Selection Indices for Simultaneous Selection for Pod Yield and Leafspot Resistance in Peanut (*Arachis hypogaea* L.)[1]

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ABSTRACT

The objective of this study was to investigate the possibility of index selection for pod yield and leafspot resistance, causal organisms *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. and Curt.) Deighton, in peanut (*Arachis hypogaea* L.). Eleven crosses were evaluated in the S_1 and S_2 generations under natural disease pressure for pod yield and disease reaction. Leafspot severity was measured by leaf necrotic area and defoliation. Variances for each trait and covariances between traits were estimated by progeny analysis. Economic weights assigned to the different characters were derived as the ratio of the pod yield for a genotype to the theoretical pod yield gain from leafspot resistance. Indices were constructed and their efficiency both as predictor of the breeding value and relative to individual selection for either trait was evaluated. Index selection for increased pod yield and reduced leafspot susceptibility was between 87% and 100% as efficient as direct selection for either trait. Combining several leafspot severity readings with pod yield did not improve the efficiency of the index. Fourteen to 17% of the breeding value of the population was accounted for by the traits combined in various indices. This indicated that there is potential for improvement of these indices.

Key Words: Index selection, leafspot resistance, pod yield

Breeders deal routinely with more than one trait and often use a variety of schemes to take into account the many characters of interest. The critical problem, however, is to maximize the concurrent selection of several traits in selected individuals (6).

Tandem selection, independent culling, and index selection are the procedures commonly described in most breeding and quantitative genetic texts for multiple trait selection. The effectiveness of index selection relative to the others has been demonstrated (5,8).

Lin (11) extensively reviewed the theory and applications of index selection for genetic improvement of quantitative characters. A variety of modifications of the technique have been published but the Hazel-Smith index seems to be preferred, especially when the relative economic values of characters combined differ a great deal (1). The latter requires, for its derivation, estimates of genetic variances and covariances and defines the aggregate genotype as a linear combination of genetic values, each weighted by the relative economic value.

Index selection has had limited use in actual plant breeding programs. Studies have been reported in soybeans (3,10), peanuts (2), alfalfa (6), and oats (4). The various results seem to indicate that index selection for improving one trait singly would be no better than direct selection for the trait itself, but might prove useful when selecting simultaneously for more than one trait.

The purpose of this study was to develop indices useful in diverse theoretical peanut leafspot disease environments for individual plant selection for increased pod yield and reduced leafspot susceptibility. The potential worth of these indices in practical breeding operations was also investigated.

Materials and Methods

The plant materials used, experimental design, and statistical analysis have been presented previously (9). Eleven of 69 crosses between high yielding and leafspot resistant peanut genotypes were chosen in the first selfed generation (S_1) on the basis of pod yield and disease reaction, measured as leaf necrotic area and defoliation. The S_2 generation was evaluated under natural leafspot infection for pod yield and disease reaction. The disease reaction was measured as percent necrotic area of the fifth fully expanded leaf from the end of the mainstem at 120 days after planting (DAP) (termed LSA) and at 140 DAP (LSB). Previous research (14) has shown a high correlation between mainstem defoliation and defoliation of cotyledonary laterals and other main branches of runner peanut plants. Therefore, percent defoliation was measured for each plant by counting the nodes on the mainstem without leaves and dividing by the total number of nodes. Variances for each trait, covariances between traits, and narrow sense heritabilities for all traits were estimated using the techniques described by Iroume and Knauft (9).

A range of theoretical leafspot disease pressures was chosen, from one in which leafspot caused no yield reduction to one in which there was a 100% reduction in yield. The economic value of leafspot severity was considered as the actual monetary loss from the yield decrease caused by the leafspot disease. To allow this economic value to be neutral across years, locations, and political boundaries, a relative economic value was assigned to both traits, derived as the ratio of the potential yield of any genotype (100% yield recovery) to the potential gain in yield (in percentage of potential yield) from the minimum level of resistance necessary to eliminate the loss in any environment. The different leafspot environments, the ratios and the relative economic values for the traits studied, are presented in Table 1.

Table 1. Derivation of relative economic values for pod yield and leafspot severity in seven theoretical leafspot environments.

Leafspot[1] environments (% yield loss)	Economic value ratios yield: resistance	Relative Economic Value	
		pod yield	leafspot severity
0	1:0	1	0
10	10:1	10	1
20	5:1	5	1
25	4:1	4	1
50	2:1	2	1
75	4:3	4	3
100	1:1	1	1

[1]Leafspot environments expressed as the theoretical reduction in pod yield expected with no leafspot control.

The indices were constructed by solving the following matrix equation:

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$b = P^{-1} G a$

where

b = vector of unknown weighting factors of the traits to be determined

P = variance - covariance phenotypic matrix

G = additive genetic variance - covariance matrix

a = vector of relative economic values assigned to the different traits.

The estimated phenotypic and additive genetic variances and covariances are presented in Table 2.

The constructed index is then

$$I = b_1 X_1 + b_2 X_2$$

or by rescaling

$$I = X_1 + b_2(b_1)^{-1} X_2 = X_1 + bX_2$$

where X_1 and X_2 are the phenotypic values for traits 1 and 2, respectively.

Indices were constructed for various combinations of pod yield with each or all leafspot severity ratings.

The efficiency of the different indices as predictors of the aggregate breeding value of the population was estimated according to the procedure described by Falconer (7) as:

$$r_{IB} = \frac{\sigma_I}{\sigma_B}$$

where

σI = standard deviation of the index

σB = standard deviation of the economic breeding value of the population

The variance of the indices was calculated by the formula:

$$\sigma^2_I = b_1 (b_1 \hat{\sigma}^2_{P_{X_1}} + b_2 \hat{Cov}_{P_{X_1X_2}} + \ldots) + b_2 (b_1 \hat{Cov}_{P_{X_2X_1}} + b_2 \hat{\sigma}^2_{P_{X_2}} + \ldots) + \ldots b_n (b_1 \hat{\sigma}^2_{P_{X_1}} \ldots)$$

The aggregate breeding value of the population was derived by assuming that all the traits (pod yield, LSA, LSB, and defoliation) contributed to the breeding value of the individual plant as

$$B = a_1A_1 + a_2A_2 + a_3A_3 + a_4A_4$$

where A_1, A_2, A_3, A_4 represent the individual contributions of pod yield, LSA, LSB, and DEF to the whole breeding value of the individual plant and a_1, a_2, a_3, and a_4 represent the economic values assigned to each of these traits, respectively. In the computations all the disease severity ratings were assumed to have the same economic weight.

The variance of the population breeding value was then computed as:

$$\hat{\sigma}^2_B = a_1 (a_1 \hat{\sigma}^2_{B_{X_1}} + a_2 \hat{Cov}_{B_{X_1X_2}} + \ldots) + a_2 (a_1 \hat{Cov}_B + a_2 \hat{\sigma}^2_{B_{X_2}} + \ldots + \ldots$$

The quantity r^2 IB which has been defined by Nordskog (14) as a measure of the expected progress in the economic breeding value of the population was also computed.

The efficiency of index selection relative to direct selection for any of the traits was calculated as:

$$E = r_{IB}(h)^{-1}$$

where h = square-root of the heritability of an individual measurement (7).

Results and Discussion

Rescaled indices involving pod yield in various combinations with LSA, LSB, and DEF for the different theoretical leafspot disease environments are presented in Table 3. LSA, LSB, and DEF were given negative weighting in almost all the indices computed. This result accounted for the negative phenotypic and genetic covariances between pod yield and leafspot severity (Table 2) and indicated that selection using index score would result in increasing pod yield while reducing leafspot susceptibility of peanut genotypes. A reversal of sign was observed in the weight of LSB in the indices combining pod yield with all the disease severity ratings in the environments with high leafspot impact. That shift seemed to suggest that the rating of percentage necrotic area late in the season (LSB) might become an indicator of the amount of disease present, rather than the breeding value of the population. It would be desirable when working in a high leafspot incidence region to take a rating of leafspot earlier in the season when differences among genotypes are maximal.

The efficiency of any selection index depends on how its values correlate with the average breeding value of the population. The estimated correlations between the different indices and the aggregate economic merit of the population ranged from 0.39 to 0.41 for all the indices and all the leafspot environments. The worth of including different leafspot severity readings in an index and the effect of the different leafspot environments on the efficiency of the indices were assessed by an analysis of variance. Combining more than one leafspot severity measurement with pod yield did not improve the value of the index as a predictor of the net merit of the population. This is an additional indication that LSA, LSB, and DEF are measuring more or less the same genetic event. Likewise, the various index combinations did not show different efficiencies from one leafspot environment to the other. This suggests that the variation in relative economic values assigned to traits in different environments had little effect on the index. A similar remark has been made by Brim *et al.* (3.) The indices including pod yield and percent leaf necrotic area ratings showed the highest efficiency value of 0.41 ($p = 0.05$).

The overall value of an index in selection is associated with the accuracy with which plants having the highest economic breeding values can be chosen by selecting directly for the index score. The quantity r^2_{IB} was computed for the various indices to serve that purpose. The results showed that a range of 14 to 17% advance would be expected per generation on the index score, depending on which index was used. This should not, however, be misinterpreted as the heritability. The relationship between r^2_{IB} and the heritability of the index h^2_I has been shown by Lin and Allaire (12). In fact, the economic index is optimal for the improvement of the economic, not the genetic, aggregate breeding value of the population. Nordskog (13) demonstrated that the squared correlation, r^2_{IB}, was always less than h^2_I, which is a measure of the genetic improvement of the population. Falconer (7) reported that the r^2_{IB} value could also be used to assess the potential for improvement of the index by inclusion of additional measurements. Interpreted as such, only 14 to 17% of the breeding value of the population was accounted for by the measurements combined in various indices.

The efficiency of index selection relative to direct selection for either trait evaluated was also investigated. The results show that index selection for increased pod yield and reduced leafspot susceptibility of peanut genotypes would be between 87 and 100% as efficient as direct selection, depending on the trait. This suggested that, if the objective of selection was to improve solely any of the traits studied, selection on the basis of an index score would be no better than direct selection for the trait itself. Similar conclusions have been reached in peanuts (2) and oats (4). It is important to note that the original objective of developing a selection index has never been to maximize genetic progress for a single trait, but to provide the breeders with an objective way for maximizing advance for several traits at a time. Index selection would thus be a useful strategy in selecting simultaneously for leafspot resistance and pod yield in early generations and would achieve per generation 87% and 90 to 100% of the progress expected when selecting singly for pod yield or leafspot resistance, respectively.

In the final analysis, the deductions about the usefulness of the constructed indices to achieve the expected goals remain, for their practical significance, dependent upon the precision with which the genetic components used have been estimated. Another potential drawback to the value of the estimated indices is the manner in which economic values for different traits are derived, as noted by Brim *et al.* (3). A review of some other internal deterrents of index selection has been made by Lin (11). A negative correlation may arise after a period of selection for positively correlated traits or two genetically uncorrelated traits, and reduce the genetic progress. A selection limit may occur with index selection even though the genetic variances of the component traits have not been exhausted.

The disease resistance parameters measured in this study, leaf necrotic area and defoliation, were both more easily measured than yield itself. Reports on the inheritance of pod yield and of leafspot resistance generally reported leafspot resistance to be more highly heritable than pod yield (15). Thus one method for selecting in early generations for high yielding, disease resistant plants would be to select for the disease resistance itself. However, such selection would also include many plants with low yield potential. Direct selection for yield was felt to be inefficient, given its low heritability and the confounding effects of different mechanisms of disease resistance and tolerance on the expression of pod yield under disease pressure. This study examined the feasibility of developing an index combining both pod yield in a leafspot environment and various parameters of leafspot resistance. It showed that an index combining pod yield and any one of the leafspot resistance parameters used in this study could be nearly as efficient as direct selection of either resistance or yield.

Further research should evaluate the different indices and determine the extent to which significant progress may be achieved and the comparative effectiveness of the procedure when contrasted with others in developing high yielding leafspot resistant peanut genotypes.

Table 2. Genetic and phenotypic variances and covariances for different leafspot resistance parameters combined in selection indices.

Characters	Necrotic area (1st reading: LSA)	Necrotic area (2nd reading: LSB)	Defoliation (DEF)	Pod yield
Necrotic area (1st reading: LSA)	0.249+0.06 (2.063∓0.05)[1]	0.198+0.03 (0.386∓0.04)	0.422+0.02 (1.528∓0.023)	-2.56+0.97 (-12.174∓1.14)
Necrotic area (2nd reading: LSB)		0.191+0.03 (1.382∓0.04)	0.413+0.09 (0.742∓0.11)	-1.60+0.79 (-5.475 ∓0.92)
Defoliation (DEF)			1.991+0.43 (14.574∓0.5)	-7.331+2.81 (-24.086 ∓3.28)
Pod yield				181.641+34.16 (1209.981∓39.86)

[1]Phenotypic values in parenthesis.

Table 3. Selected rescaled selection indices for increased pod yield and decreased leafspot severity for diverse leafspot pressure environments.

Leafspot[1] environments	Traits combined in the index Yield/LSA=I_{12}	Yield/DEF=I_{14}	Yield/LSB/DEF=$_{134}$
10%	$X_1 - 2.51X_2$	$X_1 - 1.73X_4$	$X_1 - 2.97X_3 - 1.60X_4$
20%	[2]$X_1 - 2.42X_2$	$X_1 - 1.65X_4$	$X_1 - 2.75X_3 - 1.51X_4$
25%	$X_1 - 2.39X_2$	$X_1 - 1.58X_4$	$X_1 - 2.61X_3 - 1.45X_4$
50%	$X_1 - 2.21X_2$	$X_1 - 1.38X_4$	$X_1 - 2.03X_3 - 1.25X_4$
75%	$X_1 - 2.00X_2$	$X_1 - 1.20X_4$	$X_1 - 1.41X_3 - 0.96X_4$
100%	$X_1 - 1.73X_2$	$X_1 - 0.93X_4$	$X_1 - 0.78X_3 - 0.71X_4$

[1]Leafspot environments expressed as the theoretical reduction in pod yield, expected with no leafspot control.

[2]X_1, X_2, X_3, X_4 = phenotypic values of pod yield, LSA, LSB and DEF respectively.

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