Theory of Selection for
Yield of Plants in Disease-Stress Environments

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ABSTRACT

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The effects of selection for yield in disease stress environments (Y_{DS}) on yield performance in nonstress environments (Y_{NS}) and disease resistance (X) were examined where disease losses (bX) are a linear function of disease resistance: $Y_{NS} - Y_{DS} = bX$. Genetic correlations between Y_{DS} and Y_{NS} and between Y_{DS} and bX were calculated in terms of the genetic correlation between Y_{NS} and bX and the ratio between genetic variances for bX and Y_{NS}. Correlated responses in Y_{NS} and bX to selection for Y_{DS} were compared to those predicted from optimum index selection for high Y_{NS} and low bX, with both traits having equal economic weight. Simulated selection for Y_{DS} resulted in favorable correlated responses in Y_{NS} and bX except in certain situations where the genetic correlation between bX and Y_{NS} is highly positive. Predicted responses in Y_{NS} and bX from selection for Y_{DS} compared favorably to those predicted from index selection.

Additional keywords: breeding, disease resistance, index selection.

The development of high-yielding, disease-resistant varieties is the goal of most applied plant breeding programs. Therefore, plant breeders and pathologists must be able to efficiently select genotypes that are not only disease resistant but have the capacity to yield in the absence of disease stress.

Several methods are available and have been used to improve plant populations for more than one trait. Independent culling is selection at a given intensity for several traits sequentially in the same generation (6). For example, a selection intensity of 50% is applied for disease resistance and out of those the top 20% for yield are selected for a final selection intensity of 10% (50% × 20% = 10%). Tandem selection is selection in a population for one trait for several generations until a desirable level in attained, followed by selection for a second trait for several generations (6). Both independent culling and tandem selection can be inefficient when compared to optimum index selection (15), and this disadvantage increases when traits are unfavorably correlated (3,17). Index selection, in the broad sense, means selection based on an overall estimate of a genotype's worth, where each individual trait is given a relative economic weight. The optimum selection index relies on estimates of additive genetic and phenotypic variances and covariances among traits, as well as on estimates of relative economic worth, in the calculation of weights given each trait (15). Because of the time and expense required to obtain reliable estimates of the necessary variances and covariances and the difficulty in assigning relative economic weights to traits, index selection has not been widely used for multiple-trait selection in plants (6). All three methods would require careful evaluation of genotypes for all traits selected, and in the case of disease resistance, a reliable estimate of an adequate level of resistance.

Selection for plant genotypes that yield well under disease stress could be an alternative approach to select for yield potential and disease resistance simultaneously, offering several advantages over the other methods. It would eliminate the evaluation of individual genotypes for disease resistance per se. Plots could either be naturally or artificially inoculated; as long as levels of disease stress were sufficient to affect plant yields, the only data to be obtained from plots would be harvested yield. It would also eliminate the need to set relative economic weights or acceptable levels of resistance; yield losses due to disease stress would determine the relative worth of disease resistance. Finally, it would eliminate the

time and expense of obtaining reliable experimental estimates of additive genetic and phenotypic variances and covariances necessary to construct a selection index.

Experimental data on the relative effectiveness of selection for yield in stress versus nonstress environments is sparse and not conclusive. Selection for lint yield in upland cotton was ineffective when conducted at Texas locations deficient either in heat units or soil moisture but was effective at locations where neither factor was limiting (13). Grain yield of oat lines selected under nutrient and drought stress interacted more with differing environments than did those selected under optimal conditions (4). Estimates of heritability for grain yield were higher in nonstress than stress environments, but no significant differences in grain yields were detected between groups of lines selected in the two environments (4). Later studies on the heritability of oat grain yield in nutrient stress or late-planting stress environments indicate that, in general, genetic and environmental variances both increased as environmental stress decreased so that heritabilities changed little between environments (8). Additive genetic variance for grain yield in a maize population was higher when planted at the optimal planting date in Egypt than when planted later (1). However, dominance genetic variance increased at the later planting date (1). Mass selection for seedling weight in tobacco was more effective when selection was conducted under optimal nutrient levels (16). Selection for grain yield in a wheat cross was most effective under suboptimal fertility levels (5). Moreover, lines selected under fertility stress were more adaptable than those selected under nonstress conditions (5).

Rosielle and Hamblin (14) have reported the theoretical aspects of selection for tolerance to stress, where selection is for low difference in yield between stress and nonstress environments. Based on their analysis, this selection would result in decreased yield in nonstress environments unless genetic variance for yield was much higher in stress than nonstress environments, and the genetic correlation between yield in the two environments was quite high, a highly unlikely situation according to the authors (14). The objectives of this paper were to determine the effects of selection for yield in a disease-stress environment on yield potential in nonstress environments and on disease resistance using the analytic methods of Rosielle and Hamblin (14), and to compare the relative efficiency of selection for yield under disease stress in improving yield in nonstress environments and disease resistance with index selection for both yield in nonstress environments and disease resistance.

MATERIALS AND METHODS

Assume that yield of a genotype in a disease-stress environment (Y_{DS}) is equal to the yield potential of that genotype in a nonstress environment (Y_{NS}) minus loss due to disease that is a direct function of the level of disease severity (X) on that genotype. Therefore, $Y_{NS} - Y_{DS} = bX$, where b is a constant (slope) describing the relationship between loss and disease severity. Because the variance of a sum is equal to the sum of the variances plus twice the covariance ($V_{A+B} = V_A + V_B + 2 \, COV_{A \cdot B}$) we can derive expressions for the genetic variances of Y_{DS}, Y_{NS}, bX and the genetic covariances between them:

$$V_{GNS} = V_{GDS} + V_{GbX} + 2 \, COV_{GDS,bX} \tag{1}$$

$$V_{GDS} = V_{GNS} - V_{GbX} - 2 \, COV_{GDS,bX} \tag{2}$$

$$V_{GbX} = V_{GNS} - V_{GDS} - 2 \, COV_{GDS,bX} \tag{3}$$

$$COV_{GNS,DS} = V_{GNS} - COV_{GNS,bX} \tag{4}$$

$$COV_{GDS,bX} = COV_{GNS,bX} - V_{GbX} \tag{5}$$

$$COV_{GNS,bX} = V_{GbX} + COV_{GDS,bX} \tag{6}$$

Because we are interested in the effect of selection in a disease-stress environment on each of the two components of Y_{DS}, namely Y_{NS} and bX, we are interested in the genetic correlation of Y_{DS} with Y_{NS} and bX. Thus, the genetic correlation coefficient between Y_{NS} and Y_{DS} can be described by:

$$r_{GNS,DS} = \frac{COV_{GNS,DS}}{(V_{GNS} V_{GDS})^{\frac{1}{2}}} \tag{7}$$

By setting the ratios V_{GbX}/V_{GNS} and $r_{GNS,bX}$ to constant values, $r_{GNS,DS}$ can be calculated. For example: let $V_{GbX}/V_{GNS} = 1.0$ and $r_{GNS,bX} = 0$, then

$$COV_{GNS,bX} = 0, \ V_{GbX} = V_{GNS} \tag{8}$$

By substituting equation 4 in the numerator and equation 2 in the denominator of equation 7 we have:

$$r_{GNS,DS} = \frac{V_{GNS} - COV_{GNS,bX}}{[V_{GNS}(V_{GNS} - V_{GbX} - 2 \, COV_{GDS,bX})]^{1/2}}$$

By using equation 8 and substituting equation 5, we obtain:

$$= \frac{V_{GNS}}{(2V^2_{GNS})^{1/2}}$$

$$= 0.7071$$

Values of $r_{GNS,DS}$ were then calculated for a wide range in values for V_{GbX}/V_{GNS} (0.25 − 4.00) and $r_{GNS,bX}$ (−1.0 to +1.0) (Table 1). Similarly, values for $r_{GbX,DS}$ were calculated for the same range in values for V_{GbX}/V_{GNS} and $r_{GNS,bX}$ (Table 2).

With the genetic correlations calculated above, of each kth component ($k = Y_{NS}$ or bX) with Y_{DS}, correlated responses in Y_{NS} and bX from selection for Y_{DS} were calculated by (2, p. 286): $C.R._k = i \, V_{Pk}^{1/2} \, r_{GkDS} h_k h_{DS}$ where i = standardized selection differential, $V_k^{1/2}$ = phenotypic standard deviation for the trait under indirect selection, r_{GkDS} = genetic correlation coefficient between the two traits; and h_k and h_{DS} = the square root of the heritability of the trait under indirect or direct selection, respectively. Heritabilities were calculated by $h^2 = V_G/V_P$ and $V_P = V_G + V_E$, where V_G, V_P, and V_E equal the genetic, phenotypic, and environmental variances, respectively. Correlated responses were evaluated over a range of heritabilities for each of the components, Y_{NS} and bX. The heritabilities for Y_{NS} were 0.25, 0.50, and 0.75 by setting V_{ENS} and V_{EDS} to either $3V_{GNS}$, V_{GNS}, or $1/3 \, V_{GNS}$, respectively; for bX, 0.20, 0.33, 0.50, 0.67, and 0.80 corresponding to values of the ratio, $V_{GbX}/V_{GNS} = 0.25, 0.50, 1.00, 2.00,$ and 4.00, respectively. The value of V_{EbX} was kept constant at V_{GNS}. The correlated responses of the kth component (Y_{NS} or bX) to selection for Y_{DS} were compared to the response expected from direct selection, where the direct response (R_k) $= i \, V_{Pk}^{1/2} \, h^2_k$ (2, p. 275), i.e., CR_k/R_k. The correlated response of the kth component was also expressed by dividing it by its genetic standard deviation ($V_{Gk}^{1/2}$) and i, i.e. $CR_k/(i \, V_{Gk}^{1/2})$.

Finally, expected aggregate correlated genetic gains in Y_{NS} and bX from selection for Y_{DS} calculated above were compared to those expected from optimum index selection for Y_{NS} and bX where both traits were given equal relative economic weights. Aggregate genetic gains equalled the difference between genetic gains for Y_{NS} and bX since the desired response in bX is negative (low loss to disease) and is positive for Y_{NS}. Index coefficients were calculated by $b = V_P^{-1} V_G \, a$, where b is the vector of index coefficients, V_P is the phenotypic variance–covariance matrix, V_G is the genotypic variance–covariance matrix, and a is the vector of relative economic weights (14). Genetic gains for each trait in the index were calculated by:

$$\Delta g_k = i \, (b'V_{Gk}) \Big/ {(b'V_p b)^{1/2}}$$

where Δg_k is the genetic gain for the kth trait, i is selection intensity, and V_{Gk} is the column vector of genetic covariances between the kth trait and each component trait of the index (9). Aggregate gain in Y_{NS} and bX from index selection was obtained as the difference in the genetic gains for each trait (Δg_k, $k = Y_{NS}$, bX) divided by their genetic standard deviation and i.

RESULTS

Selection for high Y_{DS} would result in a favorable (positive) correlated response in Y_{NS}, because under most conditions $r_{GNS,DS}$

TABLE 1. Genetic correlation coefficients between yield in nonstress environments (Y_{NS}) and yield in disease stress environments (Y_{DS}), $r_{GNS,DS}$, with different values of $r_{GbX,NS}$, the genetic correlation between loss to disease severity X (bX) versus Y_{NS}, and with different ratios of genetic variance for bX and Y_{NS}

Ratio:[a] $\dfrac{V_{GbX}}{V_{GNS}}$	$r^b_{GbX,NS}$								
	−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	...[c]
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

[a] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments, respectively.
[b] Genetic correlation coefficient between Y_{NS} and bX.
[c] Not calculable, since division by zero is required.

is positive (Table 1). Only when the ratio V_{GbX}/V_{GNS} is greater than 1.00 and $r_{GbX,NS}$ is highly unfavorable (≥ 0.75) would an unfavorable correlated response in Y_{NS} from selection for Y_{DS} be expected. Selection for high Y_{DS} would also result in a favorable (negative) correlated response in bX under most conditions (Table 2). Only when the ratio V_{GbX}/V_{GNS} is less than 1.00 and $r_{GbX,NS}$ is highly unfavorable (≥ 0.75) would an increase in bX (loss due to disease severity, X) result from selection for high Y_{DS}.

Correlated responses in Y_{NS} resulting from selection for Y_{DS} (Tables 3–5) increased when heritability for Y_{NS} increased from 0.25 to 0.75. However, when correlated responses in Y_{NS} were expressed as a proportion of the response expected from direct selection for Y_{NS}, correlated responses were greatest at the lowest heritability level for Y_{NS} (Table 3).

Correlated responses in bX resulting from selection for Y_{DS} (Tables 6–8) increased in magnitude (became more negative) as

TABLE 2. Genetic correlation coefficients between yield loss due to disease severity X (bX) and yield in disease stress environments (Y_{DS}), with different values of $r_{GbX,NS}$ and the ratio of genetic variances for bX and Y_{NS}.

Ratio:[a] $\frac{V_{GbX}}{V_{GNS}}$	$r^{b}_{GbX,NS}$								
	−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	...[c]
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	−0.87	−0.87	−0.88	−1.00

[a] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments.
[b] Genetic correlation coefficient between Y_{NS} and bX.
[c] Not calculable, since division by zero is required.

TABLE 3. Correlated response in yield in nonstress environments (Y_{NS}) when selection is for yield in disease stress environments (Y_{DS}), assuming environmental variances for Y_{NS} and Y_{DS} are equal to three times the genetic variance for Y_{NS} (i.e., $h^2_{NS} = 0.25$)[a]

Ratio:[b] $\frac{V_{GbX}}{V_{GNS}}$	$r^{c}_{GNS,bX}$								
	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	0.6547	0.6135	0.5706	0.5312	0.4827	0.4400	0.3891	0.3326	0.2774
	(1.309)	(1.227)	(1.141)	(1.062)	(0.965)	(0.880)	(0.778)	(0.665)	(0.555)
0.50	0.7020	0.6515	0.5925	0.5315	0.4734	0.4049	0.3338	0.2538	0.1667
	(1.404)	(1.303)	(1.185)	(1.063)	(0.947)	(0.810)	(0.668)	(0.508)	(0.334)
1.00	0.7559	0.6898	0.6152	0.5326	0.4490	0.3522	0.2500	0.1323	...[d]
	(1.512)	(1.380)	(1.230)	(1.065)	(0.898)	(0.704)	(0.500)	(0.265)	
2.00	0.8125	0.7226	0.6250	0.5204	0.4101	0.2830	0.1353	−0.0286	−0.2326
	(1.625)	(1.445)	(1.250)	(1.041)	(0.820)	(0.566)	(0.271)	(−0.057)	(−0.465)
4.00	0.8660	0.7505	0.6359	0.4981	0.3558	0.1890	0.0000	−0.2214	−0.5000
	(1.732)	(1.501)	(1.272)	(0.996)	(0.712)	(0.378)	(0.000)	(−0.443)	(−1.000)

[a] Responses are in genetic standard deviations ($V_{GNS}^{1/2}$) times the reciprocal of i, the standardized selection differential, and in proportion to direct response to selection for high Y_{NS} (in parentheses).
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments.
[c] Genetic correlation coefficient between Y_{NS} and bX.
[d] Not calculable, since $r_{GNS,DS}$ was not calculable.

TABLE 4. Correlated response in yield in nonstress environments (Y_{NS}) when selection is for yield in disease stress environments (Y_{DS}), assuming environmental variance for Y_{NS} and Y_{DS} is equal to genetic variance for Y_{NS} (i.e., $h^2_{NS} = 0.50$)[a]

Ratio:[b] $\frac{V_{GbX}}{V_{GNS}}$	$r^{c}_{GNS,bX}$								
	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	0.8321	0.7920	0.7499	0.7126	0.6634	0.6223	0.5695	0.5081	0.4472
	(1.177)	(1.120)	(1.061)	(1.008)	(0.938)	(0.880)	(0.806)	(0.719)	(0.633)
0.50	0.8629	0.8141	0.7549	0.6931	0.6352	0.5627	0.4855	0.3923	0.2811
	(1.220)	(1.151)	(1.068)	(0.980)	(0.898)	(0.796)	(0.687)	(0.555)	(0.398)
1.00	0.8944	0.8290	0.7534	0.6677	0.5797	0.4725	0.3536	0.2021	...[d]
	(1.265)	(1.172)	(1.065)	(0.944)	(0.820)	(0.668)	(0.500)	(0.286)	
2.00	0.9239	0.8324	0.7314	0.6212	0.5023	0.3588	0.1801	−0.0410	−0.3827
	(1.307)	(1.177)	(1.034)	(0.878)	(0.710)	(0.507)	(0.255)	(−0.058)	(−0.541)
4.00	0.9487	0.8297	0.7109	0.5648	0.4108	0.2236	0.0000	−0.2858	−0.7071
	(1.342)	(1.173)	(1.005)	(0.799)	(0.581)	(0.316)	(0.000)	(−0.404)	(−1.000)

[a] Responses are in genetic standard deviations ($V_{GNS}^{1/2}$) times the reciprocal of i, the standardized selection differential, and in proportion to direct response to selection for Y_{NS} (in parentheses).
[b] V_{bX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments.
[c] Genetic correlation coefficient between Y_{NS} and bX.
[d] Not calculable, since $r_{GNS,DS}$ was not calculable.

TABLE 5. Correlated response in yield in nonstress environments (Y_{NS}) when selection is for yield in disease stress environments (Y_{DS}), assuming environmental variances for Y_{NS} and Y_{DS} are equal to one-third of the genetic variance for Y_{NS} (i.e., $h^2_{NS} = 0.75$)[a]

Ratio:[b] $\dfrac{V_{GbX}}{V_{GNS}}$	$r^c_{GNS,bX}$								
V_{GNS}	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	0.9333	0.8980	0.8615	0.8322	0.7908	0.7621	0.7239	0.6816	0.6547
	(1.078)	(1.037)	(0.995)	(0.961)	(0.913)	(0.880)	(0.836)	(0.787)	(0.756)
0.50	0.9473	0.9030	0.8482	0.7917	0.7417	0.6777	0.6125	0.5505	0.4524
	(1.094)	(1.043)	(0.979)	(0.914)	(0.856)	(0.783)	(0.707)	(0.636)	(0.522)
1.00	0.9608	0.8982	0.8254	0.7421	0.6573	0.5518	0.4330	0.2711	...[d]
	(1.109)	(1.037)	(0.953)	(0.857)	(0.759)	(0.637)	(0.500)	(0.313)	
2.00	0.9726	0.8818	0.7810	0.6705	0.5502	0.4018	0.2091	−0.0511	−0.5828
	(1.123)	(1.018)	(0.902)	(0.774)	(0.635)	(0.464)	(0.241)	(−0.059)	(−0.673)
4.00	0.9820	0.8622	0.7425	0.5937	0.4357	0.2402	0.0000	−0.3240	−0.8660
	(1.134)	(0.996)	(0.857)	(0.686)	(0.503)	(0.277)	(0.0)	(−0.374)	(−1.000)

[a] Responses are in genetic standard deviations ($V_{GNS}^{1/2}$) times the reciprocal of i, the standardized selection differential, and in proportion to response to direct selection for Y_{NS} (in parentheses).
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity $X(bX)$ and for yield in nonstress environments.
[c] Genetic correlation coefficient between Y_{NS} and bX.
[d] Not calculable, since $r_{GNS,DS}$ was not calculable.

TABLE 6. Correlated response in yield due to disease severity $X (bX)$ when selection is for yield in disease stress environment (Y_{DS}), assuming environmental variance for bX equals the genetic variance for yield in nonstress environments (Y_{GNS}) and environmental variance for $Y_{DS} = 3\, V_{GNS}$ ($h^2_{NS} = 0.25$)[a]

Ratio:[b] $\dfrac{V_{GbX}}{V_{GNS}}$	$r^c_{GNS,bX}$								
V_{GNS}	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	−0.6547	−0.5566	−0.4613	−0.3522	−0.2440	−0.1250	0.0000	0.1323	0.2774
	(1.464)	(1.245)	(1.032)	(0.788)	(0.546)	(0.280)	(0.000)	(−0.296)	(−0.620)
0.50	−0.7020	−0.6175	−0.5273	−0.4326	−0.3349	−0.2261	−0.1052	0.0214	0.1667
	(1.216)	(1.070)	(0.913)	(0.749)	(0.580)	(0.392)	(0.182)	(−0.037)	(−0.289)
1.00	−0.7559	−0.6898	−0.6152	−0.5326	−0.4490	−0.3522	−0.2500	−0.1323	...[d]
	(1.069)	(0.976)	(0.870)	(0.753)	(0.635)	(0.498)	(0.354)	(0.187)	
2.00	−0.8125	−0.7623	−0.7022	−0.6394	−0.5798	−0.5068	−0.4293	−0.3379	−0.2326
	(0.995)	(0.934)	(0.860)	(0.783)	(0.710)	(0.621)	(0.526)	(0.414)	(0.285)
4.00	−0.8660	−0.8272	−0.7865	−0.7512	−0.7036	−0.658	−0.6152	−0.557	−0.5000
	(0.968)	(0.925)	(0.879)	(0.840)	(0.787)	(0.735)	(0.688)	(0.622)	(0.559)

[a] Responses are expressed in genetic standard deviations ($V_{GNS}^{1/2}$) times the reciprocal of i, the standardized selection differential, and in proportion to direct response to selection for low bX (in parentheses).
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity $X (bX)$ and for yield in nonstress environments, respectively.
[c] Genetic correlation coefficient between yield in nonstress environments and loss due to disease severity $X (bX)$.
[d] Not calculable, since $r_{GbX,DS}$ was not calculable.

TABLE 7. Correlated response in yield loss due to disease severity $X (bX)$ when selection is for yield in a disease stress environment (Y_{DS}), assuming environmental variance for bX and Y_{DS} is equal to genetic variance for yield in nonstress environment ($h^2_{NS} = 0.50$)[a]

Ratio:[b] $\dfrac{V_{GbX}}{V_{GNS}}$	$r^c_{GNS,bX}$								
V_{GNS}	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	−0.8321	−0.7185	−0.6063	−0.4725	−0.3354	−0.1768	0.0000	0.2027	0.4472
	(1.861)	(1.607)	(1.356)	(1.057)	(0.750)	(0.395)	(0.000)	(−0.452)	(−1.000)
0.50	−0.8629	−0.7717	−0.6720	−0.5642	−0.4493	−0.3143	−0.1530	0.0331	0.2811
	(1.495)	(1.337)	(1.164)	(0.977)	(0.778)	(0.544)	(0.265)	(−0.057)	(−0.487)
1.00	−0.8944	−0.8290	−0.7534	−0.6677	−0.5797	−0.4725	−0.3536	−0.2021	...[d]
	(1.265)	(1.172)	(1.066)	(0.944)	(0.820)	(0.668)	(0.500)	(0.286)	
2.00	−0.9239	−0.8781	−0.822	−0.7632	−0.7101	−0.6425	−0.5717	−0.4856	−0.3827
	(1.132)	(1.075)	(1.006)	(0.935)	(0.870)	(0.787)	(0.700)	(0.595)	(0.469)
4.00	−0.9487	−0.9145	−0.879	−0.8518	−0.8125	−0.7782	−0.7534	−0.7185	−0.7071
	(1.061)	(1.023)	(0.983)	(0.952)	(0.908)	(0.870)	(0.842)	(0.803)	(0.791)

[a] Responses are expressed in genetic standard deviations ($V_{GNS}^{1/2}$) times the reciprocal of i, the standardized selection differential, and in proportion to response to direct selection for low bX (in parentheses).
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity $X (bX)$ and for yield in nonstress environments, respectively.
[c] Genetic correlation coefficient between yield in nonstress environments and loss due to disease severity $X (bX)$.
[d] Not calculable, since $r_{GbX,DS}$ was not calculable.

heritabilities for Y_{NS} increased. This trend held true even when correlated responses were expressed as a proportion of those expected from direct selection for low bX.

Aggregate genetic gains for high Y_{NS} and low bX from selection for Y_{DS} and from optimum index selection are compared in Tables 9–11. Selection for Y_{DS} would result in greater aggregate genetic gains than would optimum index selection if the ratio V_{GbX}/V_{GNS} were one or less, regardless of the level of heritability set for Y_{NS}. Use of the optimum selection index would become increasingly superior to selection for Y_{DS} as the ratio V_{GbX}/V_{GNS} increases from one and the genetic correlation between Y_{NS} and bX becomes less favorable (increasingly positive).

DISCUSSION

In most applied plant breeding programs, selection is usually practiced for more than one trait, with disease resistance often being secondary in importance only to yield potential. Conventional multiple trait selection schemes such as tandem selection, independent culling levels, and index selection to improve a population for both disease resistance and yield potential usually rely on some rating scale for measuring disease resistance. Unfortunately, for most plant diseases, knowledge of what constitutes an adequate level of resistance (i.e., at what disease rating would no significant yield loss be expected) is lacking. This could result in inappropriate weight or importance being placed on disease resistance in these breeding schemes. Also, considerable time and effort may be expended in taking detailed data on disease resistance of the genotypes under selection. Because disease resistance is usually important only because it reduces yield losses to disease, and because of problems, mentioned above inherent in using conventional multiple trait selection schemes for improving disease resistance and yield simultaneously, we feel that the method of selection for yield in disease-stress environments deserves serious consideration by plant breeders and pathologists alike. Selection for yield in disease-stress environments appears to be a practical method of selection for genotypes with adequate levels of disease resistance (low bX) and yield potential in non-disease stress environments. Only when the correlation between Y_{NS} and bX is highly unfavorable (highly positive, >0.75) and the genetic variance for bX is greater than that for Y_{NS} would selection for Y_{DS} result in an undesirable correlated response in Y_{NS}. Although it is not possible to make statements about values of the ratio V_{GbX}/V_{GNS}, a highly negative correlation between disease resistance (low bX) and yield does not appear to be a common occurrence in plants. Estimates of genetic

TABLE 8. Correlated response in yield loss due to disease severity X (bX) when selection is for yield in a disease stress environment (Y_{DS}), assuming environmental variance for bX equals the genetic variance for yield in nonstress environments (Y_{GNS}) and environmental variance for $Y_{DS} = 1/3 \, V_{GNS}$ ($h^2_{NS} = 0.75$)[a]

Ratio:[b] $\dfrac{V_{GbX}}{V_{GNS}}$	$r^c_{GNS,bX}$								
	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	−0.9333 (2.087)	−0.8147 (1.822)	−0.6966 (1.558)	−0.5518 (1.234)	−0.3998 (0.894)	−0.2165 (0.484)	0.0000 (0.000)	0.2711 (−0.606)	0.6547 (−1.464)
0.50	−0.9473 (1.641)	−0.8560 (1.483)	−0.7550 (1.308)	−0.6444 (1.116)	−0.5246 (0.909)	−0.3785 (0.656)	−0.1930 (0.334)	0.0452 (−0.078)	0.4524 (−0.784)
1.00	−0.9608 (1.359)	−0.8982 (1.270)	−0.8254 (1.167)	−0.7421 (1.050)	−0.6573 (0.930)	−0.5518 (0.780)	−0.4330 (0.612)	−0.2711 (0.383)	...[d]
2.00	−0.9726 (1.191)	−0.9302 (1.139)	−0.8775 (1.075)	−0.8238 (1.009)	−0.7779 (0.953)	−0.7195 (0.881)	−0.6636 (0.813)	−0.6045 (0.740)	−0.5828 (0.714)
4.00	−0.9820 (1.098)	−0.9504 (1.063)	−0.9184 (1.027)	−0.8955 (1.001)	−0.8617 (0.964)	−0.8359 (0.935)	0.8254 (0.923)	−0.8147 (0.911)	−0.8660 (0.968)

[a] Responses are expressed in genetic standard deviations ($V_{GNS}^{1/2}$) times the reciprocal of i, the standardized selection differential, and in proportion to response to direct selection for low bX (in parentheses).
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments, respectively.
[c] Genetic correlation coefficient between yield in nonstress environments and loss due to disease severity X (bX).
[d] Not calculable, since $r_{GbX, DS}$ was not calculable.

TABLE 9. Aggregate genetic gain for yield in nonstress environments (Y_{NS}) and decreased yield loss (bX) due to disease severity (X) from selection for yield in a disease-stress environment (Y_{DS}) and from index selection for both traits given equal economic weight (in parentheses)[a]

Ratio:[b] $\dfrac{V_{GbX}}{V_{GNS}}$	$r^c_{GNS,bX}$								
	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	1.3094 (0.9105)	1.1701 (0.8217)	1.0319 (0.7313)	0.8838 (0.6396)	0.7267 0.5477)	0.5650 (0.4583)	0.3891 (0.3774)	0.2003 (0.3183)	0.00 (0.3035)
0.50	1.4040 (1.1509)	1.2690 (1.0317)	1.1198 (0.9082)	0.9641 (0.7796)	0.8083 (0.6455)	0.6310 (0.5060)	0.4390 (0.3642)	0.2324 (0.2364)	0.00 (0.2005)
1.00	1.5118 (1.5119)	1.3795 (1.3612)	1.2304 (1.2048)	1.0652 (1.0405)	0.8980 (0.8660)	0.7044 (0.6787)	0.5000 (0.4752)	0.2646 (0.2510)	...[d]
2.00	1.6250 (2.0199)	1.4849 (1.8403)	1.3272 (1.6556)	1.1598 (1.4626)	0.9899 (1.2583)	0.7898 (1.0402)	0.5646 (0.8065)	0.3093 (0.5607)	0.00 (0.3466)
4.00	1.7320 (2.7042)	1.5777 (2.5007)	1.4224 (2.2943)	1.2493 (2.0807)	1.0594 (1.8574)	0.8470 (1.6226)	0.6152 (1.3765)	0.3356 (1.1259)	0.00 (0.9014)

[a] Environmental variances for Y_{NS} and Y_{DS} equal three times the genetic variance for Y_{NS} (V_{GNS}) and the environmental variance for bX equals V_{GNS}. Heritability of Y_{NS} = 0.25.
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments, respectively.
[c] Genetic correlation coefficient between yield in nonstress environments and loss due to disease severity X (bX).
[d] Not calculable.

TABLE 10. Aggregate genetic gain for yield in nonstress environments (Y_{NS}) and decreased yield loss (bX) due to disease severity (X) from selection for yield in a disease-stress environment (Y_{DS}) and from index selection for both traits given equal economic weight (in parentheses)[a]

Ratio:[b] V_{GbX} V_{GNS}	$r^c_{GNS,bX}$								
	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	1.6642 (1.1180)	1.5105 (1.0294)	1.3562 (0.9371)	1.1851 (0.8412)	0.9988 (0.7416)	0.7991 (0.6394)	0.5695 (0.5371)	0.3054 (0.4420)	0.0000 (0.3727)
0.50	1.7258 (1.3223)	1.5858 (1.2074)	1.4269 (1.0856)	1.2573 (0.9557)	1.0845 (0.8165)	0.8770 (0.6667)	0.6385 (0.5062)	0.3592 (0.3418)	0.0000 (0.2269)
1.00	1.7888 (1.6330)	1.6580 (1.4924)	1.5068 (1.3416)	1.3354 (1.1785)	1.1594 (1.0000)	0.9450 (0.8018)	0.7072 (0.5774)	0.4042 (0.3162)	...[d]
2.00	1.8478 (2.0908)	1.7105 (1.9266)	1.5534 (1.7510)	1.3844 (1.5614)	1.2124 (1.3540)	1.0013 (1.1244)	0.7518 (0.8672)	0.4446 (0.5826)	0.0000 (0.3587)
4.00	1.8974 (2.7386)	1.7442 (2.5527)	1.5899 (2.3570)	1.4166 (2.1483)	1.2233 (1.9235)	1.0018 (1.6794)	0.7434 (1.4142)	0.4327 (1.1359)	0.0000 (0.9129)

[a] Environmental variances for Y_{NS}, Y_{DS}, and bX are equal to genetic variance for Y_{NS}. Heritability of $Y_{NS} = 0.50$.
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments, respectively.
[c] Genetic correlation coefficient between yield in nonstress environments and loss due to disease severity X (bX).
[d] Not calculable.

TABLE 11. Aggregate genetic gain for yield in nonstress environments (Y_{NS}) and decreased yield loss (bX) due to disease severity (X) from selection for yield in a disease-stress environment (Y_{DS}) and from index selection for both traits given equal economic weight (in parentheses)[a]

Ratio:[b] V_{GbX} V_{GNS}	$r^c_{GNS,bX}$								
	−1.00	−0.75	−0.50	−0.25	0.00	0.25	0.50	0.75	1.00
0.25	1.8666 (1.3117)	1.7127 (1.2114)	1.5581 (1.1093)	1.3840 (1.0039)	1.1906 (0.8944)	0.9786 (0.7803)	0.7239 (0.6621)	0.4105 (0.5434)	0.00 (0.4372)
0.50	1.8946 (1.5055)	1.7590 (1.3763)	1.6032 (1.2443)	1.4361 (1.0056)	1.2663 (0.9574)	1.0562 (0.7968)	0.8055 (0.6207)	0.5053 (0.4295)	0.00 (0.2583)
1.00	1.9216 (1.7889)	1.7964 (1.6335)	1.6508 (1.4739)	1.4842 (1.3039)	1.3146 (1.1180)	1.1036 (0.9100)	0.8660 (0.6695)	0.5422 (0.3789)	...[d]
2.00	1.9452 (2.2039)	1.8120 (2.0302)	1.6585 (1.8500)	1.4943 (1.6563)	1.3281 (1.4434)	1.1213 (1.2043)	0.8727 (0.9292)	0.5534 (0.6091)	0.00 (0.3781)
4.00	1.9640 (2.8062)	1.8216 (2.6207)	1.6609 (2.4254)	1.4892 (2.2157)	1.2974 (1.9875)	1.0761 (1.7358)	0.8254 (1.4552)	0.4907 (1.1492)	0.00 (0.9354)

[a] Environmental variances for Y_{NS} and Y_{DS} equal one-third the genetic variance for Y_{NS} and (V_{GNS}) and the environmental variance for bX equals V_{GNS}. Heritability of $Y_{NS} = 0.75$.
[b] V_{GbX}, V_{GNS} = genetic variances for yield loss due to disease severity X (bX) and for yield in nonstress environments, respectively.
[c] Genetic correlation coefficient between yield in nonstress environments and loss due to disease severity X (bX).
[d] Not calculable.

correlation coefficients between yield and disease resistance in maize (7,11; Carson, *unpublished*) and sunflower (10) populations have been either not significantly different from zero or favorable.

In our analysis of correlated responses to selection for Y_{DS}, we varied values of heritability for yield in nonstress environments (Y_{NS}) from low (0.25) to medium (0.50) to high (0.75) by varying values of V_{ENS} and V_{EDS}. Although it is not practical to evaluate responses to selection for Y_{DS} over all possible values of the parameters in our analysis, we are encouraged that, within the ranges tested, selection for yield under disease stress would effectively select for improved yield in nonstress environments and for low losses to disease in most cases. It is also encouraging that selection for Y_{DS} in our analysis compares favorably to index selection for high Y_{NS} and low bX, without the problems inherent in the development of an effective selection index.

Rosielle and Hamblin (14) used a similar methodology to evaluate the effects of selection for tolerance to stress, which they defined as a low difference in yields between stress and nonstress environments. This would be analogous to selection for low loss due to disease (bX) in our study. The authors did not evaluate effects of selection for yield in a stress environment as we have done, and hence the differences in conclusions.

In our analysis, our basic assumption is that yield losses due to disease are a direct function of disease severity ($Y_{NS} - Y_{DS} = bX$). It could be argued that this relationship may not be linear or that

yield loss thresholds may exist, but these problems can be remedied with an appropriate transformation of disease severity data. Further, if no relationship between disease severity and yield loss exists, then the utility of selection for disease resistance (low values of X) is questionable. If, however, the lack of relationship between disease severity and yield loss is due to disease tolerance, then this method may be effective in selecting tolerant genotypes (12).

Before selection for yield in disease stress environments can be recommended as a useful method for the selection of high-yielding, disease resistance varieties, its effectiveness must be evaluated experimentally. The effectiveness of this selection in improving disease resistance also depends on the level of disease stress in the selection environment. Therefore, every effort must be made to ensure a high level of disease stress in evaluating the efficacy of this method.

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