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An alternative approach to multivariate selection in plant breeding where genotypes are evaluated at many locations

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Summary. A new approach to genotypic selection in a plant breeding programme where the genotypes under assessment are grown in a number of environments is examined. It is assumed that these environments are a random sub-set of all possible environments where the genotypes are likely to be grown. It involves estimating the probability that each genotype will, if grown at any location, exceed predefined target values for one or more characters. The multi-normal probabilities are estimated from the genotype means and environmental variance of each variate. Where more than a single variate is to be considered, the correlation coefficients between variates are also used in the estimation. It was found that the coefficient obtain by correlating the predicted proportion of locations that genotypes would exceed the set target values, with the observed proportion of locations in a different year, were consistently higher than similar coefficients between observed proportions in different seasons. The latter were high enough to conclude that the approach would be of use in practise. Such a method may therefore be used to identify genotypes which have a high probability of being suitable over a range of locations.

Introduction

Comstock and Moll (1963) stated that "genotype by environment interaction is in some way involved in most problems of quantitative genetics and many problems of plant breeding". Genotype by environment interactions have been recognised by plant breeders for many years as reducing the efficiency of selection (Hill 1975). Limited seed supply and logistical problems involved in the handling of large numbers of progeny usually restricts the selection of early generation breeding lines to one location. Only at the later stages of a breeding programme is it possible to assess selections in a wide range of locations by which time genetic variation between selected lines may be drastically reduced.

If a single quantitative character is assessed in more than one environment the genotypic expression for that character will be:

$$y_{ijk} = \mu + \alpha_i + \gamma_j + \psi_{ij} + e_{ijk} \tag{1}$$

where y_{ijk} is the phenotypic expression of the ith genotype grown in the jth enviroment; α_i is the genotypic effect of the ith cultivar; γ_j is the effect of the jth environment and ψ_{ij} is the interaction between the ith genotype and the jth environment. The e_{ijk} term is a random error term estimated by replication within that environment, assuming a simple model where replicates are not blocked

From Eq. (1), if all ψ_{ij} values are equal to zero, all genotypes have responded equally to different environments and selection for individual characters can be carried out on the mean value, averaged over all environments. If however, genotype by environment interactions are detected ($\psi_{ij} \neq 0$) then the breeder must decide which of the environments will provide the "best" estimation for selection purposes, or perhaps must practice selection for each environment seperately.

Finlay and Wilkinson (1963) suggested that genotype by environment interactions in a plant breedings scheme could be dealt with by the model:

$$y_{ijk} = \mu + \alpha_i + \beta_i(1 + \gamma_j) + e_{ijk} \tag{2}$$

where y_{ijk} is the phenotypic expression of the ith genotype grown in the jth environment; μ is the overall mean of the trial; α_i is the effect of the ith genotype; γ_j is the effect of the jth environment and β_i is the environmental sensitivity of the ith genotype. The environmental sensitivity (β) is

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the linear regression coefficient from the regression of mean performance of a line against the mean performance of all other lines grown in a particular environment. From this model, each cultivar will have a mean effect (α_i) and an environmental sensitivity (β_i). Breeders could use these two parameters to identify cultivars which will perform well in all environments (i.e., high mean and low sensitivity). This approach however doubles the parameters of the selection equation (i.e., mean plus sensitivity rather than only the mean). Despite the disadvantages of this approach it is still the most widely used method of stability analysis (Becker 1981).

The success of a new cultivar is seldom determined by the expression of a single trait and is usually a result of the general improvement of a number of different characters over existing cultivars. When a potential new cultivar constitutes an improvement only in a single character, it must be at least as good as other cultivars for most other traits. Biological and economical constraints aside, the need to be of value for cultivation and use is now a statutory requirement in many countries including the United Kingdom.

Fisher (1936) first suggested the concept of multivariate selection indices to differentiate different species in taxonomic studies. This type of index selection was developed for use by plant (Smith 1937) and animal (Hazel 1943) breeders. It has been shown for both the case where variables in the index are independent (Hazel and Lush 1942) and where the variates are correlated (Young 1961) that multivariate index selection is theoretically more effective than selection by independent culling or tandem selection.

Very few plant breeders use index selection despite the apparent advantages in efficiency of selection. One reason for this is the need to estimate genetic correlations before selection and after one round of selection the genetic parameters in the index equation will be altered and thus need re-estimation. A second reason is that selection indices do not cope with genotype by environment interaction (Arnold and Innes 1976) in that they may not necessarily identify the most stable cultivars. The inability to define clear economic weights of the characters in the index is also often a further difficulty. Furthermore, economic weights change from time to time or vary from one location to another. For interested readers, a full and detailed review of the theory, applications and limitations to index selection is given by Lin (1978).

In this paper a different approach to selection in the later stages of a plant breeding programme, where the genotypes are grown at many locations, will be considered. It must be stressed that it is assumed that these environments are a random subset of all possible environments in which the genotypes are likely to be grown. The term genotype in this context, is assumed to mean either a clone or a homozygous inbred line as well as a heterozygous population depending on the breeding system of the crop which is being bred. The procedure involves estimating the probability that a genotype, if grown at any location, will be greater or less, than a predefined target value. First consider the case of a single trait, evaluated in many environments. If these environments are considered to be a random sample of all possible environments, then the probability of the i^{th} genotype exceeding a target value (T) will be:

$$\int_{T}^{\infty} f(x_i)\, dx_i \tag{3}$$

Similarly, the probability that the i^{th} genotype will be less than a predefined target value will be:

$$\int_{-\infty}^{T} f(x_i)\, dx_i \tag{4}$$

The probability density function $f(x_i)$ will be determined by the mean of the i^{th} genotype and the environmental variance of the i^{th} genotype. The target value (T) can be arbitrarily determined or it can be determined by the performance of standard cultivars included in the trials. It is assumed that this function is normally distributed (although the procedure is robust against non-normality) and that the probability of a line exceeding the target value set in any environment can be estimated as the sum of the normal probability integrals corresponding to the values:

$$\frac{T-\bar{x}}{\sigma} \quad \text{or} \quad \frac{\bar{x}-T}{\sigma}$$

depending on whether the predictions are for values greater than (or equal to) or less than (or equal to) the target value (T). Where $\bar{x}$ is the average performance of the genotype over all environments and σ is the square root of the environmental variance of the genotype.

This approach can be extended to cover more than one character. Consider for example, n different traits, then the probability that the i^{th} genotype will be greater than the predefined target values set for the n traits (T) will be:

$$\int_{T_1}^{\infty}\int_{T_2}^{\infty}\dots\int_{T_n}^{\infty} f(x_{i_1}, x_{i_2}, \dots x_{i_n})\, dx_{i_1}, dx_{i_2} \dots dx_{i_n} \tag{5}$$

In this case $f(x_{i_1}, x_{i_2}, \dots, x_{i_n})$ is a multivariate normal density function and will be determined by the mean expression of each trait, the environmental variance of each trait and the covariance between traits concerned. The technique of using multivariate probabilities for selection will be illustrated by a simple example taken from the potato breeding programme of the Scottish Crop Research Institute, Pentlandfield.

Material and methods

Twenty potato genotypes were grown at seven different sites in each of two seasons: four in England, at Arthur Rickwood EHF Cambridgeshire, Terrington EHF Norfolk, Gleadthorpe EHF Nottinghamshire, Stockbridge EHS Yorkshire, and three in Scotland, one in East Lothian and two in Angus. In each environment every clone was represented by two ten plant plots, grown in completely randomised blocks. The same locations and experimental design were used in both years although of course, the actual fields and randomisations used were different. Five widely grown cultivars, Pentland Crown, Desiree, Maris Piper, Wilja and Record were included in each trial. The growing conditions used at each location reflected the usual commercial practice of the area.

At harvest, the produce from each plot was mechanically dug and taken to store. In store, the tubers from each plot were visually assessed independently by two potato breeders for "overall appearance" on a 1–9 scale of increasing preference (Brown et al. 1984). The data analysed were the average scores of both breeders. The total produce from each plot was size graded into tubers less than 40 mm, 40 mm–60 mm, 60 mm–80 mm and greater than 80 mm over a square mesh riddle. Each size grade sample was weighed and saleable yield (weight of tubers greater than 40 mm, excluding those with growth cracks) estimated. The average size of tubers from each plot was also estimated by:

$$p_1 w_1 + p_2 w_2 + p_3 w_3 + p_4 w_4 \tag{6}$$

where p_1 is the proportion of weight in the 1st size grade, p_2 is the proportion in the second size grade etc. and $w_1 = 30$ mm, $w_2 = 50$ mm, $w_3 = 70$ mm and $w_4 = 90$ mm. This is therefore the proportion of the sample in each size grade multiplied by the average size of each size grade and summed. After each plot had been size graded and weighed, a three tuber sample was removed and later steam cooked. After cooking, tuber flesh blackening, tuber sloughing (i.e., disintegration on cooking) and other cooking characters were visually combined to give a general cooking quality score on a 1–9 scale of increasing desirability.

The univariate and multivariate probabilities were calculated using a computer program based on the algorithm by Schervish (1984).

Results

The mean performance of the five control cultivars for breeders' preference, saleable yield, tuber size and cooking quality in 1984 and 1985 are shown in Table 1. The means, averaged over the five control cultivars, were chosen as the target values that the genotypes under assessment had to exceed in the predictions. Although in practise the target values used may be the score of the "best" control for each variate. Inspection of the control means and values for each control shows that none of these cultivars were in fact greater than the mean for all variates examined.

Univariate

To illustrate univariate prediction the character saleable yield was chosen. The observed proportion of locations that each of the genotypes under assessment would exceed the mean saleable yield of the five control cultivars are shown in Table 2. Alongside the observed proportions are those predicted, using the mean and variance of each genotype estimated over the seven sites, and Eq. (3). Visual inspection of the data suggests that the observed or predicted proportions provided a useful indication as to the performance of genotypes in the other year.

Table 1. Mean breeders' preference, saleable yield (kg/plot), tuber size (mm) and cooking quality of the five control cultivars grown in 1984 and 1985 at 7 sites

	Breeders' preference	Saleable weight	Tuber size	Cooking quality
1984				
P. Crown	5.21	15.70	65.13	6.43
M. Piper	5.14	13.73	57.01	7.79
Record	2.82	11.04	56.93	7.64
Desiree	3.86	14.62	64.98	7.21
Wilja	5.71	10.49	57.99	7.21
Mean	4.55	13.12	60.40	7.26
Standard error	0.73	1.89	1.32	0.72
1985				
P. Crown	5.20	17.24	64.83	6.06
M. Piper	5.70	16.89	59.12	7.36
Record	2.89	13.30	59.12	7.07
Desiree	3.81	15.68	63.28	7.00
Wilja	4.50	13.64	57.41	7.29
Mean	4.29	15.35	60.75	6.96
Standard error	0.76	1.78	1.82	0.80

Table 2. Predicted (Pre.) and observed (Obs.) proportion of environments where genotypes were greater than the mean of five control cultivars for saleable yield

Genotype	1984		1985	
	Pre.	Obs.	Pre.	Obs.
G1	0.712	0.714	0.496	0.571
G2	0.681	0.571	0.583	0.571
G3	0.595	0.571	0.528	0.429
G4	0.670	0.571	0.409	0.571
G5	0.637	0.714	0.452	0.286
G6	0.694	0.429	0.571	0.857
G7	0.729	0.714	0.819	0.857
G8	0.536	0.857	0.834	0.857
G9	0.532	0.571	0.468	0.571
G10	0.571	0.571	0.606	0.714
G11	0.871	0.857	0.587	0.714
G12	0.397	0.429	0.378	0.428
G13	0.516	0.571	0.604	0.714
G14	0.648	0.571	0.610	0.571
G15	0.767	0.857	0.815	0.857
G16	0.629	0.571	0.598	0.571
G17	0.732	0.571	0.644	0.571
G18	0.142	0.142	0.187	0.142
G19	0.779	0.571	0.618	0.857
G20	0.131	0.142	0.203	0.142

Table 3. Correlation coefficients obtained by correlating predicted and observed proportion of locations that each genotype will exceed the target value (mean of five controls) set for saleable yield; all correlations are significantly greater than zero at the 5% level

	Predicted 1984	Observed 1984	Predicted 1985
Observed 1984	0.843		
Predicted 1985	0.686	0.796	
Observed 1985	0.720	0.666	0.870

Table 4. Correlation coefficients obtained by correlating breeders' preference, saleable yield, tuber size and cooking quality based on the mean over all sites in 1984 and 1985 and including all genotypes; also the range of correlation coefficients relating to the correlation over environments of each individual genotype

	All clones	Range
1984		
Breeders preference v saleable	0.772^{c}	−0.048 to 0.830
Breeders preference v tuber size	0.659^{b}	−0.769 to 0.931
Breeders preference v cooking	-0.136^{ns}	−0.779 to 0.712
Saleable yield v tuber size	0.778^{c}	−0.247 to 0.823
Saleable yield v cooking	-0.221^{ns}	−0.882 to 0.430
Tuber size v cooking	-0.183^{ns}	−0.628 to 0.739
1985		
Breeders preference v saleable	0.825^{c}	0.037 to 0.829
Breeders preference v tuber size	0.550^{a}	−0.614 to 0.797
Breeders preference v cooking	-0.171^{ns}	−0.536 to 0.795
Saleable yield v tuber size	0.475^{a}	−0.668 to 0.778
Saleable yield v cooking	0.120^{ns}	−0.688 to 0.257
Tuber size v cooking	-0.320^{ns}	−0.737 to 0.698

ns = not significant; ^{a} $0.01<p<0.05$; ^{b} $0.001<p<0.01$; ^{c} $p<0.001$

Linear regression of predicted on to observed proportions accounted for 62% and 76% of the total variation in observed proportions in 1984 and 1985 respectively. The coefficients, obtained by correlating all combinations of observed and predicted proportion of sites where each genotype would exceed the target value were all significantly greater than zero (Table 3). Examination of the relative magnitude of these correlation coefficients showed that the greatest association was between predicted in 1985 and observed in 1984. The second largest in magnitude was between predicted in 1984 and observed in 1985, while the lowest correlation coefficient was between observed in 1984 and observed in 1985. When the other three variates were examined in this way similar results were obtained in that the correlation between predicted and observed in different years consistently yielded higher coefficients than between observed in different years.

Table 5. Predicted (Pre.) and observed (Obs.) proportion of environments where genotypes were greater than the mean of five control cultivars for breeders' preference, saleable yield, tuber size and cooking quality

Genotype	1984		1985	
	Pre.	Obs.	Pre.	Obs.
G1	0.103	0.143	0.091	0.143
G2	0.202	0.143	0.085	0.000
G3	0.330	0.143	0.106	0.143
G4	0.388	0.429	0.054	0.000
G5	0.274	0.286	0.064	0.000
G6	0.045	0.000	0.199	0.286
G7	0.629	0.571	0.419	0.429
G8	0.416	0.571	0.332	0.286
G9	0.190	0.286	–	0.000
G10	0.058	0.000	0.203	0.000
G11	0.030	0.000	0.023	0.000
G12	0.088	0.143	0.079	0.000
G13	0.193	0.143	0.057	0.143
G14	0.482	0.429	0.386	0.286
G15	0.453	0.571	0.347	0.286
G16	0.339	0.429	0.557	0.571
G17	0.577	0.571	0.557	0.571
G18	0.029	0.000	0.020	0.000
G19	0.661	0.429	0.420	0.571
G20	0.046	0.000	0.034	0.000

Multivariate

The multivariate predictions were based on the genotype mean and variance over environments, but were also determined by the correlation, or covariance, between the four variates. When all the genotypes were included in the correlation, breeders' preference was found to be highly correlated with saleable yield and tuber size in both years (Table 4). Breeders' preference and cooking quality however were negatively correlated, although not significantly. Saleable yield and tuber size were significantly correlated in 1984 and 1985 and tuber size also showed a negative relationship with cooking quality. The correlation coefficients when each genotype was examined separately showed a considerable range in value (Table 4) for the pair wise comparisons.

The predicted [based on Eq. (4)] and observed proportion of locations where each of the genotypes exceeded the target value (mean of five control cultivars) set for breeders' preference, saleable yield, tuber size and cooking quality are shown in Table 5. In 1984 it was predicted that genotype G19 would exceed these target values in 66% of the environments whereas genotype G18 would only exceed the target values at three locations in every 100. In 1985 genotype G17 was predicted to be the one which would exceed the target values most frequently (at 56% of the locations) while genotype G18 was again only expected to exceed these targets on 2% of the occassions. The observed proportion of locations that each genotype exceeded the target values ranged from

Table 6. Coefficients obtained by correlating expected and observed proportion of locations where genotypes were greater than the mean of five control cultivars for breeders' preference, saleable yield, tuber size and cooking quality, all correlation coefficients are significantly greater ($p < 0.001$) than zero

	Predicted 1984	Observed 1984	Predicted 1985
Observed 1984	0.904		
Predicted 1985	0.755	0.759	
Observed 1985	0.744	0.666	0.929

0% (i.e., never exceeded the target values at any location) to 57% (i.e., exceeded the target values at four locations out of the seven).

As with the univariate example the predicted and observed proportion were highly correlated. Linear regression of predicted on to observed accounted for 82% of the total variation in 1984 and 86% of the total variation in the observed in 1985. The repeatability of selection method (observed or predicted) was again examined by the magnitude of correlation coefficient obtained between observed and predicted in different years (Table 6). The correlation coefficient between predicted in 1985 and observed in 1984 was of a similar magnitude (0.76) to that obtained between predicted in 1984 and observed in 1985 (0.74). The correlation coefficient between observed proportions in the different years was however slightly lower (0.66).

Conclusions

In a practical plant breeding scheme, selections are usually made on each year's results, and only those genotypes that are selected in one year are grown in the subsequent year. In the example shown here the predictions made in either of the years can be compared to the observed proportions of the other year. It was found that the coefficients obtained by correlating predicted and observed proportions consistently higher than similar coefficients between observed proportions in different years. This was true for univariate and multivariate proportions.

The target values used for any character can be considered as the weighting for the variate. Standard, or control, cultivars are invariably included in breeders' assessment trials and their performance can be used to set targets. For example, a breeder could ask the question: What is the probability that a given line will have higher yield than the control variety A, better quality than variety B and more disease resistance than variety C? and the statistic answer will be a single datum value which is easily interpreted (i.e., the higher the probability the greater the likelyhood of success).

Pooni and Jinks (1978) have shown that that it is possible to predict the proportion of recombinant inbred lines which would exceed the target values for a two and three characters simultaneously. These predictions were made based on genetic means, variances and covariances estimated by experimental methods. They obtained the multi-variate probabilities from tables (Owen 1956). Using computers it is not necessary to restrict such predictions to two or three characters (Powell et al. 1985). Similarly, predicting the proportion of locations that genotypes will exceed set target values for a number of characters, can now be easily and quickly calculated by computer. Only a limited amount of data from two years have been presented here to illustrate the principles of this approach. If however, similar predictions on a greater number of genotypes show good agreement to that observed in different seasons, they will provide breeders with a useful tool for selecting genotypes which will have a high probability of being superior to standard cultivars for a range of different traits over a large proportion of environments.

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