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The Inheritance of Lipoxidase Activity and Pigment Content in Durum Wheat *

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Summary. Analysis of a 10-parent diallel of durum wheat *(Triticum turgidum* L. var. *durum)* grown at two diverse locations revealed that for enzyme lipoxidase activity, wheat and predicted macaroni pigment contents, heterosis was environmentally dependent. Both additive and dominance genetic effects were significant for each of these quality traits studied, but in one location, the additive genetic effect was consistently more pronounced than the dominance genetic effect, while the reverse was the case in the other location. There was no evidence of epistatic gene effect for any of the three characters in either location.

Introduction

Yellow pigment content of durum wheat *(Triticum turgidum* L. var. *durum)* is the most important criterion of the quality of this grain for pasta production (Irvine 1971). Some of the original pigment is lost during processing of the milled durum product, semolina, into the pasta product. The rate of this pigment loss depends on the activity of the enzyme lipoxidase in the semolina (Irvine 1971). It is generally known that both pigment contents and lipoxidase activity are largely varietal characteristics, although they can also be affected by environmental factors (Irvine and Anderson 1953). The relative importance of the genotype and the environment in determining pigment content and lipoxidase activity in durum wheat has not been studied yet. Moreover, very little is known about the nature of the genetic system governing the inheritance of these important quality characteristics (Braaten, Lebsock and Sibbitt 1962). Therefore, the present study was undertaken in order to provide information regarding the nature, magnitude and stability of the genetic parameters related to wheat and macaroni pigment contents and lipoxidase activity in durum wheat.

Materials and Methods

The ten durum cultivars used in this study and their countries of origin were: Adur (A, France), Candeal Selection (C, Argentina), DT-310 (D, Canada), Iumillo (I, Italy), Kharkov Kaja (K, Russia), Leeds (L, U.S.A.), Madif (M, Italy), My-54 (My, Mexico), Naradnaja (N, Russia) and Stewart 63 (S, Canada). These cultivars were crossed in a diallel fashion and the reciprocal families were bulked to produce 45 first generation hybrids. The seed was then used to produce 45 F_2 families. Seed from the 45 F_2 families and the 10 parental cultivars was sown in May, 1971 at Winnipeg, Manitoba and at Swift Current, Saskatchewan. At each location, the diallel experiment was laid out in a randomized complete block design with two replications. Each plot consisted of three 3-meter rows with 160 seeds per row. The distance between rows was 30 cm. Single border rows of the common wheat cultivar 'Manitou' were planted between adjacent plots to equalize border effects between plots and to minimize inter-plot competition.

Approximately 20 gm. of the threshed, cleaned seed was sampled from each plot for the two quality tests. Wheat pigment content (p.p.m.) and lipoxidase activity units were determined following the methods described by Irvine and Anderson (1953). Macaroni pigment content (p.p.m.) was then calculated from the following multi-linear regression equation derived by Irvine and Anderson (1955):

$Pm = 0.807\ Pw - 0.0105\ Lw - 0.383$

where Pm = macaroni pigment, p.p.m.,
Pw = wheat pigment, p.p.m., and
Lw = lipoxidase activity, $\mu\ 10_2$/min./g.

All results presented herein are on a 14% moisture content basis.

Preliminary analysis of variance was made for each of the three quality traits in order to estimate their genotypic and environmental (i.e. replicates within each location) effects. Heterosis or hybrid performance for each of the three characters were estimated by comparing each hybrid with its midparent value. LSD values were used to test each hybrid-midparent contrast. General and specific combining ability analyses were conducted with the parental and F_2 data according to the procedure outlined by Griffing (1956) and were designated as method 2 of model I. Genetic parameters were estimated following the methods of Jinks (1954) and Hayman (1954) for the F_1 diallel excepting that the contribution of the dominance effect of the heterozygote for the F_2 generation was halved due to an additional generation of inbreeding (Lee and Kaltsikes, 1972). The narrow sense heritability estimates for each of the three characters, defined as the ratio of the additive and/or additive × additive genetic variance to the total phenotypic var-

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Table 1. Lipoxidase activity and yellow pigment contents of the ten durum cultivars grown at Winnipeg (Wpg.) and at Swift Current (S.C.)

Cultivar	Lipoxidase activity[1]		Wheat pigment[2]		Predicted Macaroni pigment[2]	
	Wpg.	S.C.	Wpg.	S.C.	Wpg.	S.C.
A	91.81	95.51	4.78	3.73	2.50	1.62
C	74.25	65.57	4.98	6.50	2.86	4.18
D	90.74	78.88	5.26	4.88	2.91	2.72
K	101.30	90.31	5.55	5.55	3.03	3.15
M	98.28	121.80	5.06	4.37	2.67	1.87
N	89.92	91.52	5.38	4.42	3.01	2.22
L	83.72	90.17	5.43	6.90	3.12	4.24
S	120.13	68.91	4.22	4.39	1.76	2.43
I	114.66	158.14	5.08	3.42	2.51	0.71
My	81.38	75.21	5.86	5.93	3.50	0.36
LSD(0.05)	12.56	13.92	0.29	0.21	0.29	0.24
LSD(0.01)	16.71	18.52	0.38	0.28	0.38	0.32

[1] $\mu 10_2$/min./g.; low value is desirable

[2] Parts per million (p.p.m.).

iance, were obtained following Crumpacker and Allard (1962). The stability of the genetic systems governing the three characters over the two locations was systematically tested according to Allard (1956) by the use of a computer programme developed by Lee and Kaltsikes (1972).

Results and Discussion

Preliminary Analysis of Variance

The variation among the 55 entries (45 F_2 families and 10 parents) was highly significant ($P \leq 0.01$) for each of the 3 characters for material grown at both locations and thus accounted for a major portion of the total phenotypic variation. This result was not unexpected since the parental cultivars were derived from extremely diverse geographic origins, and consequently, these cultivars and the progenies derived from them were expected to show diversity in both genotypes and adaptability with respect to these three characters. Replication effects were highly significant ($P \leq 0.01$) for wheat pigment for both locations and derived macaroni pigment for Winnipeg, and significant ($P \leq 0.05$) for lipoxidase activity for Winnipeg and macaroni pigment for Swift Current. However, no replication effect was evident for lipoxidase activity for Swift Current.

Parental Performance and Heterotic Effects

The parental performance for each of the three characters at each location (Table 1) revealed substantial variation among cultivars. Candeal Selection had the lowest values for lipoxidase activity at both locations while Stewart 63 and Iumillo had the highest values at Winnipeg and Swift Current, respectively. Wheat pigment for the Winnipeg material ranged from 4.22 p.p.m. (Stewart 63) to 5.86 p.p.m. (My-54). The same character for the Swift Current material ranged from 3.42 p.p.m. (Iumillo) to 6.90 p.p.m. (Leeds). Macaroni pigment from the Winnipeg material ranged from 1.76 p.p.m. (Stewart 63) to 3.50 p.p.m. (My-54) while that for the Swift Current material ranged from 0.71 p.p.m. (Iumillo) to 4.24 p.p.m. (Leeds).

From the differences in the relative parental performance (i.e. ranking) for each of the three characters over the two locations (Table 1), it was evident that the environmental complex (location) had a substantial influence in the phenotypic expression for these characters. Moreover, certain cultivars were relatively more stable over environments than others. For example, considering all three characters, Kharkov Kaja was the most stable cultivar while the reverse was the case with Iumillo.

Heterosis for each of the three characters in both locations, expressed as deviation of the hybrid value from the mid-parent value, is presented in Table 2. On the whole, the material grown in Winnipeg showed an appreciably greater frequency of significant absolute (i.e. positive and negative) heterotic effect than that grown at Swift Current. For lipoxidase activity, 21 hybrids out of the 45 showed significant absolute heterotic effect in the Winnipeg grown material while only 8 hybrids showed the same effect in the Swift Current material. For wheat and macaroni pigments, there were 21 and 28 hybrids, respectively, which showed significant absolute heterosis for Winnipeg while only

Table 2. Hybrid performance for lipoxidase activity and yellow pigment contents expressed as deviation from mid-parent value

Hybrid	Lipoxidase activity[1]		Wheat pigment[2]		Predicted Macaroni pigment[2]	
	Wpg.	S.C.	Wpg.	S.C.	Wpg.	S.C.
C × A	26.52**	-8.12	-0.36*	0.19	-0.56**	0.24*
D × A	1.32	-11.86	-0.74**	0.08	-0.60**	0.18
K × A	7.94	-7.91	-0.34*	-0.20	-0.36*	-0.09
M × A	33.32**	-1.16	-0.32*	-0.09	-0.60**	-0.06
N × A	-0.11	-3.82	-0.77**	-0.02	-0.61**	0.03
L × A	17.80*	-2.33	-0.06	-0.56**	-0.22	-0.42**
S × A	-13.21*	-10.04	-0.01	-0.18	0.14	-0.04
I × A	30.42**	20.00**	-0.84**	-0.02	-0.99**	-0.22
My × A	12.84*	4.53	-0.03	-0.39**	-0.16	-0.36**
D × C	-8.50	-5.12	0.13	-0.02	0.19	0.04
K × C	3.04	1.39	0.10	-0.08	0.06	-0.08
M × C	7.28	-23.68**	0.56**	-0.16	0.36*	0.10
N × C	8.96	-7.78	-0.04	-0.02	-0.12	0.07
L × C	5.41	6.43	0.57**	-0.01	0.41**	-0.08
S × C	-11.49	0.55	0.42**	-0.30**	0.46**	-0.24*
T × C	31.50**	-9.12	-0.14	0.05	-0.44**	0.14
My × C	31.98**	7.60	-0.01	0.21*	-0.35*	0.08
K × D	-8.45	7.32	-0.31*	0.06	-0.16	-0.02
M × D	-11.90	-24.12**	0.01	0.14	0.13	0.38**
N × D	5.05	-10.71	-0.91**	-0.10	-0.79**	0.04
L × D	-5.08	-7.18	0.06	-0.46**	0.10	-0.30*
S × D	-20.12**	10.42	0.11	-0.54**	0.30*	-0.54**
I × D	20.60**	10.48	-0.66**	-0.16	-0.75**	-0.23
My × D	-7.21	10.09	-0.28	-0.14	-0.16	-0.21
M × K	22.29**	6.06	-0.06	-0.32**	-0.28	-0.32**
N × K	2.96	-11.64	-0.38**	-0.02	-0.34*	0.11
L × K	-8.08	-0.06	0.20	-0.33**	0.24	-0.28*
S × K	-9.28	32.21**	0.56**	-0.91**	0.56**	-1.07**
I × K	28.35**	4.10	-0.28	-0.06	-0.53**	-0.09
My × K	-6.93	7.45	0.28	-0.18	0.30*	-0.23
N × M	13.78*	-18.77**	-0.33*	-0.08	-0.41**	0.12
L × M	-0.55	-14.54*	0.48**	-0.34**	0.40**	-0.12
S × M	-22.48**	-3.52	0.46**	0.05	0.60**	0.08
I × M	18.91**	-17.06*	-0.37*	0.06	-0.50**	0.22
My × M	3.84	-4.80	0.24	-0.08	0.14	-0.02
L × N	7.12	-5.46	-0.04	-0.28**	-0.10	-0.17
S × N	-11.44	2.96	0.10	-0.02	0.20	-0.04
I × N	22.84**	0.22	-0.52**	0.06	-0.65**	0.05
My × N	20.50**	11.92	-0.21	0.04	-0.38**	-0.10
S × L	-16.82**	-6.18	0.78**	-0.44**	0.81**	-0.29*
I × L	28.55**	2.54	-0.14	-0.40**	-0.41**	-0.34**
My × L	14.69	-1.28	0.03	-0.52**	-0.13	-0.41**
I × S	9.13	12.33	-0.24	0.12	-0.28	-0.03
My × S	-25.90**	17.42*	0.24	0.02	0.46**	-20
My × I	37.56**	12.67	-0.46**	-0.46**	-0.78**	-0.50**

* Significant at 5% level
** Significant at 1% level
[1] $\mu 10_2$/min./g.; negative heterosis is desirable
[2] Parts per million (p.p.m.)

15 and 14 hybrids, respectively, showed similar effect for Swift Current.

When only the desirable type of heterosis was considered (i.e. negative heterosis for lipoxidase activity and positive heterosis for both pigments), 5 hybrids showed significant heterotic effect for lipoxidase activity from both locations; 7 and 1 hybrids showed a significant heterosis for wheat pigment for Winnipeg and Swift Current, respectively, while 10 and 2 hybrids, showed a similar effect for macaroni pigment from Winnipeg and Swift Current, respectively. It seemed that the environmental conditions at Winnipeg, which had a somewhat lower mean temperature and higher moisture, were more conductive to hybrid vigour for the three quality traits than the more hot and arid conditions at Swift Current (the summer of 1971 in Winnipeg was cooler

Table 3. Estimates of combining ability effects and variances for lipoxidase activity and yellow pigment contents

Cultivar	Lipoxidase activity[1] Wpg.	S.C.	Wheat pigment[2] Wpg.	S.C.	Predicted Macaroni pigment[2] Wpg.	S.C.
General combining ability effects						
A	3.55	-0.31	-0.42	-0.62	-0.38	0.50
C	-7.07	-16.71	0.07	0.85	0.13	0.86
D	-9.58	-8.63	-0.11	-0.04	0.01	0.05
K	1.21	2.06	0.24	0.21	0.18	0.15
M	2.42	6.09	0.06	-0.27	0.02	-0.28
N	-1.32	-4.17	-0.09	-0.22	-0.06	-0.13
L	-6.64	-3.59	0.35	0.78	0.36	0.67
S	-2.16	-7.21	-0.21	-0.38	-0.15	-0.23
I	24.22	35.74	-0.29	-0.75	-0.49	-0.98
My	-4.62	-3.27	0.39	0.45	0.37	0.40
S.E.($\hat{g}i-\hat{g}j$)	2.58	2.81	0.06	0.05	0.06	0.03
Variances						
g.c.a.	1094.29**	2354.27**	0.89**	3.72**	0.95**	3.64**
s.c.a.	140.83**	81.42*	0.06**	0.04**	0.08**	0.04**

[1] $\mu 10_2$/min./g.; low value is desirable
[2] Parts per million (p.p.m.)
* Significant at 5 % level
** Significant at 1 % level

and had a higher rainfall than usual). The results in Table 2 also revealed that, in most cases, the same hybrid did not exhibit heterotic effects in both locations or that in one location it showed positive heterosis while in the other, it showed negative heterosis. It was apparent that for the three characters studied, heterosis was largely environmentally dependent. These results were in general agreement with those of Griffing and Zsiros (1971), who demonstrated that heterosis exhibited by *Arabidopsis thaliana* was biotically and environmentally dependent. Thus, it is clear that the same set of hybrids could perform quite differently under a different environmental complex. Kaltsikes and Larter (1970) found that the environment exerted a substantially greater effect on the phenotypic expression of three agronomic characters in durum wheat, although a genetic effect was also evident.

General and Specific Combining Ability

The results of analysis for the general combining ability (g.c.a.) and specific combining ability (s.c.a.) are presented in Table 3. Highly significant ($P \leqslant 0.01$) g.c.a. and s.c.a. variances were obtained for all characters in both locations excepting the s.c.a. variance for lipoxidase activity at Swift Current ($P \leqslant 0.05$). Since g.c.a. provides an estimate for additive genetic effect while s.c.a. provides estimate for non-additive genetic effect (Sprague and Tatum 1942), it is evident that both additive and non-additive gene effects exerted a significant influence in the phenotypic expression for the three characters studied in both locations.

Estimates of general combining ability effects associated with each of the ten parental cultivars for the three characters measured showed that DT-310 from Winnipeg and Candeal Selection from Swift Current were the best combining cultivars for lipoxidase activity (i.e. low value is desirable) while Iumillo is the most undesirable combining parent for this character in both locations. Practically, DT-310 would be the recurrent parent to use in a crossing program in Winnipeg if lipoxidase activity were the character of interest; similarly, Candeal Selection would be the parent to choose for Swift Current. The parent that showed the highest general combining ability effect for wheat and predicted macaroni pigments in Winnipeg was My-54 while that in Swift Current was Candeal Selection. Accordingly, these two cultivars could be preferred as the recurrent parent in a crossing program for wheat and macaroni pigments, depending on which location the program were to be carried out.

Positive and negative s.c.a. effects associated with individual crosses were noted for each of the characters, although many of them were not signifi-

Table 4. Estimates of genetic components of variance for lipoxidase activity and yellow pigment contents

Component	Lipoxidase activity[1]		Wheat pigment[2]		Predicted Macaroni pigment[2]	
	Wpg.	S.C.	Wpg.	S.C.	Wpg.	S.C.
D	174.4± 46.9**	691.2±41.9**	0.17±0.02**	1.34±0.04**	0.19±0.02**	1.27±0.04**
F	-6.3±108.4	-101.0±96.6	0.06±0.05	0.31±0.10**	0.10±0.06	0.21±0.10*
H_1	2187.5± 99.9**	678.9±89.1**	1.29±0.05**	0.57±0.09**	1.62±0.05**	0.56±0.09**
H_2	1097.8± 84.9**	495.3±75.8**	0.49±0.04**	0.45±0.07**	0.69±0.04**	0.43±0.08**
h^2	431.8± 56.9**	43.3±50.7	0.03±0.03	0.30±0.05**	0.17±0.03**	0.22±0.05**
$\frac{H_2}{4H_1}$	0.12	0.18	0.09	0.20	0.11	0.19
$\left(\frac{H_1}{D}\right)^{1/2}$	3.56	0.99	2.72	0.65	2.90	0.66
$\frac{(4DH_1)^{1/2}+F}{(4DH_1)^{1/2}-F}$	0.99	0.86	1.14	1.42	1.20	1.29
Heritability	0.06	0.37	0.11	0.79	0.10	0.73

* Significant at 5% level
** Significant at 1% level
[1] $\mu 10_2$/min/g
[2] Parts per million (p.p.m.)

cant. No particular cross showed outstanding s.c.a. effect for any of the three characters measured and consequently the g.c.a. effect of the parental cultivars could be the only useful criterion for the selection of parents to be employed in a crossing program.

Estimation of Genetic Parameters

Least squares estimates of the genetic variance components are presented in Table 4. The notations used here and the genetical theories followed are basically those of Hayman (1954). D is the component of variation due to additive effects of the genes. H_1 is the component of variation due to non-additive effects of genes while H_2 is also due to non-additive gene effects but corrected for gene distribution; h^2 represents the overall dominance effect only at the heterozygous loci; F is the covariation of additive and non-additive gene effects (a positive F value indicates an excess of dominant alleles over recessive alleles governing the character while the reverse is true with a negative F value).

Both additive (D) and non-additive (H_1 or H_2) genetic components of variation were highly significant ($P \leq 0.01$) for each of the three characters investigated for both locations. Thus, both additive and non-additive gene effects were important in influencing the phenotypes for these characters. This is also in agreement with the combining ability results (Table 3). The non-additive genetic components of variance were substantially higher in Winnipeg than those in Swift Current and this was consistent in all three characters studied. These results can explain the appreciably higher frequencies of heterosis observed for the Winnipeg hybrid material (Table 2). These findings suggest that the hot and arid conditions in Swift Current suppress the non-additive genetic effects, at least for the three quality traits that were examined.

The average degree of dominance $(H_1/D)^{1/2}$ ranged from partial dominance for wheat and macaroni pigments of Swift Current to over-dominance. All three characters exhibited over-dominance at Winnipeg while they only showed from partial to complete dominance at Swift Current. Thus dominance genetic effect for the three traits was substantially environmentally dependent.

The mean value of the product of gene frequencies of dominant ($\bar{u}$) and recessive alleles ($\bar{v}$) at the loci showing dominance is represented by $\bar{u}\bar{v} = H_2/4H_1$. If $\bar{u}\bar{v} = 0.25$, then $\bar{u} = \bar{v} = 0.50$, then $H_1 = H_2$ (i.e. the positive and negative alleles at these loci were in equal proportions in the ten parents). From Table 4, it is apparent that positive and negative values are not in equal proportions in the 10 parents for any of the quality traits studied.

Table 5. Genotype by location interaction analyses of the additive components of variation for lipoxidase activity and pigment contents

Source of variation	Degrees of freedom	Mean squares		
		Lipoxidase activity[1]	Wheat pigment[2]	Predicted Macaroni pigment[2]
Locations	1	10.4375	0.2300**	0.1240*
Reps within locations	1	190.6250	0.1841**	0.2371**
Parents	9	1346.9929**	2.0594**	2.0719**
Locations × Parents	9	609.9861**	1.0749**	0.9617**
Error	19	58.1184	0.0149	0.0183

* Significance at the 5 % level
** Significance at the 1 % level
[1] $\mu 10_2$/min/g
[2] Parts per million (p.p.m.)

The ratio of the total number of dominant to recessive genes in all the parents was estimated by $[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$. This ratio ranged from 0.86 for lipoxidase activity at Swift Current to 1.42 for wheat pigment content at the same location. Based on the results for both locations, it was evident that the ten parental cultivars carried slightly more dominant than recessive alleles for each of the two pigment contents while the reverse was true with lipoxidase activity (but note that the recessive allele is the desirable for lipoxidase activity). However, the F values were significant only for the two pigments at Swift Current. In other words, although it was shown that the then parents did not carry dominant and recessive genes in equal proportions for the three characters, statistically significant departure from equality was shown only for the two pigments at Swift Current.

Heritability Estimates

The narrow sense heritability, defined as the ratio of additive and/or additive × additive genetic variance to the total phenotypic variance, was estimated as $0.25D/[0.25(D + H_1 - F) + E]$ (Crumpacker and Allard, 1962). Heritability estimates were consistently low for all three characters of the Winnipeg material. This result was expected since non-additive genetic variance (H_1 or H_2) was many times greater than the additive genetic variance (D) for Winnipeg. On the other hand, heritability estimates were high for the Swift Current material, a reflection of the higher additive genetic variance relative to non-additive genetic variance of the material grown at this location. Wheat pigment content of the Swift Current material had the highest heritability (0.79). It seems that mass selection should be effective for improving lipoxidase activity and wheat and macaroni pigment contents under the Swift Current growing conditions while a hybrid programme might be more appropriate for exploiting the non-additive gene effects for the improvement of these characters under Winnipeg growing conditions.

Stability of the Genetic Systems Over the Two Locations

Analysis of the genetic system described above was performed separately for each of the two locations. The findings strongly indicated that both additive and non-additive genetic effects governing all three characters were environmentally-dependent. This section employs a more precise and systematic method of investigating the stability of the genetic parameters over the two environments and therefore the findings herein can be used either to confirm or refute those of the previous sections with respect to genotype by environment interactions. The method, proposed by Allard (1956), involves an analysis of variance of the parental means and array variations and covariations from the diallel cross over the two environments (locations). The analysis permits determination of the stability of three kinds of genetic parameters over environments: Additive, dominance and epistatic (additive × additive, additive × dominance or dominance × dominance) effects.

Genotype by location interaction analysis of the additive components of variation is summarized in Table 5. Location and replications within location

Table 6. Genotype by location interaction analysis of the dominance components of variation for lipoxidase activity and pigment contents

Source of variation	Degrees of freedom	Mean squares		
		Lipoxidase activity[1]	Wheat pigment[2]	Predicted Macaroni pigment[2]
Locations	1	1.4185**	1.2582**	0.9890**
Reps within locations	1	0.2134*	1.3237**	0.6611**
Dominance	1	1.8055**	0.1497**	0.2173**
Locations × dominance	1	2.5231**	1.7035**	1.8187**
Arrays	9	0.1896**	0.0293	0.0696**
Locations × arrays	9	0.1587**	0.0995**	0.1031**
Dominance × arrays	9	0.0648	0.0066	0.0116
Locations × dominance × arrays	9	0.0912	0.0069	0.0122
Error	39	0.0442	0.0179	0.0208

* Significance at the 5% level
** Significance at the 1% level
[1] $\mu 10_2$/min/g
[2] Parts per million (p.p.m.)

mean squares were significant only for the two pigment contents. These two terms have no particular genetic meaning. They simply indicate that for the two pigment contents, the overall average performance for the 55 entries (45 F_2 families and 10 parents) was significantly different between locations and between replicates within a location. Mean squares for parents were highly significant for all three characters, suggesting that for each character, certain parents carried alleles with different additive effects. Stability of additive genetic effects over locations can be tested by location × parents mean squares. Evidently, the additive genetic effects for each of the three characters were substantially unstable over locations, as indicated by the high significance in their mean squares. Accordingly, these findings are in complete agreement with those of the previous sections.

Genotype by location interaction analysis of the non-additive components of variance is summarized in Table 6. Mean squares for locations and replications within location were highly significant for all three characters, suggesting a substantial difference in the mean dominance between locations and between replicates within each location for these traits. Mean squares for dominance were highly significant for all traits studied, indicating the appreciable dominance effect on these characters. The array mean squares were highly significant only for lipoxidase activity and macaroni pigment, suggesting there were differences in the degree of dominance among the ten parental cultivars for these two characters. The highly significant mean squares for locations × arrays for these three characters suggest that the average level of dominance and/or epistatic effects for each parent was not consistent over locations. For example, the most dominant parental cultivar in one location may not be the most dominant one in the other location. Mean squares for locations × dominance were highly significant for all three characters, suggesting that the dominance effects for all characters studied here were environmentally dependent, agreeing with the results found in the previous sections. The non-significance of the dominance × arrays and locations × dominance × arrays interactions provide evidence not only for the lack of epistasis in all three traits, but also that the absence of epistasis was consistent over locations.

In general: The results of this study indicated that heterosis for lipoxidase activity and for wheat and predicted macaroni pigment contents is environmentally-dependent. The data suggested that the environmental conditions at Winnipeg, which had a relatively lower mean temperature and higher moisture, were more conducive to hybrid vigour for these quality traits than the more hot and arid conditions at Swift Current. Although both additive and dominance genetic effects were significant for each of these quality traits studied, additive genetic effect was consistently more pronounced than dominance genetic effects for the material grown at Swift Current while the reverse was

true for the material grown at Winnipeg. There was no evidence of epistatic gene effect for any of the three characters grown at either location.

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