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THE EVOLUTION OF ADAPTATION TO NUTRITIONAL FACTORS IN POPULATIONS OF HERBAGE PLANTS

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Abstract

THE EVOLUTION OF ADAPTATION TO NUTRITIONAL FACTORS IN POPULATIONS OF HERBAGE PLANTS. Plant breeders are familiar with differences in the mineral nutrition of their varieties and these can often be related to differences in varietal performance. Nevertheless, such differences in nutrition may be accidental by-products of the breeding programme and in no way related to yield. In natural populations, however, the differences are the product of powerful selection and therefore directly adaptive: there is considerable evidence of marked differentiation between populations in their adaptation to nutritional factors.

All levels of differences are found. In extreme cases populations of a species may be completely intolerant of an environment and unable to grow on it. For example, normal populations of the grass *Agrostis tenuis* cannot grow on soils contaminated with heavy metals, but it does have populations on such soils which are tolerant to these metals.

In less extreme cases two populations may both be able to grow in each of several environments, but to a different degree: on one environment two populations may behave similarly, on another environment one may be far better than another. In this case the differences that are manifest are differences in the degree of response and they can be related to the levels of nutrients in the soil. This is illustrated by work on *Agrostis*, *Dactylis* and *Lolium*. Several distinct types of response curve can be recognised. Populations may either be less reduced by low levels of nutrient or more tolerant of high levels; they may respond at various rates or the final response achieved may differ.

INTRODUCTION

Many factors contribute to yield, not least of which is the requirement that the crop should be specifically adapted to the environment in which it is grown. Such adaptation is generally regarded as of prime importance and has been reviewed by, among many others, Wilsie [1] and Whyte [2]. Nevertheless, certain aspects of the topic have been inadequately considered, and even though crop adaptation is universally recognized, very few breeding programmes have been concerned with achieving it directly. The value of such breeding programmes or their chance of success is therefore little known. In particular, nutritional adaptation is important not only because of a variety of soil types but also because of the ever increasing fertilizer usage in farm practice. Differences in the mineral nutrition of varieties are well known (for review, see Vose [3]), but such differences have been studied mostly out of physiological interest. Their adaptive value has been difficult to assess: they are often an accidental by-product of a breeding programme, and may have no relation to yield as such. For example, although Morris and Pierre [4] showed that two strains of *Lezpedeza* that differed in their calcium requirement also differed in their ability to grow on soils of low calcium status, Robinson [5] found no relation between phosphorus uptake of clones of clover and their

ability to grow on phosphorus-deficient soil. This problem is important. Hayes [6] showed that the very successful barley variety Proctor had a greater nitrogen response than the older Plumage Archer variety: it is pertinent to ask to what extent the high yield of Proctor is due to its better adaptation to high fertilizer levels. Evidence concerning the significance of nutritional adaptation is poor.

Nevertheless, a clue to the value of such adaptation can come from the study of natural or semi-natural populations growing on a wide range of habitats. Differences between such populations, should they exist, are likely to be the products of natural selection and therefore directly adaptive. This paper is an attempt to assess the extent, nature and origin of adaptation to nutritional factors from a study of herbage plants. Apart from being of economic importance, herbage plants grow over a wide range of soil types, and are therefore well suited to the study of the general phenomenon of nutritional adaptation.

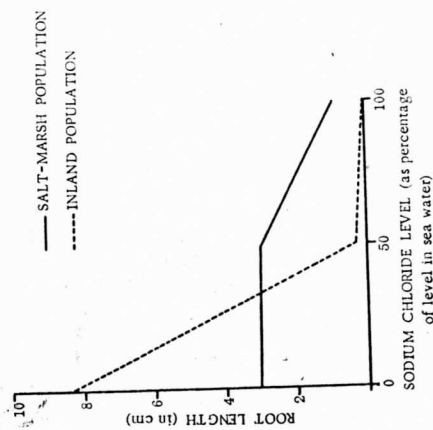


FIG. 1. Response of salt-marsh and inland populations of *Festuca rubra* to sodium chloride. (After Ref. [13])

THE EXTENT OF NUTRITIONAL ADAPTATION

All levels of differences in plant nutrition have been found between natural populations, and these differences can be related to the environments in which the plants are growing. At one extreme there are specialized populations of a species which permit that species to occupy habitats that are so extreme that the normal populations cannot grow. For example, around old mine workings there occur soils contaminated with heavy metals (e.g. lead, zinc, copper, nickel): normal populations of the grass *Agrostis tenuis* cannot grow on such soils, but the soils do carry populations which are tolerant to high concentrations of metal (Bradshaw et al. [7]). Similar populations are known in other species (Wilkins [8], Schwanz and Hahn [9, 10], Gregory and Bradshaw [11]), and Kruckeberg [12] presents evidence of ecotypic adaptation to serpentine soils in

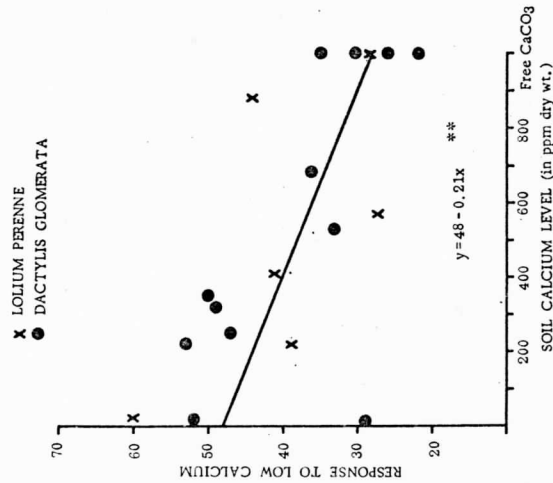


FIG. 2. Response to low calcium of populations taken from soils of different calcium level. Response measured as dry weight yield at 2 ppm Ca over yield at 54 ppm Ca, and expressed as a percentage. (Data from Ref. [19])

15 species. Saline habitats are another extreme. With the technique of measuring rooting of tillers in different solutions, normally used for the estimation of metal tolerance, Lane and Lyon [13] have demonstrated the existence on salt marshes of races of *Festuca rubra* tolerant to high salt concentrations that are nearly lethal to normal populations (Fig. 1). Similar results have been obtained by McNaughton [14].

All these populations are evidence of quite remarkable adaptation to extreme nutritional conditions, but less extreme differences are far more common. What evidence is there of adaptation to these conditions? This is best determined using a range of nutrient levels. Thus in one environment two populations may behave similarly, but in another environment one may do better than the other. When the relative performance of different genotypes depends on the environment, these are said to show different genotype-environment interactions (for full discussion see Allard and Bradshaw [15]). These were first shown by Melchers [16], in Hutchinsia, who demonstrated differences in calcium response of natural populations which could be related to the calcium content of the soils. Similar results have been obtained by Snaydon and Bradshaw [17] in *Festuca ovina*, and by Snaydon [18] in *Trifolium repens*. Furthermore, Crossley [19] showed differences in response of populations of *Lolium perenne* and *Dactylis glomerata* to calcium, phosphorus, nitrogen, aluminium and manganese. All these differences could be related to the levels of these nutrients in the environments from which the populations came, the correlation being very marked in some instances (Fig. 2).

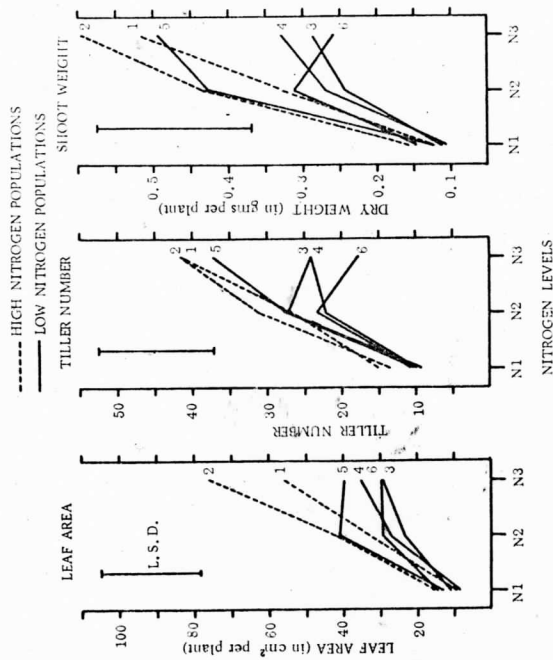


FIG. 3. Response of populations of *Lolium perenne* to nitrogen

The response of populations of *Lolium perenne* to nitrogen has been investigated in more detail. The populations used were as follows:

High nitrogen populations

- (1) S24 - Bred pasture strain in common use.
- (2) Puffin Island - Bird sanctuary, very high fertility.

Low nitrogen populations

- (3) Romney Marsh - A long-established sheep grazed pasture.
- (4) Pensarn - Poor permanent pasture.
- (5) Aber - Poor permanent pasture.
- (6) Conway - Very poor upland pasture.

These were grown in sand culture at three nitrogen levels, 9, 27 and 243 ppm, and harvests were taken after three, five and seven weeks. The plants were collected as tillers, and the material standardized by growing in normal potting compost for six months, picking uniform tillers, and removing extreme types after a week's growth in sand culture. The results for harvest one, after three weeks (Fig. 3), show marked differences between the populations, the response being consistently greater for the high nitrogen populations. Interestingly, population 2 from Puffin Island shows a greater response and yield than the cultivated variety S24. This population comes from an uninhabited island colonized by

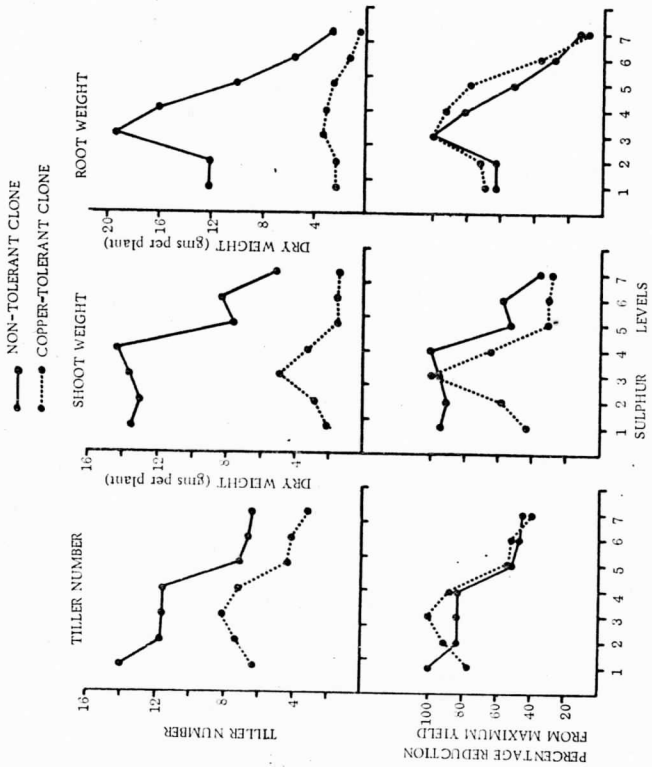


FIG. 4. Response of copper-tolerant and non-tolerant clones of *Agrostis tenuis* to different sulphur levels. The seven levels are (in ppm) 6, 12, 24, 48, 112, 144, and 240. (Data from Ref. [22])

millions of sea birds whose droppings increase the fertility of the ground enormously.

The adaptation can moreover be to several nutrients at the same time. For example, soil contaminated with heavy metals is not only high in metal ion content but, because of the antagonistic effect of the metals, low in phosphates. And mine populations, as well as being tolerant to metals, show a better growth under low phosphate than normal populations (Jowett [20], McNeilly [21]). Moreover, since the metal-carrying ores are sulphides there is high sulphur content; this nutritional factor has produced a marked difference in sulphur response of mine and normal populations (Fig. 4). The picture is therefore not only one of extreme and widespread adaptation but also one of adaptation of a specific and subtle nature. Because of the importance of mineral nutrition it is perhaps not surprising that natural selection places a great store on such adaptation.

NATURE OF ADAPTATION TO NUTRITIONAL FACTORS

The situation as outlined above may seem quite straightforward. Populations can be considered as tolerant of certain nutritional factors or as responding differently. There are, however, several difficulties.

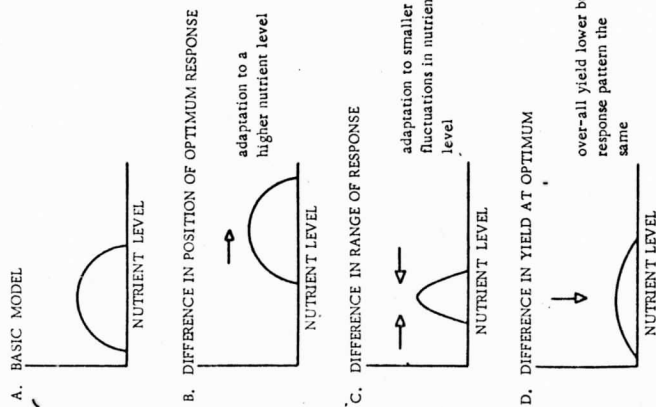


FIG. 6. The evolutionary significance of different types of response curves

not used to denote that under all conditions this level of nutrient is the best. The performance of a variety over a range of nutrients depends on other factors such as temperature, level of other nutrients, etc. Moreover, greatest performance may not be the optimum in terms of fitness (Davies [25]). Thus Snaydon and Bradshaw [26] showed that whereas lowland clover did better than upland under all fertility levels when grown as spaced plants in upland and lowland conditions, the situation was reversed when the two types were planted into an upland sward. In this case, after two years, the lowland type was eliminated, but plants of the upland type were still surviving. Competition is an important factor in studies of nutrient response (see also Crossley [19]).

The response curves of populations can differ in the following ways: The optimum of one population may be greater than that of another (Fig. 6B); this implies that the population is adapted to a higher nutrient level, without retaining any adaptation to the lower.

The spread of the response curve (i.e. the range over which growth of one population occurs may be less than that of another (Fig. 6C)). This implies that the population is adapted to less extreme fluctuations in nutrient level in its normal environment.

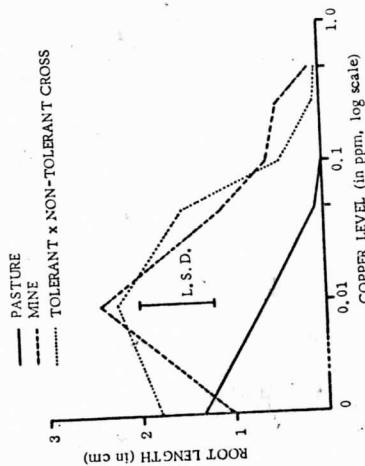


FIG. 5. Response of seedlings of copper-tolerant and non-tolerant populations of *Agrostis tenuis* to copper

The nature of tolerance

The difference between tolerance and response is obviously a matter of degree, and indeed tolerance is really one sort of response. This is well illustrated by looking at the effect of increasing copper concentrations on the root growth of tolerant and non-tolerant seedlings of *Agrostis tenuis* (Fig. 5). The tolerant populations are reduced much more slowly than the non-tolerant by increasing concentrations: it is not an all or nothing effect. Interestingly, it seems that tolerant plants show a positive response to copper at low concentrations, suggesting they have a positive "need" for copper. Similar results have been obtained for copper, zinc and lead in *Agrostis tenuis* by Barker [23] and for zinc in *Silene inflata* by Baumeister and Burghardt [24].

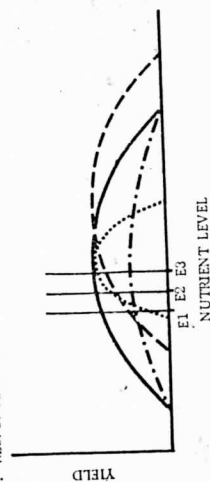
Tolerance is therefore an ability to be unaffected by those levels of a particular nutrient factor which would have adverse effects on growth of other populations, i.e. it is applied to situations where there is negative response to a nutrient.

The interpretation of general response curves

Where there are marked differences in the nutrient requirements of populations, as in metal tolerance, these differences can be meaningfully studied at one nutrient level. Where there are more subtle differences between populations, these can often only be assessed over a range of nutrients. Levels of available nutrients in soils may fluctuate from season to season; they may also fluctuate from place to place. This is the ecological population have to face and endure such variation. This is the ecological and genetical reason for studying nutrient adaptation over a range of levels.

The performance of a plant in a wide range of nutrient levels may be represented diagrammatically. Normally the response curve obtained is of the type shown in Fig. 6A; under both excessively low and excessively high nutrient levels the plant does badly, and at some intermediate nutrient level it produces its greatest or optimum yield. The word "optimum" is

A. RESPONSE OVER WHOLE NUTRIENT RANGE



B. RESPONSE OVER LIMITED NUTRIENT RANGE

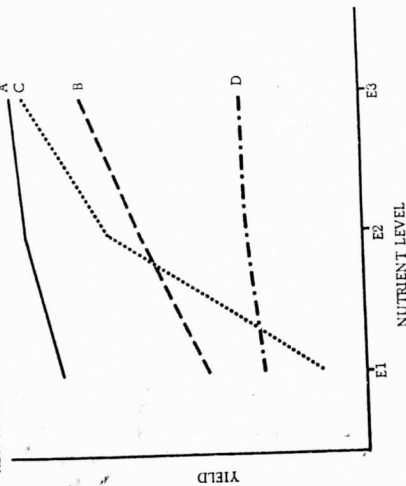


FIG. 7. Response curves over different ranges of nutrient levels (for explanation, see text)

Finally, the spread and position of the optimum may be the same, but the yield at the optimum may be lower (Fig. 6D). This suggests that the response pattern is the same but that the yield at optimum is limited by a difference in absolute growth. This could be brought about by selection for small plants, for example in exposed conditions, and may have little to do with nutrient response.

In nature the situation is obviously more complex than this. In particular, differences between response curves appear as differences in kurtosis, but they can nevertheless be usually assessed using the above models as a basis.

The main difficulty is that it is normally not practicable to measure response in a series of populations over the entire nutrient range, and if we look at response over a limited range, the situation can be very confusing (Fig. 7). If we have four populations with the four types of ideal response curves outlined above then the true pattern for these populations is as in Fig. 7A, whereas under only three levels it is then as in Fig. 7B. For example, population D seems to respond far less than any of the other populations, yet its optimum is the same as A and C, and its range the

same as A and B. It is obviously essential to have as wide a range of nutrient levels as possible.

If the optimum has been reached or at least approached by the levels used in the experiment, then plotting percentage reduction from the optimum removes the effect of different amounts of absolute growth in the two populations, and measures the performance over a range of nutrients as a percentage of best performance. If, however, the optimum is not approached by the levels used, this method of plotting the data is dangerous. The method has been used in the data presented in Figs 2 and 4. In Fig. 2 the levels were defined by a previous experiment with the calcium level ranging far above the optima for the populations concerned. Figure 4 shows how the pattern of response is clarified using this method of plotting the data.

In spite of these various difficulties, it is important that there is such good agreement between response and nutrient status of the environment from which the populations are taken. Detecting adaptation to nutrient level is fraught with difficulties, and it is therefore all the more remarkable that a picture of precise adaptation still emerges.

Response as a growth phenomenon

Response of a plant under different conditions is a function of its growth under those conditions. It may be expected on an intuitive basis that a nutrient would have a greater effect and be more efficiently used by a plant that is faster growing or initially larger. If we assume an exponential growth pattern, then the slope of log yield against time will be the growth rate, and the intercept of the line with the vertical axis will represent the starting capital. If the differential response in two varieties is lost after a log transformation (Fig. 8A and 8B), then it suggests that either the growth rate or the initial starting capital (expressed on a log scale) has been changed equally in both varieties by the nutrient treatments (Figs 8C and 8D). The variety that has the greater growth rate or the greater initial capital will be the one that, on untransformed data, will have the greater response. If we start the experiment using standard material, then the initial capital in the nutrient treatments (if not in the two varieties) is the same, and if a log transformation eliminates the differential response, this is confirmation that it is the growth rate that has been altered equally in both varieties. Differences in growth rate are probably largely responsible for the differences in response to calcium of populations of *Dactylis* and *Lolium* taken from soils of different calcium status (Fig. 2), since if we apply a log transformation to the data (Fig. 9) the relationship between response and soil calcium level disappears.

In other words, a greater absolute response can be achieved not only by a greater or more efficient utilization of the nutrient, but simply by having a greater growth rate. Selection for growth rate may, in fact, be the easiest way of achieving good response, and may explain the high degree of nutrient response in cultivated varieties. It is also well known that plants under low fertility conditions tend to be slower growing; high nutrients allow a high growth rate and therefore a high response, whereas low nutrient levels do not permit a high growth rate with the corresponding effect that the populations show a low response. However, in many cases

EFFECT OF LOG TRANSFORMATION ON RESPONSE CURVES

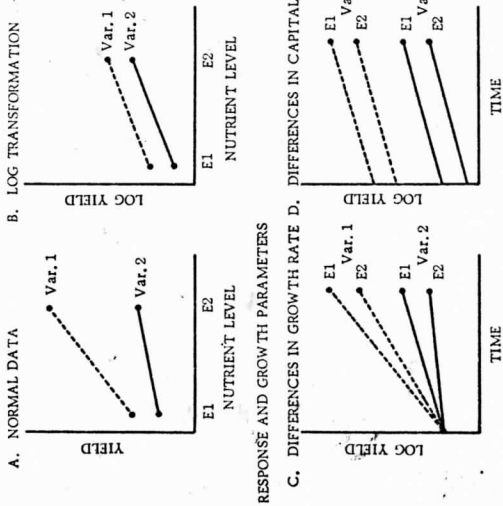


FIG. 7. Response as a growth phenomenon (for explanation, see text)

the log transformation fails to remove the interaction: this suggests that there is specifically more efficient utilization and uptake of the nutrients. Genotype X environment interactions, indicating differences in response, can be looked for on both untransformed and transformed data. Untransformed data show the actual agronomic or ecological potential of the different species, whereas using transformed data it is possible to detect the nature of the response.

Rate and time of response

It is possible to confirm the above hypothesis on growth rates by looking at response over a period of time. This also allows the detection of speed of response since an early response will be indicated by the situation illustrated in Fig. 8E. Here the difference in growth rates in the two environments occurs early, subsequently the nutrients do not affect the growth rates, and the lines obtained are parallel.

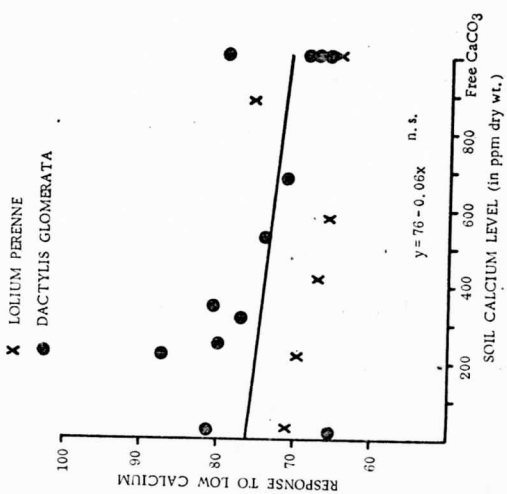


FIG. 9. Response to low calcium of populations taken from soils of different calcium level. Response measured as log of dry weight yield at 2 ppm Ca over log yield at 54 ppm Ca, and expressed as a percentage (compare Fig. 2). (Data from Ref. [19])

The experiment on nitrogen responses in a series of populations mentioned earlier is an illustration of this. The log yield of high and low nitrogen populations at three nitrogen levels plotted against time (Fig. 10) shows the following. Firstly, the lines are more or less straight; the plants are therefore still in the exponential phase. Secondly, and perhaps more interesting, the lines are more or less parallel to each other suggesting a similar growth rate but different starting capitals, but since the initial starting capital was standardized the differences in yield observed between treatments must have come about by an early response of the growth rate to nitrogen. Thirdly, the differences between high and low nitrogen populations could be accounted for either by differences in initial starting value or by differences in the initial growth rates since it is impossible to ensure uniformity of starting capital between populations. But, interestingly, the parallelism between the lines is only present in the low nitrogen populations between the later harvests and not between the earlier harvests. This suggests that these populations are still responding to nitrogen, and only reach their final growth rate after five weeks, whereas the high nitrogen populations reached it after three weeks. In other words, high nitrogen populations respond quicker to different nitrogen levels. This hypothesis is confirmed if we look at the nitrogen response on a log scale at all three harvests (Fig. 11). The difference in response is only clearly evident at harvest I, the lines getting more and more parallel in subsequent harvests.

Two important points emerge from this. Firstly, the speed of response is a very important factor in the adaptation of plants to nutrient factors. Secondly, and a corollary to this, differences in response may

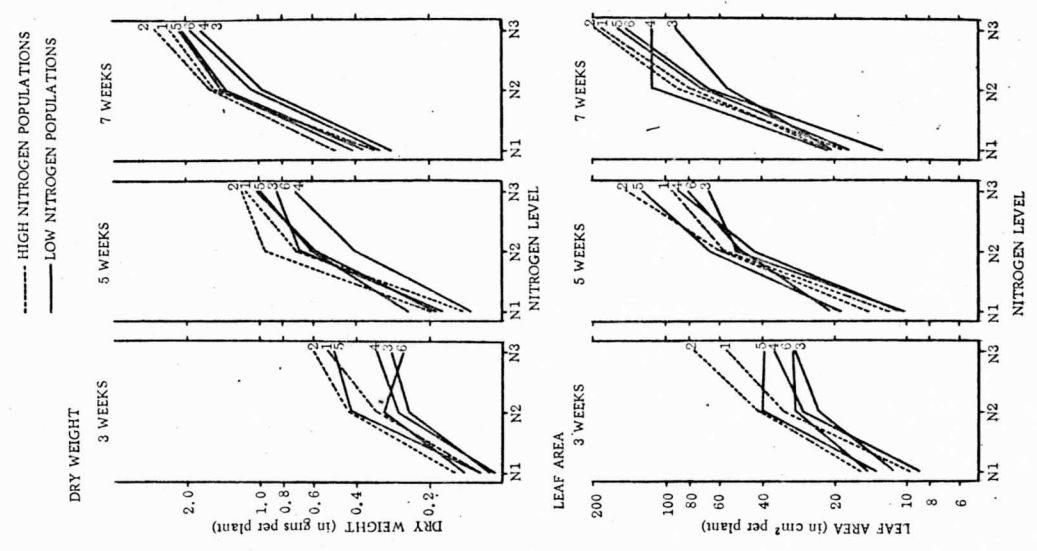


FIG. 11. Changes with time in response of populations of *Lolium perenne* to nitrogen

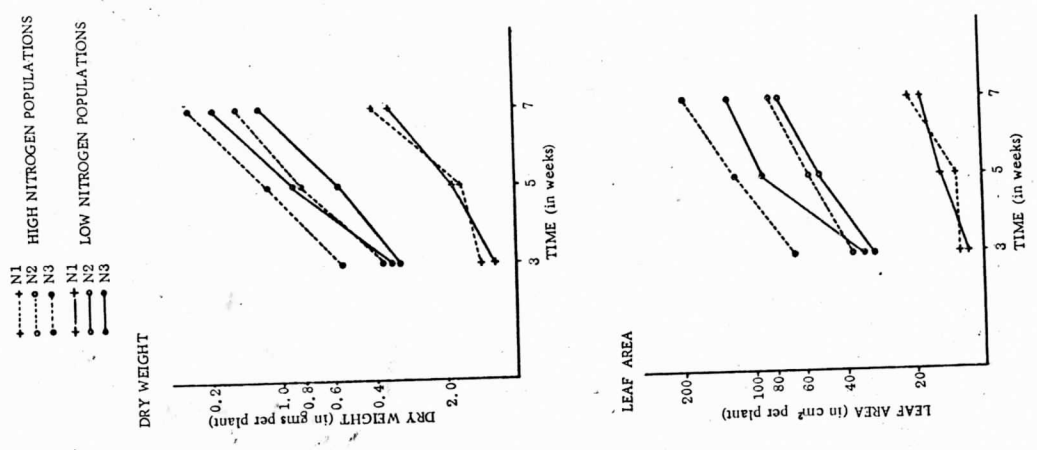


FIG. 10. Growth curves of high and low nitrogen populations under different nitrogen levels

be missed if they occur at a specific time: response studies should consider the time factor.

SELECTION FOR NUTRIENT RESPONSE

Studies on responses to nutrients in natural populations have shown that the plant is very sensitively adapted to the nutrient factors in the soil. The size of the differences between populations may give the impression that their evolution has been a long-term process. It is therefore pertinent to inquire into the effectiveness of selection in producing these differences and the speed with which they can arise. These questions have obvious relevance to breeding programmes.

An important part of the information that there is on the process of natural selection in plant population comes from a study of adaptation to a nutrient factor, namely tolerance to heavy metals. This work has shown that such adaptation does in fact arise by natural selection (Jowett [27], Bradshaw et al. [7]), that natural selection maintains differences over very short distances (McNeilly [21], Jain and Bradshaw [28]), and that the selection is largely metal specific since tolerance to one metal does not involve tolerance to another (Schwanitz and Iahm [10], Gregory and Bradshaw [11]). There is very little evidence that these features are not common to adaptation to soil factors of a less extreme nature. Thus the process of selection against edaphic ecotypes of clover when transplanted into different habitats has been demonstrated by Snaydon and Bradshaw [26]. The maintenance of differences over very short distances by selection has been shown for calcium response in *Anthoxanthum*: plants on limed and non-limed plots a few inches apart differ in their performance (see Jain and Bradshaw [28]).

Evidence of selection in natural populations can be readily obtained by comparing the properties of the established individuals in a population with those of the seedling population. Any differences between the two suggest that selection is acting to maintain the status quo of the adult population in spite of the production of unadapted types. To test therefore whether there was evidence of natural selection for response to nutrients, the behaviour of material derived from seed and tillers was compared for two populations of *Dactylis glomerata*. One population was from a region of low calcium content (15 ppm) and one from a soil containing free calcium carbonate (> 1000 ppm). The performance of seed and tiller material was compared on an acid and chalk soil. The results (Fig. 12) show that whereas the seed population shows a variability both in absolute size and in relative performance of the same genotype in the two conditions (response), the adult population is much more uniform in both respects. Here we have clear evidence that there is natural selection occurring for nutrient response, and that natural populations contain a considerable variability and therefore potential for change.

The evidence from studies on artificial selection for metal tolerance suggests that such tolerance can be evolved quite rapidly; natural populations contain individuals highly tolerant to metals that can be picked out in one generation from seed material by screening methods. It is therefore possible to select even quite extreme nutritional variants in one generation. Vose and Randall [29] have similarly found that aluminium and manganese tolerance can be significantly increased by only two generations of selection.

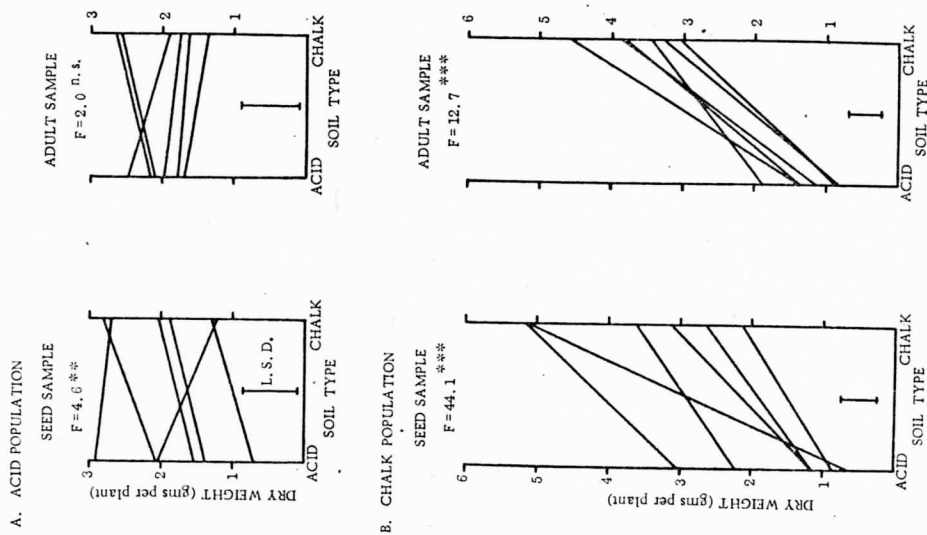


FIG. 12. Response of seed and adult samples to acid and chalk soil. "F" (variance ratio) values are for genotype \times soil interaction. Each genotype represented by a single line. (Data from Ref. [19])

The picture therefore is one of rapid change. To investigate this further the nutritional adaptation of semi-natural populations of *Dactylis glomerata* and *Lolium perenne* was examined (see Crossley [19]). Two types of situation were investigated in cultivated varieties of these two species. Firstly, comparisons were made between the performance of varieties after one generation of seed multiplication on chalk soil with the performance of the original seed stocks. Since cultivated varieties of these species are by no means homozygous, there is selection for the most adapted types during the process of seed multiplication. Secondly,

a comparison was made between acid and chalk populations of these species which were growing naturally but which had been started from a known variety. The different populations were compared for their performance on chalk and on acid soil. The results for the different populations are summarized in Table I, and show in the case of three comparisons out of eight that the populations have evolved not only differences in absolute yield but also differences in response. In two instances this has happened in populations only two years old and in the other case the populations were twelve years old. Since re-seeding has probably not occurred, or has been very limited, the differences have arisen almost certainly within one generation, either at the initial seedling establishment stage or during vegetative growth.

The speed with which such responses in nutritional adaptation have occurred is similar to those detected by Charles [30] in the proportion of different varieties of *Lolium*, *Dactylis* and *Phleum* under various conditions of management, including different nitrogen treatments.

For these reasons, the evolution of adaptation to nutritional factors seems a rapid process under natural conditions. There must therefore exist considerable genetic variation on which selection can act, as well as strong selection pressures for such adaptation. Both these features point to the feasibility and to the importance of breeding for nutritional adaptation.

CONCLUSION

The evidence presented above shows that nutritional adaptation is widespread in nature. Very often such differentiation is not reflected in the morphology of the individual and therefore is not directly visible. It is probably for this reason that such physiological adaptation has received inadequate attention. The existence of natural populations, for example of *Lolium perenne*, that respond better than cultivated varieties to high nitrogen suggests that cultivated varieties may not exploit the available fertilizer fully, and emphasize the importance of breeding directly for fertilizer response. Moreover, breeding for salt-tolerance and tolerance to low fertility could widen the use of certain crops. The situation in nature suggests that progress to selection is rapid, and that direct selection for different types of response is a practical possibility and necessity in plant breeding.

ACKNOWLEDGEMENT

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Species	Variety	Populations compared	Age of populations in years	Untransformed data		Log transformation
				Between populations	Population x soil interaction	
<i>Dactylis glomerata</i>	S 143	Basic	0	***	**	**
	S 143	Multiplied	2	***	**	**
<i>Lolium perenne</i>	S 24	Basic	0	***	**	N.S.
	S 24	Multiplied	2	***	**	**
S 24	S 24	Basic	0	N.S.	N.S.	N.S.
	S 24	Acid	12	N.S.	N.S.	N.S.
S 24	S 24	Chalk	2-3	N.S.	N.S.	N.S.
	S 24	Acid	12	N.S.	N.S.	N.S.
S 23	S 23	Basic	0	N.S.	N.S.	N.S.
	S 23	Acid	12	N.S.	N.S.	N.S.
S 23	S 23	Chalk	2-3	***	***	**
	S 23	Acid	12	***	***	**

TABLE I. EVOLUTIONARY CHANGES IN THE PERFORMANCE AND NUTRITIONAL RESPONSE OF STANDARD VARIETIES OF *LOLIUM* AND *DACTYLIS*, FOLLOWING GROWTH ON DIFFERENT SOIL TYPES

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DISCUSSION

J. B. HANSON: At the most, only a very few recessive genes appear to be involved in the selection of genotypes that are resistant to, say, toxic metals. On the other hand, reactions described at this Symposium suggest that we may be dealing with an adaptive enzyme. Could there possibly be a genetic mechanism involved which controls the selective production of a detoxification substance?

J. ANTONOVICS: Fairly extensive studies carried out by D. A. Wilkins in the United Kingdom and by German workers such as W. Broeker indicate that the resistance to toxic metals is inherited in a dominant rather than a recessive manner. Wilkins' results suggest that several genes or alleles are involved, and we suspect that we are dealing with the channelling of a physiological mechanism towards a particular end, rather than with the production of a specific enzyme.

J. B. HANSON: But the process you envisage must involve biochemical synthesis; it must involve physiological reactions resulting in inactivation or precipitation of the toxic element. Are you geneticists looking for a specific biochemical pathway by which genes control such a process?

R. G. TURNER: In my opinion, as a non-geneticist, the only way to discover whether the development of tolerance involves an adaptive enzyme or a physiological mechanism that can be graded in response to a breeding programme is to test a range of plant populations with different indices of tolerance to different metals.

P. B. VOSE: I do not think that work in this field has progressed as far as Dr. Hanson assumes, hence the difficulty in answering his question. With regard to the inheritance of resistance to toxic metals, studies that I have carried out indicate that aluminium toxicity resistance is inherited in a dominant manner. Moreover, studies with perennial ryegrass point quite definitely to polygenic inheritance.

As for the adaptive nature of the process, we found that our plants developed resistance to aluminium if the aluminium level was raised gradually. This suggests that the process may partly be one of adaptation. I personally think that enzyme systems are involved, but we are a long way from establishing this.

F. G. H. LUPTON (Chairman): I think we must distinguish between a hereditary character and one that is inherited simply on a genetic basis. Moreover, we must establish that characters are inherited at all. We have not yet reached the point where we can profitably consider how many genes or alleles are involved. That is a question for the more distant future.