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Cross prediction in bread wheat germplasm using single seed descent lines

J. Hill, W.W. Wagoire[1], R. Ortiz* & O. Stølen
*Department of Agricultural Sciences, The Royal Veterinary and Agricultural University, 40 Thorvaldsenvej, DK-1871 Frederiksberg C, Copenhagen, Denmark; [1]P.O. Box 1805, Mbale, Uganda; *author for correspondence: ICRISAT, Patancheru 502 324, Andhra Pradesh, India*

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Summary

Populations of F_6 recombinant inbred lines, generated by single seed descent from a half diallel among eight bread wheat lines adaptcd to the East African highlands, were used to identify those crosses that were more likely to produce cultivars which combined resistance to yellow rust with improved yield. Crosses having the most resistant line as one parent offered the best prospect of success, particularly those which produced F_1 hybrids exhibiting better parent heterosis. For plot grain yield there was a highly significant correlation between the observed and predicted rankings of the recombinant inbred line populations for the proportion of individual lines equalling or surpassing the target value. For yellow rust severity, however, this correlation was non-significant when a target value of zero was used. Adopting a slightly less stringent target of 0.25, coupled with the omission of two aberrant populations, increased this correlation significantly. The plant breeding implications of these results are discussed.

Introduction

Cross prediction for use in inbreeding species was first described by Jinks & Perkins (1972) and Jinks & Pooni (1976). The technique assumes that the character in question varies continuously and is normally distributed, with a mean and a standard deviation s. Regardless of whether the resultant recombinant inbred lines (RIL) are produced by conventional pedigree inbreeding, single seed descent (SSD) or dihaploidy (DH), the proportion expected to equal or exceed a specified target value (T) can be calculated from the normal probability integral corresponding to the standardized difference between T and $\bar{x}$, that is

$$(T-\bar{x})/\sqrt{S_B^2} \, or \, (\bar{x}-T)/\sqrt{S_B^2},$$

depending on whether the prediction is for higher or lower values than the target. It can be shown that S_B^2, the between lines component of variance, equals the additive genetic component of variation (Σa^2, Kearsey & Pooni, 1996; Hill et al., 1998), while, in the absence of epistasis and linkage disequilibria, $\bar{x}$ is equal to the mid-parent value (m) of the two parents in the original cross.

Despite the guidance cross prediction can provide to breeders in assessing the relative merits of their crosses, it has not been widely used in practice. In part this was because, in its original version, generations had to be produced which were not normally required in a breeding programme (Snape, 1997). Various modifications have therefore been suggested to make cross prediction more user friendly for plant breeders. Assuming that dominance and other non-additive sources of genetic variation are small, particularly in relation to the additive variation, simplifies matters considerably. Estimates of the requisite parameters can then be calculated from early generations in the selfing series (Jinks & Pooni, 1980; Kearsey, 1993; Hill et al., 1998), generations which are routinely produced during the breeding and selection of inbreeding crops. Snape (1997) has also shown how DH lines can provide the information required for prediction purposes. Here SSD lines are used to identify those crosses from which potential bread wheat (*Triticum aestivum*) cultivars adapted to the East African highlands could be developed.

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

Code name/pedigree		Source*	Yellow rust reaction
1	BURI	2nd HRWSN	Resistant
	CM58340-A-lY-3Y-2M-2Y-0M		
2	KENYA CHIRIKU	NPBRC	Resistant
	K. TEMBO/CARPINTERO ‘S’		
3	ESDA/LIRA	2nd HRWSN	Resistant
	CM78428-017M-013M-013Y-03AL-3Y-3AL-0Y		
4	VEE‘S’/JUP73/EMU‘S’//GJO‘S’	RBWONLRA	Moderately resistant
	CM74465-05AP-300AP-4AP-300AL-0AP		
5	ATTILA	4th HRWSN	Moderately susceptible
	CM85836-4Y-0M-0Y-OPZ		
6	CY8801	5th HCWSN	Susceptible
7	F60314.76/4/CNO76/7C//KAL/BB/3/PCI‘S’/5/CNO79	13th SNACWYT	Susceptible
8	CAR853/COC//VEE‘S’/3/E7408/PAM‘S’/HORK‘S’/PF73226	13th SNACWYT	Susceptible

RWSN	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.

Materials and methods

Eight bread wheat lines from the Uganda Wheat Development Project were chosen for this investigation. These lines were selected at Kalengyere, a marginal wheat growing environment in the south western highlands of Uganda regularly exposed to severe biotic stress caused by yellow rust (*Puccinia striiformis*). The pedigree of these lines, together with their response to yellow rust, is shown in Table 1.

The eight lines were intercrossed in a half diallel mating design to give 28 F_1 hybrids, from 20 of which 279 F_6 RIL were produced by SSD (Brim, 1966). The number of RIL from each hybrid ranged from 10 to 31. Although the RIL were produced in a rust-free environment, most of the missing lines were from crosses between susceptible parents (Table 2). Indeed, of the RIL actually generated none came from crosses between two susceptible parents. Apart from the RIL, the trial also included parents and F_1 hybrids. The trial was conducted at Kalengyere using a randomized block design with two replicates. Each plot comprised two rows 1.5 m long, with inter-row spacing of 0.3 m, and spacing between plants within rows of 0.15 m. Nitrogen was applied at planting at a rate of 50 kg ha^{-1}.

Two characters were recorded, yellow rust severity and plot grain yield (g m^{-2}). Yellow rust was scored on the flag leaf of individual plants when its severity on the most susceptible parent was about 100%, i.e., most of the leaf surface was covered with uredinia. The modified Cobb scale (Peterson et al., 1948) was used for scoring the percentage of possible tissue rusted (disease severity). Host response to infection was scored using T (= 0.1) for immune plants; R (= 0.2) for resistant plants showing miniature uredinia; MR (= 0.4) for moderately resistant plants exhibiting small uredinia; MS (= 0.8) for moderately susceptible plants with moderate sized uredinia (smaller than the fully susceptible type); and S (= 1) for fully susceptible plants. Disease severity and host response scores were multiplied together to give the coefficient of infection (CI) for data analysis. Whole plots were hand harvested, threshed, cleaned, sun-dried and the grain weighed at approximately 12% moisture content.

Analyses of variance were conducted on the parents and within all RIL populations for both characters. For each RIL population the between lines component of variance (S_B^2), calculated from the expectation of mean squares, equals ${}^{15}/_{16}\ \Sigma a^2 + {}^{15}/_{1024}\Sigma d^2$ (Hill et al., 1998), where Σa^2 is the additive and Σd^2 is the dominance component of genetic variation. For all practical purposes, therefore, S_B^2 measures additive genetic effects, as the dominance component may be safely ignored. Two target values were chosen for CI, zero (i.e. T = 0), indicating plants showing no visible

Table 2. Mean coefficient of infection of yellow rust and grain yield (g m^{-2}, emboldened). F_1 data in the rows above the leading diagonal; RIL data in the columns below the leading diagonal

Parent	1	2	3	4	5	6	7	8	Parental mean
1		0.50	2.15	1.10	2.10	3.00	4.00	12.00	0.25
		178.00	**163.27**	**97.15**	**95.53**	**94.60**	**66.30**	**54.37**	**130.00**
2			0.10	1.90	1.40	1.40	2.00	3.00	0.20
			112.07	**74.18**	**97.67**	**162.03**	**118.70**	**115.27**	**103.67**
3	24.44	14.59		0.20	0.60	1.20	0.50	0.50	0.00
	55.90	**83.09**		**334.00**	**183.47**	**143.53**	**129.70**	**190.80**	**150.87**
4		0.88	0.62		38.00	9.41	45.04	23.00	5.00
		99.51	**131.87**		**108.33**	**151.10**	**63.60**	**57.27**	**131.90**
5	36.86	18.00	17.24	16.80		30.00	23.00	70.00	19.50
	33.65	**69.65**	**95.17**	**81.29**		**58.23**	**72.77**	**25.70**	**91.77**
6	9.98	15.56	5.17	9.67	29.01		70.00	50.00	45.00
	75.21	**74.20**	**108.14**	**92.34**	**40.34**		**27.73**	**54.50**	**53.00**
7	6.80	19.65	50.24	9.74				70.00	35.00
	119.57	**96.40**	**21.91**	**94.43**				**10.53**	**16.63**
8		22.59	1.42	2.39					70.00
		62.41	**93.40**	**142.42**					**4.83**

symptoms of yellow rust, and a more realistic value of 0.25, the CI value of line 1 (Table 2). For the former the normal probability integral, from which the proportion of individual lines within an RIL population having a target CI value of zero is calculated, reduces to $\bar{x}/S_B$. The yield of parent 3 (150.87 g m^{-2}) was chosen as the target for this character.

Results and discussion

Means of both characters for all generations are presented in Table 2. Analyses reveal that parental differences are significant for both characters (data not shown). We can therefore conclude that additive genetic variation exists among these parents for CI and grain yield. From the F_1 data presented in Table 2 there is a discernible genetic pattern for CI. All crosses based on the resistant lines 1, 2 or 3 have low CI values. Susceptible progeny are only produced when both parents are susceptible. Crosses from array 4, the moderately resistant line, show a range of CI values. Clearly in this material resistance to yellow rust is dominant to susceptibility (see also Wagoire et al., 1998). Although a strong negative genetic correlation exists between CI and yield at Kalengyere (Hill et al., 1999), there are individual F_1's which combine relatively low yield with resistance (e.g. 2 × 4), while others are comparatively high yielding and susceptible (e.g. 4 × 5).

Cross predictions for each RIL population are set out in Table 3. No calculations are shown for those where the between lines mean square is non-significant. For CI there is apparently little to choose between the RIL populations generated here, with all populations having a significant between lines mean square expected to contain 10% or more of individual lines with no visible disease symptoms. By contrast, only four RIL populations are predicted to contain more than 10% of individual lines with a plot grain yield equal to or surpassing the target. From Table 2 the RIL population derived from the cross between the moderately resistant line 4 and the most susceptible line 8 apparently offers greatest scope for producing high yielding individual lines. But the high replicate interaction shown by the RIL within this population renders the between lines mean square non-significant.

From a breeding point of view interest in prediction methods centres on whether they can rank a series of crosses correctly, rather than on the actual proportion expected to equal or surpass a specified target value. The efficacy of the approach used here was tested by ranking the observed and expected proportions of lines within each RIL population equalling or surpassing T (Table 3), and calculating Spearman's

Table 3. Percentage F_6 SSD lines expected (% E) and observed (% O) to equal or surpass the target value (T) for yellow rust severity (CI) and plot grain yield (g m^{-2})

Cross	CI (T = 0)				(T = 0.25)		Grain yield (T = 150.87)			
	$\bar{x}$	S_B	% E	% O	% E	% O	$\bar{x}$	S_B	% E	% O
1 × 3	24.44	18.93	9.9	4.8	10.0	9.5	55.90	36.65	0.5	0.0
1 × 5	36.86	–	–	–	–	–	33.65	28.39	<0.1	0.0
1 × 6	9.98	14.70	24.8	14.3	25.4	28.6	75.21	55.10	8.5	14.3
1 × 7	6.80	5.97	12.7	0.0	13.6	8.3	119.57	–	–	–
2 × 3	14.59	17.99	20.9	15.4	21.2	23.1	83.09	44.15	6.2	15.4
2 × 4	0.88	0.99	18.6	10.5	26.1	52.6	99.51	–	–	–
2 × 5	18.00	16.77	14.1	6.3	14.4	25.0	69.65	40.73	2.3	0.0
2 × 6	15.56	–	–	–	–	–	74.20	58.62	9.1	16.7
2 × 7	19.65	–	–	–	–	–	96.40	64.24	19.8	18.2
2 × 8	22.59	19.41	12.3	0.0	12.5	10.0	62.41	–	–	–
3 × 4	0.62	0.72	19.3	27.2	30.3	54.5	131.87	49.57	35.1	18.2
3 × 5	16.94	24.25	24.2	6.5	24.6	35.5	95.17	52.13	14.3	12.9
3 × 6	5.17	4.10	10.3	8.3	11.1	33.3	108.14	57.25	22.7	25.0
3 × 7	50.24	–	–	–	–	–	21.91	–	–	–
3 × 8	1.42	1.42	15.9	18.2	20.7	36.4	93.40	39.37	7.2	9.1
4 × 5	16.80	18.89	18.7	0.0	19.0	0.0	81.29	38.15	3.4	8.3
4 × 6	9.67	15.53	26.6	0.0	27.0	0.0	92.34	33.50	4.0	6.7
4 × 7	9.74	7.85	10.7	11.8	11.3	17.6	94.43	–	–	–
4 × 8	2.39	3.78	26.3	20.0	28.5	40.0	142.40	–	–	–
5 × 6	29.01	22.55	9.9	9.1	10.1	9.1	40.34	35.32	0.1	0.0

rank correlation (r_s) between them. For plot grain yield $r_s = 0.934^{***}$, indicating close agreement between the observed and expected rankings. Which is more than can be said for the CI rankings when T = O, because $r_s = 0.260$ when all RIL populations are included. For the slightly less stringent target of 0.25, $r_s = 0.507^{*}$, which, though significant, is of little predictive value. Inspection of these data reveals two notable shortfalls in the observed proportions, namely for populations 4 × 5 and 4 × 6, where none of the individual lines reaches the target value (Table 3). Omitting these two populations increases r_s to 0.789^{***}. The non-significant correlation between the observed and expected rankings recorded for the extreme target value of zero could be due to sampling error. Such lines are, by definition, least likely to occur. There is also the possibility that the discrepancy could be due to the segregation of major genes for yellow rust resistance. Although we are not aware of the existence of such genes in this material, their effect on the prediction techniques is likely to be minimal unless the distribution of recombinant inbred lines becomes markedly non-normal.

Lawrence & Senadhira (1998) recommend a three stage strategy for the development of potential cultivars where the end products of a breeding programme are inbred lines. In the first stage those F_1 progeny exhibiting better parent heterosis are identified. Heterosis is more likely to arise from crosses between superior inbreds differing for a minority of the genes controlling the character, providing these genes exhibit directional dominance. Those F_1's displaying better parent heterosis could then be used to develop hybrid cultivars, where these are economically feasible. In any event these progeny would be selfed to produce the F_3 generation, from which the genetic information required to identify those crosses most likely to produce superior F_6 RIL can be obtained. When greater selection efficiency is the goal, the F_3 generation may be used as the starting point for generating RIL, as advocated by both Snape (1997) and Lawrence & Senadhira (1998; but see Caligari et al., 1986). Here, three crosses in particular – 3 × 4, 3 × 5 and 3 × 8 – display better parent heterosis for plot grain yield. Since line 3 is also the most resistant to yellow rust it would appear that RIL having this line as one parent offer the best prospect of produ-

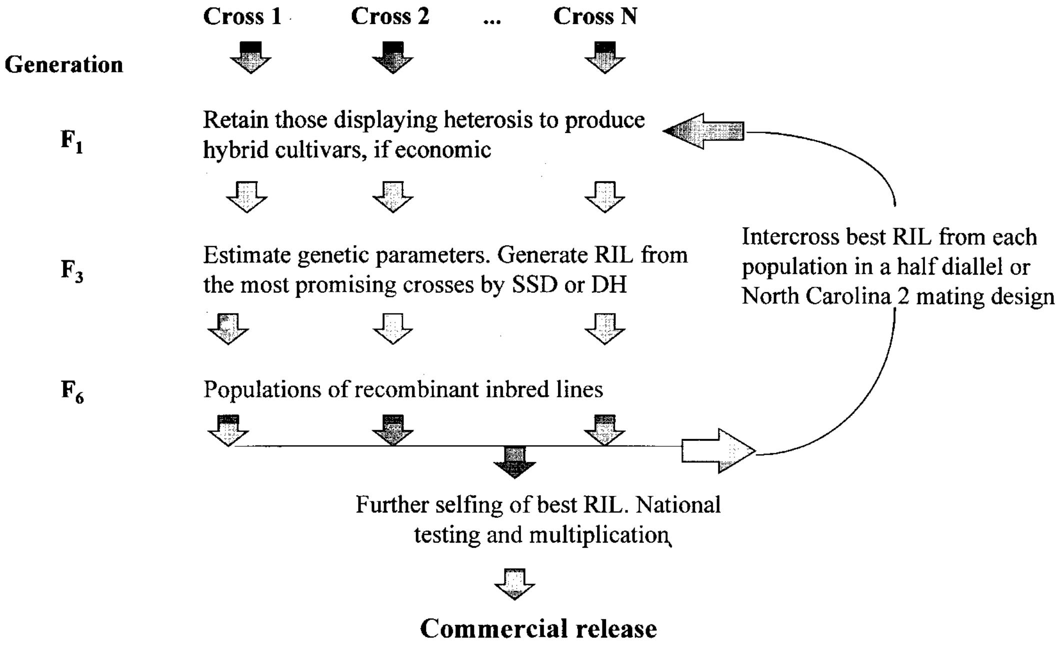

Figure 1. Diagrammatic representation of a breeding strategy for inbreeding species using recombinant inbred lines (RIL) developed by single seed descent (SSD) or dihaploidy (DH).

cing cultivars from this material adapted to rust-prone environments in the East African highlands.

Lawrence & Senadhira (1998) proposed their breeding strategy as a means for improving the yield of modern *indica* cultivars of rice. Since there is no shortage of additive genetic variation in these cultivars, they believe that the inability of breeders to breach a potential yield barrier of 10 t ha^{-1} is partly due to the use of inefficient early generation selection procedures (Lawrence & Senadhira, 1998). Evidence is now accumulating that early generation selection is not the best strategy for improving the expression of continuously varying characters in inbreeding crops (Jinks & Pooni, 1981). Extending the notion that superior RIL can be developed from heterotic F_1's, Lawrence & Senadhira's approach can be regarded as the first stage in a continuous process of improvement, which is after all what plant breeding is. Thus, those superior F_6 RIL selected as potential cultivars could be plugged into a second cycle of selection. Assuming that several RIL populations have been generated, the best individual line from each population could be intercrossed in a half diallel arrangement to identify heterotic F_1's. Admittedly the workload increases with each additional parent for this mating design, but so does the number of F_1 hybrids generated. If only two F_6 RIL populations are retained, the top lines from one population could be crossed with the best from the other population in a North Carolina 2 design, again to identify heterotic F_1's. In Uganda, however, it would be unwise to concentrate on the production of hybrid cultivars of wheat. It would be uneconomic and impractical, and would waste resources that could be better deployed in generating RIL. The main features of this approach, which is essentially an extension of Lawrence & Senadhira's proposal, are presented in Figure 1. Material could be cycled through this scheme for as long as progress is being made, taking care to ensure that the genetic base is not narrowed unduly.

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