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The Park Grass

Experiment: Insights from the Most Long-term Ecological Study

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Introduction

In 1856 J.B. Lawes and J.H. Gilbert started an experiment still in progress, which is now, undoubtedly, the most long-term ecological study in the world. The Park Grass Experiment was initially designed to determine the effects of different amounts and combinations of mineral fertilizers and organic manures on the productivity of permanent grassland. However, there were such dramatic effects of the treatments on plant species composition and plant diversity that Lawes and Gilbert (1880) quickly concluded that the experiment was of greater interest to the 'botanist, vegetable physiologist, and the chemist than to the farmer'. And this has proved to be so.

As demonstrated below, the treatments within the experiment have continued to provide insights into issues in evolutionary, population, community and ecosystem ecology. The long-term data have become increasingly powerful with each additional sampling, despite the lack of replication and randomi-

zation. However, Lawes and Gilbert can hardly be faulted for their experimental design. Important contrasts were placed adjacent to each other so that treatment effects could be directly observed all along the 80 m boundary that the two plots shared. Moreover, it was during R.A. Fisher's tenure at Rothamsted that he articulated, more than 70 years after the establishment of Park Grass, the concepts upon which modern experimental design are based (Barnett, Chapter 10).

Design of the Park Grass Experiment

The Park Grass Experiment was laid out in a four hectare area that had been maintained as grassland by grazing or mowing for hay for several hundred years before the study began (Lawes and Gilbert, 1863; see also Johnston, Chapter 2). It had also been periodically fertilized with farmyard manure. Lawes and Gilbert originally established 13 plots and later added seven more; they ranged in size from 0.05 to 0.2 ha. Initially each plot received either no nutrient addition (the control plots, Plots 3 and 12), farmyard manure (Plot 2), or various combinations and rates of annual addition of mineral nutrients (the remaining 17 plots). Some treatments were altered (Warren and Johnston, 1964) and most plots were halved first in 1903 and then in 1965 into four subplots that received different rates of liming. The most recent subdivision was to give four different levels of soil pH. A summary of the major changes in manurial history and management was given by Warren and Johnston (1964). These authors, together with Thurston *et al.* (1976) summarized both chemical and botanical results and Thurston *et al.* (1976) discussed initial effects of the liming treatments introduced in 1965. The layout of the plots, and the treatments applied to each plot, are summarized in Fig. 16.1. These treatments provide 89 plots in which the responses of plants, of herbivores, and of soil organisms, properties and processes to soil nutrients can be directly observed.

The Ecology of Park Grass: a Brief Review

The first significant papers published on the Park Grass Experiment were those of Lawes and Gilbert (1863, 1880) and Lawes *et al.* (1882). These presented results of surveys in which the relative abundances of plant species in each plot were estimated in 1862, 1867, 1872, and 1877. These papers also included soil chemistry and hay yields. Brenchley and Warington (1958) published the next major compilation of botanical data and included data from 1903, 1914, 1919, 1920, 1926, 1936, 1948 and 1949. Some plots were not sampled in some of these years and a few were sampled more frequently. Thurston (1969) and Williams (1978) have published more recent data on the botanical composition of these plots, and Crawley and co-workers have collected

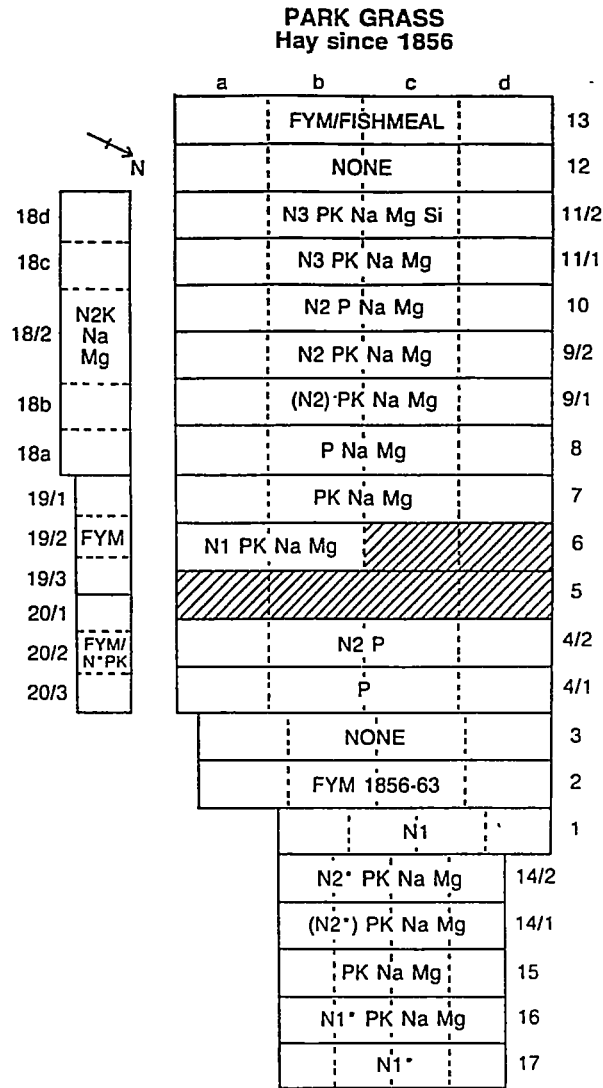


Fig. 16.1. Treatments (every year except as indicated). *Nitrogen* (applied in spring): N1, N2, N3 sulphate of ammonia supplying 48, 96, 144 kg N ha⁻¹; N1*, N2* nitrate of soda supplying 48, 96 kg N ha⁻¹; (N2), (N2*) last applied 1989. *Minerals* (applied in winter): P 35 kg; K 225 kg; Na 15 kg; Mg 10 kg ha⁻¹; Si Silicate of soda at 450 kg ha⁻¹ of water soluble powder; Plot 20, rates of manuring in years when FYM not applied: 30 kg N*, 15 kg P, 45 kg K ha⁻¹. *Organics* (each applied every fourth year since 1905): FYM, 35 t ha⁻¹ farmyard manure (bullocks) (1989, 1993); fish meal (about 6.5% N) to supply 63 kg N ha⁻¹ (1991, 1995). *Lime*: a,b,c, lime applied as needed to maintain pH 7, 6 and 5 respectively; d, no lime applied (pH range 3.5 (plot 11-1) to 5.7 (plot 17)).

the most recent data (1991-93). In addition, Cashen (1947), Smith (1960), Warren and Johnston (1964), Warren *et al.* (1965), Silvertown (1980, 1987), Tilman (1982, 1986), and others have presented analyses of both yield and botanical data. The above data and analyses, and the analyses presented below, demonstrate that:

1. In the absence of experimental perturbation, plant species composition, diversity and productivity are quasi-stable, but are influenced by climatic variation. Some usually rare species have brief periods of dominance, and a few usually dominant species have brief periods of rarity.
2. Plant community composition is highly dependent on both the rate and ratio of supply of limiting soil resources. Nitrogen, phosphorus and potassium are the major limiting soil resources for Park Grass species.
3. Soil pH, which is modified via liming and fertilization, greatly affects plant species composition and diversity.

4. Different rates of nutrient supply act as a selective force on plant populations, causing measurable evolutionary change.

These four points are discussed in the following sections.

Compositional Dynamics

Because few ecological communities have been sampled over periods of even a decade, it is difficult to know the extent to which present compositional patterns are representative of the long-term state of most plant communities. The 130-year record of plant species abundances in the control plots of Park Grass provides insight into this issue and illustrates the difficulty of establishing true experimental 'controls'. Consider, for instance, the dynamics in Plot 12 of eight of the most abundant plant species in Park Grass (Fig. 16.2). Three perennial grasses, *Festuca rubra*, *Dactylis glomerata*, and *Agrostis capillaris* generally remained the co-dominant species during this period, but their absolute and relative abundances changed from one sampling to the next. *Agrostis*, for instance, was the most abundant species at the first sampling in 1862, was the fourth most abundant species in 1949, and the second most abundant species in 1991. The least abundant of the eight species in 1862, *Arrhenatherum*, generally remained less abundant throughout the 130-year period. The shifts in the absolute and relative abundances of these species were also shown by other species during the 130 years. *Plantago lanceolata* was the most abundant species in 1919, but never in any other year; in 1877 it was the 17th most abundant species of the 29 in this plot. *Leontodon hispidus* was recorded as having 'trace' abundance through 1877, but was 10% of biomass in 1949. Its low initial abundance may have resulted from the periodic grazing of the field before the experiment began (see later discussion). *Leontodon* is a preferred forage species for cattle and would have been freed from such selective herbivory once the experiment began. Whereas many species tended to remain dominants, subdominants or rare throughout this 130-year

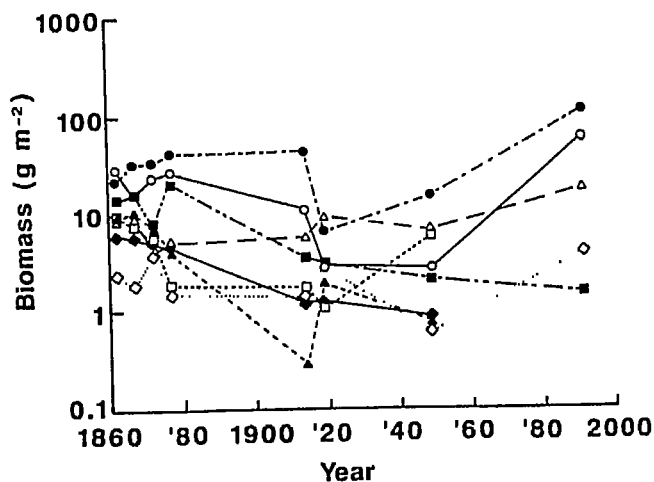


Fig. 16.2. The dynamics of eight common species in Plot 12, an unfertilized control plot. Reasons for some of the initial changes are discussed in the text. ○ *Agrostis*; □ *Alopecurus*; ◇ *Arrhenatherum*; △ *Dactylis*; ● *Festuca*; ■ *Holcus*; ◆ *Lathyrus*; ▲ *Rumex*.

period (Silvertown, 1987), occasionally a species which was rare in most years sporadically became a dominant. We do not know what caused these periodic outbreaks of usually rare plant species.

The other control, Plot 3, was sampled more frequently, and shows apparently greater variation (Fig. 16.3). Two grasses, *Festuca* and *Agrostis*, were the co-dominants throughout most of the period. In 1903 *Agrostis* seemingly declined and another grass, *Briza*, increased; but this may be a case of misidentification because these two species are difficult to distinguish vegetatively. Many species had order-of-magnitude variations in estimated biomass, and some, such as *Leontodon* and *Poterium* showed a marked pattern of increase during the initial 50-70 years of the experiment (Fig. 16.3). When viewed on a coarser scale by summing together all grasses, all legumes, or all forbs, species composition shows a long-term pattern of change on Plot 3. Grasses were initially the most dominant group, but grasses declined and forbs (non-legume, dicotyledonous species) increased until the early 1900s (Fig. 16.4). Legumes remained rare throughout and showed little directional change in relative abundances. The data in Fig. 16.4 come from visual estimates of abundances, so that some of the variation may be caused by differences in technique between observers over the 130 years. However, the major trends seem too great to be accounted for in this way. The marked increases in

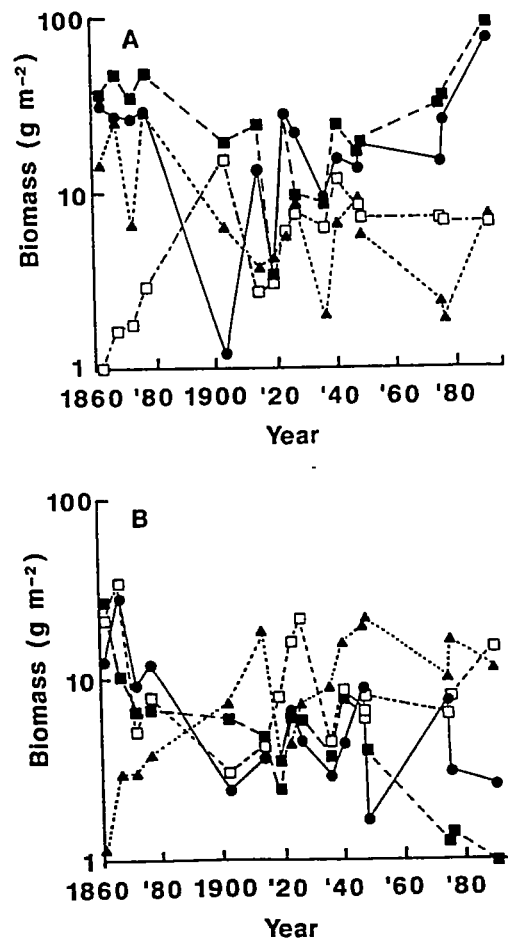


Fig. 16.3. The dynamics of eight species in Plot 3, another unfertilized control plot which was sampled more frequently than Plot 12 (Fig. 16.2). (A) ● *Agrostis*; ■ *Festuca*; ▲ *Holcus*; □ *Poterium*; (B) ● *Anthoxanthum*; ■ *Helictotrichon*; ▲ *Leontodon*; □ *Plantago*. Note that most variation is between 1 and 100 in both plots.

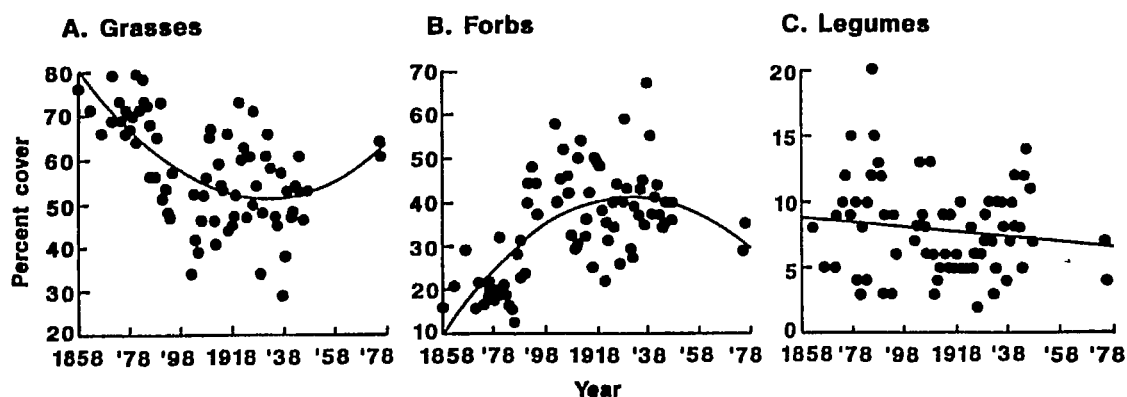


Fig. 16.4. Abundances of (A) grasses, (C) legumes, and (B) forbs in Plot 3, a control plot; estimated visually (Williams, 1978). (The fitted curves were those which gave the highest R^2 values.)

the abundances of particular forb species (Fig. 16.3) and in the relative abundances of forbs as a group (Fig. 16.4) during the first half century of the experiment has several possible explanations. The field had been both mown for hay and grazed and periodically fertilized with farmyard manure prior to 1856 after which the occasional addition of nutrients ceased. From 1856 the plots were cut for hay each year with the aftermath being grazed by sheep until 1874, from 1875 the aftermath was cut and weighed green. The changes in vegetational composition might be caused by either the cessation of manuring or herbivory or both. The changes during the first 50–70 years in Plots 3 and 12 probably reflect such effects. The dynamics since then provide a better estimate of the stability of unmanipulated grassland.

Climate and Grassland Productivity

The effect of the climate, or 'season' in agricultural terms, on aboveground net primary productivity, which is reasonably estimated by the size of the hay crop, has been frequently discussed since the early days of the experiment. In general the hay yield of English meadows tends to be strongly correlated with actual transpiration, and rainfall tends to be the most important determinant of this (Smith, 1960). This relationship is usually strongest in grasslands not receiving nitrogen fertilizer. Cashen (1947) statistically demonstrated both of these aspects of the relationship between hay yield and rainfall for the Park Grass plots in a study directed by R.A. Fisher. More recently, Jenkinson *et al.* (1994) found that meteorological variables, including rainfall, could account for only between 12% and 21% of the variance in total annual hay yield on the unlimed parts of Plots 2, 3, 12, 14 and 16 over the period from 1891 to 1958. This improved to between 45% and 63% for 1960 to 1992, during which time yields of herbage at the traditional hay-making stage of growth were estimated by cutting a part of each plot with a forage harvester. This provides a better

estimate of the dry matter of the standing crop than traditional haying methods which were continued on the remainder of the plot, although these hay yields were not determined.

The relationship between climate and hay yield is important from an ecological point of view because it demonstrates climatic effects on the plant communities. Climatic variation may affect plant community composition: (i) directly by differentially influencing the growth and death of individual plant species; or (ii) indirectly by affecting comparative growth rates between species which in turn affects composition through competitive effects among species; or (iii) indirectly through effects on nutrient dynamics, pathogen densities, litter decomposition, etc. Silvertown *et al.* (unpublished) have looked at different combinations of the relationships between rainfall, hay yield and composition (the ratio of grasses/legumes/other species) and found stronger relationships between yield variation and variation in composition than between rainfall and composition. Of twelve regression models used, the most successful was a model which explained variation in composition based on variation in hay yield in the year before composition was measured. This may mean that direct effects of rainfall were less important than indirect ones and may indicate the importance of interspecific competition or of accumulated plant litter in the response of the Park Grass communities to climatic perturbation.

Nutrient Supply and Species Composition

The addition of inorganic N, of P, and of various combinations and ratios of N, P, K, Ca, and other nutrients (Fig. 16.1 above) caused dramatic shifts in the abundances of plant species, as predicted by a theory of resource competition (Tilman, 1982). Consider, for instance, Plot 11-1, which received complete mineral fertilizer, including 144 kg N ha⁻¹ as ammonium sulphate. A perennial grass, *Holcus lanatus* (Yorkshire fog) became dominant by 1950 (Fig. 16.5A) and virtually all other species were displaced from the unlimed subplot by 1976. In contrast, Plot 14 received complete mineral fertilizer, including 96 kg N ha⁻¹ as sodium nitrate. It was dominated by *Alopecurus* and *Arrhenatherum*, but *Holcus* was extremely rare (Fig. 16.6). The difference between these two N treatments seems to be caused by the acidifying effects of N when added as ammonium sulphate. The top 23 cm of soil on the unlimed part of Plot 11-1 had a pH less than 4 in 1959, whereas that on the unlimed part of Plot 14 had a pH of 6 (Warren and Johnston, 1964). The part of Plot 11-1 which received lime every fourth year from 1903 (Fig. 16.5B) had a composition much more similar to that of Plot 14 than to Plot 11-1, from 1959 onwards. This supports the hypothesis that the dramatically different effects of the two forms of N addition came from the effects on soil pH. Further effects of liming and soil pH are discussed below.

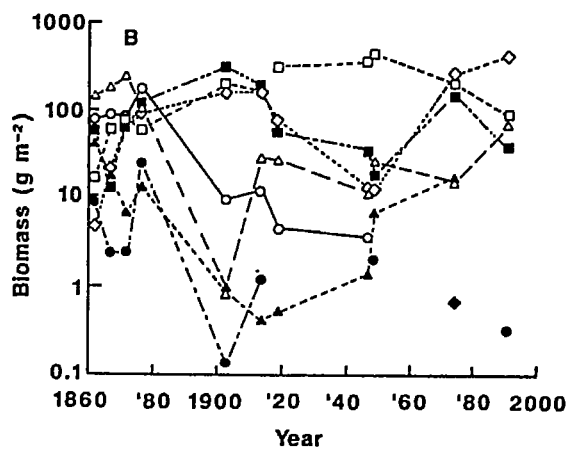
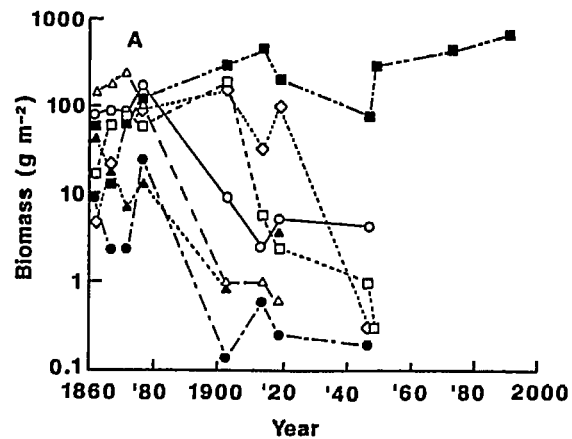


Fig. 16.5. Abundances of eight common species on Plot 11-1 which gets P K Na Mg together with 144 kg N ha⁻¹ as ammonium sulphate (see Fig. 16.1). (A) Subplot without lime. This soil became very acid (Table 16.1) and only *Holcus* was observed at the two most recent samplings. (B) Subplot with most lime, liming had a marked effect on species dominance and diversity. ○ *Agrostis*; □ *Alopecurus*; ◇ *Arrhenatherum*; △ *Dactylis*; ● *Festuca*; ■ *Holcus*; ◆ *Lathyrus*; ▲ *Rumex*.

Another critical determinant of the species composition of the plots is the N:P ratio (Tilman, 1982). Again considering the limed sections of the plots, low

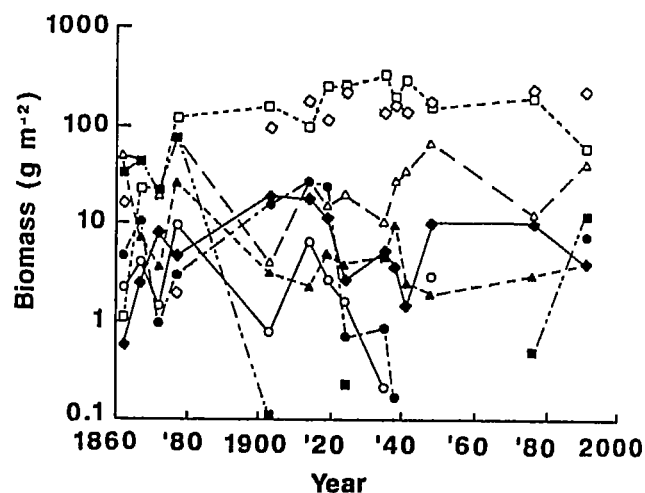


Fig. 16.6. The dynamics of eight common species in Plot 14, which received the same amounts of P, K, Na and Mg as Plot 11-1 (Fig. 16.5), but 96 kg N ha⁻¹ as sodium nitrate. The unlimed soil had pH 6.0 in 1959. ○ *Agrostis*; □ *Alopecurus*; ◇ *Arrhenatherum*; △ *Dactylis*; ● *Festuca*; ■ *Holcus*; ◆ *Lathyrus*; ▲ *Rumex*.

N:P ratios, such as created by the addition of just P (Plot 4-1) or of P, Na and Mg (Plot 8) or of P, K, Na, and Mg (Plot 15) led to markedly higher relative abundances of the legumes *Lathyrus*, *Lotus* and *Trifolium* and lower relative abundances of the grasses *Festuca rubra*, *Arrhenatherum*, and *Dactylis glomerata*. In contrast, the addition of just N (Plots 1 and 17) led to about fivefold lower relative abundances of *Lathyrus* and *Lotus* and threefold greater relative abundances of the grasses *Dactylis glomerata* and *Festuca rubra*. In general, increased productivity led to greater grass dominance and to lower legume and forb relative abundances. However, within limed plots with similar pH values, the abundances and identity of the dominant grass species depended on the ratio of supply of N and P. For instance, Plot 16, which received N and P together with K, Na, Mg, had more than 10-times the *Arrhenatherum* abundance of Plots 1 and 17, which received the same rate of N addition, but no P or K, Na, Mg. Such effects of N:P ratios on species composition and relative abundances are consistent with the theory of competition for multiple resources presented in Tilman (1982).

There are also effects of nutrients other than N and P. Consider *Taraxacum officinale*, the dandelion. Its relative abundance in Park Grass ranges from 0 in some plots to over 20% of aboveground living biomass in others. Using the data summarized in Williams (1978), the nine limed subplots receiving K had 67 times greater relative abundance of dandelions than the unlimed subplots receiving no K. The unlimed part of Plot 4-2, which received only 96 kg N ha⁻¹ as ammonium sulphate together with P, was 100% grass (*Agrostis* and *Anthoxanthum*) and the part limed to pH 5 was 99.8% grass (*Festuca*, *Agrostis* and *Poa*). Both have experienced a rain of dandelion seed from neighbouring plots, but have virtually no dandelions, possibly because they receive no K. This suggests that *Taraxacum* may be a poor competitor for K and cannot persist in soils in which K is limiting.

Productivity and Diversity

The addition of various amounts and combinations of nutrients also influenced the number of plant species occurring in these plots. Although there are some interesting exceptions, in general, the greater the productivity caused by a given fertilizer treatment, the lower the species diversity (Fig. 16.7). This effect was evident in 1862 and every year since (Tilman, 1982). However, the effect of productivity on species richness depended on soil pH. At a given level of productivity, more acidic plots had fewer species (see Table 16.1). This experimentally demonstrated inverse relationship between productivity and species richness is the opposite of the commonly reported pattern for habitats along latitudinal productivity gradients (e.g. Pianka, 1966; Tilman and Pacala, 1993). However, results similar to those observed in Park Grass have been observed in a wide variety of terrestrial and aquatic habitats that have had their

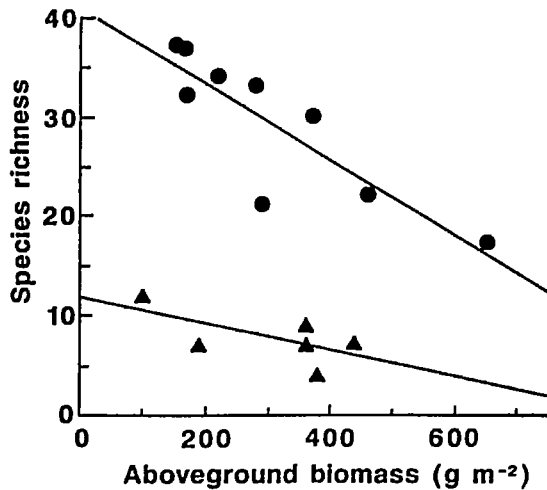


Fig. 16.7. Relationship between species richness (number of plant species recorded during a given sampling period) and productivity on soils, above (●) and below (▲) pH 4.9 (Redrawn from Tilman, 1982, using 1948 and 1949 data).

productivity increased via nutrient addition (Huston, 1979; Tilman, 1982). An explanation for this effect is that nutrient addition eliminates spatial heterogeneity and causes a large number of plant species to become limited by the same resource (often light), with the best competitor for that resource displacing all other species limited by it from the habitat (Tilman, 1982).

The Effects of Liming

Most fertilized plots were halved in 1903 to comprehensively test the effects of liming after some early tests between 1881 and 1897 (Warren and Johnston, 1964). Half of each plot was limed and half left alone. In 1965, these half plots were again halved, with the intention of achieving pH values of 7, 6, 5 on subplots a, b, c (Warren *et al.*, 1965) by periodic additions of lime. Some effects on soil pH of lime treatments introduced in 1965 were discussed by Johnston (1972) especially the slow change in mineral soil pH on plots with a 'mat' of partially decomposed plant debris.

The liming treatments started in 1903 and 1965 both dramatically illustrate the effects of an abiotic environmental factor, soil acidity, on plant species composition and diversity. Soil pH can influence the way in which other soil resources are utilized and can control the number of plant species capable of persisting on a subplot. Declining pH increases the ionic concentration of potentially toxic metals like iron and aluminium. Here we describe the effects of liming on five plots: the two unfertilized controls (Plots 3 and 12) to give an impression of the degree of background variation between plots, a plot receiving 144 kg N ha⁻¹ as ammonium sulphate (the largest rate of nitrogen tested on Park Grass; Plot 11-1), a plot receiving potassium and phosphorus but no nitrogen (Plot 7), and a plot receiving phosphorus only (Plot 8). (Plots 7, 8 and 11-1 also receive small amounts of Na and Mg which almost certainly do not affect the results reported here.) Soil pH, plant species richness and hay yields from these plots are shown in Table 16.1 for the most recent sampling (1991-93).

Table 16.1. Effects of lime treatment on soil pH, species richness and biomass at the first cut on five plots on Park Grass.^a

Plot	Soil pH in H ₂ O (0–23 cm) in 1991			
	(a) ^b	(b)	(c)	(d)
3	6.4	6.4	5.0	4.8
12	7.0	6.1	4.8	4.8
7	6.5	6.2	5.2	4.8
8	6.7	6.4	5.1	4.9
11-1	5.3	5.4	4.1	3.4
Plant species richness (total species per 10 m x 15 m area)				
3	34	33	35	35
12	44	42	34	41
7	22	23	25	25
8	32	32	28	29
11-1	11	13	9	2
Biomass (t dry matter ha ⁻¹) from the early June hay crop; 1991–93				
3	2.77	3.28	2.00	2.16
12	2.31	2.50	1.85	2.15
7	5.39	5.47	4.59	4.35
8	2.96	3.43	3.66	3.56
11-1	5.84	5.76	5.30	5.59

^a Species richness was estimated in a 10 x 15 m rectangle in the centre of each subplot so that the area used for the estimates was the same throughout.

^b Subplot (a) limed to achieve a pH of 7 since 1976 but limed since 1903; (b) limed to achieve a pH of 6 since 1965, but limed since 1903; (c) limed to achieve a pH of 5 since 1965, unlimed from 1856 to 1964; (d) unlimed since 1856.

Liming and soil pH

The aim of the liming regime introduced in 1965 was to produce three different soil pH values for each fertilizer treatment (subplots a,b,c), as discussed above, whilst subplot d would remain unlimed and its pH would depend on the various acidifying inputs. As yet it has been difficult to maintain the target pH values of 7, 6 and 5 on subplots a,b and c respectively. The liming treatments have, however, created a sequence of plots that differ in soil pH in the desired directions (Table 16.1). Soil pH has fallen below 4 only where ammonium sulphate has been applied, and liming has not raised and maintained the pH above 6 on the plot receiving 144 kg N ha⁻¹ as ammonium sulphate (Plot 11-1a). The difference in pH between subplots 3a and 12a of the

unfertilized controls is probably because of the different amounts of lime applied between 1965 and 1991.

Lime and plant species richness

There are at least two important diversity-reducing processes at work on Park Grass: (i) increasing soil acidity may reduce the number of species capable of tolerating the abiotic conditions; and (ii) increasing productivity may lead to competitive exclusion of small-stature plant species by taller species that are presumably better competitors for light (which is likely to be a major limiting factor in productive plots). Given these processes, we expect diversity to be least on acid plots with tall individual species and high biomass, and most on limed plots with small individuals and low total biomass. Comparisons of species richness, based on 1991–93 visual censuses, for Plots 11-1 and 12, and Plots 7 and 8 (Table 16.1) support this. However, this does not explain the differences between the control plots, Plot 12 is seemingly more diverse than Plot 3. The effect of acid-tolerance on the size of the species-pool is suggested by the steeply declining trend of species richness with increasing acidity on the plot (11-1) receiving most ammonium nitrogen (see also Fig. 16.5A). Of the 126 species that have been recorded at some time on Park Grass, *Holcus lanatus* was the dominant grass in 1947 when the pH was 3.8 and it now thrives below pH 3.5 with large inputs of ammonium sulphate together with P and K. This is likely to be a direct pH effect, but it may also be caused by some other factor, such as the dense layer of litter (thatch or mat) which has developed gradually on the unlimed plots receiving most ammonium nitrogen. Clearly, although the Park Grass Experiment provides evidence that is consistent with these hypothesized processes, additional studies are required to determine whether there are actually direct effects of pH and productivity on diversity, or if the observed patterns are mediated through other correlated processes.

The effect of pH on species biomass

On Plot 11-1 there is no clear trend in hay yield with pH, but there is a major impact on botanical composition (Table 16.2). The 6 t ha⁻¹ of dry matter on subplot 11-1a is made up of *Arrhenatherum*, *Alopecurus* and *Dactylis* and several tall herbs, whereas the 6 t ha⁻¹ of dry matter on subplot 11-1d is made up entirely of *Holcus lanatus*. There is no trend in hay yield with liming and hence pH on the control plots, but the more recently limed 'c' subplots have lower yields than the more long-term stable subplots. The declining pH over the course of the experiment on the unlimed control subplots suggests an effect of acid deposition. It is estimated that the soil pH of the original meadow was about 6.0. Since the industrial revolution, the pH on the unlimed subplots has declined to 4.8 on both 12d and 3d. This is associated with greater relative abundances of the grasses *Agrostis capillaris* and *Anthoxanthum odoratum*,

Table 16.2. Average dry matter yield (g m^{-2}) for 1991–93 based on quadrat sampling just prior to the first hay crop, of four grass species showing a range of responses to the application of lime. Note (a), (b), (c) and (d) refer to liming treatments; for pH values see Table 16.1.

Plot	(a)	(b)	(c)	(d)
<i>Arrhenatherum elatius</i>				
3	0.6	0	0	3.3
12	2.1	0	3.4	1.5
7	123.0	134.7	12.7	3.3
8	9.8	27.1	1.3	8.2
11-1	397.7	320.0	118.2	0
<i>Alopecurus pratensis</i>				
3	0.6	0	0	0
12	0	0.6	1.0	0
7	19.4	35.4	11.6	5.0
8	0	0	0.8	0.2
11-1	67.7	50.6	71.7	0
<i>Holcus lanatus</i>				
3	2.6	4.2	0.7	3.8
12	6.6	2.5	1.5	0.9
7	39.3	43.4	27.1	19.4
8	19.9	14.6	13.3	30.6
11-1	66.7	91.2	280.2	457.6
<i>Agrostis capillaris</i>				
3	32.0	38.4	55.2	72.8
12	55.2	50.4	54.4	65.6
7	4.8	10.4	131.2	154.4
8	32.8	16.8	80.0	72.8
11-1	0.8	0.2	37.6	0

and thus with lower relative abundances of herbs and legumes species, but not yet with changes in species richness.

Liming and abundances of selected plant species

The average dry weight at first harvest for 1991–93 of four of the more characteristic grass species are shown in Table 16.2. The species were chosen to exemplify contrasting responses to the application of lime.

Arrhenatherum elatius is the characteristic tall grass of the limed subplots receiving both P and K; in the absence of K it is rare. It grows more than 1 m high in the crop cut in June and forms the major component of the regrowth cut in October–November. It flowers in both periods. The effects of

lime are shown on high yielding plots with nitrogen (Plot 11-1) and without (Plot 7) (Table 16.2). Plot 7 yields well because of the legume component of the sward.

Alopecurus pratensis has a very similar distribution to *Arrhenatherum* but differs in its ecology in important ways. It reaches only about one-fifth of the peak biomass shown by *Arrhenatherum* in the first crop (Table 16.2) and is virtually absent from the second. It flowers only in the first crop and is a strongly early-season grass. Like *Arrhenatherum* it disappears from the sward in the absence of K when P is applied.

Holcus lanatus is ubiquitous on Park Grass, but rarely achieves high biomass with the spectacular exception of the most acid subplots of Plot 11-1 (Table 16.2). On Plot 11-1 it declines with increasing lime from a monoculture of 458 g m⁻² on subplot 11-1d to a modest 66 g m⁻² on the limed subplot 11-1a.

Agrostis capillaris has a general increase in absolute abundance with declining pH (Table 2). On control Plot 3 it more than doubled in the standing crop from subplot a to d; the trend on Plot 12 was similar but less pronounced. The increase was especially pronounced where no nitrogen but both P and K were applied; Plot 7 subplots c and d had 131 and 154 g m⁻². *Agrostis* has less absolute biomass on Plot 8 without potassium. *Agrostis* is rare on all but subplot c of Plot 11-1 (144 kg N ha⁻¹, limed to attain pH 5 since 1965). Here *Agrostis* has increased markedly since 1965.

Microevolution in the Park Grass Experiment

Because the various rates and patterns of nutrient addition to the Park Grass plots have resulted in changes in the abundances of plant species, it seems reasonable that the treatments might also act as selective forces on individual species. However, the rapidity of evolutionary change in response to such selective forces at Park Grass has been surprising. Genetic differentiation has been demonstrated in *Anthoxanthum odoratum* (sweet vernal grass) which occurs across a broad range of nutrient and pH differences on many of the Park Grass plots. Snaydon (1970) sampled tillers and collected seeds of *Anthoxanthum odoratum* in limed and unlimed parts of Plots 1, 10 and 18 and grew these in boxes of acid and calcareous soils. Plants from acid plots did better on acid soil than on calcareous soil, whereas the reverse was the case for plants from less acid plots. The results were similar for plants grown from vegetative material or seed, suggesting that differences were genetic rather than due to phenotypic carryover (e.g. Bullock *et al.*, 1993). Liming was begun in Plots 1 and 10 in 1903 and in Plot 18 in 1920. Thus, genetic differentiation occurred in less than 40 years. Following the introduction of new liming treatments on Park Grass in 1965, there were significant morphological differences between populations that had received different liming treatments for only six years.

In another experiment, Snaydon and Davies (1972) collected plants from the limed and unlimed parts of Plots 1, 3, 4, 9, 10, 17 and 18, propagated the

samples vegetatively, and then grew these in a common garden. They observed correlations between disease resistance and plot treatments. Mildew (*Erysiphe graminis*) resistance of plants in the common garden was positively correlated ($r^2 = 0.83$) with total soil nitrogen in source plots. Rust (*Puccinia poae-nemoralis*) resistance was positively correlated with vegetation height ($r^2 = 0.69$). Nitrogen fertilizer increases susceptibility to mildew, and humid atmospheric conditions (as found in tall vegetation) aids rust infection, so there appears to have been selection for resistance in those populations most exposed to each disease. However, these experiments were carried out with vegetative samples, so a genetic basis was not fully proven.

The decisive evidence that natural selection has operated on *Anthoxanthum* in Park Grass comes from reciprocal transplants between contrasting plots (Plot 3 unlimed and Plot 9 limed, Plot 1 limed and Plot 1 unlimed, Plot 8 limed and Plot 7 unlimed). Davies and Snaydon (1976) collected plants from each of the six populations, propagated them vegetatively in a garden bed and then transplanted tillers back into source plots and contrasting ones. All alien transplants had lower survival and lower tillering rates than native transplants. Selection coefficients against aliens (calculated as $1 - \text{alien/native performance}$) 18 months after transplanting were in the range 0.09–0.77 for survival and 0.23–0.57 for tillering rate.

The rapid microevolution of *Anthoxanthum* probably results from its short generation time and the large selection pressures in Park Grass. If an outcrossing (self-incompatible) species like *Anthoxanthum* can adapt to local conditions so rapidly, then it would be surprising if there was not genetic differentiation among many of the other species found in the Park Grass plots. As yet, no other species have been investigated, but Park Grass provides a unique opportunity to conduct a comparative study of microevolution among species with a variety of life histories and mating systems growing in a common set of environments with a well-documented and long-term history.

Conclusions

The experiment started by Lawes and Gilbert to determine the effects of nutrient additions on hay yield has provided a large number of unanticipated ecological and evolutionary insights. However, there are many more such insights to be gained from further studies on Park Grass. Effects of treatments on herbivorous insects, for instance, should provide insights into the validity of hypothesized relationships between productivity and the intensity of herbivory (Hairston *et al.*, 1960; Oksanen, 1990). The effects of treatments on both aboveground and belowground foodweb structure have likewise not yet been studied in the Park Grass ecosystems. Published analyses of Park Grass data have suggested a host of mechanistic explanations for the observed effects of nutrient ratios and productivity on plant species composition and diversity

(e.g. Tilman, 1982), but these hypotheses have not yet been tested. The Park Grass Experiment provides a richer and longer history than for any other site of interest to experimental ecologists. This bestows on Park Grass a unique potential to contribute to the central issues of ecology, evolution and environmental science.

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References

- Brenchley, W.E. and Warington, K. (1958) *The Park Grass plots at Rothamsted 1856-1949*. Reprinted 1969. Rothamsted Experimental Station, Harpenden, Herts.
- Bullock, J.M., Mortimer, A.M. and Begon, M. (1993) Carryover effects on the clonal growth of the grass *Holcus lanatus* L. *New Phytologist* 124, 301-307.
- Cashen, R.O. (1947) The influence of rainfall on the yield and botanical composition of permanent grass at Rothamsted. *Journal of Agricultural Science* 37, 1-10.
- Davies, M.S. and Snaydon, R.W. (1976) Rapid population differentiation in a mosaic environment. III. Measurements of selection pressures. *Heredity* 36, 59-66.
- Hairston, N.G., Smith, F.E. and Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist* 94, 421-425.
- Huston, M.A. (1979) A general hypothesis of species diversity. *American Naturalist* 113, 81-101.
- Jenkinson, D.S., Potts, J.M., Perry, J.N., Barnett, V., Coleman, K. and Johnston, A.E. (1994) Trends in herbage yields over the last century on the Rothamsted Long-term Continuous Hay Experiment. *Journal of Agricultural Science* 122, 365-374.
- Johnston, A.E. (1972) Changes in soil properties caused by the new liming scheme on Park Grass. *Rothamsted Experimental Station Report for 1971*, Part 2, 177-180.
- Lawes, J.B. and Gilbert, J.H. (1863) The effect of different manures on the mixed herbage of grassland. *Journal of the Royal Agricultural Society of England* 24, Part I, 1-36.
- Lawes, J.B. and 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* 171, 289-415.
- Lawes, J.B., Gilbert, J.H. and 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.
- Oksanen, L. (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. In: Grace, J.B. and Tilman, D. (eds) *Perspectives on Plant Competition*. Academic Press, San Diego, CA, pp. 445-474.

- Pianka, E. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100, 33-46.
- Silvertown, J.W. (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.
- Smith, L.P. (1960) The relation between weather and meadow hay yields in England. *Journal of the British Grassland Society* 15, 203-208.
- Snaydon, R.W. (1970) Rapid population differentiation in a mosaic environment. I. Response of *Anthoxanthum odoratum* to soils. *Evolution* 24, 257-269.
- Snaydon, R.W. and Davies, M.S. (1972) Rapid population differentiation in a mosaic environment. II. Morphological variation in *Anthoxanthum odoratum* L. *Evolution* 26, 390-405.
- Thurston, J. (1969) The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the yield of hay. In: Rorison, I. (ed.) *Ecological Aspects of the Mineral Nutrition of Plants*. Blackwell Scientific Publications, Oxford, pp. 3-10.
- Thurston, J.M., Williams, E.D. and Johnston, A.E. (1976) Modern developments in an experiment on permanent grassland started in 1856: effects of fertilizers and lime on botanical composition and crop and soil analyses. *Annales Agronomiques* 27, 1043-1082.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. (1986) Resources, competition and the dynamics of plant communities. In: Crawley, M.J. (ed.) *Plant Ecology*. Blackwell Scientific Publications, Oxford, pp. 51-75.
- Tilman, D. and Pacala, S. (1993) The maintenance of species richness in plant communities. In: Ricklefs, R. and Schluter, D. (eds) *Species Diversity*. University of Chicago Press, Chicago.
- Warren, R.G. and Johnston, A.E. (1964) The Park Grass experiment. *Rothamsted Experimental Station, Report for 1963*, 240-262.
- Warren, R.G., Johnston, A.E. and Cooke, G.W. (1965) Changes in the Park Grass experiment. *Rothamsted Experimental Station, Report for 1964*, 224-228.
- Williams, E.D. (1978) Botanical composition of the Park Grass plots at Rothamsted 1856-1976. Harpenden, Rothamsted Experimental Station.