Rainfall, Biomass Variation, and Community Composition in the Park Grass Experiment

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RAINFALL, BIOMASS VARIATION, AND COMMUNITY COMPOSITION IN THE PARK GRASS EXPERIMENT[1]

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Abstract. We used data on grassland plant community composition over a 90-yr period in the history of the Park Grass Experiment, England to look for relationships between variation in composition and annual variation in rainfall and biomass. This was investigated by regressions of biomass and rainfall on each other, and of these variables separately on each of three different measures of variation in plant community composition. Two of these measures, principal components analysis scores based on variation in species abundance and the ratio by mass of nongrass/grass species, showed significant relationships with biomass variation on many experimental plots, although relationships with rainfall were relatively slight or nonexistent. The third measure employed similarity indices to detect changes in species composition in response to variation in biomass, but failed to find any. Biomass was significantly increased by rainfall on all plots. We propose that variation in community composition was more closely related to biomass variation than to rainfall because rainfall selectively favored the grasses in the community, which we believe competed asymmetrically (for light) with the other species when rainfall was high. The severity of this competition would depend upon biomass more directly than upon rainfall, although it is rainfall that enhanced grass growth. In effect, asymmetric competition magnified the effect of rainfall on community composition.

Key words: biomass variation; climate change; community dynamics; competition; ecological stability; UK; grassland; long-term experiment; Park Grass Experiment; rainfall.

INTRODUCTION

Current concern about the ecological effects of projected climate change has added impetus to enquiry into the basic ecological question "How stable are communities?" (Pimm 1991). The palynological record has been invaluable in attempts to answer this question (e.g., Tallis 1991), but the time scales of palynological studies are necessarily long ones. By contrast, most ecological studies of contemporary plant communities are very short, lasting <10 yr (Delcourt and Delcourt 1988). The gap between the time scales of ecological and palynological studies leaves us largely ignorant of how stable plant communities behave on the time scale of 50–100 yr, which is precisely the time frame for most scenarios of climate change. Very few data from nonsuccessional plant communities are available to fill this gap.

In this paper we use historical records for grassland communities in the Park Grass Experiment (PGE), begun at Rothamsted in England in 1856, to look for the

impact of annual variation in rainfall on biomass and species composition. The PGE consists of a series of contiguous meadow grassland communities that share the same microclimate and original soil type, but which differ in species richness, floristic composition, and annual net primary production. These differences result from nearly a century and a half of fertilizer treatments and nearly a century of liming treatments that have affected soil reaction and soil nutrient status (Williams 1978). After an initial period of ≈40 yr adjustment to the application of fertilizers, the botanical composition of the plots reached equilibrium. Composition was stable in the sense that the ratio of grasses/legumes/other species in the annual summer hay cut persisted over many decades in the face of annual perturbation (Silvertown 1980, 1987).

The biomass of grassland ecosystems is sensitive to annual variation in weather (e.g., Smith 1960, Sala et al. 1988, Oskam and Reinhard 1992). Tilman and Downing (1994) used the change in biomass following a severe drought to measure the stability of grasslands in Minnesota and found that biomass on more species-rich plots was both more resistant and more resilient

to perturbation by drought than biomass on species-poor ones. In the PGE annual hay biomass is correlated with rainfall (Cashen 1947, Jenkinson et al. 1994) and any year's rainfall above or below average may be regarded as a perturbation with potentially measurable effects on biomass and species composition. We have found that biomass on PGE plots with acid soil is significantly more variable than on others and that more species-rich plots tend to be less variable than less species-rich ones (Dodd et al. 1994). Here, we extend the analysis by asking whether rainfall influences species composition and whether any such effect is direct or operates indirectly through the relationship between rainfall and hay biomass.

METHODS

The Park Grass Experiment

The Park Grass Experiment at Rothamsted Experimental Station in Hertfordshire, England was set up between 1856 and 1872 when a hay meadow of uniform vegetation composition and soil type was divided into 20 plots of between 0.05 and 0.2 ha. A variety of fertilizer treatments was established and continue to be applied on a regular schedule to the present day. These treatments may be conveniently divided into four main groups depending on whether, or in what form, nitrogen is applied. Seven plots receive no nitrogen, seven receive nitrogen in the form of ammonium sulphate, three receive nitrogen in the form of sodium nitrate, and three in organic form. The other nutrients applied in the fertilizer treatments are shown in Table 1. At the begining of the 20th century some plots were divided and lime was applied at regular time intervals to one-half. In 1965 the plots were divided in half again and the liming scheme was modified to achieve target pH values of 5, 6, and 7 on three of the quarters of each plot, leaving one-quarter unlimed. In this study we have only used data for the period between 1900 and 1992 to avoid the major trends in species composition and biomass that occurred before this.

Biomass and rainfall

The hay biomass of each plot was measured in a cut each summer and autumn. The summer hay cut was normally taken in the middle of June, but the actual date varied from early June to mid-July. The "autumn" hay cut was taken between September and the following January. Since 1960 hay biomass has been estimated from samples cut with a forage harvester in two strips across each plot at each harvest. First-cut biomass (summer hay cut alone) as well as total biomass (summer + autumn hay cuts) were analyzed because the first hay cut was made soon after botanical samples were taken.

Monthly totals of rainfall from 1900 to 1992 calculated at the time of collection from the 4 m² (1/1000th acre) rain gauge were used (Penman 1974). Monthly rainfall was summed for the period March–May, which covered the majority of the growing period before the summer hay cut, and March–August, which covered most of the growing period for the summer and autumn cuts combined.

The relationship between biomass and rainfall for each plot was investigated as follows. First, both variables were detrended using regression models of these variables on time (e.g., Fig. 1a, b) and then the relationship between the biomass and rainfall residuals was investigated using regression. A linear model was used for detrending rainfall, but for biomass the curvilinear model, biomass $= a(e^{b \cdot year})$, where a and b are parameters to be estimated, gave a better fit than a linear model. (The curvilinear model was fitted by regressing ln biomass on year using ordinary least squares.) Detrending biomass was potentially complicated by the fact that all values of biomass per plot increased when the harvesting method used to estimate this changed in 1960. We therefore compared separate regressions of ln biomass on year for the data of 1900–1959 and 1960–1992 with a single regression covering the whole period 1900–1992. Residuals were very similar and so the overall 1900–1992 regression was used.

Response of community composition

The record of community composition in the PGE is far from complete and only very recently has the species composition of every plot and modern subplot been sampled in the same year. Three grades of compositional data are available in the period 1900–1992. (1) Quantitative data on species composition by dry mass for occasional samples (years shown in Fig. 1c) taken before the summer hay cut. Different subsets of plots were sampled in different years and some plots were much more frequently sampled than others. (2) Species composition of some plots sampled by mass (as 1) every year for a run of years for limited periods in the 1920s and 1930s. (3) Annual separations into "grass," "legume," and "other species" (GLO) components by dry mass for continuous periods of up to 47 yr at the begining of the 20th century. Among the three grades of data there is an inverse relationship between the degree of botanical detail available and the time span of continuous records. In order to use each of the three grades of data to full effect, three different measures were used to detect community responses to biomass and rainfall. The relationship between each of the three measures of response and the degree of perturbation was determined by separate regressions for each plot of each measure on hay biomass and on rainfall residuals. Overall relationships between perturbation and response were investigated by calculating an overall P value for a particular regression model across all plots using Fisher's method (Sokal and Rohlf 1981: Chapter 18).

TABLE 1. Fertilizer treatments applied to the main Park Grass plots used in this study (data from Williams 1978). Minor applications of other fertilizers given near the start of the experiment are not shown. With the exception of farmyard manure and fishmeal, which were applied every 4th yr, fertilizers were applied annually.

Nitrogen fertilizer	Plot	Other nutrients applied
None	2	None
	3	None
	12	None
	4/1	P
	7	P, K, Na, Mg
	8	P, Na, Mg
	15	P, K, Na, Mg
Ammonium sulphate supplying N at		
48 kg/ha	1	None
96 kg/ha	4/2	P
96 kg/ha	9	P, K, Na, Mg
96 kg/ha	10	P, Na, Mg
96 kg/ha	18	K, Na, Mg
144 kg/ha	11/1	P, K, Na, Mg
144 kg/ha	11/2	P, K, Na, Mg, Si
Sodium nitrate supplying N at		
48 kg/ha	17	None
48 kg/ha	16	P, K, Na, Mg
96 kg/ha	14	P, K, Na, Mg
Farmyard manure (35 Mg/ha)	19	None
+ fishmeal supplying N at		
63 kg/ha	13	None
48 kg/ha	20	P, K

Measure 1: Principal components analysis.—The species composition on each of the plots varied in many dimensions depending on the number of species and their individual proportions in each year. Principal components analysis (PCA) was used to reduce the number of dimensions of this variability. This method of measuring community response could be applied to isolated records of community composition. The percentages of each species were used from all plots that were recorded at least 12 times between 1900 and 1992. These were the unlimed (U) and limed (L) halves of plots 3, 7, 8, 9, 10, and 14; the unlimed halves of 15 and 17 and the parts of plots 18, 19, and 20 receiving no lime (U), low lime (LL), and high lime (HL). A principal components analysis was carried out (using GENSTAT 5), for each plot separately. The eigenvectors (loadings) of each species for the first two axes were examined to see which individual species had the most effect on each axis. To remove the effects of long-term changes such as nutrient loss or soil acidification principal component scores and biomass were both detrended.

The residuals from the detrending of the first two principal components were then regressed against (1) detrended rainfall, (2) the curvilinear detrended biomass (first cut and total) obtained in the year of the botanical survey, (3) the curvilinear detrended biomass (first cut and total) obtained in the year before the botanical survey.
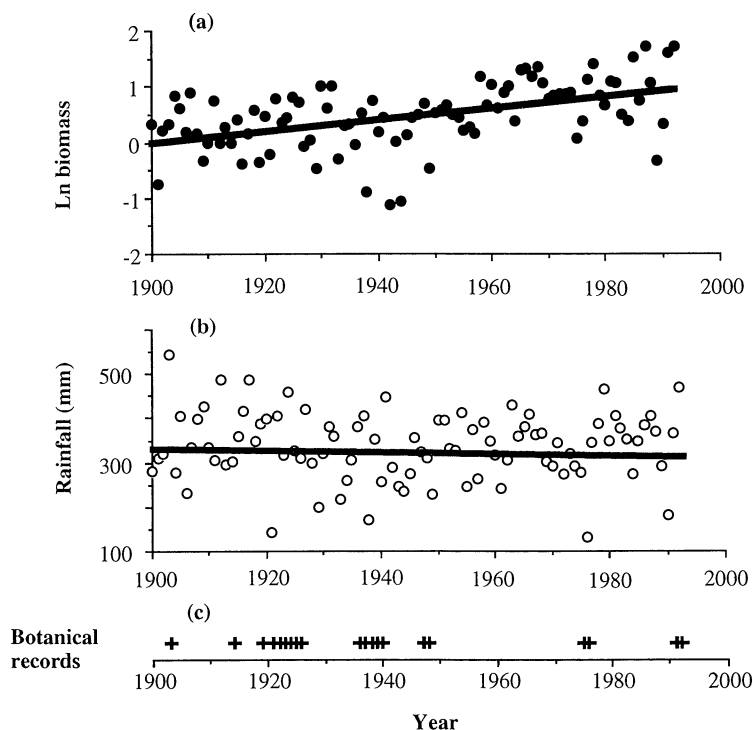

FIG. 1. Time series 1900–1992 and linear regressions for (a) ln biomass (Mg/ha) on plot 3 (unlimed) ($y = 0.01045x - 19.85$), (b) total rainfall (mm) March–August ($y = -0.120x + 571$). (c) Years when botanical records were made by separation of species from the hay, indicated by a cross.
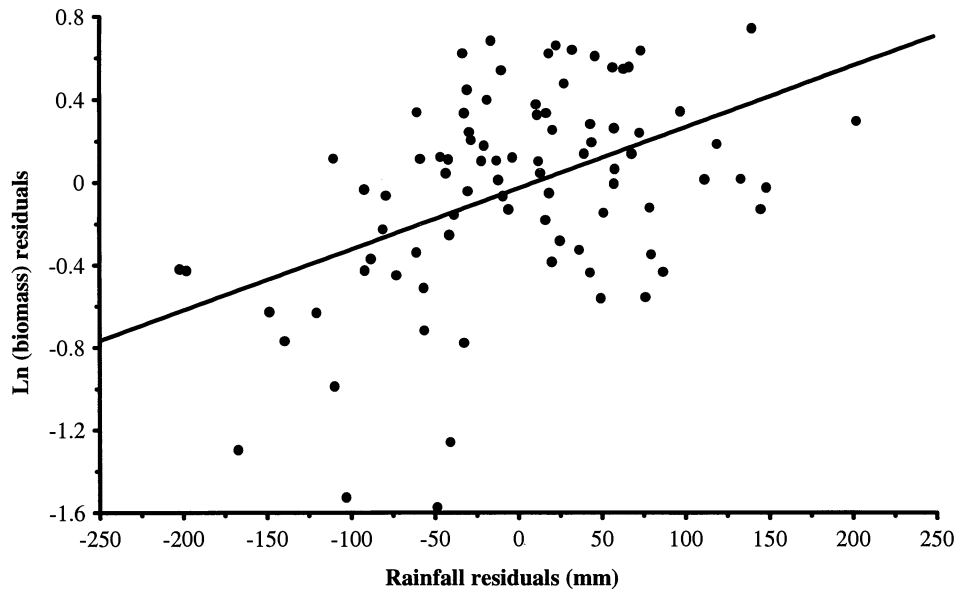
Fig. 2. Relationship between rainfall residuals and ln(total biomass) residuals for plot 3 (unlimed) after detrending of the two variables. The regression line shown has a zero intercept and is: $y = 0.0029x$; $r^2 = 0.18$, $n = 93$, $P < 0.001$.

Measure 2: (Legumes + other)/grass ratio. — The log of the ratio (legumes + other)/grass was regressed on detrended rainfall and on detrended biomass residuals (first cut and total) in the year of GLO measurement and in the year before. Use of a log transformation for a ratio avoids the curved response that arises from a finite range and tends to give a more linear relationship with other variables.

Measure 3: Similarity. — This analysis required compositional data for runs of two or three successive years. These data were available only for a period in the 1920s and 1930s; unlimed parts of plots 3, 7, 8, 9, 10, and 14 were used. The 3 yr in a run were designated years A, B, and C. Rainfall and biomass residuals for year B were used as a measure of perturbation. The "resistance" of a community gauges its immediate response to perturbation and we measured this using a quantitative similarity index (Gower 1971) that compared plot composition in years A and B. The "resilience" of a community gauges its recovery from perturbation, and we measured this using the similarity index to compare plot composition in years A and C.

One might expect inverse relationships between the degree of perturbation and the value of resistance or resilience. There were insufficient data points to look for such relationships on individual plots, so we pooled plots for the purpose and regressed similarities on biomass residuals (first cut and total).

RESULTS

Biomass and rainfall

Regressions of total biomass on rainfall were significant ($P < 0.05$) and positive in all 43 plots tested. An example is shown in Fig. 2. Regressions of first-cut biomass on rainfall showed a significant positive relationship in 21 of 43 plots (Table 2). This relationship occurred more often on plots not receiving nitrogen (9 of 14 plots) than on those receiving nitrogen (11 of 29 plots) (Table 2). Liming had an effect on the slope of the relationship between biomass and rainfall, which can be seen by comparing plots receiving the same fertilizer treatment (Table 2); for the regressions involving total biomass the slope was greater on unlimed than on limed plots in 7 out of 7 comparisons of plots receiving ammonium. For first-cut biomass this was true for 5 out of 7 comparisons. Plots not receiving ammonium did not show this trend.

Response of community composition

Measure 1: Principal components analysis. — The first two axes combined accounted for between 57 and 96% of the variance in species composition. None of the regressions of PCA axes on rainfall were significant overall. The regression of PCA axis 2 on biomass in year t was significant over the 23 plots in the analysis for both first and total hay cuts (model 9, Table 3). The regression of PCA axis 2 on total biomass in year $t - 1$ was just significant overall (model 10, Table 3).

Measure 2: (Legumes + other)/grass ratio. — The regressions of the log ratio (legumes + other)/grass on March–May rainfall in year t were significant overall (model 5, Table 3). On two individual plots receiving no nitrogen (plots 3L and 8U) rainfall significantly increased the proportion of grass, while on two plots receiving nitrogen (plots 9U and 14U) the proportion of grass decreased (model 5, Table 3). All the regressions of the log ratio (legumes + other)/grass on bio-

TABLE 2. Regressions of biomass on rainfall for first-cut hay biomass on rainfall March–May and total biomass on rainfall March–August. Codes for fertilizer treatments are, Nitrogen treatments: n = No nitrogen, A = Ammonium nitrogen, N = Nitrate, F = Farmyard manure. Codes for liming treatments attached to plot numbers are: U = Unlimed, L = limed (HL, high rate or LL, low rate of lime applied).

N Treatment	Plot	Period of treatment (yr)	First-cut biomass			Total biomass		
			Slope	P	% var	Slope	P	% var
A	1U	93	0.0058	<0.001	13.8	0.0048	<0.001	30.7
A	1L	90	0.0024	0.002	9.1	0.0022	<0.001	19.6
n	2U	93	0.0021	0.024	4.4	0.0029	<0.001	21.4
n	2L	90	0.0036	0.001	11.9	0.0029	<0.001	18.4
n	3U	93	0.0020	0.033	3.8	0.0029	<0.001	18.2
n	3L	90	0.0033	0.001	10.0	0.0028	<0.001	19.1
N	4/1U	93	0.0025	0.004	7.6	0.0030	<0.001	22.8
n	4/1L	90	0.0029	0.005	7.4	0.0030	<0.001	22.3
A	4/2U	93	0.0044	0.014	5.4	0.0029	0.002	8.9
A	4/2L	90	0.0012	0.065	2.7	0.0016	<0.001	18.6
N	7U	93	0.0010	0.147	1.2	0.0022	<0.001	23.4
n	7L	90	0.0012	0.057	3.0	0.0018	<0.001	18.5
N	8U	93	0.0012	0.103	1.8	0.0023	<0.001	20.6
n	8L	90	0.0029	0.001	11.0	0.0029	<0.001	26.3
A	9U	93	0.0017	0.213	0.6	0.0019	0.005	7.4
A	9L	90	0.0011	0.027	4.4	0.0011	0.001	10.1
A	10U	93	0.0023	0.043	3.4	0.0025	<0.001	17.6
A	10L	90	0.0010	0.037	3.8	0.0014	<0.001	21.1
A	11/1U	92	0.0003	0.841	−1.1	0.0016	0.014	5.5
A	11/1L	90	0.0004	0.405	−0.3	0.0011	<0.001	16.1
A	11/2U	93	−0.0003	0.771	−1.0	0.0011	0.008	6.5
A	11/2L	90	0.0000	0.901	−1.1	0.0010	0.001	11.5
N	12U	93	0.0016	0.071	2.5	0.0027	<0.001	18.6
n	12L	28	0.0017	0.121	5.5	0.0042	<0.001	46.7
F	13U	93	0.0017	0.003	8.6	0.0020	<0.001	22.4
F	13L	90	0.0018	0.004	8.3	0.0019	<0.001	16.8
N	14U	93	−0.0001	0.701	−0.9	0.0008	0.004	7.7
N	14L	73	0.0001	0.780	−1.3	0.0011	<0.001	16.0
N	15U	93	0.0018	0.026	4.3	0.0024	<0.001	20.9
n	15L	73	0.0016	0.023	5.7	0.0022	<0.001	19.9
N	16U	93	0.0009	0.070	2.5	0.0015	<0.001	16.4
N	16L	90	0.0010	0.048	3.3	0.0014	<0.001	16.3
N	17U	93	−0.0003	0.711	−0.9	0.0018	<0.001	13.9
N	17L	73	0.0018	0.012	7.2	0.0026	<0.001	29.9
A	18U	93	0.0062	<0.001	15.8	0.0051	<0.001	27.9
A	18LL	73	0.0010	0.182	1.1	0.0025	<0.001	26.4
A	18HL	73	0.0003	0.708	−1.2	0.0016	0.002	11.7
F	19U	93	0.0007	0.267	0.3	0.0019	<0.001	17.7
F	19LL	73	0.0008	0.190	1.0	0.0022	<0.001	21.9
F	19HL	73	0.0012	0.098	2.5	0.0021	<0.001	18.4
F	20U	93	0.0009	0.061	2.7	0.0017	<0.001	20.7
F	20LL	73	0.0019	0.080	2.9	0.0018	<0.001	21.1
F	20HL	73	0.0013	0.011	7.5	0.0021	<0.001	25.3

mass were significant overall (models 11 and 12, Table 3).

All significant regressions on biomass for individual plots were of negative slope (Table 3) and occurred both on plots receiving and on plots not receiving nitrogen.

Measure 3: Similarity.—Values of resistance and resilience tended to be higher on plots with fewer species and also increased on plot 9 between 1922 and 1939 as this plot lost species (Table 4). No significant relationships were found between the pooled data for resistance or resilience and biomass residuals.

DISCUSSION

Our results show that rainfall affected the floristic composition of plots in the PGE directly, but that the indirect effect was stronger. The evidence of a direct effect was confined to one of the two models tested on GLO (model 5, Table 3) and PCA analysis provided no evidence that rainfall affected composition (Table 3). It is noteworthy that the significant effect on GLO showed that March–May rainfall and not March–August rainfall affected composition and that no time lag occurred. Determinations of species composition were made in June, so an effect of rainfall in the period March–May is to be expected if rainfall has a direct effect.

The strength of the indirect relationship between rainfall and composition, operating through biomass as an intermediary, is indicated by significant relationships between rainfall and total biomass for all PGE plots (Table 2) and several significant regressions of

TABLE 3. Results of regressions of PCA axes and log([legumes + other]/grass) on rainfall and first-cut and total biomass. All variables were detrended and separate regressions were run on 23 plots for PCA and 25 plots for log([legumes + other]/grass). Overall P for the regressions was calculated as described in *Methods: Response of community composition*.

Model	Independent variable	Dependent variable	Rainfall March–May, first hay cut		Rainfall March–August, total biomass	
			Overall P	Significant plots† and sign	Overall P	Significant plots† and sign
			Rainfall			
1.	yr t	PCA axis 1	0.976	none	0.913	none
2.	yr $t-1$	PCA axis 1	0.891	none	0.753	+19U
3.	yr t	PCA axis 2	0.814	none	0.273	+14U
4.	yr $t-1$	PCA axis 2	0.938	none	0.884	+14L
5.	yr t	$\log \dfrac{L+O^*}{G}$	0.004	−3L, −8U, +9U, +14U	0.238	−10L
6.	yr $t-1$	$\log \dfrac{L+O^*}{G}$	0.527	+10U	0.103	−3L, −7U, +10U
			Biomass			
7.	yr t	PCA axis 1	0.528	none	0.392	−10L, +18LL
8.	yr $t-1$	PCA axis 1	0.220	−9L, +20LL	0.715	+9L, +20LL
9.	yr t	PCA axis 2	0.005	−7U, +8U, +9U, +9L	0.001	+3L, −7U, +9U, +9L, −17U, +18HL
10.	yr $t-1$	PCA axis 2	0.081	+9L, −10L, +14L	0.038	+7U, +9L, +10L
11.	yr t	$\log \dfrac{L+O^*}{G}$	0.037	−9L, −18LL, −18HL	<0.001	−3L, −9L, −10L, −18LL, −18HL
12.	yr $t-1$	$\log \dfrac{L+O^*}{G}$	0.029	−18HL	<0.001	−3L, −7U, −17U, −18LL, −18HL, −19LL, −19HL, −20LL, −20HL

* O = other species; L = legumes; G = grass.

† L = plots receiving lime, U = plots receiving no lime; LL = plots receiving low lime, HL = plots receiving high lime.

TABLE 4. Similarities for the unlimed parts of six plots for the "B" years shown and the biomass residual on each plot in the year calculated from linear detrending of first and total biomass 1900–1992.

Plot	Year	No. spp.	Similarity (%)		Biomass residual (Mg/ha)	
			Resistance	Resilience	First cut	Total
3	1922	34	82.0	79.9	−0.0190	0.8202
	1925	38	80.9	76.8	0.1615	0.7892
	1937	35	76.9	75.8	−0.0403	−0.0095
7	1922	27	76.9	77.4	−1.1902	−0.4070
	1936	31	79.0	73.6	−0.7608	−0.2662
	1939	26	75.8	77.0	0.2942	1.4289
8	1936	34	79.1	76.6	−0.7877	−1.0264
	1939	33	79.1	76.1	−0.0900	0.1154
9	1922	14	75.4	85.7	−3.124	−1.468
	1925	11	73.1	72.0	0.378	0.741
	1928	9	86.4	77.5	−0.720	−1.047
	1931	9	84.3	100	2.268	3.782
	1936	6	96.7	98.9	−0.265	−0.049
	1939	8	96.4	85.8	−0.851	0.645
10	1936	9	87.1	93.8	−0.199	−0.1246
	1939	7	78.6	71.1	−0.412	0.3866
14	1921	12	91.1	89.0	0.073	−1.0708
	1924	17	89.3	87.0	0.939	−0.2601
	1936	14	91.9	90.9	0.033	0.3437
	1939	14	91.8	92.9	−0.075	0.7764

composition on biomass. The latter were more frequent than direct relationships between rainfall and composition and occurred with both PCA and GLO as dependent variables (Table 3, models 7–12). This suggests that biomass as a measure of perturbation is an effective integrator of the effects of rainfall and other climatic variables that were not explicitly included in our analyses. The most successful of the 12 models was the regression of GLO on total biomass in the year before GLO determination (model 12, Table 3). This model was significant on 9 of the 25 plots analyzed and showed that the proportion of grass increased in the year after a season of high total biomass. The relationship between variation in biomass and variation in GLO within plots over time is particularly interesting because biomass is correlated with composition in a similar manner between plots at any one sampling date (Silvertown 1980). Communities on plots with high average biomass have a higher proportion of grass by mass than plots with low average biomass. The fact that these variables are also correlated within plots over time demonstrates that the between-plot relationship is dynamically determined.

Using similarity as a measure of response to perturbation over the period 1920–1940 we could find no evidence that there was a general relationship between perturbation of biomass on a plot and changes in its species composition. There are several possible reasons for this lack of a relationship. Firstly, similarity is not a good measure of compositional stability. This seems

particularly likely in communities that differ so much in diversity because plots with few species and low equitability will inevitably measure as "more stable" than plots with more species and greater equitability. However, there seems no other way of measuring compositional stability in this instance. Frank and Mc-Naughton (1991) used a similarity index to show that drought had less effect on more diverse plant communities in Yellowstone than on less diverse ones. Secondly, it may be that we don't have a good measure of ecological perturbation, though in our other analyses total biomass did appear to be a good measure. Thirdly, the plots are very stable, whether this is measured in terms of resistance or resilience. There is good evidence that the composition of the Park Grass plots is resilient in terms of the major GLO components (Silvertown 1980, 1987), though the species composition of these components has been observed to change over periods of time when the ratio of the components themselves did not. Silvertown (1980) concluded from this that the abundance of species and the abundance of components were independently regulated. The present findings are consistent with this.

The following overall picture emerges from this study. Rainfall in the growing period before the first hay cut increased the biomass and the proportion of grass in that cut on some of the plots not receiving nitrogen, but had less effect on biomass and favored other species on some of the nitrogen-fertilized plots. Total rainfall, including that occurring after the first hay cut (and after sampling of species composition), had a greater effect on hay biomass than rainfall before June (Table 2) but, surprisingly, this rainfall appears not to have influenced GLO at the next determination in the following year (model 6, Table 3). Nevertheless, total biomass (including the second cut) and total biomass in year t − 1 both affected GLO.

Why is biomass a better predictor of compositional variation than rainfall? One obvious explanation is that rainfall is an important but not the exclusive influence on plant growth. More, or more sophisticated, climatic variables might explain more of the variance in composition. However, we have found that potential soil moisture deficit, which is usually a good correlate of grass growth (e.g., Coleman et al. 1989), performs little better than rainfall as an explanatory variable in the PGE (M. Dodd, unpublished data). An alternative explanation is that rainfall controls competitive interactions among the grasses, legumes, and other species, and that the ratio of these components is thus affected by two mechanisms: the first is due to the preferential effect of rainfall on grass growth, and the second is due to the competitive suppression of legumes and other species when grass growth increases, which the success of model 12 (Table 3) suggests probably operates with a time lag of a year. Thus we propose that biomass has a stronger effect on the (legumes + other)/grass ratio than does rainfall because biomass is highly correlated

with grass growth and it multiplies the rainfall effect. This kind of positive feedback favoring better competitors is known to occur among plants when competition is asymmetric, as is to be expected when light is the limiting resource (Weiner 1990). This interpretation of our results raises the possibility that asymmetric competiton between species will magnify the effects of climate change on the composition of plant communities and suggests that these effects will first become apparent in fertile habitats where competition for light is strongest. A greater response to perturbation in communities where interspecific competition is strong than in communities where it is weak is consistent with the prediction arising from computer simulations of communities that the more interactive a community is the less stable it is likely to be (May 1973).

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