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Effectiveness of indirect selection for wheat yield in a stress environment

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Abstract Effectiveness of indirect selection for grain yield was investigated among eight bread wheat lines, selected in a stress environment in the East African Highlands, where they showed a wide response to yellow rust, the biotic factor causing the stress. The lines were intercrossed to give an $8 \times 8 F_1$ diallel, which was grown in this same environment for three consecutive growing seasons during 1994 and 1995. Half of the last trial was sprayed with fungicide. From the estimates of narrow-sense heritabilities for yield and yellow rust severity, and the genetic correlation between them, indirect selection for yield in the unsprayed plots, obtained by choosing the most resistant 5% of this material was, on average, 12% higher than selecting for yield itself. In the fungicide-treated plots, indirect selection was only 73% as efficient as direct selection. The implications of these results for selecting for yield in stress environments are discussed.

Key words Bread wheat lines · Coheritability · Diallel cross · Direct selection · Indirect selection · Yellow rust · Yield

Introduction

The expected response (R) to direct selection for a primary character (x) is

$$R = ih^2_{\mathrm{nx}}\sqrt{V_{\mathrm{Px}}} \tag{1}$$

where i is the selection intensity, expressed in standardized units, h^2_{nx} is the narrow-sense heritability and $\sqrt{V_{\mathrm{Px}}}$ is the phenotypic standard deviation of the primary character. The correlated, or indirect, response in the primary character (CR_{x}) resulting from selection for a secondary character (y) equals

$$CR_{\mathrm{x}} = ih_{\mathrm{nx}}h_{\mathrm{ny}}\mathrm{r_A}\sqrt{V_{\mathrm{Px}}} \tag{2}$$

where h_{nx} and h_{ny} are the square roots of the narrow-sense heritabilities of x and y, and $\mathrm{r_A}$ is the additive genetic correlation between the two characters (Falconer and Mackay 1996). The term $h_{\mathrm{nx}}h_{\mathrm{ny}}\mathrm{r_A}$ is called the coheritability (Falconer and Mackay 1996) because it is equivalent to h^2_{nx} in Eq. (1). Indirect selection is rarely as effective as direct selection for the primary character (Gallais 1984). It will only be so if the secondary character has a substantially higher narrow-sense heritability than the primary character and if the additive genetic correlation between the two characters is high (Falconer and Mackay 1996), that is if $\mathrm{r_A}h_{\mathrm{ny}} > h_{\mathrm{nx}}$. Practical considerations can also influence this choice. For example, the secondary character may be cheaper and easier to measure. Consequently, it may be possible to handle larger populations of, and hence apply greater selection pressure to, the secondary character. Indirect selection may also be useful for selecting a primary character expressed late in the life cycle. Nevertheless, genetic considerations remain paramount.

In practice, indirect selection may be used in two different ways. Conventionally, selection pressure is applied to a secondary character to assess the correlated response in the primary character in that same environment. Gallais (1984) concluded from his own studies on forage maize, and other published results, that single-trait indirect selection for grain yield was no more efficient, and generally ineffective, than direct selection. Efficiency of selection for yield in rapeseed (*B. napus*), under drought stress was improved by

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constructing an index based on yield, siliquae number and flowering time (Richards and Thurling 1979), while in grain maize a combination of yield plus ear height was more effective than direct selection for yield alone (Moll et al. 1975: for details of index selection see Baker 1986). LeRoy et al. (1991) working with soybean (*Glycine max* L.) found that direct and indirect selection for small seed, by pod width, were equally effective in the temperate and tropical environments they studied. These examples indicate that a primary quantitative character may be the result of, or affected by, secondary characters as a consequence of common or sequential physiological processes.

The second, and perhaps more interesting, use of indirect selection is when the same character is measured in two different environments, as it can then be regarded for practical purposes as two different characters (Falconer and Mackay 1996). This raises the question of the choice of optimum environment for selection purposes, because genotype-environment interactions can complicate selection procedures (Jinks and Connolly 1973; Gallais 1984; Ceccarelli and Grando 1991). Cooper et al. (1997) investigated how nursery environments, structured so as to impose different levels of water and nitrogen limitation, predicted the yield of lines from the Queensland wheat breeding programme in on-farm target environments. Yield in low-stress nurseries effectively predicted yield in similar target environments, but not in target environments exposed to moderate or severe water stress. Yield in the stress nurseries was a poor predictor of yield in any of the target environments.

The investigation presented here compared the response to direct and indirect selection for yield in wheat, grown in a stress environment in the East African Highlands where yellow rust (*Puccinia striiformis* Westend.) is one of the main biotic factors limiting yield.

Materials and methods

Experimental

Eight bread wheat lines from the Uganda Wheat Development Project were chosen for this investigation. The lines were selected at Kalengyere, a location with a high incidence of yellow rust, where they exhibited a wide response to this disease (Table 1). All the parents grown in these experiments derive directly or indirectly from trials conducted by the International Maize and Wheat Improvement Centre (CIMMYT) and have, therefore, been bred for wide adaptation, including resistance to various diseases (Rajaram et al. 1996). Parents were intercrossed and selfed to give a complete 8×8 diallel, which was subsequently grown in three consecutive seasons at Kalengyere, located 2400 metres above sea level in the south western highlands of Uganda. During the trial period the average daily temperature was 16° C. Precipitation was bimodal, with relatively low rainfall (480 mm) in season (A), lasting from March to August, and high rainfall (750 mm) during season (B) from September to March. A randomized, complete block design with two replicates was used in the 1994B and 1995 A growing seasons. For the 1995B experiment a split-plot design with two replicates was employed, in which the main plots were either treated with fungicide (FT) or unsprayed controls (C). The 64 families were allocated to sub-plots. The fungicide 'FOLICUR 250 EC' was applied to the FT plots with a knapsack sprayer at Zadok's growth stages (GS)37 and 63 (Roelfs et al. 1992) at the manufacturer's recommended rate of 150 ml ha^{-1} active ingredient. Experimental plots comprised two rows of 1.5 m length and 0.3 m inter-row spacing. Spacing between plants was 0.15 m. Nitrogen was applied at planting at a rate of 50 kg ha^{-1}.

Yellow rust severity was scored on the flag leaf of individual plants when the rust on the most susceptible parent was about 100% and most of the leaf surface was covered with uredinia. Disease severity was recorded between the late milk and early dough stages (GS 77–83) using the modified Cobb scale to estimate the percentage of possible tissue rusted (Peterson et al. 1948). Host response to infection was scored using T ($=0.1$) to indicate immunity; R ($=0.2$) to indicate resistance in plants showing miniature uredinia; MR ($=0.4$) to indicate moderate resistance in plants exhibiting small uredinia; MS ($=0.8$) to indicate moderate susceptibility in plants with moderate-sized uredinia (smaller than fully susceptible type); and S ($=1$) for complete susceptibility (Wagoire 1997). Disease severity and host response scores were multiplied together to give the coefficient of

Table 1 Designation, parentage, pedigree and rust response of the parents

Code name/pedigree	Source[a]	Yellow rust reaction
1 BURI CM58340-A-1Y-3Y-2M-2Y-0 M	2ndHRWSN	Resistant
2 KENYA CHIRIKU K.TEMBO/CARPINTERO"S"	NPBRC	Resistant
3 ESDA/LIRA CM78428-017M-013M-013Y-03AL-3Y-3AL-0Y	2ndHRWSN	Resistant
4 VEE"S"/JUP73/EMU"S"//GJO"S" CM74465-05AP-300AP-4AP-300AL-0AP	RBWONLRA	Moderately resistant
5 ATTILA CM85836-4Y-0M-0Y-OPZ	4thHRWSN	Moderately susceptible
6 CY8801	5thHCWSN	Susceptible
7 F60314.76/4/CNO76/7C//KAL/BB/3/PC1"S"/5/CNO79	13thSNACWYT	Susceptible
8 CAR853/COC//VEE"S"/3/E4708/PAM"S"/HORK"S"/PK73226	13thSNACWYT	Susceptible

[a] HRWSN, High Rainfall Wheat Screening Nursery, CIMMYT, Mexico; NPBRC, National Plant Breeding Research Centre, Njoro, Kenya; RBWONLRA, Regional Bread Wheat Observation Nursery for Leaf Rust Accessions, ICARDA, Syria; HCWSN, Hot Climate Wheat Screening Nursery, CIMMYT, Thailand; SNACWYT, Screening Nursery for African Cooperative Wheat Yield Trial, CIMMYT, East Africa

infection (CI) for data analysis. Experimental plots were hand-harvested and the grain threshed, cleaned, sun-dried and weighed at approximately 12% moisture content. Yield was expressed as g m^{-2}.

Genetical

Variation between the 64 families for CI and yield was partitioned into differences between males, between females and the interaction between them. The corresponding mean cross products were also computed from an analysis of covariance between these two characters. After equating the observed mean squares and cross products with their expected values, the components of variance and covariance for males, females and males x females were calculated, from which estimates of the additive genetic (V_{A}), dominance (V_{D}), environmental (V_{EC}) and phenotypic (V_{P}) components were obtained. It can be shown that in an inbred diallel cross such as this, the components of variance have the following genetic expectations (Hill et al. 1998):

Component of variance	Genetic expectation
Between males (σ^2_{M})	$\frac{1}{2}V_{\mathrm{A}}$
Between females (σ^2_{F})	$\frac{1}{2}V_{\mathrm{A}}$
Males × females (σ^2_{MF})	V_{D}.

From these and the corresponding components of covariance the appropriate genetic, phenotypic and environmental correlations were calculated, together with estimates of narrow-sense heritability (h^2_{n}) for the two characters. Finally, the expected response to direct selection for yield (x), was estimated from Eq. (1) while the correlated, or indirect, response in yield, resulting from selection for yellow rust severity (y), was calculated from Eq. (2).

Results and discussion

Mean squares and cross products for the three unsprayed and one sprayed trial are presented in Table 2. As expected, widespread significant differences occur between males and females for both characters when rust is unchecked. The application of fungicide reduces the level of variability for CI to the extent that only differences between females remain significant, while for yield only the male effect is significant. In the unsprayed trials males and females interact significantly for CI, indicating that both additive and non-additive genetic variation exists for this character (Wagoire et al. 1998). For yield, only in the 1994B season, when disease incidence was unusually low, is there convincing evidence of non-additive genetic variation (Wagoire 1997).

Equating the mean squares and cross products to their expected values, given in Table 2, yields estimates of the genetic, environmental and phenotypic components of variance and covariance, from which the corresponding correlations and narrow-sense heritabilities can be calculated (Table 3). Expected responses to direct and indirect selection, assuming a selection

Table 2 Mean squares for the coefficient of infection (a), yield (b) and mean cross products (c), together with their corresponding expectations (d), for the F_1 diallels

Item	*df*	1994	1995		
		B	A	B(C)[a]	(FT)[b]
a					
Males (M)	7	816.62***	10 077.22***	6 692.34***	50.54 ns
Females (F)	7	1 218.73***	10 302.79***	7 804.65***	80.77*
M × F	49	97.66***	1 106.58***	680.53***	17.39 ns
Error	63	30.88	29.93	154.29	28.03
b					
Males (M)	7	48 627.85***	10 536.06***	12 930.35***	25 996.02*
Females (F)	7	42 816.31***	15 230.33***	16 928.90***	20 347.94 ns
M × F	49	6 801.29***	1 475.69*	3 302.97 ns	13 002.54 ns
Error	63	2 009.38	863.64	2 323.95	9 582.22
c					
Males (M)	7	−5 379.80	−8 798.47	−8 979.82	−353.85
Females (F)	7	−6 036.96	−11 410.43	−9 518.11	−687.74
M × F	49	−308.83	−414.65	−756.90	−165.83
Error	63	6.60	1.77	−63.76	−29.06
d[c]					
Males (M)	$\sigma^2_{\mathrm{E}} + 2\sigma^2_{\mathrm{MF}} + 16\sigma^2_{\mathrm{M}}$				
Females (F)	$\sigma^2_{\mathrm{E}} + 2\sigma^2_{\mathrm{MF}} + 16\sigma^2_{\mathrm{F}}$				
M × F	$\sigma^2_{\mathrm{E}} + 2\sigma^2_{\mathrm{MF}}$				
Error	σ^2_{E}				

ns, *, *** indicates non-significance and significance at the 5% and 0.1% levels of probability, respectively

[a] C, Control or untreated plots

[b] FT, Fungicide-treated plots

[c] σ^2_{M} = males' variance component, σ^2_{F} = females' variance component, σ^2_{MF} = males' × females' interaction component, σ^2_{E} = error (environmental) variance component

Table 3 Estimates of the genetic, environmental and phenotypic components of variance and covariance for the coefficient of infection (CI) and yield (Y) from the F_1 diallels, together with the corresponding correlations and narrow-sense heritabilities

	1994B		1995A		1995B(C)[a]		1995B(FT)[b]	
	CI	Y	CI	Y	C	Y	CI	Y
Variance component								
Additive (V_A)	115.0	4 865.1	1 135.4	1 425.9	821.0	1 453.3	6.0	1 271.2
Dominance (V_D)	33.4	2 396.0	538.3	306.0	263.1	489.5	−5.3	1 737.2
Environmental (V_{EC})	30.9	2 009.4	29.9	863.6	154.3	2 324.0	28.0	9 528.2
Phenotypic (V_P)	179.3	9 270.4	1 703.7	2 595.6	1 238.4	4 266.8	28.7	12 536.6
Narrow-sense heritability (h_n^2)	0.64	0.53	0.67	0.55	0.66	0.34	0.21	0.10
Component of covariance								
Additive	−674.9		−1211.2		−1061.5		−44.4	
Dominance	−157.7		−263.0		−225.1		−68.4	
Error	6.6		1.8		−63.8		−29.1	
Phenotypic	−826.1		−1472.5		−1350.4		−141.8	
Correlations								
Additive (r_A)	−0.90		−0.95		−0.97		−0.51	
Dominance (r_D)	−0.56		−0.65		−0.63		–	
Environmental (r_E)	0.03		0.01		−0.11		−0.06	
Phenotypic (r_P)	−0.64		−0.70		−0.59		−0.24	

[a] C, Control or untreated plots

[b] FT, Fungicide-treated plots

Table 4 Direct (D) and indirect (I) response in yield (g m^{-2}) to 5% selection intensity, together with trial means for the coefficient of infection (CI) and yield for the F_1 diallels

	1994B		1995A		1995B(C)[a]		1995B(FT)[b]		Average of unsprayed trials	
	D	I	D	I	D	I	D	I	D	I
	104.3	104.0	57.7	60.5	45.9	62.2	23.4	17.1	65.1	73.2
Mean CI	7.90		30.17		24.48		2.29		20.85	
Mean yield	143.06		54.59		113.54		396.11		103.73	

[a] C, Control or untreated plots

[b] FT, Fungicide-treated plots

intensity of 5% ($i = 2.063$; Falconer and Mackay 1996), are shown in Table 4. In the three unsprayed trials, indirect selection for yield is expected to be at least as effective, and in two of these trials, more effective than direct selection. Averaged across the three trials, response to indirect selection is approximately 12% higher than direct selection. The reasons for this success are the high additive genetic correlation between the two characters, combined with the higher narrow-sense heritability of the secondary character, particularly in the control plots of the 1995B trial when indirect selection is most effective. It is also apparent from Table 4 that the season in which indirect selection is least effective, relative to direct selection, (1994B), coincides with an unusually low incidence of the disease. This suggests that the greater the stress, the more effective indirect selection for yield may be. By comparison, in the sprayed trial, indirect selection is only 73% as effective as direct selection.

Overall response to direct and indirect selection for yield was also calculated from a combined analysis of variance of the three unsprayed trials at Kalengyere. This gave an additive genetic correlation of less than −1.00 and narrow-sense heritabilities of 0.504 for CI and 0.302 for yield. Assuming an r_A value of −1.00 and a selection intensity of 5%, indirect selection was 29% more effective than direct selection, with the respective gains being 59.0 and 45.6 g m^{-2}.

A stress environment represents an extreme environment in which the genetic architecture displayed by yield will be that of a character exposed to directional selection, with additive genetic variation predominating (Jinks et al. 1973; Mather 1973). Indeed, this has already been established from a more detailed study of the inheritance of yield in this material at this location (Wagoire et al. in press). Consequently, there is a prospect of a high genetic correlation between yield (x) and tolerance to the stress factor (y), one of the pre-conditions which favours indirect selection. Furthermore, it may be still worthwhile considering indirect selection, even if the narrow-sense heritability of the secondary character only equals that of yield. Relative to direct selection the correlated response would then equal the genetic correlation for a given value of *i*. Tolerance to the stress factor can be assessed earlier in the growing season, is usually more accurately measured and may be less susceptible to genotype-environment interactions than yield. Moreover, some reduction in the effectiveness of indirect selection can often be compensated for by growing larger populations and hence increasing the selection intensity on the secondary character. Thus, if indirect selection is only 75% as effective as direct selection, selection intensity would have to be raised from 2.063 to 2.751, assuming an initial selection pressure of 5%. This is approximately equivalent to a 1% selection pressure, which is not impractical. There are, therefore, a number of genetical and practical reasons why indirect selection for yield may be feasible in a stress environment. It could be more effective, particularly when cyclical or recurrent selection are being practiced, while available resources may be more efficiently utilized.

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