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The effect of combining scald resistance genes on disease levels, yield and quality traits in barley

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Abstract Pairwise combinations of genes for resistance to scald in barley were developed using linked isozyme markers to test whether such combinations conferred improved resistance to the pathogen, *Rhynchosporium secalis*. The resistance genes originally derived from *Hordeum vulgare* ssp. *spontaneum*. The combinations were bred into an essentially similar genetic background because the scald-susceptible, Australian barley cultivar 'Clipper' was the recurrent backcross parent in their ancestry. In field tests of the recombinants over 2 years, disease levels were lower in three of six doubly resistant lines than in backcross lines carrying a single resistance gene, which in turn were less diseased than either 'Clipper' or recombinants that lacked the marked resistance genes. All resistant lines significantly outyielded 'Clipper' but did not themselves differ significantly. Lines resistant to scald had significantly higher grain size and grain weight. Gains for malt yield of about 1% were detected in the higher disease environment. Resistance was not accompanied by any obvious "cost" in terms of yield or quality. Protection against scald is therefore a significant requirement for new malting barley cultivars in scald-prone areas.

Key words Pyramiding · *Hordeum vulgare* ssp. *spontaneum* · *Rhynchosporium secalis* · Backcross lines · Isozyme marker genes

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Introduction

Scald is one of the more damaging leaf and stem diseases of barley when the crop is grown over winter in areas with winter rainfall. The great diversity in pathogenicity of its casual agent, the fungus *Rhynchosporium secalis* (Shipton et al. 1974; Ali et al. 1976; Brown 1985; 1990; Goodwin et al. 1990), and the tendency for field resistance to scald in new cultivars to lessen with time hampers control of the disease. One possible way to increase the durability of resistance to scald is to combine or "pyramid" different resistance genes together into a single cultivar (McDonald et al. 1988). However two issues immediately arise in adopting such a strategy. The first is the difficulty of recognizing the presence of different resistance genes when manipulating them in a crossing program. The second issue concerns whether a yield penalty attends an increase in the number of resistance genes in a cultivar. Closely linked gene markers supply an ideal solution to the first issue (Melchinger 1990; Haley et al. 1994; Adam-Blondon et al. 1994), whereas the second issue can only be addressed in replicated field trials of specific comparable stocks (Pedersen and Leath 1988).

The wild progenitor of barley (*Hordeum vulgare* ssp. *spontaneum*) is a rich source of genes for scald resistance, with major genes located on at least four different chromosomes (Abbott et al. 1992). Further, wild barley is a rich source of molecular polymorphisms (Brown 1991), some of which are linked to these resistances (Abbott et al. 1992, 1995). These linked polymorphisms make it possible to combine several different resistances and to test for improved durability of resistance in the field. However, some previous combinations of isozyme-marked segments from wild barley in backcrosses can give unfavorable epistasis for yield (Brown et al. 1988). These early combinations were planned on other bases than to contain multiple resistance to scald. We therefore developed a new set of F_3 families from crosses between scald-resistant BC_3 lines. The families were

selected to carry different numbers of wild barley-derived isozyme marker genes and hence also to possess different numbers of scald resistance genes as well, in an otherwise relatively common genetic background. This paper reports the field performance of these lines with respect to disease levels, yield and malting quality.

Materials and methods

A set of backcross (BC_3) lines was derived from crossing accessions of *H. spontaneum* with barley cultivar 'Clipper' and backcrossing thrice to 'Clipper' while selecting only for a specific wild barley isozyme marker (Brown et al. 1988). Thus, the lines were approximately 90% recurrent parent. The segment of wild genes surrounding the isozyme locus is expected to comprise about 50% of remaining genome that forms the total remaining from the nonrecurrent donor (Brown et al. 1989). By chance, several of these BC_3 lines were resistant to scald when tested as seedlings under glasshouse conditions (Abbott et al. 1991, 1992). Further, the resistance genes were linked to the selected donor isozyme in several BC_3 families. The barley chromosome locations of these resistances (with the equivalent homoeologous Triticeae H-designations) and recombination frequencies between the isozyme loci and the resistance genes of the parental lines in this study are presented in Table 1.

Pairs of resistant lines were crossed, and F_2 individuals double-homozygous for various isozyme alleles were isolated and multiplied for field testing at Wagga Wagga, New South Wales, a district where scald is common on barley crops. The particular crosses were: BC30 × BC35; BC30 × BC53; BC35 × BC53; BC35 × BC59; BC11 × BC200; and BC30 × BC200. From the cross between BC lines 30 and 35, all four possible double-homozygous classes were selected. From the other crosses, only the double homozygotes for the *H. spontaneum* allozyme markers were isolated. In each case 4 or 5 separate lines were isolated. In 1992, the yield trial included four different parental BC_3 lines along with 32 recombinant lines from four crosses among them. The 1993 trial included five parental BC_3 lines and 37 recombinant lines from five crosses. The trial sites were in a barley-growing district on acid clay loam following a grazed oat crop that had been ploughed in the previous spring. Sowing dates were 15 May 1992 and 7 June 1993. Each trial had three replicates arranged in three sections in 1992 and six sections in 1993, with two-dimensional neighbor analysis balanced designs. Plot size was seven rows × 10m. Fertilizer and herdicide were applied at standard rates. As the 1993 site carried a high load of take-all (*Gaemannomyces graminis* var *'tritici'*) inoculum, the seed was sown with a biocontrol agent.

Scald disease levels were assessed as percentage leaf damage on three occasions during the growth of the crop over 42 days in 1992, and four times over 71 days in 1993. Twenty random plants were scored in each plot. The averages of these individual scores were integrated over the season to measure the overall level of disease, expressed as the Area Under the Disease Progress Curve (AUDPC) as outlined elsewhere (Abbott et al. 1991). Plots were machine-harvested for yield measurement. For quality assessment, samples from the 1992 trial were harvested by hand from each plot in two replicates because the plots were lodged. The 1993 grain for quality assessment came directly from the machine-harvested seed. Plot yield data were analyzed by TwoD (Cullis and Gleeson 1991).

Grain samples were measured for the following properties: 1000-grain weight; grain size as the percentage remaining after screening through a sieve of 2.5 mm; and grain protein as percentage fresh weight. Malting quality parameters were measured on a sample of grain retained above a 2.2-mm screen. Grain protein and moisture content were determined on ground barley by near infra-red reflectance using calibrations developed previously (Glennie Holmes 1991). Micromalting was carried out in a computer-controlled micromalter (Glennie Holmes et al. 1990) using 40-g samples. Malt yield was measured and expressed as a percentage dry weight of the malted grain; fine hot water extract (FHWE) was determined using the EBC procedure modified for test-tube mashing (Glennie Holmes unpublished) and expressed as extract percentage of total soluble solids on a dry weight basis. Free alpha amino nitrogen (FAAN) in the FHWE was determined using the method detailed in Analytica-EBC (1975) and expressed in milligrams per liter. Diastatic power (DP) in millimoles per second per kilogram, a combined indicator of alpha- and beta-amylases, alpha-glucosidase and limit dextrinase, was measured using Henry's method (1984) on a 1.0-g sample of the malt ground as for the FHWE. Standard errors for line means were computed from analysis of variance of plot values.

Table 1 Chromosomal location, linked isozyme marker and recombination fraction of scald resistance loci in each of the six 'Clipper' third-backcross (BC_3) lines in this study (see Abbott et al. 1992)

Backcross line	Barley chromosome	Isozyme locus	Recombination
BC11	4 (4H)	*Acp 2*	0.07
BC30	6 (6H)	*Dip 1*	0.29
BC35	4 (4H)	*Acp 2*	0.18
BC53	3 (3H)	*Est 2*	0.33
BC59	4 (4H)	*Acp 2*	0.35
BC200	1 (7H)	*Est 5*	0.15

Results

Parental lines

Table 2 lists the means for the field response to disease, yield, grain and malting quality characters for the six scald resistant, parental BC_3 lines and the control recurrent parent 'Clipper' for both 1992 and 1993. In both years, the susceptible cultivar 'Clipper' developed substantial levels of disease; values for AUDPC in 'Clipper' exceeded 1600, implying a seasonal average of 40% and 25% leaf area damaged in 1992 and 1993 respectively. However, values of AUDPC are cumulative figures essentially for comparison among lines within a single experiment. As such, they do not fully reflect the fact that the scald epidemic was noticeably more severe in the 1992 trial than in the 1993 trial.

Five of the six resistant backcross lines repeated their disease response of earlier trials (Abbott et al. 1991). The exception was BC-line 200 in which the resistance appeared to be ineffective in the year it was included. The AUDPC was consistently lowest in BC-line 30. Scald resistance in BC-line 59 was only moderate. The field responses to scald in the set of seven experimental lines thus constitute a range of reactions, from susceptible 'Clipper' to the strong resistance of BC-line 30.

Grain yields in the resistant backcross lines exceeded those of the susceptible cultivar, in most cases significantly. The comparison of 'Clipper' with the resistant backcross parents indicated that disease reduced yields by about 30% in 1992 and about 15% in 1993, which are margins similar to those published previously (Abbott et al. 1991). Scald damage also lowered malting quality, first by reducing grain size. In 1992, the heavy level of scald disease on 'Clipper' resulted in about 50% of the grain by weight being unacceptably small (passing

Table 2 Scald disease level (AUDPC), yield, grain and malting quality characters for the recurrent parent 'Clipper' (Cl) and six scald resistant third-backcross lines

	Cl	11	30	35	53	59	200	Average SE
AUDPC	1710[a] a		110 d	280 c	160 cd	1020 b		80
	1600 a	360 bc	80 d	590 c	110 cd		1670 a	110
Yield (tph)	2.6 a		4.2 bc	4.0 bc	4.4 c	3.5 b		0.2
	3.3 a	3.6 ab	3.5 ab	4.3 b	4.1 b		3.8 b	0.3
Grain size (%)	49 a		76ab	89 b	91 b	73 ab		7
	87	84	77	89	87		80	2.5
Grain weight (g)	37.6 a		43.3 b	44.9 b	46.7 b	43.2 b		1.3
	42.6 a	42.9 a	43.9 ab	48.0 c	46.4 c		45.7 bc	0.6
Grain % protein	14.9 a		15.6 a	13.8 b	14.4 ab	15.1 a		0.25
	13.1	14.1	13.9	13.2	13.9		14.2	0.6
Malt yield (%)	92.4 a		93.4 b	92.6 ab	92.5 a	93.5 b		0.3
	88.9	89	88.9	88.4	88.7		88.9	0.6
FHW extract	75 ab		73 a	76 b	77 b	73 ab		0.7
	79	79	77	80	81		79	1.7
Free alpha amino N	109		108	109	117	108		8
	112 a	115 a	127 ab	126 ab	145 b		118 a	5
Diastatic power	5.3		5.5	5.9	5.4	5.2		0.6
	7	8.5	7.7	7.5	7.2		6.7	0.5

[a] The values for the 1992 trial are given above those for the 1993 trial. Values within rows with different letters are significantly different

through a 2.5 mm sieve). Second, disease lowered malting quality by reducing grain weight, which was about 15% lower in 'Clipper' than in the resistant lines in 1992. Disease also reduced grain weight in 1993, but only by about 7%.

The remaining characters listed in Table 2 were assessed on samples of acceptably large screened grain, the same screening that occurs in the malthouse. They generally showed very few statistically significant differences that were related to disease status. For example, BC-line 53 appeared to have a higher level of free alpha-amino nitrogen than 'Clipper' but other resistant lines had values similar to 'Clipper'. The overall conclusion is that disease level had little direct effect on the biochemical malting quality parameters *per se*. Rather, its major effect was to reduce both the proportion of grain of acceptable size for malting, on top of its lowering of the total yield of grain. Thus, in a year of high scald, the loss of malt per acre due to disease could exceed 60%.

Recombinant lines

Disease

Table 3 lists the means of the nine disease, yield and quality variables for the nine sets of progeny (recombinant) lines. The lines are doubly homozygous for various isozyme markers linked to different resistance genes that were selected from the F_2 generation of the six crosses. In both years the average level of disease (AUDPC) differed among the lines according to marker genotype. The group of lines that were homozygous for both *H. spontaneum* allozymes in the cross between BC30 and BC35, and therefore likely to carry two resistance genes, had less disease damage in both years than had the comparable reconstituted single gene lines (30 + Cl, Cl + 35; Table 3). The relative performance of these two reconstituted single lines (Table 3) paralleled that of the parents (Table 2) in that the gene in BC30 gave greater protection than that in BC35. On average, leaf damage in the reconstituted singly resistant lines exceeded that of their parent BC line. Similarly, disease in the reconstituted susceptible lines (Table 3) was less than in 'Clipper' (Table 2). Both these effects were presumably due to recombination between the resistance loci and the loosely linked isozyme tags that were used to select the resistances. From this, we infer that the performance of the double *H. spontaneum*-isozyme homozygotes underestimates that of the truly isogenic, doubly resistant lines that are potentially extractable from each cross.

As the comparable reconstituted single-gene lines were not isolated from the other five crosses, the level of disease in their combinations of resistances could not be strictly gauged in relation to the single resistances. However, comparisons are available with the AUDPC values of the parental lines (Table 2). In only two cases (30 + 53 in 1992 and 11 + 200 in 1993) out of seven tests did the combinations have less disease than their more resistant parent. Lowered resistance on average in sets of doubly resistant lines, relative to the original parents, could be due to the occasional recombination between isozyme marker and resistance gene during their synthesis.

Table 3 Scald disease level (AUDPC), yield, grain size and malting quality for various recombinant lines from six crosses between scald resistant backcross lines

	Cl[a] + Cl	Cl[a] + 35	30 + Cl[a]	30 + 35	30 + 53	35 + 53	53 + 59	11 + 200	30 + 200	Average SE
Number of lines	5	5	5	5	4	4	4	5	4	
AUDPC	1360[b] a	440 bc	260 cd	50 d	90 d	360 bc	760 b			130
	1300 a	590 b	260 cd	180 cd	80 d	410 bc		180 cd	320 bc	110
Yield	2.9 a	4.0b	4.0 b	4.2 b	4.2 b	4.2 b	3.6 b			0.18
(tph)	3.2 a	3.5 ab	3.5 ab	3.6 ab	4.0 b	4.0 b		3.4 ab	3.5 ab	0.16
Grain	43 a	74 b	69 b	73 b	70 b	79 b	71 b			5.3
size (%)	84 bc	84 c	79 b	77 b	79 b	85 c		88 c	70 a	1.4
Grain	35.2 a	40.1 b	40.4 b	41.3 b	41.6 b	42.2 b	40.4 ab			1.3
weight (g)	42.6 a	42.9 ab	43.7 ab	43.5 ab	44.5 b	44.9 b		47.7 c	44.8 b	0.5
Grain %	15.2 a	14.5 ab	15.1 a	15.0 ab	15.1 a	13.8 b	14.2 ab			0.31
protein	14.0 bc	14.0 bc	14.8 a	14.1 b	14.6 a	13.3 c		14.1 b	14.7 b	0.23
Malt (%)	91.4 a	92.4 bc	92.4 bc	93.0 d	92.9 cd	91.8 ab	92.8 bcd			0.24
yield	88.7	88.7	88.8	88.7	89.0	88.0		88.8	89.1	0.15
FHW	74.9 bc	75.3 ab	74.1 bc	73.8 bc	74.5 bc	77.8 a	76.5 a			0.48
extract	78.2	77.9	77.4	77.1	77.9	79.4		77.3	77.1	0.44
Free alpha	113 a	105 ab	108 a	95 b	102 ab	110 a	107 a			4.1
amino N	126 ab	126 ab	129 ab	120 bc	126 ab	133 a		111 c	120 bc	3.4
Diastatic	6.2 a	5.6 ab	5.9 ab	5.3 b	5.5 ab	6.1 ab	5.6 ab			0.3
power	7.1 b	7.7 b	7.8 b	7.2 b	7.3 b	7.4 b		8.6 a	7.6 b	0.2

[a] The abbreviation Cl signifies the lines that have the 'Clipper' isozyme genotype for a specific locus, whereas the number indicates the wild isozyme genotype from that specific parent

[b] The values for the 1992 trial are given above those for the 1993 trial

Yield

Of the nine possible means for doubly marked and likely doubly resistant lines in Table 3, six had an average yield that significantly exceeded that for the reconstituted susceptible. Indeed, in neither year was there a significant reduction of yield (relative to singly resistant lines) in lines carrying a double wild barley isozyme segment. This result indicates that there was no substantial yield penalty associated with combining resistance genes in pairs compared with using them singly. The yields of the lines that were double homozygotes for the 'Clipper' allozymes (Cl + Cl, Table 3) were significantly less than the best resistant lines in both years, reflecting the benefit of protection against disease (about 25% on average in 1992 and 10% in 1993).

Grain physical characters

In the same manner as in Table 2 for the parental lines, the most prominent difference among the group means in Table 3 was that between the scald susceptible genotypes (Cl + Cl) and the remainder, particularly for seed size and weight in a disease-prone environment. The two reconstituted singly resistant lines of the set of four were superior to reconstituted 'Clipper'. The fact that this pattern mirrored the results for the original parental lines is additional evidence that the effect of disease on yield and quality traits is a direct one, and unlikely to be due to an indirect correlation from residual "linkage drag" in the backcrossing pedigree.

Malting quality

The remaining characters are measured on the fraction of the grain sample that a 2.2 mm sieve retains, which is the fraction of grain sufficiently plump for the malthouse. Despite this preselection of "acceptable" grain there is a suggestion for both the backcross parental (Table 2) and recombinant progeny (Table 3) lines that the grain from diseased plants gives lower values for malt yield. However, the effect of resistance genotypes on these micromalting measures of quality was relatively small.

Correlation between characters

Table 4 presents the product-moment correlation coefficients estimated from the individual plot values for all the lines. The correlations for the 37 lines tested in 1992 are shown above the diagonal, while the data for the 43 lines tested in 1993 are below the diagonal. In the more heavily diseased crop (1992), a strong negative correlation was present between the amount of disease (AUDPC) and yield per plot (−0.93), and significant unfavorable correlations were present between disease level and grain size and weight (about −0.6 in each

Table 4 Matrix of product moment correlation coefficients between characters

	AUDPC	Yield	Grain size	Grain weight	Grain protein	Malt yield	FHW Extract	Free AA N	DP
AUDPC	–	−0.93[a]	−0.64	−0.58	0.04	−0.52	0.15	0.26	0.27
Yield	−0.29	–	0.72	0.65	−0.17	0.45	0.06	−0.33	−0.21
Grain size	0.14	0.06	–	0.95	−0.55	0.55	0.44	−0.20	−0.51
Weight	−0.32	0.28	0.36	–	−0.47	0.54	0.42	−0.20	−0.54
Protein	−0.23	−0.02	−0.57	−0.12	–	−0.23	−0.77	0.16	0.45
Malt	−0.16	0.11	−0.41	−0.01	0.31	–	−0.15	−0.53	−0.74
Extract	0.19	0.38	0.49	0.09	−0.60	−0.29	–	0.09	−0.15
FAAN	−0.03	0.31	0.00	−0.09	0.03	−0.02	0.17	–	0.40
DP	−0.39	−0.17	0.16	0.24	0.22	0.07	−0.30	−0.21	–

[a] The correlation values for the 1992 heavily scalded trial are above the diagonal and those for the 1993 lightly diseased trial are below. Correlation coefficients larger than 0.325 in 1992 and 0.300 in 1993 are significantly different from zero at the 0.05 level

case). Malt yield was also negatively correlated with disease. These patterns were either weaker or absent in the 1993 trial, probably due to the lower disease incidence in that year. The remaining quality characters (protein, extract, FAAN and DP) were unrelated to disease. The negative correlation between extract and protein in both years is the usual relationship when there is major variation in grain filling.

The difference in disease levels between the two trials had additional indirect effects on the relationships between the characters. Since the impact of scald was greater in 1992, the higher variance in disease response in that trial led to inflated intergenotypic variance in seed size (Tables 2 and 3). On the whole this led to more appreciable correlations between grain dimensions and malting quality parameters. In 1992 more disease was associated with smaller seeds of higher protein and FAAN content, lower malt yield and extract and higher diastatic power (DP). All but the last of these relationships have adverse effects on malting quality. The result for DP probably reflects the dry matter basis of the measurement and the fact that smaller seeds have less starch reserves, which is responsible for the usual positive correlation of DP with protein.

Discussion

Markers closely linked to several resistance genes provide a precise and efficient method of obtaining experimental material for testing the pyramiding hypothesis of genes for disease resistance. Their use circumvents both the need for a range of pathotypes that discriminate between the individual resistance genes during the crossing program and the need for extensive progeny testing when resistance is a dominant character.

In this experiment we tested the effects of pyramiding scald resistance genes using isozyme loci as genetic markers. Because of the restricted number of isozyme loci in the genome, it is usually the case that isozymes will provide only moderately to loosely linked tags for resistance genes. However, the ease with which large numbers of plants can be screened enabled the generation for field evaluation of populations of recombinant lines with higher frequencies of resistance than if no indirect selection were made. It was possible to test the general effects of pyramiding in this host-pathogen system despite the occurrence of crossing over and breaking of the linkage between tag and resistance gene in a few of the lines. Clearly, the potential exists to extract the multiply resistant recombinant homozygous lines more precisely, once closely linked molecular tags are available.

In the detailed study of one combination of two resistances (BC30 and BC35), a significant improvement in disease resistance was obtained in the doubly resistant lines. In the other cases the combining of resistance genes did not lead to unilateral improvement in resistance. However, in deciding whether pyramiding is a beneficial strategy, the tests should also check whether useful resistance is more prolonged when genes are combined than when they are used singly. In the present case, performance was tested in only 2 years. More generally, we would expect a benefit to be evident over longer time-frames, provided that there was no yield penalty to combining resistance genes ("cost of resistance") in years when scald was not prevalent. In these trials, no negative effects of resistance on yield or quality were evident, in either year.

The range of disease responses shown by several lines with a similar genetic background (the cultivar 'Clipper') in the trials enabled us to examine the effect of scald disease on malting quality in barley. The evidence indicates that scald damage lowered yield and grain quality, and hence malting quality. This conclusion parallels that of Khan and Crosbie (1988) who tested the effect of controlling scald with fungicide on malting quality.

Thus, the damage that scald inflicts can entail substantial losses to the farmer. Grain yield is depressed as is grain size and concomitant carbohydrate yield. It is clear that to realize their full potential for malt, future barley cultivars will need the protection from scald that combinations of several resistance genes afford. Further

suitably tagged genes will be at a premium in barley improvement programs. Such tagged resistances will allow the combination of resistance as one key strategy for meeting the challenge of this highly variable pathogen (Burdon et al. 1994).

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