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Genetic analysis of a two-row × six-row cross of barley using doubled-haploid lines

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Abstract A study was conducted on a two-row/six-row cross of barley to (1) determine the yield potential, (2) detect epistasis and genetic correlations, (3) estimate the heritabilities of six agronomic traits, and (4) study the effect of the *V* locus on the agronomic traits in the barley cross. The effects of five other marker loci (*Re2*, *s*, *R*, *Est1*, and *Est5*) on the six agronomic traits were also studied. One hundred and ninety doubled-haploid (DH) lines were derived from a 'Leger'/CI9831 cross using the bulbosum method. The DH lines and the two parents were tested for grain yield, test weight, seed weight, plant height, lodging, and heading/maturity at two locations in Eastern Canada in 1993. Additive × additive epistasis and genetic correlations were detected for some of the agronomic traits. Many of the heritability estimates were high; however, significant progress in yield improvement would be difficult to achieve because of a low mean yield of the DH lines. Under the growing conditions in Eastern Canada, six-row lines outyielded two-row by 20–27%. Six-row lines, however, were associated with low test weight, low seed weight, and severe lodging. Some two-row lines yielded higher than the two-row parent CI9831, but none of the six-row lines yielded higher than the six-row parent 'Leger'. The *R*, *s*, and *Est5* loci were associated with the six agronomic traits, but the *Est1* locus was apparently not associated with the agronomic traits. The effect of the *Re2* locus was probably due to its close linkage with the *V* locus. Further studies are needed to determine if superior six-row lines can be developed from two-row/six-row crosses.

Key words Barley · Haploids · Two-row · Six-row · Quantitative trait loci

Introduction

Barley varieties can be classified into two types, two-row versus six-row, according to their spike characteristics. The most popular variety in Western Canada, 'Harrington', is a two-row. In contrast, six-row varieties predominate in Eastern Canada. Barley breeders sometimes make two-row/six-row crosses in an attempt to transfer desirable genes such as disease resistance, straw stiffness, or high protein from one type to another. Harlan et al. (1940), however, observed that two-row/six-row crosses were 'strikingly inferior'. Not only did six-row selections from 149 two-row/six-row crosses yield lower than six-row selections from 209 six-row/six-row crosses, but two-row selections from the two-row/six-row crosses also yielded lower than two-row selections from 21 two-row/two-row crosses. In contrast, Lambert and Liang (1952) were able to identify lines from a two-row/six-row cross that were outstanding in yield, test weight, and stiffness of straw. Improved varieties have been developed from two-row/six-row crosses in Canada (e.g., 'Tukwa' spring barley and McDiarmid winter barley) and elsewhere (Aikasalo 1988). Therefore, more studies on the yield potential of two-row /six-row crosses are warranted.

The two-row versus six-row characteristic is controlled by a single locus (*V*). As demonstrated by Wells (1962), simply replacing the *VV* (two-row) alleles in an

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improved variety with the *vv* (six-row) alleles does not necessarily result in a good six-row, or vice versa. The effect of the *V* locus on agronomic traits has been studied by several workers, but their findings are inconsistent. Some studies have shown an association between the *v* allele and high yield (Harlan et al. 1940; Wiebe et al. 1961), while in others there was no such association (Powell et al. 1990). The association between the *v* allele and high yield varies with the genetic background (Wells 1962; Takahashi et al. 1975).

Doubled-haploid (DH) lines are ideal material for genetic analysis because they are completely homozygous and homogeneous. Therefore, DH lines were derived from a two-row/six-row cross for use in this investigation. Our objectives were to (1) study the yield potential of the two-row/six-row cross, as measured by the cross mean and the number of superior lines; (2) detect epistasis and genetic correlations, and estimate heritabilities of six agronomic traits; and (3) detect the effect of the *V* locus on the six agronomic traits (grain yield, test weight, seed weight, plant height, lodging, and heading/maturity) in the barley cross. In addition, the effects of five other marker loci: *Re2* (purple lemmas), *s* (short rachilla hairs), *R* (rough awns), *Est1* (esterase 1), and *Est5* (esterase 5) on the six agronomic traits were also studied.

Materials and methods

Plant material

One hundred and ninety DH lines were derived from the F_1 hybrids of a ‘Leger’/CI9831 cross of barley by the bulbosum method (Choo et al. 1992). ‘Leger’ is a variety well adapted to Eastern Canada, while CI9831 is an introduction resistant to net blotch. Leger possesses the *v*, *re2*, *s*, *r*, *Est1Ca*, and *Est5Te* genes. In contrast, CI9831 possesses the V^t, *Re2*, *S*, *R*, *Est1Pr*, and *Est5Ri* genes. For simplicity, the symbol *V* is used throughout this paper to denote the *deficiens* form of two-row barley (V^t). The 190 DH lines can be classified into 12 marker classes according to the six marker loci (Table 1). The *V* and *Re2* loci are located on chromosome 2 with a recombination value of 0.11 (= *VVRe2Re2*:*VVre2re2*:*vvRe2Re2*:*vvre2re2* = 85:9:12:84). The *r* and *s* loci are located on chromosome 7 with a recombination value of 0.30 (= *SSRR*:*SSrr*:*ssRR*:*ssrr* = 69:30:27:64). The *Est5* gene segregates distortedly, but all the other genes segregate at random (Choo et al. 1992).

Testing procedures

The two parents and the 190 DH lines were first increased for seed at Ottawa in 1992. Then, they were seeded on May 10 and May 12, 1993, at Charlottetown (Prince Edward Island) and Ottawa (Ontario), respectively, in a randomized complete block design with four replications at each location. The two parents were each entered five times in each replication. Each experimental plot at Charlottetown consisted of four 3-m rows with a row spacing of 17.8 cm. Each plot at Ottawa consisted of four 2.5-m rows with a row spacing of 23 cm. All four rows were harvested at Charlottetown for yield determination, but only the central two rows were harvested at Ottawa. Standard cultural practices were followed at each location. Grain yield, test weight, seed weight, plant height, and lodging were recorded for each plot at both locations. In addition, heading date was recorded at Charlottetown; while maturity date was recorded at Ottawa.

Table 1 Classification of the 190 DH lines derived from a ‘Leger’/CI9831 cross of barley into 12 marker classes on the basis of six marker loci

Locus	Chromosome	Number of DH lines	
		Leger genotype[a]	CI9831 genotype
V	2	96	94
Re2	2	93	97
s	7	94	96
R	7	91	99
Est1[b]	3	71	62
Est5[b]	1	83	50

[a] ‘Leger’ possesses the *v* (six-row), *re2* (yellow lemmas), *s* (short rachilla hairs), *r* (smooth awns), *Est1Ca*, and *Est5Te* genes. CI9831 possesses the *V* (two-row), *Re2* (purple lemmas), *S* (long rachilla hairs), *R* (rough awns), *Est1Pr*, and *Est5Ri* genes

[b] The allelic identity of the other 57 lines was not determined

Statistical analysis

Data from each location were analyzed separately. The mean of the 190 DH lines was compared with the parental mean by the *F*-test to detect whether or not additive × additive epistasis was present (Choo et al. 1986). Any DH line showing a mean value outside the parental range was considered to be a transgressive line. A superior line was defined as a transgressive line with grain yield or test weight higher than that of ‘Leger’, seed weight greater than CI9831, plant height shorter than ‘Leger’, lodging resistance better than ‘Leger’, or heading/maturity date earlier than CI9831 on the basis of the *t*-test. The variance components were estimated by equating the expected mean square to its appropriate mean square. The heritability (h^2) on a plot basis was estimated from the following equation: $h^2 = \sigma_G^2/(\sigma_G^2 + \sigma_E^2) \times 100\%$ where σ_G^2 and σ_E^2 are the genotypic variance and environmental variance, respectively. The standard errors for the variance components and heritability were estimated according to the principles outlined by Kendall and Stuart (1967).

Phenotypic correlation was used to detect genetic linkage and/or pleiotropy. Assume that X and Y are the characters under consideration and that h_X^2 and h_Y^2 are the heritabilities of X and Y, respectively. Falconer (1960) showed that phenotypic correlation (r_p) between X and Y is a linear combination of genetic correlation (r_A) between X and Y, and environmental correlation (r_E) between X and Y. Mathematically, $r_p = h_X h_Y r_A + e_X e_Y r_E$ where $e_X^2 = 1 - h_X^2$ and $e_Y^2 = 1 - h_Y^2$ (see Falconer 1960, Eq. 19.1). When an identical set of DH lines is grown at locations as diverse as Charlottetown (C) and Ottawa (O), and the two characters X and Y are measured separately at two diverse locations, then the environmental correlation becomes negligible or zero (i.e., $r_E = 0$). Consequently, the resulting phenotypic correlation is due solely to the genetic correlation. Using this method, we obtained two phenotypic correlation coefficients between X and Y, one was between X at C and Y at O and the other was between X at O and Y at C. The two correlation coefficients varied somewhat dependent upon the heritability values.

The effects of the six marker loci on agronomic traits were studied by comparing the 2 marker classes for each of the six marker loci. The between classes mean square was tested against the within-classes mean square by the *F*-test (Choo 1983). If means of the 2 marker classes of DH lines were significantly different, then this would suggest the presence of either linkage between the marker

Table 2 Agronomic traits of the 190 DH lines derived from a 'Leger'/CI9831 cross of barley

Trait	Mean[a]			Number of transgressive DH lines	
	Leger	CI9831	DH	Inferior	Superior
Charlottetown					
Yield (t ha^{-1})	4.8 a	3.0 b	(3.2)[c]	45	0
Test weight (kg hl^{-1})	65.2 a	64.9 a	(62.0)	137	5
Seed weight (mg)	39.6 a	47.6 b	42.0	90	73
Height (cm)	109.5 a	114.7 a	(107.7)	13	56
Lodging (1–9)[b]	4.5 a	4.9 a	4.8	58	77
Heading (days)	60.2 a	60.2 a	60.8	92	46
Ottawa					
Yield (t ha^{-1})	3.6 a	2.2 b	(2.3)	22	0
Test weight (kg hl^{-1})	62.8 a	62.5 a	(59.7)	97	4
Seed weight (mg)	34.6 a	44.2 b	40.1	31	52
Height (cm)	95.1 a	89.1 a	93.0	0	0
Lodging (1–9)	0.5 a	0.6 a	0.9	12	0
Maturity (days)	93.6 a	93.1 a	92.9	0	15

[a] Means for the same characteristic followed by different letters were different at the 0.05 level

[b] 1 = no lodging, 9 = severe lodging

[c] Means in parentheses were different from their respective mean values of parents at the 0.05 level

locus and quantitative trait loci (QTL), or a pleiotropic effect of the marker gene. The variance component between classes and variance component within classes were estimated by equating the expected mean squares to their observed mean squares. The effect of the marker genes was further studied by determining the percentage of the variance component between-classes over the total variance (i.e., sum of between-classes and within-classes variance components).

Results

The two parents differed only in two of the six agronomic traits i.e., grain yield and seed weight (Table 2). 'Leger' outyielded CI9831 by 60% at Charlottetown and 61% at Ottawa. In contrast, CI9831 seed outweighed 'Leger' seed by 20% at Charlottetown and 28% at Ottawa. The mean yield of the two parents was 25% higher than that of the DH lines at both locations. Similarly, the mean test weight of the two parents was 5% higher than that of DH lines at both locations. On average, the two parents were 4% taller than the DH lines at Charlottetown and were as tall as the DH lines at Ottawa. The DH lines, on average, did not differ from the mid-parental value for seed weight, lodging, and heading/maturity at the two locations. There were many transgressive lines, but the majority of them were inferior. All of the DH lines yielded significantly less than 'Leger', at Charlottetown. Likewise, all but 8 of the DH lines yielded significantly lower than 'Leger' at Ottawa. Nine and 6 two-row lines, however, yielded significantly higher than the two-row parent CI9831 at Charlottetown and Ottawa, respectively. On average at the two locations, the two-row DH line Legci 28 outyielded CI9831 by 31%. For test weight, 4 of the 5 superior lines were two-row at Charlottetown, and 2 of the 4 superior lines were two-row at Ottawa. For seed weight, all superior lines were two-row at both locations. On average at the two locations, the best two-row line Legci 59 was 24% higher than the two-row parent CI9831 in seed weight. At Charlottetown, only 1 six-row line had higher seed weight than 'Leger', and 90 six-row lines had significantly lower seed weight; while at Ottawa, 9 six-row lines had higher seed weight than 'Leger', and 31 six-row lines had significantly lower seed weight. On average, the six-row line Legci 167 was 9% higher in seed weight than 'Leger'.

Variation among DH lines was significant for all six agronomic traits at Charlottetown (Fig. 1), it was also significant for grain yield, test weight, seed weight, and maturity, but not for plant height and lodging at Ottawa (Fig. 2). The growing conditions appeared to be more favorable at Charlottetown compared with Ottawa in 1993, thus barley plants grown at Charlottetown were taller, produced higher seed weight and higher yield, but lodged more severely than those grown at Ottawa. In most cases, the frequency distributions of the 190 DH lines were unimodal. The frequency distribution for seed weight was bimodal at both locations and that for lodging resistance appeared to be bimodal or multi-modal at Charlottetown. More six-row lines had high yield, but more two-row lines had high test weight, high seed weight, tall plant height, and good lodging resistance. The frequency distribution of the six-row lines was almost separated from that of the two-row lines for seed weight.

The environmental variance was small and the genotypic variance was large for all six traits at Charlottetown; thus, all the heritability estimates were very high (Table 3). In contrast, the genotypic variance was negligible for height, lodging, and maturity at Ottawa. Consequently, the heritability estimates at Ottawa ranged from very low for the three traits to high for test weight and seed weight. The 96 six-row lines had

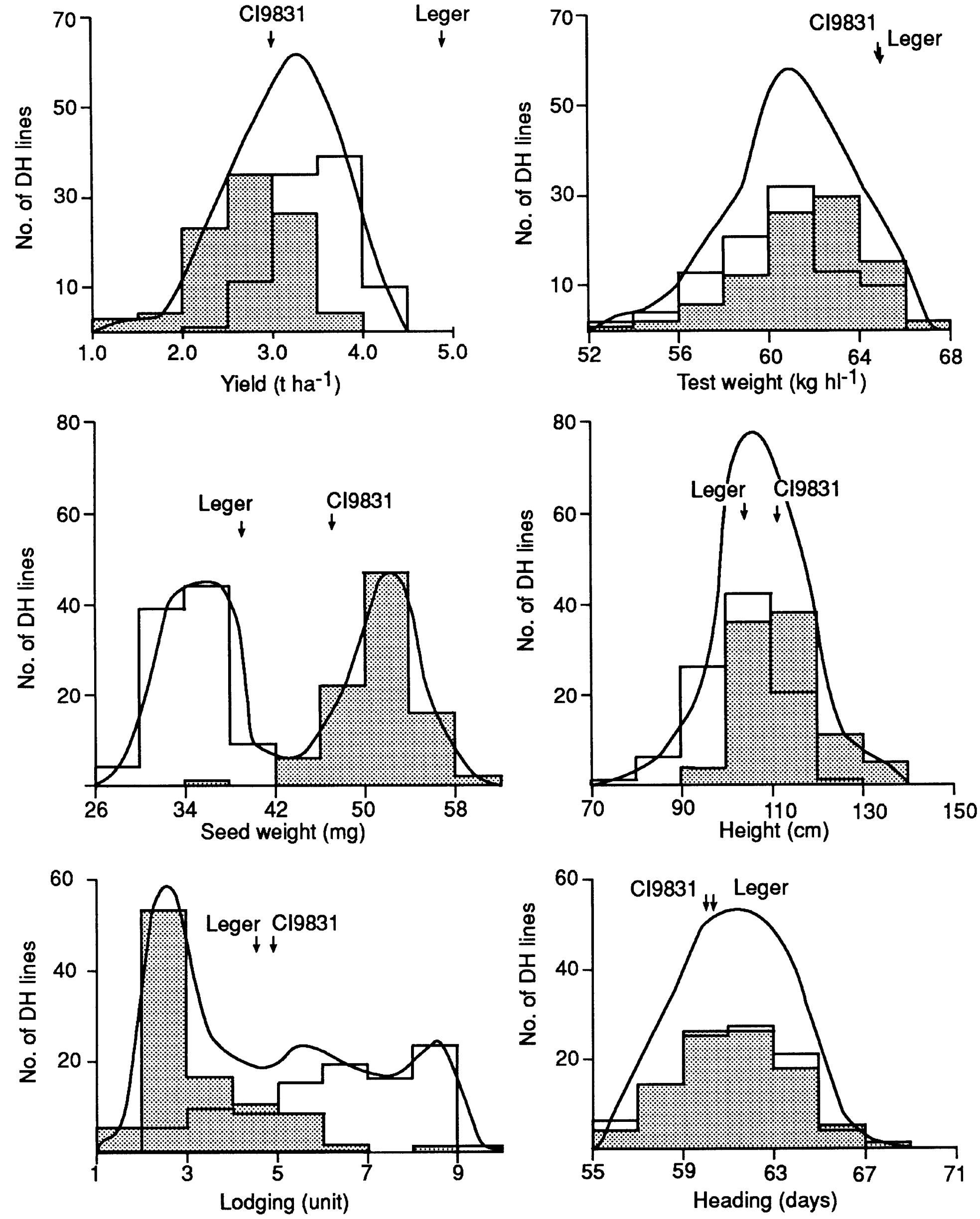


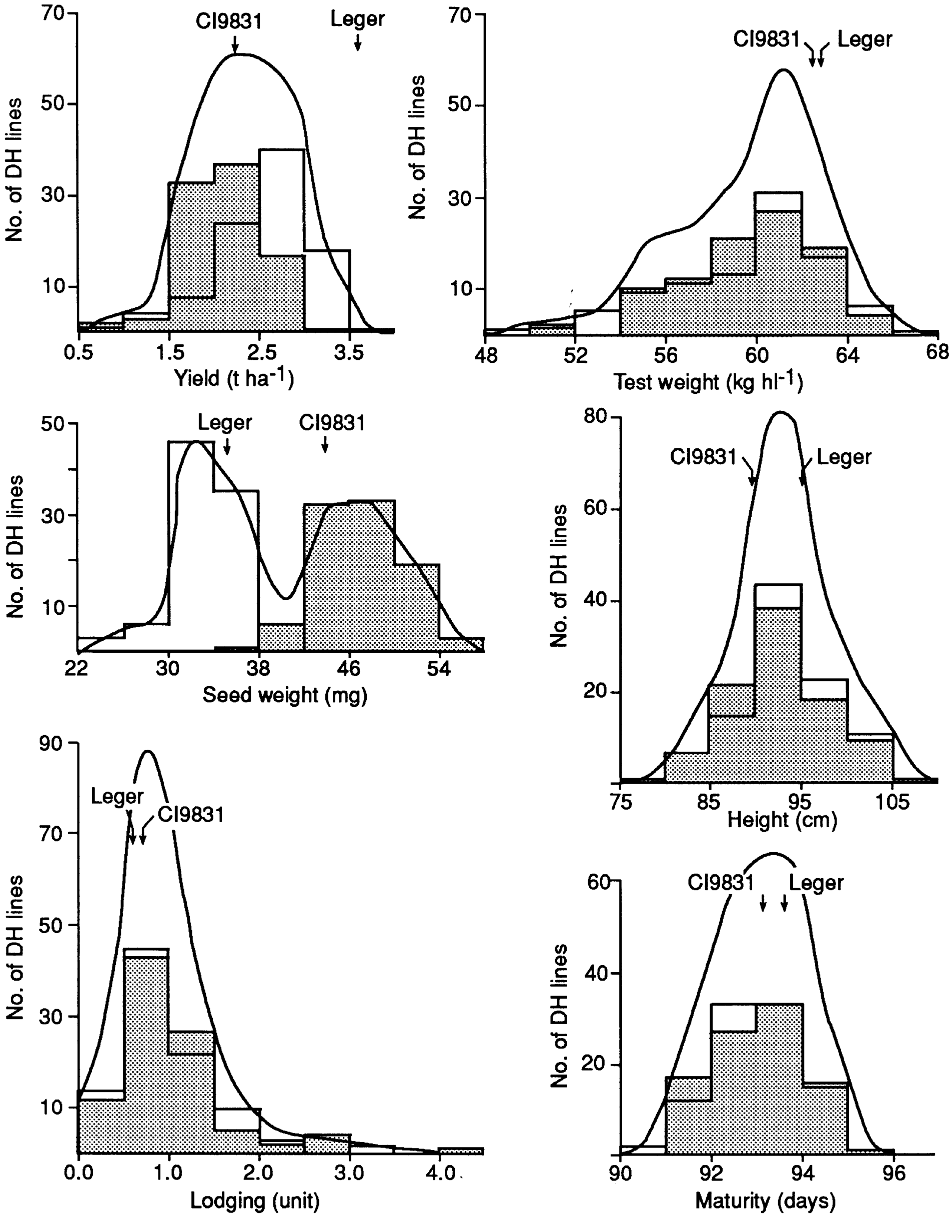
Fig. 1 Frequency distributions for six agronomic traits among the 190 barley doubled-haploid (DH) lines derived from a 'Leger'/ CI9831 cross grown at four replications at Charlottetown in 1993. The *solid lines* represent the frequency distributions of the 190 DH lines. *Shaded distributions* show the frequency of the 94 two-row lines, while *unshaded distributions* show the frequency of the 96 six-row lines

similar heritabilities as the 94 two-row lines, but both six- and two-row lines had lower heritabilities than the pooled 190 DH lines.

Grain yield was positively correlated with test weight in the pooled DH lines, two-row lines, and six-row lines (Table 4). Grain yield was correlated negatively with seed weight, in the pooled DH lines but positively in the two-row lines, it was not correlated with seed weight in the six-row lines. Grain yield was correlated with plant height only in the six-row lines. Test weight was positively correlated with plant height in four of the six cases. Lodging resistance was correlated only with grain yield and seed weight in the pooled DH lines. Grain yield was negatively correlated with heading, but it was not correlated with maturity.

The esterase 1 locus had no effect on all six agronomic traits, thus data concerning the esterase 1 locus are not presented here. All the other five marker loci had a major effect on grain yield in these DH lines (Table 5). Six-row lines on average outyielded two-row ones by 27% at Charlottetown and by 20% at Ottawa. Six-row lines, however, were associated with low test weight, low seed weight, short plant height, and severe lodging. The *re2re2* genotype outyielded the *Re2Re2* genotype by 24% and 19% at Charlottetown and Ottawa, respectively. Like the six-row lines, the *re2re2* genotype was also associated with low test weight, low seed weight, short plant height, and severe lodging. The *SS* genotype had a 7% higher yield than the *ss* genotype at both locations, it had high test weight but low

Fig. 2 Frequency distributions for six agronomic traits among the 190 barley doubled-haploid (DH) lines derived from a 'Leger'/ CI9831 cross grown at four replications at Ottawa in 1993. The *solid lines* represent the frequency distributions of the 190 DH lines. *Shaded distributions* show the frequency of the 94 two-row lines, while *unshaded distributions* show the frequency of the 96 six-row lines



seed weight. The *RR* genotype outyielded the *rr* genotype by 8% and 11% at Charlottetown and Ottawa, respectively; it had high test weight, low seed weight, short plant height, poor lodging resistance, and earliness. The *RiRi* genotype outyielded the *TeTe* genotype by 9–10%. The *RiRi* genotype was also associated with high test weight, low seed weight, and tall plant. Both the *V* and *Re2* loci had a major effect on seed weight, accounting for approximately 90% and 70%, respectively, of the total variation in seed weight.

Discussion

Previously, Harlan et al. (1940) reported that two-row selections from two-row/six-row crosses yielded lower than selections from two-row/two-row crosses. In this study, at least some two-row lines outyielded the two-row parent CI9831. In fact, 1 two-row line, Legci 28, outyielded CI9831 by 31%. While none of the six-row lines yielded higher than the adapted, six-row parent, 'Leger', some six-row lines (e.g., Legci 129 and Legci 167) had a higher test weight and a higher seed weight. Thus, they may have a better chemical composition than 'Leger'. The chemical composition of the 190 DH lines is currently being analyzed, and the results will be reported in due course. 'Leger' outyielded CI9831 by 60%. Perhaps, CI9831 was a poor parent and had few high-yielding genes to contribute. Therefore, more studies on two-row/six-row crosses using different adapted parents are needed in order to determine if superior six-row lines can be developed from two-row/six-row crosses.

Table 3 Estimates of variance components and heritability of the 190 doubled-haploid lines derived from a 'Leger'/CI9831 cross of barley

Trait	Charlottetown			Ottawa		
	σ_E^2	σ_G^2	h^2	σ_E^2	σ_G^2	h^2
Pooled six-row and two-row lines						
Grain yield	0.08 ± 0.00	0.31 ± 0.03	99 ± 1	0.19 ± 0.01	0.21 ± 0.03	53 ± 5
Test weight	1.08 ± 0.06	7.63 ± 0.81	88 ± 2	3.57 ± 0.21	9.68 ± 1.09	73 ± 3
Seed weight	1.40 ± 0.08	80.63 ± 8.33	98 ± 0	8.88 ± 0.53	57.54 ± 6.15	87 ± 2
Height	30.61 ± 1.82	80.21 ± 9.05	72 ± 3	114.60 ± 6.81	0.00	0
Lodging	1.12 ± 0.07	4.62 ± 0.50	80 ± 2	1.34 ± 0.08	0.02 ± 0.02	1 ± 13
Heading/maturity[a]	0.65 ± 0.04	5.77 ± 0.61	90 ± 1	2.76 ± 0.16	0.30 ± 0.11	10 ± 10
96 six-row lines						
Grain yield	0.10 ± 0.01	0.15 ± 0.02	59 ± 6	0.23 ± 0.02	0.19 ± 0.04	45 ± 8
Test weight	1.47 ± 0.12	7.20 ± 1.10	83 ± 3	3.78 ± 0.32	11.79 ± 1.85	76 ± 4
Seed weight	1.37 ± 0.12	7.12 ± 1.08	84 ± 3	6.53 ± 0.95	7.73 ± 1.38	54 ± 8
Height	36.21 ± 3.04	59.52 ± 9.98	62 ± 6	117.72 ± 9.86	0.00	0
Lodging	1.25 ± 0.11	3.06 ± 0.49	71 ± 4	1.14 ± 0.09	0.02 ± 0.05	2 ± 33
Heading/maturity	0.62 ± 0.05	5.70 ± 0.85	90 ± 2	2.48 ± 0.21	0.38 ± 0.15	13 ± 13
94 two-row lines						
Grain yield	0.06 ± 0.00	0.19 ± 0.03	78 ± 3	0.14 ± 0.01	0.15 ± 0.01	52 ± 6
Test weight	0.70 ± 0.06	7.27 ± 1.09	91 ± 1	3.32 ± 0.28	7.63 ± 1.24	30 ± 3
Seed weight	1.40 ± 0.12	13.09 ± 1.97	90 ± 2	11.17 ± 0.95	10.73 ± 2.00	49 ± 7
Height	24.85 ± 2.10	66.76 ± 10.71	73 ± 4	110.78 ± 9.38	0.00	0
Lodging	0.98 ± 0.08	1.17 ± 0.21	54 ± 7	1.56 ± 0.02	0.00 0	
Heading/maturity	0.68 ± 0.06	5.87 ± 0.89	90 ± 2	2.99 ± 0.25	0.24 ± 0.16	7 ± 17

[a] Heading date for Charlottetown, maturity date for Ottawa

Table 4 Correlation coefficients between agronomic traits in the 190 doubled-haploid lines derived from a 'Leger'/CI9831 cross of barley

Charlottetown	Ottawa					
	Yield	Test weight	Seed weight	Height	Lodging	Maturity
Pooled six- and two-row lines						
Yield		0.25**	– 0.57**	0.09	– 0.01	0.01
Test weight	0.19**		0.21**	0.04	0.02	– 0.02
Seed weight	– 0.36**	0.08		– 0.04	0.06	0.01
Height	0.01	0.35**	0.47**		0.11	– 0.00
Lodging	0.37**	– 0.12	– 0.64**	– 0.03		– 0.03
Heading	– 0.25**	– 0.08	0.08	0.01	– 0.14	
96 six-row lines						
Yield		0.46**	– 0.08	0.23*	0.06	0.01
Test weight	0.25		0.06	0.14	– 0.03	0.04
Seed weight	– 0.04	0.11		0.14	0.01	0.10
Height	0.42**	0.50**	0.33**		0.12	0.06
Lodging	0.13	– 0.12	– 0.06	0.13		– 0.16
Heading	– 0.13	0.04	0.23*	– 0.08	– 0.09	
94 two-row lines						
Yield		0.26*	0.19	– 0.11	– 0.04	0.03
Test weight	0.43**		– 0.06	– 0.02	0.07	– 0.08
Seed weight	0.25*	0.20*		0.06	0.22*	– 0.03
Height	0.05	0.23*	0.06		0.29	– 0.06
Lodging	0.03	– 0.19	0.13	– 0.10		0.13
Heading	– 0.38*	– 0.23	– 0.06	0.11	– 0.18	

*, **Significantly different from zero at the 0.05 and 0.01 level, respectively

One of the objectives of this cross was to transfer net blotch resistance genes from CI9831 to 'Leger'. Five lines were found to be resistant to all three isolates (WRS102, WRS858, WRS857) of *Pyrenophora teres* (Ho et al. 1996), and 1 of them was six-row (i.e., Legci 68). Unfortunately, Legci 68 yielded lowest among the six-row lines at both locations. The two-row line Legci 184 was resistant to all three isolates of *P. teres* and it also yielded 9% higher (although not statistically significant) than CI9831. Thus, Legci 184 may be a good

Table 5 Agronomic traits of ten classes of the 190 barley doubled-haploid lines grown at Charlottetown (C) and Ottawa (O) in 1993

Comparison	Yield (t ha^{-1})[a]		Test weight (kg hl^{-1})		Seed weight (mg)		Height (cm)		Lodging (1–9)[b]		Heading/maturity (days)[c]	
	C	O	C	O	C	O	C	O	C	O	C	O
Spike type												
Two-row (*VV*)	2.7 a	2.1 a	62.6 a	60.0 a	51.1 a	47.0 a	112.0 a	92.4 a	3.1 a	0.9 a	61.2 a	92.9 a
Six-row (*vv*)	3.5 b	2.6 b	61.3 b	60.0 a	34.4 b	33.4 b	103.6 b	93.5 a	6.2 b	0.9 a	61.0 a	92.9 a
%[d]	60	29	9	0	93	89	33	0	67	0	0	0
Lemma color												
Purple (*Re2Re2*)	2.8 a	2.2 a	62.7 a	59.9 a	49.2 a	45.7 a	111.2 a	92.4 a	3.6 a	0.9 a	61.2 a	93.0 a
Yellow (*re2re2*)	3.5 b	2.6 b	61.5 b	59.8 a	36.0 b	34.4 b	104.6 b	93.6 a	5.8 b	0.8 a	60.9 a	92.9 a
%	43	20	10	0	72	71	22	1	42	0	0	0
Rachilla hairs												
Long (*SS*)	3.2 a	2.4 a	62.3 a	60.3 a	42.2 a	39.6 a	108.1 a	92.7 a	4.7 a	0.9 a	61.1 a	93.8 a
Short (*ss*)	3.0 b	2.2 b	61.6 b	59.1 b	43.2 a	40.8 b	107.4 a	93.3 a	4.6 a	0.8 a	61.1 a	94.0 a
%	2	4	2	6	0	0	0	0	0	0	0	0
Awn type												
Rough (***RR***)	3.3 a	2.5 a	62.3 a	60.3 a	40.8 a	38.8 a	106.9 a	92.4 a	5.0 a	0.9 a	60.8 a	93.9 a
Smooth (***rr***)	3.0 b	2.2 b	61.6 b	59.1 b	44.6 b	41.7 b	108.6 b	93.5 a	4.3 b	0.9 a	61.4 b	93.9 a
%	14	9	2	7	8	6	1	1	4	0	2	0
Esterase 5												
TeTe	3.1 a	2.3 a	61.7 a	58.7 a	43.0 a	40.5 a	107.6 a	92.1 a	4.8 a	0.9 a	60.7 a	93.8 a
RiRi	3.3 b	2.5 b	62.6 b	61.3 b	40.6 b	38.2 b	107.4 a	94.2 b	4.8 a	0.9 a	60.8 a	93.9 a
%	4	6	4	27	2	2	0	7	0	0	0	0

[a] Means in each comparison followed by different letters were different at the 0.05 level

[b] 1 = no lodging, 9 = severe lodging

[c] Heading data for Charlottetown, maturity date for Ottawa

[d] $\% = \sigma^2_{\mathrm{M}}/(\sigma^2_{\mathrm{M}} + \sigma^2_{\mathrm{W}}) \times 100\%$, where σ^2_{M} = variance between marker classes and σ^2_{W} = variance within marker classes

parent for a crossing program for breeding net blotch resistance.

The DH lines on average were lower in grain yield, test weight, and height than the mean of the two parents, indicating the presence of additive × additive epistasis. This study, however, did not permit us to estimate the amounts of additive genetic variance and additive × additive genetic variance. Therefore, the relative importance of additive × additive epistasis in controlling these three agronomic traits is unknown. Genotypic correlations were detected among some of these agronomic traits, but it is not known whether these correlations were due to linkages among QTL or pleiotropy, or both. Test weight was positively correlated with grain yield in all cases, indicating that test weight may be a good selection criterion for high yield. Many of the heritability estimates ranged from high to very high and selection for these traits would be effective. However, as the cross mean was low, significant progress in yield improvement would be difficult to achieve.

Under the growing conditions in Eastern Canada, six-row lines outyielded two-row ones by 20–27%. This study seems to support the early findings of Harlan et al. (1940) and Wiebe et al. (1961). Six-row lines, however, were associated with low test weight, low seed weight, short plant height, and severe lodging. It has been reported that the *V* locus also had a major effect on kernel size and shape in the 'Leger'/CI9831 cross (Frégeau-Reid et al. 1996), on 12 quantitative traits (days to heading, height of tallest culm, width and area of penultimate leaf, number of tillers per plant, spike length, awn length, spike density, vegetative biomass, kernel weight, kernel-size index, and harvest index) (Allard 1988), and on spike length, plant height, number of kernel per main stem, seed weight, and straw weight (Powell et al. 1990). Therefore, as pointed out by Allard (1988), the *V* locus 'affects developmental processes in ways that leave few quantitative traits untouched'. The effect of the *Re2* locus was smaller than that of the *V* locus and both loci were closely linked. Therefore, the effect of the *Re2* locus on the six agronomic traits is probably due to its close linkage with the *V* locus.

In this study, the *RR* genotype was found to be associated with high yield, high test weight, low seed weight, short plant height, poor lodging resistance, and earliness. It has been reported that yield increase can be achieved by transferring the *rr* alleles from one variety to another (Suneson et al. 1952; Everson and Schaller 1955; Suneson and Stevens 1957). Everson and Schaller (1955) concluded that the association between the *rr* alleles and high yield was due to linkage with the factor or factors for increased yield, which was located between the *R* and *s* loci and closer to the *R* locus. Similarly, there could be QTL that are linked with the *R* locus in the 'Leger'/CI9831 cross. The effect of the *s* locus was smaller than that of the *R* locus, and both the *R* and *s* loci were linked. This suggested that the QTL was more closely linked with the *R* locus than with the *s* locus. Also, Jensen (1989) identified a QTL affecting seed weight, *Kw*1, which was located closer to the *R* locus than to the *s* locus. This study showed no association between *Est1* and the six agronomic traits. Kjær et al. (1991) also failed to detect any association between *Est1* and 23 quantitative traits. The effect of the *Est5* locus was significant on grain yield, test weight, seed weight and, perhaps, plant height. The *Est5* locus segregates distortedly in the 'Leger'/CI9831 cross (Choo et al. 1992). The effect of non-random segregation on the variance between classes at the *Est5* locus is not known.

In conclusion, this study suggests that it would be possible to transfer desirable genes from six-row varieties to two-row ones and that further studies are needed to determine if superior six-row lines can be developed from two-row/six-row crosses. Under the growing conditions in Eastern Canada, six-row lines outyielded two-row ones by 20–27%. Six-row lines, however, were associated with low test weight, low seed weight, and severe lodging. The *RR* genotype was found to be associated with high yield, high test weight, low seed weight, short plant height, poor lodging resistance, and earliness. The *Est1* locus had no effect on the agronomic traits, but the *Est5* could have a significant effect on grain yield, test weight, seed weight, and plant height. Additive × additive epistasis and genetic correlations were detected for some of these agronomic traits. Although many of the heritability estimates were high, significant progress in yield improvement would be difficult to achieve because of a low mean yield of the DH lines.

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