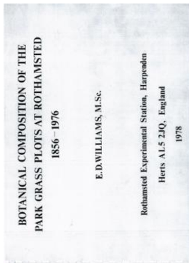
Botanical Composition of the Park Grass Plots at Rothamsted 1856-1976



Full Table of Content

Dicussion and Conclusions

Rothamsted Research

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3. COMPARISON OF THE BOTANICAL COMPOSITION OF PLOTS 3, 7 AND 14 IN 1975 AND 1976

(Tables 42, 43, 44 and 45)

The present botanical composition of these plots has already been discussed when successional changes were presented and the very different weather conditions preceding the 1975 and 1976 harvests have also been emphasised.

There was nevertheless good agreement between the results for the two seasons especially for the major components on the plots. For example, on the unlimed half of Plot 3 (Unmanured), *Festuca rubra* contributed 32-33% in both seasons and *Agrostis* on the unlimed half of Plot 7 (PKNaMg) was 29 and 31% in 1975 and 1976 respectively. Also on the unlimed half of 14 (N_2 *PKNaMg) *Arrhenatherum* and *Alopecurus* were co-dominant but on the limed half *Arrhenatherum* was dominant in both 1975 and 1976. The unlimed half of Plot 7 consisted of 30% *Arrhenatherum* in 1975 and although only partial analysis was done in 1976 (Table 44) about three-quarters of the grass fraction (40%) appeared to consist of *Arrhenatherum* in that year.

There were also some differences between seasons. The most significant of these was the increase in % other species on the limed half (L) of Plot 3 and the large increase in % legumes on the limed half of Plot 7 in 1976 compared with 1975. The increase in other species on 3L in 1976 was mainly at the expense of the grasses but the increase in legumes on 7L was accompanied by a decrease in other species so evidently the drought induced different reactions in different communities. Particular species e.g. *Hypochaeris* and *Leontodon* were much encouraged in 1976; *Dactylis* and *Lolium* also appeared more abundant than usual and *Arrhenatherum* was more plentiful on 14L in 1976 than in 1975.

DISCUSSION AND CONCLUSIONS

CHANGES WITH TIME

As pointed out in the Introduction the present analyses were initiated to quantify the changes in botanical composition on those sub-plots which had received new or increased rates of lime under the new liming scheme. The analyses were then extended to include plots with unchanged treatment to assess whether and how much they had changed since the previous hay analyses during 1948 and 1949. At the same time it became clear that a better appraisal of the present-day flora would be achieved by considering it not only in relation to changes in the immediate past but also in relation to the main changes on the plots throughout the duration of the experiment. The scope of the work was, therefore, widened from a presentation of the results of the 1973-1976 analyses to include also a review of past results. However, because of the large amount of accumulated data the results section dealt only with those changes which were deemed large enough or to have continued for long enough to be obviously 'significant'. It is likely that other changes have occurred especially in minor components which the method of analysis was not sensitive enough to detect. Plot yields have changed (usually decreased) slowly with time but except in the early (1862-77) and late (1973-76) analyses the amounts of species per unit area of land were not calculated; in view of the yield changes it is possible that over a period of time the changes in the amount of species might be somewhat greater or smaller than the percentage figures suggest. Although percentage composition can be compared throughout, because of the change

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in the method of estimating yield (hay before 1960 but dry weight since then) the absolute amount of species after 1960 cannot be compared with that before that date.

With the introduction of the four-year liming scheme in 1903 and the new liming scheme on some plots in 1965 the parts of the plots with unchanged treatment have become progressively smaller; thus for the ammonium sulphate plots the continuously unlimed section is now only a quarter of that during the first 47 years and on other plots half that at the outset. Nevertheless, despite the smaller area, because of the large differences between treatments and the length of time they have continued, it is possible to ascertain what successional changes are occurring.

Although many of the major differences between plots were established in the early years and have persisted throughout the duration of the experiment the dynamic nature of the vegetation on the plots has also long been recognised. Commenting on the 1858 results, particularly on the proportion of *Lolium* in the samples, Lawes and Gilbert (1859) stressed that "it must not be supposed that figures which represent the proportion of flowering and seeding stem of a certain plant at a given period of the season are at the same time accurate indications of the relative development of the total plant under all the conditions in question. It must be borne in mind that the numerous plants which constitute the complex herbage of our meadows have each their natural period of flowering and seeding. It must be remembered that by cutting time some plants are grown up and disappeared whilst others may escape the scythe. Plants may be present in diminished numbers or in such limited growth that they are not obvious at all times when observations are made and still less are they found in the samples. When circumstances become favourable again they re-appear". Brenchley (1937) also pointed out "that the botanical composition of the herbage of any particular area of grassland is by no means static, but is in a constant flux, varying not only from year to year, but also from one season of year to another. This is true even when the treatment of these plants is the same for many years". Apart from these short-term variations between and within seasons, the available evidence, including that from recent analyses, shows that long-term changes are also occurring on most plots. That is, botanical composition continues to change systematically despite unchanging treatment. The extent, rate and direction of the changes, however, vary between treatments. On some plots definite increases or decreases in certain components have occurred during the last 30 years, on others a complete change in dominant species has occurred, on others the changes have been cyclical such that the present-day botanical composition more closely resembles that sixty than thirty years ago and on yet others few changes have occurred in the dominant species although changes may have occurred in more minor components. The fact that groups of plots are behaving similarly confirms that the changes are genuine, and not haphazard.

The unlimed halves of the unmanured plot (3) and of those receiving PKNaMg (7) or PNaMg (8) had much more *Festuca rubra* during 1975 and 1976 than they had during 1948 and 1949. On the unmanured plot the 32% recorded was larger than any in the past although the species exceeded 20% during 1872-1903; on the other two plots similar or larger values were recorded in the past but not since 1935 on 7 (PKNaMg) and 1941 on 8 (PNaMg). On the limed halves of the unmanured and PNaMg plots there was also much more *Festuca* during 1975 and 1976 than during 1947 and 1948 but on the PKNaMg plot only small amounts were present, as previously. It is unlikely that these increases were merely seasonal since there was good agreement between the two contrasting seasons. On Plots 3 and 7, % grasses also appears to have increased

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recently. Some of these changes could be explained by the plots becoming more acid but this possibility is ruled out by the fact that recent analyses (Table 3) have shown the pH on these plots to be largely unchanged since 1959. *Dactylis* has also decreased generally in this group of plots except possibly on the PNaMg plot, where it has always been very infrequent and *Helictotrichon* and *Rumex* have also decreased. However, not all changes have been similar : whereas *Holcus* has decreased on the unmanured plot, especially on the unlimed half, it has increased greatly on the other two plots.

The unlimed halves (or quarter-plots since 1965) of all plots given the intermediate amount of ammonium sulphate, except the one not given phosphate, have become dominated by *Anthoxanthum* since the last analyses in 1948 and 1949. Visual survey suggests that they became so during the late 50's and early 60's. Even on the plots not given phosphate (Plot 1 (N_1) and Plot 18 (N_2KNaMg) the amount of *Anthoxanthum* has increased substantially. On these plots however, a similar precentage of *Anthoxanthum* has occurred in the past: on Plot 1 *Anthoxanthum* increased to about 15% and remained at that level until after 1919 and then declined, but on Plot 18 only in one other year (1920) was as much *Anthoxanthum* recorded as in 1973. However, since past records and present analyses show much seasonal variation in this species further analyses would be required to ascertain whether the increases on these two plots are transient or permanent. Also, although *Anthoxanthum* has evidently dominated the unlimed halves and later sub-plots *d* of Plots 4^2, 9 and 10 for the last 10-15 years, it is not clear whether the proportion (70%) now on the plots represents an equilibrium position with *Agrostis* or whether the species is still increasing to a completely dominant position as *Holcus* has done on Plots 11^1 and 11^2. Further analyses in 5-10 years time would be needed to assess this.

Most of the plots now dominated by *Arrhenatherum* and *Alopecurus* have shown systematic variations in these components in the past. On the limed halves of Plot 9 (N_2PKNaMg) and 11^1 (N_3PKNaMg) where *Arrhenatherum* is now dominant or co-dominant with *Alopecurus* respectively, the relative proportions of the two species in 1974 and 1976 more closely approximated to those in 1914 (ten years after the start of the main liming scheme) than they did in most of the intervening years, when *Alopecurus* was dominant. As on Plot 9, *Arrhenatherum* is also now dominant on 11^2. A decline in *Alopecurus* also occurred during the 1930s and 1940s on plots given FYM, especially on the unlimed and lightly limed sub-plots of Plot 19 which did not receive inorganic fertilisers. In contrast on Plot 20, which received NPK as well as FYM, there was less decline in *Alopecurus* and this did not occur on the unlimed sub-plot. On Plot 18 (N_2PNaMg), which lacks K, a very pronounced decline in *Alopecurus* occurred on both lightly and heavily limed sub-plots.

Amongst the half-plots that have shown little change during the last fifty years or so are those unlimed and given the largest amount of ammonium sulphate and PKNaMg (Plots 11^1 and 11^2) which are dominated by *Holcus*. The unlimed and limed half-plots of Plot 14 (N_2 as sodium nitrate) and 7 (PKNaMg), which are dominated by *Alopecurus* and *Arrhenatherum* respectively, have also been relatively stable although some decline in *Dactylis* has occurred recently compared to the level during the 1940s. It will be of great interest to see whether these plots remain stable in the future; in particular, whether *Anthoxanthum* which has appeared to increase on 11^1d since the 1973 analysis will continue to do so.

10R

CHANGES WITH LIME

Comparison of treatments and discussion of the effects of lime under the main schemes have, as mentioned earlier, been made several times in the past. The present analyses were not undertaken primarily to provide further evidence of these differences, and since only a limited number of plots were analysed in any one year, the results do not lend themselves readily to valid detailed comparisons of all treatments. It is, however, apparent in view of the many long-term changes already noted on some plots and relative stability on others, that differences between treatments will also be affected. However, such detailed comparisons would probably be applicable only to the particular site in question whereas a study of succession within particular types of communities would be expected to be more widely applicable. Except on the plots given sodium nitrate, the effects of lime are very pronounced but the differences between unlimed and limed half-plots are often not much greater than those which have occurred with time on the unlimed half-plots as they have become gradually more acid. For example, the botanical composition of the unlimed half of Plot 11^1 in 1903 was qualitiatively similar to that of the limed sub-plots *a* in 1974.

In so far as comparison is possible the effects of lime under the new scheme, particularly where it has been applied to previously unlimed sub-plots, have appeared in general larger than the effects in 1914 of lime applied under the old scheme in 1903 and 1907. The reason for this is that between that time and 1965, when the new scheme was started, the unlimed halves of the plots in question became progressively more acid; this was reflected in their botanical composition : whereas a wide range of species were present in 1903, in 1965 the unlimed sub-plots were dominated by single acid-tolerant grasses. The initial effect of lime applied in 1903 was to encourage or discourage differentially species already present but lime applied under the new scheme also allowed species which were absent at the time or present in extremely small amounts to be introduced or to increase on the newly-limed sub-plots. The increase in pH also at the same time caused a marked reduction in the dominant species. One of the effects of fresh lime during 1965-68 was to allow re-introduction of species previously present on the plots before they became so acid. For example, *Festuca*, much increased on 1*c*, was very abundant on Plot 1 unlimed during 1939 and 1940, the composition of 18*c* in 1973 resembled that of the unlimed sub-plot in 1923, 4^2c in 1973 probably resembled that of the unlimed half during the 1920s (it was not analysed between 1914 and 1949), 10*c* that of 10 unlimed in 1948, 9*c* that of 9 unlimed during 1926 and 1927, 11^1c that of 11^1 unlimed in 1903 and 11^2c that of 11^2 unlimed during the first ten years of the century. This provides further evidence that the effects of lime have not been much greater than changes which have occurred naturally with time. This was also so on sub-plots given increased rates of lime. The effect of lime on these plots was to accentuate the trends already occurring with time: the decline of *Alopecurus* already occurring since 1948 was increased by increased rates of lime. It is likely, however, that sub-plots which have received lime under the new scheme are still in a state of change, albeit a slower one than during the first seven years. Brenchley (1937), describing the effects of lime, states "that the initial effect may be accentuated with time until a certain position" (presumably of relative stability) "is reached as far as effect of liming is concerned, although seasonal conditions will still cause fluctuations in the normal way".

In general, lime in the new scheme has shown that under acid conditions relatively small changes in soil pH (Thurston, Williams & Johnston, 1976) in the uppermost soil

11 L

layers may bring about fairly large changes in the botanical composition. For example, the changes in botanical composition on Plot 18*c* were associated with only 0.2 pH unit increase in the uppermost 7.5 cm of soil in 1971, although the pH of the 'mat' of partially decomposed organic matter was raised from 3.9 to 6.3 (Johnston, 1972). The effects of recent lime on the botanical composition of the swards has, in general, been more consistent than on yield since it has been less subject to seasonal variations. Also, although in 1973 recent lime on 11^1 increased yield of sub-plot *c* compared to *d* by only about 20%, but by as much as 70% on 11^2, changes in botanical composition were similar. The reduction in the acid-tolerant grasses and replacement by other species was accompanied by large increases in yield, especially at the first cut on sub-plot *c*. However, changes in the proportion of grasses already present e.g. on sub-plot 11^2b had little effect on yield, although pH was raised from 4.7 to c.6.0 in the uppermost 22.5 cm.

Although the unlimed sub-plots of plots 4^2, 9 and 10 were very similar, consisting of c.70% *Anthoxanthum*, and although this was decreased to 5-10% by lime, the species was replaced by different amounts of different species on the different sub-plots. On 4^2c *Anthoxanthum* was replaced mainly by *Festuca rubra* on 9*c* by *Holcus* and on 10*c* by both. It is clear therefore that a prediction of the effects of lime entails not only knowledge of the existing flora and extent of pH change but also previous fertiliser application or nutrient status of the soil as well as the proximity of other species. The presence of *Festuca rubra* on K-deficient soil in the pH range 4.7-5.5 on the Park Grass plots confirms this association on other soils and under other management conditions (*e.g.* Castle & Holmes, 1960; Murphy, 1960; Heddle, 1967; Smith, Elston & Bunting, 1975; Arnold, Hunter & Gonzalez-Fernandez, 1976). The relatively small effect of lime under the new scheme on % *Agrostis* on plots receiving N_2 is similar to the effects at the start of light lime on Plot 19, where there was also no reduction during the first 8 years although there were large reductions later. It is, however, not clear why lime should increase the amount of *Holcus* on sub-plots 9*c* and 10*c* whilst decreasing it on 11^1c and 11^2c.

It is now abundantly clear that, although some species are plentiful in very acid conditions whilst others are absent, great caution needs to be exercised in categorising species simply into those that are discouraged or encouraged by liming. The distribution of species is influenced by the relative preferences and tolerances of other species and also the influence of lime depends on the pH range and extent of change and on what other nutrients are applied. For example, although *Holcus* dominates the unlimed acid sub-plots of 11^1 and 11^2 this may not be because it prefers acid conditions *per se* but because it is better able to survive and is not subjected to competition from other species in such conditions. There have been some instances, as already noted, where the amount of *Holcus* has been increased by lime on Park Grass. Similarly, *Rumex*, which may appear to prefer acid conditions, also grows well on limed soils but is subject to increased competition there (Brenchley, 1935).

ASSOCIATION BETWEEN BOTANICAL COMPOSITION AND YIELD

Although the experiment was set up as an agricultural investigation and the treatments induced large changes in yield these were soon associated with conspicuous changes in botanical composition. However, the fact that complete fertilisers (N_3PK) increased yield three-fold even in the first year suggests that this was achieved by the response of species already present at the outset,

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since it is unlikely that large changes would have occurred in the botanical composition during the first year. As the unmanured plot became increasingly impoverished, *Lolium* and *Holcus* decreased to very minor components and *Agrostis* and *Festuca* became the main grasses; other species have been abundant. It is possible that through growing slowly the species may make small demands on the environment and/or that they may be very efficient in the use of mineral nutrients. The presence of large numbers of low-growing dicotyledonous species may also be a form of adaptation to the fertiliser and management regime – only a small part of this vegetation would be removed during harvest, perhaps enabling nutrients to be conserved and recycled within the community.

The larger yield on the plot given PKNaMg than on the unmanured plot has for most of the time been associated with more *Dactylis* and legumes and the still larger yield on the limed half of this plot, with even more vigorous growth of *Lathyrus* and also *Arrhenatherum* and *Alopecurus*. However, when yields of hay in individual years between 1900-1950 are plotted against % legumes in those years on both unlimed and limed half plots there appears to be no correlation between yield and legume content. Brenchley (1935), however, using data from four selected years postulated a correlation between the two parameters but it is clear that although high yields in particular years may be associated with much legume, there are many other years where large yields are associated with little legume and small yields with much legume. When potassium was omitted from this treatment, yield declined to about 50% of that with K, legumes became less frequent and latterly *Leontodon* and *Plantago* more frequent. On the plot given the smallest amount of ammonium sulphate without P and K, and where *Agrostis* has been dominant since c. 1940, yield has been smaller than on the unmanured plots. However, it cannot be deduced from this that *Agrostis* is a low-yielding species *per se* since its presence on this plot may merely reflect that it is better able to survive under these conditions than its competitors. The species was in fact, especially in the early years of the experiment, also associated with plots of higher fertility and is also frequent now on plots receiving N_2. The plot given N_2PKNaMg yielded about 4.0 t ha^{-1} of hay during the first 30 years but yield then declined progressively to about 2.8 t ha^{-1} during the 1950's. This decline was associated, at least during the first quarter of the century, with larger amounts of and subsequent dominance by *Holcus* for another thirty years before *Anthoxanthum* became dominant. The variations in yield on the limed half from the 1920's to the 1940's were not associated with any changes in botanical composition.

Omitting K from this treatment (i.e. N_2PNaMg) resulted in a sharp decline in yield which was associated with a decrease in *Poa trivialis* and *Dactylis* and increases in *Alopecurus, Arrhenatherum* and *Festuca* which continued until about 1920. Afterwards yield continued to decline while *Holcus* was dominant during the next 15 years or so and then while *Anthoxanthum* and *Agrostis* were the main constituents. Yield on the limed half-plot declined only very slowly and this was associated during the mid-40's to mid-50's with an increase in *Festuca* and a decrease in *Alopecurus*. On the N_3PKNaMg plots (11^1 and 11^2) Cashen's statistical analysis (1947) suggested that there was no significant falling off in yield during the first fifty years. Whilst this is probably true for the plot receiving N_3PKNaMgSi it is less likely to be so for Plot 11^1 (N_3PKNaMg). Examination of ten-year means for yields of this plot showed a gradual but consistent decrease from the outset: statistical analyses of the first fifty

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years were probably distorted by the abnormally high yields during the fifth decade. After the rapid increase and subsequent dominance of *Holcus* appreciable decreases in yield occurred. Although the larger yields on the limed halves were associated with *Alopecurus* and *Arrhenatherum*, changes in yield with time could not be correlated with changing botanical composition.

On plot 17, receiving sodium nitrate, yield has declined continuously although botanical composition has been relatively stable. However, on Plot 14, receiving the larger amount of sodium nitrate and PKNaMg, moderately stable yields have been associated with relatively stable botanical composition.

Although evidently it is possible to associate differences in yield on the Park Grass plots with differences in botanical composition and to outline changes in yield with time in relation to concurrent botanical changes it is clear that the relationship between yield and botanical composition is very complex and it is very difficult to establish causal relationships between the two. The complexity of the situation is due to the large number of species present, insufficient botanical data for some periods (e.g. 1877 to 1903), difficulties of estimating hay yield accurately on low-yielding plots and of satisfactorily eliminating the effects of variable and changing weather conditions. In addition, until 1960 estimates of yield were also affected by weather during hay-making. Another reason for the difficulty in correlating yield and botanical composition is that both are affected by a third factor, the fertiliser treatment and hence nutrient status of the soil. Yield is the indirect consequence of the effects of the fertiliser treatments on the responses and interactions or competition of the species present and depends on the fact that whereas some species may have very specific requirements and do not seemingly respond to increased fertility others may be less specific in their requirements and be able to respond to increased fertility.

Despite these difficulties it is nevertheless possible to characterise the extreme situations. In general, low-yielding plots, e.g. the unmanured and the PNaMg plots, have large numbers of low-growing dicotyledonous species together with unproductive grasses, or where conditions are acid and P and/or K are deficient, only acid-tolerant grasses are present, whereas the higher-yielding plots are now dominated by *Alopecurus* and *Arrhenatherum*. However, plots with roughly similar botanical composition may yield differently whilst others with similar total yields have very different botanical compositions.

RELATIONSHIP BETWEEN FERTILISER TREATMENT AND BOTANICAL COMPOSITION

The experiment is best known for the way in which the different fertiliser regimes have changed the presence and balance of species on the different plots. The subject has been comprehensively presented in many previous publications (Lawes, Gilbert & Masters, 1882; Brenchley, 1924; Brenchley & Warington, 1958) and need not be repeated here.

However, it must be emphasised that conclusions about the preferences of individual species and their response to various factors should take account of other factors involved and also of changes that have occurred with time. The distribution of species is not governed solely by the response to the presence or absence of one particular nutrient although data from Park Grass can be used to pinpoint some of the major determinants within a given situation. Additionally, the frequency of a given species may be determined as much by the response through competition of

12 R

other species, as by the preferences of the species itself. In such situations further experiment is needed to determine the relative importance of the two factors. As pointed out previously, although *Holcus* is dominant on the acid conditions of the N_3PK plots this may be a reflection of differential survival and tolerance under these conditions and cannot be interpreted as a reflection of the preferences of the species. *Holcus* is now infrequent where potassium is not given (Plot 10) but was so dominant during the 1920s and 1930s that Brenchley and Warington (1958) concluded that the species was encouraged by omission of potassium. However, in the absence of nitrogen the species continues to be more plentiful without than with potassium. Similarly, without nitrogen and under fairly acid conditions (pH approx 5) *Arrhenatherum* is more abundant where K is withheld but when the plots are limed the opposite is now true, though not in the past. Also, on the limed sections of Plot 10, given N_2PNaMg, omitting K decreases % *Arrhenatherum* but the species appears to be increasing on this treatment. *Alopecurus,* often described in the past as requiring complete fertilisers, was dominant for 30-40 years at the beginning of the century on two plots (4^2 and 10 limed) which had not received K for about fifty years previously. Evidently, the species is able to survive under fairly low levels of K; its replacement by *Festuca rubra* might be because *Festuca* can tolerate even lower levels of K or it is better favoured by the increase in pH which occurred between 1923 and 1959 on these plots (Warren & Johnston, 1964)

A further example of a different response at different time is shown by the colonisation of *Chamaenerion angustifolium* on the plots. Following much damage to the vegetation of the unlimed half-plots receiving ammonium sulphate during the severe winter of 1928/29, more *Chamaenerion* established on plot 4^2 than on 11^1 and Brenchley & Heintze (1933) attributed this to the greater competitive ability of the vegetation on 11^1 than on 4^2. However, botanical analyses of the plots following the very cold winter of 1946/47 showed that much more *Chamaenerion* then established on 11^1 than on 4^2.

EFFECT OF SEASON ON BOTANICAL COMPOSITION

Since almost all the major differences between plots are apparent every year it is clear that seasonal differences are small compared to those due to treatments and in only abnormal seasons is the influence of treatment out-weighed by weather. Nevertheless, large effects occur in some seasons, but these are usually reversible e.g. following the drought of 1871 there was a large amount of *Bromus* on Plot 14 but it soon decreased afterwards. Also, following the droughts of 1921 and 1976, *Alopecurus* was much increased on the unlimed half of Plot 14 during 1922 and 1977. On the unmanured and other plots in 1938 and 1976, % other species was larger than usual and the relative increase in this group in dry seasons has long been recognised. This effect is noted in the White Books for the 1872 season: "With regard to the weedy herbage these also have necessarily been retarded in growth but the ill effects of a dry season are less felt by many of them than by the graminaceous or leguminous plants on account of the faculty which some of them possess for retaining and storing in periods of plenty through the agency of their fleshy roots a sufficiency of moisture and nutrient to supply the parent plant in time of scarcity like that which prevailed during the present year". Temperature may, as well as rainfall, affect the proportion of the three main groups of plants. In 1921 the proportion of grasses was high on most plots despite low rainfall presumably because of high temperatures; low

13 L

temperatures early in the season tend to reduce the proportion of grasses. Seasonal variations in yield, however, cannot easily be related to differences in botanical composition at least as far as the three main groups of plants are concerned (Brenchley, 1935).

The weather conditions preceding the 1937 and 1938 and the 1975 and 1976 harvests were similar in many respects, the spring of 1937 and 1975 being very wet but 1938 and 1976 very dry. In 1938, % other species was high on both limed and unlimed halves of the unmanured plot but in 1976 only on the limed half; *Poterium, Plantago* and *Leontodon* were all increased. In 1976 only *Leontodon* had a greater % on the unlimed half than in 1975. The relatively small increase in % other species on the unlimed half in 1976 compared with 1975 (35% as against 29%) contrasts strongly with the increase in 1938 compared to 1937 (67% as against 35%) but the reason for this is unclear. *Arrhenatherum* on Plot 14 (N_2*PKNaMg) limed increased in 1938 and 1976 compared to the levels in 1937 and 1975 but it decreased on Plot 9 with equivalent treatment where N is given as ammonium sulphate. Different depths of rooting of the same species on the two plots (Lawes & Gilbert, 1871) may possibly account for the different result. On both halves of the unmanured plot % legumes was about 2% less in 1976 than in 1975 but on the limed half of the PKNaMg plot there was very much more legume in 1976 than in 1975. Both these results are in accord with Cashen's conclusions (1947) from past data: these were that an extra 25 mm of rain increased % legumes by 0.5% on the unmanured plot and that a greater proportion of leguminous plants would be expected to occur on the plot receiving mineral manures *following* a dry year. (1975 was very dry from mid-May onwards).

Although seasonal effects are often in themselves not permanent they may precipitate developments and changes already occurring on the plots. It is possible for example that the large permanent decreases in *Holcus* on the unlimed halves of Plot 10 (N_2PNaMg) after 1938 and of Plot 9 (N_2PKNaMg) after 1962 and the increasing amount and eventual dominance of *Anthoxanthum* on these plots might, to a large degree, be associated with the extreme weather conditions in both years, the summer of 1938 being exceptionally dry and the 1962/63 winter exceptionally cold. It would be of great interest to know the mechanism of increase of *Anthoxanthum* on Plot 9– whether it was by rapid increase of the 'ecotypes' already present on it or whether there was incursion from nearby Plot 10.

GENERAL

There were large changes in yield and botanical composition of the plots during the early years; changes in yield were possible from the outset because of the presence of appreciable amounts of species like *Holcus* and *Lolium* which responded to the increased fertility and in botanical composition because of the large number of species present. Since the changes depended on both the range and type of species present initially, the potential for such rapid change might not exist in all vegetation types. For example, it is likely that if the experiment were now started on land whose botanical composition resembled the present day unmanured plot, changes in yield at least would be smaller since many of the species may have become adapted to the low nutrient status and so could not respond to increased supplies. Some evidence in support of this comes from results from the microplot experiment on Plot 5[1] (unmanured 1897-1963 following N_2 as ammonium sulphate) where increased supplies of nitrogen have resulted in only small increases in yield (Johnston, personal

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communication). Although the unmanured plot can be regarded as a control plot and is the closest approximation to the state of the whole field at the outset, it is important to realise that it continues to change with time. Yield is now only half that at the start, the dominant grasses are different and there is a relatively much larger contribution of other species, three of which (*Leontodon, Plantago & Poterium*) are now abundant. It is also important to bear in mind that the botanical composition of the plots is not only a function of the fertiliser treatment but also of the management in general. Although this has remained fairly constant throughout, some changes have nevertheless occurred e.g. a change in method of cutting from scythe to mowing machine, and abandonment of grazing the aftermath after 1872. It is therefore possible that these changes in husbandry may have had some influence on changes in botanical composition with time.

Small differences in management e.g. slightly more frequent cutting, as on access strips for studies of the Entomology department in 1973 and 1974, may have profound influence on the botanical composition of the swards (Thurston, Williams and Johnston, 1976). This serves to emphasise the extreme plasticity of the grass sward with each new treatment imposed giving rise to a different species balance.

FUTURE WORK

Examination of the data from hay analysis over the duration of the experiment shows that although the rate of change has decelerated an end-point in botanical composition (plagioclimax) has not been, and possibly may not be, reached on most plots. Changes are also still occurring as a result of the new liming scheme and are likely to continue as new plots are brought into it. The scheme of differential liming was introduced to enable comparisons of the botanical and chemical compositions of the herbage to be made at several pH values for all manurial treatments (Warren, Johnston & Cooke, 1965). It is therefore desirable that assessments and/or surveys should continue to be done to provide some of the information for which the new liming scheme was designed and which it is now yielding. Such information is all the more valuable since the vegetation has been well documented in the past. At the same time a measure of long-term changes on plots not yet in the new scheme and a base line for future changes on the plots would be obtained.

It is clear, however, from comments made in the Introduction that the problem of how best to assess the changes in botanical composition is a very real one since although visual surveys give information on the relative amount of heading of different species at particular points of time they provide only limited information on the contribution of the species to the yield of the plots. Analyses of hay samples, on the other hand, whilst giving a better indication of contribution to yield at one particular point in time, are too laborious and time-consuming to be done regularly. Other methods e.g. point quadrat (Warren Wilson, 1960) would involve too much disturbance of the swards especially those of the taller-growing plots. However, despite these shortcomings it is clear that, when many changes are occurring, visual surveys may give a reasonable indication of them but are less successful at detecting changes in components already present. For example, visual surveys between 1965 and 1972 (Williams, 1974) gave a good indication of change on sub-plots *c* but not on sub-plots *b*. It is possible that botanical separations might be done more easily on fresh or frozen herbage than on air-dried material but this would require more people and much storage space, because such samples would be bulkier than hay samples. It would be desirable that if

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and when a change be made in the method of analysing the vegetation, comparison be made with the traditional method of analysis if the results are to be compared with those in the past.

Since the large number of sub-plots now precludes hay analysis being used routinely to monitor the vegetation, a more worthwhile approach, as previously explained, is to use the method to try to answer specific questions for a limited number of plots and treatments. In the early years of the experiment and again following the liming scheme of 1903 when major changes were occurring on the plots it was clearly of greatest interest to quantify the changes in species composition of the plots and this remains so for plots when new treatments are imposed. However, the emphasis has now changed: whereas this aspect was of paramount importance at the outset, data on the distribution and contributions of the different species may now serve as a background to more detailed studies of individual species and factors affecting the distribution of groups of species.

The Park Grass plots provide within a small area of relatively constant soil-type, a range of discrete types of vegetation which receive similar weather and management. They give ample opportunity for work to ascertain why some species are confined to particular habitats whilst others occur on a wide range of plots. Species may be confined to particular habitats either because of a direct preference for or adaptation to particular conditions or because they are less adversely affected than other species and so are at a competitive advantage under such conditions. The wide distribution of other species might be the result of a wide tolerance within the species as a whole or because morphologically and physiologically different populations have evolved on the plots. Such intraspecific variation for many heritable characteristics has been shown to occur in *Anthoxanthum* by Snaydon and Davies (Davies, 1975; Davies and Snaydon, 1973a, 1973b, 1974, 1976; Snaydon, 1970; Snaydon and Davies, 1972, 1976) in a significant lead on this type of work on species with a wide distribution on the Park Grass plots. The species has increased its contribution on many plots in recent years : the facts that it produces viable seed before the first cut and is cross-pollinated must contribute to the speed of differentiation within the species. Similar studies of other species e.g. *Festuca rubra* would not only help to explain their distribution on the Park Grass plots but also add to the understanding of the mechanisms of adaptation and differentiation within plant species. Populations of *Holcus* from the different plots are also now being used by the Unit of Comparative Plant Ecology (Natural Environment Research Council) at Sheffield University in a study of the variation of response within the species to different nitrogen sources.

Apart from the autecology and ecological genetics of individual species, studies of the comparative ecology and competition between pairs of species should also help to elucidate their distribution on the plots. Some species e.g. *Alopecurus* and *Arrhenatherum* usually occur together and appear to have roughly similar requirements but *Arrhenatherum* tends to become dominant at the higher pH values. However, on some plots e.g. 11^1 and 11^2 the relative amount of the two species has fluctuated with time despite unchanging pH. *Holcus* and *Anthoxanthum* also have very similar ecological requirements and at different times have dominated the same plots : *Holcus* was dominant for 30 years on Plot 9 and also for a shorter length of time on Plot 10 before being replaced by *Anthoxanthum*. The rapidity of transition suggests that the species have fairly similar requirements since it is unlikely that there would be any large differences in nutrient status of the soil during the time of change-over of species.

14R

Studies of the comparative biology of related species which appear to have different ecological requirements would also be worthwhile. These would include comparisons of *Poa pratensis* with *Poa trivialis* and of *Taraxacum* with *Leontodon hispidus*. Lawes, Gilbert & Masters (1882) concluded that *Poa pratensis* benefitted from nitrogen in the form of ammonium sulphate but not as sodium nitrate, whereas *Poa trivialis* declined markedly on plots given ammonium sulphate, but remained prominent on plots given sodium nitrate. Although these differences have been generally true for much of the experiment, they are less clear-cut than in the past. For example, during 1947 and 1948 *Poa pratensis* was much more widespread on Plot 14 unlimed (nitrogen as sodium nitrate) than was *Poa trivialis* and during 1974 there was much more *Poa trivialis* than *Poa pratensis* on the limed half, especially the sub-plot receiving increased rates of lime, of plot 11^2 (nitrogen as ammonium sulphate). Fundamental studies of the response of the two species to different soil reactions and nitrogen sources should help in explaining their different distribution. Whilst *Taraxacum* and *Leontodon* are both absent from the most acid soils, *Taraxacum* is plentiful only on plots given potassium fertiliser whereas *Leontodon* is most abundant on plots lacking potassium. Experiments under controlled conditions should help explain to what extent differences in efficiency of uptake and utilisation of this cation can account for the different distribution of the two species and whether other factors such as competition with other species are also implicated.

It is possible that by now some of the changes that are occurring on the plots may be related to changes in supply and availability of minor elements. Since all the produce is removed every year and there is no replenishment, cumulative depletion of these elements must occur. Additionally, under the very acid conditions of plots given ammonium sulphate without lime, differential tolerance of species to such factors as aluminium toxicity (Hewitt, 1952; Rorison, 1975) must also be a factor in delineating the distribution of species and should be investigated.

The Park Grass plots now represent a range of sward types to be found in many areas of the British Isles. It would be of great interest to know what the likely outcome of ploughing and reseeding such areas would be in terms of regeneration from the previous vegetation. This would depend, in part, on the accumulation of seed of different species on the plots. Assessments of the number and type of viable seeds incorporated into the soil of the different plots would not only help in predicting this but would also contribute to an understanding of the role of buried seeds in regenerating and maintaining species under permanent pasture conditions. Only a very limited study of the buried weed seeds on Park Grass has previously been done (Brenchley, 1918).

In the early years of the experiment a measure of the value of the herbage on the different plots was obtained, at least of the aftermath, by the number of sheep the plots would support and the amount of liveweight gain made by them. Since then, although much work has been done on the botanical and chemical composition of the swards and yields have been estimated annually, no attempts have been made to determine the value of the vegetation, hay or individual species as animal feed although Brenchley (unpublished) applied the figures for individual species given by de Vries, Hart & Kruijne (1942) to estimate the quality of produce from the plots. This lack of information contrasts with the position for the Palace Leas field at Cockle Park at Newcastle (Elliott & Thomas, 1934; Thomas, Holmes & Clapperton, 1955a, 1955b), where less attention has been given to the botanical composition but more to the

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nutritive value of the herbage. Estimates of the nutritive value and digestibility of the material would greatly enhance the value of existing data. The value of a particular grassland species may, of course, depend upon where it is being grown and for what purpose and may also change with time. Although *Holcus* has been used in hill-land reclamation, it is nowadays considered undesirable in lowland pastures; Lawes & Gilbert (1859) state that "some consider it as almost a weed". Similarly, *Arrhenatherum* described by them as not growing abundantly except upon poor soil and being of "somewhat questionable value" is now abundant upon the high fertility plots of the experiment. It was, however, considered a useful hay grass by Smith (1924) and rated highly in de Vries' et al (1942) evaluation scores.

As far as can be foreseen it is likely that the botanical composition of many of the Park Grass plots will continue to change during the next 20-30 years, albeit at different rates for different plots, as a result of both natural succession and recent lime. If beyond that the flora became completely stable or the changes were of insufficient interest to continue recording, useful information would be obtained by changing the treatments on some plots, especially where there are two plots receiving almost the same treatment. For example, it would be of great interest to know what would be the effects on both yield and botanical composition of additions of nutrients to the now very impoverished Plot 2 (unmanured since 1863). This would not repeat the original investigation, because, as detailed previously, the vegetation at the outset differed in many respects from the present-day unmanured plots. Plots 3 and 12 (unmanured from the start) would continue as 'control' plots. As these plots are unique in not having any additions of nutrients for longer than 120 years, not only in the Park Grass but also in a wider context, it would seem desirable that they be maintained in such a state. The reverse situation where a plot given complete fertiliser e.g. N_3PK would be given no fertiliser would also be of interest. This could possibly be done on Plot 11^1 or 11^2 with the other plot continuing to receive N_3PK or alternatively by splitting Plot 9 ($N_2PKNaMg$) with one half continuing to receive the same fertiliser treatment as before and the other half none. However, soil acidity on the unlimed halves would be likely to limit the introduction of many species. Another possibility is that, where it is thought that a deficiency of a minor element is now influencing botanical composition and/or yield, judicious additions of such an element to a plot or part of it might reveal whether this is so. Plots 4^2 and 10 which receive similar treatment and have similar botanical compositions could also be used if any change of treatment were contemplated.

The fact that there are so many contrasting treatments in close proximity makes the experiment a rich source of plant material and this is likely to continue to be so.

Finally, it is clear that monitoring the botanical composition now serves a different purpose from that in the early years. In the past it provided new information of general application. However, as the experiment progressed, and with unchanged treatment, the contrasted processes of enrichment and depletion of nutrients on the different plots limited the applicability of much of the data to present-day agriculture. However, ecologically the data has become increasingly valuable and now serves as a source of information and ideas for more detailed studies of the behaviour of individual species. The usefulness of any future data on the botanical composition of the plots will be enhanced if steps are taken, as far as possible, to ensure that it not only describes the flora and changes in plant associations of a unique site but that it enables this data to be used to predict changes at other sites, and also attempts to describe the mechanisms of distribution and change within those associations.

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