grasslands and savannas is primarily determined by precipitation quantity. Recent research, motivated by predictions of changes in the distribution of rainfall events by global climate change models, indicates that ANPP may be affected by rainfall distribution as much as by annual totals. Grazing and community composition are also known to affect grassland ANPP. The manner in which interactions between rainfall distribution, grazing, and community composition affect the relationship between precipitation and ANPP represents a critical knowledge gap. The effects of community composition and grazing on aboveground growth responses to intraseasonal variation in water availability were investigated at seven grassland sites with a nonselective clipping experiment. The aboveground growth of the dominant C_4 species at each site was measured at regular intervals for 2–3 growing seasons in the presence or absence of regular defoliation. In the absence of defoliation, there was a general lack of synchrony of intraseasonal growth among co-occurring species. Variation in growth rates was high and was only partially explained by variation in rainfall. Regular defoliation increased growth synchrony at all sites, but changes in growth responses to rainfall varied between sites. These results suggest that community composition will be important in determining ANPP–precipitation relationships under conditions of altered rainfall distribution. However this effect appears to be a result of species responding differently to soil water or other resources rather than to rainfall per se. Grazing may override the effects of community composition by reducing differences in growth patterns between species and has the potential to weaken precipitation controls on ANPP.

Key words: aboveground net primary productivity; community composition; grasslands; grazing; precipitation.

Introduction

Net primary productivity (NPP) is a fundamental process of ecosystems, providing the habitat structure and energy that sustains all other trophic levels and regulating the exchange of carbon dioxide and water with the atmosphere. With the advent of global climate change, the role of climate in determining NPP has become a topic of much interest. In grasslands and savannas, aboveground NPP (ANPP) is primarily determined by precipitation, and long-term data show a significant linear relationship between annual precipitation quantity and annual ANPP for sites around the world (Smoliak 1986, Lauenroth and Sala 1992, McNaughton et al. 1993, Briggs and Knapp 1995, Jobbagy and Sala 2000, O'Connor et al. 2001, Chidumayo 2003, Knapp et al. 2006, Nippert et al. 2006). Global climate change models predict not only changes in annual precipitation (Houghton et al. 2001) but also increases in "extreme events," with rainfall more likely to fall in larger but less frequent events (Gordon et al. 1992, Easterling et al. 2000, Meehl et al. 2005). Previous research on the effects of such changes in the distribution of rainfall events indicates that this effect can rival effects of changes in rainfall amount, even in mesic grasslands (Knapp et al. 2002, Swemmer and Knapp 2007).

In addition to precipitation, herbivory and plant community composition can affect ANPP substantially. While these determinants have received less attention than precipitation, both grazing by ungulates (often simulated by clipping and mowing) and community composition have been shown to alter productivity–precipitation relationships at an annual timescale (grazing, Coughenour 1991, Biondini et al. 1998, Heitschmidt et al. 1999, Frank et al. 2002, Chidumayo 2003; community composition, Kelly and Walker 1976, O'Connor et al. 2001). Grazing and community composition are also likely to affect ANPP responses to rainfall distribution, as the ability of individuals to exploit (or endure) intraseasonal variation in the availability of water may depend on whether they have recently been defoliated and on genotype. For example, co-occurring grass species often reach peak biomass at different times of the season (Grunow et al. 1980, Sala et

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al. 1981, Dye and Walker 1987), which may be a result of species-specific differences in responses to intraseasonal variation in rainfall.

Interactions between these determinants of ANPP are made more complex by the potential for feedbacks between them. Interannual variation in precipitation has been shown to alter community composition (Snyman and Opperman 1983, Gibson and Hulbert 1987, O'Connor 1991), particularly during drought (Weaver 1954, Herbel et al. 1972, Snyman and van Rensburg 1990, Fynn and O'Connor 2000), and these compositional changes may then alter the relationship between ANPP and annual precipitation. Likewise, substantial changes in community composition in response to grazing can occur (Snyman and Opperman 1983, O'Connor 1991, Collins and Steinauer 1998, Fynn and O'Connor 2000, Bullock et al. 2001). Predicting the response of ANPP to climate change, in grass-dominated ecosystems, therefore requires an understanding of not only the overall effect of annual precipitation, but also the various potential interactions between rainfall distribution, herbivory, and community composition.

To investigate the potential effects of grazing and community composition on the relationship between aboveground productivity and within-season rainfall distribution, we conducted a defoliation experiment at a number of grassland sites ranging from semiarid to mesic. The short-term, aboveground growth responses of co-occurring grass species was measured in both the presence and absence of defoliation, during intervals of high and low rainfall. In both the control and defoliation treatments, the synchrony of intraseasonal variation in growth provided a simple test of differences in species responses to intraseasonal variation in rainfall: if all species respond in a similar way (the null hypothesis) then they should all grow at the same time (i.e., when water availability is low all species should show low growth rates and when water availability increases they should show high growth rates). In contrast, a lack of synchrony could indicate that responses are species-specific. Regular defoliation was expected to disrupt any synchrony, as co-occurring graminoid species are known to vary in terms of defoliation tolerance (McNaughton and Chapin 1985, Wallace et al. 1985, Klink 1994, Banyikwa 1998), and those less tolerant were expected to become less responsive to intraseasonal variation in water availability.

METHODS

Sites

Data were collected from seven sites located in pristine, unplowed perennial grasslands or savannas dominated by C_4 perennial grasses. Two of the sites were located in the United States: one in a mesic grassland in eastern Kansas and one in a semiarid grassland in central Colorado. The remaining sites were located in South Africa: three in savannas within the Kruger National Park and two in grasslands within the Suikerbosrand Nature Reserve. Appendix A summarizes the main environmental conditions at the sites. All of the sites were fenced and ungrazed and, with the exception of Konza, had a long history of grazing prior to the start of the experiment.

Experimental design

At each site, the four most common C_4 grass species were selected for sampling (see Appendix B for species names). All except one were perennial. Six of the 28 species selected occurred at more than one of the sites. Two pairs of sites had two of these species, while a different two pairs of sites each shared one species. For all analyses, these overlapping species were treated independently at each site.

Sampling was conducted for three growing seasons (between September 2003 and July 2006). Due to logistical constraints, the following periods could not be sampled: the second half of the first growing season at the Basalts and Sands sites, the control plots at Satara, and for three species in the control treatment at Shabeni. Similarly, for the second half of the third growing season, sampling was not possible at Konza and Boulder. These represented no more than 15% of the possible measurements that could have been made over the three-year study period.

A defoliation treatment and control treatment were established at each site with two plots per treatment. Each defoliation plot was located adjacent to a control plot. The proximity of each pair of defoliation and control plots varied from adjacent (Basalts and Sands) to ~100 m (Konza). Defoliation treatment plot sizes varied from 3 × 3 m (Basalts and Sands) to 5 × 5 m (Konza). Control plots were larger, extending away from the adjacent clip plots as far as was required to locate sufficient numbers of individuals to sample. None of the plots contained large trees or were shaded by canopies of nearby trees.

Individual tufts within each plot were clipped at regular intervals (18–50 d) during the growing season. Most of the species were caespitose "bunchgrasses" or weakly rhizomatous with clearly defined tufts. For four strongly rhizomatous species, an individual was defined as a cluster of tillers that appeared to originate from the same rhizome. For two stoloniferous species, any growth produced by rooted nodes of stolons was included, provided there was still a live connection between the node and the parent plant. Sampling intervals were deliberately shortened during wet periods when growth was more rapid in an attempt to measure a similar amount of growth in each interval. The aim of this variable clipping frequency was to produce regrowth patterns similar to those observed in heavily grazed patches that were maintained in a short state by cattle or natural grazers in areas adjacent to each site.

In the control treatment, a new pair of control plots was established for each growing season and, in most cases, these were either burnt or clipped down to crown height prior to the start of the season. After a few weeks of growth, individual tufts were randomly selected, clipped down to the crown, and marked with a flag. For each subsequent sample, only individuals that were not marked with a flag (i.e., had not been clipped during that season) were selected. Thus all clipped material in the control treatment consisted of the current season's growth, up to the date of sampling. For one season at the Sands and Basalts sites and for all three seasons at Nkuhlu, control plots were neither burnt nor clipped prior to the start of the growing season. Material harvested in these seasons was separated into senesced material from the previous season and material from the current season (on the basis on the color of senesced leaves), and the former were discarded.

In the defoliation treatment, plots were clipped to a height of 2–3 cm prior to the start of the first growing season. Randomly selected tufts were then marked and clipped to a height of 2–3 cm at the end of each sampling interval. Clipped biomass therefore consisted of the regrowth of the marked individuals since the previous harvest. The clipping height used represents the typical grazing height for nonselective grazers in these systems. Individuals were marked and labeled using a plastic-coated loop of wire placed around the base of the tuft. After the marked tufts were clipped at the end of an interval, all other grass tufts and forbs in the plots were clipped down to the same height and this biomass removed from the plot. If a marked individual died, a replacement was selected from the same plot and marked, thus maintaining a constant number of replicates per plot. For some of the less common species, a shortage of additional individuals resulted in a reduction in replicates by the end of the experiment. Appendix B provides the number of individuals marked and the percentage of these that died.

In both treatments, seven or eight individuals per species were typically clipped per plot, at each sampling interval. Clipped material was dried to a constant mass (at 60°–80°C) and weighed.

Precipitation measurement

Precipitation data were obtained from automatic rain gauges. At the five South African sites these were located on site. For Boulder, data were obtained from a weather station of the National Wind Technology Center, ~3.5 km from the site and at approximately the same elevation (data *available online*).[4] For Konza, data were obtained from an automatic rain gauge located ~800 m from the site. For some intervals at some of the South Africa sites, data from the nearby weather station was used to substitute for missing data (three intervals at Basalts, five at Nkuhlu, and one at Shabeni).

Statistical analysis

In the control treatment, growth was calculated as the increment in average biomass (live + senesced) for each species, from one interval to the next. For each species in each interval, *t* tests of ln-transformed data revealed no significant difference (alpha = 0.05) between the mean biomass of individuals in each control plot for the majority (>90%) of intervals. Data from each control plot were therefore combined to achieve a more accurate species-specific estimate of average biomass for each interval. Average biomass was calculated as the geometric mean because distributions were generally skewed to the right (using median biomass produced similar results). For the defoliation treatment, the average growth for each species was calculated simply as the geometric mean biomass of all individuals at each sampling interval. Again replicates from both plots were combined. For the first interval (in the first growing season), data for the defoliation plots was treated as control data, as individuals in these plots had not been clipped previously. As the sample size for the first interval was only three individuals per plot (for each treatment), the total number of replicates for the control treatment for this interval was approximately the same as for subsequent intervals.

To assess the synchrony of growth, pairwise correlations of the average growth for each species were calculated for each pair of species, in each treatment at each site, using Pearson's product-moment *r*. Sample sizes (i.e., the number of sampling intervals for each species) ranged from nine to 18 in the control treatment and nine to 17 in the defoliation treatment (refer to Appendix B for sample sizes for each species). The pairwise correlation coefficients from both treatments were then entered into a factorial ANOVA to test the effects of defoliation and site. To account for differences in sample sizes used to calculate the coefficients, each was weighted by its respective sample size.

To analyze species' growth responses to rainfall, growth rates were calculated as growth per interval length (in days) to account for differences in interval lengths. Interval rainfall was calculated as the total rainfall for an interval (any rain that fell in the last three days of an interval was excluded and included in the following interval's total). Pearson's product-moment correlations of growth rate vs. rainfall were calculated for each species in each treatment. For the control treatment this was simply done with a single correlation for each species. For the defoliation treatment, the effect of repeated measurements was accounted for with separate correlations for each marked individual. The biomass of each individual was first divided by interval length, to obtain individual growth rates for each interval, and individual growth rates were then correlated with interval rainfall to obtain an *r* value for each individual of each species. The least squares mean of the individual *r* values was then calculated for each species, using a factorial ANOVA with species and plot as the

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[4] ⟨www.nrel.gov/midc/nwtc_m2⟩

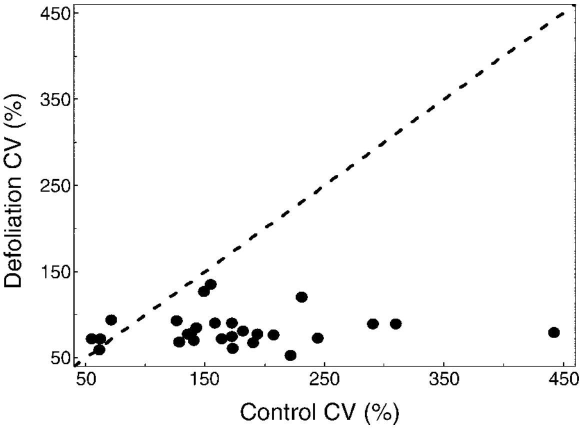

FIG. 1. The coefficient of variation (CV) of growth rates in the control and defoliation treatments calculated from the 9–18 intervals sampled across the seven sites. Each point represents the CV for one of the 28 species in each treatment. The dashed line shows unity. Defoliation thus decreased the CV for almost all species. One site was located in a mesic grassland in eastern Kansas and one in a semiarid grassland in central Colorado, USA. Three sites were located in savannas within the Kruger National Park and two in grasslands within the Suikerbosrand Nature Reserve, South Africa.

independent variables (refer to Appendix B for the number of individuals used per species). As a result of individuals dying and being replaced during the course of the experiment, some individuals were not measured for the entire experimental period and therefore did not experience the full range of water availability encountered. To account for this in the ANOVA, each r value was weighted by the range of interval rainfall that the individual experienced. Individuals with less than three measurements were excluded, and the maximum number of measurements was 18. A factorial ANOVA was used to test for the effects of defoliation and site on the growth–rainfall correlation coefficients.

All analyses were conducted using Statistica version 7.0 (Statsoft, Tulsa, Oklahoma, USA). For the ANOVA, homogeneity of variance was checked using Cochran's C test, and the distribution of residuals was determined with half-normal probability plots.

RESULTS

Synchrony

Variation in aboveground growth rates, calculated as the coefficient of variation from one interval to the next, was large for most species in the control treatment (Fig. 1). Many species in this treatment produced >50% of total seasonal production in a single sampling interval, with low or zero growth thereafter. Regular defoliation resulted in more uniform growth and greatly reduced the intraseasonal variation in growth rates for almost all 28 species. (Appendix C provides plots of average biomass per interval for each treatment, for selected species.) Total biomass produced over the experimental period was greater in the defoliation treatment for seven of the 28 species. Expressed as a percentage of total biomass in the control treatment, production in the defoliation treatment was greater for species with larger intraseasonal variation in the control treatment (Fig. 2). Species with highly variable short-term growth rates were therefore little affected by, or even benefited from, regular defoliation over multiple-season timescales.

Synchrony of growth, measured as the strength of the correlation of interval growth between pairs of species, was generally weak in the control treatment (0.25 ± 0.24 [overall mean ± SD]; Fig. 3), but increased with regular defoliation at all seven sites (0.70 ± 0.18). A weak interaction effect of defoliation and site on the synchrony coefficients (Table 1) was the result of smaller increases in synchrony at the two U.S. sites (Boulder and Konza) and one of the South African sites (Satara).

Rainfall correlations

Correlation coefficients of interval growth rate with rainfall during that interval varied greatly among species, as did the effect of regular defoliation on these correlations (Fig. 4, Appendix B). Synchrony of growth was lower for pairs of species that had a larger difference between the growth–rainfall coefficient of each species. Thus the greater the difference in growth responses to rainfall between a pair of co-occurring species, the weaker the correlation of their growth rates. This relationship was evident in the control treatment ($r = -0.40$, $P < 0.01$) but not the defoliation treatment ($r = -0.11$, $P = 0.50$), indicating that the greater synchrony in the defoliation treatment was not a result of uniformly stronger growth responses to rainfall among co-occurring species.

The strength of the correlations between growth rate and rainfall were dependent on both site and treatment (Table 2), with correlations being consistently stronger

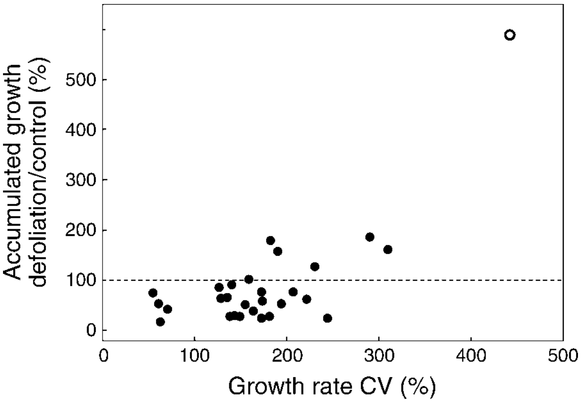

FIG. 2. Biomass accumulation over the entire experimental period for the defoliation treatment, expressed as a percentage of the control treatment production, plotted against the CV of growth rates in the control treatment ($r = 0.57$, $P < 0.01$). Values of biomass accumulation >100 indicate that more biomass was produced in the defoliation treatment. Removal of the potential outlier point (open circle) had little effect on the strength of the correlation ($r = 0.51$, $P < 0.01$).

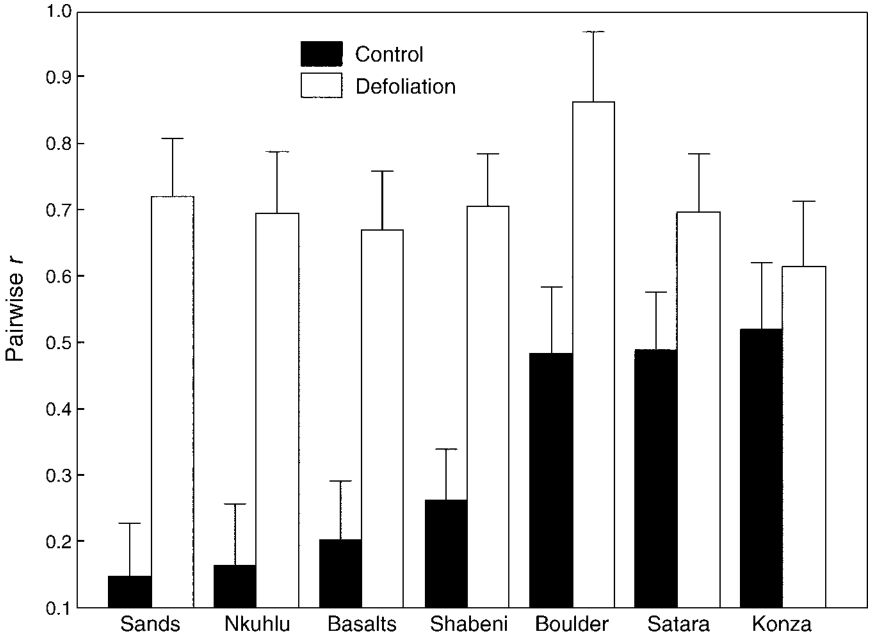

FIG. 3. Correlation coefficients for growth between the six pairwise comparisons of the four species at each site (mean + SE). Data are shown for both control and defoliation treatments. For the calculation of the mean coefficient for each treatment at each site, the pairwise coefficients were weighted by the number of intervals of measurement for each pair of species at the site. See Table 2 for ANOVA results.

in the defoliation treatment at two sites (Sands and Satara), but weaker at a third (Konza, the most mesic site; Fig. 4). Defoliation treatment differences at these sites were significant at the 5% level, according to a least significant difference (LSD) test.

DISCUSSION

In the absence of defoliation there was substantial variation in the aboveground growth dynamics of common, co-occurring C_4 grass species at a range of sites spanning two continents. This suggests that community composition is likely to be a key determinant of ANPP responses to changes in rainfall distribution, and rainfall distribution may in turn drive changes in community composition (feedback that could either enhance or mitigate responses to future changes in precipitation, depending on the species involved). These results also lend support to studies showing that greater diversity leads to greater productivity in grasslands (Tilman et al. 1996, Hector et al. 1999). More diverse communities are likely to be more productive over a range of rainfall distribution patterns, either because they are more likely to contain species that are productive for a given rainfall distribution (a selection effect sensu Drake [2003]) or because of niche complementarity (Tilman et al. 2001). While evidence of niche complementarity for nitrogen use has been found at one grassland site (Tilman et al. 1996), our results suggests that it may also result from differentiation of water use, i.e., co-occurring species utilize water at different times of the growing season, resulting in greater community-level efficiency of water use.

The general lack of aboveground synchrony in the control treatment could only be partly attributed to differences in rainfall responses between co-occurring species. Many co-occurring species differed in the time at which peak biomass was reached, thus weakening synchrony regardless of rainfall. Certain species grew rapidly following adequate rainfall early in the growing season, but then ceased growth well before the end of the growing season, regardless of water availability, resulting in large intraseasonal variation in growth rates, poor correlation of growth with rainfall, and low synchrony with co-occurring species. Many factors may have constrained the growth of these species prior to the end of the growing season, e.g., self-shading (Knapp and

TABLE 1. The effect of site and defoliation treatment on aboveground growth synchrony.

Effect	SS	df	*F*	*P*
Defoliation	37.9	1	62.6	<0.01
Site	7.4	6	2.0	0.07
Defoliation × Site	6.4	6	1.8	0.12
Error	42.4	70		

Notes: A factorial ANOVA was conducted using pairwise growth correlation coefficients for the six pairs of species at each site ($F_{13,70} = 7.08$, $P < 0.01$). One site was located in a mesic grassland in eastern Kansas and one in a semiarid grassland in central Colorado, USA. Three sites were located in savannas within the Kruger National Park and two in grasslands within the Suikerbosrand Nature Reserve, South Africa.

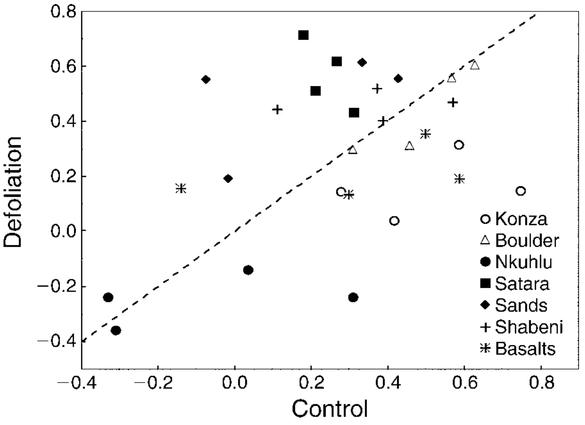

FIG. 4. Correlation coefficients for growth vs. rainfall plotted for the control and defoliation treatments for each species. Species are labeled according to site. The dashed line shows unity.

Seastedt 1986), phenology (some species appeared to stop growing once they had flowered), competition (greater shading by neighbors), and declining soil nutrient availability (Dodd et al. 2000).

Utilization of water from different soil depths (Holmes and Rice 1996) may have also been responsible for lack of synchrony and poor correlation with rainfall. Species that showed more consistent growth through the season and reached peak biomass towards the end of the season were often not responsive to rainfall early in the growing season (A. Swemmer, *personal observation*). This may have been the result of these species requiring deeper soil water to obtain high growth rates. At the South African sites, the warm, dry dormant season leads to deep soil layers being dry at the start of the growing season and thus, deep-rooted species would require sufficient rainfall for infiltration to occur to depth before significant growth can occur (Knapp et al. 2006). At the U.S. sites, where winter precipitation results in high water availability throughout the soil profile in the spring (Knapp et al. 1998), deep-rooted species could achieve rapid growth regardless of rainfall in the first part of the growing season. Uncoupling of aboveground production and growing-season rainfall, due to reliance on water stored in deeper layers, has previously been suggested for other grassland systems (Sala et al. 1992, Paruelo and Sala 1995). In systems in which different species utilize primarily either shallow or deep soil water, the role of community composition in determining ANPP responses to altered rainfall regimes may therefore depend on how intraseasonal variation in rainfall translates into both temporal and spatial (depth) variation in soil water availability.

Regular defoliation clearly reduced intraseasonal variation in aboveground growth, both within and between species, and increased synchrony among co-occurring species. This treatment effect occurred despite many control plots being defoliated (by fire or clipping) in the dormant season. This suggests that ANPP responses to altered rainfall distributions will be less complex for sites where regular grazing occurs during the growing season. A similar effect of grazing on spatial variation in intraseasonal growth has been found for semiarid grasslands, where grazing reduced horizontal variation in aboveground production created by soil heterogeneity (Milchunas and Lauenroth 1989, Coffin and Lauenroth 1992). Grazing may therefore reduce both the spatial and temporal variation of production in grasslands, making predictions of ANPP less complex at larger spatial scales as well.

Regular clipping homogenized growth patterns among species, and changes in community composition in heavily grazed environments (resulting from the defoliation or other factors) are therefore predicted to be less important for determining ANPP–precipitation relationships. The greater synchrony created by regular defoliation was not necessarily a result of stronger growth responses to rainfall among co-occurring species. While growth responses to rainfall were stronger for some species, they were weaker for others, with site-specific factors having an overriding effect. This indicates that defoliation does not lead to stronger growth responses to large rainfall events for grass species in general, nor creates a common shift towards utilization of shallow soil water (as might be expected from reductions in root growth). Rather than creating uniform responses to rainfall, the strongest effect of regular clipping appeared to be to constrain the growth patterns of the fast-growing, high-variance species to those of the more consistent, slower-growing species, whose short-term growth was little affected by large rainfall events. This suggests that, for certain systems, the major effect of regular, non-selective grazing may simply be to uncouple ANPP from precipitation quantity, with the rapid growth responses to rainfall precluded for all species and ANPP constrained to low levels even in wet years.

Regular defoliation also lengthened the duration of growth for many species (Appendix C). While many individuals stopped growing before the end of the growing season in the control treatment, the majority in the defoliation treatment produced at least some regrowth following clipping, even at the end of the growing season. Similar results have been found for tillering (Butler and Briske 1988) and green-leaf

TABLE 2. The effects of site and defoliation treatment on species' growth responses to rainfall.

Effect	SS	df	*F*	*P*
Defoliation	0.0009	1	0.03	0.87
Site	2.12	6	10.5	<0.01
Defoliation × Site	0.75	6	3.67	<0.01
Error	1.42	42		

Note: A factorial ANOVA was conducted using the "interval growth vs. rainfall" correlation coefficients for all 28 species ($F_{13,42} = 6.52$, $P < 0.01$).

duration (Baruch and Bilbao 1999). For some species with highly variable growth rates in the absence of defoliation, this extension actually resulted in a greater total production over the course of a number of growing seasons, despite lower short-term growth rates. These results have important implications for the coevolution of grasses and grazers and provide an additional mechanism for intensive grazing resulting in greater ANPP in certain systems (McNaughton 1985). By returning to the same patch to feed, grazers may incur a cost of a lower quantity of forage earlier in the growing season but benefit from a more consistent supply, with at least some regrowth available for consumption for the entire duration of the growing season. Repeated grazing of the same patch could even lead to a greater quantity of forage over the entire season (Fig. 2), as has been documented in the Serengeti ecosystem (McNaughton 1985).

Finally, while the clipping treatment in this experiment simulated nonselective grazing, the effects of selective grazing are likely to add complexity to ecosystem responses to climate change. Selective grazing can lead to a rapid decline of palatable species (Anderson and Briske 1995), which could strengthen or weaken ANPP–precipitation relationships, depending upon the rainfall responses of the unpalatable species that become dominant.

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APPENDIX A

Locations and environmental variables for the seven sites where the experiment was conducted (*Ecological Archives* E089-163-A1).

APPENDIX B

Species and intervals sampled at the seven sites (*Ecological Archives* E089-163-A2).

APPENDIX C

Mean aboveground biomass of individual tufts clipped each interval for three consecutive growing seasons (*Ecological Archives* E089-163-A3).