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# THE DYNAMICS OF A GRASSLAND ECOSYSTEM: BOTANICAL EQUILIBRIUM IN THE PARK GRASS EXPERIMENT

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## SUMMARY

(1) The published results of the Park Grass Experiment (PGE), begun in 1856, provide up to 30 yr of annual data which may be used to determine whether the botanical composition of these grasslands was at equilibrium. Data covering a period exceeding 80 yr are available to test for relationships between hay yield (biomass), species diversity, species number and time.

(2) Species diversity and species number show negative relationships with plot biomass and with pH. These relationships were constant over time. The effects of biomass and pH on species number and species diversity were additive.

(3) Analysis of the flora of nine plots, each divided into grasses, legumes and a miscellaneous component showed that these components were at equilibrium.

(4) The effect of various endogenous factors on this botanical equilibrium was examined. No regular or irregular cycles of component biomass operating between years were detected and it is inferred that populations were regulated by processes operating within individual years.

(5) The biomasses of all three components were positively correlated within an unfertilized plot but the floristic components of plots receiving a fertilizer treatment showed few within-plot correlations. By contrast between-plot correlations of components were common for all plots with the exception of those receiving nitrogen fertilizer.

(6) The mechanisms of population regulation which maintained the Park Grass ecosystem at equilibrium are discussed and tests for these are proposed.

## INTRODUCTION

Theoretical discussions of the relationship between the diversity of ecological communities and their stability (e.g. Margalef 1968; May 1974) have taken place largely in the absence of any conclusive evidence of whether such communities are stable or not in the long term. There is a dearth of the type of studies of ecosystems which can provide such evidence, and the most useful data in this respect come from experiments on plagioclimax vegetation (Jones 1933, 1967; Milton 1940; Milton & Davies 1947; Brenchley & Warington 1958). These studies of pastures and hay-meadows have demonstrated that their botanical composition may be controlled by altering the grazing and fertilizer regime. The longest-running experiment on the effect of different fertilizer regimes on hay-meadow grassland, the Park Grass Experiment at Rothamsted, in Hertfordshire, U.K. also

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suggests that such ecosystems reach equilibrium after a period of management (Brenchley & Warington 1958).

Various studies of the effects of exogenous factors on the botanical composition of plots in the Park Grass Experiment (PGE) have been published. Cashen (1947), employing statistical techniques developed by Fisher (1925), reported that rainfall influenced the annual yield of hay from the grassland but that no major influence of rainfall on annual changes in the ratio of legume:grass:other taxonomic components of the flora was detectable. Dramatic increases in the populations of individual species following years of exceptional drought (1871, 1921, 1976) have been recorded (Williams 1978) but these perturbations were rapidly stabilized by the subsequent decrease of the species concerned. The effects of fertilizer applications on botanical composition have been discussed by many authors, two of the most recent accounts being by Thurston (1969) and Williams (1978). The second of these two authors also described recent changes in the botanical composition of the PGE due to the experimental alteration of pH by the controlled application of lime. The general conclusion to be drawn from these studies of the PGE is that all perturbations of the botanical composition of these plots by exogenous factors result in either only a temporary excursion from the existing floristic equilibrium or alternatively in the establishment of a new equilibrium in the ratio of taxonomic components in the flora. Although several authors (Lawes, Gilbert & Masters 1882; Brenchley 1935; Williams 1978) have commented on the dynamic nature of these equilibria, endogenous changes in the botanical composition of the plots which may control these equilibria have received little attention.

The present study sets out to determine the effect of various endogenous factors on the equilibrium botanical composition of the PGE. Correlations between the hay yield of plots and their species diversity (as measured by species number and Shannon function) and changes in these correlations with time are examined. The stability of the botanical composition of plots is determined by analyses of changes in the annual quantities of legumes, grasses and other species in hay crops. Negative correlations of these quantities within plots in successive years is sought as potential evidence of feedback processes capable of maintaining an equilibrium in botanical composition.

## MATERIALS AND METHODS

### *The experiment*

The Park Grass Experiment was begun in 1856 with the object of determining the effect of different fertilizer regimes on the yield of hay from permanent grassland. Seventeen plots were established in species-rich grassland of reputedly uniform botanical composition (Lawes, Gilbert & Masters 1882). These plots were subdivided and supplemented during the course of the following 100 yr (Rothamsted Experimental Station 1970). Initially there was no systematic replication of treatments but plots were subdivided in 1964 (Williams 1978) to provide a series of liming and fertilizer treatments. The present analysis is confined to the period before these changes were introduced.

In the early years of the experiment, Lawes, Gilbert & Masters (1882) noticed significant changes in the botanical composition of the plots according to the fertilizer regimes that they were applying. Samples of hay were taken for botanical analysis from all plots for the first time in 1862. These samples were dried, separated into species and weighed to give an estimate of the absolute and percentage composition of each species in the total cropped biomass. This procedure was repeated at irregular intervals until 1949 with separation of the herbage into three categories (grasses, legumes, miscellaneous species) performed in some intervening years.

Published results from the experiment (Brenchley & Warington 1958; Reps. Rothamsted Experimental Station) provide a source of annual data on the relative proportions by weight of the three vegetation components in nine plots over periods of up to 30 yr. The treatments administered annually to these plots are shown in Table 1. At the beginning of the experiment all plots were 0·05–0·1 ha in extent, but half the area of plots 3, 7, 8, 14, 15, 19, 20 received a dressing of lime, in addition to the usual fertilizer treatment, every 4 yr beginning in 1903. Only data from the unlimed half of these plots are used in the present analysis. Other, minor, differences in the application of treatments to the nine plots are given in Table 1. Details of treatments administered to other plots are given below as required.

TABLE 1. Fertilizer applications to nine Park Grass plots

| Plot number | Treatment | Years* | Number of botanical analyses† | Notes |
|---|---|---|---|---|
| 3 | Unfertilized | 1906–38 | 33 | |
| 4·1 | P | 1906–19 | 14 | |
| 6 | PKNaMg | 1906–19 | 14 | After Ammonium sulphate 1856–68 |
| 7 | PKNaMg | 1906–38 | 33 | |
| 8 | KNaMg | 1906–19 | 14 | |
| 14 | 2 NPKNaMg | 1919–36 | 18 | |
| 15 | PKNaMg | 1906–21 | 13 | No data 1916 |
| 19 | FYM | 1915–37 | 23 | |
| 20 | NPK/FYM | 1915–35 | 21 | FYM every 4th year only. |

* Refers to periods of continuous, annual botanical analysis, dividing the vegetation into legumes, grasses and other species.

† Number of analyses carried out in the period given.

*Annual quantities of fertilizer applied*

| | |
|---|---|
| P | 392 lb Superphosphate containing 29·3 lb P |
| N | 26 lb Sodium nitrate |
| 2N | 52 lb Sodium nitrate |
| K | 300 lb Potassium sulphate (120 lb K) 1856–78 · 500 lb. Potassium sulphate (200 lb K) 1879–1938. |
| Na | 100 lb Sodium sulphate containing 14 lb Na |
| Mg | 100 lb Magnesium sulphate containing 10 lb Mg. |
| FYM | Farmyard manure every 4 yr since 1905 (Equivalent to 200 lb N) |

The treatments administered to the Park Grass plots selectively increased some species present in the original grassland whilst others have been greatly reduced or entirely eliminated (Warren & Johnston 1964). Virtually no new species have entered the experimental area as a whole so that the species composition of each plot during the period under analysis here was a subset of the species present in the grassland before the experiment began.

## *Species number, species diversity and biomass*

The above-ground biomass (hay yield) of the PGE varied between plots according to treatment, and within plots, between years according to rainfall (Cashen 1947). A long-term decline in the biomass of most plots was observed between 1856 and the 1940s (Brenchley & Warington 1958). The relationship between the mean biomass of a plot (taken over a 10-yr period where sufficient data were published) and its species number

(*N*) and Shannon function (*H*) was analysed at six intervals over 87 yr of the PGE and is reported here. It was impossible to control for the effect of plot size on *N* in this study. Variable plot size should have a little or no effect in between plot comparisons of *H* since this diversity measure is independent of sampling area. Both *N* and *H* were calculated from the results of botanical analyses published in the sources referred to above. Biomass data were obtained from the same sources and converted to units of g $m^{-2}$.

Ammonium sulphate applied as fertilizer to some plots severely acidified the soil and brought about a large drop in species diversity (*H*) in plots falling below a critical pH value of 4·5 (Fig. 1). The effect of ammonium sulphate on the value of *H* and *N* in the plots to which it was applied was separated out from any biomass relationship by treating plots receiving ammonium sulphate and those not receiving this fertilizer as separate samples. A linear regression of *N* on biomass and *H* on biomass was carried out for each sample and intercepts and slopes of the two regressions were compared by an analysis of covariance (Snedecor 1956).

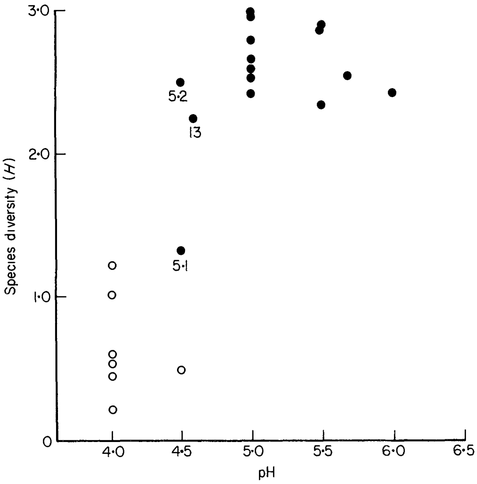

FIG. 1. Species diversity (*H*), corrected for biomass, in twenty-two plots of the PGE plotted against soil reaction. Data for 1948/49. ○ = plot which received ammonium sulphate regularly. ● = plot which did not receive ammonium sulphate regularly. Plots 5.1, 5.2 and 13 received ammonium sulphate till 1897, 1897 and 1904 respectively.

## *Establishing the existence of an equilibrium in botanical composition*

The continuous periods of annual botanical analysis carried out for nine plots of the PGE (Table 1) provide the data necessary to establish whether an equilibrium between the grass, legume and miscellaneous components of the vegetation existed during the period of observation. Regulation (*sensu* Lack 1954) of the quantity of components in the Park Grass plots must have occurred if it can be shown that there was no trend in the biomass of any of the three components with time, or that such long-term trends as did occur were insignificant in determining the biomass of a particular vegetation component, by comparison with yearly fluctuations in the biomass of components. Linear regression of the biomass (g $m^{-2}$) of each component on time (yr) was performed on the data for each of the nine plots.

The regression coefficients (*b*) obtained were used to correct data for both significant and non-significant trends. This was done by adding *b* × time to each observed value, setting time to zero in the first year of the relevant period for each plot. Data corrected by this method was employed in all subsequent analyses.

### *The detection of regulatory processes and negative feedback in annual changes of component biomass*

Analysis directed at detecting negative feedback and the regulatory processes which evidently maintained an equilibrium in the nine plots discussed above was divided into three parts: tests for regular cycles of component biomass, tests for non-random numbers of increases or decreases in component biomass and tests for irregular periodicity in changes of component biomass. The tests were performed on both the biomass of components and on the proportions of components in a plot. The two parameters are referred to collectively as component 'quantities'.

#### *The detection of regular cycles in component quantities*

Serial correlation was used to detect regular cycles occurring with a lag-time of from 1 to 12 yr. The formula for serial correlation used was that of Moran (1952).

#### *The frequency of increases and decreases in component quantities*

Regulation of the quantity of a component may occur as a regular, annual event or as an intermittent process operating when the quantity of a component approaches an upper or lower limit. The latter kind of regulatory mechanism should result in unequal numbers of increases and decreases in component quantities. A chi-square test of the number of increases between successive years against the number of decreases between successive years was used, employing the null hypothesis that increases and decreases were equally likely events.

#### *The detection of irregular periodicity*

Having established the frequency and direction of changes in the quantity of components it is also necessary to test these changes to see if they occurred in random order, since a non-random ordering would suggest irregular cycles of change. A one sample runs test (Siegal 1956) was used for this purpose, employing the null hypothesis that increases and decreases were randomly ordered.

### *Correlations between components in the same plot*

A correlation matrix was compiled from pairwise correlations of the three components in each plot. Negative correlations between the biomass of components would be consistent with a regulatory mechanism involving the interaction of different taxa. Alternatively, a different response by each component to some exogenous environmental factor such as rainfall might also result in a negative correlation between the biomass of components.

### *Correlation between plots*

A correlation matrix was also used to test for inter-plot relationships. Correlation between the biomass of a component in one plot and the biomass of the same component in other plots would suggest that environmental factors induced synchrony in the biomass changes of those components.

Correlation between plots for the biomass of each component was carried out on two sets of data. The first set of data covered the 14 yr, 1906–19 for plots 3, 4.1, 6, 7, 8.

The second set of data covered 17 yr from 1919–35 for plots 3, 7, 14, 19, 20. It was not possible to perform correlations between all plots over the same period because of the lack of concurrent data for all nine of them. All plots receiving nitrogen fall into the second period of analysis and are absent from the first period.

## RESULTS

### *Species number, species diversity and biomass*

The relationships between species number ($N$), Shannon function ($H$) and plot biomass at six intervals during the course of the PGE are shown in Fig. 2. A single negative regression accounts for the relationship between biomass and $N$ for all plots in 1862, irrespective of fertilizer treatment. Regression coefficients and intercepts are given in Table 2. The elevation of the regression line for $N$ on biomass for acidified plots fell progressively below that of the non-acidified plots as species were lost with time, though the slope of the two lines and hence the general relationship between $N$ and biomass remained the same from 1862 to 1948/9. A similar pattern of change for the acidified and non-acidified samples is observed for the regressions of $H$ on biomass. These trends show that the effect of pH and biomass on both $N$ and $H$ were additive.

TABLE 2. Regression data for the relationship between species number and biomass in the Park Grass Experiment from 1862 to 1949

| Year(s) of botanical analysis | Biomass ($g\,m^{-2}$) averaged over period | Plots with ammonium salts | | | | Plots without ammonium salts | | | | Analysis of covariance $n_1 \times n_2$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $n_1$ | $b$ | $a$ | $P$ | $n_2$ | $b$ | $a$ | $P$ | $Pb$ | $Pa$ |
| (a) 1862 | 1856–1865 | 7 | $-3·1 \times 10^{-2}$ | 48·2 | ** | 12 | $-3·9 \times 10^{-2}$ | 53·7 | ** | n.s. | n.s. |
| 1877 | 1868–1877 | 8 | $-3·4 \times 10^{-2}$ | 42·8 | * | 14 | $-4·2 \times 10^{-2}$ | 57·5 | *** | n.s. | *** |
| 1903 | 1896–1903 | 4 | $-1·3 \times 10^{-2}$ | 22·9 | n.s. | 8 | $-3·3 \times 10^{-2}$ | 49·1 | ** | n.s. | *** |
| 1919 | 1916–1919 | 8 | $-2·1 \times 10^{-2}$ | 20·3 | * | 15 | $-3·1 \times 10^{-2}$ | 37·5 | *** | n.s. | *** |
| 1933/36 | 1926–1935 | 2 | — | — | — | 7 | $-5·0 \times 10^{-2}$ | 40·9 | * | — | — |
| 1948/49 | 1946–1949 | 8 | $-3·0 \times 10^{-2}$ | 16·3 | n.s. | 15 | $-3·4 \times 10^{-2}$ | 38·3 | ** | n.s. | *** |
| (b) 1862 | 1856–1865 | 7 | $2·6 \times 10^{-4}$ | 2·1 | * | 12 | $-1·3 \times 10^{-3}$ | 3·1 | ** | * | n.s. |
| 1877 | 1868–1877 | 8 | $-2·0 \times 10^{-4}$ | 2·0 | n.s. | 14 | $-1·2 \times 10^{-3}$ | 3·1 | ** | n.s. | *** |
| 1903 | 1896–1903 | 4 | $-7·6 \times 10^{-5}$ | 1·5 | n.s. | 8 | $-1·3 \times 10^{-3}$ | 3·2 | n.s. | n.s. | *** |
| 1919 | 1916–1919 | 7 | $-1·9 \times 10^{-3}$ | 2·3 | * | 15 | $-2·5 \times 10^{-3}$ | 3·2 | *** | n.s. | *** |
| 1933/36 | 1926–1935 | 2 | — | — | — | 7 | $-2·4 \times 10^{-3}$ | 3·2 | * | — | — |
| 1948/49 | 1946–1949 | 8 | $-3·4 \times 10^{-3}$ | 1·7 | * | 15 | $-2·1 \times 10^{-3}$ | 3·2 | ** | n.s. | *** |

$n$ = number of plots included in sample; $b$ = slope of regression line; $a$ = intercept of regression line; $P$ = significance level.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$; n.s. not significantly different.

The regression coefficients for the relationships between $N$ and biomass in the non-acidified plots in 1862 and 1948/9 are not significantly different (Table 3) despite the loss of some fifteen species per plot throughout the experiment. Most of this difference in the intercepts of the two regression line arose after 1903 when plots were divided for liming. A decline in species-number was a general feature of the PGE which occurred to some extent in most plots, irrespective of the treatment that they received.

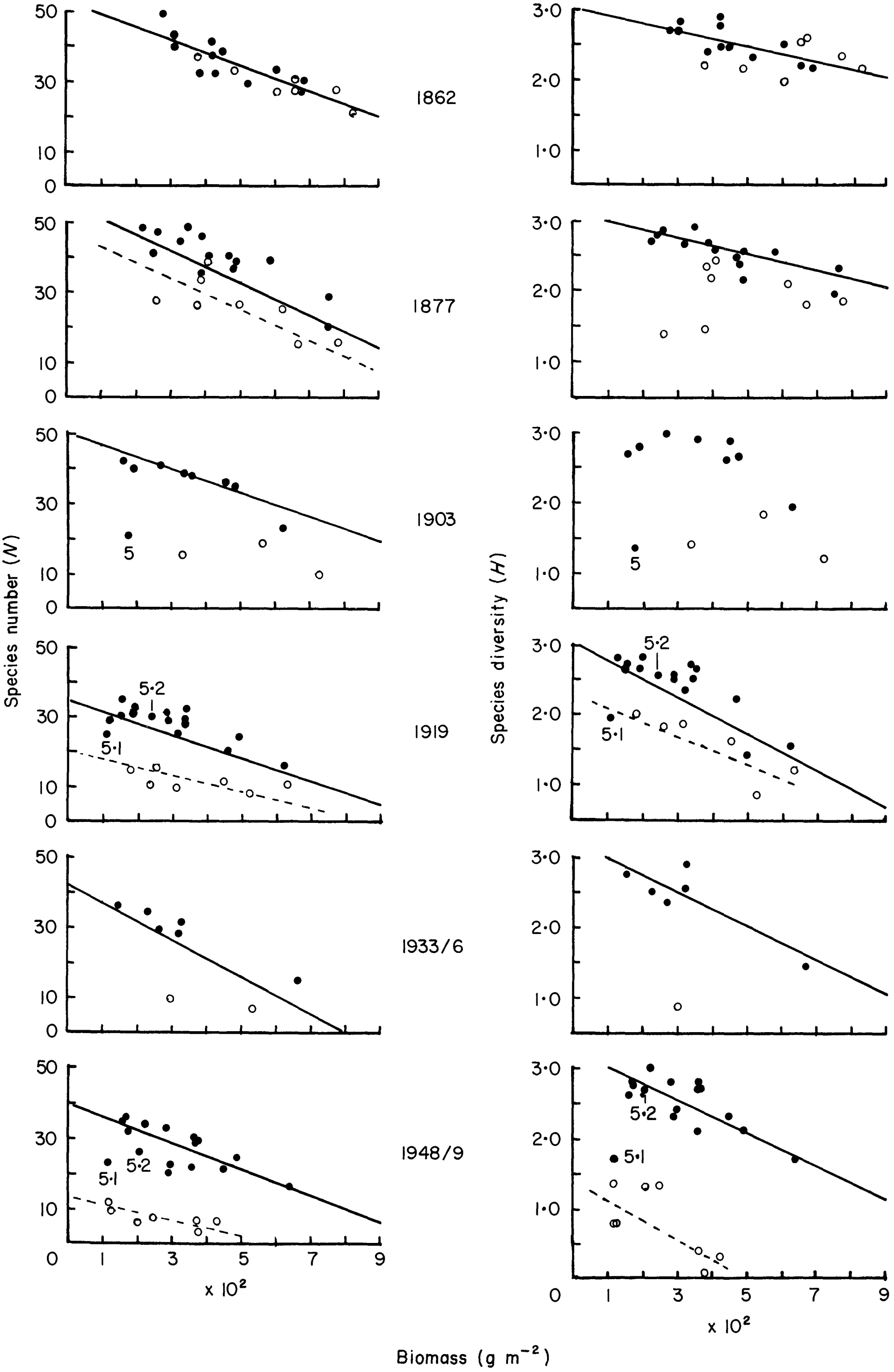

FIG. 2. Linear regressions of Shannon function and species number on biomass for non-acidified plots in the PGE from 1862 to 1948/49. ○ = plot which received ammonium sulphate regularly. ● = plot which did not receive ammonium sulphate regularly. Regression statistics are given in tables 2a and 2b.

TABLE 3. Analysis of covariance for the regressions of $N$ on biomass and $H$ on biomass in 1862 and 1948/9

| | | d.f. | f | $P$ |
|---|---|---|---|---|
| Species number ($N$) on biomass | Elevation | 1,31 | 70·9 | *** |
| | Slope | 1,30 | $9{\cdot}2 \times 10^{-2}$ | n.s. |
| Shannon function ($H$) on biomass | Elevation | 1,24 | 5·9 | * |
| | Slope | 1,23 | 1·3 | n.s. |

* $P < 0{\cdot}05$; *** $P < 0{\cdot}001$; n.s. not significantly different.

A comparison of the regression of $H$ on biomass for the same plots in 1862 and 1948/9 gives similar results to those obtained for $N$ on biomass at the two dates (Table 3). However, the difference in elevation for the $H$ on biomass regressions is considerably less significant than the difference for the $N$ on biomass regressions. This may indicate the differential sensitivity of the statistics $N$ and $H$ to the division of plots which took place between 1862 and 1948/9.

### *Establishing the existence of an equilibrium in botanical composition*

Linear regression showed no significant trends in any miscellaneous component; with time, four significant trends were found amongst the nine legume components and three amongst the nine grass components (Silvertown 1979). Six of the seven significant trends were negative and of the order of $-1$ to $-9\ \mathrm{g\ m^{-2}\ yr^{-1}}$. Plot 20, receiving farmyard manure, increased the biomass of its grass component by $9{\cdot}3\ \mathrm{g\ m^{-2}\ yr^{-1}}$. All significant trends in component biomass were at least an order of magnitude below the annual variation in the biomass of components. The majority of components therefore appear to have been at equilibrium whilst the remainder were subject to slight trends in biomass with time, superimposed upon annual fluctuations.

### *The detection of processes regulating component biomass*

Serial correlation revealed no regular cycles in the quantities of any component in any plot. Non-random periodicity was also absent from yearly fluctuations in component proportions and component biomass in all plots (Silvertown 1979).

### *Correlation between components in the same plot*

The correlation coefficients for all possible pairs of components in each plot are given in Table 4. The biomasses of all components were correlated ($P < 0{\cdot}01$) with each other in the unfertilized plot (plot 3) and in the plot receiving KNaMg (Plot 8, $P < 0{\cdot}05$). The grass components of plot 4.1 (P) and plot 6 (PKNaMg) were correlated with the miscellaneous component, and the legume and grass components of plot 6 were also correlated. There were no correlations between components in any plots receiving nitrogen.

### *Correlation between plots*

Correlation coefficients are given in Table 5. In the first period no plots received nitrogen and the biomass of the grass components of all of them were correlated with each other with the exception of plots 8 (KNaMg) and 7 (PKNaMg). Five correlations between legume components occurred and significant correlation ($P$ 0·01) was also found between the biomasses of the miscellaneous components of all plots in the first period. Fewer between plot correlations occurred in the second period when plots receiving nitrogen

TABLE 4. Correlations between grass (G), legume (L) and miscellaneous (M) components within nine Park Grass plots

| Plot no. | Treatment | Years | | Grass | Legumes |
|---|---|---|---|---|---|
| 3 | Unfertilized | 33 | G | 1·00 | |
| | | | L | 0·73** | 1·00 |
| | | | M | 0·63** | 0·64** |
| 4·1 | P | 14 | G | 1·00 | |
| | | | L | 0·20 | 1·00 |
| | | | M | 0·69** | 0·39 |
| 6 | PKNaMg | 14 | G | 1·00 | |
| | | | L | 0·66** | 1·00 |
| | | | M | 0·56* | 0·25 |
| 7 | PKNaMg | 33 | G | 1·00 | |
| | | | L | 0·20 | 1·00 |
| | | | M | 0·03 | 0·18 |
| 8 | KNaMg | 14 | G | 1·00 | |
| | | | L | 0·59* | 1·00 |
| | | | M | 0·53* | 0·53 |
| 14 | NPKNaMg | 20 | G | 1·00 | |
| | | | L | 0·14* | 1·00 |
| | | | M | 0·02* | −0·03 |
| 15 | PKNaMg | 15 | G | 1·00 | |
| | | | L | 0·02 | 1·00 |
| | | | M | 0·41 | −0·36 |
| 19 | FYM | 24 | G | 1·00 | |
| | | | L | −0·20 | 1·00 |
| | | | M | 0·36 | −0·07 |
| 20 | FYM/NPK | 22 | G | 1·00 | |
| | | | L | −0·08 | 1·00 |
| | | | M | 0·38 | 0·33 |

* $P < 0·05$; ** $P < 0·01$.

were included in the analysis. Correlations between the grass components of plots 3 (unfertilized) and 7 (PKNaMg) and the legume components of these plots remained although the miscellaneous components of these plots were no longer correlated. Correlations between plots 19 and 20 may have been an artefact induced by the application of farmyard manure at the same four-yearly intervals.

## DISCUSSION

### *Equilibrium properties of the Park Grass ecosystem*

In the *Origin of Species* Darwin (1859) wrote: ‘Battle within battle must be continually recurring (in nature) with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another’. Analysis of the botanical composition of the PGE over long periods of time reveals two features of this equilibrium referred to by Darwin. In the first instance the three major floristic components of the grasslands remained in dynamic equilibrium despite the occurrence of annual fluctuations in the biomass of these components large enough to produce correlations between plots. In the second instance analysis of the relationship between species diversity and biomass in the PGE demonstrates a remarkable consistency over a period exceeding 80 yr (regressions of $H$ and $N$ on biomass had the same slope in 1862 and 1948/9). This suggests that there were strict rules governing the number and relative abundance of species in any single equilibrium collection of species.

TABLE 5. Correlation coefficients between plots for each component

| | | | First | period | 1906–1919 | (14 yr) |
|---|---|---|---|---|---|---|
| Component | Treatment | Plot no. | 3 | 4·1 | 6 | 7 |
| Grass | Unfertilized | 3 | 1·00 | | | |
| | P | 4·1 | 0·76** | 1·00 | | |
| | PKNaMg | 6 | 0·77** | 0·91** | 1·00 | |
| | PKNaMg | 7 | 0·90** | 0·88** | 0·88* | 1·00 |
| | KNaMg | 8 | 0·67** | 0·62* | 0·59* | 0·52 |
| Legumes | Unfertilized | 3 | 1·00 | | | |
| | P | 4·1 | 0·37 | 1·00 | | |
| | PKNaMg | 6 | 0·57* | 0·07 | 1·00 | |
| | PKNaMg | 7 | 0·72** | −0·006 | 1·61* | 1·00 |
| | KNaMg | 8 | 0·67** | 0·35 | 0·72** | 0·51 |
| Misc. | Unfertilized | 3 | 1·00 | | | |
| | P | 4·1 | 0·90** | 1·00 | | |
| | PKNaMg | 6 | 0·68** | 0·68* | 1·00 | |
| | PKNaMg | 7 | 0·69** | 0·80** | 0·75** | 1·00 |
| | KNaMg | 8 | 0·89** | 0·96** | 0·75** | 0·81** |
| | | | Second | period | 1919–1935 | (17 yr) |
| | | | 3 | 7 | 14 | 19 |
| Grass | Unfertilized | 3 | 1·00 | | | |
| | PKNaMg | 7 | 0·57* | 1·00 | | |
| | NPKNaMg | 14 | 0·35 | 0·25 | 1·00 | |
| | FYM | 19 | 0·29 | 0·30 | 0·28 | 1·00 |
| | FYM/NPK | 20 | −0·06 | 0·13 | −0·14 | 0·53* |
| Legumes | Unfertilized | 3 | 1·00 | | | |
| | PKNaMg | 7 | 0·60* | 1·00 | | |
| | NPKNaMg | 14 | 0·06 | 0·50* | 1·00 | |
| | FYM | 19 | 0·01 | −0·18 | −0·39 | 1·00 |
| | FYM/NPK | 20 | 0·24 | 0·40 | 0·54* | 0·18 |
| Misc. | Unfertilized | 3 | 1·00 | | | |
| | PKNaMg | 7 | 0·15 | 1·00 | | |
| | NPKNaMg | 14 | 0·27 | −0·08 | 1·00 | |
| | FYM | 19 | 0·39 | −0·39 | 0·65** | 1·00 |
| | FYM/NPK | 20 | 0·53* | −0·18 | 0·37 | 0·71** |

* $P < 0·05$; ** $P < 0·01$.

The constancy of the relationships between biomass, Shannon function and species-number and the fact that the effects of pH and biomass on $N$ and $H$ were directly additive (the regression coefficients of $N$ and $H$ on biomass for the samples of low and high pH are the same) also suggests that there is a generality about these relationships which is independent of the specific identities of the species present in the grassland. Applications of nitrogen fertilizer and minerals in varying quantities and combinations determined the abundance of particular species but this did not disrupt the $N$ and $H$ regressions on biomass. Most plots included in the data received different treatments. These observations indicate that grassland ecosystems may have emergent properties (Salt 1979) which are not dependent on the presence of specific elements in the flora.

### *Population regulation and the mechanisms of botanical equilibrium*

Though the PGE data demonstrated that these grasslands were at botanical equilibrium, the correlative tests applied to annual abundances of plot components have failed to reveal the equilibration mechanism in operation. The absence of negative feedback between botanical components measured in different years strongly points to a mechanism which regulates plant populations within individual years. Unfortunately there are insufficient data on within-year population changes in the PGE for this hypothesis to be tested at present. There are some suggestive observations however. Shifts in the phenology of species and botanical components due to annual changes in seasonal rainfall and temperature have frequently been observed (e.g. Williams 1978; R. Gulliver pers. comm.) and these testify to rapid changes in the abundance of plant populations within individual years. Correlative methods of the kind employed here on annual data should be applied to similar data collected at more frequent intervals to investigate these changes. The temporal niche differences between *Trifolium repens* and *T. fragiferum* found by Harper & Clatworthy (1963) illustrate the kind of temporal partitioning and competition for space which could be involved in the regulation of plant populations in the PGE.

### *Limiting factors and the role of nutrients in population regulation*

Equilibrium in the grass: legume: miscellaneous species ratio was attained in all nine of the plots analysed, despite the loss of species due to the effects of fertilizer applications to some of them. The equilibrium in the proportion of the three components in these plots concealed non-equilibrium changes in the species composition of each component (Williams 1978). An equilibrium between components in a plot need not reflect an equilibrium between constituent species within each component.

The three divisions used to analyse the vegetation of the plots are, in the case of the grass and legume families, natural ones which contain ecologically similar species. It is quite conceivable that each of these families reached an equilibrium with the others determined by the availability of its own limiting resource: nitrogen in the case of grasses and minerals in the case of legumes, for example. The balance between species within each family is likely to be determined by different factors from those limiting the group as a whole and so constituent species may not achieve equilibrium at the same time as the components reach this state. This situation is consistent with the findings of Turkington, Cavers & Aarssen (1977) in which particular grass species were found to be positively associated with particular legume species and negatively associated with other grasses, suggesting that complementarity occurs between grass and legume species whilst species from the same family are incompatible.

This independence in the factors controlling components (families) and their constituent species suggests a model of resource division in grassland in which these two taxonomic levels represent (or map on to) independent dimensions of niche-space. Such a model is illustrated in Fig. 3, where component abundance in plot 3 and species abundance in each component of the plot form the two axes of a two-dimensional niche space (Whittaker 1965). It is clear from such a model how the relative abundance of species within a component may vary independently of changes in component biomass in a plot.

A two-dimensional model cannot possibly represent the full complexity of resources division in grassland, though this model, and the evidence upon which it is based, does suggest that the factors limiting population size may be nested in a fashion similar (or possibly equivalent) to the nesting of taxonomic groups (i.e. family, genus, species). Thus, suppose that nitrogen availability limits the total biomass of the Gramineae present in a plot, whilst different limiting factors, perhaps the availability of germination sites or micro-nutrients, limit each population of the grass species which together make up the grass component. If any of these species should be released from its specific limiting factor, its population may only increase to the level at which it meets a new limiting factor. It may never exceed the limitation placed upon the Gramineae as a whole by

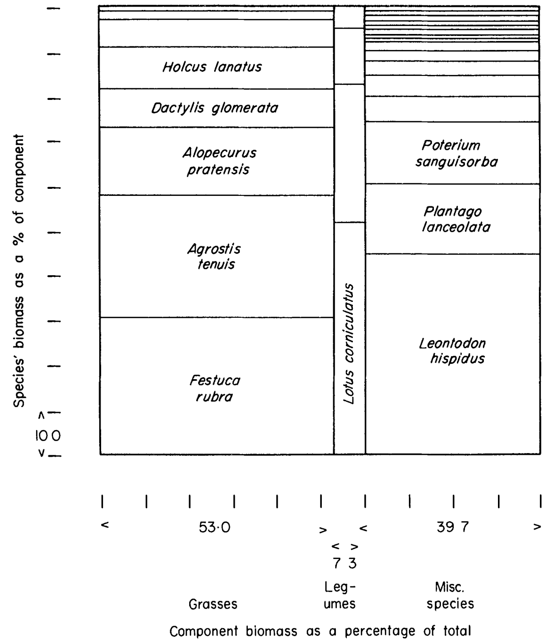

FIG. 3. A model of the division of niche-space along two principle dimensions in grassland. The model is applied to data from plot 3 (unfertilized) of the PGE, 1948. Only the principle species in each component are named.

nitrogen availability. Such increases in a species' abundance must deplete the supply of nutrients and space which form limiting factors for other grasses and consequently reduce or eliminate them.

This hypothetical system of nested limiting factors is consistent with the conclusions of the competitive-exclusion principle (Williamson 1957) that, at equilibrium, only one species may be limited by a single limiting factor, since nitrogen only becomes the sole limiting factor of a grass species when it is the only grass present.

The fact that regulation of botanical composition largely occurred within years means that a component which may have benefited from an increased supply of a limiting factor in one year did not increase its biomass in the following year by this advantage. Some indication of the factors limiting different components in the PGE have been obtained from observations on trends in species abundance with fertilizer regime (Thurston 1969).

The correlation between the biomass of components within plots reveals the extent to which component biomass was influenced by fluctuations in the total quantity of available resources. Where the biomass of all three components was positively correlated, components increased their biomass as a result of an increase in the total available resources. Where correlation is absent or negative, biomass changes in one component may have occurred largely at the expense of other components competing for the same resource.

There are strong positive correlations between all components in the unfertilized plot (3) and slightly weaker correlation between all components in the plot receiving minerals alone (plot 8). Cashen (1947) found that the total biomass of these plots was increased by 35 g $m^{-2}$ per additional 2·5 cm of rain above the mean in April. The positive correlation between all components in these plots demonstrates that additional biomass due to rainfall was a result of an increase of a resource which limited all three components to some extent. A similar effect of rainfall on the yield of wheat was found by Fisher (1925) who suggested it was due to additional nitrate released in the soil after spring rainfall. Fisher also found that additional rainfall in the autumn may depress yield by leaching nitrate from the soil. Such an effect in the PGE would have reinforced the correlated behaviour of vegetation components. The significance of nitrogen as a factor in determining correlations between components is also suggested by the complete absence of such correlations within plots which received nitrogen fertilizer.

Correlations of the kinds discussed above suggest that plant nutrients play an important role as the ultimate factors limiting plant populations at higher levels of the suggested hierarchy of nested limiting factors. Detailed experimental studies are required to determine the identity of the factors limiting individuals species' populations. On the basis of studies of population regulation in animals (e.g. *Parus major*, Perrins 1979) it seems likely that different geographical populations of the same species may be regulated by different limiting factors. Whatever the specific factors limiting populations at a particular site are, the emergent properties of the meadow-grassland ecosystem (the constant relationship between biomass and species diversity and species number) may turn out to have a generality beyond the confines of the Park Grass Experiment.

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