Long-term oscillations in grassland productivity induced by drought

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Abstract
Disturbances such as drought have immediate impacts on ecosystem functioning, but little is known about long-term dynamic consequences of disturbance. Here, we show that a major drought perturbed prairie grassland from nearly constant average annual production, and induced 9 years of oscillations with a 2-year period. This pattern occurred in unmanipulated plots in many widely separated fields that were part of two different long-term studies. Using direct and indirect tests, we could reject the hypothesis that the oscillations were externally imposed by climate or herbivores. Weak evidence supported the hypothesis that oscillations were internally generated, caused by a litter and nitrogen dependent feedback on productivity. This hypothesis was supported by the results of two other long-term studies, in which burning and, separately, nitrogen addition eliminated the 2-year oscillations in plant production. However, more direct evidence failed to support the litter hypothesis. A final, but untested hypothesis was suggested by the observation that production tended to be synchronized amongst dominant plants. Drought may have synchronized production dynamics amongst plants with biennially greater allocation to above-ground growth. Regardless of the specific mechanism, our results show that a single disturbance may have long-lasting effects on the dynamics of plant production.

Keywords
ANPP, community dynamics, disturbance, drought, litter, long-term research, nitrogen, oscillations, primary production, synchronous production.

INTRODUCTION
Primary production is regulated by many factors, among them temperature (Raich et al. 1997), precipitation (Rosenzweig 1968; Sims & Singh 1978; Deshmukh 1986; Sala et al. 1988; Pandey & Singh 1992; Knapp & Smith 2001), light (Knapp & Seastedt 1986; Seastedt et al. 1991), length of growing season (Leith 1975), nutrient availability (Chapin et al. 1986; Tilman 1988), plant diversity (Tilman et al. 1996; Hector et al. 1999), and herbivory (McNaughton 1983, 1985; Williamson et al. 1989; Holland et al. 1992; Pandey & Singh 1992; Frank & McNaughton 1993; Turner et al. 1993; Ritchie et al. 1998; Belovsky & Slade 2000). These factors and their interactions are likely to determine the level of primary production in any ecosystem (Lauenroth & Whitman 1977; Breman & deWit 1983; Hurlbert 1988; Briggs & Knapp 1995; Blair 1997; Epstein et al. 1997). Much research has focused on how the levels of these various factors combine to influence plant production, usually over short time periods. In this paper, we ask how these factors may regulate long-term dynamics of plant production after disturbance caused by drought.

Drought, heavy rainfall, and fire may all have large immediate effects on ecosystem dynamics, and may cause pulses of high primary production during or just after disturbance (Noy-Meir 1973; Reiners 1983; Seastedt & Knapp 1993; Blair 1997; Knapp & Smith 2001). These disturbances may also lead to longer-lasting impacts. Multi-year studies have demonstrated that it may be two or more years before productivity returns to predisturbance levels (Polis et al. 1997; Herbert et al. 1999). Drought in particular often has severe, negative effects on short-term plant production (e.g. Albertson & Weaver 1942; Herbel et al. 1972; Tilman & Downing 1994; Briggs & Knapp 1995), and on longer-term plant production (Lauenroth & Sala 1992) and plant diversity (Tilman & El Haddi 1992).
Few studies have investigated longer-term transient dynamics of plant community production after disturbance. Milchunas & Lauenroth (1995) provide one example of how a short period of disturbance can have a long-term influence on community dynamics. In a grassland experiment, they found that the abundance of the dominant grass and the plant community composition recovered rapidly after treatments of water and nitrogen had been applied for 5 years. However, in 16 years of monitoring their plots after cessation of treatments, they found periods of convergence and divergence amongst treated and untreated plots in the abundance of the dominant grass and in plant community composition.

We studied the transient dynamics of prairie plant communities for 19 years—6 years before and 12 years following a 50-year drought. Grasslands have the greatest potential for large variation in above-ground net primary productivity (ANPP) in response to precipitation, because of high production potential and high rainfall variability (Knapp & Smith 2001). Using direct and indirect evidence collected in concurrent studies, we tested hypotheses that the dynamics of plant production following drought were regulated by two groups of factors. First, the dynamics could be regulated by externally imposed factors, such as climate or herbivores. Second, the dynamics could be internally regulated, caused by litter or nutrient dependent feedbacks, or by the population dynamics of individual plant species. With regard to plant population dynamics, the drought could act to either synchronize production (especially if grassland plants are prone to irregular intervals of seed crop production, such as in ‘masting’), or could cause asynchronous dynamics amongst competitors. To test our hypotheses, we used data gathered within many unmanipulated grassland plots, as well as in grassland experiments that are part of the Cedar Creek Long-Term Ecological Research site.

**METHODS**

We studied the dynamics of ANPP in two separate long-term studies at Cedar Creek Natural History Area, Minnesota, USA. First, we studied control plots from a nitrogen addition experiment in three successional grassland fields (Fields A, B, and C, which had been abandoned from agriculture in 1968, 1957 and 1934, respectively; Tilman 1987). The experiment was established in 1968 to examine the long-term effects of nutrient addition on prairie plant communities. The site was moved each year so that no area was clipped twice in the same year. We obtained data from the Cedar Creek weather station, approximately 8 km from Cedar Creek. A small number of gaps in the data were supplemented with observations from the Cambridge weather station, approximately 15 km from Cedar Creek. These data can be obtained on the internet at: http://www.ncdc.noaa.gov/

Where possible, we used direct evidence from the grassland control plots and the successional plots to test hypotheses about the effects of internally generated and externally imposed factors on the dynamics of ANPP at Cedar Creek. When such direct data were not available, we used indirect evidence that was gathered in three other long-term studies. First, to determine the effects of litter accumulation on ANPP dynamics, we analyzed ‘burned grassland plots’ (field D in Tilman (1987)) that were burned two out of every three years. These ten 1.5 × 4.0 m plots were the controls of a nitrogen addition experiment and were established simultaneously with the grassland control plots (again, five plots were true controls, and five received a mixture of P, K, Ca, Mg, S and trace metals, but no nitrogen). Above-ground, living plant biomass was collected as in the other grassland control plots. Second, to determine the effects of nutrient availability on ANPP dynamics, we analyzed data from a nitrogen addition study in Fields A, B, and C, which included 162 plots from three successional fields that were fertilized annually with eight different levels of nitrogen: 0.0, 1.0, 2.0, 3.4, 5.4, 9.5, 17.0, or 27.2 g m⁻² year⁻¹. (Note that plots that received no nitrogen are the grassland control plots.) At Cedar Creek, nitrogen is the...
primary limiting resource in plant communities (Tilman 1988). Above-ground, living plant biomass was collected as in the grassland control plots. For analysis, we divided plots into those that received low (< 6 g m$^{-2}$ year$^{-1}$) and high (> 9 g m$^{-2}$ year$^{-1}$) levels of nitrogen addition.

Third, to determine the influence of herbivores on the dynamics of plant biomass, we analysed abundances of two of the most important herbivore groups at Cedar Creek, small mammals and grasshoppers. Data on both groups were collected in 19 fields, including each of the fields that contained the successional plots. Herbivore data were collected along four permanent transects that were 40 m long, were separated from each other by 25 m, and were adjacent to the permanent plots where plant biomass was measured. Small mammal data were collected every August from 1984 to 2000. In each field, five traps were spaced 10 m apart along each transect (20 traps per field). Traps were set for three consecutive nights, followed by three days of rest, followed by three consecutive nights of trapping. On each morning following trapping, small mammals were identified to species and counted. Grasshopper data were collected monthly from June to September from 1987 to 2000. Each transect was swept 50 times with a standard 15 inch diameter light muslin net (200 sweeps per field). All grasshoppers were identified to species and counted.

**Analysis**

Our inferences are drawn mainly from patterns of plant biomass over time. First, we examined patterns of autocorrelation in biomass with a time lag of 1–5 years (Royama 1992). Next, we analysed the effects of growing season precipitation (calculated as the total precipitation summed from May to July) and growing degree days, calculated as the sum of the difference between the mean temperature and 15 °C (Thorntwaite & Mather 1955), on plant biomass in simple regressions and in multiple regressions using both variables. We determined the effects of litter and herbivores on plant biomass in simple regressions. We examined autocorrelation in plant biomass after the effects of precipitation and herbivore numbers had been controlled. Finally, we analysed correlations in plant biomass amongst dominant plant species.

**RESULTS**

For the first 5 years in the grassland control plots (1982–86), mean plant biomass was remarkably constant (Fig. 1A). However, the third worst drought of the past 150 years occurred at Cedar Creek in 1987–88 (Fig. 2; see also fig. 2 in Tilman & El Haddi, 1992). In the grassland control plots and the successional plots, we observed strong and regular oscillations in plant biomass after the drought with a 2 year period (Fig. 1). We detrended the data and determined the autocorrelation of biomass with a time lag of 1–5 years. In the grassland control plots, we found significant, negative autocorrelation in biomass with a 1 year time lag ($N=17$, $r=-0.50$; $P=0.05$), but not with longer time lags (lag 2, $r=0.45$; lag 3, $r=-0.27$; lag 4, $r=0.21$; lag 5, $r=-0.43$). However, autocorrelations did reverse sign in successive lags as is characteristic of oscillatory dynamics. When only data from the years of oscillations during and after the drought were considered, autocorrelations were stronger and all were significant ($P<0.05$; lag 1, $r=-0.91$; lag 2, $r=0.82$; lag 3, $r=-0.73$; lag 4, $r=0.82$; lag 5, $r=-0.90$). In the successional plots, which had fewer data points, autocorrelations were not significant at any time lag (lag 1, $r=-0.16$; lag 2, $r=0.0$; lag 3, $r=-0.18$; lag 4, $r=0.62$; lag 5, $r=0.56$). Again, when only data from years of oscillations were considered, autocorrelations were stronger (lag 1,
In the grassland control plots, oscillations in plant biomass began in the two drought years. The increase in biomass in 1987 may have been caused by higher sunlight or temperature during the first year of the drought, when there was still surplus ground water that could be exploited by the plant community (a similar result was found by Briggs & Knapp 1995). In the grassland control plots and the successional plots, the 2-year period oscillations in plant biomass lasted for 8 years following the drought. Even after the drought, oscillations in plant biomass were large, as much as 64% of total biomass. In the successional plots, the oscillations were evident for 8 post-drought years in 6 of 12 fields, and for 7 post-drought years in the other 6 fields. The probability of such regular oscillations occurring in one field for 8 years would be equal to $0.57 \times 0.008$. That the same pattern occurred in many fields suggests that the pattern was not random.

**Tests of hypotheses predicting externally imposed oscillations**

**Hypothesis 1: Oscillations were caused solely by weather fluctuations**

Using local data on precipitation and growing degree days (Fig. 2), we found that plant biomass was significantly related to precipitation in the grassland control plots ($N = 19$, $F = 5.53$, $R^2 = 0.41$, $P = 0.01$; $y = 168.25 + 9173.36/x - 3201825.3/x^2$) and the successional plots ($N = 13$, $F = 5.33$, $R^2 = 0.33$, $P = 0.04$; $y = 154.30 - 11059.05/x$). In both studies, we assumed an asymptotic relationship between precipitation and plant biomass because of the large negative effect of drought on plant biomass, and because plant biomass can not rise without limit as precipitation increases to high levels. After controlling for precipitation in a multiple regression analysis, growing degree days was not significantly related to plant biomass. After controlling for the effects of precipitation, the 2-year oscillations in plant biomass were still evident for 8 years in the grassland control plots, and for 7 of 8 years in the successional plots (Fig. 3). Autocorrelations were not significant for either the grassland control plots, perhaps because of the apparent rise in biomass during years of oscillations, or successional plots, which had fewer data points. Precipitation did not eliminate the pattern, however, and we rejected the hypothesis that the oscillations were caused by weather.

**Hypothesis 2: Oscillations were caused by top-down effects of dominant herbivores on the plant community**

Small mammal numbers and biomass peaked in 1986, 1990, 1995 and 1999, and grasshopper numbers peaked in 1990 and 1996 (Fig. 4). Abundances of neither were significantly correlated with plant production in simple regressions. However, after controlling for precipitation in the grassland control plots, grasshopper abundances were significantly, negatively related to plant biomass ($N = 14$, $F = 6.84$, $R^2 = 0.36$, $P = 0.02$; $y = 28.35 - 0.0098x$). After controlling for precipitation and grasshopper numbers, residual biomass still showed 8 years of oscillations (Fig. 3A; autocorrelations were not significant in the smaller data set with grasshoppers; $r_1, r = -0.41$; $r_2, r = 0.29$; $r_3, r = -0.31$; $r_4, r = 0.20$; $r_5, r = -0.24$). In the successional plots, there was no relationship between grasshopper numbers and plant biomass. Taking the two studies together, we concluded that there was no evidence to support the hypothesis that top-down effects of small mammals or grasshoppers, two major herbivore groups at Cedar Creek, caused oscillatory dynamics in biomass. Other large herbiv-
ores, such as deer, were excluded from the grassland control plots, but were not excluded from the successional plots, and the oscillations were present in both studies. We did not have data on plant pathogens, which may have regulated plant production.

**Tests of hypotheses predicting internally generated oscillations**

**Hypothesis 3: Oscillations were caused by litter and nutrient dynamics**

According to this hypothesis, the drought would initially lead to low ANPP and accumulation of soil nutrients. These nutrients would then lead to high ANPP in the year following the drought, which would lead to high litter production and heavy ground cover. Litter accumulation would limit light penetration and sequester nutrients, causing low production in the second year following the drought. Litter decomposition would then provide a source of nutrients to increase production in the third year following the drought, and so on. Tilman & Wedin (1991) found that litter caused seemingly chaotic oscillations in biomass of one species in heavily fertilized plots at Cedar Creek, due to litter effects on light limitation. Others have also found that litter accumulation can affect plant population dynamics (e.g. Bergelson 1990; Molofsky et al. 2000).

This hypothesis would be partially supported if, after the drought, litter production one year was negatively related to biomass the following year, and biomass was positively related to litter production in the same year. The dynamics of litter biomass only weakly supported the hypothesis that litter controlled oscillations in plant biomass. First, the dynamics of litter production did not show the same oscillating patterns as shown by the dynamics of plant biomass (data not shown). Second, in a plot-by-plot analysis, litter production was significantly, positively related to plant biomass in the same year ($N = 636; R^2 = 0.14, P = 0.001$). The relationship was even stronger when data were analysed by year, and current year plant production explained as

![Figure 3](image3.png)

**Figure 3** Residual plant biomass in (A) grassland control plots after controlling for effects of precipitation and grasshopper abundances, and (B) successional plots after controlling for effects of precipitation.

![Figure 4](image4.png)

**Figure 4** Community dynamics of dominant herbivores, including (A) small mammals and (B) grasshoppers. Data were collected in 19 fields, including all of the successional plots. Each point represents the summed number of individuals from all fields.
much as 50% of the variation in current year litter biomass. In a plot-by-plot analysis, there was a weaker, but unexpectedly positive relationship between litter biomass in one year and plant community biomass in the next year ($N = 600; R^2 = 0.06, P = 0.001$). This occurred because some plots were consistently more productive than others, both in their production of plant biomass and of litter. One reason that our data only weakly support the hypothesis that the 2-year oscillations were caused by dynamics of litter may have been that we measured litter biomass in summer, rather than at the beginning of the following growing season when its biomass should best predict its effects on plant production.

Additional evidence supporting the litter and nutrient dynamics hypothesis came from burned grassland plots (Fig. 5). Burning removes litter and releases nutrients to the soil (Kucera & Ehrenreich 1962), and lack of burning leads to accumulation of inorganic and mineralizable nitrogen (Blair 1997). As in the grassland control plots and the successional plots, the drought had a negative impact on plant production in the burned grassland plots (Fig. 5). However, the long-term dynamics of plant biomass in the burned grassland plots differed from the dynamics in unmanipulated plots. After an initial increase in plant biomass over the first 6 years of the study, plant biomass has since begun a 3 year pattern of oscillatory dynamics, peaking in years when plots are burned. This pattern of plant production suggests that litter may limit production, and provides further evidence to refute the hypothesis that the oscillations were controlled only by precipitation. This is because the peaks in biomass in the burned plots were asynchronous with rainfall. For example, biomass in the burned grassland plots was low only in one of two dry years (1992, but not 1994) when the plots were not burned.

We did not have nutrient data from the grassland control plots or the successional plots to examine their dynamics directly. However, we were able to examine the effects of nitrogen indirectly through analysis of a nitrogen addition experiment. We expected to find that if nitrogen availability was controlling oscillations in plant production, then plots with high levels of nitrogen addition would not show long-term, regular patterns of oscillations. We add the caveat that long-term nitrogen addition has also changed plant species composition (Tilman 1988), limiting inference that can be drawn from this analysis. Our results supported our expectations, in that low nitrogen plots showed regular oscillations that were sustained for 8 years following the drought (Fig. 6). The regular oscillations were not evident in heavily fertilized plots because (1) in 1992, productivity did
not decrease in high nitrogen plots, and (2) the oscillations were much more irregular in high nitrogen plots, with a sharper response to the drought, and a more erratic pattern of plant community production both before and after the drought (Fig. 6).

**Hypothesis 4: Oscillations were caused by plant composition, or by a single plant species or functional group**

Because of the wide fluctuations in biomass – even after the drought, by as much as 64% of total biomass – the fluctuations must have been caused by changes in biomass of dominant plant species. Epstein et al. (1996) found variation in responses of dominant grassland species to climatic gradients, and variable plant responses may have influenced the transient dynamics of the total plant community in this study. In the grassland control plots and the successional plots, as well as in other fields at Cedar Creek, dominant species included three grasses, *Poa pratensis*, *Schizachyrium scoparium*, and *Agropyron repens*. We examined patterns of plant production in each of these grasses, as well as in forbs, which were pooled as a group. These species made up 90–96% of total biomass in the grassland control plots and 71–83% of total biomass in the successional plots.

The 2-year periodic oscillations in biomass were most consistent in forbs (the patterns of oscillations held for 8 years following the drought in each study, Fig. 7G,H) and in *A. repens* (oscillations held for 7 of 8 years following the drought in each study, Fig. 7E,F). Oscillations by *P. pratensis* biomass followed the community-wide pattern for 3 (grassland control plots) and 8 (successional plots) years following the drought (Fig. 7C,D). Oscillations by *S. scoparium* biomass followed the community-wide pattern for 6 (grassland control plots) and 7 (successional plots) years following the drought (Fig. 7A,B). Interestingly, although not all plant species showed 8 full years of oscillations following the drought, their years of peak and trough production were synchronized. Although plant species’ biomasses were not typically correlated, signs of the correlation coefficient were always positive (Table 1). We did not observe asynchronous interspecific production that might be expected due to competitive effects on plant production. Thus, we rejected the hypothesis that oscillations were caused by the individualistic response of a single plant species, or to changes in species composition following the drought.

**DISCUSSION**

Our results show that severe perturbation caused by drought led to 9 years of oscillations in ANPP, and oscillations had a 2-year period. The regularity and amplitude of the oscillations – after very stable levels of production before the drought – would occur with very low probability in even one field. That the pattern was consistent across 15 fields in two different studies suggests that the drought caused long-term oscillations that appear to only recently have subsided.

The reason that oscillations ended is unclear, and is not obviously related to weather. The year the oscillations ended (1997), *P. pratensis* showed its largest drop in biomass after long-term trends in grassland control plots and successional plots had led to very high levels of production. Biomass of *A. repens*, another C3 grass, also dropped sharply in 1997. Perhaps the end of oscillations was caused by weather during spring or late summer, when C3 grasses are most productive, or due to density-dependent population regulation on the abundance of *P. pratensis* in particular.

In only one previous study by Milchunas & Lauenroth (1995) did we find evidence of sustained cycles in plant production that were not caused by recurrent disturbance (i.e., repeated fire). In other long-term studies of plant community production that have examined transient dynamics after disturbance, regular long-term oscillations have not been observed. In 52 years of data collected in shortgrass steppe in Colorado, Lauenroth & Sala (1992) found low primary production caused by drought. Their results showed a several-year time lag until plant production recovered to pre-drought levels. In 19 years of data collected at the Konza Prairie LTER, Briggs & Knapp (1995) found that two of the three most productive years across all fields followed two different droughts. This response to drought was similar to the initial response that we detected in our study; however, Briggs & Knapp (1995) did not find longer-term effects on production dynamics. In an analysis of 30 years of data from the Park Grass experiment, Silvertown (1980) found no evidence of regular cycles in plant biomass.

Oscillations have been reported in plant population dynamics, where density-dependent oscillations are caused by limitation on plant growth and seed set (Symonides et al. 1986; Thrall et al. 1989; Crone & Taylor 1996). However, there has been some debate about the likelihood of cyclic dynamics in plant populations (Rees & Crawley 1989, 1991; Silvertown 1991), and they are considered most likely in annuals grown in fertile soils, whose seeds are not dormant and have high survivorship. The dominant species in this study are perennials, and unmanipulated plots contained infertile soils.

Several previous papers have examined the response of the Cedar Creek grasslands to drought (Tilman & El Haddi 1992; Tilman & Downing 1994; Tilman 1996). Plant species richness declined in grassland control plots following the drought by about one-third (Tilman & El Haddi 1992), and was approaching pre-drought levels in 1993 (Tilman 1996). However, the transient dynamics of plant species richness was a steady recovery rather than oscillatory. Importantly,
more diverse plots were more stable, and their biomass decreased proportionately less during drought than in less diverse plots (Tilman & Downing 1994; Tilman 1996). Diverse plots in those studies included the grassland control plots in this study. Although these plots were more resistant to change in biomass production during the drought and on average had lower year-to-year variation in biomass production (see fig. 3, Tilman 1999), production in diverse plots exhibited synchronized and regular oscillations.

Of the hypotheses that we tested about mechanisms that may have caused the oscillatory pattern in plant production, we were able to reject those that propose externally imposed oscillations caused by weather or top-down effects of herbivores. Precipitation and herbivores did explain large amounts of variation in biomass, but, after controlling for these effects, oscillations were still present. We found weak support for internally generated dynamics. The one hypothesis for which we found partial support was that the 2-year oscillations in ANPP were caused by time lags in the feedback of litter and/or nutrients on production following drought. This hypothesis is consistent with other results from long-term studies of plant production (Briggs &

Figure 7 Dynamics of production by four dominant species or species groups in the grassland control plots and the successional plots. Each point represents mean biomass per plot of (A, B) *Schizachyrium scoparium*, (C, D) *Poa pratensis*, (E, F) *Agropyron repens*, and (G, H) all forbs pooled together.
Knapp 1995). Blair (1997) found that accumulation of nutrients between fires was most important in creating higher levels of plant production following fire. He asserted that a similar phenomena could occur in response to periodic drought. Molofsky et al. (2000) found that litter could impact plant population dynamics, lengthening cycles of population oscillations.

One striking result from this study was the broad-based pattern in oscillations. The pattern was synchronized amongst many different unburned plots. The plots were spread across 15 different fields that spatially covered much of the 22 km² area of Cedar Creek. This suggests strongly that the pattern was not due to chance fluctuations. The pattern was also synchronized across dominant functional groups of plants, including C3 and C4 grasses, and forbs. The oscillatory patterns in plant production were not present in all plant species in all years. Still, the peak and trough years of production were synchronized between species.

Based on the synchronous oscillations exhibited by different species of dominant plants, we developed another hypothesis that we could not test. Some plant species may allocate more to above-ground production – including reproduction – one year, and to below-ground production – including storage – the following year. Production of mast seed crops on an every-other-year basis could be a cause of such a pattern. Interannual variability in seed production has been found in many other plant species (Kelly 1994; Herrera et al. 1998), including grasses and forbs (e.g. Kelly et al. 2000). In our study, forbs, showed 2-year oscillations even before the drought. These oscillations were dominated by fluctuations of biennial, early successional species that disappeared from the experiment in later years. Regardless, it suggests that two year oscillations in productivity may be characteristic of some species at Cedar Creek. Synchronization in these patterns of production induced by drought would then explain our observed pattern in ANPP dynamics.

The regular, consistent, and robust patterns of sustained oscillations in plant production following drought in our study add to evidence showing that ecosystem function can be impacted long beyond the occurrence of a major disturbance. Other recent studies have also reported long-term impacts of severe weather events (Polis et al. 1997) and other disturbance (Milchunas & Lauenroth 1995). Additional studies are now needed to explore whether disturbance induces oscillations in plant production in other ecosystems, and to test which internally generated mechanisms drive the oscillatory dynamics of plant production following disturbance.

ACKNOWLEDGEMENTS

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REFERENCES


Table 1 Correlations in biomass amongst dominant species or species groups during the 10-year period of oscillations: (a) grassland control plots from 1987 to 1996, and (b) successional plots from 1988 to 1996. Data were first detrended with respect to temporal trends in biomass. *P < 0.05; **P < 0.01.

(a) Grassland control plots

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