GENETIC ADAPTATION OF GRASSES AND LEGUMES TO TROPICAL ENVIRONMENTS

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ABSTRACT

The breeding of tropical pasture plants is discussed. In particular, the need for accurate definition of breeding objectives is stressed. The indirect nature of most selection procedures is emphasized, as well as the need for more information on heritabilities, genetic correlations, and genotype-environment interactions.

INTRODUCTION

Nobody can deny that plant breeding has been a successful undertaking in many species. Most of these have been crop or horticultural plants where most effort has been concentrated and where objectives are usually easily and clearly defined. Nevertheless, it has been well demonstrated that plants can be modified and adapted successfully to pasture situations. For temperate conditions, the many releases from the Aberystwyth program, the work of Burton in Georgia, and the C.S.I.R.O. program in Canberra show the progress that has been made.

Examples of successful pasture plant breeding in the tropics and subtropics are hard to find. One reason is that there are fewer plant breeders in these areas than in temperate areas! However there are a number of features which combine to make tropical pasture plant breeding a difficult exercise. Firstly, the plants themselves are mostly in an "undeveloped" state, not having enjoyed the benefits of years of breeding and selection. Secondly, the growth habit and size of the plants (mainly twining legumes and tufted grasses) makes it difficult to grow large populations without creating huge problems of weed control and data gathering. Thirdly, the almost continuous growing season, with its attendant extremes of temperature and moisture creates further difficulties. Nevertheless, the production of Siratro, Narok setaria, and Krish sorghum by workers at C.S.I.R.O. Cunningham Laboratory are demonstrations of the progress that can be made. In addition to these released cultivars, there are advanced breeding lines of lucerne, leucaena, *Desmodium*, *Macroptilium*, and *Digitaria* which should make important contributions in the near future.

Most tropical plant breeders are faced with the problem of improving an already fairly successful species, due to the careful evaluation and successful screening of large numbers of introductions by workers in that field. Thus it is probably harder to produce a new variety of a species already in use than to introduce successfully a new species itself. However, once a species has been extensively grown over a long period of time, its problems become more obvious (and thus better defined). It may then be possible to breed quickly and efficiently for their solution.

BREEDING OBJECTIVES

The definition of breeding objectives has been, and still is, one of the greatest problems in any plant breeding program. Although breeding objectives are often discussed they are rarely actually defined. Whose responsibility is it to do this? Is it the breeder's? The breeder has a good knowledge of the plant but may not appreciate its weakness in a grazed pasture. Conversely, the agronomist may know the weak points of a plant but be unable to define causes which can be rectified through breeding. Ideally, the agronomist should identify the causes of a problem, such as non-

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persistence in a legume, before asking a breeder to work towards its solution. This course of action would ensure that the breeder does not choose characters which readily respond to selection but bear little relevance to maximising animal production from pasture.

What characteristics are important in a pasture plant? McWilliam (1969) has listed some of the important requirements for pasture plants in Australian conditions. These are:

1. Ability to maintain production over extended periods, particularly when for reasons of temperature or moisture stress the growth of the associated species is severely limited.

2. Ease and reliability of establishment from seed, coupled with good competitive ability of young seedlings.

3. Persistence under grazing and rapid regeneration after defoliation.

4. Wide adaptability over a wide range of sites, seasonal conditions, and management practices, with tolerance to stresses imposed by such factors as drought, low temperature (including frost), waterlogging and soil pH.

5. High seed yields and ease of harvest.

6. Resistance to disease and insect pests.

7. Satisfactory quality and freedom from toxic properties injurious to the health of the grazing animal.

8. Efficient nitrogen fixation in legumes coupled with a substantial feed back of nitrogen to the soil system.

9. Compatability between legume and grass in order to maintain an adequate and vigorous legume component in the pasture.

10. Ability to respond to applied fertilizers.

In tropical pasture situations it is probably easier to define the requirements for legumes than for grasses, since apart from cool season production, grass growth is unlikely to limit animal production. Indeed, Hutton (1968) has suggested that it may be feasible to breed less vigorous tropical grasses that will allow greater proportions of legume in the pasture.

INDIRECT SELECTION

When breeding objectives have been defined, it is then up to the plant breeder to select for the characters concerned. In some situations the breeder will select directly for the character in which he is interested (e.g. seed retention in *Phalaris*, disease resistance in lucerne). These are characters which have a direct bearing on the usefulness and possible economic future of any new variety. However, in pasture plant breeding in many cases it is not really the particular character that we are selecting for that we are interested in, but rather the increase in animal liveweight gain that will result from the incorporation of this character in a cultivar. Consequently it may be considered that a great deal of selection carried out by plant breeders (e.g. Dry matter yield, IVD) is in reality indirect selection for potential animal weight gain.

Another aspect of indirect selection as it affects plant breeding is the "performance" of genotypes under different agronomic conditions. Selections made by the plant breeder as mono-specific spaced plants will be ultimately grown as swards, in competition with other species. Different management systems are another example where selection may have been made for performance in one environment, with practical evaluation in another.

The implications of indirect selection in plant breeding need further consideration. The theoretical aspects of indirect selection are well known (see e.g. Falconer, 1960).

We are concerned with estimating the change in a character Y if we select for another character X. The response of character X, directly selected for, is:

$$R_x = i\, h_x^2\, \sigma_{px} \qquad \text{.......................1}$$

where i represents intensity of selection

h_x^2 is the heritability of X (a measure of "usability" of variation in X)

and σ_{px} is the phenotypic standard deviation of X.

It can be shown that the correlated response of character Y is:

$$CR_y = i\, h_x\, h_y\, r_a\, \sigma_{py} \qquad \text{.......................2}$$

where h_y is the square root of the heritability of Y, σ_{py} is the phenotypic standard deviation of Y, and r_a is the genotypic correlation between X and Y. (Formula 2 can also be written

$$CR_y = i\, h_x\, r_a\, \sigma_{ay} \qquad \text{.......................3}$$

where σ_{ay} is the genotypic standard deviation of Y.)

What parameters must be determined before correlated response can be estimated? It is necessary to have information concerning genotypic and phenotypic variation in both characters (from which heritabilities can be calculated if needed), and an estimate of the genotypic correlation between the two characters.

Some examples will serve to illustrate the concept of indirect selection.

1. *Physiological characters.* It has sometimes been advocated that breeders should select for physiological characters, such as photosynthetic rate or leaf angle. Unless an advance in this 'basic' character leads to a genetic advance in the yield of the plant, selection is useless. In many characters of this type there are so many compensatory and feedback mechanisms involved that no advance in yield is likely.

2. *Spaced plants vs. swards.* In many grass breeding programs, digestibility, as well as many other characters, is often evaluated in spaced plants, or small plots of spaced plants. In our buffel grass program, selections have been made on samples taken from plots of plants spaced at 0.6 m square. We want to know what progress will be made in improving digestibility in swards by selecting on spaced plants. Since digestibility varies greatly with season and age of regrowth, and may be subject to a range of sampling errors its heritability may not be high. My calculations from unpublished data of A. J. Pritchard indicate a heritability of about 0.3, based on four harvests (or replications). It should be noted that this is a low value by comparison with most published reports in temperate species, where most estimates are in the region of 0.5 to 0.6 (e.g. Oram, Clements & McWilliam 1974). J. B. Hacker (unpublished data) has also obtained higher estimates for setaria. A population of 150 introductions had a phenotypic standard deviation of about 3 units, as spaced plants.

With a selection intensity of 10% we would expect progress in spaced plants to be 1.6 units, although if the heritability were very high (say 0.9) a gain of 4.8 units would be expected. It is clear from formulae 1 and 2 that, if h_x^2 and h_y^2 are similar, and if σ_{px} and σ_{py} are similar, then progress for Y will always be less than for X—i.e. progress in swards will be less than in spaced plants. If, however, the heritability and phenotypic standard deviation change, then the actual response varies with the magnitude of those changes.

Figure 1a shows the progress to be expected in swards, assuming σ_{px} and σ_{py} to be the same for different heritabilities and a range of genotypic correlations. If meaningful progress is to be made (say 3 units) heritability must be high both in sward and spaced plants, and there must be a high genetic correlation. With an apomict such as buffel grass it is possible to increase the selection intensity without fear of problems caused by inbreeding. Figure 1b shows for an intensity of 1% the expected progress which is approximately 50% larger than that of Figure 1a. Selection differentials of this latter magnitude are unlikely to be achievable in most cross pollinating grasses.

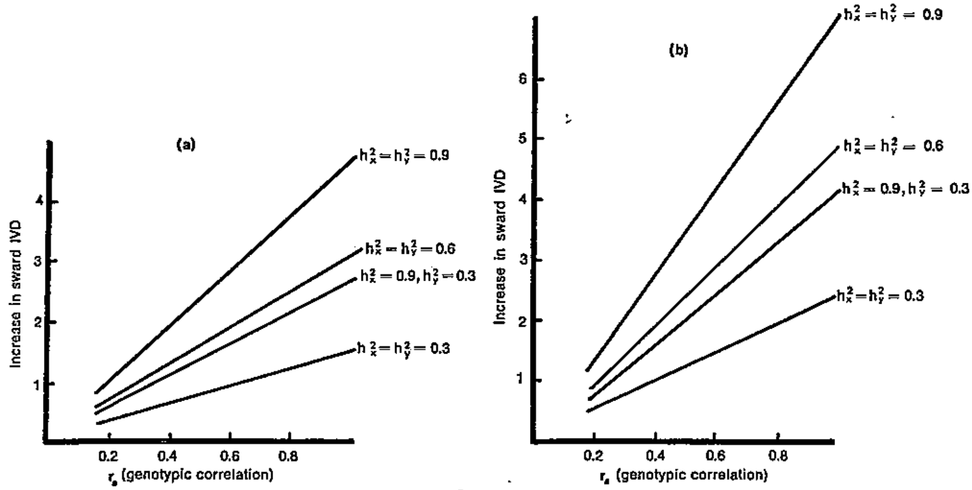

FIGURE 1

The effect of heritability and genotypic correlation on the response to selection; (a) $i = 1.76$ (10% selection); (b) $i = 2.67$ (1% selection).

The expected progress referred to above represents only one generation of selection. Recurrent selection for several generations will be possible in most cases to provide greater cumulative progress.

3. *Sward evaluation vs. animal performance.* Having achieved a sward of higher digestibility, how does this relate to the performance of animals grazing that sward? Once again, these two attributes of any genotype have a genetic correlation. Selection for IVD (or some other character) of the sward may (or may not) produce a related change in animal performance. Once again unless the genetic correlations are high, and variation significant, selection may be of little use.

Data pertinent to the above situations are conspicuous in the literature by their absence. Sedcole and Clements (1973) obtained a genetic correlation for yield of rye grass at wide and close spacings of the order of 0.8, while McWilliam and Latter (1970) found the genetic relationships between yield of spaced plants and swards to vary between 0.42 and 0.78 depending on the season. Several estimates of genetic correlations between characters at different plant age are available. Clements (1973), found that in *Phalaris tuberosa* the genetic correlation between *in vitro* digestibility of organic matter at two stages (heading and mature) was 0.39. Sleper (1974) showed a low (0.20) genetic correlation between digestibility of Rhodes grass at two weeks and six weeks regrowth.

Why are not more estimates of this type available? The experimental procedures, although relatively simple, are time consuming, tedious, and demanding of field facilities and analytical services. As an example, to determine relevant genetic relationships for IVD between spaced plants and swards in buffel grass might need 35 genotypes, 4 replications, 2 spacings, 3 locations, and 6 harvests, or a total of 5040 IVD determinations. Similar efforts would be required for other characters, such as dry matter yield. Nevertheless, such experiments must be done so that the chance of effective breeding work can be assessed.

CHOICE OF CHARACTERS

What characters can be effectively selected for? The question is perhaps better rephrased as: What are the requirements for a 'selectable' character?

1. It must be possible to grow large populations to screen for the character.
2. Evaluation should be easy and precise.

3. There must be genetic variation in the breeder's plots (plants).
4. There must be genetic variation in a meaningful field situation.
5. There must be a reasonable genetic correlation between expression in the breeder's plots and expression in the field.

These five requirements are all represented or implied in the equation $R_Y = i\, h_x\, r_a\, \sigma_{ay}$ (formula 3). Obviously the intensity of selection possible is of great importance. Although it may be desirable statistically to increase it as much as possible, there are genetic reasons in many cases for using lower values. These include possible inbreeding effects, narrowing of the genetic base, and random gene drift effects. If very large populations can be grown, as when screening seedlings for disease resistance, then selection intensities can be made high, but a broad base still maintained. Thus in disease resistance breeding in lucerne, the selection of 100 seedlings from 10,000 is a high intensity, but genetically acceptable.

The precision of estimate of a character and the extent of genetic control interact to give an estimate of heritability. Obviously high heritability for the character in question is desirable, since simple breeding methods then apply. However progress can be made at low heritabilities although family selection or progeny testing may be necessary (Latter 1964).

Real advances will be achieved only when selection in the breeding program gives meaningful results in terms of the pasture situation. Characters such as yield, IVD, or "acceptability" measured by the breeder may not relate well to field situations. Perhaps characters such as seedling vigour, frost tolerance, disease resistance, or speed of regrowth, where one might reasonably expect good relationships between performance in breeder's evaluations and under grazing are the ones that we should concentrate on.

OTHER GENETIC RELATIONSHIPS

Genetic correlations

There are other genetic relationships of interest besides those already discussed. It is important to know the genetic relationship between characters, so that any adverse response can be anticipated (e.g. the common negative relationship between yield and nitrogen content). Also of interest are the relationships between the same character at different stages of growth (e.g. will selection for high IVD at 4 weeks regrowth give an increase at 6 weeks regrowth). This also applies to correlations between different parts of the plant.

In many cases the genetic correlation situation may be very complex. In the previously cited example of sward and animal performance, the correlation might well change with season, associated species etc. Any correlation may also depend on the animal population, both genetically (e.g. breed differences) and physiologically (e.g. lactation status). The concept of a single value for the correlation is probably not tenable, and it must be realised that estimates of correlations (and heritabilities) are population—and environment—dependant.

On many of the above aspects of pasture plant breeding knowledge is almost totally lacking. This is perhaps understandable as the obtaining of data, especially under grazing, would be difficult. Nevertheless, it is desirable to have available, for all plants likely to be of interest, data on genetic variation, genetic correlations, and heritabilities.

Genotype × environment interaction

We have considered above the performance of lines at different spacings and under different management regimes. What of their performance in different climatic environments? The breeder cannot undertake selection or evaluation in every environment likely to be of interest, and there is ample evidence of plant performance differing over locations. This genotype × environment interaction represents one of the most important problems that the breeder has to overcome.

We are once again faced with the problem of indirect selection. Genotypes selected for some characteristic in one (or a few) environments are grown in others —will the selected lines be superior? What is the correlated response to selection in the original environment?

The question of understanding and 'dealing with' genotype × environment interactions has been the subject of a great deal of research. Much of the work has been based on the classic paper of Finlay & Wilkinson (1963). This was the first real progress in quantifying the responses of genotypes to a range of environments and the interactions which occur. The general principle used by Finlay & Wilkinson was to fit a linear regression model for each variety using an environmental index based on environmental means as the independent variable. In many cases the regression on individual yields on environmental index accounts for a significant proportion of the interaction, and enables each variety to be characterised as 'stable' or otherwise, depending on the value of its regression co-efficient, deviations from regression, and the individual definitions of the authors concerned. The general principle has been widely used with crop plants (e.g. Eberhardt and Russell 1966; Baker 1969) and can also be applied to pasture situations (Burt & Haydock 1968; Samuel *et al.* 1970).

Recently, Mungomery, Shorter & Byth (1974) have used the grouping and ordination techniques popularised by W. T. Williams to approach this problem. In their work, significant regressions of yield on environmental index were not found. However, using grouping techniques it was possible to group varieties with similar responses to a range of environments. This should lead to economy of testing, and the ability to predict the performance of a particular line in a particular environment. Of course, this should also be possible from the regression approach if linear regressions account for a substantial part of the genotype × environment interaction. However, before it is possible to reach this stage, a large amount of data must be accumulated, both in characterizing varieties and environments. The accumulation of this data is most time consuming, but necessary.

Obviously, the breeder cannot test his lines in all environments, and he must therefore choose as wide a range as he can handle within the climate of likely adaptation of his material. In Queensland, we have a vast range of environments, and to sample these adequately is virtually impossible. If large genotype × environment interactions occur, then it would be desirable to produce varieties specifically adapted to each environment. This is probably impractical at the present stage of development of our pastoral and seed production industries. The breeder must therefore compromise with a broadly adapted variety, of good average performance, even though this may mean the loss of potentially outstanding performance in some environments.

FUTURE DEVELOPMENTS IN TROPICAL PASTURE PLANT BREEDING

What future developments are likely in tropical pasture plant breeding? This is dependent on several factors.

a. *The provision of new genetic material.* As plant introduction techniques continue to improve, so the supply of novel and usable variation to the breeder improves. It is important that any breeder have available a comprehensive collection of genetic variability which he can screen as the need arises.

b. *New methods of producing and manipulating variation.* For some species (e.g. tobacco) methods of anther and pollen culture have enabled the large scale production of haploids, and thus homozygous diploid lines. In tobacco the main use of these lines is in the production of hybrids, but for pasture plant breeding such methods show considerable promise simply as a rapid means of generating homozygous lines. However, the culture techniques are not yet available for any of our pasture species.

Methods of cell hybridization may seem to offer the opportunity of making wide crosses to create new variation. However, most breeding programs already have more variation than they can handle, and the problem is in evaluating the variation, rather than creating it.

Of more potential interest to breeders are the various attempts being made to induce apomixis in sexual species. Apomixis, which can be broadly defined as reproduction by seed without sexual recombination, results in plants reproducing true-to-type. If the reproductive system can be manipulated in such a way that crosses can be made between promising parents, and the best of these crosses fixed by apomixis, then the breeder has an ideal system. At present buffel grass probably comes closest to this ideal. Sexuality is controlled by 2 genes (Taliaferro & Bashaw 1966) and crosses between apomictic and sexual plants segregate for apomixis. Thus the screening of large F_1 populations may provide the desired combination of agronomic characters together with apomixis. The discovery of similar systems in other species would be of immense practical value.

c. *New (or more efficient) methods of selection and testing.* Most plant breeding programs are limited by the size of population that can be handled. It is generally accepted that an area of about 4 ha year^{-1} is necessary for an effective breeding program in a tropical legume, just for the evaluation of breeding material. Such a field program requires a high level of support, both in field and laboratory staff. Any advances that can be made in reducing generation time or increasing precision of selection would be useful. This includes not only statistical techniques but also the possibility of selection based on biochemical, physiological or plant architectural criteria.

Pasture plant breeding is necessarily a long-term enterprise, 10 to 20 years being a not unreasonable timescale for the production of a new variety. Such an interval between the inception and completion of a program raises the possibility that because of changing economics or agricultural systems, the variety produced may not be wanted. If this is so, it is important to recognise this early before a breeder commits too much of his time.

Progress in current plant breeding programs is restricted by three main factors —lack of definition of breeding objectives, lack of basic knowledge of the quantitative genetics of the plants, and the lack of labour to handle the large populations necessary. However, pasture plant breeding in the tropics is still in its infancy. The potential contributions in this field are enormous, but will not come quickly or without a great deal of work, entailing extensive co-operation between disciplines and the commitment of extensive resources.

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REFERENCES

BAKER, R. J. (1969)—*Can. J. Plant Sci.* **49**: 743.
BURT, R. L. and HAYDOCK, K. P. (1968)—*J. Aust. Inst. Agric. Sci.* **34**: 228.
CLEMENTS, R. J. (1973)—*Aust. J. Agric. Res.* **24**: 21.
EBERHARDT, S. A. and RUSSELL, W. A. (1966)—*Crop Sci.* **6**: 36.
FALCONER, D. S. (1960)—Introduction to quantitative genetics. Ronald. NY.
FINLAY, K. W. and WILKINSON, G. N. (1963)—*Aust. J. Agric. Res.* **14**: 742.
HUTTON, E. M. (1968)—*J. Aust. Inst. Agric. Sci.* **34**: 203.
LATTER, B. D. H. (1964)—*In* "Grasses and Grasslands." Ed. C. Barnard, Lond., MacMillan.
MCWILLIAM, J. R. (1969)—*J. Aust. Inst. Agric. Sci.* **35**: 90.
MCWILLIAM, J. R. and LATTER, B. D. H. (1970)—*Theor. Appl. Genet.* **40**: 63.

MUNGOMERY, V. E., SHORTER, R. and BYTH, D. E. (1974)—*Aust. J. Agric. Res.* **25**: 59.
ORAM, R. N., CLEMENTS, R. J. and MCWILLIAM, J. R. (1974)—*Aust. J. Agric. Res.* **25**: 265.
SAMUEL, C. J. A., HILL, J., BREESE, E. L. and DAVIES, A. (1970)—*J. Agric. Sci.* **75**: 1.
SEDCOLE, J. R. and CLEMENTS, R. J. (1973)—*J. Agric. Sci.* **80**: 97.
SLEPER, D. A. (1974)—*Soil Crop Sci. Soc. Fla. Proc.* **33**: 5.
TALIAFERRO, C. M. and BASHAW, E. C. (1966)—*Crop Sci.* **6**: 473.