PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Stability in the Plant Communities of the Park Grass Experiment: The Relationships between Species Richness, Soil pH and Biomass Variability

Mike E. Dodd, Jonathan Silvertown, Kevin McConway, Jacqueline Potts and Mick Crawley

Phil. Trans. R. Soc. Lond. B 1994 **346**, 185-193
doi: 10.1098/rstb.1994.0140

Stability in the plant communities of the Park Grass Experiment: the relationships between species richness, soil pH and biomass variability

MIKE E. DODD[1], JONATHAN SILVERTOWN[1], KEVIN McCONWAY[2], JACQUELINE POTTS[3] AND MICK CRAWLEY[4]

[1]*Biology Department and* [2]*Department of Statistics, The Open University, Walton Hall, Milton Keynes MK7 6AA, U.K.*
[3]*Department of Statistics, Rothamsted Experimental Station, Harpenden, Herts AL5 2JQ, U.K.*
[4]*Department of Pure and Applied Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, U.K.*

SUMMARY

The Park Grass Experiment (PGE), begun at Rothamsted Experimental Station in 1856 and still running, affords a unique opportunity to test for the influence of species number and soil reaction on biomass variability in a suite of comparable plant communities. Biomass variability was measured by calculating the coefficient of variation (*CV*) over time of annual hay yield in an eleven-year moving window. *CV* and species number were both strongly negatively correlated with biomass; both relations were affected by time and pH. Multiple regression of *CV* on species number and mean biomass for non-acidified plots in 42 years between 1862 and 1991 showed a relationship between biomass and *CV* which was negative in most years and significantly so in nearly three quarters of them (30/42). We are unable to tell how much of this effect is intrinsic to the statistical relation between the mean and *CV* of biomass. Species number was negatively correlated with *CV* in 29/42 years, but this was statistically significant on only three occasions. Because this relation was highly significant in the year (1991) for which we have the largest sample size (34 plots), we tentatively conclude that biomass variability may be lower in more species-rich communities, although the effect is possibly a weak one. We suggest that physiological stresses imposed by low pH may explain the greater variability of plots with acidified soil. An increase in the variability of biomass that occurred across plots with time may be due in part to acidification across the whole experiment. Three hypotheses are proposed to explain the relationship between species richness and biomass variability: (i) biomass variability on more species-rich plots is better buffered against climatic variation because species differ in their response to climatic conditions: (ii) there are fewer species on plots with greater biomass variability because species have been lost by competitive exclusion in years when biomass reaches high values; (iii) species richness and variability are both correlated with a third variable, for example soil moisture deficit within a plot. All three hypotheses are susceptible to testing within the PGE.

1. INTRODUCTION

The stability of ecological communities is a subject that has preoccupied ecologists for more than sixty years (Elton 1927; May 1974; Connell & Sousa 1983; Pimm 1991). Elton (1958) believed that communities with fewer species, such as in the Arctic, would be less stable than more complex ones. This suggestion gave rise to theoretical investigations of the relationship between stability and diversity (May 1974; DeAngelis 1975), and some empirical studies (Wolda 1978; McNaughton 1993), but the investigation of the problem has been hampered by a dearth of suitable long-term data, to the point where Connell & Sousa (1983) were able to argue that the evidence for ecological stability itself was very scanty. Silvertown (1987) pointed out that data from one of the longest-running experiments in the world, the Park Grass Experiment at Rothamsted, England, provided good *prima facie* evidence of stability that Connell & Sousa (1983) had overlooked.

A community is stable in the mathematical sense if it returns to equilibrium after a perturbation. In practice communities may be judged stable if they have characteristics that persist for a reasonable length of time in the face of measured perturbation. The evidence for stability in the PGE is that different communities in the experiment have maintained characteristic ratios of grasses : legumes : other species over many decades, despite the fact that ratios vary from year to year in response to weather (Silvertown 1987). Biomass per plot in the PGE may be shown to be stable in an equivalent manner, although up to 30% of its annual variation is attributable to variation

Phil. Trans. R. Soc. Lond. B (1994) **346**, 185–193
Printed in Great Britain

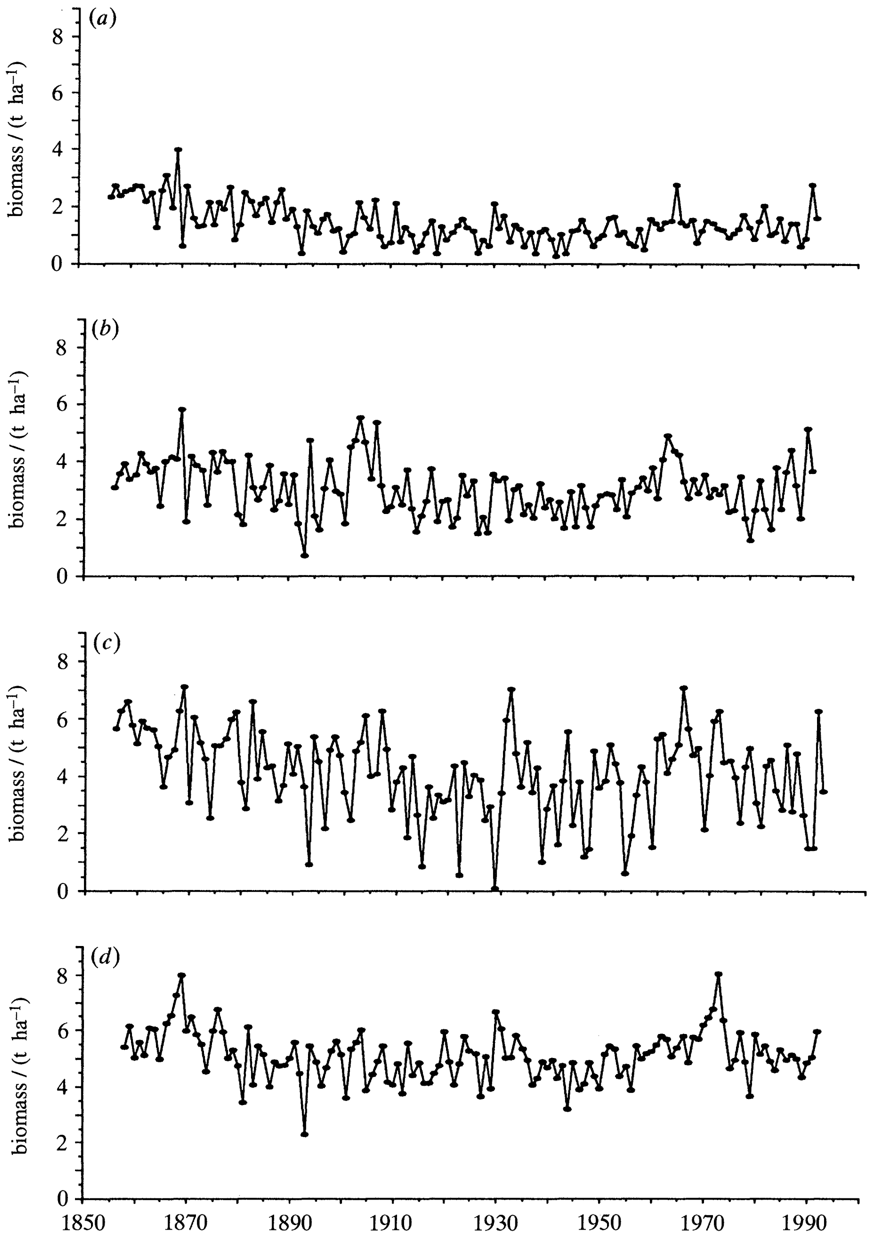

Figure 1. Time-series 1856–1992 for annual measures of biomass in the summer hay cut on four typical unlimed plots in the Park Grass Experiment. (*a*) Plot 3, receiving no fertilizer treatment; (*b*) Plot 7, fertilized with PKNaMg; (*c*) Plot 9, fertilized with ammonium sulphate and PKNaMg; (*d*) Plot 14, fertilized with sodium nitrate and PKNaMg.

in rainfall (Silvertown *et al.* 1994). The behaviour of a stable system may be described by its resilience to perturbation, by its resistance to perturbation and by its variability (Pimm 1991). Ideally, one would measure all three properties but resistance and resilience are very difficult to measure because real communities like those of the PGE are continually perturbed, making it very difficult to isolate recovery following a particular perturbation from the more immediate effects of subsequent ones (Connell & Sousa 1983). Variability is more easily measured and it may be particularly informative if, as in the PGE, it is possible to ask why some communities are more variable than others.

Long-term data do exist for a wide range of plant communities (White 1985; Goldberg & Turner 1986), but most of these are successional and their dynamics are dominated by directional changes in species composition (Burrows 1990; Olff & Bakker 1991). The Park Grass Experiment (PGE), begun in 1856 at Rothamsted in Hertfordshire, England, is by far the longest-running of only a handful of long-term studies of non-successional vegetation. Grasslands of a wide range of species composition are represented within the experiment, and the botanical composition of many plots has been at dynamic equilibrium since about 1900 (Silvertown 1980). The different communities are all within a single meadow that was of uniform soil type when the experiment began (Lawes & Gilbert 1880, Lawes *et al.* 1882). Fertilizer treatments have altered the soil properties in different plots, but other physical influences on the stability of the plant communities, such as mowing and climate, have been experienced in common by all communities. The PGE now contains communities that range in species richness from two or three species to more than thirty. The PGE therefore provides a unique opportunity to compare the relative variability in the long term of adjacent communities with widely different numbers of species.

Various kinds of data have been collected at various intervals and for varying lengths of time on the Park Grass communities, but the only complete data set is for the biomass of the plant community on each plot at the annual hay cut in summer (figure 1). Fortuitously, biomass is a good aggregate measure of the performance of the plant community because it incorporates the performance of individual species and guilds. The biomasses of three separate guilds (grasses, legumes and 'other' species) are positively correlated with one another *within* plots (Silvertown 1980; M. Dodd *et al.*, unpublished); this correlation means that we lose little information by using total biomass as a measure of community dynamics. There is also good evidence that the ratios of grasses : legumes : other spp. in the PGE has remained at equilibrium within plots since 1900 despite some notable changes in the species composition of the guilds (Silvertown 1980, 1987). As a measure of *community* dynamics, then, total biomass has the very useful property that it is not excessively influenced by secular changes in the abundance of one or two species. This paper is concerned with two general questions. (i) What relationship, if any, exists between the number of species in a community and biomass variability? (ii) Is there a correlation between soil pH and biomass variability? A subsequent paper will look at the stability of community composition.

2. METHODS

(*a*) *The Park Grass Experiment*

The Park Grass Experiment was set up between 1856 and 1872, when a hay meadow of uniform vegetation composition and soil type at Rothamsted was divided into 20 plots of between 0.1 and 0.2 ha. Fertilizer treatments were applied to 18 plots and two plots (numbers 3 and 12) were kept as unfertilized controls. Fertilizers continue to be applied on a regular schedule to the present day. Full details of the fertilizer treatments are given by Williams (1978). Methods of fertilizer application, hay cutting and other details of experimental procedure in the nineteenth century are given by Lawes & Gilbert (1863, 1880; Lawes *et al.* 1882). For the purposes of the present study the important details are that 11 of the original plots have received a nitrogen fertilizer, and in 8 of these it was applied as ammonium sulphate, which progressively acidified the soil (Johnston *et al.* 1986). By the end of the nineteenth century some degree of acidification and species loss was observed on all plots and a liming scheme was introduced. Plots were divided and lime was applied at regular time intervals to one half. In 1965 plots were divided in half again and three of the sub-plots were limed. One quarter of the original area of each plot has never had lime. Quarter plots are now between 80 and 500 m^2 in area.

The hay biomass of each plot has been measured annually in summer since 1856, providing a continuous record of how experimental treatment and year-to-year changes in weather have affected the biomass of communities as a whole. The number and abundance of plant species on different plots was first determined in 1862 by taking samples from the hay. Each sample was dried, separated into species and then weighed. This procedure has been repeated at irregular intervals until the present day.

(*b*) *Data*

Numbers of species per plot have been recorded at irregular intervals, and rarely on all plots in the same year. In the analyses described below, all available published data on biomass and species number for most of the limed and unlimed plots were used (Lawes and Gilbert 1863, 1880; Lawes *et al.* 1882; Rothamsted Experimental Station 1934, 1935, 1936, 1937, 1938, 1952; Brenchley & Warington 1958; Warren & Johnston 1964; Warren *et al.* 1965; Williams 1978). The only plots omitted were those that had been recorded less than twice (up to 1991) and three plots which were only recorded for short periods in the early part of the experiment. Some additional, unpublished data for the number of species per plot on a variable number of plots during the period 1871–1883 were found in the archives at Rothamsted. The most complete data for any year were from our own field survey conducted in 1991 (M. Crawley, unpublished data). In total, 45 plots and sub-plots recorded intermittently between 1862 and 1991 gave 678 plot–year combinations. The individual analyses used appropriate subsets of the full data set, as described below.

Biomass variability was measured as the coefficient of variation of biomass, measured over time, for the first cut each year (usually taken in early June). Several alternative measures of variability were considered, each one involving the variance and mean of a time series of biomass determinations on the same plot. *CV* was chosen because it has the advantage of being scale-free. Within a single, stable population it might well be reasonable to assume that the mean and standard deviation of biomass would be independent. In that situation it would be reasonable to expect a negative correlation between mean biomass and *CV*. However, the aim in the present study is to describe the relation between mean and *CV* over a number of different populations. Although the variance is clearly strongly dependent on the mean, there is no *a priori* basis on which to build a model of the relation between the two across different populations in this type of unreplicated experiment. In the absence of a justifiable model, we have not attempted any ecological explanation of the relation between *CV* and mean biomass. The empirical relation between *CV* and mean biomass was used in our analysis in order that the relations between species richness, soil pH and *CV* at constant biomass could be investigated and interpreted ecologically.

Mean biomass and coefficient of variation (*CV*) of first-cut hay biomass were calculated over an 11 year period centred on the year of the species count. (A centred interval was chosen for the calculation of the *CV* to avoid prejudging the causal direction of the relationship between species richness and biomass variability.) At the end of the data run (i.e. 1991), 5 year means and *CV*s were used. Other variables such as pH have also been measured at Park Grass although less frequently (Warren & Johnston 1964; Johnston *et al.* 1986).

(*c*) *Analysis*

The main determinants of species richness in the PGE are soil pH and biomass, both of which are in turn determined by fertilizer treatment (Silvertown 1980). Therefore, in looking for a relation between variability and species richness we first quantified relations between species richness and biomass and pH, biomass and variability.

Multiple linear regression was carried out by using GENSTAT5 computer programs. Plotting of the data indicated that the usual multiple regression models fitted the data adequately. Regression models were constructed with the number of species per plot, and coefficient of variation of biomass per plot as dependent variables. In each instance terms were added to the model until further additions proved to be non-significant (table 1). Preliminary analysis of the data indicated that two binary factors should be included. The first of these (labelled as A in tables 1 and 2) indicated plots that received the soil-acidifying fertilizer ammonium sulphate, but did not receive liming treatment. The second (labelled as B) indicated plots that received ammonium sulphate together with lime (from 1906 onwards). In comparisons between years, year was also treated as a factor. The same regression technique was used to fit the model *CV* = biomass + species number for each individual year. Data from the same plots were restricted to be at least 11 years apart to avoid spurious serial correlation between *CV* measurements.

3. RESULTS

(*a*) *Species number*

Species number per plot (*n*) in 1862 was negatively correlated with mean biomass (figure 2*a*). A simple

Table 1. *Regression models used in the analysis*

(A indicates the inclusion of a factor for plots receiving ammonium sulphate and no lime, B indicates the inclusion of a factor for plots receiving lime and ammonium sulphate.)

model	dependent variable	terms	overall *f*	(d.f.)	*P*	*f* (d.f.) for added term		*P*	% variance accounted for
1.	*n* 1862	biomass	69.75	1,17	<0.001	—	—	—	79.3
		+A	46.14	2,16	<0.001	5.22	1,16	0.036	83.4
		+A · biomass	35.28	3,15	<0.001	2.86	1,15	0.112	85.1
2.	*n* 1991	biomass	1.26	1,39	0.269	—	—	—	0.6
		+A	71.68	2,38	<0.001	137.70	1,38	<0.001	77.9
		+A · biomass	51.98	3,37	<0.001	3.43	1,37	0.072	79.3
		+B	86.89	4,36	<0.001	37.55	1,36	<0.001	89.6
		+B · biomass	67.76	5,35	<0.001	0.09	1,35	0.771	89.3
3.	*n* 1862 and 1991	biomass + A + biomass · A	7.43	3,56	<0.001	—	—	—	24.7
		+year + year · A	86.70	3,54	<0.001	147.32	2,54	<0.001	87.9
		+year · biomass	77.62	6,53	<0.001	4.46	1,53	0.039	88.6
		+year · biomass · A	65.61	7,52	<0.001	0.23	1,52	0.631	88.5
4.	*CV* 1862	biomass	16.60	1,17	<0.001	—	—	—	46.4
		+A	16.06	2,16	<0.001	8.35	1,16	0.011	62.6
		+A · biomass	10.10	3,15	<0.001	0.07	1,15	0.796	60.3
5.	*CV* 1991	biomass	97.59	1,39	<0.001	—	—	—	70.7
		+A	111.32	2,38	<0.001	36.42	1,38	<0.001	84.7
		+A · biomass	75.89	3,37	<0.001	1.59	1,37	0.216	84.9
		+B	77.28	4,36	<0.001	12.25	1,36	<0.001	88.4
		+B · biomass	72.22	5,35	<0.001	6.32	1,35	0.017	89.9
6.	*CV* 1862 and 1991	biomass + A + biomass · A	39.70	3,56	<0.001	—	—	—	66.3
		+year + year · A	59.93	5,54	<0.001	29.55	2,54	<0.001	83.3
		+year · biomass	68.78	6,53	<0.001	18.11	1,53	<0.001	87.3
		+year · biomass · A	58.75	7,52	<0.001	0.72	1,52	0.398	87.3
7.	*CV* all years	biomass + n + year	25.16	51,625	<0.001	—	—	—	64.6
		+biomass · year + *n* · year	12.66	145,531	<0.001	2.60	94,531	<0.001	71.4

Table 2. *Values of* t *and associated* P*-values for the full regression models used in the analysis of 1991 data (table 1, Models 2 and 5)*

(A indicates the inclusion of a factor for plots receiving ammonium sulphate and no lime; B indicates the inclusion of a factor for plots receiving lime and ammonium sulphate.)

	Species number		*CV*	
term	*t*	*P*	*t*	*P*
constant	20.22	<0.001	21.46	<0.001
biomass	−6.72	<0.001	−13.42	<0.001
A	−9.20	<0.001	1.17	0.250
A • biomass	2.25	0.031	2.16	0.038
B	−1.65	0.108	−1.19	0.242
B • biomass	−0.29	0.774	2.51	0.017

regression of n on mean biomass accounted for 79.3% of the variance in species richness. With ammonium treatment as a factor in the model, the variance accounted for increased to 83.4% and intercepts differed significantly for the two types of plot (table 1, Model 1). Including the ammonium × biomass interaction showed that slopes did not differ significantly between the two types of plot (table 1, Model 1).

In 1991 there were parallel relations between n and biomass for non-ammonium and limed ammonium plots, and a quite different slope and intercept for the relation in unlimed, ammonium plots (figure 2*e*). In statistical terms, this is demonstrated by the fact that adding a term to distinguish between the intercept for the limed ammonium plots and those for the other plots produces a significant improvement in the fit of the model, whereas adding another term to distinguish the slope for those plots does not (table 1, Model 2). The *t*-values for the full model (table 2) generally confirm these features. Although the *t*-values for the slope and intercept for the limed ammonium plots are not significant in the full model, the sequential modelling process (table 1, Model 2) indicates that the lack of significance for both these terms in the full model is an artefact of their collinearity, and the most parsimonious interpretation of the regression calculations is that the lines of non-ammonium and limed ammonium plots differ in intercept but not necessarily in slope. Fitting a model to the data from 1862 and 1991 taken together (omitting the limed ammonium nitrogen plots) leads to the conclusion that the corresponding lines for 1862 and 1991 differ in slope (table 1, Model 3).

Intermediate years between 1862 and 1991 (figure 2*b*–*d*) showed a gradual reduction in number of species per plot, with this process proceeding significantly faster on ammonium nitrogen plots than on others. Regression lines shown in figure 2 are for the maximum number of significant terms from the modelling process. This indicated parallel relations with significantly different intercepts for ammonium and non-ammonium plots in 1877, 1919 and 1948.

(*b*) *Coefficient of variation of biomass*

Biomass and its coefficient of variation were negatively correlated in 1862 (figure 3). For a given biomass, the eight plots receiving ammonium sulphate were significantly more variable than the 11 other plots in the sample. Intercepts for the two groups of plots differed ($p < 0.05$), but slopes did not. The overall regression model accounted for 62.6% of the variance in *CV* (table 1, Model 4).

In 1991 the unlimed part of plot 18 was highly acidified, with large bare patches in the vegetation. This plot had an extreme *CV* and was omitted from the sample. The remaining 40 plots fell into three distinct groups: ammonium plots with no lime, ammonium plots with lime, and the rest (figure 3). A simple regression model of *CV* on biomass, which made no distinction between the three types of plot, accounted for 70.7% of the variance in *CV* (table 1, Model 5). Adding terms that allow different intercepts and slopes for the relation between *CV* and biomass (b) for the three types of plot leads to a model that accounts for 89.9% of the variance in *CV* (table 1, Model 5). The conclusion is that the three lines are not parallel, and that the difference in gradient is statistically significant. Again, the corresponding lines for 1862 and 1991 differ in slope.

Intermediate years between 1862 and 1991 (figure 3) showed a gradual increase in biomass variability, with this process proceeding significantly faster on ammonium nitrogen plots than on others. Regression lines shown in figure 3 are for the maximum number of significant terms from the modelling process. As for the relations between n and b, relations between *CV* and b in 1877, 1919 and 1948 were parallel, with significantly different intercepts for ammonium and non-ammonium plots.

(*c*) *CV, species number, pH, biomass and year*

The species-rich plots were also the ones with the lowest biomass. Plots with low biomass were the most variable. Because *CV* and species number were both negatively correlated with biomass, one would expect *CV* and species richness to be positively correlated. This is not what we observe. Taking into account all years for which data were available, the Pearson correlation coefficients for *CV* and species number with biomass were −0.65 and −0.40, respectively; however, the correlation between *CV* and species richness was also negative (just) at −0.06.

An overall model for *CV* fitting biomass, species number, year and interactions between biomass and year, and number and year for all available data on non-acidified plots indicates that the relation between *CV* and species number and biomass differed significantly between years (table 1, Model 7), so it is not possible to draw any simple conclusion from this model in which years are combined. To explore the relation further, we therefore fitted the model $CV =$ biomass + species number to each year's data set independently. Recall that the mean biomass and the

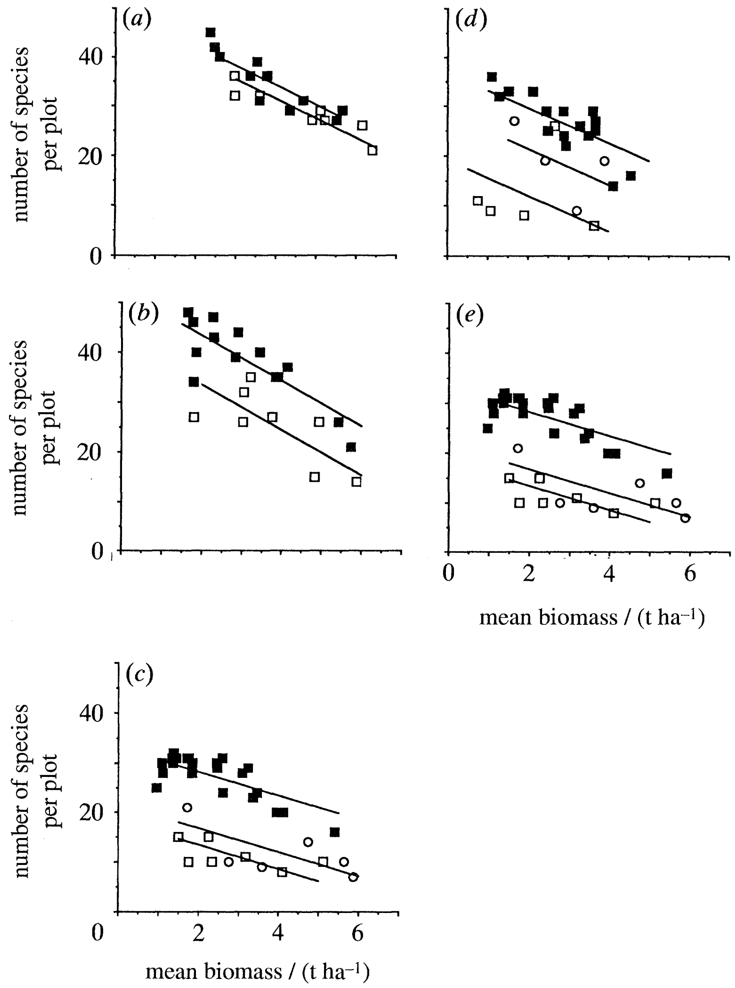

Figure 2. Relations between number of species per plot (n) and mean biomass (b) 1862–1991. Open squares are plots receiving ammonium sulphate; open circles are plots receiving ammonium sulphate and lime after 1906; filled squares are plots receiving neither ammonium sulphate nor lime. Regression parameters are as follows. (a) 1862. Non-ammonium plots $n = 50.08 - 3.971b$; ammonium plots $n = (50.08 - 2.85) - 3.971b$. ($b$) 1877. Non-ammonium plots $n = 52.49 - 4.553b$; ammonium plots $n = (52.49 - 9.90) - 4.553b$. ($c$) 1919. Non-ammonium plots $n = 33.13 - 2.408b$; ammonium, limed plots $n = (33.13 - 11.52) - 2.408b$; ammonium plots $n = (33.13 - 14.88) - 2.408b$. ($d$) 1948. Non-ammonium plots $n = 36.70 - 3.55b$; ammonium, limed plots $n = (36.70 - 8.28) - 3.55b$; ammonium plots $n = (36.70 - 17.59) - 3.55b$. ($e$) 1991. Non-ammonium plots $n = 32.86 - 2.955b$; ammonium, limed plots $n = (32.86 - 6.14) + (-2.955 - 0.28)b$; ammonium plots $n = (32.86 - 27.63) + (-2.955 + 2.211)b$.

CV for any given year were calculated over a period around the year in question. The t-values and coefficients for models of the 42 years in which data on four or more plots are available are given in table 3.

Plots with higher biomass were less variable in most years. On the non-acidified plots (table 3a) there was a small reduction in variability with increased number of species in 29 of the 42 years, although this was significant only in 1877, 1882 and 1991, and in one year (1928) there was a significant increase in variability with n. There were fewer plot–year combinations available for the acidified treatments and in only six of the ten years was there a reduction in variability with increased number of species (table 3b). Because years differ in the relation between variables (table 1, Model 7) and sample sizes vary widely between years, we cannot compute an overall significance for the relation between *CV*, biomass and species number. However, the overall trends are clear.

4. DISCUSSION

The relationship between species richness (n) and variability (*CV*) in the plant communities of the Park Grass Experiment is bound up with two other variables that correlate with both n and *CV*. The present analysis and a previous study (Silvertown 1980) show that there is a strong relation both between biomass of the community (hay biomass) and species richness and between soil pH and species richness. It now appears that biomass variability is also strongly related to biomass itself and to pH. These correlations are of interest in their own right (see below). Using multiple regression to partition the effects of biomass and species number on variability, we found that biomass and *CV* had a significantly

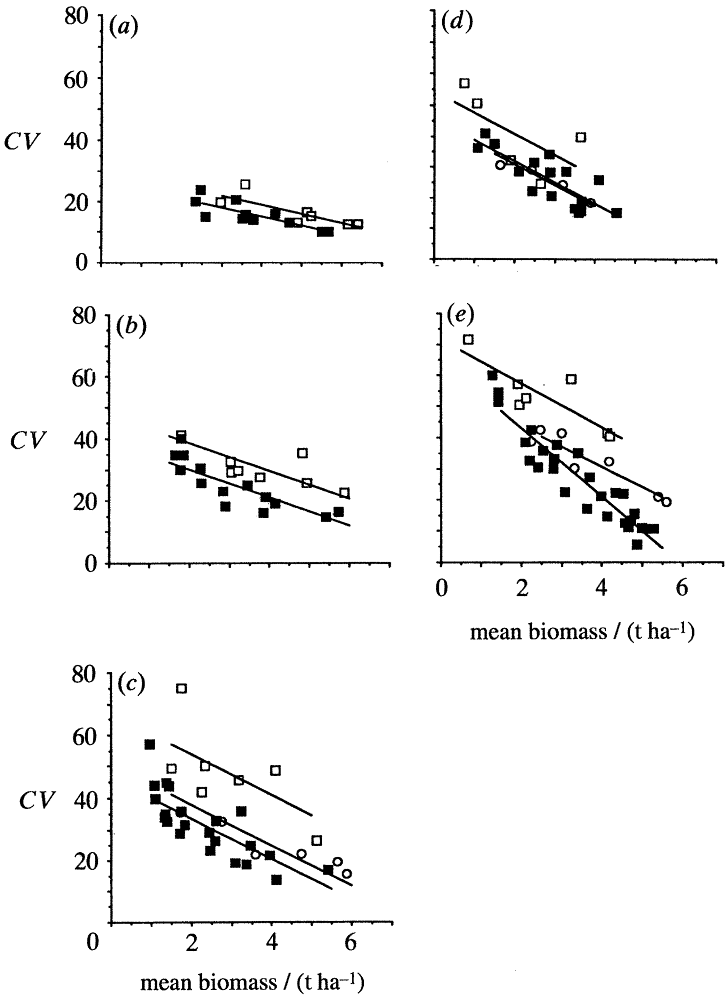

Figure 3. Relations between coefficient of variation (CV) and mean biomass (b) 1862–1991. Symbols as for figure 2. Regression parameters are as follows. (*a*) 1862. Non-ammonium plots $CV = 26.71 - 2.911b$; ammonium plots $CV = (26.71 + 3.79) - 2.911b$. (*b*) 1877. Non-ammonium plots $CV = 39.01 - 4.487b$; ammonium plots $CV = (39.01 + 8.44) - 4.487b$. (*c*) 1919. Non-ammonium plots $CV = 46.57 - 6.507b$; ammonium, limed plots $CV = (46.57 + 4.33) - 6.507b$; ammonium plots $CV = (46.57 + 20.36) - 6.507b$. (*d*) 1948. Non-ammonium plots $CV = 45.60 - 6.86b$; ammonium, limed plots $CV = (45.60 - 0.94) - 6.86b$; ammonium plots $CV = (45.60 + 8.81) - 6.86b$. (*e*) 1991. Non-ammonium plots $CV = 64.93 - 10.955b$; ammonium, limed plots $CV = (64.93 - 8.24) + (-10.995 + 4.47)b$; ammonium plots $CV = (64.93 + 6.57) + (-10.995 + 3.95)b$.

negative relation with CV over most of the timespan from 1862 to the present. Higher-biomass plots have generally been less variable than lower-biomass ones, although we cannot tell how much of this effect is intrinsic to the statistical relation between the mean and CV of biomass.

The multiple regressions offer a less clear-cut conclusion about the relation between species richness and variability. After allowing for the effect of biomass, the observed relation between species richness and CV was negative in 29 of the 42 years analysed, but this relation was significant on only three occasions. This includes the year for which we have the largest sample size (34 plots), which is also the year of our own survey of the PGE (1991). Had we been reporting the results of a one-off survey in 1991 we might have concluded that the negative relation between species richness and variability was the best support yet for the hypothetical relation between variability and diversity, coming as it does from 34 adjacent and clearly comparable communities. As it is, we have a historical record of these communities dating from near their point of common origin in a single meadow community of the early 1850s and this forces us to a more tentative conclusion. The hypothesized relationship between species richness and variability may exist, but if so it is a weak one. Of course, coefficient of variation of hay biomass is not the only possible measure of variability we might have used, but it is the simplest available and therefore the easiest to interpret. A study based on variability of species composition, for which there are much less extensive data in the record of the PGE, will be the subject of a separate report (J. Silvertown *et al.*, unpublished).

The relation between soil acidification and variability was a strong one. One explanation for the greater variability of plots with acidified soil is that the physiological stresses imposed by low pH make the plants in these communities more susceptible to adverse weather conditions. Known interactions between soil reaction, plant nutrition and soil

Table 3. *Values of* t *and coefficients for the models* CV= *constant* + *biomass* + *no.* spp., by year.

((*a*) Non-ammonium plots 1862–1991, including ammonium plots receiving lime from 1903; (*b*) ammonium nitrogen plots without lime, 1862–1991. Significance levels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; d.f. = no. plots −3.)

(*a*)	*t*-values for terms			Coefficients	
Year	biomass	no. spp.	no. plots	biomass	no. spp.
1862	−2.11	−0.45	11	−3.77	−0.152
1867	−4.35**	−1.38	11	−8.56**	−0.655
1871	−0.68	−0.22	4	−15.4	−1.54
1872	−2.12	0.14	14	−7.53	0.12
1874	−4.73*	1.15	5	−12.2*	0.397
1875	−6.46***	−0.38	8	−12.85***	−0.103
1876	−4.76**	−0.64	8	−9.82**	−0.141
1877	−6.52***	−3.12**	14	−8.61***	−0.709**
1878	−4.97***	−1.78	12	−8.56***	−0.526
1879	−5.01***	−2.00	11	−8.95***	−0.924
1880	−5.71***	−1.35	11	−6.96***	−0.239
1881	−7.61***	−2.16	10	−6.992***	−0.52
1882	−6.58***	−2.52*	10	−9.06***	−0.768*
1883	−2.61	−0.62	6	−6.04	−0.239
1903	−5.80***	−0.14	9	−7.46***	−0.032
1914	−6.29***	−0.96	29	−8.92***	−0.2
1919	−5.81***	−1.58	29	−7.27***	−0.363
1921	−5.13***	−1.69	20	−6.46***	−0.454
1922	−2.98*	−0.67	16	−6.64*	−0.34
1923	−2.54*	1.00	18	−4.37*	0.28
1924	−2.75*	0.70	16	−6.09*	0.268
1925	−2.42*	0.69	18	−4.31*	0.198
1926	−3.02*	−0.34	13	−8.05*	−0.155
1927	−2.42*	0.13	12	−3.97*	0.041
1928	0.67	2.78*	8	0.81	0.507
1929	−5.08*	−3.11	6	−9.35**	−0.972
1931	−1.48	−0.81	5	−6.37	−0.615
1933	1.04	1.59	5	6.34	2.03
1935	−1.27	0.37	8	−3.55	0.154
1936	−2.41*	−0.38	10	−6.70*	−0.153
1937	−1.78	0.12	10	−7.18	0.068
1938	−3.70**	−0.18	10	−7.13**	−0.052
1939	−4.33**	−0.92	11	−8.70**	−0.258
1940	−3.56**	0.31	11	−7.14**	0.082
1941	−2.81	−0.32	5	−9.30	−0.149
1946	−3.47*	1.60	9	−12.84*	1.091
1947	−3.44**	0.16	16	−6.85**	0.052
1948	−5.21***	−0.97	20	−7.66***	−0.202
1949	−5.40***	−0.63	17	−7.03***	−0.127
1975	−1.77	−0.86	12	−3.18	−0.432
1976	−1.30	−0.98	6	−4.57	−0.861
1991	−11.07***	−3.14**	34	−12.25***	−0.759**

(*b*)	*t*-values for terms			Coefficients	
Year	biomass	no. spp.	no. plots	biomass	no. spp.
1862	−1.00	0.18	8	−2.37	0.124
1867	−3.53*	3.03*	9	−3.077*	0.618*
1872	−5.00**	−0.36	8	−5.82**	−0.069
1877	−4.51**	−2.76*	8	−5.61**	−0.611
1914	−1.65	−0.54	7	−12.00	−1.38
1919	−5.09**	−3.49*	7	−12.26**	−4.13
1947	−1.76	0.29	6	−3.80	0.41
1948	−1.47	−1.19	5	−6.79	−0.806
1973	−1.17	−2.33	8	−1.93	−1.052
1991	−2.80*	0.11	7	−7.18*	−0.19

moisture deficit certainly make this likely. With time, *CV* increased significantly across plots, independently of biomass (compare elevations in figure 3 for 1862 and 1991). Some of this increase may have been due to reductions in plot size which took place in the early 1900s and in 1965 when plots were divided for liming treatments, but this is unlikely because the trend of increasing variability through time was evident as early as 1877 (compare elevations in figure 3 for 1862 and 1877), before plots were divided. Even the divided plots remained large by the standards of most ecological experiments. It is known that pH has fallen on all plots in the PGE, including those not receiving ammonium sulphate fertilizer (Johnston *et al.* 1986), and this is a likely explanation for the general trend of increasing variability in the PGE communities as a whole.

If the relation between species number (n) and *CV* is a real one, what might be its cause? There are three possibilities: (i) n directly affects *CV*; (ii) *CV* directly affects n; (iii) correlation between n and *CV* is the indirect effect of separate correlations between n, *CV* and a third variable. Case (i) would occur if species differed in their optimum climatic conditions for growth. The total biomass of a plot with many species would then be better buffered against climatic variation than that of a plot with fewer species. In case (ii) where the causative arrow is reversed, a lower species richness in less stable plots could be the result of competitive exclusion in years of unusually high community productivity. Many of the less competitive species characteristic of unproductive grassland would be particularly susceptible. In case (iii) both species loss (and hence n) and biomass variability may be linked through correlation with a third, driving variable. This could explain why the correlation between *CV* and n is a fairly weak one. Our analysis suggests that the third variable cannot be biomass *per se* because the correlation between variability and n occurs after the linear effect of biomass has been allowed for (table 3). We suggest that the unknown variable, if it exists, may be response to drought. Annual variation in the productivity of English hay meadows correlates strongly with rainfall (Smith 1960), and rainfall interacts with nitrogen fertilizer treatment in affecting plot biomass within the PGE (Cashen 1947). Plots that are particularly susceptible to drought will have a more variable biomass and may also lose species in dry years. It is not possible to choose among cases (i)–(iii) on present evidence, but all the hypotheses advanced under these three scenarios are susceptible to tests using PGE data, including botanical records of the early years of the PGE when most extinctions occurred. This, and other explorations of the unique records of the PGE, will be the subject of future publications.

This work was supported by a research grant from the Natural Environment Research Council. J. Potts acknowledges the support of the Leverhulme Trust. We thank Gavin Ross, Joe Perry and J. Bastow Wilson for comments on the manuscript.

REFERENCES

Brenchley, W.E. & Warington, K. 1958 *The Park Grass Plots at Rothamsted 1856–1949*. Harpenden, Herts: Rothamsted Experimental Station.

Burrows, C.J. 1990 *Processes of vegetation change*. London: Unwin Hyman.

Cashen, R.O. 1947 The influence of rainfall on the yield and botanical composition of permanent grass. *J. agric. Sci.* **37**, 1–10.

Connell, J.H. & Sousa, W.P. 1983 On the evidence needed to judge ecological stability or persistence. *Am. Nat.* **121**, 789–824.

DeAngelis, D.L. 1975 Stability and connectance in food web models. *Ecology* **56**, 238–243.

Elton, C.S. 1927 *Animal Ecology*. London: Sidgwick & Jackson.

Elton, C.S. 1958 *The ecology of invasions by animals and plants*. London: Methuen (1972; subsequent reprints by Chapman & Hall, London).

Goldberg, D. and Turner, R.M. 1986 Vegetation change and plant demography in permanent plots in the Sonoran desert. *Ecology* **67**, 695–712.

Johnston, A.E., Goulding, K.W.T. & Poulton, P.R. 1986 Soil acidification during more than 100 years under permanent grassland and woodland at Rothamsted. *Soil Use Mgnt* **2**, 3–10.

Lawes, J.B. & Gilbert, J.H. 1863 The effect of different manures on the mixed herbage of grassland. *J. R. agric. Soc.* **24**, 131–164.

Lawes, J.B. & Gilbert, J.H. 1880 Agricultural, botanical and chemical results of experiments on the mixed herbage of permanent meadow, conducted for more than twenty years in succession on the same land. Part 1. The agricultural results. *Phil. Trans. R. Soc. Lond.* **171**, 289–415.

Lawes, J.B., Gilbert, J.H. & Masters, M.T. 1882 Agricultural, botanical and chemical results of experiments on the mixed herbage of permanent meadow, conducted for more than twenty years in succession on the same land. Part II. The botanical results. *Phil. Trans. R. Soc. Lond.* **173**, 1181–1413.

May, R.M. 1974 *Stability and complexity in model ecosystems*. Princeton, New Jersey: Princeton University Press.

McNaughton, S.J. 1993 Biodiversity and function of grazing ecosystems. In *Biodiversity and ecosystem function* (ed. E.-D. Shulze & H. A. Mooney), pp. 361–383. Berlin: Springer-Verlag.

Olff, H. & Bakker, J.P. 1991 Long-term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *J. appl. Ecol.* **28**, 1040–1052.

Pimm, S.L. 1991 *The balance of nature?* Chicago, Illinois: Chicago University Press.

Rothamsted Experimental Station 1934 *Rothamsted Experimental Station Report for 1934*. Harpenden, Herts: Rothamsted Experimental Station.

Rothamsted Experimental Station 1935 *Rothamsted Experimental Station Report for 1935*. Harpenden, Herts: Rothamsted Experimental Station.

Rothamsted Experimental Station 1936 *Rothamsted Experimental Station Report for 1936*. Harpenden, Herts: Rothamsted Experimental Station.

Rothamsted Experimental Station 1937 *Rothamsted Experimental Station Report for 1937*. Harpenden, Herts: Rothamsted Experimental Station.

Rothamsted Experimental Station 1938 *Rothamsted Experimental Station Report for 1938*. Harpenden, Herts: Rothamsted Experimental Station.

Rothamsted Experimental Station 1952 *Results of the field experiments 1939–1947*. Harpenden, Herts: Rothamsted Experimental Station.

Silvertown, J. 1987 Ecological stability: a test case. *Am. Nat.* **130**, 807–810.

Silvertown, J. 1980 The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *J. appl. Ecol.* **17**, 491–504.

Silvertown, J., Dodd, M.E., McConway, K., Potts, J. & Crawley, M. 1994 Rainfall, biomass variation and community composition in the Park Grass Experiment. *Ecology*. (In the press.)

Smith, L.P. 1960 The relation between weather and meadow hay yields in England. *J. Brit. Grassland Soc.* **15**, 203–208.

Warren, R.G. & Johnston, A.E. 1964 The Park Grass Experiment. *Rothamsted Experimental Station Report for 1963*, pp. 240–262. Harpenden, Herts: Rothamsted Experimental Station.

Warren, R.G., Johnston, A.E. & Cooke, G.W. 1965 Changes in the Park Grass Experiment. *Rothamsted Experimental Station Report for 1964*, pp. 224–228. Harpenden, Herts: Rothamsted Experimental Station.

White, J. 1985 The census of plants in vegetation. In *The population structure of vegetation* (ed. J. White), pp. 33–88. The Hague: Dr W. Junk.

Williams, E.D. 1978 *Botanical composition of the Park Grass plots at Rothamsted 1856–1976*. Harpenden, Herts: Rothamsted Experimental Station.

Wolda, H. 1978 Fluctuations in abundance of tropical insects. *Am. Nat.* **112**, 1017–1045.

Received 28 February 1994; accepted 18 May 1994