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Quantitative-genetic analysis of reciprocal crosses between a winter and a spring cultivar of common wheat (*Triticum aestivum* L.)

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Abstract The winter wheat cultivar Sakhalin (parent A) and the spring wheat cultivar Khush-hal (parent B), assumed to be both nuclear-genetically and plasmotypically different, were reciprocally crossed and the F_1 generation of the reciprocals backcrossed to either parent. The populations $(A \times B)F_1$, $(A \times B)F_2$, $[(A \times B)F_1 \times A]F_1$ and $[(A \times B)F_1 \times B]F_1$, and their reciprocals $(B \times A)F_1$, $(B \times A)F_2$, $[(B \times A)F_1 \times A]F_1$ and $[(B \times A)F_1 \times B]F_1$, assumed to have the plasmotypes of the parents A and B respectively, were spring sown in the same field from unvernalized (experiment #1) and vernalized (experiment #2) seeds. The results of the analyses of variance of the data recorded in the two experiments are fairly similar. In both the experiments the plasmotypically A populations have produced more heads and higher grain yields per plant than their plasmotypically B reciprocals. The components of the family means and of half the differences between the reciprocals within the families show that vernalization has not affected the efficiency of the nuclear genes of parent A but has reduced the efficiency of the nuclear genes of parent B in both the homozygous and the heterozygous states. This in turn has affected the components of family mean squares and those of the family × reciprocals interaction mean squares in the analysis of variance tables.

Key words Genotype · Plasmotype · Families Reciprocals · Vernalization

Introduction

Character-measurement differences between reciprocal crosses have been observed in a number of plant species. Procedures of quantitative-genetic analysis of such crosses were formulated and/or applied by Chandraratna and Sakai (1960), Sakai et al. (1961), Durrant (1965), Mather and Jinks (1971), Jinks et al. (1972), Aksel (1974), Smith and Aksel (1974), Soomro and Aksel (1974), Patel and Bains (1984 a,b), Poni et al. (1987) and others. The materials used for the present study were produced in connection with a project to investigate the inheritance of quantitative characters in arrays of reciprocal crosses between sets of winter and spring cultivars of common wheat. The occurrence of hybrid grass-clump dwarfness (see, e.g., Canvin and Newetty 1976) in the F_1 generation of a number of crosses, and some other circumstances, have prevented the implementation of the project as initially planned.

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Materials and methods

The common wheat cultivars Sakhalin (winter type) and Khush-hal (spring type) were reciprocally crossed and the F_1 generation of the reciprocal crosses was backcrossed to either parent. The materials, consisting of F_1 and F_2 generations of reciprocal crosses and of their backcrosses, were spring sown at the Ellerslie Genetics Field Station of the University of Alberta in two experiments: experiment #1 grown from unvernalized seeds and experiment #2 grown from vernalized seeds. Both experiments, of four randomized blocks each, were space-seeded (30 cm between rows, 15 cm within rows) and located side by side in the same field. At heading time the dominance of the spring habit of growth was found to be monogenically controlled. In experiment #1 (unvernalized) the winter cultivar Sakhalin did not produce any heads; about 25% of the plants in the F_2 generation of the reciprocal crosses between the winter cultivar Sakhalin and the spring cultivar Khush-hal and about 50% of the plants in the backcrosses to winter cultivar Sakhalin also did not. In experiment #2 (vernalized) all the plants, including those of the winter type Sakhalin, headed and produced seeds. At maturity all the head-bearing plants were harvested by hand and their numbers in each plot were recorded. The quantitative characters considered for study were:

(a) The number of heads per plant and (b) the yield of grain (in grains) per plant. With respect to both the characters a and b it was assumed that:

(1) The parents Sakhalin (A) and Khush-hal (B) are homozygous and differ from one another both genotypically and plasmotypically.
(2) The nuclear genes controlling the character have different effects in different plasmotypes.

(3) The plasmotype of the hybrid is the same as that of its female parent and maintains its reaction norm in the subsequent generations of self-pollination.
(4) The parents differ at more than one locus and the nonallelic genes are independent in their action.

The crosses made for this study were the reciprocal crosses A×B and B×A, and their backcrosses (A×B) F_1×A and (A×B) F_1×B and (B×A) F_1×A and(B×A) F_1×B, where the female parent is always written first. The sets consisting of one, or more than one, filial generation of the above pairs of crosses can be symbolized generally as:

Set 1. $\sum_{G \varepsilon I}$(A×B, B×A)F_G,

Set 2. $\sum_{G \varepsilon J}$[(A×B)F_1×A, (B×A)F_1×A]F_G and

Set 3. $\sum_{G \varepsilon K}$[(A×B)F_1×B, (B×A)F_1×B]F_G,

respectively, where G is the generation index, ε means "*belongs to*", and I, J and K are the index sets. The equally indexed (i.e., belonging to the same filial generation) pairs of crosses in sets 1, 2 and 3, respectively, will be referred to as *reciprocals* in the sense that genotypically they are the same but by virtue of the assumptions made are expected to have different plasmotypes and character-measurements. The i-th pair ($i=1, 2,...n_i$) of such reciprocals will be referred to as the i-th family. The total number of such families in the experiment is $n_i=\#I+\#J+\#K$ where $\#I$, $\#J$ and $\#K$ are the numbers of elements (indexes G) in the index sets I, J and K. With the reciprocals considered apart, a field experiment of n_k randomized blocks consists of $2n_in_k=N$ plots with n_p plants in the p-th plot ($p=1,2,...,N$). The character-measurement mean ($\bar{x}$) of the n_p plants in the p-th plot, i.e., $\bar{x}_p$, can be denoted more specifically as $\bar{x}_{ijk}$ where the subscripts refer to the j-th reciprocal ($j=1, 2$) of the i-th family ($i=1, 2, ..., n_i$) located in the k-th block ($k=1, 2, ..., n_k$); $j=1$ if the female parent of the cross is A or (A×B)F1 and $j=2$ if the female parent of the cross is B or (B×A)F1.

In the experiments conducted for this study the numbers of plants and, implicitly, the numbers of observations per character in the plots, were not the same. The analysis of variance of the experimental data was performed by using Scheffe's approximate method (Scheffe 1959), viz., the $2 \times n_i \times n_k$ table of plot means was treated as though all the means had the same variance, the estimate of which is:

$$c(MS'_e) = (N^{-1} \sum_p n_p^{-1}) \, [\sum_p (ss)_p \, (\sum_p n_p - N)^{-1}] \qquad (1)$$

where $(ss)_p$ is the sum of squares and n_p is the number of observations in the p-th plot. In the analysis of variance table this variance is referred to as the *error mean square* (*EMS*, $df=\sum_p n_p - N$).

In the analysis of variance table of $2n_in_k=N$, plot means ($\bar{x}ijk$), the families sum of squares (*FSS*), the reciprocals sum of squares (*RSS*), and the (families) × (reciprocals) interaction sum of squares [$(F\,R)SS$], are devoid of block effect differences since they were computed from the plot means averaged over blocks (viz., from $X_{ij.}$). The sums of squares in question and their respective degrees of freedom (*df*) are:

$$FSS=2n_k \sum_i (\bar{x}_{i..}-\bar{x}_{...})^2,\ df=n_i-1 \qquad (2)$$

$$RSS=2n_in_k\,(\bar{x}_{.\Delta.})^2,\ df=2-1=1 \qquad (3)$$

$$(F{\times}R)SS=2n_k \sum_i (\bar{x}_{i\Delta.}-\bar{x}_{.\Delta.})^2,\ \mathrm{df}=n_i-1 \qquad (4)$$

where: $\bar{x}_{i..}=2^{-1}(\bar{x}_{i1.}+\bar{x}_{i2.})$, $\bar{x}_{...}=2^{-1}(\bar{x}_{.1.}+\bar{x}_{.2.})$, $\bar{x}_{.\Delta.}=2^{-1}(\bar{x}_{.1.}-\bar{x}_{.2.})$, and $\bar{x}_{i\Delta.}=2^{-1}(\bar{x}_{i1.}-\bar{x}_{i2.})$, the dots substituting for the subscripts over which the data were averaged and delta (Δ), as a subscript, referring to half the difference between the two reciprocals. The sums of squares divided by the corresponding degrees of freedom give the respective variances or means squares (*MS*); the mean squares divided by the error mean square [*EMS*, see (1)] give the respective F ratios. The observations on parents A and B were not included in the analysis since they did not have reciprocals as defined for this study.

On the assumption of independence of gene action the expected mean measurement of the i-th family (i.e., data averaged over blocks and reciprocals) can be expressed as:

$$u_i[aa]_.+(1-u_i)[bb]_.+q_i[h]_.=E\,\bar{x}_{1i..} \qquad (5)$$

where $[aa]_.$ and $[bb]_.$ are the mean character-measurements of the sets of homozygous loci, the same as those constituting the genotypes of the parents A and B, respectively, and $[h]_.$ is the dominance deviation, i.e., $[h]_.=[ab]_.-2^{-1}([aa]_.+[bb]_.)$ where $[ab]_.$ is the character-measurement of the set of heterozygous loci, the same as that constituting the genotype of the first generation of the cross between the A and B parents.

If, instead of the mean, half the difference $1/2(\bar{x}_{i1.}-\bar{x}_{i2.})=\bar{x}_{i\Delta.}$ between the reciprocals of the i-th family is considered then its expected value is:

$$u_i[aa]_\Delta+(1-u_i)[bb]_\Delta+q_i[h]_\Delta=E\bar{x}_{i\Delta.} \qquad (6)$$

where $[aa]_\Delta$ and $[bb]_\Delta$ are half the differences of the character measurements of the genomes of the parents A and B acting in conjunction with the plasmons of the parents A and B respectively, and $[h]_\Delta$ is half the difference between the dominances in plasmotypically A and B reciprocals.

In both equations (5) and (6) the coefficients u_i and q_i are such that: u_i=0.5 and $q_i=2^{1-G}$ if the i-th family belongs to set 1 of filial generations, u_i=0.75 and $q_i=2^{-G}$ if the i-th family belongs to set 2 of filial generations, and u_i=0.25 and $q_i=2^{-G}$ if the i-th family belongs to set 3 of filial generations.

The solution of n_i equation (5) with $E\bar{x}_{i..}=\bar{x}_{i..}$ obtains the parameter estimates $[\hat{a}\hat{a}]_.$, $[\hat{b}\hat{b}]_.$ and $[\hat{h}]_.$, and the solution of n_i equation 6 with $Ex_{i\Delta.}=x_{i\Delta.}$ obtains the parameter estimates $[\hat{a}\hat{a}]_\Delta$, $[\hat{b}\hat{b}]_\Delta$ and $[\hat{h}]_\Delta$. Expressed in terms of parameter estimates the value of the mean of the i-th family is $u_i[\hat{a}\hat{a}]_.+(1-u_i)[\hat{b}\hat{b}]_.+q_i\,[\hat{h}]_.$ which differs from the observed mean $\bar{x}_{i..}$ by $\tau_{i..}$ so that

$$u_i[\hat{a}\hat{a}]_.+(1-u_i)[\hat{b}\hat{b}]_.+q_i[\hat{h}]_.+\tau_{i..}=\bar{x}_{i..} \qquad (7)$$

where the $\tau_{i..}$ differences (or residuals) are independently distributed with mean zero and variance ≥0. Therefore the overall mean of n_i family means is:

$$u_.[\hat{a}\hat{a}]_.+(1-u_.)[\hat{b}\hat{b}]_.+q_.[\hat{h}]_.=\bar{x}_{...} \qquad (8)$$

The difference between (7) and (8) is

$$(u_i-u_.)([\hat{a}\hat{a}]_.-[\hat{b}\hat{b}]_.)+(q_i-q_.)[\hat{h}]_.+\tau_{i..}=\bar{x}_{i..}-\bar{x}_{...} \qquad (9)$$

Appropriate substitution in (2) gives:

$$FSS=2n_k\sum_i\{(u_i-u_.)([\hat{a}\hat{a}]_.-[\hat{b}\hat{b}]_.)+(q_i-q_.)[\hat{h}]_.\}^2+2n_k\sum_i\tau^2_{i..} \qquad (10)$$

On the same grounds and by the same procedure one obtains for (3) and (4) respectively:

$$RSS=2n_in_k\,\{u_.[\hat{a}\hat{a}]_\Delta+(1-u_.)[\hat{b}\hat{b}]_\Delta+q_.[\hat{h}]_\Delta\}^2 \qquad (11)$$

and

$$(F{\times}R)\,SS=2n_k\sum_i\{(u_i-u_.)([\hat{a}\hat{a}]_\Delta-[\hat{b}\hat{b}]_\Delta)+(q_i-q_.)[\hat{h}]_\Delta\}^2+2n_k\sum_i\tau^2_{i\Delta.} \qquad (12)$$

Whenever sets 2 and 3 consist of the same filial generations,i.e., whenever the index sets J and K are the same, $u_.=0.5$ *and* $\sum_i(u_i-u_.)(q_i-q_.)=0$. Therefore equations (10) and (12) become respectively:

$$FSS=2n_k([\hat{a}\hat{a}]_.-[\hat{b}\hat{b}]_.)^2\sum_i(u_i-u_.)^2+2n_k[\hat{h}]^2\sum_i(q_i-q_.)^2+2n_k\sum_i\tau^2_{i..} \qquad (13)$$

and

$$(F{\times}R)SS=2n_k\,([\hat{a}\hat{a}]_\Delta-[\hat{b}\hat{b}]_\Delta)^2\sum_i(u_i-u_.)^2+2n_k[\hat{h}]^2_\Delta\,(q_i-q_.)^2+2n_k\sum_i\tau^2_{i.\Delta.} \qquad (14)$$

The corresponding mean-square and the F ratios are obtained as: $FMS=FSS/(n_i-1)$, $F=FMS/EMS$; *and* $(F{\times}R)MS=(F{\times}R)SS/(n_i-1)$, $F=(F{\times}R)MS/EMS$. With $u_.=0.5$ and $df=1$ equation (11) gives $RSS=RMS$ and, therefore,

$$RMS=2n_in_k\,\{0.5([\hat{a}\hat{a}]_\Delta+[\hat{b}\hat{b}]_\Delta)+q_.[\hat{h}]_\Delta\}^2 \qquad (15)$$

The parametres $[\hat{a}\hat{a}]_.$, $[\hat{b}\hat{b}]_.$ and $[\hat{h}]_.$ in n_i equation (5) and the parametres $[aa]_\Delta$, $[bb]_\Delta$ and $[h]_\Delta$ in n_i equation (6) have the same coefficients u_i, $(1-u_i)$ and q_i, respectively. The numerical values of these coefficients particular to this study are listed in Table 1.

Experimental results

The results of the analyses of variance of data recorded for both the characters a=the number of heads per plant and b=yield of grain (in grams) per plant are given in Tables 2 and 3.

The values of the family means $2^{-1}(\bar{x}_{i1.}+\bar{x}_{i2.})=\bar{x}_{i..}$ and of those of half the differences between the reciprocals within the families, i.e., of $2^{-1}(\bar{x}_{i1.}-\bar{x}_{i2.})=\bar{x}_{i\Delta}$ are given in Table 4 for both the characters a (number of heads per plant) and b (grams of grain yield per plant) in experiments #1 and #2.

The linear equations expressing the parametric composition of the family means ($\bar{x}_{i..}$) and of half the differences between the reciprocals within the families ($\bar{x}_{i\Delta}$) are given in Table 1 for the experiments #1 and #2. Appropriate substitutions from Table 4 and subsequent solution of these equations obtain the parameter estimates as listed in Table 5.

In both the experiments #1 and #2 the number of blocks is n_k=4, the number of families is n_i=4 and, as obtained from Table 1, $\sum_i(u_i - u_.)^2$=1/8, and $\sum_i(q_i-q_.)^2$=3/16. By taking into account the above values and substituting the appropriate parameter estimates, listed in Table 5, into equations (13) and (14) and then dividing by $df=n_i-1=3$ one obtains the values of the first two components of FMS and of $(F{\times}R)MS$. The subtraction of these value from FMS and $(F{\times}R)MS$ respectively yields the contributions of the residuals (see Tables 6 and 7).

The values of the components of the $FSS/(n_i-1)=FMS$ ratios [see (13), the analysis of variance tables and Table 5] are given in Table 6.

The values of the components of the $(F{\times}R)SS/(n_i-1)=(F{\times}R)MS$ ratios [see (14), the analysis of variance tables and Table 5] are given in Table 7.

Results

The results of the analysis of variance of the number of heads per plant (character a) and the grain yield (in grams)

Table 1 Experiments 1 and 2

i	Family	$[aa]_{..}[aa]_\Delta$ u_i	$[bb]_{..}[bb]_\Delta$ $(1\text{-}u_i)$	$[h]_{..}[h]_\Delta$ q_i	Known terms: $\bar{x}_{i..}, \bar{x}_{1\Delta}$
1	$\{A{\times}B, B{\times}A\}F_1$	0.5	0.5	1	$\bar{x}_{1..}, \bar{x}_{i\Delta}$
2	$\{A{\times}B, B{\times}A\}F_2$	0.5	0.5	0.5	$\bar{x}_{2..}, \bar{x}_{2\Delta}$
3	$\{(A{\times}B)F_1\ A,(B{\times}A)F_1\ A\}F_1$	0.75	0.25	0.5	$\bar{x}_{3..}, \bar{x}_{3\Delta}$
4	$\{(A{\times}B)F_1\ B,(B{\times}A)F_1\ B\}F_1$	0.25	0.75	0.5	$\bar{x}_{4..}, \bar{x}_{4\Delta}$
	Means:	$u_.$=0.5	0.5	$q_.$=0.625	$\bar{x}_{...}, \bar{x}_{.\Delta}$

Table 2 Experiment #1 (unvernalized)

Source of var.	df	Character a		Character b	
		MS	F	MS	F
Families (F)	3	10.6694	2.4752+	135.3856	7.1659**
Reciprocals (R)	1	206.6036	47.9303**	741.2213	39.2324**
Blocks (B)	3	20.3395	4.7186**	88.0026	4.6529**
F×R	3	7.7113	1.7890	31.0734	1.6447
F×B	9	7.8267	1.8157	16.1804	0.8564
R×B	3	20.3695	4.7256**	73.1626	3.8725**
F×R×B	9	4.8270	1.1198	13.9402	0.7378
Error (E)	1391	4.3105	–	18.8931	–

+ P=0.10; ** P=0.01

Table 3 Experiment #2 (vernalized)

Source	df	Character a		Character b	
		MS	F	MS	F
Families (F)	3	21.9675	13.5035**	168.8779	21.9756**
Reciprocals (R)	1	29.7413	18.2821**	134.6030	17.5155**
Blocks (B)	3	5.8090	3.5708*	45.6104	5.9351**
F×R	3	0.8866	0.5450	2.9713	0.3866
F×B	9	1.2606	0.7749	7.8498	1.0215
R×B	3	1.2334	0.7582	5.5078	0.7167
F×R×B	9	2.3802	1.4631	6.2247	0.8100
Error (E)	1438	1.6268	–	7.6848	–

* P=0.05; ** P=0.01

Table 4 The values of $x_{i..}$ and $x_{i\Delta}$

Experiment #1 (unvernalized)

i	Family	$1/2(\bar{x}_{i1.}+\bar{x}_{i2.})=\bar{x}_{i..}$		$1/2(\bar{x}_{i1.}+\bar{x}_{i2.})=\bar{x}_{i\Delta}$	
		a	b	a	b
1	{A×B, B×A}F_1	21.201,25	44.292,50	2.533,75	3.917,50
2	{A×B, B×A}F_{21}	18.633.75	35.206,25	2.906,25	5.066,25
3	{(A×B)F×A,(B×A)F_1 A}F_1	18.898,75	36.575,00	1.201,25	2.837,50
4	{(A×B)F_1×B,(B×A)F_1 B}F_1	19.710,00	36.790,00	3.522,50	7.435,00
	$\bar{x}_{...}$	19.610,937,5	38.217,187,5	–	–
	$\bar{x}_{.\Delta.}$	–	–	2.540,937,5	4.812,812,5

Experiment #2 (vernalized)

i	Family	$\bar{x}_{i...}$		$\bar{x}_{.\Delta.}$	
		a	b	a	b
1	{A×B, B×A}F_1	13.667,50	26.831,25	1.235,00	2.676,35
2	{A×B, B×A}F_2	12.971,25	23.435,00	0.498,75	1.292,50
3	{(A×B)F_1×A,(B×A)F_1 A}F_1	14.312,50	27.083,70	0.952,50	1.853,75
4	{(A×B)F_1×B,(B×A)F_1 B}F_1	10.522,50	17.218,75	1.170,00	2.381,25
	$\bar{x}_{...}$	12.868,437,5	23.642,175	–	–
	$\bar{x}_{.\Delta.}$	–	–	0.964,062,5	2.050,937,5

Table 5 The parameter estimates for $x_{i..}$ and $x_{i\Delta}$

Experiment #1 (unvernalized) (*DF*=1)

	Character a	Character b		Character a	Character b
$[\hat{a}]_.$	16.149±1.139	27.868±2.508	$[\hat{a}]_\Delta$	0.232±0.925	1.716±0.119*
$[\hat{b}]_.$	17.772±1.139	28.298±2.508	$[\hat{b}]_\Delta$	4.874±0.925	10.911±0.119**
$[\hat{h}]_.$	4.24±1.264	16.214±2.783	$[\hat{h}]_\Delta$	−0.019±1.026	−2.401±0.132*

(*)P=0.05;(**) P=0.01

Experiment #2 (vernalized) (*DF*=1)

	Character a	Character b		Character a	Character b
$[\hat{a}]_.$	15.32±0.941	28.192±2.182	$[\hat{a}]_\Delta$	0.295±0.956	0.481±1.402
$[\hat{b}]_.$	7.747±0.941	8.462±2.182	$[\hat{b}]_\Delta$	0.730±0.956	1.536±1.1402
$[\hat{h}]_.$	2.131±1.044	8.504±2.421	$[\hat{h}]_\Delta$	0.723±1.061	1.668±1.556

Table 6 The values of the components of the *FSS*/(n_i−1)=*FMS* ratios

Experiment #1, components of *FMS*	Character a	Character b
$([\hat{a}]_. - [\hat{b}]_.)^2\, 2n_k\sum_i(u - u_{..})^2/(n_i - 1)$	0.8781 (8.23%)	0.0619 (0.05%)
$[\hat{h}]^2\, 2n_k\sum_i(q_i - q_.)^2/(n_i - 1)$	8.9930 (84.29%)	131.4469 (97.09%)
$2n_k\sum r^2_{i..}/(n_i - 1)$	0.7983 (7.48%)	3.8768 (2.87%)
Total: $FSS/(n_i - 1)=FMS$	10.6694 (100%)	135.3856 (100%)**

(+) P=0.1; (**) P=0.01

Experiment #2, components of *FMS*	Character a	Character b
$([\hat{a}]_. - [\hat{b}]_.)^2\, 2n_k\sum_i(u_i - u_.)^2/(n_I - 1)$	19.1522 (87.18%)	129.7576 (76.84%)
$[\hat{h}]^2\, 2n_k\sum_i(q_i - q_.)^2/(n_i - 1)$	2.2705 (10.34%)	36.1590 (21.41%)
$2n_k\sum_i r^2_{i..}/(n_i - 1)$	0.5448 (2.48%)	2.9613 (1.75%)
Total: $FSS/(n_i - 1)=FMS$	21.9675 (100%)**	168.8779 (100%)**

(**)P=0.01

Table 7 The values of the components of $(F{\times}R)SS/(n_i{-}1)=(F{\times}R)MS$ ratio

Experiment #1, components of$(F{\times}R)MX$	Character a	Character b
$([a\hat{a}]_{\Delta}-[b\hat{b}]_{\Delta})^2\, 2n_k\sum_i(u_i-u_{..})^2/(n_i-1)$	7.1827 (93.15%)	28.1827 (90.70%)
$[\hat{h}]_{\Delta}\, 2n_k\sum_i(q_i-q_{.})^2/(n_i-1)$	0.0002 (0%)	2.8824 (9.28%)
$2n_k\sum_i r^2_{i\Delta.}/(n_i-1)$	0.5284 (6.85%)	0.00083 (0.02%)
Total: $(F{\times}R)SS/(n_i-1)=(F{\times}R)MS$	7.7113 (100%) $^{(+)}$ P=0.1; $^{(**)}$P=0.01	31.0734 (100%)
Experiment #2, components of $(F{\times}R)MS$	Character a	Character b
$([a\hat{a}]_{\Delta}-[b\hat{b}]_{\Delta})^2\, 2n_k\sum_i(u_i-u_{..})^2/(n_i-1)$	0.0631 (7.12%)	0.3710 (12.48%)
$[\hat{h}]_{\Delta}\, 2n_k\sum_i(q_i-q_{.})^2/(n_i-1)$	0.2614 (29.48%)	1.3911 (46.82%)
$2n_k\sum_i(r^2_{i\Delta.}/(n_i-1)$	0.5621 (63.40%)	1.2092 (40.70%)
Total: $(F{\times}R)SS/(n_i-1)=(F{\times}R)MS$	0.8866 (100%)	2.9713 (100%)

per plant (character b) in the two experiments are fairly similar (Tables 2 and 3). For both characters the family mean squares are significant in both experiments #1 and #2, and so are the reciprocals and blocks mean squares. Of the interaction mean squares only reciprocals × blocks mean square is significant for both the characters a and b in experiment #1 but not in #2.

As to be expected the plot means for the characters a and b are positively correlated, namely, r_{ab}=+0.94 (*df*=30, *P*=0.01) in experiment #1 and r_{ab}=+0.96 (*df*=30, *P*=0.01) in experiment #2. This correlation is reflected in the results of the analysis of variance of the data recorded on the two characters in question. The coefficients of correlation between the *F* ratios for the characters a and b are: r_{ab}=0.99 (*df*=5, *P*=0.01) in experiment #1 and r_{ab}=+0.94 (*df*=5, *P*=0.01) in experiment #2.

The experiments #1 and #2 were spring sown at the same time in the same field with the materials consisting of the same families. The overall means ($\bar{x}_{...}$) given in Table 4 show that vernalization (experiment #2) has reduced the degree of expression for both the characters, viz., by 19.61–12.87=6.74 heads and by 38.22–23.64=14.58 grams of grain yield per plant.

Half the differences ($\bar{x}_{i\Delta..}$) between the plasmotypically A (Sakhalin) and B (Khush-hal) reciprocals listed in Table 4 show that the same sets of genotypes when acting in conjunction with the plasmotype of the parent A have produced more heads and higher grain yields per plant, viz., on the average $2\bar{x}_{.\Delta.}$=5.08 more heads and $2\bar{x}_{.\Delta.}$=9.63 grams more grain per plant in experiment #1; the respective figures in experiment #2 are 1.93 more heads and 4.10 grams more grain per plant.

The estimated values of the components of family means and those of half the differences between the reciprocals (plasmotypes) within the families are listed in Table 5 for both the characters in experiments #1 and #2. The parameter estimate $[a\hat{a}]_.$ in experiment #2 is more or less the same as in experiment #1 for both the characters in question, but the parameter estimates $[b\hat{b}]_.$ and $[\hat{h}]_.$ are considerably lower. This suggests that vernalization has affected the degree of character expression of the nuclear genes of parent *B* (Khush-hal) but not those of parent *A* (Sakhalin).

The estimated values of the parameters $[a\hat{a}]_{\Delta}$ and $[\hat{h}]_{\Delta}$ for the character a (no. of heads/plant) in experiment #1 are not significant, which means that the nuclear genes of the parent A when homozygous are expected to produce the same number of heads per plant regardless of the plasmotype, and the dominance $[\hat{h}]_.$ to be the same in the reciprocals. With $[b\hat{b}]_{\Delta}$=4.874±0.925 the nuclar genes of parent B, when homozygous, are expected to produce $[b\hat{b}]_.+[b\hat{b}]_{\Delta}$=22.646±1.735 heads per plant when acting in conjunction with the plasmotype of parent A and $[b\hat{b}]_.-[b\hat{b}]_{\Delta}$=12.898±1.735 heads per plant when acting in conjunction with the plasmotype of its own kind. The observed number of heads per plant produced by parent B is 10.11±0.47 (*df*=80) which is not significantly different from the estimated 12.898±1.735 heads per plant. For the character b (grams of grains/plant) all three parameter estimates $[a\hat{a}]_{\Delta}$, $[b\hat{b}]_{\Delta}$ and $[\hat{h}]_{\Delta}$ are significant and, as such, the components of the means of the plasmotypically A reciprocals are expected to be $[a\hat{a}]_.+[a\hat{a}]_{\Delta}$=29.584±2.530 and $[b\hat{b}]_.+[b\hat{b}]_{\Delta}$=39.209±2.530 grams of grain per plant, and the dominance deviation to be 13.813±2.786. The respective values for the plasmotypically B reciprocals are: 26.152±2.530, 17.387±2.530 and 18.615±2.786. Parent B has produced 13.595±1.370 (*df*=80) grams of grain per plant which is not significantly different from the estimated value of 17.387±2.530.

In experiment #2 (vernalized) none of the parameter estimates $[a\hat{a}]_{\Delta}$, $[b\hat{b}]_{\Delta}$ and $[\hat{h}]_{\Delta}$ is significant and so is $[\hat{h}]_.$ The observed character measurement means of the parents A (Sakhalm) and B (Khushhal) are, respectively, 15.27±2.02 and 9.83±0.72 heads per plant, and 29.25±4.69 and 11.64±1.04 grams of grain per plant. The expected values for nuclear genes of parent A when homozygous and acting in conjunction with their own plasmotype are $[a\hat{a}]_.+[a\hat{a}]_{\Delta}$=15.622±1.341 heads and 28.673±2.599 grams of grain per plant which are not significantly different from the observed values of 15.27±2.02 and 29.25±4.69, respectively (*df*=50). The expected values for the nuclear genes of parent B when homozygous and acting in conjunction with their own plasmotype are $[\hat{b}\hat{b}]_{.}+[\hat{b}\hat{b}]_{\Delta}=7.017\pm1.343$ heads per plant and 6.926 ± 2.590 grams of grain per plant which differ significantly from their respective observed values of 9.83 ± 0.72 heads and 11.64 ± 1.04 grams of grain per plant ($df=67$).

As shown in Table 6, the family mean-square (*FMS*) and the (family) × (reciprocals) interaction mean-square [$(F{\times}R)MS$] in the analysis of variance Tables 2 and 3 each consist of three component parts. If it is assumed that there is no dominance, i.e., that the parental genes contribute additively, the character-measurement of the F_1 generation of the cross between the parents A and B is expected to be equal to the mean of the character-measurements of the parents A and B, viz., $[\hat{a}\hat{b}]_{.}=2^{-1}([\hat{a}\hat{a}]_{.}+[\hat{b}\hat{b}]_{.})$, and the component $([\hat{a}\hat{a}]_{.}-[\hat{b}\hat{b}]_{.}{}^{2}2n_k\sum_i(u_i-u_{.})2/(n_i-1)$ of the *FMS* to constitute its additive part. In experiments #1 and #2 this component accounts for 8.23% and 87.18%, respectively, of the *FMS* in the case of character a (no. of heads/plant) and for 0.05% and 97.09%, respectively, of the *FMS* in the case of character b (grams of grain/plant). With dominance $[\hat{h}]_{.}\neq0$, a second component of *FMS* has to be considered, viz., $[\hat{h}]^2 2n_k \sum_i(q_i-q_{.})^2/(n_i-1)$. The contributions of this dominance component to the *FMS* in Tables 2 and 3 (experiments #1 and #2) are, respectively, 84.29% and 10.34% in the case of character a (no. heads/plant) and 97.09% and 21.41% in the case of character b (grams of grain/plant). The respective contributions of the residuals $2n_k\sum_i r_i^2/(n_i-1)$ to the *FMS* are:7.48% and 2.87% for the characters a and b in Table 2 (experiment #1), and 2.48% and 1.75% for the character a and b in Table 3 (experiment #2). The figures listed in Table 6 show that in Table 2 the dominance component $[\hat{h}]^2 2n_k\sum_i(q_i-q_{.})^2/(n_i-1)$ alone is sufficient to render *FMS/EMS*=F ratio significant, particularly in the case of character b; in Table 3 (experiment #2) the additive component $([\hat{a}\hat{a}]_{.}-[\hat{b}\hat{b}]_{.})^2 2n_k\sum_i(u_i-u_{.})^2/(n_i-1)$ alone is enough to make the *FMS/EMS*=F ratio significant for both the characters a and b.

The relative value (in %) of the $FMS-2n_k\sum_i r_i^2/(n_i-1)$ difference shows how well the family means $(\bar{x}_{i..})$ fit the expectation (5). In experiment #1 this expectation accounts for 92.52% of the *FMS* in the case of character a, and for 97.14% of the *FMS* in the case of Character b.

With $\bar{x}_{i..}=2^{-1}(\bar{x}_i 1+\bar{x}_{i2})$ and $\bar{x}_{i\Delta}=2^{-1}\bar{x}_{i1}-\bar{x}_{i1})$ and, implicitly, $\bar{x}_{i1.}=\bar{x}_{i..}+\bar{x}_{i\Delta}$ and $\bar{x}_{i2.}=\bar{x}_{i2.}-\bar{x}_{i\Delta}$, the (family)×(reciprocals) interactions mean square [$(F{\times}R)MS$] takes the form of the mean square of half the differences between the reciprocals within the families [see (4)]. In both experiments the $(F{\times}R)MSs$ turn out not to be significant. Nevertheless, in order to check the expectation (6) the components of half the differences between the reciprocal within the families, i.e., of $\bar{x}_{i\Delta}$'s (see Table 5) were estimated and the components of $(F{\times}R)MSs$ were computed [see (14) and Table 7]. Table 7 is similar to Table 6 with the differences that instead of the parameters $[\hat{a}\hat{a}]_{.}$, $[\hat{b}\hat{b}]_{.}$ and $[\hat{h}]_{.}$ estimated from family means $(\bar{x}_{i..})$, the parameters $[\hat{a}\hat{a}]_{\Delta}$, $[\hat{b}\hat{b}]_{\Delta}$ and $[\hat{h}]_{\Delta}$ estimated from half the differences between the reciprocals within the families, are used (see Table 5). As shown in Table 7, the additive component $([\hat{a}\hat{a}]_{\Delta}-[\hat{b}\hat{b}\ ]_{\Delta})^2$ $2n_k\sum_i(u_i-u_{.})^2/(n_i-1)$, the dominance component $[\hat{h}]^2 2n_k\sum_i(u_i-u_{.})^2/(n_i-1)$ and the residuals component $2n_k\sum_i r_{i\Delta}^2/(n_i-1)$ in experiment #1 (Table 2) account fo r 93.15%, 0% and 6.85%, respectively, of the $(F{\times}R)MS$ in the case of character a (no. heads/plant) and for 90.70%, 9,28% and 0.02%, in that order, in the case of character b (grams of grain/plant). In experiment #2 (Table 3) the corresponding values are 7.12%, 29.48% and 63.40% in the case of character a, and 12.48%, 46.82% and 40.70% in the case of character b.

The relative values (in%) of the $(F{\times}R)MS-2n_k\sum_i r_{i\Delta}^2$ difference are 93.15% for character a, and 99.98% for character b in experiment #1; and only 36.60% for character a and 59.30% for character b. The above figures show that in experiment #1 half the differences between the reciprocals in the families fit expectation (6) well, but not in experiment #2.

In both experiments #1 and #2 the reciprocal mean squares (*RMS*) are significant for character a as well as for character b. The values of the *RMSs* are obtained by substituting the appropriate values of the components of half the differences between reciprocals in the families from Table 5 in expression (15). For both the characters a and b in experiment #1 the main contributor to the *RMS* is the parameter estimate $[\hat{b}\hat{b}]_{\Delta}$. In contrast to experiment #1, in experiment #2 all three parameter estimates $[\hat{a}\hat{a}]_{\Delta}$, $[\hat{b}\hat{b}]_{\Delta}$ and $[\hat{h}]_{\Delta}$ have positive values and their joint contribution renders the *RMS* significant, although considered individually none of them is significant.

Discussion

The degree of expression of quantitative characters – the number of heads and grams of grain per plant in the present case – depends on growing conditions and the ideotypic ability of individuals or groups of individuals to use them efficiently.

The experiments #1 (unvernalized) and #2 (vernalized) were spring-sown at the same time in the same field using the seeds of the same families. However, because of the vernalization of the seeding materials for experiment #2, the development of the plants in the two experiments was not the same. In experiment #1 the winter-type parent Sakhalin and all the plants in the families with a winter growth habit have not headed; the plants with a spring growth habit in either the homozygous or the heterozygous state have headed and produced seeds. In experiment #2, grown from vernalized seeds, all the plants in the families, including those of the winter-type parent Sakhalin, have headed and produced seeds. The vernalization was needed to induce the winter-type plants in the population to head. For the genotypically spring-type plants in the families, in both the homozygous and heterozygous state, vernalization was not necessary but, because some of the seeds in the materials were expected to produce winter-type plants, all the seeds, including those of the spring-type parent Khush-hal used as a check, were vernalized. Although the winter-type plants have not contributed to character-measurement means of the families in experiment #1, the genotypic composition for the two characters, number of heads and grain yield per plant, was assumed to be the same in the two experiments. For both the characters, the family means and half the differences between the plasmotypically winter-type Sakhalin and spring-type Kush-hal reciprocals in the families are considerably higher in experiment #1 (unvernalized). This shows that vernalization has reduced the degree of expression of the family means and the differences between the plasmotypically winter-type Sakhalin and plasmotypically spring-type Khush-hal reciprocals within the families. The estimated values of the components of family means and those of half the differences between the reciprocals within the families show that in experiment #1 (unvernalized) the highest number of heads and the highest grain yield per plant are expected to be produced by the plants which are nuclear genetically the same as the spring-type parent Khush-hal when acting in conjunction with the plasmotype of the winter-type parent Sakhalin, viz., 22.65 heads and 39.21 grams of grain per plant. When acting in conjunction with their own plasmotype these amounts are reduced to 12.90 heads and 17.39 grams of grain per plant. The respective figures for the plants nuclear genetically the same as the winter-type parent Sakhalin are 16.38 heads and 29.58 grams of yield, and 15.92 heads and 26.15 grams of grain yield per plant. In experiment #2 the vernalization has drastically reduced the degree of expression of the plants nuclear genetically the same as the spring-type parent Khush-hal, but seems not to have affected the degree of expression of the plants nuclear genetically the same as the winter-type Sakhalin. These plants, notwithstanding plasmotypes and vernalization, are expected to produce the same number of heads and the same amount of grain yield per plant as the winter-type parent Sakhalin grown from vernalized seeds.

The results of the analysis of variance in the two experiments are fairly similar but the component parts of the family mean squares and the (family reciprocals) interaction mean squares are not the same. In experiment #1 (unvernalized), with respect to both the characters in question, most of the family mean squares (*FMS*) is due to dominance whereas in experiment #2 (vernalized) it is due to the additive component. In experiment #1 most of the (family×reciprocals) interaction mean squares [$(F{\times}R)MS$] is contributed by its additive part of variation for both the characters, number of heads and the grain yield (in grams) per plant, whereas in experiment #2 it is due mostly to its nonheritable part, i.e., to residuals.

In both experiments #1 and #2 a very low rate of seeding was used, viz., one seed per 450 cm^2 or 100 seeds per 4.5 m^2. Such a low rate of seeding most likely precluded competition between the plants so that, provided that the growing conditions are adequate, all the plants perform according to their ideotypic ability. The experimental results obtained in the two experiments are on a single plant basis. In breeding work the yielding ability of wheat and, in general, of cereal strains is judged on the basis of yield obtained per unit area, the usual rate of seeding being 350–400 seeds per m^2.

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