THE UNIVERSITY OF MANITOBA

THE INHERITANCE AND INTERRELATIONSHIPS OF QUANTITATIVE CHARACTERS IN DURUM WHEAT (*TRITICUM TURGIDUM* L. VAR. *DURUM*)

by

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PREFACE

This thesis is divided into two sections. The first section concerns the genetic system controlling the inheritance of the quantitative characters in durum wheat while the second section deals with the interrelationships among these characters.

A modified form of the first section is intended for publication in the Zeitschrift für Planzenzuchtung (German Journal of Plant Breeding) while the second section will be submitted for publication in the Canadian Journal of Plant Science. The manuscripts are presented in the format required by the respective Journals.

ABSTRACT

Lee, James Hin Foon, Ph.D., The University of Manitoba, May, 1973. The inheritance and interrelationships of quantitative characters in durum wheat (Triticum turgidum L. var. durum). Major Professor: Dr. P. J. Kaltsikes, Department of Plant Science.

Ten durum wheat cultivars (Triticum turgidum L. var. durum) of diverse geographic origin were crossed in a diallel fashion. The parents and the 45 F_1 and F_2 populations were grown at two contrasting locations for two consecutive years. Heterosis, combining ability, the mode of inheritance of and interrelationships among yield, components of yield and several related agronomic characters were investigated.

Significant mid-parent heterosis was found for all characters but it was not consistent over environments or generations. Inbreeding depression was evident in the F_2 populations, particularly for yield and number of kernels per plant. General and specific combining ability variances were significant or highly significant for all characters. Cultivars with promising combining abilities were identified for most characters.

Additive and dominance genetic effects were of consi-

derable importance in controlling the phenotypic expression of all characters while epistatic effects were important only for some characters. However, the dominance effect was not consistent either in magnitude or in direction over loci in these polygenic characters. The magnitude of the various genetic parameters was susceptible to environmental changes. Averaging over environments, the narrow-sense heritability for yield was 16% and 30%, respectively, for the F_1 and F_2 population. Number of florets per spike had the lowest heritability while plant height had the highest.

The cultivars used in the present investigation represented very promising germplasm for the improvement of durum wheat in Canada with respect to yield and a number of agronomic attributes. The prevalence of additive genetic variance for these traits indicated that selection procedures leading to the isolation of superior homozygous lines could be effectively practiced in breeding for the improvement of any of these characters.

All of the agronomic characters were highly associated with yield; most of these characters were also correlated amongst themselves. The expression of yield, and of number of spikes and kernels per plant was simultaneously influenced by some common underlying factors. Based on both the F_1 and F_2 populations, number of spikes per plant, plant height and kernel weight were the most important predictor characters for grain yield.

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INTRODUCTION

In a recent review on the genetical and agronomic aspects of durum wheat, Bozzini (1970) concluded that (i) the genetic variability existing among several subspecies and botanical varieties related to this crop is still far from being utilized to improve the germplasm of the durum wheat population, and (ii) that only a rather modest effort has been made for improving yield and the economically important attributes in this species, particularly when compared to the progress achieved in Triticum aestivum. Thus, although in Western Canada the production of durum wheat has increased from 479 million kilograms in 1965 to 2,000 in 1972 and the acreage from 0.324 million hectares to 1.296 (Statistics Canada, 1965-1972), very little is known about the mode of inheritance of the agronomic characters and their interaction with the environmental complex (Kaltsikes and Larter, 1970; Kaltsikes and Lee, 1971; Lee and Kaltsikes, 1972c). This is probably reflected in the fact that the average yield per hectare has remained stationary during this period at least in Western Canada.

Clearly for a successful breeding program a breeder must

effectively select the best possible parents for hybridization, subsequently identify the most promising hybrids and then accurately predict the rate and amount of genetic advance under selection. To accomplish this he needs accurate estimates of the genetic parameters relating to the characters under improvement so that he can assess their relative importance and utilize them effectively. From the beginning he is confronted with two problems:

(1) Grain yield and other economically important characters are polygenically controlled with the result that the effects of the individual genes contributing to the phenotypic expressions of the characters are too small to be recognized separately. The breeder has to work with the average effect of all the genes controlling that character. Furthermore, the genetic effect of a polygenic character is invariably confounded with that of the environmental complex;

(2) More often than not there is a marked genotype x environment interaction which, unless experiments aimed at estimating genetic parameters are replicated in time and space, renders these estimates almost worthless.

Statistical methods have been devised to deal with the overall average effect of the genes and to separate the genetic effect from that of the environment. The diallel cross analysis, one of the statistical procedures, was developed for early gen-

eration evaluation of the parental lines in a breeding program by assessing the relative importance of the additive and non-additive effects of genes controlling the expression of polygenic traits (Jinks and Hayman, 1953; Jinks, 1954). The method was extended to consider in greater detail the dominance effects of genes as well as the dominance relationships among the parents (Hayman, 1954; 1957; 1958). The diallel crossing system was also used by Griffing (1956) to estimate the general and specific combining abilities of the parental lines. Allard (1956) and Crumpacker and Allard (1962) further extended the diallel cross analysis to estimate the stability of various genetic parameters in different environments.

The present investigation, utilizing ten durum cultivars of diverse geographic origin, was undertaken in order to: (1) provide estimates of heterosis and combining abilities and subsequently assess the relative importance of the additive and non-additive effects of the genes controlling the phenotypic expression of grain yield, yield components and other related agronomic attributes; and (2) assess the stability or consistency of these genetic parameters by growing two filial generations in four diverse and unpredictable environments. A further objective was to compare the performance of these ten cultivars and the hybrid families derived from them with that of Hercules, a current commercial cultivar in Western Canada (Leisle, 1971) to see whether or not some of the cultivars included in this study represent promising breeding material for the improvement

of durum wheat.

LITERATURE REVIEW

As there was only a very limited amount of genetic information available on durum wheat, it was decided that heterosis and the genetic parameters of hexaploid wheat was to be included in the literature review. Since both durum and hexaploid wheats are long established allopolyploids which behave like diploids in segregation and both are essentially self-pollinating, it was assumed that the genetic system controlling metrical traits for both species were fairly similar. The methods of cultivation are also generally similar for both crops (Leisle, 1973).

I. Heterosis

Interest in the degree of heterosis in wheat has been stimulated by the prospect of employing cytoplasmic male-sterility and the fertility restoration system in the commercial production of hybrid wheats. However, if the production of hybrids is to become a success on a commercial scale, a maximum degree of heterosis will have to be attainable to offset the cost of seed production.

A comprehensive survey of heterosis in wheat was made by Briggle (1963). Among the 23 publications surveyed, the

magnitude of heterosis reported in wheat ranged from no heterosis at all to 100 percent heterosis. However, the studies for the most part were limited in scope and application. Many were based on a few plants grown in greenhouses. Field experiments were based on single F_1 rows with few or no replicates. Heterotic effects on height, maturity and yield components were more often measured than grain yield. The early studies surveyed by Briggle seemed to have only limited usefulness for predicting the performance of commercial hybrids because measurements of heterosis were frequently based on non-commercial unproductive cultivars. Economic levels of heterosis in wheat must be based upon comparisons of hybrid performance with that of the most productive commercial cultivar available.

Further studies on heterosis in wheat were continued by other workers subsequent to the 1963 review by Briggle. A selection of these reports will be summarized. Observations on heterosis were made by Brown et al. (1966) in a study of crosses among seven hard and soft winter wheat cultivars. Hill plantings were used to simulate normal seeding rates. Yield heterosis relative to the high parents was observed in five of the 16 hybrids, and 12 exceeded their respective midparents. The yielding capacity of the hybrids ranged from 96 to 131% of the high parent means. Less heterosis occurred for number of spikes and kernel weight than was observed for yield. In general, their results suggested that considerable heterosis for

grain yield may occur in certain wheat hybrids but not in others. Heterotic effects in the hybrids derived from an 8-parent spring wheat diallel experiment for several agronomic characters were examined by Bhatt (1971). He found that the level of heterosis was considerably different among different hybrids and the degree of heterosis was different for each character. Maximum heterosis was expressed by kernel weight and number of kernels per spike. On the other hand, similar characters in the F_1 and F_2 hybrids from a 6-parent hard red spring wheat diallel revealed no promising heterotic effects for any character in either generation (Knott and Sindagi, 1969). Similarly, Kaltsikes and Lee (1971) found no significant heterotic effect for ten agronomic characters in the F_1 hybrids derived from a space planted 6-parent durum wheat diallel experiment. Widner (1968) found that 17 out of 45 F_1 durum wheat hybrids exhibited significant heterosis for grain yield. Some F_1's yielded up to 84% more than their high-yielding parent. However, significant inbreeding depression occurred in the F_2 populations in certain hybrids.

The performance of hybrids derived from crosses involving nine hard red winter wheat cultivars was evaluated in replicated field tests over a three-year period (Livers and Heyne, 1966). The hybrids were grown in single-row plots three feet in length and were seeded at the rate of 50.4 kilograms per hectare. The mean yield of the hybrids exceeded that of the parental cul-

tivars by 20, 37, and 33% respectively, over the three year period. On the basis of these results, it was concluded that certain hard red winter wheat hybrids grown under normal planting conditions can express heterosis comparable to other crops although heterosis fluctuated considerably from year to year. Heterosis for grain yield, plant height and heading date was studied in the F_1, F_2, F_3, BC_1, and BC_2 generations of four durum wheat crosses (Amaya et al., 1972). The experiment, based on three years data, revealed that heterosis was particularly evident for grain yield in the F_1 generation, which exceeded their high-yielding parents by an average of 25%. Heterosis was of lesser magnitude in the expression of plant height and heading date. However, the heterotic effects for all three characters were susceptible to environmental changes; i.e. the magnitude of heterosis was not consistent over years.

McNeal et al. (1965) reported that the F_1 and F_2 generations from some hard red spring wheat crosses were intermediate to the parents for both agronomic and quality characters. No single hybrid exhibited significant high-parent heterosis for any character. These results suggested that closely related parents may result in little or no heterosis and the need of genetic diversity was emphasized in the development of vigorous hybrids. Johnson et al. (1966) observed heterosis for yield and yield component characters in the F_1, F_2 and both backcross generations from a cross between two hard red winter

wheat varieties which differred greatly in all of these attributes and therefore were considered to be genetically divergent. Higher yields were obtained for the F_1, F_2 and one backcross populations than for either parent. For kernel weight, the F_1 mean was significantly greater than that of either parent while the F_2 mean approached that of the high parent. Both the F_1 and F_2 means for spikes per plant exceeded that of either parent.

Based on the foregoing results, some general conclusions concerning heterosis in yield and agronomic characters can be drawn: (i) Most of the heterosis studies in wheat have been carried out under conditions of space-planting and have involved rather small populations; (ii) conflicting results were reported by different workers in predicting heterosis from hybrids derived from similar genetic material; and (iii) the expression of yield and other agronomic characters was considerably dependent upon the environmental complex.

II. Combining Ability and Gene Action

A number of studies on combining ability and gene action in wheat have been conducted. A diallel experiment conducted by Kronstad and Foote (1964) revealed general combining ability variances to be considerably greater than specific combining ability variances for all traits studied with the exception of kernel weight. The genetic variation for each character excepting kernel weight was therefore largely due to additive gene action. The relative magnitudes of general and specific combining ability estimates obtained in a 5-parent winter wheat diallel study conducted by Brown et al. (1966) also led to the conclusion that additive genetic effects accounted for most of the total genetic variability. A 7-parent diallel cross using soft red, soft white and hard red winter wheat cultivars showed both general and specific combining abilities to be of considerable importance in controlling yield, components of yield and a number of agronomic characters (Gyawali et al., 1968). An 8-parent diallel cross analysis of spring wheat showed that general combining ability was more important than specific combining ability in controlling the expression for six of the seven agronomic characters studied (Bhatt, 1971). A study of ten metrical traits in the F_1 generation resulting from a diallel cross of six durum wheat cultivars indicated that general combining ability effects were more important than specific combining ability

effects and that the average parental performance could be used to predict hybrid performance (Kaltsikes and Lee, 1971).

Yield and yield components were studied in the F_1 and F_2 generations of a diallel cross among four spring wheat cultivars by Whitehouse et al. (1958). Primarily, additive genetic effects were observed in each of the yield components, although dominance effects were noted in the F_1 generation for grains per spikelet and spikelet per spike. Yield, on the other hand, was strongly influenced by non-allelic interactions in both the F_1 and F_2 populations. In a diallel study involving F_1 and F_2 populations derived from crossing six winter wheat cultivars, Lupton (1961) found yielding ability to be influenced mainly by dominance and epistatic gene action . Yield and yield component analysis of a diallel cross of spring wheat cultivars indicated that a large part of the total genetic variation for all characters was predominantly additive while the dominance effect of genes had only minor influence in the inheritance of these agronomic characters (Knott and Sindagi, 1969; Hsu and Walton, 1970). Similarly, an 8-parent diallel cross analysis of spring wheat showed that in the inheritance of yield and its components additive gene action was of paramount importance for all characters while dominance was noted only for yield and number of kernels per spike (Walton, 1971).

Crumpacker and Allard (1962) studied the inheritance of heading date based on F_1 data from a 10-parent diallel cross

among spring wheat cultivars over a 3-year period. Genetic variability was attributable to both additive and dominance gene effects. Epistasis was not observed to be an important feature of the genetic system. Yield and kernel weight was studied in the F_1 and F_2 generations of 22 spring wheat crosses over two years (Wells and Lay, 1970). These authors concluded that additive gene action seems to be the only factor governing the inheritance of these two metrical traits in both years.

Four cultivars of durum wheat, representing diverse levels of genetic relationship and geographic origins, were crossed to produce six segregating generations (Jackson et al., 1968). Five metrical characters were studied in the F_2 and F_4 generations grown in separate years. It was concluded that dominance variance predominated in two of the six populations in the F_2 but became minimal in the F_4 generation. Additive genetic variance generally constituted the major source of genetic variance in all of the populations. However, the magnitudes of the various genetic parameters fluctuated considerably between years. Lebsock and Amaya (1969) also concluded that the genetic parameters governing several characters in durum wheat were substantially inconsistent over years. Amaya et al. (1972) studied the mode of inheritance associated with yield, plant height and heading date in the F_1, F_2, F_3, BC_1, and BC_2 generations derived from four crosses of durum wheat. The experiment was repeated in three consecutive years. In

general, the dominance genetic effect was relatively more important than the additive effect in the inheritance of yield while the reverse was true in the inheritance of plant height and heading date. Epistatic effects occurred only in certain generations and in certain environments. All of the genetic parameters estimated were somewhat inconsistent over generations and environments.

A number of spring wheat cultivars grown in the Tselinograd region in the U.S.S.R. over several years revealed that the genotypic variability of yield among the cultivars depended largely on the environmental complex. Heritability for yield and for number of kernels per spike varied considerably from year to year; heritability also decreased for these characters in the unfavorable years (Mamonov, 1970). Similarly, a number of F_2 and F_3 populations of a set of crosses involving 17 wheat parents were evaluated under different environments (Roy and Murty, 1969). They found that days to heading was the only character of the 7 agronomic characters recorded that was phenotypically stable and highly heritable under all environments. For the remaining characters, heritability was not only low but also fluctuated considerably in these environments. Kaltsikes and Larter (1970) found that the environmental effect was substantially greater than the genetic effect in influencing the phenotypic expressions of three agronomic traits in durum wheat.

In summary, numerous investigations have been conducted

to assess the relative importance of the various types of action of genes controlling quantitative characters in wheat. These studies employed both diallel cross analyses and analyses based on early segregating generations of crosses between inbred lines. In the diallel crossing systems, the effects of gene action were estimated either in terms of general and specific combining ability (Griffing, 1956) or by the variance-covariance techniques (Hayman, 1954; Jinks, 1954). In the combining ability analysis all of the reports estimated the additive and non-additive genetic effects in terms of general and specific combining ability variances, respectively. However, it was pointed out by Griffing (through personal communication, 1972) that the relative magnitudes of additive and non-additive genetic effects should be estimated by the relative magnitudes of the variance components due to general and specific combining ability effects, respectively. When the combining ability variances rather than their components were used, non-additive genetic effects would be underestimated.

In general, additive genetic effects have been found to be of major importance in the inheritance of quantitative characters although in many instances non-additive effects have also been found to be of some importance. The environment also exerted a substantial influence over the genetic parameters controlling these metrical characters. The implications and limitations of investigations of this type with respect to plant breed-

ing have been ably discussed by Matzinger (1963).

MATERIALS AND METHODS

The ten durum wheat (Triticum turgidum L. var. durum) cultivars used in this study and their respective country of origin were: Adur (France), Candeal Selection (Argentina), DT-310 (Canada), Iumillo (Italy), Kharkov Kaja (Russia), Leeds (U.S.A.), Madif (Italy), My-54 (Mexico), Narodnaja (Russia) and Stewart (Canada). The cultivars were chosen specifically to represent germ plasm sources from several distinct geographic regions throughout the world and were therefore assumed to be broadly divergent genetically. These cultivars were crossed in a diallel fashion with reciprocal families bulked to yield 45 F_1 and subsequently 45 F_2 families. Hercules, a commercial cultivar in Canada (Leisle, 1971), was included in the study as a standard in order to compare the relative performance of the ten cultivars and the hybrids derived from them. Altogether, there were 56 entries (11 cultivars and 45 hybrids) in each of the two diallel generations.

Seeds were sown at Winnipeg, Manitoba and at Swift Current, Saskatchewan in May of 1971 and 1972. At each of the four environments, the F_1 and F_2 diallel experiments were separately laid out in a randomized complete block design with two replications as follows: Each F_1 plot consisted of a single

3-meter row with 15 seeds space planted. The number of plants which survived at harvest ranged from 2 to 15 but most plots had 8 to 12 plants. Each F_2 plot consisted of three 3-meter rows with 160 seeds sown per row. The seeding rate for the F_2 population was approximately 75 kilograms per hectare. The seeding rate used for the F_2 population simulates normal commercial seeding rates, which range from 70 to 100 kilograms per hectare (Leisle, 1973). A guard row of the cultivar Manitou was sown between plots to minimize inter-plot competition. Two plots were sown for each of the eleven parents. The inter-row and inter-plot distances for both diallel generations was 30 centimeters.

The following characters were measured from each plot:

(1) Grain yield. In the F_1 diallel, grain yield (gm) per plant was derived by dividing plot yield by the number of plants survived at harvest. In the F_2 diallel, yield observations consisted of the weight (kg) of seeds from each plot which was converted into kilograms per hectare.

(2) Number of spikes per plant. In the F_1 diallel, the number of fertile spikes per plant was determined by dividing the total number of fertile spikes in each plot by the number of plants survived at harvest. In the F_2 the number of fertile spikes per linear meter row was determined by direct count. This value was then divided by 53 to obtain number of spikes per plant since there were about 53 plants per linear meter.

(3) 1,000 kernel weight (gm)

(4) Number of spikelets per spike

(5) Number of florets per spike

(6) Number of kernels per spike

(7) Percent of florets bearing seeds

(8) Number of kernels per spikelet (fertility)

Characters (4) through (8) were taken from primary spikes. Two and ten primary spikes were randomly sampled from each of the F_1 and F_2 plots, respectively.

(9) Number of kernels per plant. In the F_1 diallel, the number of kernels per plant was obtained by direct count from a random sample of two plants from each plot. In the F_2, the number of kernels per plant was estimated by multiplying the number of kernels per spike by number of spikes per plant.

(10) Days to heading. The number of days to heading was recorded as the number of days from planting to approximately 75% of the plants had their first head completely emerged from the boot. Days to heading was recorded only at Winnipeg.

(11) Days to maturity. The number of days to maturity was recorded as the number of days from planting to approximately 75% of the plants that had matured.

(12) Plant height. Height of the plant (cm) was taken from ground to the tip of the tallest tiller, excluding awn, on individual plants in the F_1 and on 10 randomly chosen plants in the F_2.

RESULTS

I. Genotypic and Environmental Variation

Preliminary analysis of variance was conducted for both the F_1 and F_2 diallels to estimate the variation among genotypes, replications, locations, years, and the various interactions among them. The statistical model assumed to explain the sources of variation in the experiment was:

$$X_{ijkl} = \mu + R_i + G_j + L_k + Y_l + (GL)_{jk} + (GY)_{jl} + (LY)_{kl} + (GLY)_{jkl} + E_{ijkl}$$

where X_{ijkl} is a plot in the l^{th} year in the k^{th} location in the j^{th} genotype in the i^{th} replicate, and $i = 1,2$; $j = 1, 56$; $k = 1, 2$; $l = 1,2$.

The other symbols represent the contribution of the effect in question to X_{ijkl} are as follow:

μ = general mean,

R_i = contribution of the effect of the i^{th} replicate,

G_j = contribution of the effect of the j^{th} genotype,

L_k = contribution of the effect of the k^{th} location,

Y_l = contribution of the effect of the l^{th} year,

$(GL)_{jk}$ = contribution of the interaction effect between the j^{th} genotype and the k^{th} location,

$(GY)_{jl}$ = contribution of the interaction effect between the j^{th} genotype and the l^{th} year,

$(LY)_{kl}$ = contribution of the interaction effect between the k^{th} location and l^{th} year,

$(GLY)_{jkl}$ = contribution of the interaction effect among the j^{th} genotype and the k^{th} location and the l^{th} year, and

E_{ijkl} = random contribution of the environment in the $ijkl^{th}$ plot.

The effect of the genotype was considered fixed while all other effects were considered random. Therefore, information derived from the present investigation must be restricted to the experimental material included here and inferences to other cultivars of durum wheat should not be made.

The form of the analysis of variance and the expectations of mean squares was given in Table 1. The appropriate error term for testing the significance of various sources of variation was as follows:

(1) Replication effect.

$F_{(\alpha,\ 1,223)} = \frac{R}{Error}$, where α refers to the probability level.

(2) Genotypic effect. Since no single mean square could be used as an appropriate error term to test for genotypic effect,

Table 1. Analysis of Variance and Expected Mean Squares Associated With Each of the 12 Agronomic Characters

Source of variation	Degrees of freedom+	Mean square	Expected value for mean square
Replication	1	R	$\sigma^2 + lyg\sigma^2_R$
Genotype	55	G	$\sigma^2 + r\sigma^2_{GLY} + ry\sigma^2_{GL} + rl\sigma^2_{GY} + rly\sigma^2_G$
Location	1	L	$\sigma^2 + rg\sigma^2_{LY} + rgy\sigma^2_L$
Year	1	Y	$\sigma^2 + rg\sigma^2_{LY} + rgl\sigma^2_Y$
G x L	55	GL	$\sigma^2 + r\sigma^2_{GLY} + ry\sigma^2_{GL}$
G x Y	55	GY	$\sigma^2 + r\sigma^2_{GLY} + rl\sigma^2_{GY}$
L x Y	1	LY	$\sigma^2 + rg\sigma^2_{LY}$
G x L x Y	55	GLY	$\sigma^2 + r\sigma^2_{GLY}$
Error	223	Error	σ^2

+Days to heading was taken only from Winnipeg. The error degrees of freedom is 111 and the mean squares for location and interactions with location do not apply to this character.

an approximate F- test was used (Cochran, 1951; Satterthwaite, 1946).

$$F_{(\alpha,\ n_1, n_2)} = \frac{G + GLY}{GL + GY}$$

where $n_1 = \dfrac{(G + GLY)^2}{\frac{G^2}{55} + \frac{(GLY)^2}{55}}$ and $n_2 = \dfrac{(GL + GY)^2}{\frac{(GL)^2}{55} + \frac{(GY)^2}{55}}$

(3) Location effect. $F_{(\alpha,\ 1,\ 1)} = \frac{L}{LY}$

(4) Year effect. $F_{(\alpha,\ 1,\ 1)} = \frac{Y}{LY}$

(5) G x L interaction. $F_{(\alpha,\ 55,\ 55)} = \frac{GY}{GLY}$

(6) G x Y interaction. $F_{(\alpha,\ 55,\ 55)} = \frac{GY}{GYL}$

(7) L x Y interaction. $F_{(\alpha,\ 1,\ 223)} = \frac{LY}{Error}$

(8) G x L x Y interaction. $F_{(\alpha,\ 55,\ 223)} = \frac{GLY}{Error}$

The Error, with 223 degrees of freedom, was a composite term consisting of interactions with replication. This term will further be partitioned at a later section. In all of the statistical analyses, the standard notation for significance was used, i.e. * = significant at the 5% level of probability and ** = significant at the 1%.

Mean squares associated with each of the 12 characters were summarized in Tables 2 and 3. Genotypic variation was statistically significant for all of the characters in both generations excepting the number of fertile spikes per plant

Table 2. Mean Square Values for 12 Agronomic Characters of 56 Parent and F_1 Populations of Durum Wheat

Source of variation	Plant yield	No. fertile spikes/ plant	1,000 kernel weight	No. spikelets/ spike	No. florets/ spike	No. kernels/ spike	% florets with seeds	No. kernels/ spikelet	No. kernels/ plant	Days to heading	Days to maturity	Plant Height
Replication	625**	37.1**	18.2	0.9	717**	101	235	0.23	70915*	2.0	98	375
Genotype	127*	7.0	99.1**	4.9**	115*	152**	155**	0.37**	27052+	6.1**	307	415*
Location	64918*	1976.5*	6337.5	56.8	2391	9919	10060	20.57	7751794*	-	46022518*	1284643
Year	303	0.1	5150.3	0.4	4494	4602*	1313	14.53	1957.5	590.0**	28448	689073
G x L	93*	6.5	31.8	1.3*	64	57*	66	0.14*	20666	-	307**	341*
G x Y	65	6.5	33.4	2.3**	68	54*	64	0.11	23115	1.6**	81	181
L x Y	45	1.2	1224.9**	108.5**	2942**	162	1724**	0.54*	23977	-	28447**	400205**
G x L x Y	62*	5.6*	30.2	0.8	58	32	65	0.08	18711**	-	81**	210
Error	45	3.4	23.7	1.2	63	47	72	0.10	11226	1.0	50	223

+Significant at 7% level

Table 3. Mean Square Values for 12 Agronomic Characters of 56 Parent and F_2 Populations of Durum Wheat

Source of variation	Plot yield	No. fertile spikes/ plant	1,000 kernel weight	No. spikelets/ spike	No. florets/ spike	No. kernels/ spike	% florets with seeds	No. kernels/ spikelet	No. kernels/ plant	Days to heading	Days to maturity	Plant height
Replication	22148	12	10.6	1.6*	202**	13	80	0.00	417173	0.5	22	514
Genotype	144225*	404	76.7**	3.8**	80**	90**	86**	0.28**	1659249*	8.3**	417	1068**
Location	128393632**	362578*	18046.7*	392.2*	19391*	13876*	31289*	18.19	1158022131*	-	39972751*	570001
Year	203662	2345	6005.0	20.6	10308*	269	553	2.86	106232	271.2**	13508	468014
G x L	72418**	145	13.7**	0.4	26	24	31	0.07	572842	-	416**	612**
G x Y	33392**	598**	18.4**	1.0**	30*	15	16	0.03	976381*	1.2**	61	316
L x Y	14996	702*	79.5**	0.3	14	75**	77	0.17*	3952007**	-	13407**	141432**
G x L x Y	13534*	199**	5.7	0.5	19	17**	25	0.05**	567481**	-	61**	237
Error	9204	110	7.7	0.4	23	11	24	0.03	288098	0.6	32	242

and days to maturity, which were not significant in either generation. This result was expected since the 11 cultivars had diverse geographic origins and their genotypic and adaptive characteristics therefore would have been distinct. The lack of significance in genotypic variation for the number of spikes per plant in the F_1 was due to the substantial interaction of genotypes with both years and locations; in the F_2 the high interaction with year alone resulted in the absence of significant genotypic variation for this character. For days to maturity, significant genotype x location interaction caused non-significance in genotypic variation. As there was no significant genotypic variation associated with these two characters, they were omitted from further genetic analysis.

The characteristics of the 11 parents, averaged over years and locations, are summarized in Table 4. Hercules, one of the current commercial cultivars in Canada, ranked sixth in terms of grain yield. Cultivar DT-310 outyielded Hercules by 455 Kg/ha and the difference was highly significant. Candeal Selection outyielded Hercules by 222 kg/ha but the difference was not significant. Based on the average over years and location, 15 of the 45 hybrids outyielded Hercules but only three hybrids outperformed this cultivar significantly. These three best yielding hybrids were DT-310 x Candeal Selection (3771 kg/ha), DT-310 x Narodnaja (3526 kg/ha) and DT-310 x Adur (3315 kg/ha).

Table 4. Characteristics of the Eleven Durum Wheat Cultivars[1]

Cultivar	Yield (Kg/Ha)	Spikes/ plant	1,000 kernel weight	Spikelets/ spike	Florets/ spike	Kernels/ spike	% florets with seeds	Kernels/ spikelet	Kernels/ plant	Days to heading	Days to maturity	Height (cm)
Adur	2812	1.70	43.2	16.2	47.4	36.0	77	2.22	63	60	102	112
Can-Sel	3200	1.98	31.8	16.0	59.8	46.6	80	2.91	95	58	101	99
DT-310	3433	1.94	39.4	17.2	56.2	43.1	78	2.49	87	60	101	98
Kharkov Kaja	3037	1.70	43.2	15.2	49.5	39.3	80	2.56	70	58	100	100
Madif	2656	1.74	44.8	16.5	53.9	39.6	75	2.40	70	60	103	104
Narodnaja	3104	1.88	37.1	15.5	53.5	39.8	76	2.55	79	60	100	101
Leeds	2697	1.70	37.8	15.9	49.0	35.1	73	2.21	62	60	100	97
Stewart	2808	1.92	40.3	16.8	51.7	38.7	75	2.28	79	60	103	116
Iumillo	2642	1.82	33.2	16.6	48.0	33.9	72	2.03	64	62	101	99
My-54	2986	1.92	35.8	14.8	48.1	37.5	79	2.53	75	58	101	72
Hercules	2978	1.74	42.6	16.4	50.8	36.5	73	2.21	67	58	100	96
LSD (0.05)	301	0.18	2.35	0.50	4.13	2.86	4.2	0.14	9.1	0.6	4.8	13.2
LSD (0.01)	354	0.21	2.79	0.60	4.90	3.39	5.0	0.16	10.8	0.8	5.8	15.8

[1]All values were averaged over the four environments. Seeding rate was approximately 75 kilograms per hectare

For 1,000 kernel weight, three cultivars outperformed Hercules but no cultivar or any hybrids derived from them outperformed the commercial cultivar significantly. The three best hybrids for 1,000 kernel weight were Madif x Leeds, Madif x Adur and Kharkov Kaja x Adur, with values 44.6, 44.5 and 44.4 gm., respectively, as compared to 42.6 for Hercules.

For number of kernels per plant, Candeal Selection, DT-310, Narodnaja and Stewart significantly outperformed Hercules. The five hybrids which had significantly more kernels per plant than Hercules were Candeal Selection x My-54, Candeal Selection x Adur, Candeal Selection x Iumillo, Candeal Selection x Stewart and DT-310 x Adur, with values 86, 85, 83, 82 and 79, respectively, as compared to 67 for Hercules.

The number of kernels per spikelet, Candeal Selection, DT-310, Kharkov Kaja, Madif, Narodnaja and My-54 were all significantly superior to Hercules. Thirty one of the 45 hybrids significantly outperformed Hercules for this character. Among the 31 hybrids, the best ones were Candeal Selection x DT-310, Candeal Selection x My-54 and DT-310 x Narodnaja with values 2.79, 2.77 and 2.64, respectively, as compared to 2.21 for Hercules. For the remaining metrical characters, Hercules ranked about intermediate among the 11 cultivars and among the 45 hybrids.

The location effect was significant for plant yield,

number of spikes and kernels per plant and days to maturity in the F_1 while it was significant for all characters excepting the number of kernels per spikelet and plant height in the F_2. The effect of year seemed to be of lesser importance in influencing the expression of all characters. It was significant only for the number of kernels per spike and days to heading in the F_1 and for the number of florets per spike and days to heading in the F_2 generation. (In 1972 there was a few days of cold spell about mid-June which had induced the plants to have headed not only earlier but more uniformly than in the previous year).

The interaction effects of genotype x year, genotype x location, year x location, and genotype x year x location were significant for some of the characters only. These interaction effects were, on the whole, slightly more prevalent in the F_2 generation. Thus, grain yield in the F_1 showed significant genotype x location interaction only while the same character in the F_2 showed significant genotype x location and genotype x year interactions.

II. Heterosis

Heterosis for the characters studied was measured by comparing each hybrid with its mid parent value for the F_1 and F_2 generations first from each of the four environments. Adjusted L.S.D. values were used to test each hybrid-mid-parent contrast due to the fact that hybrid means were based on only half as many observations as the mid-parental means. Thus, L.S.D. = $t_{(\alpha,\ n)}S_{\bar{d}}$, where α is the probability level with n degrees of freedom (n = 54 for individual environments and n = 223 for averaged over environments). $S_{\bar{d}}$ is the standard error of the difference between the two means, which is equal to

$$\sqrt{\frac{\sigma_e^2}{n_1} + \frac{\sigma_e^2}{n_2}}$$

where σ_e^2 is the error mean square from the analysis of variance. For individual environment, $n_1 = 2$ since there were 2 F_1 values which made up the hybrid mean (one from each of the two replicates), and $n_2 = 4$ since there were 4 parental values which made up the mid-parental mean (two from each of the two replicates). For the averaged over the four environments, $n_1 = 8$ and $n_2 = 16$.

Almost all of the hybrids for each of the ten characters deviated either positively or negatively from their respective mid-parental means. The number of hybrids which showed statistically significant positive or negative heterosis varied con-

siderably from character to character and from environment to environment. Moreover, different hybrids exhibited significant heterosis under different environments. The only discernable pattern regarding heterosis in the individual environments was that for most characters a greater number of F_2 hybrid showed significant heterosis when compared to the F_1. However, this result was attributed to the greater prevalance of negative heterosis exhibited in the F_2 hybrids. The overall average performance of the 45 hybrids was not significantly different from that of the ten parents for any character derived from any environment in either generation.

Heterosis expressed as percent of the mid-parent value (i.e. 100 x hybrid/midparent) based on the average over the four environments for the F_1 and F_2 populations was calculated. The number of hybrids out of the 45 individual crosses for each generation showing significant heterosis is summarized in Table 5.

Table 5. Number of Hybrids Out of the 45 Crosses Showing Significant Mid-parent Heterosis[1]

Character	F_1 Heterosis			F_2 Heterosis		
	Positive	Negative	Range[2]	Positive	Negative	Range
Yield	1	2	75-134	1	11	73-111
Kernels/plant	2	4	67-137	1	10	79-117
1,000 kernel weight	8	2	86-121	11	2	91-116
Kernels/spikelet	3	16	84-112	5	9	85-111
% floret with seeds	1	9	82-111	5	9	89-107
Spikelets/spike	1	6	95-106	19	4	97-106
Florets/spike	0	2	88-108	6	2	89-113
Kernels/spike	1	9	78-119	12	5	84-117
Plant height	2	1	91-110	0	0	93-114
Days to heading	4	3	90-121	3	7	92-110

[1]Heterosis, expressed as the percent of the mid-parent value, was based on the average over the four environments.

[2]The range indicates the values of the most negative and positive heterotic hybrids, respectively, among the 45 crosses.

From Table 5, the following patterns regarding heterosis emerged: The total number of hybrids which showed significant heterosis, ignoring sign, were considerably greater in the F_2. The only exceptions were the number of kernels per spikelet and plant height. Inbreeding depression was evident for grain yield, number of kernels per plant and days to heading. Thus, only 2 hybrids of the 45 showed significant negative heterosis for yield in the F_1 generation while 11 hybrids exhibited significant negative heterosis for this character in the F_2 generation. For number of kernels per plant, the number of hybrids showing significant negative heterosis in the F_1 and F_2 generations were 4 and 10, respectively. For days to heading, 3 and 7 hybrids exhibited significant negative heterotic effects in the F_1 and F_2 generations, respectively.

It was also noted that the number of plants which made up an F_2 plot was about 30 times greater than the number of plants per F_1 plot. Therefore, the environmental error in the F_2 was substantially less than that in the F_1 population(Table 6). Since the l.s.d. value was a direct function of the environmental error(i.e. the error mean square from the analysis of variance), it is obvious that a much smaller heterotic effect in the F_2 would have been declared statistically significant. Take the number of kernels per spike as an example. The range of heterosis among the 45 F_1 hybrids(78%-119%) was greater

than that in the 45 F_2 hybrids (84% - 117%), yet the number of hybrids which exhibited significant heterosis was considerably more in the F_2 population. The result was, of course, due to the fact that the environmental error associated with the number of kernels per spike in the F_1 was four times greater than that in the F_2 population (Table 6).

Table 6. The Environmental Error Associated with Each of the 10 Characters in the F_1 and F_2 Populations+

Character	Environmental Error F_1	Environmental Error F_2
Yield	44.7	9.2
Kernels/plant	11226	5800
1000 Kernel weight	23.7	7.7
Kernels/spikelet	0.10	0.03
% floret with seeds	72	24
Spikelets/spike	1.2	0.4
Florets/spike	64	24
Kernels/spike	47	12
Plant height	223	242
Days to heading	1.00	0.64

+ See Appendix 2

More convincing evidence for inbreeding depression in the F_2 generation can be obtained by comparing the range of heterosis in both generations (Table 5). In the F_1 population, the best hybrid among the 45 crosses consistently out performed that in the F_2 population, excepting the number of florets and kernels per spike and plant height. Thus, for grain yield, the

best hybrid in the F_1 yielded 34% more than its mid-parent value while in the F_2, 11%; for number of kernels per plant, the best hybrid outperformed its mid-parent by 37% while in the F_2 by 17%.

There were several hybrids which outperformed their corresponding high-parents, particularly for grain yield and number of kernels per plant. However, no statistical significance was obtained in any of the cases.

III. Combining Ability Analysis

The term 'general combining ability' refers to the average performance of a cultivar in a set of hybrid combinations while 'specific combining ability' refers to the performance of a particular hybrid in comparison to the average performance of a set of hybrids derived from the same parent. The combining ability effects and variance components associated with these effects, estimated according to Method 2 of Model I of Griffing (1956) were summarized in Table 7. In accordance with Model I, inference of genetic information is restricted only to the ten cultivars used in this particular study since they were considered as a fixed set rather than a random sample from a population of durum cultivars.

The variance components[1] for both general and specific combining abilities were highly significant for all traits studied with a few exceptions. The magnitudes of the variance components associated with specific combining ability were in most cases greater than that for general combining ability. Since general combining ability provides an estimate of additive gene action while specific combining ability, of non-additive

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[1]The term 'variance component' used here and in all subsequent sections should be interpreted in a restricted sense since it refers to the genetic effect which was considered fixed; i.e. Model I.

gene action (Sprague and Tatum, 1942), the results implied that non-additive genetic effect was of considerable importance in controlling the phenotypic expression for those metrical traits. The relative magnitudes of the variance components for general and specific combining abilities were susceptible to environmental changes as can be seen from their considerable inconsistencies over the four environments and between generations. Thus, a negative estimate was obtained for the specific combining ability variance component associated with the F_1 population for yield at Winnipeg, 1971 while the same estimate was highly significant in all other environments.

The estimates of general combining ability effects associated with each of the ten parental cultivars for the ten metrical characters revealed considerable differences among parents in terms of the combining abilities (Table 7). The results thus implied that certain cultivars were desirable combiners while others were not. A large positive general combining ability effect indicates that the cultivar is a desirable combiner and therefore the one to be selected as a recurrent parent in a breeding program. However, as with the variance components, the relative magnitudes of these effects were, by and large, not consistent over environments or between generations.

DT-310, the highest yielding parental cultivar (Table 4) was also a good combining cultivar in the F_2 generation at Swift

Table 7. Estimates of Combining Ability Variance Components and Effects Derived From the Diallel Cross Analysis

Character	Generation	Environment	Variance Component GCA	Variance Component SCA	GCA effects A	C	D	K	M	N	L	S	I	My	S.E.$(\hat{g}_i - \hat{g}_j)$
Grain yield	F_1	W71	20.3**	0[1]	2.6	-1.7	-3.2	1.3	-6.1	3.1	0.2	5.4	6.8	-8.5	2.68
		W72	1.8**	29.3**	1.3	0.7	0.8	-0.4	-1.7	0.2	-1.5	4.0	-2.1	-1.2	1.73
		S71	0.6**	2.7**	-0.4	0.4	1.0	-0.4	-1.4	-0.8	0.2	1.6	-0.4	0.2	0.60
		S72	0.8**	5.4**	-0.6	-0.2	0.1	-1.2	-0.6	0.1	-0.3	-0.1	0.1	2.6	0.62
	F_2	W71	8.5**	21.2**	0.8	1.1	1.0	0.2	-0.5	1.0	-0.8	-0.5	-1.4	-1.0	0.34
		W72	7.2**	3.5**	-0.2	0.4	1.4	0.2	-0.5	0.2	-0.4	-0.9	-1.4	1.2	0.25
		S71	0.7**	3.4**	0.2	0.4	0.3	0.2	-0.1	0.1	-0.3	-0.5	-0.3	0	0.15
		S72	0.4**	13.8**	-0.2	0.2	0.2	-0.4	0	-0.1	-0.1	0	0	0.4	0.08
Kernels/ plant	F_1	W71	5.5**	13.6**	59.9	23.4	26.8	-23.1	-57.0	-25.9	-19.8	64.6	107.7	-156.6	28.90
		W72	1.4**	7.7**	14.2	20.0	37.6	-18.5	-29.5	-8.9	-60.3	47.2	-41.8	39.9	25.30
		S71	1.0**	2.8**	-24.6	38.1	45.2	-42.6	-5.8	-32.7	-22.8	27.7	14.5	3.0	1.83
		S72	1.5**	7.3**	-7.0	22.1	54.7	-50.9	-12.1	-7.4	-45.8	8.0	-27.0	65.5	19.46
	F_2	W71	16.6**	21.3**	43	862	93	-441	-374	337	-420	291	-23	-368	155
		W72	27.6**	23.9**	-266	812	646	-435	82	-179	-187	-286	-813	625	122
		S71	2.7**	8.5**	113	300	127	-161	126	56	-110	-205	-74	-171	41
		S72	5.5**	16.0**	-92	321	298	-528	151	-59	-127	67	-56	25	81
1,000 kernel weight	F_1	W71	7.9**	4.2*	3.0	-2.6	0.1	4.3	0.1	1.4	-0.6	1.8	-1.9	-5.6	0.91
		W72	4.1**	21.8**	-0.4	3.4	1.6	3.4	0.7	-0.6	-0.3	1.9	-3.6	0.9	1.32
		S71	1.6**	6.6**	2.1	-1.1	-0.1	1.5	0.2	-1.8	-0.3	1.1	-2.0	0.5	0.67
		S72	5.4**	9.9**	1.3	-0.2	-0.4	4.5	1.5	-1.4	0.5	-0.3	-5.1	-0.4	0.97
	F_2	W71	5.2**	4.8**	3.2	-2.6	-0.1	2.6	1.3	-0.7	-0.1	1.5	-4.4	-0.6	0.41
		W72	8.1**	0.4	1.8	-5.1	0.5	1.8	4.9	-1.2	-0.1	2.2	-3.7	-1.0	1.00
		S71	2.0**	1.6**	1.9	-2.1	0.2	1.4	0.2	-0.4	0.3	-2.2	-0.9	1.7	0.45
		S72	5.0**	2.7**	1.0	-3.6	0.4	2.1	4.3	-1.4	0	0.2	-2.8	-0.3	0.62
Kernels/ spikelet	F_1	W71	1.4**	8.1**	7.3	27.0	-2.4	-16.4	3.3	1.0	-12.3	9.5	-7.8	-9.3	5.77
		W72	1.3**	3.2**	-4.8	18.0	5.3	-7.3	2.4	5.6	-13.9	12.7	-23.0	16.5	8.16
		S71	1.7**	4.0**	7.4	10.4	6.6	-18.6	12.1	10.0	-11.0	-10.1	-21.7	15.0	5.77
		S72	1.0**	0.7	-3.8	12.2	9.0	3.9	8.0	-3.8	-5.2	-2.0	-23.3	13.1	7.07
	F_2	W71	2.2**	2.0**	-8.6	27.5	0.3	-13.4	-6.0	14.5	-11.0	2.7	-21.3	15.1	2.89
		W72	2.0**	2.7**	-10.4	26.5	9.2	-19.1	3.0	3.6	2.9	-1.8	-23.2	9.3	4.08
		S71	1.6**	1.8**	-5.5	20.4	8.8	-9.5	10.4	3.1	-0.7	-12.1	-23.1	8.1	1.19
		S72	0.8**	1.7**	0	15.5	11.4	1.8	5.1	-0.6	-11.3	-5.6	-9.9	-6.5	0.96
% florets with kernels	F_1	W71	-[2]	-	-	-	-	-	-	-	-	-	-	-	-
		W72	7.0**	23.0*	-0.1	3.0	2.9	-2.0	0.8	1.8	-4.0	0.3	-5.5	2.8	2.04
		S71	6.0**	10.0*	3.3	1.4	1.8	-4.8	-0.5	1.0	-3.3	-1.5	-1.0	3.7	1.83
		S72	7.0**	17.0**	-0.8	3.4	2.1	0	1.2	2.0	1.1	-0.3	-6.0	3.5	1.29
	F_2	W71	2.0**	2.0*	1.3	1.6	0.1	-2.0	-1.3	1.6	-1.8	1.4	-2.2	1.2	0.76
		W72	4.0**	7.0	0.5	3.2	1.6	-4.0	-0.6	-0.1	0.8	1.4	-4.0	1.0	1.58
		S71	3.0**	9.0**	0.7	2.5	2.3	-2.3	0.7	-0.5	-0.2	-1.3	-2.8	0.8	0.01
		S72	5.0**	7.0**	0.6	3.7	3.9	-0.1	-1.4	0.1	-2.9	-0.8	-2.3	-0.8	0.01

GCA and SCA represent, respectively, general and specific combining abilities.
S.E.$(\hat{g}_i - \hat{g}_j)$ is the standard error of the difference between 2 GCA effects.
A = Adur; C = Candeal Selection; D = DT-310; K = Kharkov Kaja; M = Madif; N = Narodnaja; L = Leeds; S = Stewart 63; I = Iumillo; My = My-54.
W71 = Winnipeg 1971; W72 = Winnipeg 1972; S71 = Swift Current 1971; S72 = Swift Current 1972.

[1] Negative estimate, i.e. environmental variance component exceeds genetic component.

[2] No significant genotypic variation.

Table 7. (Continued)

Character	Generation	Environment	Variance Component GCA	SCA	GCA effects A	C	D	K	M	N	L	S	I	My	S.E. $(\hat{g}_i - \hat{g}_j)$
Spikelets/ spike	F_1	W71	0.4**	0.5*	0.6	-0.2	0.8	-0.3	0.4	-0.9	-0.1	0.4	0.3	-1.2	0.29
		W72	0.1**	0.5**	0.4	-0.4	0	-0.3	0.1	-0.1	-0.1	0.6	-0.2	-0.2	0.18
		S71	0.6**	0.3**	0.2	-0.4	1.0	-0.3	0.9	1.3	0	0.7	0.4	-1.2	0.18
		S72	0.1**	0	0.6	0.1	0.4	-0.5	0.4	-0.2	-0.4	0.1	-0.1	-0.3	0.27
	F_2	W71	0.3**	0.2**	0.1	-0.3	0.4	-0.2	0.4	-1.0	0	0.8	0.3	-0.5	0.10
		W72	0.1**	0.2*	-0.2	0.3	0.5	-0.2	0.3	-0.7	-0.1	0.4	0.1	-0.3	0.24
		S71	0.3**	0.3**	0.1	-0.1	0.5	-0.5	0.2	-1.0	-0.1	0.7	0.6	-0.4	0.09
		S72	0.1**	0.2*	0.3	0.1	0.3	-0.2	0.2	-0.3	-0.2	0.3	0.2	-0.7	0.15
Florets/ spike	F_1	W71	8.1**	0	2.0	5.6	2.9	-0.9	2.6	-4.2	-2.4	1.4	-0.1	-6.8	3.34
		W72	0.8**	6.0**	0.6	0.3	-1.4	-1.0	0.3	-0.2	-0.2	2.2	-1.4	0.7	0.90
		S71	11.2**	19.6**	-0.4	-0.3	3.9	-1.4	7.2	-3.1	0.3	1.6	-3.4	-4.3	1.55
		S72	1.7**	0	1.9	0.4	1.7	-2.8	2.3	-0.2	-1.5	0.1	-1.2	-0.8	1.35
	F_2	W71	3.4**	7.2**	-1.8	3.4	1.4	-2.0	0.8	-1.5	-1.1	2.3	-2.0	0.4	0.87
		W72	5.4**	0	-3.9	5.2	3.1	-1.9	2.2	-1.8	-0.4	-0.6	-2.1	0.3	2.12
		S71	2.3**	4.1**	-0.8	1.8	1.7	-1.9	2.3	-1.9	-0.2	0.4	-1.2	-0.1	0.45
		S72	2.7**	10.3**	0.5	1.0	0.6	-0.3	3.4	-1.3	-0.9	0.2	-0.1	-3.1	0.56
Kernels/ spike	F_1	W71	9.8**	26.0**	3.3	4.2	2.2	-3.8	1.7	-2.6	-2.2	2.8	-0.4	-5.2	1.50
		W72	4.4**	14.1**	0.2	2.3	0.9	-2.1	0.6	0.9	-2.8	2.1	-4.7	2.6	1.68
		S71	7.6**	15.7**	1.8	0.7	3.9	-4.1	4.9	-1.7	-2.0	0	-2.9	-0.4	1.18
		S72	4.0**	1.4	0.8	2.1	2.6	-2.0	2.2	-1.1	-1.8	-0.2	-4.2	1.4	1.41
	F_2	W71	4.7**	8.6**	-1.0	3.7	1.2	-2.7	0.1	-0.3	-2.0	2.7	-2.9	1.1	0.63
		W72	7.8**	2.4	-2.4	5.5	2.9	-4.0	1.2	-1.3	0.3	0.6	-3.8	0.8	1.38
		S71	3.5**	5.3**	-0.4	2.7	2.4	-2.6	2.1	-1.8	-0.3	-0.3	-2.1	0.3	0.45
		S72	2.9**	5.3**	0.6	2.6	2.4	-0.2	1.3	-0.8	-2.1	-0.2	-1.2	-2.4	0.50
Plant height	F_1	W71	24.7**	11.3**	7.4	-4.0	0.7	0	0.8	-1.0	-3.9	8.3	0.1	-8.4	1.25
		W72	17.0**	11.0**	6.3	0.3	-0.3	-1.9	0.6	-0.4	-2.1	5.6	0.6	-8.6	0.48
		S71	29.5**	23.4**	5.6	-3.1	-1.2	-0.2	0.6	-2.0	0.1	14.5	-2.0	-9.4	1.06
		S72	13.8**	10.5	8.0	1.2	-1.9	-4.5	2.3	2.1	0.1	1.9	-6.2	-3.0	2.40
	F_2	W71	36.9**	17.7**	7.3	-2.3	-1.9	-1.0	0.7	-0.7	-1.5	11.6	-0.6	-11.6	0.91
		W72	38.4**	16.6**	6.9	-1.1	-0.4	-1.4	-0.6	-1.1	-2.1	12.1	-0.4	-12.0	0.46
		S71	13.0**	9.7**	4.6	-2.5	-1.8	-0.3	2.6	0.1	-1.7	6.7	-2.2	-5.4	0.89
		S72	12.5**	17.9**	4.1	0.6	-0.7	1.6	5.0	-1.8	-1.3	3.2	-4.0	-6.6	1.22
Days to heading	F_1	W71	0.3**	0.4	0.5	-0.8	-0.1	-0.7	0.8	-0.7	0	0.2	1.0	-0.3	0.35
		W72	0.4**	1.2**	0.1	-1.0	0.3	-0.8	0.8	-0.2	-0.4	-0.2	1.0	0.4	0.18
	F_2	W71	0.8**	1.3**	0	-0.9	-0.6	-1.5	0.2	-0.4	0.3	1.0	1.7	0.1	0.18
		W72	0.3**	1.3**	-0.1	-0.8	-0.1	-0.8	-0.1	-0.2	0.3	0.6	1.1	0.2	0.13

Current. Thus, DT-310 can be considered as a prospective recurrent parent to be used in some hybridization program at Swift Current for the improvement of yield. DT-310 and Candeal Selection had consistently high general combining ability effects in all environments and in both filial generations for the number of kernels per plant. Since these two cultivars also out performed all others in terms of grain yield and number of kernels per plant (Table 4), they should, in all probability, be promising germ plasm sources for the improvement for yield or for number of kernels per plant. On the other hand, although Stewart and Iumillo were the two best combiners for grain yield in the F_1 at Winnipeg, 1971, these cultivars were themselves not high yielders.

Kharkov Kaja had consistently high general combining ability for 1,000 kernel weight. Since this cultivar also performed relatively well in kernel weight, it should be considered as promising genetic material for the improvement of this metrical character. Candeal Selection not only out performed all other cultivars in terms of the number of kernels per spikelet, but was also the best combiner for this character. Thus, using Candeal Selection as a recurrent parent in a breeding program should in all likelihood improve fertility in durum wheat.

Positive and negative specific combining ability effects were present in all hybrids for each of the metrical characters studied. However, these effects were not consistent over environ-

ments nor were they consistent over generations. Although a number hybrids showed statistically significant positive or negative effects, very few could be considered outstanding.

IV. The Genetic System

A. Testing the Validity of Assumptions Underlying the Diallel Analysis

The theoretical basis of the diallel analysis as developed by Jinks (1954) and Hayman (1954) is based on a number of hypotheses or simplifying assumptions regarding the genetic system of the experimental material. These assumptions include: (1) Homozygous parents; (2) diploid segregation; (3) no reciprocal differences, i.e. absence of maternal or cytoplasmic effect; (4) no epistasis; (5) genes are independently distributed among the parents, i.e. no linkage; (6) no multiple allelism; and (7) no genotype-environment interaction within location or year. The validity of the diallel analysis is thus based on a simple additive-dominance genetic model with additive environmental effects and independence of genes in action and in distribution in the experimental material (a set of inbred lines and the hybrid families derived from crosses among these lines).

Certain of these assumptions may be considered valid for the material used in the present study. Parental homozygosity is essentially assured due to the self-pollinating habits of tetraploid wheat. Also, durum wheat is an old, established allo-tetraploid that has become a functional diploid over a great period. While strict validity of the assumption

regarding the absence of reciprocal differences is not ensured, maternal influences on the expression of most quantitative traits in wheat crosses are unusual. A few cases have been described in connection with a certain type of chlorophyll deficiency associated with plastid inheritance in hexaploid wheat (Sears, 1948). Nonetheless, it is unlikely that such effects could bias the diallel analysis in any significant way.

Some bias to the diallel analysis is possible due to the lack of an adequate procedure for obtaining separate and unambiguous evaluations of the assumptions regarding epistasis, linkage, and multiple allelism. Hayman (1954, 1957, 1958) has investigated the individual effects of epistasis, linkage, and multiple allelisin on the diallel analysis from a theoretical standpoint. He has shown that epistasis of the complementary type inflates the estimate of $(H_1/D)^{\frac{1}{2}}$, the average degree of dominance, but has little effect on the estimate of $H_2/4H_1$, the average frequency of positive and negative alleles in the parents. On the other hand, epistasis of the duplicate type has negligible effect on these two estimates. $(H_1/D)^{\frac{1}{2}}$ is deflated by the associated type of correlated gene distribution (alleles of like effects together in one parent) while this estimate is inflated by dispersion linkage (alleles of unlike effect located in same parent). However, $H_2/4H_1$ is relatively independent of either type of linkage (Hayman, 1954). In the absence of epistasis, Hill (1964) demonstrated that the associated type of linkage

produces an upward curvature on the diallel regression graph while dispersion type of linkage has no effect on the regression. Multiple allelism may cause a slight curvature on the diallel regression graph but does not appear to produce any serious source of bias in the diallel analysis (Hayman, 1957). Furthermore, Crumpacker and Allard (1962) demonstrated, on theoretical grounds, that bias due to failure of any one of these three assumptions is inconsequential as long as there is no significant deviation of the diallel regression slope from unity. Alternatively, if the assumptions on which the diallel theory is based were valid, the quantity Wr-Vr would be constant over all arrays (Hayman, 1954 ; Mather and Jinks, 1971). Wr and Vr are, respectively, the covariance between an array with its non-recurrent parent and variance of an array in the diallel table. Thus, if the diallel assumptions hold, i.e. Wr-Vr constant over arrays, the Wr = constant + Vr for all arrays. Consequently, the regression of Wr on Vr would be a straight line with unit slope.

The general test of the validity of the above assumptions was therefore conducted by means of an analysis of variance of the quantity Wr-Vr. This quantity was calculated for each of the ten arrays in each of the two replicates in each environment and generation. In the analysis of variance table, the sources of variation were replicates, arrays, and error with 1, 9, and 9 degrees of freedom, respectively. Heterogeneity of

Table 8. Analysis of Variance for the Homogeneity of (Wr-Vr) Over Arrays

Source of variation	Mean squares[1]																					
	F_1				F_2				F_1				F_2				F_1				F_2			
	W71	W72	S71	S72	W71	W72	S71	S72	W71	W72	S71	S72	W71	W72	S71	S72	W71	W72	S71	S72	W71	W72	S71	S72
	Yield								1000 kernel weight								Spikelets/spike							
Replications	19454*	696	81	5	1266**	13	0.3	609	4	598	255	412	39	594*	34	1	4.59	0.04	0.21	0.26	0.07	0.08	0.07	0.01
Arrays	4939	1007	54	42	490**	2470	14.5**	119	167**	692	134	215	30	93	16	30	1.69	0.70*	0.32	0.10	0.04	0.36	0.06	0.05
Error	3182	3060	80	38	88	3982	2.6	191	21	565	71	221	13	66	9	24	1.95	0.20	0.13	0.12	0.04	0.13	0.04	0.07
	Florets/spike								Kernels/spike								% florets with seeds							
Replications	157*	24	67	14	45	233	33	434*	8419	826	1	106	12	14	133*	39	$<10^{-4}$	1.00**	0.70*	1.00**	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$
Arrays	54	164	1062	136	127	276	13	166	1428	1044	846	147	84	227	47	51	$<10^{-4}$	0.11	0.05	0.22*	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$
Error	24	92	708	88	82	1403	23	68	2365	690	465	50	46	439	24	41	$<10^{-4}$	0.10	0.10	0.05	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$
	Kernels/spikelet								Days to maturity								Plant height							
Replications	0.040*	0.006	0.004	0	0	0	0.005	0	0.02	1.27*	9.24	0.08	4.75	37	21	0.15	1039*	1	2	2219	144	134	153	1120
Arrays	0.004	0.004	0.004	0.002	0.003	0.002	0.003	0.002	0.64	0.30	7.50	0.24	2.72	17	17	0.14	416	113**	1058	1265	516	402**	52	638
Error	0.005	0.003	0.003	0.001	0.003	0.003	0.003	0.003	0.85	0.27	5.18	0.20	4.10	14	7	0.24	168	11	414	1603	449	56	186	440
	Days to heading																							
Replications	2.82	0.13	-	-	0	3.30*	-	-																
Arrays	0.62	0.33**	-	-	1.02	0.86	-	-																
Error	0.86	0.08	-	-	1.12	0.33	-	-																

[1] The degrees of freedom associated with replicates, arrays, and error are 1, 9 and 9, respectively

Wr-Vr over arrays was indicated by the significance of the variance-ratio of arrays over error (Table 8). If the variance-ratio for arrays is statistically significant, failure of one or more of the diallel assumptions is indicated, resulting in a decrease in precision of the diallel analysis.

Partial failure of one or more of the diallel assumptions is indicated for the following characters: F_2 grain yield from both locations in 1971; 1000 kernel weight in the F_1 from Winnipeg, 1971; F_1 spikelets per spike from Winnipeg, 1972; proportion of florets bearing seeds of the F_1 data from Swift Current, 1972; plant height in both generations from Winnipeg, 1972 and days to heading in the F_1 from Winnipeg, 1972. When a particular set of data fails to conform to the assumptions imposed by the diallel genetic model, the data can be adjusted to achieve conformity by successively eliminating different array(s)[2] until the offending array(s) have been discarded so that the remaining data fit these assumptions (Hayman, 1954). However, no such attempt was made on the present data since such a procedure is, at best, of questionable logic.

On the whole, the results obtained from the test of diallel assumptions were not comparable for the generations or the environments used and, therefore, such tests should be conducted for each particular set of data. Again, since there is no test available which can evaluate unambiguously the presence of epis-

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[2]An array in the diallel context refers to the means of all crosses involving a given parent (recurrent parent), including the mean of the parent itself.

tasis[3], linkage and multiple allelism, the foregoing general test of assumptions must be regarded as, at best, insensitive and approximate. Moreover, a non-significant heterogeneity of Wr-Vr over arrays does not necessarily imply absence of epistasis, linkage and multiple allelism in the genetic system of the experimental material; rather, it may indicate that these effects, individually or accumulatively, may be too low for statistical detection, or that one effect may have nullified another - but, only so far as this test is concerned. One can never be certain that they do not bias the estimates of the various genetic parameters. Nevertheless, the effects of partial failure of some of the foregoing assumptions seemed unlikely to be large enough to seriously bias the genetic analysis of the data (Crumpacker and Allard, 1962).

The assumption of no genotype x environment interaction within location or year was tested by the mean square ratio of replicate x genotype to replicate x genotype x location and replicate x genotype x year effects, respectively. From Table 1, the error term implicitely consisted of the following sources of variation:

Source of variation	Degrees of freedom
Error	223
R x G	55
R x L	1
R x G x L	55
R x Y	1
R x G x Y	55
R x L x Y	1
R x G x L x Y	55

[3] The presence of epistasis and its stability in different environments will be evaluated in a later section.

Table 9. Analysis of Variance for the Test of Lack of Genotype x Environment Interaction Within Year or Location

Source of variation	Degrees of freedom	Yield		1000 kernel weight		Spikelets/ spike		Florets/ spike		Kernels/ spike		% florets with seeds		Kernels/ spikelet		Days to maturity		Plant height		Days to heading	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Ho: No genotype x environment interaction within year																					
Genotype x replicate	55	49	8217	22	9	1.6	0.3	60	22	57	9	76	24	0.12	0.03	52	37	220	38	1.04	0.75
Genotype x replicate x year	55	40	8868	28	7	1.1	0.3	46	20	52	16	72	16	0.12	0.03	38	26	226	27	0.76	0.53
Ho: No genotype x environment interaction within location																					
Genotype x replicate	55	49	8217	22	9	1.6*	0.3	60	22	57*	8	76	24	0.12*	0.03	52	37	220	38	-	-
Genotype x replicate x location	55	45	10535	29	8	1.0	0.3	67	16	34	10	55	27	0.07	0.03	52	37	253	37	-	-

Therefore, the 223 degrees of freedom associated with the error term were further partitioned to obtain the mean squares for R x G x L and R x G x Y to be used as the denominators for replicate x genotype interaction in the variance-ratio tests (Table 9).

The results indicated that the assumption regarding the absence of genotype x environment interaction within a year was valid for all of the characters studied. However, the genotype x environment interaction effect within location was statistically significant in the F_1 data for number of spikelets and kernels per spike and for number of kernels per spikelet. Differences in the relative performances for these three characters between the two replicates within a location were minor compared to the magnitude of genotypic differences and therefore such interaction effect seems unlikely to have introduced more than trivial bias into the genetic analysis.

B. Estimation of Genetic Parameters

If the tests for the diallel assumptions provide no serious reason to doubt the adequacy of the genetic model, the various genetic components of variance and their standard errors can be estimated (Hayman, 1954; Jinks, 1954, 1956; Mather and Jinks, 1971). The statistics generated from the Jinks-Hayman-Mather technique may be interpreted in terms of defined genetic parameters. The necessary computations, based on the ten parental cultivars and their F_1 and F_2 family means in the present study, include the variance of the parents entering into the diallel cross (Volo), the variance of the r^{th} array corresponding to each of the r parents (Vr), the covariance of the progeny in each array with the non-recurrent parents (Wr), the covariance between the parents and the mean of their progeny (WoLol), the mean variance of all arrays (VlLl), the variance of array means (VoLl), and the square of the overall difference between the mean of the parents and the mean of their progeny $(M_{Ll}-M_{Lo})^2$.

The genetical expectations associated with each of the above statistics is as follows:

$$
\begin{aligned}
\text{Volo} &= D + E \\
\text{WoLol} &= \tfrac{1}{2}D - \tfrac{1}{4}F + \frac{1}{n}E \\
\text{VlLl} &= \tfrac{1}{2}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}F + E \\
\text{VoLl} &= \tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2 - \tfrac{1}{4}F + (n-1)E/n^2 \\
(M_{Ll}-M_{Lo})^2 &= \tfrac{1}{4}h^2 + (n-1)\ E/n^2 \\
\text{Vr} &= \tfrac{1}{4}D + \tfrac{1}{4}H_1 + E \\
\text{Wr} &= \tfrac{1}{2}D + \frac{1}{n}E
\end{aligned}
$$

The genetic components of variation obtained by least squares computations from the second degree statistics given above is as follows:

$$\hat{D} = \text{VoLo} - E$$

$$\hat{F} = 2\,\text{VoLo} - 4\,\text{WoLol} - \left(2 - \frac{4}{n}\right) E$$

$$\hat{H}_1 = \text{VoLo} - 4\,\text{WoLol} + 4\,\text{VlLl} - (5n-4)E/n$$

$$\hat{H}_2 = 4\,\text{VlLl} - 4\,\text{VoLl} - 4\,(n^2-n+1)\,E/n^2$$

$$\hat{h}^2 = 4\,(M_{Ll}-M_{Lo})^2 - 4(n-1)\,E/n^2$$

D is defined as the genetic component of variation due to the additive effects of genes and H_1 due to the dominance effects of genes; $H_2 = H_1((1-(u-v)^2))$ where u and v are respectively the proportions of positive and negative alleles distributed amongst the parents. Thus, H_2 can be considered as the component of variation due to the dominance effects of genes corrected for the assymmetry of gene distribution amongst the parents; F is the average covariation of the additive and dominance effects of genes over all arrays; h^2 is the square of the net overall dominance effect, over all loci; E is the environmental component of variance; and n is the number of parents.

The genetic components of variance, as defined above, provide estimates of the following ratios:

$$\left(\frac{\hat{H}_1}{D}\right)^{\frac{1}{2}} = \text{mean degree of dominance over all loci,}$$

$\widehat{\frac{K_D}{K_R}} = \left[(4\ DH_1)^{\frac{1}{2}} + F\right] \Big/ \left[(4\ DH_1)^{\frac{1}{2}} - F\right]$ = the ratio of the total number of dominant and recessive genes in the parents,

$\frac{\widehat{0.5F}}{\left[D(H_1-H_2)\right]^{\frac{1}{2}}}$ is used to estimate the relative consistency of of the ratio of h to d over all loci. h and d are, respectively, the dominance and additive effects of individual genes, sign considered,

$\widehat{\frac{h_2}{H_2}}$ = estimate of the number of major groups of genes which control the character and exhibit dominance to some degree,

$\frac{\frac{1}{2}D + \frac{1}{2}\widehat{H_1} - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F + E}$ is the estimate of the narrow sense heritability as defined by Mather and Jinks (1971).

The "quasi least squares" method of Hayman (1954) was used to estimate the precision (e.g. standard errors) associated with each of the above genetic components.

The analysis of the F_2 diallel data follows the same general form as that of the F_1 except that the contribution of the dominance effect of the heterozygote, h, is halved on account of a generation of inbreeding (Johnson and Aksel, 1959; Lee and Kaltsikes, 1972a). All of the computations of the diallel analysis were carried out using a computer program developed by Lee

and Kaltsikes (1972a). The results are summarized in Table 10.

B.1. Additive and Dominance Genetic Components of Variance

The additive genetic component of variance, D, was either significant or highly significant at some environments in all characters studied. However, for most characters, the magnitude of this component varied considerably among environments and between generations (Table 10). Thus, for grain yield, the additive genetic component was not significant in both generations at Swift Current, 1971, but was highly significant in the other three environments; similarly, number of kernels per plant in the F_1 showed significant additive genetic effect in all four environments but no significance was obtained in the F_2 at Swift Current, 1971. The environment exerted the most noticeable influence in the additive genetic effect on the percent of florets bearing kernels, for it ranged from no significant genotypic variation in the F_1 grown at Winnipeg, 1971, to highly significant additive effect in the F_2 material grown at Winnipeg, 1971 and at Swift Current, 1972. By contrast, neither the environment nor generation seem to have influenced the additive gene effect for plant height and days to heading. In general, the amount of fixable genetic effects present in these ten durum cultivars strongly suggests that improvement of any of the characters studied is possible through selection.

Table 10. Components of Genetic Variance and Other Statistics Derived From the Diallel Cross Analysis

Character	Generation	Environment	Genetic components				Proportional values					Heritability (x 100)
			D	H_1	H_2	F	$\left(\frac{H_1}{D}\right)^{\frac{1}{2}}$	$\frac{Vr}{Wr}$	$\frac{0.5F}{[D(H_1-H_2)]^{\frac{1}{2}}}$	$\frac{h^2}{H_2}$	$\frac{K_D}{K_R}$	
Grain yield	F_1	W71	121 ± 27**	0+	9 ± 49	41 ± 23*	0	0.97	0.62	0	3.8	28
		W72	48 ± 18**	235 ± 37**	187 ± 32**	91 ± 41*	2.2	6.41	0.94	0	2.5	3
		S71	30 ± 32	206 ± 7**	200 ± 59**	4 ± 75	2.6	4.66	0.14	0	1.0	14
		S72	13 ± 3**	32 ± 5**	25 ± 5**	14 ± 6*	1.6	4.64	0.73	0.5	2.1	18
	F_2	W71	13 ± 7*	361 ± 15**	310 ± 13**	-28 ± 17*	5.2	3.13	-0.54	0.4	0.6	34
		W72	24 ± 2**	105 ± 5**	103 ± 4**	-14 ± 5**	2.1	1.09	-1.01	0.1	0.7	38
		S71	1 ± 30	60 ± 2**	52 ± 2**	-3 ± 3	7.9	8.02	-0.53	0.6	0.1	25
		S72	3 ± 1**	31 ± 1**	25 ± 1**	4 ± 1**	3.2	2.48	0.47	0.1	1.5	23
Kernels/ plant	F_1	W71	45 ± 7**	99 ± 14**	76 ± 12**	43 ± 15**	1.4	1.66	0.66	0	1.9	39
		W72	17 ± 3**	76 ± 6**	60 ± 5**	25 ± 6**	2.1	4.08	0.75	0.1	2.1	20
		S71	6 ± 1**	20 ± 2**	17 ± 2**	4 ± 2*	1.8	2.37	0.47	0	1.5	36
		S72	18 ± 3**	54 ± 6**	41 ± 5**	22 ± 6**	1.7	3.95	0.71	0	2.1	29
	F_2	W71	76 ± 12**	734 ± 26**	481 ± 22**	114 ± 28**	3.1	1.85	0.41	0.2	1.6	42
		W72	116 ± 12**	705 ± 25**	452 ± 21**	119 ± 27**	2.5	1.25	0.34	0.1	1.5	49
		S71	3 ± 3	170 ± 7**	140 ± 6**	-8 ± 8	8.0	4.83	-0.42	0.7	0.7	35
		S72	25 ± 5**	335 ± 12**	286 ± 10**	20 ± 12	3.7	2.33	0.28	0.1	1.2	25
1,000 Kernel weight	F_1	W71	25.2 ± 3.8**	45.7 ± 8.1**	32.7 ± 6.9**	1.3 ± 8.8	1.3	1.22	0.03	0.3	1.0	50
		W72	56.3 ± 9.9**	154.6 ± 21.0**	111.6 ± 17.9**	78.4 ± 22.8**	1.6	4.39	0.79	0.1	2.4	18
		S71	7.6 ± 4.1	41.7 ± 8.8**	34.1 ± 7.5**	6.0 ± 9.5	2.3	4.44	0.39	0	1.4	25
		S72	8.6 ± 6.4	73.6 ± 13.7**	64.8 ± 11.6**	-8.1 ± 14.8	2.9	3.01	-0.46	0	0.7	32
	F_2	W71	23.6 ± 2.0**	95.6 ± 4.3**	87.2 ± 3.6**	9.4 ± 4.6*	2.0	1.01	0.33	0.3	1.2	32
		W72	22.9 ± 4.7**	0	2.9 ± 8.5	-28.3 ± 10.9**	0	0.90	-1.73	0.2	0.1	65
		S71	7.4 ± 1.6**	47.5 ± 3.4**	43.0 ± 2.9**	-0.5 ± 3.7	2.5	1.27	-0.04	0	1.0	32
		S72	24.9 ± 2.2**	87.5 ± 4.6**	68.3 ± 3.9**	17.1 ± 4.9**	1.9	0.85	0.39	0.6	1.4	38
Kernels/ spikelet	F_1	W71	29.6 ± 3.4**	52.3 ± 7.1**	30.5 ± 6.1**	44.6 ± 7.8**	1.3	3.08	0.87	0.4	3.6	23
		W72	1.5 ± 2.4	36.0 ± 5.2**	29.9 ± 4.4**	-0.4 ± 5.6	4.9	5.85	-0.06	0.3	0.9	21
		S71	6.5 ± 2.4**	23.6 ± 5.1**	20.0 ± 4.3**	1.0 ± 5.5	1.9	3.07	0.10	0.1	1.1	34
		S72	0.2 ± 1.1	4.3 ± 2.4*	2.6 ± 2.0	-3.5 ± 2.6	4.5	3.35	-3.01	1.5	0.3	27
	F_2	W71	8.4 ± 0.7**	55.7 ± 1.5**	44.9 ± 1.2**	2.8 ± 1.6*	2.5	1.19	0.14	0	1.1	40
		W72	6.6 ± 1.9**	86.8 ± 4.1**	60.0 ± 3.5**	7.1 ± 4.4	3.6	1.97	0.26	0.1	1.3	44
		S71	6.6 ± 0.6**	52.6 ± 1.3**	35.0 ± 1.1**	7.1 ± 1.4**	2.8	1.38	0.32	0.1	1.3	49
		S72	7.9 ± 0.7**	53.6 ± 1.5**	36.6 ± 1.3**	17.8 ± 1.6**	2.6	1.22	0.76	0.2	2.5	28
% floret with kernels	F_1	W71	-++	-	-	-	-	-	-	-	-	-
		W72	7 ± 14	208 ± 30**	171 ± 25**	3 ± 32	5.5	10.59	0.09	0.5	1.1	18
		S71	20 ± 10*	58 ± 21**	39 ± 18*	9 ± 23	1.7	4.04	0.23	0	1.3	23
		S72	10 ± 9*	128 ± 20**	109 ± 17**	-12 ± 22	3.5	3.42	-0.43	0.2	0.7	30
	F_2	W71	6 ± 2**	69 ± 4**	60 ± 4**	-18 ± 5**	3.5	1.90	-1.22	0	0.4	42
		W72	10 ± 9	183 ± 19**	104 ± 16**	-29 ± 21	4.2	13.20	-0.51	0	0.4	47
		S71	5 ± 9	370 ± 20**	229 ± 17**	41 ± 22*	8.8	18.85	0.77	0.1	2.9	43
		S72	38 ± 4**	263 ± 8**	153 ± 7**	81 ± 9**	2.6	1.69	0.62	0.1	2.4	40

+Negative estimate, i.e. the environmental component of variance exceeds the genetic variance component.

++Genotypic variation was not significant

Table 10. (Continued)

Character	Generation	Environment	Genetic components				Proportional values					
			D	H_1	H_2	F	$\left(\frac{H_1}{D}\right)^{\frac{1}{2}}$	$\frac{Vr}{Wr}$	$\frac{0.5F}{\left[D(H_1-H_2)\right]^{\frac{1}{2}}}$	$\frac{h^2}{H_2}$	$\frac{K_D}{K_R}$	Heritability (x 100)
Spikelets/ spike	F_1	W71	1.9 ± 0.6**	5.3 ± 1.2**	3.6 ± 1.0**	1.8 ± 1.3	1.7	2.06	0.50	0	1.8	33
		W72	0.3 ± 0.3	2.6 ± 0.6**	2.5 ± 0.5**	-0.1 ± 0.6	2.9	4.48	-0.29	0.6	0.9	21
		S71	1.2 ± 0.2**	1.8 ± 0.4**	1.6 ± 0.3**	-1.6 ± 0.4**	1.2	1.24	-1.66	0.1	0.3	66
		S72	1.0 ± 0.2**	0	0	0.8 ± 0.4*	0	1.22	-	0	2.9	10
	F_2	W71	1.1 ± 0.1**	3.8 ± 0.2**	3.3 ± 0.2**	0.4 ± 0.2*	1.8	0.87	0.27	0.9	1.2	41
		W72	0.1 ± 0.2	4.8 ± 0.4**	2.9 ± 0.3**	-0.1 ± 0.4	7.0	5.10	-0.11	0.3	1.0	42
		S71	1.4 ± 0.1**	6.3 ± 0.2**	5.4 ± 0.2**	1.1 ± 0.2**	2.1	1.04	0.49	0.6	1.4	30
		S72	0.1 ± 0.1	3.1 ± 0.2**	2.2 ± 0.2**	-0.3 ± 0.2	5.0	3.21	-0.50	0	0.6	45
Florets/ spike	F_1	W71	45.5 ± 26.4*	0	0	-36.2 ± 61.0	0	2.16	-	0.5	0.5	23
		W72	6.6 ± 4.5	47.4 ± 9.7**	41.4 ± 8.2**	7.5 ± 10.5	2.7	5.61	0.59	0.3	1.5	11
		S71	47.7 ± 14.6**	127.9 ± 30.3**	116.4 ± 25.8**	-3.3 ± 32.9	1.6	2.43	-0.07	0	1.0	35
		S72	23.2 ± 4.3**	0	0	21.6 ± 9.9*	0	2.00	-	0	9.1	2
	F_2	W71	12.4 ± 4.0**	204.7 ± 8.5**	176.5 ± 7.2**	5.7 ± 9.2	4.0	2.12	0.15	0.4	1.1	25
		W72	19.9 ± 11.9	0	0	12.5 ± 27.4	0	2.10	-	0.2	1.9	7
		S71	11.9 ± 1.7**	89.0 ± 3.7**	79.5 ± 3.2**	10.1 ± 4.0*	2.7	1.47	0.43	0.4	1.4	23
		S72	8.0 ± 4.6*	249.1 ± 9.7**	180.6 ± 8.3**	22.0 ± 10.6*	5.6	8.41	0.47	0.1	1.6	36
Kernels/ spike	F_1	W71	134 ± 19**	192 ± 41**	120 ± 35**	162 ± 44**	1.2	1.81	0.82	0.3	3.0	28
		W72	6 ± 12	144 ± 26**	120 ± 22**	3 ± 28	4.9	6.94	0.12	0.7	1.1	18
		S71	26 ± 10**	95 ± 21**	83 ± 18**	-2 ± 23	1.9	3.04	-0.06	0.1	1.0	35
		S72	8 ± 4*	7 ± 9	3 ± 8	-6 ± 10	0.9	2.36	-0.53	0.2	0.4	27
	F_2	W71	16 ± 3**	206 ± 7**	169 ± 6**	9 ± 7	3.5	1.98	0.18	0.3	1.1	31
		W72	16 ± 7**	98 ± 15**	24 ± 13*	-6 ± 16	2.5	1.83	-0.08	0.8	0.9	62
		S71	12 ± 2**	132 ± 5**	99 ± 4**	9 ± 6	3.3	1.88	0.22	0.1	1.3	40
		S72	17 ± 3**	146 ± 6**	94 ± 5**	34 ± 6**	2.9	1.85	0.57	0.2	2.0	39
Plant height	F_1	W71	104 ± 8**	73 ± 17**	64 ± 14**	4 ± 18	0.8	0.98	0.06	0	1.0	61
		W72	96 ± 3**	53 ± 7**	44 ± 6**	41 ± 7**	0.7	0.88	0.69	0	1.8	70
		S71	178 ± 12**	145 ± 25**	108 ± 21**	101 ± 27**	0.9	0.83	0.62	0.1	1.9	58
		S72	78 ± 15**	41 ± 32	38 ± 27	29 ± 35	0.7	1.74	0.94	1.0	1.7	25
	F_2	W71	213 ± 8**	429 ± 18**	333 ± 15**	195 ± 19**	1.4	1.66	0.68	0.1	1.9	38
		W72	218 ± 6**	359 ± 12**	203 ± 10**	220 ± 13**	1.2	0.62	0.59	0.4	2.3	59
		S71	104 ± 6**	312 ± 13**	215 ± 11**	166 ± 14**	1.7	0.72	0.82	0	2.7	22
		S72	65 ± 9**	499 ± 20**	430 ± 17**	63 ± 21**	2.7	1.44	0.47	0.1	1.4	22
Days to heading	F_1	W71	1.7 ± 0.4**	1.5 ± 0.8*	1.0 ± 0.7	1.0 ± 0.7	0.9	2.28	0.27	0	1.4	33
		W72	1.5 ± 0.2**	4.8 ± 0.4**	4.6 ± 0.3**	-0.2 ± 0.4	1.8	2.25	-0.18	0	0.9	38
	F_2	W71	2.3 ± 0.4**	29.1 ± 0.9**	22.5 ± 0.8**	0.5 ± 1.0	3.5	2.00	0.06	0	1.0	41
		W72	0.8 ± 0.3**	27.4 ± 0.7**	19.9 ± 0.6**	2.0 ± 0.8**	5.8	9.76	0.40	0	1.5	38

The dominance genetic component, H_1, was either significant or highly significant at some environments in all characters but for some traits this component showed substantial inconsistency in magnitudes over the four environments and between the two generations. Grain yield exhibited highly significant dominance effect on all four environments and in both generations excepting the F_1 grown at Winnipeg 1971, which had a negative estimate. This exemplifies the great influence the environment can exert on the dominance effect, since a negative estimate can only result if the environmental effect was larger than the genetic one. Dominance genetic effect governing the number of kernels per plant and per spikelet and days to heading were consistently significant in all environments and generations. Thus the effect of the dominant genes on the expression of the phenotypes for these three traits seemed to be independent of the environment and generation. For the remaining six characters the dominance effect interacted with both the environment and generation, but more noticeably with the former. On the whole, the dominance effect was of some importance in the genetic system of the ten durum cultivars and therefore, the exploitation of heterozygotic effects through some hybridization program could be feasible. The moderate proportion of hybrids showing significant positive or negative heterosis (Table 5) in fact, attests to this.

H_2 is the dominance component of variance, corrected for

the unequal allelic distributions amongst the ten parental cultivars, i.e. certain parents carried more dominant alleles while others, more recessive. The statistical consequence of unequal distribution of alleles among the parents is that H_1 is always greater than H_2, as can be shown from the following expectations:

$$H_1 = \sum 4uvh^2$$

and $$H_2 = \sum 16u^2v^2h^2$$

It can be demonstrated that $H_1=H_2$ if and only if $u=v=0.5$; otherwise, $H_1>H_2$. In an intentionally chosen set of parents, i.e. fixed set, as was the case in this and probably in all other diallel experiments, the set of parents are invariably chosen because they were considered genetically different from one another. Consequently, $u\neq v\neq 0.5$ and $H_2<H_1$. Thus, H_2 is an estimate of the true dominance genetic component in such a situation. As shown in Table 10, although the magnitude of H_2 was in most cases smaller than that of H_1, as expected, the pattern of statistical significance was similar between these two statistics, excepting the F_1 population for number of kernels per spikelet from Swift Current, 1972 and days to heading from Winnpeg, 1971, where H_2 was not significant. Thus, the general conclusion concerning dominance as drawn by H_2 was similar to that drawn by H_1.

B.2. Distribution of Alleles

F was used to estimate the relative frequencies of domi-

nant and recessive alleles distributed among the ten parents. Thus, if the positive alleles were in overall excess in the parents, i.e. u>v, and the positive alleles were also dominant, F is positive. Similarly, if the negative alleles were in overall excess, i.e. v>u, and were also dominant, F will again be positive. In other words, F will be positive whenever there were more dominant alleles present in the parents, irrespective of whether or not the dominant alleles were positive or negative. Conversely F will be negative when the recessive alleles were in excess in the parents while F approaches zero when the dominant and recessive alleles were distributed in equal proportions among the parents.

Actually, a more quantitatively exact statistic, K_D/K_R, which is a function of F, estimates the ratio of the total number of dominant to recessive genes in the ten parents. Moreover, these two statistics can be used in a complementary way. Thus, for the F_1 grain yield grown at Winnipeg in 1971 and in 1972, the approximate ratio of dominant and recessive genes in the parents were 3.8 and 2.5, respectively, and they were statistically greater than unity, as indicated by the F-statistic (Table 10). It can be seen that in many of the characters included in the present investigation, the dominant and recessive alleles were not in equal proportions among the ten parents, although the environment and generation were likely to have confounded the estimation of these two statistics. This was parti-

cularly apparent in grain yield: In the F_1 generation, the ratios of dominant and recessive alleles were unity or greater than unity while the reverse was true with the F_2 data.

B.3. Degree of Dominance

The additive (D) and dominance (H_1) genetic components of variance of each character presented in the previous section were defined as the sums of the squares of the additive (d) and dominance (h) effects of individual loci controlling a polygenic character. That is, $D = \sum_i 4uvd_1^2$ and $H_1 = \sum_i 4uvh_i^2$, where u and v are, respectively, frequencies associated with the dominance and recessive alleles. Since H_1 and D have the same coefficient for allelic frequencies, the square root of their ratio, i.e. $(H_1/D)^{\frac{1}{2}}$, can be used to estimate $|h| / |d|$, the overall average degree of dominance, ignoring the sign of heterozygote effects in individual loci. The degree of dominance estimated by this ratio does not take into account the sign of the deviation of each of the 45 hybrid families from their respective mid-parent values.

Implicitely, overdominance, i.e. $(H_1/D)^{\frac{1}{2}} > 1$, indicates that on the average, the absolute dominance effect, $|h|$, was greater than the absolute additive effect $|d|$ of genes, while the reverse would be true with partial dominance, i.e. $(H_1/D)^{\frac{1}{2}} < 1$. No dominance, i.e. $(H_1/D)^{\frac{1}{2}} = 0$ could only result when each of the 45 hybrids exactly equaled their respective mid-parent

values, in which case, $H_1 = \sum_i 4uvh_i^2 = 0$ (i.e. all of the h's were zero). However, when the environmental effect intermixes with the dominance effect, $H_1 = 0$ does not necessarily mean that each of the 45 hybrids exactly equaled its respective mid-parent value; rather H_1 could be a negative estimate (which is taken as zero) when the environmental component of variation exceeded that of the genetic. As a case in point, $H_1 = 0$ (actually negative) was found for grain yield in the F_1 grown at Winnipeg, 1971; yet, every one of the 45 hybrids deviated slightly from their respective mid-parent value.

The overall mean degree of dominance for the ten characters ranged from no apparent dominance (as a consequence of negative estimate for H_1) to overdominance (Table 10). A large majority of characters exhibited over-dominance excepting the F_1 generation for plant height, where dominance was partial. The degree of dominance, as was the case with the additive and dominance genetic components of variance, depended on the macro-environmental factors, i.e. years and locations, and on the generation involved.

In the F_2 the expected reduction of dominance by a factor of ½ relative to the F_1 was not observed in the present material. This could have been attributed to a variety of reasons. For example, the two generations may have responded to the environmental complex in a different manner. However, there were differences in the seeding rate between F_1 and F_2.

The F_1 plots were space planted at the rate of 15 seeds per 3-meter row while solid planting at the rate of 160 seeds per 3-meter row was used in the F_2 plots. It is not inconceivable that under the more intensive inter-plant competition that obtained in the F_2, the hybrid families performed better than the inbreds. Jain and Allard (1960) presented evidence for heterozygote advantage in competition populations of barley. Leffel and Hanson (1961) had suggested that unequal contributions of dominance effects among individuals in a heterogenous population, i.e. F_2, may cause over-estimation of dominance. Also, the F_1 generation is not affected by linkage whereas linkage exerts its effect in the F_2 (Griffing, 1950). In the event that linkage does exist in this material, H, the dominance genetic component, would be redefined in the F_2 (Mather and Jinks, 1971). Thus for a digenic case:

$$H = \Sigma h^2 + 2\Sigma\left[(1-2p)^2 \; h_a h_b\right] \quad \text{in } F_2 \text{ while}$$

$$\therefore H = \Sigma h^2 \quad \text{in } F_1,$$

where p is the recombination value. Thus, unless $p = 0.5$, i.e. no linkage or linkage in equilibrium, the estimation of H in the F_2 would be inflated by $2\Sigma\left[(1-2p)^2 \; h_a h_b\right]$.

Nevertheless, it is not possible with the present data to ascertain whether the greater-than-expected degree of dominance shown in the F_2 is truly a consequence of heterozygote superiority under intensive inter-plant competition or merely a

result of the over-estimation of dominance. The only way to untangle these two possibly confounded variables would be to grow out the F_1 and F_2 generations in the same manner.

On the whole, the apparent over-dominance seemed to be a salient characteristic of the present data. However, Allard (1956) suggested that overdominance shown by the ratio $(H_1/D)^{\frac{1}{2}}$ may be confounded with particular types of genic interactions. When such interactions occur, Vr will likely increase disproportionately relative to Wr, particularly for the more recessive arrays. Almost all of the characters, irrespective of environment or generation, which exhibited over-dominance also had ratios of Vr/Wr substantially greater than unity (Table 10). For example, percent florets with kernels in the F_2 from Swift Current, 1971 had a value of 8.8 for degree of dominance and Vr/Wr was 18.85, suggesting a great amount of genic interaction. Following Jones' (1917) theory of heterosis, Hayman (1954, 1958) demonstrated on theoretical basis that particular combinations of unidirectional dominance (i.e. all heterozygotic effects in each locus contribute positively, or negatively, to the expression of a polygenic character) and dispersion linkage seriously inflate the estimate of $(H_1/D)^{\frac{1}{2}}$. Therefore, it is not unreasonable to suggest that some or all of the foregoing factors may have contributed to the prevalent apparent over-dominance in the present data. Again, the diallel cross analysis affords no unambiguous separations and evaluation for all forms of epistasis or linkage.

(An approximate test for the evaluation of epistasis and its stability over environments will be carried on in a later section). One thing is certain: the display of heterozygotic effect was undeniable as revealed by the number of hybrids exhibiting heterosis (Table 5).

B.4. Consistency of the Dominance Effects Over Loci

It was pointed out in the previous section that the estimate of the degree of dominance, $(H_1/D)^{\frac{1}{2}}$, was actually an estimate of $|h|/|d|$. $|h| = \Sigma\left(h_1^2 + h_2^2 + \cdots + h_n^2\right)^{\frac{1}{2}}$ = sum of the squares of individual heterozygote effect over n loci, the sign of which is ignored since these values are squared. In other words, $|h|$ is the overall average effect of dominance in a polygenic character but no information is provided regarding the relative magnitudes of these individual h's. For example, partial dominance, $0 < (H_1/D)^{\frac{1}{2}} < 1$, in a polygenic character could result from over-dominance at some loci and little or no dominance at others, or partial dominance at all individual loci. In the former, the ratio of $|h_i| / |d_i|$ is not consistent over loci while in the latter, the ratio is relatively more consistent over loci. In view of the foregoing, Mather and Jinks (1971) suggested a statistic to evaluate the consistency of the dominance effects over loci. Accordingly, if the ratio of $|h_i| / |d_i|$ is consistent over loci, the absolute value of

$$\frac{\frac{1}{2}F}{\left[D(H_1-H_2)\right]^{\frac{1}{2}}}$$

has the expectation of one while random distribution of $|h_i| / |d_i|$ over loci renders this statistic close to zero (Note that this statistic is not estimable when $H_1 = H_2$ or when $D = 0$).

From Table 10 it can be seen that the absolute levels of dominance were in most cases not consistent over loci. In fact, random distribution of $|h_i| / |d_i|$ over loci was strongly indicated for 1000 kernel weight in the F_1 from Winnipeg, 1971 and F_2 from Swift Current, 1971; and kernels per spikelet in the F_1 from Winnipeg, 1972 and Swift Current, 1971. Similar results were obtained for percent florets with kernels, spikelets, florets and kernels per spike, plant height and days to heading in certain generations and at certain environments. It is then possible that both environment and generation effects exerted important influences on the consistency of the levels of dominance over loci.

B.5. Consistency in Direction of Dominance Over Loci and the Estimation of the Number of Gene Groups

In the previous section, the consistency of the level of dominance over loci was considered. However, no information was given regarding the direction, i.e. positive or negative, of dominance in individual loci controlling a polygenic trait. When in a polygenic character, some alleles exhibit positive while others exhibit negative dominance effects, the "net" dominance effect can be zero due to bi-directional cancellation of these effects.

With this theoretical background in mind Jinks (1954) and Hayman (1954) employed the ratio of h^2/H_2 to estimate the number of major gene groups which control a polygenic character and exhibit some degree of dominance. The implicit short-comings of this estimate is that if dominance levels in individual loci differ in sign (some positive and some negative), the ratio will be under-estimated. Also, it provides no information about loci exhibiting little or no dominance. A numerical example should make this ratio and its two short-comings more explicit: Suppose a polygenic character is controlled by 5 loci each with equal allelic frequencies (u=v=0.5); let the dominance effect for each of 4 heterozygotic loci equal 2 and that for the fifth heterozygotic locus equal 0. Case 1: The dominance level is unidirectional over all loci. Case 2: Two loci exhibit positive dominance while the other two, negative. Then it can be demonstrated that D, H_1, H_2, F, $(H_1/D)^{\frac{1}{2}}$ and $0.5F/\left[D(H_1-H_2)\right]^{\frac{1}{2}}$ are all identical for both cases but h^2/H_2 is substantially different.

Case 1: $$\frac{h^2}{H_2} = \frac{(h_1 + h_2 + h_3 + h_4)^2}{(h_1^2 + h_2^2 + h_3^3 + h_4^2)} = \frac{(2+2+2+2+0)^2}{4+4+4+4+0} = 4$$

Case 2: $$\frac{h^2}{H_2} = \frac{\left[2 + 2 + (-2) + (-2) + 0\right]^2}{4 + 4 + 4 + 4 + 0} = 0.$$

The main points of the above example were: (1) h^2/H_2 provided no information about the fifth gene which shows no dominance;

hence Case 1 provided an estimate of 4 genes for a 5-gene controlled character; (2) Case 2 illustrated both short-comings of h^2/H_2. Thus according to Case 2, no gene groups were involved in controlling this polygenic character, which, in fact, was a 5-gene controlled trait.

The estimate of h^2/H_2 (Table 10) ranged from zero for several characters to 1.5 for number of kernels per spikelet in the F_1 from Swift Current, 1972. The remaining cases had values all below one. On the whole, it would appear from the present study that (i) no major gene groups were involved in controlling any of these characters which also exhibited dominance to some degree, or (ii) the cancelling effect due to bi-directional dominance was great; i.e. Case 2 in the example. Possibility (i) is obviously ruled out since the dominance effect of genes (H_1 or H_2) was significant at some environments for all characters studied (Table 10). Therefore, the only explanation for the low values associated with h^2/H_2 was the prevalence of cancelling effect of genes due to bi-directional dominance since a large number of hybrids showed either positive or negative heterosis for these characters (Table 5).

B.6. Heritability Estimates

The narrow sense heritability, defined as the ratio of additive and/or additive x additive genetic variance to the phenotypic variance, was estimated according to Mather and Jinks

(1971). The results of the heritability estimates, expressed in percentages, are presented in Table 10.

In general, these estimates were relatively low in magnitude and varied considerably in different environments, again confirming the importance of the environmental effect on the phenotypic expressions of these metrical characters. Averaging over environments, the heritability estimates for grain yield were 16% and 30%, respectively, for the F_1 and F_2 generations. Number of florets per spike had the lowest estimate, yield and yield component characters, intermediate, while plant height the highest. On the whole, heritability estimates were higher in the F_2 than those found in the F_1 generation excepting plant height. As the number of plants per plot in the F_2 was 30 times greater than in the F_1 the environmental sampling error was expected to be considerably smaller in the F_2. Other things being equal this would have resulted in a higher heritability estimate in the F_2 population.

C. Stability of Genetic Parameters in Different Environments

In the previous sections, the analysis of the genetic systems controlling the expression of the ten metrical traits was performed separately for each of the four environments. Because of the inconsistencies of the estimates obtained for the various genetic parameters over these environments, it was suggested that for many of these characters both the additive

and non-additive genetic effects were largely environmentally dependent. However, no information was provided as to whether or not the inconsistencies of estimates over environments were, in fact, statistically significant.

The general method of testing the stability of genetic parameters over diverse environments proposed by Allard (1956) was employed on the present data. The stability of the additive genetic component over environments was tested by the analysis of the means of the parental lines from a replicated diallel experiment. Dominance, epistasis and their stabilities over environments were tested by the analysis of variance based on the second degree statistics generated from a replicated diallel experiment. It was assumed that all of the basic diallel assumptions mentioned previously were met, excepting the assumption of no epistasis. When epistasis is present in the genetic system the method not only detects its occurrence but also assesses its stability over environments.

The data from the present investigation were subjected to the foregoing in order to test for the stability of the various genetic parameters controlling each of the ten metrical characters. All computations of this analysis were carried out by the use of a computer program developed by Lee and Kaltsikes (1972b).

Genotype x environment interaction analysis of the additive components of variation for each of the F_1 and F_2 generations

is summarized in Table 11.

Significance of the mean squares associated with environments and replications within environments have no particular genetic meaning. They simply indicate that for that character, the overall average performance for the 10 parents was significantly different among the 4 environments and between the two replicates within an environment, respectively. Thus, there was significant variation between replicates within an environment in the F_1 for grain yield, number of kernels per spikelet and plant height, and in the F_2 for number of kernels per plant, 1000 kernel weight, and number of spikelets, florets and kernels per spike. On the other hand, the average performance of the ten parents was significantly different over the four environments for each of the ten characters studied in both generations, confirming once again the enormous influence of the environment (location and year) on the phenotypic expression of metrical or polygenic characters. Significance of the mean squares associated with parents indicates that the ten parental genotypes have different additive and/or epistatic genetic effects. Since the parents are homozygous lines, epistatic effects would be those resulting from interactions between homozygous loci, that is, the additive by additive type of interaction. It can be seen that the ten parents have different additive and/or additive x additive genetic effects controlling all of the metrical characters studied, irrespective of generations, thus confirming the differences in

Table 11. Genotype x Environment Interaction Analysis of the Additive Components of Variation

Source of variation	Degrees of freedom	Mean Squares									
		Grain yield		Kernels/plant		1000 kernel weight		Kernels/spikelet		% florets with seed	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Rep within environment	4	74	4	62	70*	24	16**	20*	1	6	1
Environment	3	3968**	8207**	5184**	6688**	703**	1124**	258**	92**	79**	216**
Parent	9	155**	40	491**	233**	87**	152**	42**	48**	10*	7**
Environment x parent	27	122**	25**	257**	75**	38**	12**	16**	4**	6	3**
Error	36	27	4	113	23	22	3	7	1	4	1

Table 11 (Continued)

Source of variation	Degrees of freedom	Mean Squares									
		Spikelets/spike		Florets/spike		Kernels/spike		Plant height		Days to heading	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Rep within environment	4	1	11**	61	51**	73	19*	65*	3	32	9
Environment	3	14**	234**	538**	1657**	1041**	613**	1264**	4509**	1056**	506**
Parent	9	6**	43**	159*	134**	196**	113**	842**	1102**	61**	56**
Environment x parent	27	1	10**	78	21*	68*	17**	66**	50**	12	12**
Error	36	1	1	58	11	36	6	20	7	13	3

Days to heading was taken only from Winnipeg. The degrees of freedom for rep within environment is 2, environment is 1, parent is 9, env't x parent is 9 and error is 18.

the general combining abilities among parents examined previously (Table 7). Stability of the additive with/or additive x additive genetic effects over environments was tested by the mean squares associated with environment x parent. Evidently, the additive and/or additive x additive effects for each of the ten characters in both generations were substantially unstable over the four environments, excepting the F_1 for percent florets with seeds, number of spikelets and florets per spike and days to heading; therefore the suspected instability of additive gene effects over environments was confirmed.

Genotype by environment interaction analysis of the non-additive components of variance (Table 12) showed the mean squares for environments and replications within environment to be significant for all characters in both generations, with a few exceptions, suggesting substantial instability in the mean dominance over the four environments and between the two replications within environment. Mean squares for dominance were highly significant for all traits in both F_1 and F_2, excepting the F_2 plant height, reaffirming the prevalence of dominance effects found in the previous section. Mean squares for dominance x environment were significant for all characters in both generations, excepting the number of kernels per spike in the F_2 and days to heading in the F_1, thus confirming the suspected instability of dominance effects over environments.

The array mean squares were significant only for certain

Table 12. Genotype x Environment Interaction Analysis of the Dominance Components of Variation

Source of variation	Degrees of freedom	Mean Squares									
		Grain yield		Kernels/plant		1000 Kernel weight		Kernels/spikelet		% florets with seed	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Rep within environment	4	1.71**	0.56*	1.27**	0.26	24.37**	0.65**	1.57**	0.43**	6.44**	4.40**
Environment	3	1.48**	6.44**	0.22	16.51**	20.37**	0.35**	3.86**	0.74**	1.54*	5.50**
Dominance	1	21.17**	46.46**	19.40**	38.81**	58.92**	1.87**	40.21**	4.65**	85.47**	80.22**
Dominance x environment	3	1.77**	8.18**	0.86**	10.97**	13.04**	0.26*	3.37**	0.46**	1.37*	9.13**
Array	9	0.19	1.51**	0.19	1.00**	0.86	0.12	0.78**	0.08	0.46	0.33
Array x environment	27	0.21	0.72**	0.16	0.95**	0.89	0.11	0.28	0.09	0.64	1.22
Array x dominance	9	0.11	0.56**	0.15	0.91**	0.78	0.08	0.24	0.04	0.09	0.36
Array x dominance x environment	27	0.14	0.31	0.08	0.60**	0.68	0.06	0.15	0.05	0.28	0.76
Error	76	0.23	0.20	0.17	0.28	1.32	0.08	0.21	0.08	0.45	0.48

Table 12 (Continued)

Source of variation	Degrees of freedom	Mean Squares									
		Spikelets/spike		Florets/spike		Kernels/spike		Plant height		Days to heading	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Rep within environment	4	2.95**	0.58**	1.80**	0.10	0.68*	0.55**	0.33**	0.04	0.07	1.59**
Environment	3	5.57**	1.67**	2.62**	1.27**	2.69**	0.52**	0.19**	0.37**	1.60**	0.97**
Dominance	1	19.18**	13.31**	24.06**	26.25**	31.31**	11.69**	0.37**	0.07	5.54**	26.39**
Dominance x environment	3	4.25**	3.43**	2.42**	2.19**	3.11**	0.16	0.36**	0.52**	0.17	4.59**
Array	9	0.07	0.11	0.18	0.36*	0.45*	0.23	0.11**	0.20**	0.52**	0.58**
Array x environment	27	0.23	0.16	0.15	0.19	0.32	0.10	0.01	0.03	0.18**	0.25
Array x dominance	9	0.29	0.12	0.09	0.24	0.16	0.09	0.02	0.02	0.04	0.32*
Array x dominance x environment	27	0.21	0.11	0.22	0.16	0.18	0.09	0.02	0.01	0.04	0.14
Error	76	0.25	0.11	0.26	0.15	0.21	0.12	0.02	0.03	0.06	0.16

characters and in certain generations, suggesting that for these characters there were appreciable differences in the degree of dominance among the ten parental cultivars (Table 12). Significance of the array x environment mean squares associated with days to heading in the F_1 and grain yield and number of kernels per plant in the F_2 suggests that for these characters the average level of dominance for each parent was not consistent over environments. For example, the most dominant parental cultivar in one environment may not be the most dominant one in another. (Of course, this is only possible if the effect of the environment is such that it suppresses, or induces, the expression of certain dominant genes).

The presence of epistasis in a genetic system and the stability of epistasis over environments were tested by the mean squares associated with array x dominance and array x dominance x environment, respectively (Table 12). Thus, epistasis was appreciable in the genetic system controlling grain yield and days to heading in the F_2 generation but no instability of epistasis in different environments was detected for these two traits. For number of kernels per plant, epistasis was of some importance but its magnitude may have depended on environmental factors.

In considering the results of the above analyses, it must be pointed out again that a lack of statistical signifi-

cance associated with a genetic effect does not necessarily imply complete absence of that effect; it may imply that the effect was too low for statistical detection. Nevertheless it could have exerted some influence on the phenotypic expression of a character.

D. Verification of the Predictive Ability of the Diallel Analysis

One of the functions of the diallel cross analysis as a statistical genetics method is to assess the importance of the dominance effect of genes controlling polygenic characters and also to evaluate the dominance relationships among the parents (i.e. the relative ranking of dominance among the parents) in early generations (Hayman, 1954; 1958). Having conducted such an assessment and if dominance effects of genes were found to be of significance, the breeder may decide to exploit this effect by, for example, crossing the most dominant parent with the most recessive. Barring the cancelling effect of dominant genes (i.e. some loci show positive dominance effect while others negative within a polygenic character), a hybrid between two such genetically divergent parents should have the theoretical expectation of exhibiting maximum heterosis. The opposite would, of course, be true for a hybrid from two genetically similar parents (i.e. dominant x dominant or recessive x recessive). Similarly, an F_2 population derived from crossing between two genetically divergent parents would be expected to show much more genetic segregation than that derived from crossing two genetically similar parents. To test these hypotheses the data pertaining to plant height were utilized.

Diallel analysis of the F_1 plant height data derived from Winnipeg 1971 revealed that the dominance effect was of major im-

portance in controlling the expression of this metrical character (Table 10). Hence the relative magnitudes and differences in the array covariances and variances, weighted by the parental variance (i.e. (Wr + Vr)/Volo for each array) provide, respectively, a measure of the order of dominance in the ten parents and an evaluation of genetic diversity among these parents (Crumpacker and Allard, 1962). Thus, the lower the (Wr + Vr)/Volo value for a parent the greater the proportion of dominant genes it carries. Based on these values (Table 13) Narodnaja was selected as the most dominant parent with Candeal Selection as the moderatly dominant while My-54 and Adur were selected as the two most recessive parents.

Table 13. Level of Dominance Among the 10 Parents Based On the F_1 Plant Height Data From Winnipeg, 1971

Level of Dominance	Parent	(Wr + Vr)/Volo
Dominant	Naroknaja+	48
"	Kharkov Kaja	49
Moderately dominant	Stewart	67
" "	Candeal Selection+	72
" "	DT-310	73
" "	Leeds	76
Moderately recessive	Iumillo	96
Recessive	My-54+	105
"	Madif	112
"	Adur+	115

+Indicates the parents used in the 1972 space-planted experiment grown at Winnipeg

The genetic divergence among the four parents, as measured by the differences among their respective (Wr + Vr)/ Volo values (Table 13) was as follows:

Adur - Narodnaja	=	67
Adur - Candeal Selection	=	43
Adur - My-54	=	10
My-54 - Narodnaja	=	57
My-54 - Candeal Selection	=	33
Candeal Selection - Narodnaja	=	24

From the six possible F_2 populations among the four selected parents Candeal Selection x Narodnaja, Candeal Selection x Adur, Narodnaja x Adur and My-54 x Adur were selected as representing the various combinations between and within the dominant and recessive parents, i.e. hybrids derived from crossing between genetically divergent and genetically similar cultivars. The four parents and the four F_2 families were grown out in Winnipeg in 1972 in the following manner:

Approximately 200 seeds were space-planted for each of the four parents. The four F_2 families were each replicated three times. Each replicate consisted of approximately 150 seeds sown per F_2 family. All inter-plant distances within a plot was 30 cm. Distance between plots was 60 cm. Plant height data (in cm) were recorded individually on all surviving plants.

While the decision regarding which parents and hybrids were to be chosen for the study conducted in 1972 was by necessity based on the diallel analysis of the Winnipeg, 1971 data,

The comparison was made between the 1972 space-planted experiment and the 1972 Winnipeg diallel results. This was done to eliminate the confounding effect of the environment (year) upon the estimation of the genetic parameters.

The 1972 data (Tables 10 and 14) showed the dominance effect to be highly significant and the parents from both years ranked essentially in the same order with respect to dominance (Spearman's rank correlation = 0.81**).

Table 14. Level of Dominance Among the 10 Parents Based On the F_1 Plant Height Data From Winnipeg, 1972

Level of Dominance	Parent	(Wr + Vr)/Volo
Dominant	Narodnaja+	16.99
"	Stewart	20.95
"	Kharkovkaja	21.98
Moderately dominant	DT-310	29.53
" "	Iumillo	30.81
Moderately recessive	Leeds	37.28
" "	Madif	40.67
" "	Candeal Selection+	42.38
Recessive	Adur+	45.68
"	My-54+	47.31

+Indicates the parents used in the 1972 space-planted experiment grown at Winnipeg

Two hypotheses were advanced and tested:

(1) A cross between two genetically dissimilar parents produces hybrids which show considerable heterosis.

It was found that Adur x Narodnaja, i.e. the cross between the two most genetically divergent parents, showed the highest negative heterosis while Adur x My-54, the cross between the two most genetically similar parent, showed positive heterosis. The two remaining hybrids exhibited heterosis intermediate in magnitude (Table 15). Thus, a general relationship seemed to have existed between genetic divergence and heterosis. However, none of the four hybrids showed statistically significant heterosis, as tested by $t\ (0.05,\ 2) = \bar{h}/S.E.(\bar{h})$, where $\bar{h}$ = mean heterosis over the three replicates and $S.E.(\bar{h})$ = standard error of $\bar{h}$, estimated from the variation of $\bar{h}$ over replicates.

(2) A cross between two genetically divergent parents produces maximum genetic segregation.

Genetic segregation in the F_2 population was measured by the individual plant variance within the F_2 family (Table 15). However, since the variance of an F_2 population contained both genetic and environmental components, the latter must be estimated to ascertain the occurrence of genetic segregation in the F_2 population. The environmental variance associated with each of the F_2 population was estimated by the weighted variance of the parents from which the particular F_2 family was derived. Thus, the environmental variance associated with Adur x Candeal Selection = $[(143 \times 16) + (140 \times 25)] / (143 + 140) = 19$. Similarly, the environmental variance for Adur x My-54, Adur x Narodnaja and Candeal Selection x Narodnaja was, respectively,

Table 15. Summary Results of the Four Parents and Four F_2 Hybrids Based on the Plant Height Data From Winnipeg, 1972

Parent or F_2 hybrid	No. of observations	Mean plant height (cm.)	Plant to plant variation	Genetic divergence[1]	Heterosis (%)
Adur	143	120	16	-	-
Candeal Selection	140	102	25	-	-
My-54	109	73	30	-	-
Narodnaja	135	105	23	-	-
A x C	273	109	157	3.30	-2.0
A x M	266	99	84	1.60	+2.5
A x N	262	109	222	28.69	-3.5
C x N	272	102	195	25.39	-1.5

[1] Genetic divergence was measured by the difference between the two values of (Wr + Vr)/Volo taken from Table 14 pertaining to the parents involved in the cross; L.S.D. (0.05) = 42, for plant to plant variation in the F_2.

22, 20 and 24. The variance-ratio test showed that genetic variance, i.e. genetic segregation, was highly significant for each of the four F_2 populations. For example, the variance ratio associated with Adur x Candeal Selection = 157/19 = 8** with 272 and $\left[0.5 \times (143 + 140)\right] - 1$ degrees of freedom.

The analysis of variance used to test the significance of differences among the four F_2 individual-plant variance had the following layout:

Source	Degrees of freedom
Replication	2
F_2-variance	3
Error	6

The F- ratio for the F_2-variance was significant ($P \leq 0.05$) and the L.S.D. was found to be 42 (Table 15). An implicit assumption associated with the above variance analysis was that the environmental variance exerted on each of the four F_2 families was similar in magnitude (i.e. homogeneity of variance associated with the 'error' term). This assumption was valid since the four environmental variances (19, 22, 20, 24) were statistically homogeneous (Bartlett, 1937; Lee and Campbell, 1969).

In summary, the relative magnitudes of the observed individual plant variance of the F_2 populations agreed with the genetic divergence between parents derived from the diallel analysis (Table 15). Based on the present data, the diallel cross analysis seems to be a valuable statistical genetics method

in assessing the dominance relationships among the parents and predicting the segregation patterns of hybrids derived from these parents.

GENERAL DISCUSSION

I. GENOTYPIC AND ENVIRONMENTAL VARIATION

The phenotypic expression of a quantitative character is invariably determined by the effect of the genotype, the environment and their interatcion. Consequently, the same genotype, when grown in a set of environments, always produces a variety of phenotypes due to the differential environmental effects exerted on it (Lee and Kaltsikes, 1972 d). Similarly, the relative performance of a set of genotypes grown in a series of environments will not be consistent due to genotype x environment interaction. The twelve metrical characters included in the present investigation were, in general, influenced by the environmental complex. The magnitude of the influence, however, was also dependent upon the particular quantitative character involved. Thus, the F_1 genotypes associated with the number of spikelets per spike interacted significantly with both locations and years while no such interaction was statistically significant in the case of percent of florets bearing seeds (Table 3).

Environment and genotype x environment interaction effects associated with agronomic characters are well documented for

both self- and cross-pollinated species (Johnson and Aksel, 1959; Jones et al., 1960; Nei, 1960; Kaltsikes and Larter, 1970) and the implications of these effects on plant breeding have been ably discussed by Comstock and Moll (1963) and Matzinger (1963). In general, the presence of the masking effect of the environment compounded with genotype x environment interaction hinders progress through selection since the value of a genotype is dependent upon the type of environment under which it is grown.

Various methods have been employed to separate the effect of the environment upon the phenotypic expression of a metrical character so that a better estimate of its true genotypic value could be obtained. One such method, the stratification of the environment, has been used with some success. The region for which a breeder is developing improved varieties can often be so sub-divided that the environment in a sub-region is somewhat more homogeneous than that of the original area. Stratification is usually based on such macro-environmental differences as temperature gradients, rainfall distribution and soil types. An alternative approach aimed at separating the effect of the environment on the phenotypic expression of a metrical character is the use of control plots (Shebeski, 1967; Briggs, 1969). An inherent assumption for such a method is that the magnitude of the environmental effect exerted on the control plot is the same with that exerted on the genotype of interest, i.e. absence

of genotype x environment interaction within that confined area. However, even with the refinement of such methods as stratification or the use of control plots, the varying environmental and genotype x environment interaction effect with respect to different years probably remains appreciable and certainly unpredictable. The data presented herein showed that both the phenotypic expression and the genetic parameters of all of the metrical characters fluctuated considerably between years (Tables 3, 4, 8, 11).

II. HETEROSIS AND COMBINING ABILITIES

The number of hybrids which exhibited significant heterotic effects and the significance of the variance components associated with general and specific combining abilities for each of the agronomic characters strongly indicated the feasibility of exploiting the additive or non-additive genetic effects in a breeding program involving the ten cultivars of durum wheat included in the present investigation. However, since the expression of general combining ability in the parents and specific combining ability or heterosis in the hybrids were differentially affected by the environment (Tables 6 and 8), a breeder must take into account the relative consistency as well as the magnitude of each of those estimates over environments as his selection criteria. A good example is provided by the general combining ability effects of the ten cultivars associated with plant height in the F_1 generation (Table 6). The general

combining ability values for the parent Adur over the 4 environments were, respectively 7.4, 6.3, 5.6, and 8.0 while those for Stewart were 8.3, 5.6, 14.5, and 1.9. Although the sum of the effects over environments was higher for Stewart (30.4) as compared to that for Adur (27.3), the general combining ability effect for the latter parent was substantially more resistant to environmental changes than that of the former. Consequently, Adur might be considered a more desirable parent for general combining ability.

The degree of emphasis given to stability as opposed to the overall average performance of genetic parameters over environments as selection criteria would, in the final analysis, depend on the general breeding objective, such as whether a variety is being bred for a wide range of environmental conditions, or for cultivation under certain specified environments. Finlay and Wilkinson (1963) and Eberhart and Russell (1966) have discussed these selection criteria in some detail.

III. THE GENETIC SYSTEM: AN OVERVIEW

The Jinks-Hayman diallel analysis revealed that both additive and dominance genetic effects were important in controlling each of the ten metrical characters. These results were in general agreement with those obtained from the combining ability analysis. This was to be expected since the general and specific combining abilities estimate, respectively, the addi-

tive and non-additive gene action.

The degree of dominance ranged from negligible to over-dominance but for the majority of the cases, overdominance genetic effect exhibited in these data was not matched by a preponderance of hybrids showing high-parent heterosis although significant mid-parent heterosis was obtained for a number of hybrids in each metrical character. One reason for the result was the internal cancelling effect of genes showing dominance (i.e. certain loci showed positive dominance while others, negative). Furthermore, the estimation of dominance may have been biased upward. Possible reasons for this bias were demonstrated either empirically or from the associated results derived from the analysis. The most probable factors for the bias in the overestimation of dominance couldhave been some form of epistasis in the F_1 population and epistasis and linkage or some particular combination of both in the F_2 population. Therefore, the H_1 obtained from the diallel analysis consisted not only of dominance genetic variance, but also of variances due to epistasis and/or linkage. Thus, many of the estimates obtained were undoubtedly inflated.

For each of the ten polygenic characters, dominance was neither consistent in magnitude nor in direction over individual loci, the latter confirming the preponderance of positive and negative heterosis and the virtual absence of significant high-parent heterosis obtained in the present study.

A statistically systematic analysis of the interaction between the various genetic components and the environment revealed a general susceptibility of the additive and dominance genetic effect to environmental changes. The degree of instability depended upon the particular agronomic character involved. Furthermore, this analysis showed that the epistatic effect was an important genetic parameter for certain characters and that for some characters epistasis was stable over environments while for others it was not.

IV. SOME COMMENTS ON THE DIALLEL ANALYSIS

The diallel analysis, as any other biometrical genetics method in use today, is based on a series of simplifying assumptions at both the statistical and genetical level. In a diallel experiment, a statistical design is first set up to estimate the appropriate variances and covariances among relatives, then these second degree statistics are translated into the genetic parameters of interest, and finally some statistical test of hypotheses is conducted on the estimators of the genetic parameters so obtained. These were the procedures used in the analysis of data obtained from the present investigation.

The basic assumptions underlying the testing of hypotheses in parametric statistics are that the variable of interest is normally distributed with equality of variance and independence in error (Eisenhart, 1947). The implications on the genetical

results obtained when these assumptions are not met were discussed by Nelder (1953) and Gilbert (1958) and need not be reiterated here. In general, violations of the assumptions may result in the reduction of statistical efficiency. For example, an estimate of a genetic parameter so obtained may not have minimum variance, or when testing for the significance of a particular estimate, the apparent level of significance may not equal that of the true level; e.g. D declared significant at the 5% probability level may in fact be significant at the 8% level. Thus, it can be seen that inefficient estimates may produce misleading results and erroneous conclusions.

The basic genetic assumptions underlying the diallel theory have been touched upon in a previous section. Two points had been emphasized: (i) The estimation of the dominance variance component, H_1, and the degree of dominance $(H_1/D)^{\frac{1}{2}}$ may be biased by the presence of intergenic interaction and correlated gene distribution among the parents and (ii) the lack of statistical significance associated with the heterogeneity of (Wr-Vr) over arrays does not necessarily imply the absence of intergenic interaction and correlated gene distributions. These two points will be further examined here in the light of the results obtained in the present investigation. It was apparent that in most cases, H_1 was greater than D and overdominance seemed to be a predominant feature in the genetic system controlling almost all of the metrical traits studied.

Yet significant high-parent heterosis was virtually absent in these characters. How can these results be reconciled? Of course, one could argue that the cancellation effects of the heterozygotes showing dominance in different loci were overwhelming. Cancelling effects were indeed found to have been enormous and therefore this may well be a feasible explanation. But it is equally likely that the estimation of the degree of dominance was substantially biased upward by intergenic interaction and correlated gene distributions. Grain yield, the complex character, is used for this argument. In chromosome substitution studies, Kuspira and Unrau (1957) concluded that at least one yield gene is present in each of the 21 chromosomes in hexaploid wheat. If this can be extrapolated to tetraploid wheat, there should be at least 14 genes controlling grain yield in these ten durum cultivars. Since there were at least 1.5 times as many genes controlling yield as there were cultivars, some of the 14 genes would be shared by a number of parents and consequently the effect of correlated gene distribution in the F_2 families would be a certainty. Yet, there was no statistical significance in the heterogeneity of Wr-Vr over arrays for the F_2 of this metrical character. According to the diallel theory (Hayman, 1954), there was no correlated gene distribution (or epistasis) associated with grain yield and therefore, the estimation of the degree of dominance was not biased. How can this be reconciled? This writer has no answer nor does he think an unambigous answer exists in view of the present

state of biometrical genetics methodology, where the individual genes controlling a polygenic character are unrecognizable. Furthermore, the number of gene groups controlling yield was found to be less than one (a gross underestimation). Of course, this result was due to enormous amount of cancelling effect in those heterozygotic loci exhibiting dominance. Perhaps another assumption underlying the diallel analysis should be put forward: Equality in magnitude and direction of dominance effects over loci. But even if this assumption were completely satisfied, the number of gene groups controlling a polygenic character could still be underestimated since h^2/H_2 (the estimator for number of gene groups) cannot identify those heterozygotic loci exhibiting no dominance.

The foregoing discussion illustrated some aspects of the shortcomings of all diallel analyses. Caution should therefore be exercised in interpreting the estimates of the various genetic parameters so obtained. However, in spite of these shortcomings, the diallel analysis probably still is the most useful biometrical genetics method that can be employed to evaluate the overall genetic system controlling a polygenic character. For what other method can produce such a thorough assessment of the genetic system based on data generated from only one generation? The diallel experiment is probably most useful when used as an integral part of a plant breeding program. Gilbert

(1958) suggested that a plant breeder, faced with a large number of cultivars, would do well to first conduct a replicated trial in order to pick out 10 to 15 promising cultivars. With these cultivars, he might conduct a diallel experiment to assess the overall genetic system controlling the character(s) of interest, and then make his decision concerning the type of breeding program to pursue(See Appendix 1).

V. PRACTICAL OBJECTIVES OF THE PRESENT STUDY

In addition to the evaluation of the genetic system controlling yield and related agronomic characters, a more practical objective for the undertaking of the present study has been to ascertain whether or not some of the ten durum cultivars could represent promising breeding material for the improvement of durum wheat in Canada. Therefore, Hercules, one of the current Canadian commercial cultivars, was included in the investigation as a basis for comparison of the performance of these cultivars and their hybrids. Based on the average performance over all environments, it was found that for all the characters studied, Hercules performed only intermediate with respect to the other ten cultivars and their hybrids, but no one cultivar surpassed Hercules for all characters. Since the diallel analysis revealed that both the additive and non-additive genetic effects were of considerable importance for all of these characters, the production of a cultivar which would exceed the performance of Hercules is very possible by any breeding program which exploits either or both additive and

non-additive genetic effects.

SUMMARY

Ten cultivars of durum wheat (Triticum turgidum L. var. durum) originating from different geographic regions of the world were intercrossed in a diallel fashion. The resulting F_1 and F_2 families were grown at two contrasting locations for two years. Heterosis, combining ability and the mode of inheritance associated with yield, components of yield and several related agronomic characters were examined. It was found that:

(1) Significant mid-parent heterosis was obtained in a number of hybrids for each character studied. Inbreeding depression was evident in the F_2 families, particularly for grain yield and the number of kernels per plant. In general, heterosis was found to be environmentally dependent. That is, most hybrids exhibited significant heterosis only under certain environments.

(2) Additive and dominance genetic effects were of considerable importance in controlling the phenotypic expression of each of the characters while epistatic effect was important only for some characters. The magnitude of these genetic parameters was influenced by environmental changes. Averaging these over environments, the narrow-sense heritability for grain yield

was 16% and 30%, respectively, for the F_1 and F_2 generations. Number of florets per spike had the lowest heritability while plant height had the highest.

(3) Populations derived from hybridization of genetically divergent parents generally showed greater heterotic effect and produced maximum genetic segregation as opposed to those derived from crossing of genetically similar parents.

(4) The durum cultivars usedin the present investigation represented very promising germ plasm for the improvement of durum wheat with respect to yield and a number of related agronomic characters. The prevalence of additive genetic variance for the traits studied indicated that selection procedures leading to the isolation of superior homozygous lines could be effectively practiced in breeding for the improvement of any of these characters.

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INTERRELATIONSHIPS AMONG YIELD AND RELATED AGRONOMIC ATTRIBUTES IN DURUM WHEAT (*TRITICUM TURGIDUM* L. VAR. *DURUM*)

ABSTRACT

Correlation, multiple regression and factor analyses were conducted on grain yield and a number of related agronomic attributes in the parental, F_1 and F_2 populations originating from a 10-parent diallel cross in durum wheat. In both generations all agronomic characters were highly associated with yield; most of these characters were also correlated amongst themselves. Four common factors were extracted which explained 96% and 97% of the total variance among the 10 correlated characters in the F_1 and F_2 populations, respectively. Grain yield, the number of spikes and kernels per plant all had high loadings on the most important factor. Based on both generations, number of spikes per plant, plant height and kernel weight were the most potent predictors for grain yield.

INTRODUCTION

Selection for high yield is the ultimate objective of any wheat breeding program. However, the yielding ability of a plant depends on a number of related agronomic attributes. A breeder thus records data and makes his selection on the basis of a large number of agronomic characters among which significant positive and negative correlations may exist (Lebsock and Amaya, 1969; Kaltsikes and Larter, 1970; Kaltsikes and Lee, 1971; Lee and Kaltsikes, 1973). Consequently, any analytical method which could result in a reduction of the number of agronomic characters to be recorded without sacrificing a significant amount of information would be major asset to the breeder. Correlation analysis could be employed for this purpose. However, a correlation between two characters does not necessarily imply a cause-and-effect relationship since many unknown factors could have produced their numerical association. Factor analysis, a multivariate statistical procedure, is useful in explaining the inter-correlations among a set of characters (Lawley and Maxwell, 1963; Harman, 1967). This method also helps in identifying the number and the nature of the common causative influences which produced the inter-correlations among the set of characters. Practically, factor analysis can be used to select a set of fewer characters based on the struc-

tural inter-relationships among the original set of characters. Alternatively, multiple regression analysis can be useful when the main interest is on the prediction of the performance of the response character from a number of predictor characters. Grain yield is logically chosen as the response character while the other agronomic attributes serve as its predictors.

The present study, utilizing information from the F_1 and F_2 generations resulting from the diallel cross of 10 cultivar of durum wheat (Triticum tungidum L. var. durum), had two objectives: (i) To ascertain whether a smaller set of common causative influences (factors) could be isolated which would explain the inter-relationships among the original set of characters; and (2) To identify the agronomic characters which are important predictors for grain yield.

MATERIALS AND METHODS

Ten durum cultivars (Triticum turgidum L. var. durum) were crossed in a diallel fashion with reciprocal families bulked to produce 45 F_1 and subsequently 45 F_2 families. The ten parental cultivars represented germ plasms originating from diverse parts of the world. The names of these cultivars and their respective country of origin were: DT-310 (Canada), Stewart (Canada), Leeds (U.S.A.), My-54 (Mexico), Candeal Selection (Argentine), Adur (France), Iumillo (Italy), Madif (Italy), Kharkov Kaja (Russia) and Narodnaja (Russia). Hercules, a commercial cultivar in Canada (Leisle, 1970) was also included in the study. Altogether, there were 56 entries(11 cultivars and 45 hybrids) in each of the two generations.

Seeds were sown at Winnipeg, Manitoba and at Swift Current, Saskatchewan in 1971 and 1972. At each of the four environments, the F_1 and F_2 diallel experiments were separately laid out in a randomized complete block design with two replications as follows: Each F_1 plot consisted of a single 3-meter row with 15 seeds space-planted. The number of plants which survived at harvest ranged from 2 to 15 but most plots had 8 to 12 plants. Each F_2 plot consisted of three 3-meter rows with 160 seeds sown per row. A guard row of the common wheat culti-

var Manitou was sown between each plot to minimize inter-plot competition. Two plots were sown for each of the 11 parents. The inter-row and inter-plot distances for both diallel generations was 30 centimeters.

The following characters were measured from each plot:

(1) Grain yield. In the F_1 generation, grain yield (gm) per plant was derived by dividing plot yield by the number of plants survived at harvest. In the F_2 generation, yield observations consisted of the weight (kg.) of seeds from each plot.

(2) Number of spikes per plant. In the F_1 generation the number of fertile spikes per plant was determined by dividing the total number of fertile spikes in each plot by the number of plants survived at harvest. In the F_2 the number of fertile spikes per linear meter row was determined by direct count. This value was then divided by 53 to obtain the number of spikes per plant since there were about 53 plants per linear meter row.

(3) 1,000 kernel weight (gm).

(4) Number of spikelets per spike.

(5) Number of florets per spike.

(6) Number of kernels per spike.

(7) Number of kernels per spikelet.

(8) Percent of florets bearing seeds. Characters (4) through (8) were taken from primary spikes. Two and ten primary spikes were randomly sampled from each of the F_1 and F_2

plots, respectively.

(9) Number of kernels per plant. In the F_1 generation, the number of kernels per plant was obtained by direct count from a random sample of two plants from each plot. In the F_2, the number of kernels per plant was estimated by multiplying the number of kernels per spike by number of spikes per plant.

(10) Plant height. Height of the plant (cm) was taken from ground to tip of the tallest tiller, excluding awn, on individual plants in the F_1 and on 10 randomly chosen plants in the F_2.

Values for all characters were averaged over each plot (448 and 536 F_1 and F_2 plots in all, respectively) prior to all statistical analyses. The values from the F_1 and F_2 generations were separately subjected to the product-moment correlation and to factor analyses. In the latter, extraction of the original factor matrix was by principal factoring with iterations (Cattell, 1965). The initial estimate of the communality entry was the squared multiple correlation of each character with every other in the original correlation matrix. The criterion used to determine the number of factors to be retained was an eigen-value of 0.20 or higher. The factor matrix so obtained was rotated to a simpler structure (i.e. more easily interpretable) by the varimax method (Harman, 1967). The multiple regression analysis was carried out according to Draper and Smith (1966). According to this method, the multiple regression equa-

tion and multiple coefficient of determination were obtained by adding one predictor character at a time according to their relative importance in predicting the response variable (grain yield). Termination of analysis occurred when the introduction of a new predictor character resulted in explaining less than 1% of the variance associated with yield.

RESULTS

INTER-CHARACTER ASSOCIATION

F_1 generation

All of the agronomic characters were positively correlated ($p \leq 0.001$) with grain yield (Table 1). The most striking correlations were the number of spikes and kernels per plant vs. yield. Kernel weight, number of kernels per spike and per spikelet, % florets with seed and plant height showed intermediate associations with yield while the number of spikelets and florets per spike had the lowest correlation with yield.

Most of the agronomic characters also showed significant correlation amongst themselves. The highest correlation was between number of spikes per plant and number of kernels per plant and between number of kernels per spike and number of kernels per spikelet. No significant association was found for kernel weight vs. number of florets with seed, for % florets with seed vs. number of spikelets and florets per spike.

Four common causative influences (factors) which produced the inter-correlations among yield and various characters were extracted (Table 2). Together these four factors accounted

Table 1. Phenotypic Correlation Matrix Among 10 Agronomic Characters In A 10 x 10 F_1 And F_2 Diallel of Durum Wheat[1]

	Yield (gm)	No. spikes/ plant	1,000 Kernel weight (gm)	No. spikelets/ spike	No. florets/ spike	No. kernels/ spike	% florets with seed	No. kernels/ spikelet	No. kernels plant	Plant height(cm)
Yield (gm)	-	0.81[2]	0.47	0.29	0.25	0.50	0.46	0.45	0.82	0.63
No. spikes/ plant	0.91	-	0.42	0.27	0.22	0.43	0.40	0.38	0.93	0.55
1,000 Kernel weight	0.70	0.65	-	0.14	-0.04^{NS}	0.15	0.25	0.10*	0.40	0.42
No. spikelets/ spike	0.61	0.56	0.58	-	0.65	0.52	0.05^{NS}	0.13**	0.38	0.46
No. florets/ spike	0.59	0.58	0.68	0.75	-	0.72	-0.02^{NS}	0.53	0.42	0.34
No. kernels/ spike	0.72	0.65	0.48	0.70	0.73	-	0.67	0.91	0.70	0.48
% florets with seed	0.16	0.07^{NS}	-0.28	-0.08^{NS}	-0.37	0.35	-	0.76	0.56	0.34
No. kernels/ spikelet	0.59	0.52	0.29	0.33	0.51	0.90	0.52	-	0.63	0.35
No. kernels/ plant	0.91	0.95	0.63	0.65	0.69	0.83	0.18	0.72	-	0.58
Plant height(cm)	0.78	0.70	0.70	0.68	0.55	0.62	0.08^{NS}	0.42	0.72	-

[1]Values appear above the diagonal belong to the F_1 diallel while those below the diagonal belong to the F_2.

[2]All values were significant at the 0.1% level excepting those indicated otherwise; i.e. ** $p \leq 1\%$; * $p \leq 5\%$; NS = not significant.

for 96% of the variability for the 10 correlated characters[+]. The communalities, or the amount of variance of a character accounted for by all factors taken together, ranged from 0.39 for kernel weight to 1.00 for the number of kernels per spike and per plant and number of kernels per spikelet. For the purpose of interpretation, only those characters with loadings greater than 0.5 in a factor were considered important. With this criterion, no characters excepting grain yield loaded on more than one factor (Tables 2 and 3).

The most important factor (factor 1) contained the characters yield and number of spikes and kernels per plant (Tables 2 and 3). This result implied that the expression of these three characters was simultaneously influenced by some common underlying force. The magnitude of the influence of a factor on a character is the factor loading for that character; that is, the proportion of the variance of a character accounted for by a factor is the square value of the factor loading. Thus, factor 1 accounted for 34.8%, 65.6% and 79.2% of the variance for yield, number of kernels and spikes per plant, respectively. Similarly, factor 2 contained number of kernels per spike and per spikelet and % florets with seed; factor 3 contained number of florets and kernels per spike; factor 4, the least important factor, contained yield, kernel weight and plant height (Table 3).

[+]The importance of a particular factor as indicated by the variance accounted for by that factor in the initial or unrotated factor matrix is of no interest in the terminal or rotated factor matrix as the result of rotation. Therefore, they were not reported. Nevertheless, the relative importance of the factors is still reflected by their order; i.e. factor 1 is the most important factor while factor 4 is the least important.

Table 2. Varimax Rotated Factor Matrices For Yield And Agronomic Characters In a 10 x 10 Diallel of Durum Wheat

Character	Factor 1	2	3	4	Communality
Parent and F_1					
Yield (gm)	0.59	0.25	0.14	0.59	0.79
Spikes/plant	0.89	0.16	0.06	0.38	0.98
1,000 kernel weight	0.24	0.07	-0.10	0.56	0.39
Spikelets/spike	0.11	0.02	0.32	0.19	0.98
Florets/spike	0.13	0.11	0.91	0	0.99
Kernels/spike	0.23	0.73	0.55	0.15	1.00
% florets with seed	0.20	0.92	-0.17	0.22	0.99
Kernels/spikelet	0.22	0.84	0.49	0.08	1.00
Kernels/plant	0.81	0.38	0.23	0.34	1.00
Plant height (cm)	0.26	0.18	0.20	0.64	0.64
Parent and F_2					
Yield (gm)	0.78	0.29	0.27	0.04	0.91
Spikes/plant	0.94	0.22	0.20	-0.04	0.99
1,000 kernel weight	0.46	0.16	0.26	-0.36	0.82
Spikelets/spike	0.33	0.18	0.80	-0.14	0.86
Florets/spike	0.32	0.52	0.54	-0.39	1.00
Kernels/spike	0.38	0.74	0.54	0.14	1.00
% florets with seed	0.07	0.31	-0.02	0.80	0.89
Kernels/spikelet	0.21	0.93	0.09	0.25	1.00
Kernels/plant	0.81	0.43	0.33	0.01	0.99
Plant height (cm)	0.52	0.14	0.45	0.04	0.82

Table 3. Summary of Factor Loadings for Yield and Agronomic Characters in a 10 x 10 Diallel of Durum Wheat

Factor	Characters of the parents and F_1 population
1	Yield; number of spikes and kernels per plant
2	Number of kernels per spike; % florets with seed; number of kernels per spikelet
3	Number of florets and kernels per spike
4	Yield; 1,000 kernel weight and plant height
	Characters of the parents and F_2 population
1	Yield; number of spikes and kernels per plant; plant height
2	Numbér of florets and kernels per spike; number of kernels per spikelet
3	Number of spikelets, florets and kernels per spike
4	% florets with seed

F_2 generation

All of the agronomic characters were highly associated ($p \leq 0.001$) with grain yield (Table 1). The highest correlation was found between the number of spikes and kernels per plant and yield. The remaining agronomic characters showed intermediate correlations with yield excepting % florets with seed which had a low correlation with yield.

Most of the agronomic characters were highly correlated ($p \leq 0.001$) amongst themselves (Table 1). The highest association was the number of kernels per plant vs. number of spikes per plant and number of kernels per spikelet vs. number of kernels per spike. No significant correlation was found for the number of spikes per plant, number of spikelets per spike and plant height vs. % florets with seed. Kernel weight was negatively correlated with % florets with seed.

Four common factors which produced the inter-correlations among the 10 characters were isolated (Table 2). Together they accounted for 97% of the variability for the 10 correlated characters. The communalities ranged from 0.82 for kernel weight and plant height for 1.00 for number of florets and kernels per spike and number of kernels per spikelet. For the purpose of interpretation, only those characters with loadings greater than 0.5 in a factor were considered important. With this criterion, no characters excepting the number of florets and kernels per

spike loaded on more than one factor (Tables 2 and 3).

The most important factor (factor 1) contained yield, number of spikes and kernels per plant and plant height (Table 3). This result indicated that these four characters were simultaneously influenced by some common underlying force. This factor accounted for 60.8%, 88.4%, 65.6% and 27.0% of the variance for yield, number of spikes and kernels per plant and plant height, respectively. Similarly, factor 2 contained number of florets and kernels per spike and number of kernels per spikelet; factor 3 contained number of spikelets, florets and kernels per spike; factor 4 contained only the % florets with seed.

PREDICTION FOR GRAIN YIELD

F_1 generation

The number of kernels per plant, plant height, number of florets per spike and kernel weight were, in that order, the four most important predictor characters for grain yield. Together they accounted for 73% of the variability associated with yield (Table 4). When the five remaining characters were included in the regression equation, only an additional 1% of the variability for yield was explained. Clearly these characters were of very limited value in predicting grain yield in the present genetic material.

The best multiple linear regression equation derived from the data was

$$Y = 0.05\ X_1 + 0.2\ X_2 - 0.17\ X_3 + 0.18\ X_4$$

$$(R^2 = 0.73***)$$

where y = grain yield; X_1 = number of kernels per plant; X_2 = plant height; X_3 = number of florets per spike; and X_4 = kernel weight. The multiple coefficient of determination (R^2) was only moderately high since 27% of the variability associated with yield was not accounted for by the above regression equation.

Table 4. Partial Regression Coefficients From the Stepwise Multiple Regression Analysis on Grain Yield In A 10 x 10 Diallel of Durum Wheat

Parent and F_1 population

Kernels/plant	Plant height(cm)	Florets/spike	1,000 Kernel weight	R^2
0.06 ± 0.002***	-	-	-	0.67***
0.05 ± 0.002***	0.29 ± 0.04***		-	0.70***
0.06 ± 0.002***	0.31 ± 0.04***	-0.21 ± 0.04***	-	0.72***
0.05 ± 0.002***	0.27 ± 0.04***	-0.17 ± 0.04***	0.18 ± 0.05***	0.73***
(0.66)	(0.17)	(0.13)	(0.10)	

Parents and F_2 population

Spikes/plant	Plant height(cm)	Kernels/spikelet	1,000 Kernel weight	R^2
16.02 ± 0.30***	-	-	-	0.83***
12.74 ± 0.39***	9.36 ± 0.78***	-	-	0.87***
11.63 ± 0.39***	8.85 ± 0.73***	231.69 + 28.59***	-	0.88***
11.01 ± 0.40***	7.15 ± 0.81***	247.88 ± 28.26***	6.61 ± 1.47***	0.89***
(0.62)	(0.20)	(0.13)	(0.09)	

Characters explained less than 1% of the variance for grain yield were not included in the table.

Value enclosed in the bracket is the standardized partial regression coefficient

*** $p \leq 0.001$

F_2 generation

The number of spikes per plant, plant height, number of kernels per spikelet and kernel weight were, in that order, the four most potent predictors for grain yield (Table 4). Together, they accounted for 89% of the variability associated with grain yield. When the five remaining characters were introduced into the regression equation, only an additional 1% of the variability for yield was explained.

The best prediction equation for yield derived from these data was

$$Y = 11.01 X_1 + 7.15 X_2 + 247.88 X_3 + 6.61 X_4$$

$$(R^2 = 0.89***)$$

where y = grain yield; X_1 = number of spikes per plant; X_2 = plant height; X_3 = number of kernels per spikelet; X_4 = kernel weight. According to this prediction equation, 11% of the variability associated with yield could not be explained by the above four predictor characters.

DISCUSSION

In both generations, all of the yield components and agronomic characters were highly associated with grain yield and most of these characters were also highly correlated amongst themselves. These results were in general agreement with the correlation results reported in the literature. Thus, Parodi and Joshi (1970) found grain yield in wheat was highly correlated with the components of yield and the components were highly associated amongst themselves. Bridgeford and Hayes (1931) found yield to be positively associated with kernel weight. Similarly, Shebeski (1966) found yield in wheat to be significantly correlated with each component of yield. Fonseca and Patterson (1968) showed that the components of yield in winter wheat were all significantly correlated with kernel weight and yield. However, negative correlations among component characters also exist.

In six durum wheat cultivars and their F_1 hybrids, Kaltsikes and Lee (1971) found that grain yield was positively correlated with a number of agronomic attributes excepting plant height and number of spikelets per spike. On the other hand, Kaltsikes and Larter (1970) found a significant correlation between plant height and grain yield from a study of five durum

cultivars grown in the Canadian Western Co-operative Test. Lebsock and Amaya (1969) found correlation between height and yield only in certain crosses and generations in durum wheat. Therefore it seems that the relationship between two metrical characters is dependent on the particular genetic material used as well as on the environmental conditions under which the material was grown.

Factor analysis of the results of the yield and agronomic attributes from the two generations indicated that the importance of each of the factors extracted and the characters belonging to individual factors were by and large not consistent over the two generations, particularly those characters associated with the less important factors (Table 3). However, yield, number of spikes and kernels per plant all had high loadings on the most important factor (factor 1) in both generations. Therefore, the expressions of these three characters were simultaneously influenced by some common underlying force and this influence seemed to have been unchanged over generations. Similar results were obtained by Lee and Kaltsikes (1973) with these durum wheat cultivars based on data from one year only.

The results obtained from the multiple regression analysis for the F_1 generation indicated that the most potent predictors for grain yield were, in that order, number of kernels per plant, plant height, number of florets per spike and kernel weight; the most important predictors for grain yield in the F_2

was found to be number of spikes per plant, plant height, number of kernels per spikelet and kernel weight. Since the number of spikes per plant was highly correlated with the number of kernels per plant ($r = 0.93^{***}$) in the F_1 population, the former character could in all probability replace the latter as the predictor character for grain yield. Therefore, based on both generations, it is suggested that the three characters, i.e. number of spikes per plant, plant height and kernel weight, in that order, be given due importance as predictors for grain yield in selection programs for durum wheat. Since the number of spikes per plant and plant height can be recorded easily prior to harvest, concentration on these two predictors as selection criteria should, according to the present data, be effective in identifying superior durum genotypes with respect to yield.

In general, minor differences were observed from the results obtained over the two generations. Thus, the correlation coefficients in the F_2 were in general larger than those obtained in the F_1 generation. The four common factors in the F_2 accounted for 97% of the variance of the 10 correlated characters as opposed to 96% in the F_1 generation. Similarly, the predictor characters accounted for 89% of the variability for grain yield in the F_2 as compared to only 73% in the F_1 generation. The slight inconsistency of the results between the two generations can be attributed to several possible causes: (1) There is no genetic segregation in the F_1 whereas segregation

occured in the F_2. Therefore, the latter population was subjected to a genetic sampling error; (2) The F_1 population was space-planted whereas solid-planting was used in the F_2 material; (3) Perhaps the most important factor is that plot size differed considerably between the two generations. There were 480 plants per F_2 plot as compared to 15 plants per F_1 plot. Obviously, the F_1 population was subjected to a much greater environmental error which resulted in the lower phenotypic correlations among characters and also the inferior predictive ability of the predictor characters on grain yield.

In the discussion of "logical correlated characters" in numerical taxonomy, Sokal and Sneath (1963) stated that "we must exclude as redundant any property (character) which is a logical consequence of another". In a real sense, this applied to the phenotypic correlations among characters as well. From this point of view, perhaps the most important aspect of multiple regression and factor analyses as statistical tools is their ability to reduce redundancy in character recording. The multiple regression analysis identified three characters as the most potent predictors for grain yield. Then the remaining characters included in the present investigation could be thought of as redundant information. Similarly, from the factor analysis of the F_1 population, there should be no reason to take all three characters (yield, number of spikes and kernels per plant), when measurement of any one will suffice. Thus, selecting one charac-

ter from each factor with high loadings on more than one character will in all likelihood preserve most of the information. If the primary objective were to isolate common factors which could better explain the inter-relationships among a set of correlated characters and subsequently to select a set of fewer characters without sacrificing a significant amount of information, factor analysis is useful. On the other hand, if the primary interest were to predict the performance of the response character (grain yield), multiple regression analysis would be a more appropriate statistical method.

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APPENDIX

Appendix 1

Practical Utility of Diallel Crossing Experiments: A Personal View

During the course of the present study, this writer has come to the realization that the diallel experiment, if conducted with the sole purpose of estimating genetic parameters, has little practical value. After having read the numerous diallel papers which have published in the various scientific journals, this writer is convinced that most of these studies were carried out with the objective of assessing the genetic system controlling quantitative traits but without giving much regards to the practical values of their results. For example, a few, if any, of the diallel experiments conducted have employed a truly random sample of cultivars. The genetic material used in the diallel cross were almost invariably a selected population (i.e. Model I). According to statistical theory, the genetic information derived from these experiments must be restricted only to the population being investigated and no inference can be made to other populations. Furthermore, since the genetic parameters controlling quantitative traits are generally susceptible to environmental changes, the genetic information should also be restricted only to the environment(s) under which the experiment was conducted.

In view of the following, this writer has been pondering over this question: In what manner can the diallel experiment be conducted so that the information derived from it be most useful to the plant breeder? The following is a collection of his thoughts...

The main objectives of any breeding program for self-pollinating crops are (1) identification of promising hybrids and (2) isolation of promising homozygous lines in advanced generations derived from these hybrids. The diallel cross, if used as an integral part of a breeding program, can be a useful method in accomplishing the first objective. For example, a breeder given a large number of cultivars may first conduct a replicated trial to pick out, say, 8 to 10 promising ones. Using these lines he may then conduct a diallel cross experiment to identify the most promising hybrid(s). A good hybrid should offer the greatest probability of producing the most superior homozygous lines in the advanced generation. Some of the criteria for such a hybrid are as follows:

(1) High performance. The relative performance of the hybrid as compared to the best parent used in the diallel cross and to the current commercial cultivar.

(2) Amount of heterosis. If heterosis were due only to dominance and/or overdominance effects, it should not be given much consideration since these effects will be dissipated in the advanced(homozygous) generations. Of course, if heterosis

is of sufficient magnitude and consistency, direct use of this effect(i.e. hybrid wheat) should be considered.

(3) General combining ability(gca) effect: It should be moderately large. Since gca effect estimates additive and/or additive x additive gene actions, the two parents with good gca effect should be the ones carrying a high proportion of the desirable heritable genes.

(4) Specific combining ability(sca) effect: It should be moderately large. Since the sca effect estimates non-additive gene action, some of which will be epistatic, there should be a greater likelihood for transgressive segregation, particularly in the F_2 generation.

(5) Amount of epistasis in the two parents as estimated from the diallel variance-covariance graph should be at least greater than the average. Reason: Same as item(4).

(6) Genetic divergence between the two parents as estimated from the dominance relationships based on the diallel variance-covariance graph should be large. Reason: A cross between two genetically diverse parents should show greater amount of genetic segregation and consequently greater plant-to-plant variation in the F_2 population for selection(This hypothesis was experimentally tested to be valid. See section IV.D.: Verification of the predictive ability of the diallel analysis).

(7) Items 1 through 6 should be relatively stable over environments. This of course necessitates that the diallel experiment be replicated in time and space.

The importance attributed to each of the foregoing criteria is at the discretion of the breeder for it depends on a specific set of circumstances involved. In any case, objective evaluation of their relative importance requires further investigations at both the theoretical and experimental levels.

Appendix 2

Clarification of Results

The discrepancy of results on the error variance (environmental error) presented in Tables 3 and 6 requires clarification.

The error variance associated with yield and number of kernels per plant in the F_2 population was 9204 and 288098, respectively(Table 3) and 9.2 and 5800, respectively(Table 6).

These differences were attributed to the following:

Results based on the analysis of plot yield(kg/plot) data were reported in Table 3 while those based on the analysis of plant yield(kg/plant) data were reported in Table 6.

Results based on the analysis of the number of kernels per linear meter and per plant were reported in Tables 3 and 6 , respectively.