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Theoretical Aspects of Selection for Yield in Stress and Non-Stress Environments[1]

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ABSTRACT

The question of choice of selection criterion when lines are grown in stress and non-stress environments is examined from a theoretical standpoint in this paper. Tolerance to stress is defined as the difference in yield between stress and non-stress environments, while mean productivity is the average yield in stress and non-stress environments. Equations are developed for the genetic correlations of tolerance and mean productivity with one another and with yields in stress and non-stress environments in terms of the ratio of genetic variances and the genetic correlations between yields in stress and non-stress environments. These equations show that selection for tolerance to stress will generally result in a reduced mean yield in non-stress environments and a decrease in mean productivity. Selection for mean productivity will generally increase mean yields in both stress and non-stress environments. Tolerance and mean productivity show negative genetic correlations when the genetic variance in stress environments is less than the genetic variance in non-stress environments. This result provides an explanation for the positive correlations often reported between regression coefficient stability and mean productivity; a line with high tolerance to stress normally would have a low regression coefficient stability and genetic variances in stress environments are generally lower than in non-stress enviornments.

Additional index words: Mean productivity, Regression coefficient stability, Selection criteria, Tolerance.

SELECTION for yield or production traits in stress and non-stress environments is a problem which continues to perplex plant breeders. Several selection criteria have been proposed to assist in this task.

The most widely used criteria for selecting for high and stable performance are mean yield, regression response on site mean yield, and deviations from regression (Eberhart and Russell, 1966; Finlay and Wilkinson, 1963; Freeman, 1973; Langer et al., 1979). Finlay and Wilkinson (1963) proposed that regression coefficients approaching zero indicated stable performance. Eberhart and Russell (1966), however, point out that varieties with a regression coefficient below 1.0 usually have mean yields below the grand mean and that selection for regression coefficients near zero results in selection for low mean yields. They proposed selection for high mean yield, unit regression ($b = 1.0$), and low deviations from regression. Positive correlations between mean yields and regression coefficients are common (Perkins and Jinks, 1968, Fatunla and Frey, 1974; Eagles and Frey, 1977; Langer et al., 1979). The decision whether to select for high mean yield with either unit regression or low regression depends on circumstances. In subsistence agriculture, stable performance is more important than high yields in favorable environments. In commercial agriculture, high average performance with subsequent high average return is often the desired objective.

Recently, Langer et al. (1979) proposed use of variety ranges (highest mean yield minus lowest mean yield) as a crude measure of stability across variable environments. They found regression coefficients and variety ranges were highly correlated ($r = 0.76$ to 0.90) and suggested varieties could be grown in two extreme environments to measure stability. The technique proposed by Langer et al. (1979) simplifies selection for yield in stress and non-stress environments. If stress and non-stress conditions can be readily controlled, for example through varying irrigation treatments, the measured response would be to specific environmental factors. The techniques used by Simons (1966) for measuring tolerance to crown rust of oats by growing lines in rusted and rust-free plots is a variation of the technique proposed by Langer et al. (1979). However, implicit in these techniques is that selection for tolerance to stress is worthwhile, and this implication seems never to have been seriously questioned.

The objective of this paper is to examine theoretical consequences of selection under stress and non-stress conditions. In particular, we consider (a) selection for tolerance to stress where tolerance is defined by a small difference in productivity between stress and non-stress environments, and (b) selection for mean performance in stress and non-stress environments.

THEORETICAL

Define yield (or the trait of interest) in the non-stress environment as Y_1 and yield in the stress environment as Y_2. Selection for tolerance to stress is equivalent to selection for low yield depression or low $Y_1 - Y_2$ or high $Y_2 - Y_1$ (where high $Y_2 - Y_1$ will normally mean low negative values). Define tolerance as Y_3 where

$$Y_3 = Y_2 - Y_1$$

Selection for mean productiviity in stress and non-stress environments is equivalent to selection for high $(Y_1 + Y_2)/2$. Define mean productivity as Y_4 where

$$Y_4 = (Y_1 + Y_2)/2$$

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We now examine genotypic correlations between Y_1, Y_2, Y_3, and Y_4 using procedures similar to those developoed by Turner and Young (1969) for determining expected correlations of ratio traits with their components. The genetic correlation between Y_3 and Y_1 is

$$r_{G13} = G_{13}/(G_{11}\,G_{33})^{1/2} \quad [3]$$

where G_{xx} is the genotypic variance of trait x and G_{xy} is the genotypic covariance between trait X and trait Y. Expanding terms gives

$$r_{G13} = (G_{12} - G_{11})/(G_{11}^2 + G_{11}\,G_{22} - 2G_{11}G_{12})^{1/2} \quad [4]$$

On dividing the numerator and denominator by G_{11} (not equal to zero), we have

$$r_{G13} = (r_{G12}\,K_G - 1)/(1 + K_G^2 - 2\,r_{G12}\,K_G)^{1/2} \quad [5]$$

where

$$K_G^2 = G_{22}/G_{11} \quad [6]$$

Similarly

$$r_{G23} = (K_G - r_{G12})/(1 + K_G^2 - 2\,r_{G12}\,K_G)^{1/2}, \quad [7]$$

$$r_{G14} = (r_{G12}\,K_G + 1)/(1 + K_G^2 + 2\,r_{G12}\,K_G)^{1/2}, \quad [8]$$

$$r_{G24} = (K_G + r_{G12})/(1 + K_G^2 + 2\,r_{G12}\,K_G)^{1/2}, \quad [9]$$

and

$$r_{G34} = (K_G^2 - 1)/(1 + 2\,K_G^2 + K_G^4 - 4\,r_{G12}^2\,K_G^2)^{1/2} \quad [10]$$

We now have five equations [5, 7, 8, 9, and 10] describing the genetic correlations of tolerance and mean productivity with one another and with each of their components in terms of the ratios of genetic variances in stress and non-stress environments (K_G^2) and the genetic correlation between yield in stress and non-stress environments (r_{G12}). We now examine and discuss the properties and consequences of these equations in terms of selection for tolerance (high $Y_2 - Y_1$) or mean productivity (high $(Y_1 + Y_2)/2$).

RESULTS

Selection for tolerance (high Y_3) normally means that mean yield in non-stress environments (Y_1) will decrease because under most circumstances r_{G13} is negative (Table 1). It can be seen from equation [5] that for r_{G13} to be positive, $r_{G12}\,K_G^2$ must be greater than 1. Because r_{G12} cannot be greater than 1, $r_{G12}\,K_G^2 >$ implies $K_G^2 > 1$ (note that $K_G^2 > 0$) and that r_{G12} is positive and high. These results mean that for a yield increase to occur in non-stress environments the genetic variance in stress environments must be greater than that in non-stress environments. Also, the genetic correlation between yields in stress and non-stress environments must be positive and high. If the genetic variance in stress environments is lower than that in non-stress environments, selection for tolerance must be accompanied by a decrease in mean yield in non-stress environments.

Selection for tolerance generally means that mean yield in stress environments will increase because, under most circumstances, r_{G23} is positive (Table 2). The only situation where this will not occur is when K_G^2 is less than 1 and r_{G12} is highly positive. On the other hand selection for mean productivity (Y_4) will normally be accompanied by an increase in mean yield in both stress and non-stress environments (Tables 3 and 4). Selection for mean productivity will only decrease mean yield in non-stress environments when K_G^2 is greater than 1 and when the genetic correlation of yields in stress and non-stress environments is highly negative. Selection for mean productivity will decrease mean yield in stress environments, however, when K_G^2 is less than 1 and when the genetic correlation of yields in stress and non-stress environments is highly negative.

Selection for tolerance will decrease mean productivity if K_G^2 is less than 1 and increase mean productivity if K_G^2 is greater than 1 (Table 5). If $K_G^2 = 1$, selection for tolerance will have no effect on mean productivity.

Table 1. Genetic correlations between tolerance to stress and yield in non-stress environments (r_{G13}) for various values of K_G^2 (ratio of genetic variances in stress and non-stress environments) and r_{G12} (genetic correlation between yields in stress and non-stress environments).

	r_{G12}								
K_G^2	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	−1.00	−0.97	−0.94	−0.92	−0.89	−0.88	−0.87	−0.88	−1.00
0.50	−1.00	−0.96	−0.91	−0.86	−0.82	−0.77	−0.73	−0.71	−1.00
1.00	−1.00	−0.94	−0.87	−0.79	−0.71	−0.61	−0.50	−0.35	0.00
2.00	−1.00	−0.91	−0.81	−0.70	−0.58	−0.43	−0.23	0.06	1.00
4.00	−1.00	−0.88	−0.76	−0.61	−0.45	−0.25	0.00	0.35	1.00

Table 2. Genetic correlations between tolerance to stress and yield in stress environments (r_{G23}) for various values of K_G^2 and r_{G12}.

	r_{G12}								
K_G^2	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	1.00	0.88	0.76	0.61	0.45	0.25	0.00	−0.35	−1.00
0.50	1.00	0.91	0.81	0.70	0.58	0.43	0.23	−0.06	−1.00
1.00	1.00	0.94	0.87	0.79	0.71	0.61	0.50	0.35	0.00
2.00	1.00	0.96	0.91	0.86	0.82	0.77	0.73	0.71	1.00
4.00	1.00	0.97	0.94	0.92	0.89	0.88	0.87	0.88	1.00

Table 3. Genetic correlations between mean productivity and yield in non-stress environments (r_{G14}) for various values of K_G^2 and r_{G12}.

	r_{G12}								
K_G^2	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	1.00	0.88	0.87	0.88	0.89	0.92	0.94	0.97	1.00
0.50	1.00	0.71	0.73	0.77	0.82	0.86	0.91	0.96	1.00
1.00	0.00	0.35	0.50	0.61	0.71	0.79	0.87	0.94	1.00
2.00	−1.00	−0.06	0.23	0.43	0.58	0.70	0.81	0.91	1.00
4.00	−1.00	−0.35	0.00	0.25	0.45	0.61	0.76	0.88	1.00

DISCUSSION

Magnitudes of selection responses and correlated responses will depend on heritabilities and phenotypic standard deviations as well as genetic correlations. We have only considered direction of correlated responses to

Table 4. Genetic correlations between mean productivity and yield in stress environments (r_{G24}) for various values of K_G^2 and r_{G12}.

	r_{G12}								
K_G^2	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	−1.00	−0.35	0.00	0.25	0.45	0.61	0.76	0.88	1.00
0.50	−1.00	−0.06	0.23	0.43	0.58	0.70	0.81	0.91	1.00
1.00	0.00	0.35	0.50	0.61	0.71	0.79	0.87	0.94	1.00
2.00	1.00	0.71	0.73	0.77	0.82	0.86	0.91	0.96	1.00
4.00	1.00	0.88	0.87	0.88	0.89	0.92	0.94	0.97	1.00

Table 5. Genetic correlations between tolerance and mean productivity (r_{G34}) for various values of K_G^2 and r_{G12}.

	r_{G12}								
K_G^2	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	−1.00	−0.75	−0.65	−0.61	−0.60	−0.61	−0.65	−0.75	−1.00
0.50	−1.00	−0.47	−0.38	−0.34	−0.33	−0.34	−0.38	−0.47	−1.00
1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2.00	1.00	0.47	0.38	0.34	0.33	0.34	0.38	0.47	1.00
4.00	1.00	0.75	0.65	0.61	0.60	0.61	0.65	0.75	1.00

selection, which will not be altered by variation in heritabilities or phenotypic standard deviations. Direction of a correlated response to selection is uniquely determined by the genetic correlaton.

Lines with high tolerance to stress would be expected to have low regression coefficient stability parameters. This is supported by the data of Langer et al. (1979) showing a correlation between regression coefficients and ranges in productivities of lines in two extreme environments. The results in this paper suggest that regression coefficient stability parameters and mean productivities will be positively correlated when the genetic variance in stress environments is less than that in non-stress environments (Table 5). A necessary condition for lines to show a positive relationship between tolerance and mean productivity is that the genetic variance in stress environments is greater than in non-stress environments. This does not appear to be a common occurrence (Frey, 1964; Gotoh and Osani, 1959; Johnson and Frey, 1967; Mederski and Jeffers, 1973).

It is important that breeders be aware of the implications of the equations presented in this paper. If stress and non-stress environments occur randomly but equally frequently throughout a breeding region then selection for tolerance to stress might be considered worthwhile. However, if stress environments show smaller genetic variances than non-stress environments then selection for tolerance will always decrease mean yields in non-stress environments. Selection for mean productivity under these circumstances will increase mean yields in both stress and non-stress environments unless the genetic correlation between yields in stress and non-stress environments is highly negative, in which case yields in stress environments will be decreased. A choice of selection criterion must be made depending on the circumstances of the program. If it is imperative that yields in stress environments be increased, then selection for tolerance may be worthwhile; but it should be recognized that this selection will generally decrease both mean productivity and yield in non-stress environments. If improvement in mean productivity is the objective, then direct selection for mean productivity should achieve it even though yields in stress environments may decrease and selected lines will tend to have low tolerance to stress. These considerations would be of greatest importance in recurrent selection programs and in early stages of selection where the breeder aims to move the population mean in a specific direction.

The situation most favorable to plant breeders would be one in which genetic variances in stress environments are greater than those in non-stress environments and genetic correlations between yields in stress and non-stress environments are highly positive. Under these circumstances mean productivity and tolerance will be positively correlated with one another and with yields in both stress and non-stress environments. Unfortunately, these situations appear to be rare. They could occur, for example, with disease stress where disease is the primary factor causing variability in yields and where genetic variability is limited in the low disease-stress environment.

As used herein, a stress environment is considered a single environment, but in most situations a range of stress conditions, due to varying factors, is likely to be encountered. Extension of the results to a population of environments should be made with caution. However, the results of this paper are supported by the frequently reported positive correlations between the regression coefficient stability parameter (measured over a range of environments) and mean yields. To the extent that selection for high mean yield is a desirable objective, selection for a low regression coefficient will act counter to this aim. In our view, the most desirable approach would be to choose testing sites to be representative of the production conditions for which a breeder wishes to improve mean yield. For example, if stress conditions occur randomly in one of three crops in a breeding region then ideally one of three testing sites would be a stress environment and selection should be practiced for mean yield. Alternatively, an index selection procedure (Hazel, 1943) could be used where each testing site is weighted according to the relative economic value of the crop normally produced under these condtions. The latter procedure would have the advantage that variation in heritabilities as well as genetic and phenotypic variances and covariances would be used to develop an optimum selection procedure.

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