



Community Stability: A 60-Year Record of Trends and Outbreaks in the Occurrence of Species in the Park Grass Experiment

Mike Dodd; Jonathan Silvertown; Kevin McConway; Jacqueline Potts; Mick Crawley

Journal of Ecology, Volume 83, Issue 2 (Apr., 1995), 277-285.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28199504%2983%3A2%3C277%3ACSA6RO%3E2.0.CO%3B2-D>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://uk.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Journal of Ecology is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://uk.jstor.org/journals/briteco.html>.

Journal of Ecology

©1995 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor@mimas.ac.uk.

©2003 JSTOR

Community stability: a 60-year record of trends and outbreaks in the occurrence of species in the Park Grass Experiment

MIKE DODD, JONATHAN SILVERTOWN, KEVIN McCONWAY,*
JACQUELINE POTTS† and MICK CRAWLEY‡

Biology Department, and *Department of Statistics, The Open University, Walton Hall, Milton Keynes, MK7 6AA, †Department of Statistics, Rothamsted Experimental Station, Harpenden, Herts. and ‡Department of Pure & Applied Biology, Imperial College, Silwood Park, Ascot, Berks., UK

Summary

1 A 60-year time-series of species recorded in visual surveys of the plant communities of the Park Grass Experiment is analysed to detect changes through time in the frequency of species on seven plots with acidified soil and on 35 non-acidified plots.

2 Of 14 species recorded on the acidified plots, eight decreased with time, one (*Agrostis capillaris*) increased, four showed no trend and one (*Chamerion angustifolium*) showed an outbreak with a peak in 1946. Of the 43 species recorded on the non-acidified plots, six increased, five decreased, 10 showed outbreaks and 22 showed no trend.

3 We used discriminant analysis to try to identify combinations of seven life-history and two habitat variables that would correctly classify species according to how their frequency changed on the non-acidified plots. Habitat variables (mean pH and mean hay yield of plots) were poor discriminators, but some life history variables (notably ruderalness, mating system and flowering time) were more successful.

4 Species which increased were more outcrossing whereas outbreak species were more selfing than the average for all species, both were more ruderal than average. We speculate that the ruderal species were all well equipped to spread across plots, but that only outcrossing species possessed sufficient genetic variation to be able to sustain a broad distribution in the heterogeneous environment represented by the PGE.

5 In view of the otherwise stable nature of the Park Grass communities we suggest that the existence of outbreaks in a significant number of species calls for a re-evaluation of the concept of the stable plant community.

Keywords: genetic variation, mating system, ruderal, stability, time-series

Journal of Ecology (1995) **83**, 277–285

Introduction

The stability of ecological systems, defined as the tendency to return to an equilibrium state following perturbation, is a property of central interest in population and community ecology, but the limited state of our knowledge is neatly captured by the interrogative title of Pimm's (1991) recent book on the subject: 'The balance of nature?'. The situation is arguably worse for plant communities because the concept of succession has so dominated the study of these communities through time. This is not to deny that change is the prevailing state of plant communities in the long term, but only to point out that even successional communities may show some stab-

ility in the face of external perturbation. If we know little about the stability properties of plant communities, we know even less about how individual species behave within stable communities.

The plots of the Park Grass Experiment (PGE) at Rothamsted, England are probably the best candidates anywhere for the status of stable, equilibrium plant communities. The today PGE contains an array of different grassland plant communities that originate from the repeated application of different fertilizer treatments to plots within a uniform hay meadow community (Dodd *et al.* 1994a). Following the start of the experiment in 1856 changes in botanical composition were initially rapid, but by the beginning of the twentieth century most of these changes had

ceased and no significant trends were detectable in the proportions by weight of grasses, legumes and ‘other species’ (their GLO ratio) in the hay on seven of the nine plots tested (Silvertown 1979, 1980). Each plot had its own characteristic GLO ratio, although this ratio did vary considerably from year to year on all plots (Silvertown 1987), driven by annual variation in hay biomass and rainfall during the growing season (Silvertown *et al.* 1994). These observations are evidence of stability because they demonstrate that a range of long-term equilibria in community composition were maintained despite measurable external perturbation by the weather.

Although the GLO ratio in PGE communities was apparently in dynamic equilibrium there is evidence of trends in the abundance of some of the plant species within the components which make up the GLO categories (Williams 1978). Silvertown (1980) drew the conclusion from this that the abundance of GLO components was regulated independently of the abundance of their individual, constituent species. Using annual variation in the hay biomass of plots as another measure of stability in the PGE we have found a strong tendency for more species-rich plots to be more stable (i.e. less variable) than less species-rich ones (Dodd *et al.* 1994b).

Until now our knowledge of the dynamics of individual species in the PGE this century has been derived from a very patchy series of records based on the separation and weighing of species in the hay. No continuous record of individual species for more than a few years at a time has been available. In this paper we present the first analysis of a newly available dataset that records the species noted in visual surveys of every plot each year between 1920 and 1979. These data are used to detect trends and outbreaks (increases followed by decreases) for individual species in PGE communities, some of which have hitherto been regarded as stable.

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 0.1 and 0.2 ha. Fertilizer treatments were applied to 18 plots and two plots (nos 3 and 12) were kept as unfertilized controls (Fig. 1). Fertilizers continue to be applied on a regular schedule to the present day. Methods of fertilizer application, hay cutting and other details of experimental procedure in the nineteenth century are given by Lawes & Gilbert (1863, 1880, 1882) and later details are reviewed by Williams (1978). By the end of the nineteenth century some degree of acidification and species loss was observed on all plots and a liming

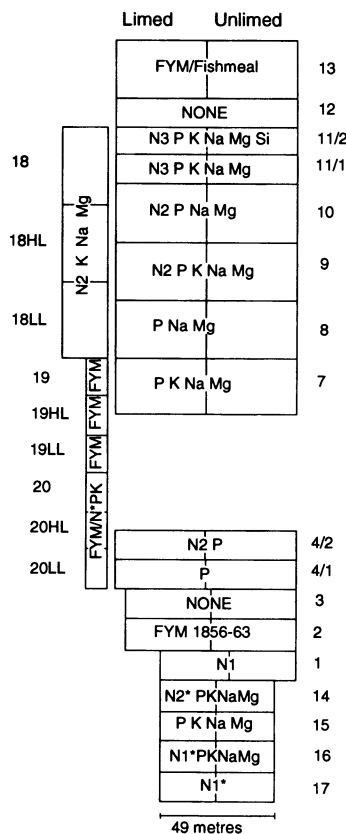


Fig. 1 Plan of the Park Grass Experiment showing fertilizer and liming treatments of those plots used in the analysis. Asterisks indicate plots where nitrogen was applied in the form of sodium nitrate. Other nitrogen treatments were applied as ammonium sulphate.

scheme was introduced (Johnston *et al.* 1986). 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 subplots were limed. One quarter of the original area of each plot has never had lime. The subplots which resulted from the division of the original plots into quarters in 1965 were between 160 and 500 m² in area. Only those plots which were recorded throughout the whole of the 1920–79 period were used in our analysis so those parts of the original plots given new liming treatments in 1965 have been omitted. The 43 plots used in the analysis are shown in Fig. 1.

VISUAL SURVEYS 1920–79

Visual surveys of the species present on every plot were carried out every year between 1920 and 1979. The surveys were not exhaustive; only species in flower and those which were obvious in the vegetative state were recorded and, on average, fewer species were detected than in the botanical analysis of hay samples (Williams 1978). Nevertheless, the surveys do provide a useful means of describing changes with time in the occurrence of particular species. The surveys were carried out by four people (Brenchley, Warington, Thurston and Williams) each one training the

following worker. Surveys were done from the edge of the plot to avoid damage to the vegetation. In the early years there were many surveys per year but the frequency was subsequently reduced and standardized at two (or sometimes three) surveys per year (Fig. 2). The number of samples per year had little effect on the total number of species recorded per plot per year except during the first few years when the early spring recording found vernal species such as *Cardamine pratensis*, *Carex caryophylla*, *Fritillaria meleagris*, *Hyacinthoides non-scripta* and *Ranunculus ficaria*. These species were not usually found in the later samples and as they were also generally rare in the experiment as a whole they were excluded from the analysis. The remaining species were scored as present on a plot in a particular year if they were recorded there in any survey during that year.

DATA ANALYSIS

Presence/absence records were accumulated across seven acidified plots (those in Fig. 1 receiving ammonium-N and no lime) and 36 non-acidified plots (all others labelled in Fig. 1) separately to give a frequency of occurrence for each species in each year on the two types of plot. Change in the frequency of individual species with time was analysed by logistic regression. A hierarchical approach was adopted. Firstly linear trends were tested, then if none were significant, a quadratic regression model was used. Four patterns of change were tested: (1) upward or (2) downward trends were tested using linear regression models and (3) outbreaks were tested by quadratic regression after the linear effect was removed. (4) A lack of change was identified when the fit of both linear and quadratic models was rejected. In preliminary analyses we also compared patterns on limed vs. unlimed plots and on nitrogen vs. no-nitrogen plots. Neither of these contrasts indicated that lime or nitrogen on their own affected species' patterns.

Though the model used to identify outbreaks was a simple one, in practice quadratic curves fitted the data adequately. Since the position of the maximum of a quadratic curve is a simple and smooth function of the coefficients of the curve, and since estimates of those coefficients and their standard errors were

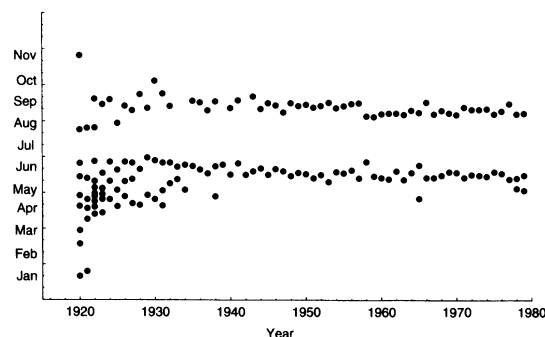


Fig. 2 Sampling dates for visual surveys made 1920–79.

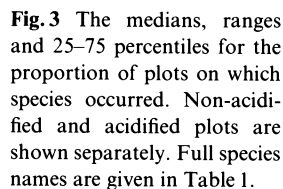
calculated in the regression, it was possible to estimate the positions of the maxima for those species where an outbreak was identified using a two-term Taylor series approximation (see e.g. Meyer 1965; p. 128). Similarly, the standard errors of these estimated peak years can be estimated. The accuracy of the approximation involved was increased by using (year – 1950) instead of simply (year) as the explanatory variable in the regressions. This has the effect of reducing the correlation between the estimates of the linear and quadratic coefficients.

Because a large number (114) of regressions were carried out, we adopted $P < 0.0005$ as a stringent criterion for statistical significance. As the data were collected from the same plots in each year residuals from the linear + quadratic regression for each species were tested for autocorrelation with lags 1–15.

As an hypothesis-generating tool to explain why species on the non-acid plots behaved differently from each other we used discriminant analysis (in the computer package STATISTICA) to try to identify combinations of seven life-history and two habitat variables that would correctly classify species into each of the four groups. The two habitat variables calculated for each species were the mean hay yield of PGE plots (1920–79) where the species occurred and the mean pH of those plots. The latter was calculated using CANOCO (ter Braak 1987; McConway *et al.* unpublished). Life history variables used were: (1) maximum height; (2) earliest and (3) latest month of flowering; (4) mating system on an ordinal scale from 1 for obligately outcrossing to 5 for obligate selfing; (5) seed weight; and numerical scores for (6) stress-tolerance and (7) ruderalness. Variables 1–4 were obtained from the Ecological Flora Database (Fitter & Peat 1994) and 5–7 were taken from Grime *et al.* (1987). Separate discriminant analyses were performed using the habitat variables alone, the life-history variables alone and all nine variables together.

Results

The frequencies of most species were very variable over the 60-year period (Fig. 3), even where no significant trends were apparent. Half the species (22/43 spp.) on non-acidified plots and about a quarter (4/14 spp.) of those on acidified plots showed no trends or outbreaks (Table 1). Nearly a quarter of species (10/43 spp.) on non-acidified plots displayed an outbreak while only one species (*Chamerion angustifolium*) did so on acidified plots (Table 1). Most species showing a trend on acidified plots declined in frequency (8/9 spp.) while almost equal numbers of species increased (5/11 spp.) or decreased (6/11 spp.) on non-acidified plots (Table 1). Examples of these patterns are shown in Figs 4 and 5. Maps showing how *Tragopogon pratensis* increased and then decreased across non-acidified plots during an outbreak are shown in Fig. 6. Regression statistics are presented in Tables 2 and 3



Classification of species into the four groups using discriminant analysis based on only the two habitat variables was unsuccessful (Table 4). None of the six species that increased or the five that decreased were assigned to their correct group and the overall percentage correct was only very slightly (3%) above that achieved by assigning all species to the single most common group. The life history variables were more successful discriminators, and in particular 'late flowering' ($P = 0.021$), 'mating system' ($P = 0.018$) and 'ruderalness' ($P = 0.040$) all varied significantly between groups (Table 4). The discriminant analysis using all nine variables performed no better than the analysis using only the seven life-history variables (results not shown).

The time series for species' frequencies provide an overview of patterns present over a long period across many plots and complement the information previously obtained from botanical separations which afford only occasional snapshots of the quantitative composition of individual plots. The new perspective obtained from the time series shows that outbreaks were surprisingly common among species on the non-acidified plots; a result that could not have been predicted from the sparse data available from botanical separations. In fact this result is unique because ecological time series half the length of ours would normally be regarded as 'long-term', but would not be long enough to detect the outbreaks we have found. Of course we still cannot tell whether the trends and outbreaks detected are part of longer-term changes or cycles.

Life history variables were reasonably successful in correctly classifying increasing species (67% correct, Table 4) but classified only one decreasing species correctly (20% correct, Table 4). Increasing species flowered (and were therefore capable of setting seed) later into the year, were more out-crossing and more ruderal than the average (Table 4). These traits sug-

Table 1 Trends 1920–79 in the number of acid and non-acid plots occupied by species in the PGE. The peak year for outbreak species is shown in brackets \pm 95% confidence limits

Trend	Acid (7 plots)	Non-acid (35 plots)
Increase	<i>Agrostis capillaris</i>	<i>Anthoxanthum odoratum</i> <i>Heracleum sphondylium</i> <i>Leontodon hispidum</i> <i>Plantago lanceolata</i> <i>Ranunculus acris</i> <i>Trifolium pratense</i>
<i>n</i>	1	6
Decrease	<i>Arrhenatherum elatius</i> <i>Alopecurus pratensis</i> <i>Conopodium majus</i> <i>Centaurea nigra</i> <i>Dactylis glomerata</i> <i>Festuca rubra</i> <i>Galium verum</i> <i>Rumex acetosa</i>	<i>Ajuga reptans</i> <i>Filipendula ulmaria</i> <i>Primula veris</i> <i>Stellaria graminea</i> <i>Veronica chamaedrys</i>
<i>n</i>	8	5
Outbreak	<i>Chamerion angustifolium</i> (1946 \pm 3)	<i>Agrimonia eupatoria</i> (1947 \pm 2) <i>Bromus hordeaceus</i> (1948 \pm 1) <i>Cerastium fontanum</i> (1945 \pm 2) <i>Festuca rubra</i> (1954 \pm 2) <i>Galium verum</i> (1949 \pm 2) <i>Pilosella officinarum</i> (1942 \pm 4) <i>Leucanthemum vulgare</i> (1933 \pm 12) <i>Linum catharticum</i> (1949 \pm 4) <i>Lotus corniculatus</i> (1948 \pm 2) <i>Tragopogon pratensis</i> (1952 \pm 1)
<i>n</i>	1	10
No trend	<i>Anthoxanthum odoratum</i> <i>Holcus lanatus</i> <i>Poa pratensis</i> <i>Potentilla reptans</i>	<i>Agrostis capillaris</i> <i>Alopecurus pratensis</i> <i>Arrhenatherum elatius</i> <i>Achillea millefolium</i> <i>Anthriscus sylvestris</i> <i>Briza media</i> <i>Conopodium majus</i> <i>Centaurea nigra</i> <i>Dactylis glomerata</i> <i>Festuca pratensis</i> <i>Holcus lanatus</i> <i>Helictotrichon pubescens</i> <i>Knautia arvensis</i> <i>Luzula campestris</i> <i>Lathyrus pratensis</i> <i>Poa pratensis</i> <i>Potentilla reptans</i> <i>Pimpinella saxifraga</i> <i>Prunella vulgaris</i> <i>Rumex acetosa</i> <i>Sanguisorba minor</i> <i>Trifolium repens</i>
<i>n</i>	4	22
Total spp.	14	43

gest that increasing species may have been those that were better equipped to produce seed in the regrowth after the June hay crop and that this, perhaps combined with the greater genetic variation among progeny that is to be expected in outcrossing species, predisposed them to spread through the PGE plots. ‘Ruderals’ are defined by Grime *et al.* (1987) as plants exploiting disturbed environments where physiological stress is low.

Outbreaks are the most difficult pattern to explain in a system otherwise at equilibrium. Two events in the management of the PGE that might explain outbreaks should be considered. Liming was initiated on just over half the plots in 1903, seventeen years before the first visual survey. This appears not to be responsible for initiating outbreaks because outbreaks were also present on unlimed plots. From 1960 onwards, two thirds of the way through our time series, the

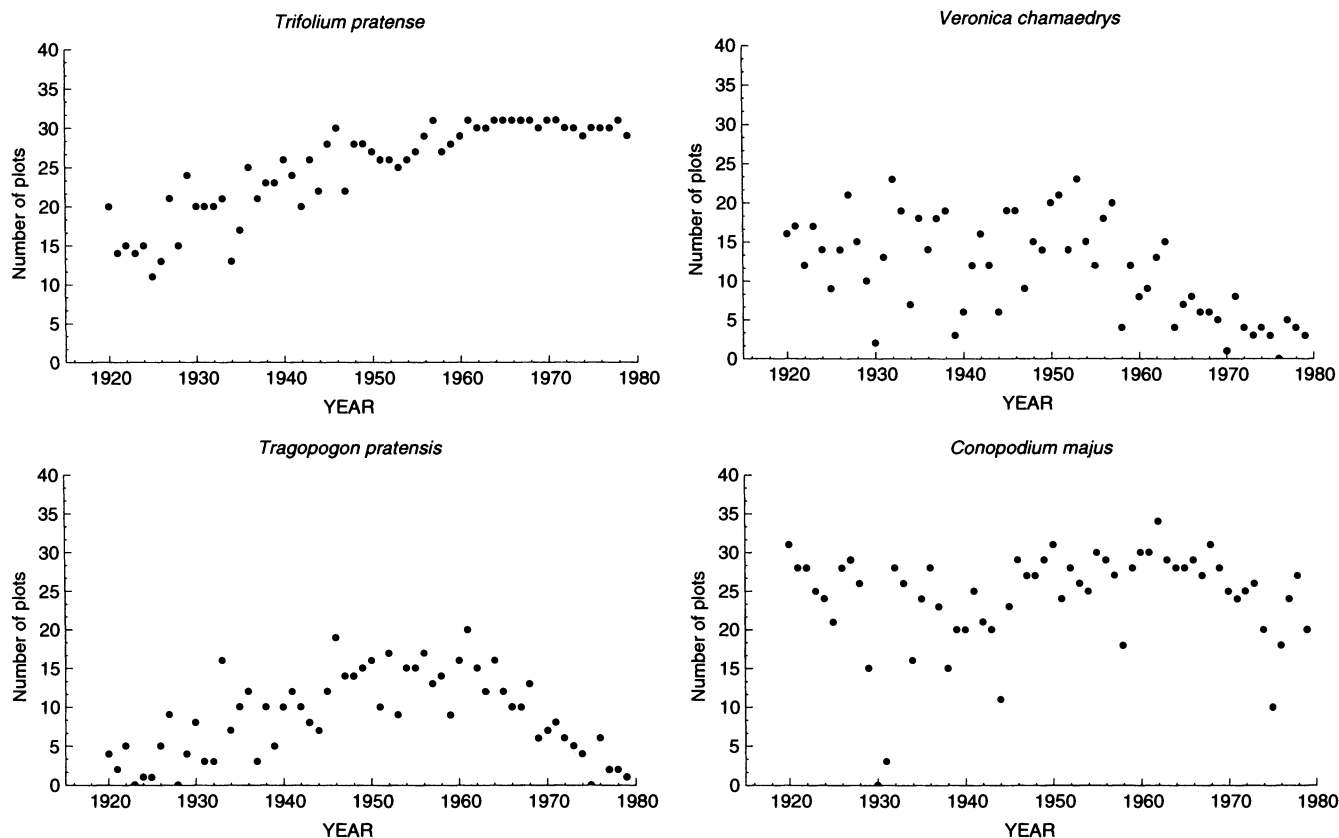


Fig. 4 Changes in the frequency of some representative species on non-acidified plots: (a) increase in *Trifolium pratense*; (b) decrease in *Veronica chamaedrys*; (c) outbreak in *Tragopogon pratensis*; (d) fluctuation in *Conopodium majus*.

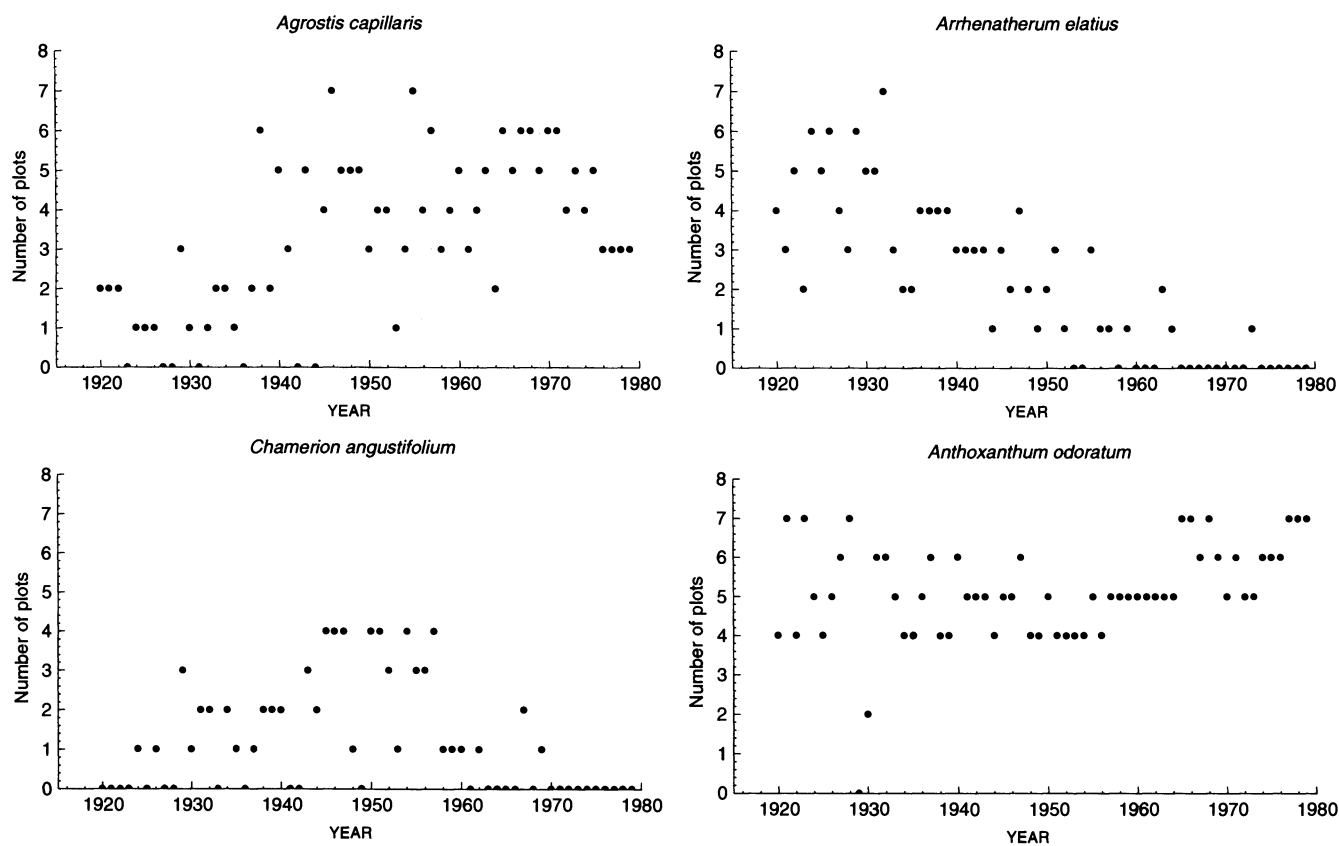


Fig. 5 Changes in the frequency of some representative species on acidified plots: (a) increase in *Agrostis capillaris*; (b) decrease in *Arrhenatherum elatius*; (c) outbreak in *Chamerion angustifolium*; (d) fluctuation in *Anthoxanthum odoratum*.

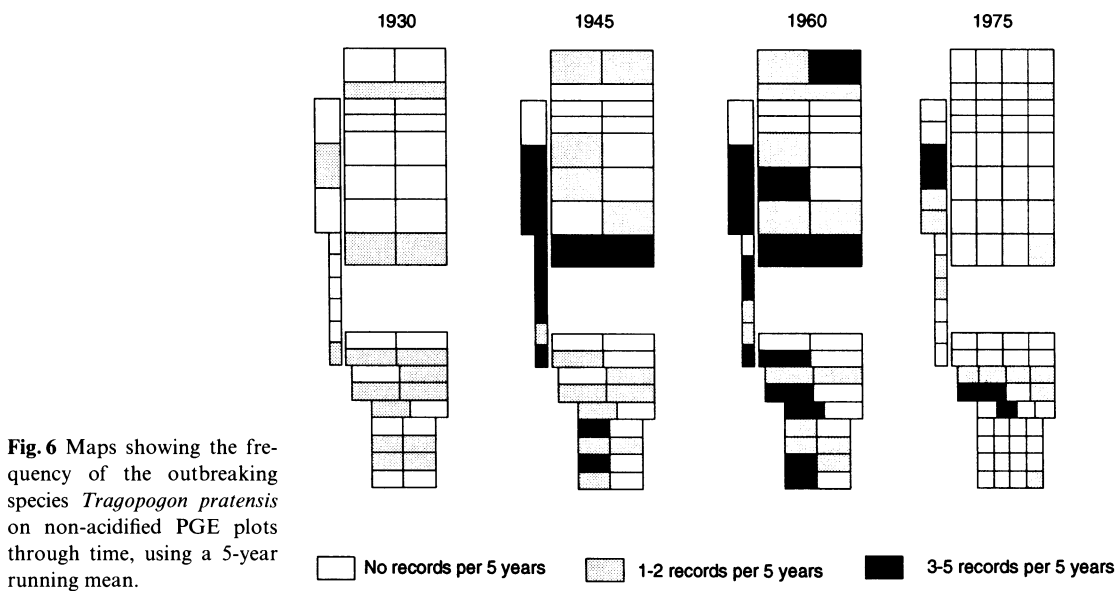


Fig. 6 Maps showing the frequency of the outbreaking species *Tragopogon pratensis* on non-acidified PGE plots through time, using a 5-year running mean.

Table 2 Coefficients (*b*) and probability levels (*P*) for linear regressions and linear (*b*₁, *P*₁) and quadratic (*b*₂, *P*₂) terms for quadratic regressions for the acid plots. Species with significant autocorrelation (lag 1 or 2) are indicated by crosses: +, *P* < 0.05; ++, *P* < 0.01; +++, *P* < 0.001. All significant autocorrelations were positive

Species	Linear regression		Quadratic regression			
	<i>b</i>	<i>P</i>	<i>b</i> ₁	<i>b</i> ₂	<i>P</i> ₁	<i>P</i> ₂
<i>Agrostis capillaris</i>	0.043	0.0000	0.045	−0.00151	0.0000	0.0095
<i>Alopecurus pratensis</i>	−0.130	0.0000	−0.131	0.00000	0.0000	*
<i>Anthoxanthum odoratum</i>	0.019	0.0139	0.024	0.00136	0.0011	0.0061
<i>Arrhenatherum elatius</i>	−0.086	0.0000	−0.113	−0.00198	0.0000	0.0052
<i>Centaurea nigra</i>	−0.027	0.0001	−0.029	−0.00023	0.0004	0.5952
<i>Chamerion angustifolium</i>	−0.011	0.3200	−0.037	−0.00545	0.0000	0.0000
<i>Conopodium majus</i>	−0.058	0.0000	−0.065	−0.00059	0.0000	0.3486
<i>Dactylis glomerata</i>	−0.049	0.0000	−0.068	−0.00155	0.0000	0.0416
<i>Festuca rubra</i>	−0.024	0.0001	−0.028	−0.00139	0.0000	0.0001
<i>Galium verum</i>	−0.053	0.0001	−0.092	−0.00234	0.0001	0.0337
<i>Holcus lanatus</i> +	0.000	0.9435	−0.002	−0.00200	0.0033	0.0008
<i>Poa pratensis</i>	−0.024	0.0434	−0.028	−0.00054	0.1049	0.4973
<i>Potentilla reptans</i>	0.003	0.6958	0.002	−0.00163	0.0062	0.0016
<i>Rumex acetosa</i> +++	−0.054	0.0000	−0.058	−0.00175	0.0000	0.0101

harvesting method was changed and the crop was thereafter cut with a forage harvester. All of the outbreaks identified by our analysis peaked and had begun to decline before this date and so this event is also unable to explain these patterns. Most of the outbreaking species peaked at around the same time in the late 1940s to early 1950s, the only exception being *Leucanthemum vulgare* (1933 ± 12) which had the widest confidence limits on the estimate of its peak year.

Having ruled out, so far as we can, changes in management as a cause of the outbreaks on non-acid plots we can apply similar questions to those already employed on species with a directional trend: did outbreak species tend to occur on plots of a particular kind, or did they share a particular type of life history? Once again, the life history variables were much better than the habitat variables in correctly classifying spec-

ies (60% and 30%, respectively, of outbreak spp. correctly classified, Table 4). Outbreak species were more ruderal and more selfing than any other group. As with the increasing species, one might expect ruderal species to be well-equipped to spread across plots, but unlike those species the outbreak species were selfing. Could the low genetic variation expected among the progeny of selfing species explain the failure of outbreaking species to sustain themselves in all the plots to which they spread at their peak?

It has often been suggested in an evolutionary context that the short-term genetic advantage of selfing is offset by a long-term cost due to the inability of such species to adapt to a changing environment (e.g. Maynard Smith 1978). In an environment as heterogeneous as the PGE, could such an effect lead to a boom and bust within as short a time as 60 years? We believe it might if pathogens play a role in reg-

Table 3 Coefficients (b) and probability levels (P) for linear regressions and linear (b_1 , P_1) and quadratic (b_2 , P_2) terms for quadratic regressions for the non-acid plots. Species with significant autocorrelation (lag 1 or 2) are indicated by crosses: +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$. All significant autocorrelations were positive

Species	Linear regression		Quadratic regression			
	b	P	b_1	b_2	P_1	P_2
<i>Achillea millefolium</i>	0.011	0.1485	0.011	-0.00053	0.1970	0.2795
<i>Agrimonia eupatoria</i>	-0.007	0.3118	-0.012	-0.00188	0.0001	0.0000
<i>Agrostis capillaris</i>	0.004	0.6435	0.004	-0.00082	0.3902	0.1981
<i>Ajuga reptans</i> +	-0.027	0.0000	-0.028	-0.00027	0.0000	0.4183
<i>Alopecurus pratensis</i> +++	0.018	0.0005	0.020	0.00043	0.0011	0.1998
<i>Anthoxanthum odoratum</i> ++	0.023	0.0003	0.023	0.00034	0.0010	0.3767
<i>Anthriscus sylvestris</i>	-0.002	0.5800	-0.001	0.00062	0.0118	0.0035
<i>Arrhenatherum elatius</i> ++	0.019	0.0013	0.019	0.00000	0.0060	0.9984
<i>Briza media</i>	-0.000	0.9305	-0.001	-0.00026	0.4618	0.2169
<i>Bromus hordeaceus</i> ++	-0.006	0.5180	-0.011	-0.00275	0.0000	0.0000
<i>Centaurea nigra</i>	0.005	0.4504	0.005	-0.00030	0.5790	0.4693
<i>Cerastium fontanum</i>	-0.012	0.0172	-0.014	-0.00152	0.0000	0.0000
<i>Conopodium majus</i> +++	0.007	0.2685	0.007	-0.00030	0.4198	0.4717
<i>Dactylis glomerata</i>	0.019	0.0180	0.015	-0.00136	0.0011	0.0045
<i>Festuca pratensis</i>	0.010	0.3759	0.010	0.00046	0.5593	0.5367
<i>Festuca rubra</i>	0.015	0.0412	0.014	-0.00183	0.0000	0.0000
<i>Filipendula ulmaria</i>	-0.041	0.0001	-0.045	-0.00040	0.0003	0.5531
<i>Galium verum</i>	-0.002	0.7206	-0.005	-0.00193	0.0000	0.0000
<i>Helictotrichon pubesce</i>	0.022	0.0016	0.021	-0.00044	0.0042	0.3131
<i>Heracleum sphondylium</i>	0.028	0.0000	0.028	0.00026	0.0000	0.3054
<i>Holcus lanatus</i>	0.014	0.0163	0.013	-0.00076	0.0070	0.0414
<i>Knautia arvensis</i>	0.004	0.4312	0.003	-0.00005	0.7264	0.8743
<i>Lathyrus pratensis</i>	0.006	0.2924	0.006	-0.00060	0.1577	0.1087
<i>Leontodon hispidus</i>	0.020	0.0000	0.020	-0.00077	0.0000	0.0004
<i>Leucanthemum vulgare</i>	-0.049	0.0002	-0.173	-0.00619	0.0000	0.0000
<i>Linum catharticum</i>	-0.002	0.7607	-0.006	-0.00228	0.0002	0.0000
<i>Lotus corniculatus</i>	-0.004	0.3472	-0.006	-0.00128	0.0000	0.0000
<i>Luzula campestris</i> ++	-0.023	0.0048	-0.021	0.00061	0.0094	0.2274
<i>Pilosella officinarum</i>	-0.019	0.0137	-0.033	-0.00219	0.0000	0.0000
<i>Pimpinella saxifraga</i>	0.016	0.0054	0.016	0.00028	0.0159	0.4377
<i>Plantago lanceolata</i>	0.032	0.0000	0.027	-0.00123	0.0000	0.0000
<i>Poa pratensis</i> +	0.008	0.2918	0.007	-0.00137	0.0077	0.0034
<i>Potentilla reptans</i>	-0.029	0.0168	-0.032	-0.00034	0.0539	0.6822
<i>Primula veris</i>	-0.061	0.0000	-0.052	0.00069	0.0000	0.2036
<i>Prunella vulgaris</i> ++	-0.009	0.5007	-0.013	-0.00125	0.3179	0.1764
<i>Ranunculus acris</i> ++	0.030	0.0000	0.029	-0.00020	0.0000	0.5275
<i>Rumex acetosa</i> ++	-0.012	0.1105	-0.011	-0.00075	0.0701	0.0961
<i>Sanguisorba minor</i>	-0.006	0.0285	-0.007	-0.00027	0.0278	0.1223
<i>Stellaria graminea</i>	-0.054	0.0000	-0.076	-0.00160	0.0000	0.0201
<i>Tragopogon pratensis</i>	0.009	0.1859	0.011	-0.00284	0.0000	0.0000
<i>Trifolium pratense</i>	0.044	0.0000	0.041	-0.00044	0.0000	0.0214
<i>Trifolium repens</i> ++	-0.003	0.7049	-0.003	-0.00003	0.9297	0.9519
<i>Veronica chamaedrys</i>	-0.026	0.0000	-0.032	-0.00133	0.0000	0.0003

ulating the population density of outbreak species. In 1993 we observed a remarkable increase in the abundance on some PGE plots of *Tragopogon pratensis*, a species belonging to the outbreak group (Fig. 6). This species, which normally exists in very small amounts (< 1%) on a wide range of non-acidified plots, exploded in abundance on the limed parts of plot 18–18% of biomass. Plants at this density were heavily attacked by a rust, probably *Puccinia hysterium*. Because frequency and abundance are correlated, such violent changes in abundance would also be likely to affect distribution among plots.

The single species that experienced an outbreak on the acid plots was *Chamerion angustifolium*, an early

perennial colonist of disturbed and waste ground (Myerscough 1980). There was a great increase in this species on bombed sites in the London area during the Second World War (Lousley 1944) and since *C. angustifolium* has small, wind-blown seeds, its appearance at Park Grass at the same time, culminating in a peak in 1946, may have been more than a coincidence.

About half the species on the non-acid plots showed no trend with time and the vegetation of many of the PGE plots certainly displays some of the behaviour to be expected of stable communities (see evidence given in the Introduction). The unique time-series analysed in this paper shows that outbreaks by individual species may occur even in communities that

Table 4 Means of nine variables and the success (%) of discriminant analyses based on these in correctly classifying species that belonged to groups that increased, decreased, displayed an outbreak or did not change in the visual surveys of the PGE from 1920 to 1979

	Species group				Overall mean	P
	Increase	Decrease	Outbreak	No change		
Number of species*	6	5	10	19		
Habitat variables						
Mean plot yield (t ha ⁻¹)	4.03	3.44	3.32	3.92	3.72	0.218
Mean pH	5.63	5.65	5.71	5.66	5.66	0.973
Correct classifications using habitat variables	0%	0%	30%	86%	51%	
Life history variables						
Maximum height (cm)	85	62	64	80	74	0.280
Earliest flowering (month)	5	4.6	5.6	5.4	5.3	0.103
Latest flowering (month)	8.8	7.4	8.3	7.5	7.9	0.021
Mating system (category)	1.5	2.4	3.5	2.2	2.4	0.018
Seed wt. (category)	3.67	2.60	3.00	3.37	3.23	0.832
Stress – tolerance (category)	1.33	1.60	1.20	1.21	1.28	0.241
Ruderalness (category)	1.17	0.40	1.40	0.74	0.93	0.040
Correct classifications using life history variables	67%	20%	60%	68%	60%	

*Three species were unavailable for the analysis as they contained missing data

are otherwise stable. At the moment we can only speculate as to the causes of such outbreaks, but their occurrence calls for a re-evaluation of the concept of the stable plant community.

Acknowledgements

This work was supported by a research grant from the Natural Environment Research Council. J. Potts acknowledges the support of the Leverhulme Trust.

References

- ter Braak, C.J.F. (1987) *CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis*. TNO Institute of Applied Computer Science, Wageningen, The Netherlands.
- Digby, P.G.N. & Kempton, R.A. (1987) *Multivariate Analysis of Ecological Communities*. Chapman & Hall, UK.
- Dodd, M., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1994a) Application of the British National Vegetation Classification to the communities of the Park Grass Experiment through time. *Folia Geobotanica et Phytotaxonomica*, **29**, 321–334.
- Dodd, M., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1994b) Stability in the plant communities of the Park Grass Experiment: the relationships between species richness, soil pH and biomass variability. *Philosophical Transactions of the Royal Society B*, **346**, 185–193.
- Fitter, A.H. & Peat, H.J. (1994) The ecological flora database. *Journal of Ecology*, **82**, 415–425.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (1987) *Comparative Plant Ecology*. UK, Allen & Unwin.
- 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 and Management*, **2**, 3–10.
- Lawes, J.B. & Gilbert, J.H. (1863). The effect of different manures on the mixed herbage of grassland. *Journal of the Royal Agricultural Society of England*, **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 I. The agricultural results. *Philosophical Transactions of the Royal Society (A & P)*, **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. *Philosophical Transactions of the Royal Society (A & B)*, **173**, 1181–1413.
- Lousley, J.E. (1944) The pioneer flora of bombed sites in central London. *Report of the Botanical Society and Exchange Club of the British Isles*, **12**, 528–531.
- Maynard Smith, J. (1978) *The Evolution of Sex*. Cambridge, Cambridge University Press.
- Meyer, P.L. (1965) *Introductory Probability and Statistical Applications*. Addison-Wesley, Reading, MA.
- Myerscough, P.J. (1980) Biological flora of the British Isles. *Epilobium angustifolium* L. *Journal of Ecology*, **68**, 1047–1074.
- Pimm, S.L. (1991) *The Balance of Nature?* Chicago, Chicago University Press.
- Silvertown, J. (1979) *The maintenance of species diversity in grassland, with particular reference to chalk grassland*. PhD thesis, University of Sussex.
- Silvertown, J. (1980) The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *Journal of Applied Ecology*, **17**, 491–504.
- Silvertown, J. (1987) Ecological stability: a test case. *American Naturalist*, **130**, 807–810.
- Silvertown, J., Dodd, M., McConway, K., Potts, J. & Crawley, M. (1994) Rainfall, biomass variation, and community composition in the Park Grass Experiment *Ecology*, **75**(8), 2430–2437.
- Williams, E.D. (1978) *Botanical Composition of the Park Grass Plots At Rothamsted 1856–1976*. Harpenden, Rothamsted Experimental Station.

Received 10 June 1994

Revised version accepted 19 September 1994