HERITABILITY AND COMBINING ABILITY OF FLAG LEAF AREA AND FLAG LEAF AREA DURATION AND THEIR RELATIONSHIP TO GRAIN YIELD IN WINTER WHEAT

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PART I

HERITABILITY OF FLAG LEAF AREA AND FLAG LEAF AREA DURATION AND THEIR RELATIONSHIP TO GRAIN YIELD IN WINTER WHEAT

HERITABILITY OF FLAG LEAF AREA AND FLAG LEAF AREA DURATION AND THEIR RELATIONSHIP TO GRAIN YIELD IN WINTER WHEAT[1]

ABSTRACT

Heritability of grain yield in winter wheat (Triticum aestivum L.) is generally considered to be low especially when dealing with unreplicated and/or early generation material. Flag leaf area (FLA) and flag leaf area duration (FLAD) have both been reported to have high heritability and to be positively correlated with grain yield. Both traits may be useful as potential selection criteria to increase grain yield. The objectives of this study were to determine the heritability of FLA and FLAD and to examine their relationship to grain yield.

Head rows of two F_3 populations resulting from crosses of 'NR391-76' x 'Payne' and 'NR391-76' x 'Vona', respectively, were seeded in the fall of 1981. Flag leaf area was measured on all 96 head rows per population and 25 high and 25 low selections for FLA were made from each population. Each set of 50 selections were grown in replicated trials in the F_4 generation for 2 years (1982 and 1983) at one location and again as F_5's for 1 year (1983) at two locations. Flag leaf area, grain yield, tiller number, number of kernels per spike, kernel weight, plant height, and heading date were measured in the F_4 and F_5 generations.

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[1] To be submitted for publication in Crop Science.

Flag leaf duration (FLD), determined in 1983 only, was calculated as the number of days from heading to senescence while FLAD was calculated as the product of grain yield and FLD.

Parent-offspring regression and realized heritabilities were calculated for FLA, FLAD, and grain yield. Flag leaf area had low heritability values when selection was based on unreplicated F_3 head rows and higher heritability values when selection was based on data from replicated F_4 plots. FLAD also had moderate to high heritability when selection was based on replicated F_4 data. However, grain yield had higher heritability than either FLA or FLAD. Phenotypic correlation coefficients among entry means indicated that FLA and grain yield were not correlated while FLAD was positively correlated to grain yield at only one location. FLD was positively correlated to grain yield in every case. Responses of grain yield to selection for FLA was negative, often significantly so while response of grain yield to selection for FLAD was positive and nearly always significant.

Since heritability for FLA and FLAD was lower than heritability for grain yield itself and since FLA showed no significant correlation to grain yield while FLAD showed inconsistent correlation to grain yield, it appears that indirect selection for grain yield through selection for FLA or FLAD would not be as successful as selection for grain yield itself.

Additional index words: realized heritability, parent offspring regression, <u>Triticum</u> <u>aestivum</u> L.

INTRODUCTION

Accurate selection for grain yield in winter wheat is limited by the large environmental effect on its expression. Grain yield in wheat has been reported to have low heritability by some (17, 21, 26) and high heritability by others (3, 20). Briggs and Shebeski (6) found heritability of grain yield to vary from low to high depending upon the population, generation, and year while Baker et al. (2) found heritability to vary proportionately with the number of replications. Response to direct selection for yield has been of limited success (21, 25, 39). The yield components of wheat, i.e., tiller number, number of kernels per spike, and kernel weight, have been shown to have higher heritabilities than grain yield (8, 13, 17, 26) and to be highly correlated to grain yield (8, 17). This suggests that a higher gain in grain yield should result from selection for yield components than from selection for yield itself. However, subsequent research has shown negative correlations between these yield components which would complicate selection (17, 25, 31, 35). Some researchers have shown interest in morpho-physiological traits and their relationship to grain yield. A number of attempts have been made to elucidate the physiological control of yield in wheat and it has been generally concluded that the carbohydrates for grainfill come almost entirely from photosynthesis after ear emergence in the green plant parts above the flag leaf node (28, 44, 45, 48). The estimated contribution of each part to grainfill varied with experimental method (27, 43). Generally the contribution of the flag leaf blade, the flag leaf sheath, and the peduncle has been estimated at 60 to 80% and the contribution of the ear at 20 to 40%. The contribution of the ear has been found to be larger in barley than in wheat (7, 27, 45, 47).

Selection for morphological characters associated with yield had been suggested as a more effective method of increasing yield than selection for yield itself (20). Smocek (39, 40) and Voldeng and Simpson (46) suggest that selection indices including the flag leaf lamina, flag leaf sheath, peduncle, and ear area would be most successful in predicting yield. However, accurate measurement of all these traits would be difficult and time consuming in a breeding program. The flag leaf blade alone has been shown to contribute a proportionately large amount to grainfill (14, 22, 44) and the flag leaf blade area can be easily and accurately measured in the field or greenhouse. Flag leaf area (FLA) has been shown to be highly correlated with grain yield (13, 20, 32, 37, 46) and Smocek (40) reported FLA to be indirectly correlated to yield through its significant correlation with kernel number and kernel weight. The heritability of FLA has been estimated to be high (0.51 to 0.75) by some (13, 18, 19) while McNeal and Berg (30) reported low heritability estimates for this plant character. Improvement in yield through indirect selection for FLA has been suggested by some (18, 40, 46) while others have suggested that productivity assessment on the flag leaf alone may be insufficient to predict yield (22, 30, 32, 39).

Both the size and the longevity of the flag leaf are considered important to grainfill (4, 14, 27, 43, 48). Longevity, or green area duration, measured as the product of the area of the photosynthetic system and the length of time the tissue remains green, is often considered in terms of G which is the ratio of grain dry weight per unit area to the green area duration. Watson et al. (47), Welbank et al.

(48), and Singh and Chatterjee (38) have found G to vary with cultivar. A number of workers have reported the green area duration of the flag leaf to be under the control of the sink capacity in the grain (9, 24, 27, 34, 40), however, other data refute this hypothesis (1, 29, 42, 45). Under field conditions leaf area duration is much shorter in semi-arid conditions than in more temperate climates or in the greenhouse (10, 16, 27, 49). Wiegand and Cuellar (49) and Sofield et al. (42) found temperature to have great effect on the duration of grainfill. Flag leaf area duration (FLAD) has been shown to vary with cultivar (28, 42, 44, 47) and to be highly correlated with grain yield in wheat (5, 13, 16, 23, 37, 43). Drake (13) found that the heritability of FLAD was of intermediate magnitude. Provided other circumstances are favorable, genotypes with greater leaf area duration should produce higher grain yield (4, 38, 43, 44).

The purpose of this study was to determine the heritability of FLA and FLAD in winter wheat and to determine their relationship to grain yield.

MATERIALS AND METHODS

Head rows of two F_3 populations resulting from crosses of 'NR391-76' x 'Payne' and 'NR391-76' x 'Vona', respectively, were seeded in the fall of 1980. NR391-76 is a European cultivar with a high flag leaf area (FLA) value (30 cm^2) while Payne, an Oklahoma release, and Vona, a Colorado release, are both adapted to the semi-arid southern Great Plains and have low FLA (20 and 16 cm^2, respectively). Each population consists of 96 unreplicated 1.22 m head rows. Flag leaf area was measured on three main tillers per row with a Licor Portable Area Meter and grain yield was recorded for each row. Twenty-five high and 25 low selections were made in each population based on FLA values. Each set of 50 selections were planted in two row plots 3 m long in a randomized complete block design (RCB) with three replications at Stillwater, OK on 29 October 1981 and on 11 November 1982. Seed harvested from the 1981 F_4 plots was bulked by selection and planted in two row plots 3 m long in a RCB design with three replications at Stillwater on 11 November and at Lahoma on 1 November 1982. Nitrogen, as NH_4NO_3, was broadcast in a split application preplant in the fall and then in the early spring. The soil type was a Norge loam in Stillwater and a Grant silt loam in Lahoma.

Flag leaf area was measured with a Licor Portable Area Meter on 10 randomly selected tillers for each F_4 and F_5 plot within 2 weeks after heading. Grain yield was recorded and seed purity was maintained. Plant height was measured in cm and the number of seed bearing tillers (tiller number) was counted for 100 cm of row per plot. Heading data was recorded as days after 30 April when 75% of the heads in a plot were extruded from the boot. The date senesced was recorded as days after 30

April when 75% of the flag leaves in a plot were senesced. Kernel weight, measured as the average weight of 100 seeds, was recorded and the number of kernels per spike calculated from plot grain yield, tiller number per plot, and single kernel weight. Flag leaf duration (FLD), determined as the number of days between heading date and the date when 75% of the flag leaves had senesced, was measured in 1983 only. Flag leaf area duration (FLAD) was calculated as the product of FLA and FLD.

Analyses of variance were used to test for significance of main treatment effects and interactions. Because of significant interaction, separate analyses of variance were conducted for each year, generation, location, and population. In order to measure realized heritability, 10 high and 10 low selections were identified in the F_4 generation from both years for each of the response variables. This allowed for the calculation of realized heritability estimates from F_4 and F_5 data. Realized heritability was derived according to Falconer (15) from the original heritability equation to fit special situations. He defined realized heritability as the ratio of response from selection to the selection differential. Dhanasobhon (12) further derived Falconer's formula as the ratio of the difference between the mean values of the high ($\bar{x}$H) and low ($\bar{x}$L) selections in the generation of response (F_t) to the difference between the means of the high and low selections in the generation selection is applied (F_{t-1}):

$$h^2 = (F_t\bar{x}H - \bar{x}L)/F_{t-1}\bar{x}H - \bar{x}L).$$

Heritability estimates were also obtained from parent-offspring regression in which means of the F_5 generation were regressed on means of the F_4 generation for each response variable. Phenotypic correlations among entry means were computed for all traits measured for each generation, location, year, and population.

The difference between the means of the high selections and the low selections were calculated for each of three characters to determine the direct and indirect effects of selection for FLA and FLAD. A test of the mean difference for each character was provided by the selection type source of variation from analysis of variance. There were two selection types in this study - high selections and low selections.

RESULTS AND DISCUSSION

Analysis of variance for FLA over all locations, generations, years, populations, selection types (high vs. low), and selections (Table 1) showed highly significant mean squares for selection type and selection as well as for interactions of year x location x generation, year x location x generation x population, year x location x generation x population x selection. The means utilized to calculate realized heritability came from separate analyses of variance for each generation, in each year at each location, and for each population.

Realized Heritability

Realized heritability estimates for FLA were low (0.06 to 0.16) when selections were based on data from unreplicated F_3 head rows (Table 2). However, realized heritability estimates increased to a moderate level (0.21 to 0.65) for FLA and were moderate (0.43 to 0.84) for FLAD and moderate to high (0.32 to 1.02) for grain yield when selections were based on means of replicated F_4 plots. Simmonds (36) stated that heritability values can be increased by experimental design that reduces environmental variance such as the use of larger plots or more replications. This could account for some of the inconsistency in the literature on heritability of grain yield. Reported heritabilities have tended to be low when estimates were based on early generation material in unreplicated plots and higher when estimates were based on data from replicated plots (11, 25, 33, 41).

In the present study, when selection was based on replicated F_4 data, heritability values for FLA ranged from low to intermediate for population II (0.03 to 0.49) but intermediate to high for population I

(0.48 to 0.65) while heritability for grain yield was intermediate to high for population I (0.32 to 0.68) but intermediate to very high for population II (0.53 to 1.02). Heritability estimates also varied with location, being generally higher in Lahoma than Stillwater for population I and higher in Stillwater than Lahoma for population II. These points illustrate that heritability estimates depend upon the material being studied, the location, and the experimental method utilized (36).

Heritability of FLAD was intermediate for population I (0.43 and 0.50) and intermediate to high for population II (0.49 and 0.84) when selection was based on mean data from replicated F_4 plots (Table 2). Generally, heritability values for FLAD were intermediate to those of FLA and grain yield.

Heritability estimates based on parent-offspring regression (Table 3) were similar to the realized heritability estimates (Table 2). FLA had intermediate to high heritability for population I (0.41 to 0.57) and low to intermediate heritability for population II (0.10 to 0.55) while heritability estimates for grain yield were intermediate to high for population I (0.48 to 0.67) and intermediate to very high for population II (0.46 to 1.15). Heritability estimates for FLAD were 0.46 and 0.50 for populations I and 0.50 and 0.90 for population II.

Correlations

Phenotypic correlations among entry means for each generation, location, year, and population show FLD positively correlated with grain yield in most cases (Tables 4, 5, 6, and 7). FLAD and grain yield were positively correlated for both populations grown in Stillwater but were not correlated with either population in the Lahoma test. FLA was not significantly correlated with grain yield or FLD, but in every case their relationship was negative suggesting that high FLA cultivars might tend to have a shorter grainfilling period (low FLD) and therefore a lower grain yield in semi-arid conditions. All other correlations among the three flag leaf traits were significant and positive. FLAD was negatively correlated with heading date in most cases while FLD was positively correlated with kernel weight in all cases and negatively correlated with heading date in all cases. Early maturity appeared to be associated with high FLD values. Perhaps in our semi-arid environment temperature influences the senescence of flag leaves and therefore grainfill and grain yield to the detriment of late maturing cultivars.

Response to Selection

Grain yield did not respond significantly to selection for FLA although it showed a slight negative response in every case (Table 8). There was also no significant response to selection for FLA, except in Stillwater in 1983. Low heritability for FLA when selection was based on unreplicated single F_3 head rows could explain the lack of successful selection for FLA under these conditions. Response of grain yield to reselection for FLA in the F_4 generation was negative in all cases (Table 9) and significantly so for several cases. It appears that selection for FLA based on replicated F_4 data was successful. Reselection for FLAD in the F_4 generation resulted in a significant and positive response of grain yield in three of four cases (Table 10). Response of FLAD to reselection for FLAD was significant in only two cases. Grain yield had a greater positive response than FLAD to selection for FLAD and a negative response to selection for FLA.

Conclusions

From the results of this study it appears that neither FLA nor FLAD are sufficiently related to grain yield to expect much gain in grain yield from their selection. Although heritability estimates were high for these traits when selection was based on replicated F_4 data, the heritability estimates for grain yield itself were higher. Some response of grain yield to selection for FLA and FLAD was noted but the response to selection for grain yield itself would be expected to be greater. FLD was highly correlated with grain yield and might prove to be an aid to selection for grain yield especially in semi-arid environments.

High heritability for grain yield when selection is based upon replicated later generation material is an indication that wheat breeders are successful in yield selection under these conditions. However, low heritability for grain yield when selection is based on unreplicated early generation material is an indication of limited success in selection for grain yield under those conditions. Unfortunately, initial selection for grain yield in a breeding program is often on unreplicated early generation material and it is at this stage that large amounts of material are evaluated and a large percentage discarded. Under these conditions then much promising material is, no doubt, lost. A trait that is highly correlated with grain yield and which has a high heritability, even when selection is based upon unreplicated early generation material, would be advantageous to wheat breeders, however, neither FLA or FLAD appear to be such a trait.

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LIST OF TABLES

Table 1. Analysis of variance for flag leaf area (FLA) over all locations, generations, years, populations, selection types (high vs. low) and selections.

Source	df	Mean Square
population	1	1.54 ns
year x location x generation	3	4826.24 **
year x location x generation x population	3	207.55 **
rep (year x location x generation x population)	16	13.53 **
selection type	1	237.93 **
selection x selection type	48	34.99 **
year x location x generation x selection type	3	11.06 ns
year x location x generation x selection x selection type	144	5.45 *
population x selection type	1	1.57 ns
population x selection x selection type	48	22.26 **
year x location x generation x population x selection type	3	8.20 ns
year x location x generation x population x selection x selection type	144	8.28 **
error	784	4.39

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 2. Realized heritability estimates for flag leaf area (FLA), flag leaf area duration (FLAD), and grain yield in populations I and II at Stillwater and Lahoma.[†]

	Population I			Population II		
	FLA	FLAD	Grain yield	FLA	FLAD	Grain yield
	h^2					
$\frac{\text{1982 } F_4 \text{ 25 high - 25 low}}{\text{1981 } F_3 \text{ 25 high - 25 low}}$	.07	--	--	.06	--	--
$\frac{\text{1983 } F_4 \text{ 25 high - 25 low}}{\text{1981 } F_3 \text{ 25 high - 25 low}}$	.14	--	--	.16	--	--
$\frac{\text{1983 } F_5 \text{ 10 high - 10 low}}{\text{1982 } F_4 \text{ 10 high - 10 low}}$	.48	--	.62	.03	--	.86
$\frac{\text{1983 } F_5 \text{ 10 high - 10 low}}{\text{1983 } F_4 \text{ 10 high - 10 low}}$	.56	.43	.60	.49	.84	.67
$\frac{\text{1983 } F_5 \text{ 10 high - 10 low[‡]}}{\text{1983 } F_4 \text{ 10 high - 10 low}}$	.58	--	.68	.21	--	1.02
$\frac{\text{1983 } F_5 \text{ 10 high - 10 low[‡]}}{\text{1983 } F_4 \text{ 10 high - 10 low}}$	.65	.50	.32	.45	.49	.53

[†] Population I = NR391-76/Payne, Population II = NR391-76/Vona.

[‡] Lahoma data.

Table 3. Heritability estimates for flag leaf area (FLA), flag leaf area duration (FLAD), and grain yield from parent-offspring regression for populations I and II at Stillwater and Lahoma.[†]

	Population I			Population II		
	FLA	FLAD	Grain yield	FLA	FLAD	Grain yield
	h^2					
1983 F_5 on 1982 F_4	.41	—	.64	.10	—	1.02
1983 F_5 on 1983 F_4	.53	.50	.67	.45	.92	.61
1983 F_5[‡] on 1982 F_4	.46	—	.63	.27	—	1.15
1983 F_5[‡] on 1983 F_4	.57	.46	.48	.55	.50	.46

[†] Population I = NR391-76/Payne, Population II = NR391-76/Vona.

[‡] Lahoma data.

Table 4. Phenotypic correlations among entry means from the F_4 generation at Stillwater in 1982 for populations I and II.

	Flag leaf area	Grain yield	Tiller number	Kernels/ spike	Kernel weight	Plant height	Heading date
Flag leaf area		-.26[†] -.141	-.182 -.214	-.256 -.095	.121 .069	.211 .140	.056 .128
Grain yield			.559 ** .488 **	.629 ** .275	.319 * .300 *	.046 .222	-.288 * -.309 *
Tiller number				-.034 -.065	-.157 -.285 *	-.037 .089	.016 .095
Kernels/spike					-.116 -.186	.025 -.084	-.196 -.156
Kernel weight						.057 -.147	-.584 ** -.535 **
Plant height							.251 .517 **
Heading date							

*,** Significant at the 0.05 and 0.01 levels, respectively.

[†] Values above are for Population I (NR391-76/Payne), values below are for Population II (NR391-76/Vona).

Table 5. Phenotypic correlations among entry means from the F_4 generation at Stillwater in 1983 for populations I and II.

	Flag leaf area	Flag leaf duration	Flag leaf area duration	Grain yield	Tiller number	Kernels/ spike	Kernel weight	Plant height	Heading date
Flag leaf area		-.123† -.201	.547** .289*	-.219 -.079	-.419** -.109	.174 -.073	.047 .135	.406** .022	.209 .043
Flag leaf duration			.761** .878**	.533** .524**	.269 .295*	.107 .004	.476** .574**	.056 -.442**	-.502** -.857**
Flag leaf area duration				.309* .475**	-.053 .181	.221 -.021	.429** .634**	.317* -.424**	-.285* -.811**
Grain yield					.615** .310*	.119 .589**	.694** .531**	.105 -.117	-.417** -.359*
Tiller number						-.471** -.267	.289* -.076	.052 -.239	-.179 -.235
Kernels/spike							-.212 .034	.070 .114	.001 .151
Kernel weight								.074 -.117	-.479** -.562**
Plant height									.350* .653**
Heading date									

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above from Population I (NR391-76/Payne), value below from Population II (NR391-76/Vona).

Table 6. Phenotypic correlations among entry means from the F_5 generation at Stillwater in 1983 for populations I and II.

	Flag leaf area	Flag leaf duration	Flag leaf area duration	Grain yield	Tiller number	Kernels/ spike	Kernel weight	Plant height	Heading date
Flag leaf area		-.246†	.540**	-.232	-.385**	.143	.096	.222	.295*
		.289*	.656**	-.001	-.524**	.077	.432**	-.114	-.304*
Flag leaf duration			.680**	.572**	.288*	.097	.426**	-.021	-.588**
			.911**	.464**	-.042	.336*	.382**	-.600**	-.860**
Flag leaf area duration				.324*	-.040	.187	.453**	.159	-.298*
				.380**	-.244	.300*	.490**	-.506**	-.799**
Grain yield					.510**	.326*	.656**	.157	-.399**
					.301*	.629**	.550**	.054	-.257
Tiller number						-.199	.026	.036	-.281*
						.250	-.276	.099	.066
Kernels/spike							-.022	.155	.180
							.156	-.056	-.079
Kernel weight								.217	-.389**
								.033	-.365**
Plant height									.347**
									.668**
Heading date									

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above from Population I (NR391-76/Payne), value below from Population II (NR391-76/Vona).

Table 7. Phenotypic correlations among entry means from the F_5 generation at Lahoma in 1983 for populations I and II.

	Flag leaf area	Flag leaf duration	Flag leaf area duration	Grain yield	Tiller number	Kernels/ spike	Kernel weight	Plant height	Heading date
Flag leaf area		-.126† -.210	.641** .480**	-.256 -.250	-.434** -.272	.123 -.186	.037 .208	.067 .377**	.174 .237
Flag leaf duration			.678** .753**	.259 .429**	.076 .267	-.162 -.097	.317* .392**	.005 -.035	-.469** -.775**
Flag leaf area duration				.017 -.194	-.258 .036	-.027 -.223	.273 .497**	.071 -.035	-.216 -.552**
Grain yield					.548** .422**	.207 .549**	.189 .111	-.091 .107	.214 -.082
Tiller number						-.339* -.124	-.060 -.335*	.028 -.098	-.010 -.101
Kernels/spike							-.582** -.417**	-.388** -.038	.330* .267
Kernel weight								-.333* .268	-.386** -.366**
Plant height									.400** .519**
Heading date									

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above from Population I (NR391-76/Payne), value below from Population II (NR391-76/Vona).

Table 8. Mean response of two traits to high and low selection for flag leaf area (FLA) in the F_3 generation in 1981 for two populations at Stillwater (25 high and 25 low selections).

Measured character	Selection type		Difference	$\frac{(\text{High} - \text{Low})}{\text{High}} \times 100$
	High	Low	(High - Low)	
1982 F_4				
FLA (cm^2)	18.87†	18.38	.49 ns	2.60
	16.42	16.03	.39 ns	2.38
Yield (g/plot)	243.17	254.16	-10.99 ns	-4.52
	195.72	205.47	-9.75 ns	-4.98
1983 F_4				
FLA (cm^2)	26.42	25.51	.91 *	3.44
	27.38	26.15	1.23 **	4.49
Yield (g/plot)	448.05	456.75	-8.70 ns	-1.94
	353.52	363.49	-9.97 ns	-2.82

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above from Population I (NR391-76/Payne), value below from Population II (NR391-76/Vona).

Table 9. Mean response of two traits to reselection for flag leaf area (FLA) in the F_4 generation in 1982 and 1983 for two populations (10 high and 10 low reselections).

	Selection type		Difference	$\frac{\text{(High - Low)}}{\text{High}}$ x 100
Measured character	High	Low	(High - Low)	
STILLWATER				
1983 F_5†				
FLA (cm^2)	25.40 §	22.56	2.48 **	11.18
	25.51	25.26	.25 ns	.98
Yield (g/plot)	417.47	451.53	-34.07 **	-8.16
	349.00	380.23	-31.23 *	-8.95
1983 F_5‡				
FLA (cm^2)	25.45	22.01	3.44 **	13.35
	25.86	23.36	2.50 **	9.67
Yield (g/plot)	417.57	435.46	-17.89 ns	-4.28
	327.73	373.33	-45.60 **	-13.91
LAHOMA				
1983 F_5†				
FLA (cm^2)	26.51	23.06	3.45 **	13.01
	26.50	24.92	1.58 **	5.96
Yield (g/plot)	568.00	627.90	-59.90 **	-10.55
	529.43	575.83	-46.40 **	-8.76
1983 F_5‡				
FLA (cm^2)	26.81	22.78	4.03 **	15.03
	26.51	24.21	2.30 **	8.68
Yield (g/plot)	567.03	616.53	-49.50 **	-8.73
	534.90	547.67	-12.80 ns	-2.39

*,** Significant at the 0.05 and 0.01 levels, respectively.

†,‡ Reselection in the 1982 F_4 and in the 1983 F_4, respectively.

§ Value above from Population I (NR391-76/Payne), value below from Population II (NR391-76/Vona).

Table 10. Mean response of two traits to reselection for flag leaf area duration (FLAD) in the F_4 generation in 1983 for two populations at Stillwater and Lahoma (10 high and 10 low reselections).

Measured character	Selection type High	 Low	Difference (High - Low)	(High - Low) x 100 High
Stillwater 1983 F_5				
FLAD (days cm^2)	23.70†	23.06	.64 ns	2.70
	25.83	24.08	1.75 **	6.76
Yield (g/plot)	443.63	411.00	32.63 *	7.34
	395.07	320.90	74.17 **	18.77
Lahoma 1983 F_5				
FLAD (days cm^2)	25.72	24.50	1.22 *	4.74
	25.85	25.89	-.04 ns	.16
Yield (g/plot)	601.40	587.03	14.37 ns	2.39
	555.40	522.07	33.33 *	6.00

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above for Population I (NR391-76/Payne), value below for Population II (NR391-76/Vona).

PART II

GENERAL AND SPECIFIC COMBINING ABILITY FOR FLAG LEAF AREA AND FLAG LEAF AREA DURATION AND THEIR RELATIONSHIP TO GRAIN YIELD IN WINTER WHEAT

GENERAL AND SPECIFIC COMBINING ABILITY FOR FLAG LEAF AREA AND FLAG LEAF AREA DURATION AND THEIR RELATIONSHIP TO GRAIN YIELD IN WINTER WHEAT[1]

ABSTRACT

Both flag leaf area (FLA) and flag leaf area duration (FLAD) have been reported to be highly correlated to grain yield and are being considered as possible selection criteria for increasing grain yield potential in wheat. If these traits are to be utilized effectively in a breeding program, their inheritance should be known and their relationship to grain yield defined. It was the purpose of this study to determine the general (GCA) and specific (SCA) combining ability for FLA, FLAD, and grain yield and to determine the relationship of FLA and FLAD to grain yield.

Nine winter wheat (<u>Triticum</u> <u>aestivum</u> L.) parents chosen to represent a range of FLA values were crossed in a diallel mating system. The resulting F_1's were grown in hill plots in three different field environments. The F_2 generation was grown in two 3 m row plots at two locations in 1 year. Flag leaf area, grain yield, tiller number, number of kernels per spike, 100 kernel weight, plant height, heading date, and flag leaf senescence date were recorded. Flag leaf area was measured

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with a portable area meter. Flag leaf duration (FLD) was calculated as the difference in days between heading date and flag leaf senescence date while FLAD was the product of FLA and FLD.

General combining ability effects were highly significant for FLA, FLAD, and grain yield. Although SCA effects were often statistically significant, GCA effects were of a greater magnitude for FLA and FLAD while GCA and SCA effects were of comparable magnitude for grain yield. Generally the parents with high FLA values had the highest positive GCA for FLA and FLAD and the highest negative GCA for grain yield. The best combiners for high grain yield were those parents with low and intermediate FLA values. Relative GCA and SCA variances for each parent aided in the choice of the best combiners. Little or no correlation was noted for either FLA or FLAD with grain yield. This finding was consistent with the results obtained from the combining ability analyses. FLD, however, was positively correlated with grain yield.

Since additive gene action appeared to play a large role in the expression of FLA and FLAD as opposed to grain yield it would appear that FLA and FLAD would be more desirable as selection criteria than grain yield itself. However, their lack of correlation with grain yield would bring into question their use as selection criteria for increased grain yield.

Additional index words: Triticum aestivum L., phenotypic correlations, diallel mating system.

INTRODUCTION

Sprague and Tatum (15) defined general combining ability (GCA) as the average performance of a line in hybrid combination and therefore GCA is considered to be a measure of additive gene action (9). Specific combining ability (SCA) describes those cases in which certain combinations do relatively better or worse than expected on the basis of the GCA of the parents (15) and is generally considered to be a measure of non-additive gene action (9). General combining ability and SCA are utilized in both outbreeding and inbreeding species to predict the performance of parents in hybrid combinations. Genetic interpretation of GCA and SCA effects as indicators of additive and non-additive gene action has been questioned by Baker (1) who concluded that genetic interpretation was possible only if there was random mating, no linkage, and no epistasis. Since these conditions are rarely satisfied, Baker (1) suggested that combining ability analysis should be used to predict hybrid performance only where interpretation of GCA and SCA requires no genetic assumptions. If SCA is nonsignificant the parental performance can be adequately predicted by GCA alone and the best hybrid combinations should result from a cross of two parents with high GCA, however, when SCA is significant the accuracy of prediction based upon GCA depends upon the ratio of GCA to SCA. For a fixed model Baker (1) suggested a ratio of GCA and SCA component mean squares and the greater the ratio the more predictable the parental performance from GCA.

Several methods of analysis are accepted for a diallel mating system. Baker (1) reviewed the advantages and disadvantages of these methods and found Griffing's analyses (6) to have an advantage in terms of meeting genetic assumptions. Both Baker (1) and Griffing (6) agree that Griffing's Method 4 Model 1 where parents are not included in the analysis gives less biased estimates than Griffing's other methods.

Simmonds (12) reported that GCA values depend upon the chosen materials and therefore combining ability estimates should be used numerically only in the context in which they were calculated. If parents are not randomly chosen, conclusions should not be made in terms of the entire crop population but should be limited to comparisons of the parents used in the experiment.

Kronstad and Foote (9) found combining ability analysis to be a promising technique for classifying parental lines of small grains in terms of their hybrid performance and to give a better understanding of the nature of quantitatively inherited traits such as grain yield. Kaltsikes and Lee (8), Kronstad and Foote (9), and Walton (17) found SCA to be highly significant for grain yield in wheat parents they studied while Brown et al. (2) found SCA for grain yield not significant for winter wheat parents in their study. Yet all agree that additive gene action is more important than non-additive gene action for expression of grain yield.

Direct selection for grain yield per se in early generations has met with limited success and breeders are seeking new selection criteria that might be more successful in increasing grain yield potential of wheat. The carbohydrates for grainfill come almost entirely from photosynthesis after ear emergence in the green plant parts above the flag leaf node. Several traits related to photosynthesis in the flag leaf and ear have been suggested as selection criteria for grain yield. These include flag leaf area (FLA), flag leaf area duration (FLAD), and peduncle length. Both the flag leaf size and its longevity are considered important for grainfill (10, 14, 18) in winter wheat and both have been found to be highly correlated with grain yield (14, 16). If traits such as FLA and FLAD are to be useful as selection criteria, the inheritance of these traits should be known. Hsu and Walton (7) found a large part of the total genetic variation for flag leaf traits to be additive. Walton (17) found no significant SCA effects for FLA but GCA effects were highly significant. Ellison et al. (4) found highly significant GCA for five flag leaf photosynthetic parameters and concluded that the magnitude of GCA variance compared to SCA variance reflected the importance of additive gene action in inheritance of these characters.

In this study nine winter wheat parents were crossed in a diallel mating system to determine the GCA and SCA effects for FLA, FLAD, and grain yield so that predictions of parental performance and superior hybrid combinations could be made, and to determine the relationship of FLA and FLAD to grain yield.

MATERIALS AND METHODS

Nine winter wheat (Triticum aestivum L.) parents, chosen to provide a range in flag leaf area (FLA) (Table 1), were crossed in a diallel mating system. 'NR391-76', 'Burgas 2', and 'Sadovo 1', all European cultivars, were chosen as high FLA parents. 'Priboy', also a European cultivar, 'OK754615A', an Oklahoma breeding line, and 'TAM W-101', a Texas release, were chosen as intermediate FLA parents. OK754615A and TAM W-101 are adapted to the southern Great Plains. 'Payne' and 'Triumph 64', both Oklahoma releases, and 'Plainsman V', a Seed Research Incorporated release, are all adapted to the southern Great Plains and were chosen as low FLA parents. Crosses were made in the greenhouse in 1981 and 1982 and the F_1 hybrids and their parents were seeded in 31 cm square hill plots with 10 seeds per hill in a randomized complete block (RCB) design with six replications at Stillwater on 11 November 1981 and 16 November 1982 and at Lahoma on 1 November 1982. Seed from the 1981 hill plots were bulked by entry and seeded in two row plots 3 m in length in a RCB with three replications at Stillwater on 16 November and at Lahoma on 1 November 1982. Nitrogen, as NH_4NO_3, was broadcast at 60 kg/ha in a split application both preplant in the fall and then in the early spring. Soil type was a Norge loam at Stillwater and a Grant silt loam at Lahoma.

Flag leaf area was measured with a Licor Portable Area Meter (Lambda Inc.) in cm^2 on the flag leaves of 10 main tillers per plot within 2 weeks after heading. The heading date was recorded as days after 30 April when 75% of the heads in a plot were extruded from the boot. The number of days after 30 April when 75% of the flag leaves in a plot were senesced was also recorded and flag leaf duration (FLD) was calculated as the difference in days between heading date and senescence date. Flag leaf area duration (FLAD) was calculated as the product of FLA and FLD. Seed bearing tillers (tiller number) were counted on 1 m of row per plot and plant height was measured in cm. Kernel weight was measured as the weight of 100 kernels, and the number of kernels per spike was determined as the average for three main tillers per F_1 plot and calculated from other agronomic data for F_2 plots. A wet spring in 1982 prevented accurate measurement of FLD and therefore FLAD. Hence, these results are not reported for that year.

The F_1 hill plots were planted with a hand operated corn planter, harvested by hand, and threshed with a belt thresher. For the F_2 study, plots were seeded with a tractor mounted cone seeder, harvested with a Suzue mower-binder, and threshed with a Vogel thresher. Seed purity was maintained. Rain delayed harvest in 1982 and a wet spring delayed maturity and therefore harvest in 1983.

Analysis of variance was conducted for each test, year, generation, and location. Diallel analyses of variance were conducted using Griffing's Method 4, Model 1 and GCA and SCA variance estimates were calculated for each parent. Mean square components were calculated according to Griffing (6) Method 4, Model 1 and phenotypic correlations were calculated among entry means by computer analysis. Frey (5) found that the hill plot method could be used efficiently for early generation testing of small grains. Small quantities of F_1 seed precluded the use of row plots while an abundance of F_2 seed allowed establishment of two row plots. Cisar et al. (3) demonstrated the applicability of diallel analysis of variance to F_2 data as well as F_1 data of a self-pollinated crop.

RESULTS AND DISCUSSION

General and Specific Combining Ability Mean Squares

General combining ability mean squares for FLA were highly significant for each year, generation, and location while SCA mean squares for FLA were significant in all cases except for the F_2 generation at Lahoma (Table 2). The ratios of GCA to SCA mean square components for FLA were relatively high ranging from 3.85 to 10.82. Nonsignificant SCA in one case as well as high mean square component ratios in the other cases indicate that additive gene action is of a greater magnitude than non-additive gene action for FLA.

General combining ability mean squares for FLAD were also highly significant in every case while the SCA mean squares were highly significant for the F_1 generation, but nonsignificant for the F_2 generation. The ratio of GCA to SCA mean square components was low ranging from 2.34 to 2.65 for the F_1 generation which would indicate the importance of both additive and non-additive gene action in the expression of FLAD. However, nonsignificant SCA mean squares in the F_2 generations at both locations indicate that additive gene action is of a greater magnitude than non-additive gene action for FLAD. According to Baker (1) the most reliable test for additive vs. non-additive gene action is when SCA is nonsignificant. Additive gene action was of approximately twice the magnitude of non-additive gene action for FLAD.

Grain yield had significant GCA mean squares in every case while the SCA mean squares were significant in all cases except for the F_2 generation at Lahoma. The ratio of GCA to SCA mean square components was very low ranging from 0.12 to 1.43 indicating similar magnitudes of both additive and non-additive gene action for grain yield. However, nonsignificant SCA in Lahoma in the F_2 generation indicates a slight edge for additive gene action in expression of grain yield. Non-additive gene action appeared to be of greater magnitude relative to additive gene action for the expression of grain yield than for the expression of FLA and FLAD.

General Combining Ability Effects

Estimates of GCA effects for FLA of each parent are given in Table 3. Sadovo 1 and NR391-76 had high positive GCA effects in most cases (2.05 to 5.01) while Burgas 2 had high positive GCA in some cases (0.94 to 3.43). Triumph 64 and Plainsman V had high negative GCA effects (-2.32 to -4.99) for FLA in all cases except in the F_1 generation in Stillwater in 1982 when Payne had the highest negative GCA effects (-3.57). The high FLA parents were the best combiners for high FLA while the low FLA parents were the best combiners for low FLA.

General combining ability, SCA, and error components of variance (Tables 6 and 7) and the relative magnitude of GCA variance to SCA variance for FLA of each parent support the evidence that the high FLA parents were the best combiners for high FLA and the low FLA parents were the best combiners for low FLA. Although the SCA variances for each parent were similar, the high FLA and low FLA parents had large GCA variances relative to their SCA variances.

Estimates of GCA effects for FLAD for each parent (Table 4) show that the four European cultivars had the highest positive GCA in every case (9.88 to 100.65). Triumph 64 and Plainsman V had high negative GCA effects (-36.17 to -97.32) while TAM W-101 and OK754615A also had relatively high negative GCA effects (-13.48 to -49.55) for FLAD. Estimates of parental GCA and SCA variances (Table 8) support the evidence that the high FLA parents were the best combiners for high FLAD while the lowest FLA parents were the best combiners for low FLAD. Priboy was a fairly good combiner for high FLAD.

General combining ability estimates for grain yield of each parent are given in Table 5. OK754615A had high positive GCA (0.61 to 44.89) in almost every case while TAM W-101, Payne, Priboy, Plainsman V, and Triumph 64 also had high positive GCA in several cases. Burgas 2 had a higher positive GCA (5.06) than all other parents for grain yield for the F_1 generation in Stillwater in 1983 but Burgas 2 as well as Sadovo 1 had high negative GCA in every other case (-3.89 to -65.57). Generally, the intermediate to low FLA parents were the best combiners for high grain yield while the high FLA parents were poor combiners for high grain yield. GCA and SCA variances of each parent for grain yield (Tables 6 and 7) also indicate that the intermediate and low FLA parents were the best combiners for high grain yield while the high FLA parents were poor combiners for high grain yield.

Specific Combining Ability Effects

The best single hybrid combination for positive expression of a trait would be expected to come from a cross of two high positive GCA parents for that trait but if SCA effects are significant the predictability of parental performance based on GCA alone is decreased. The SCA estimate for an F_1 from a cross of two parents gives the deviation of the F_1 from the expected performance based on parental GCA. It is possible but not often found that the F_1 of two poor combiners (low GCA) would have a high enough positive SCA to outperform an F_1 of two good combiners. Shrivastava and Seshu (11) found that crosses between two good combiners with high positive GCA may not always result in good F_1 combinations if there is also a large negative SCA effect. However, the single best hybrid combination for positive expression of a trait would most often come from a cross involving at least one high positive GCA parent. In order to find the single best hybrid combination both the GCA of the parents and SCA of the F_1 should be considered. High positive parental GCA and high positive SCA would result in the best hybrid combination for expression of a high level of a trait. Estimates of SCA for FLA, FLAD, and grain yield can be found in Tables 9 through 14.

Several F_1 combinations showed high positive SCA effects for FLA. Considering both the GCA effects as well as the SCA effects, the hybrid combinations which resulted in the highest FLA values were Sadovo 1/OK754615A for the F_1 generation at Stillwater in 1982, Burgas 2/OK754615A for the F_1 generation at Stillwater in 1983, Sadovo 1/Payne for the F_1 generation at Lahoma in 1983, Sadovo 1/NR391-76 for the F_2 generation at Stillwater, and Burgas 2/NR391-76 for the F_2 generation at Lahoma. Generally, the best hybrid combinations for high FLA involved only one high positive GCA parent except where SCA effects were nonsignificant in which case the GCA effects accurately predicted hybrid performance.

High positive SCA effects for FLAD resulted from several F_1 combinations for each generation, year, and location. Considering both GCA and SCA effects, the hybrid combinations which resulted in the highest FLAD were Burgas 2/OK754615A for the F_1 generation at

Stillwater, Sadovo 1/Payne for the F_1 generation at Lahoma, Priboy/TAM W-101 for the F_2 generation at Stillwater, and Burgas 2/NR391-76 for the F_2 generation at Lahoma. Generally, the best hybrid combination for high FLAD involved at least one high positive GCA parent.

High positive SCA estimates for grain yield resulted from several crosses for each generation, year, and location. Considering both GCA and SCA effects, the hybrid combinations which resulted in the highest grain yield were Triumph 64/Burgas 2 for the F_1 generation at Stillwater in 1982, Burgas 2/Plainsman V for the F_1 generation at Stillwater in 1983, OK754615A/NR391-76 for the F_1 generation at Lahoma, Payne/Triumph 64 for the F_2 generation at Stillwater in 1983, and OK754615A/Plainsman V for the F_2 generation at Lahoma in 1983. Generally, for grain yield only one high GCA parent was involved in the best hybrid combinations except when the SCA mean squares were nonsignificant in which case GCA estimates of the parents alone were good predictors of hybrid performance.

Phenotypic Correlations

Phenotypic correlations among entry means are given in Tables 15 and 16. Correlations between FLA and grain yield were inconsistent and nonsignificant in the majority of cases. For the F_2 generation at Lahoma, grain yield and FLA were negatively correlated. FLA and FLAD were positively correlated in every case and FLA and FLD were not correlated in the F_1 generation, but were negatively correlated for the F_2 generation. FLA was highly positively correlated to heading date.

Generally, FLAD was not strongly correlated to grain yield, FLD nor heading date while FLD was correlated with grain yield in all cases except for the F_2 generation at Stillwater. Negative correlations between FLD and heading date indicate that early maturity may be a factor affecting the magnitude of FLD. Temperature and moisture stress have been found to limit grainfill in semi-arid environments (13, 19) but Wiegand and Cuellar (19) found that temperature had a greater effect than moisture on the duration of grainfill. Since moisture was fairly adequate in both years of this study, temperature appeared to be the major limiting factor for grainfill through its effect on FLD. Once high temperatures were reached, flag leaves senesced regardless of their area or heading date. FLD appeared mainly dependent upon early maturity and appeared to be more important to grain yield than FLA.

The correlations obtained in this study suggest that the best parents for FLA and FLAD would likely not be the best parents for grain yield. Combining ability estimates also show that high FLA parents were good combiners for FLA and FLAD but poor combiners for grain yield. The best combiners for grain yield were the intermediate to low FLA parents which were mostly adapted to a semi-arid climate and were generally found to outyield the high FLA parents which were of European descent and apparently less well adapted to a semi-arid environment. The data suggest that the early maturity of adapted parents might allow for greater FLD and therefore better grainfill and higher grain yield.

Conclusions

Generally, GCA effects were of a higher magnitude than SCA effects for FLA and FLAD even though SCA effects were often statistically significant while both GCA and SCA effects were of a similar magnitude for grain yield. According to GCA estimates alone, high FLA parents were the best combiners for high FLA and high FLAD while intermediate to low FLA parents were the best combiners for high grain yield. The best hybrid combinations based on GCA and SCA estimates for FLA were Sadovo 1/OK754615A, Burgas 2/OK754615A, Sadovo 1/Payne, Sadovo 1/NR391-76, and Burgas 2/NR391-76 while the best hybrid combinations based on GCA and SCA estimates for FLAD were Burgas 2/OK754615A, Sadovo 1/Payne, Priboy/Tam W-101, and Burgas 2/NR391-76. In three out of four cases the best hybrid combination for FLAD was also the best hybrid combination for FLA. Triumph 64/Burgas 2, Payne/Plainsman V, OK754615A/NR391-76, Payne/Triumph 64, and OK754615/Plainsman V were the best hybrid combinations for high grain yield. The best hybrid combinations for FLA, FLAD, and grain yield were from crosses involving only one high positive GCA parent except when SCA was nonsignificant in which case GCA alone accurately predicted hybrid performance and the best hybrid combination was between two high GCA parents. This reflects the effects of significant SCA mean squares on accurate prediction of parental performance based on GCA estimates alone. Phenotypic correlation analyses supported GCA estimates showing FLA and FLAD to be generally uncorrelated to grain yield.

The relatively large role that additive gene action appeared to play in expression of FLA and FLAD as opposed to grain yield would indicate that FLA and FLAD are more desirable as selection criteria than grain yield itself, however, their lack of correlation to grain yield would exclude them as selection criteria in a breeding program concerned with increasing grain yield potential. FLD was highly correlated to grain yield and more research should be done to determine the potential of FLD as a selection criteria to increase grain yield.

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Table 1. Mean flag leaf area (FLA) of nine winter wheat parents in field trials at Stillwater in 1982 and 1983 and in Lahoma in 1983.

	cm^2
NR391-76	29.52
Sadovo 1	28.63
Burgas 2	24.31
Priboy	23.95
TAM W-101	21.02
OK754615A	19.84
Payne	19.50
Triumph 64	17.60
Plainsman V	16.62

Table 2. Mean squares for general and specific combining ability, error mean squares, and mean square component ratios from a nine parent diallel cross.

Trait	GCA	SCA	Error	Mean square component GCA/SCA
FLA				
1982 ST F_1[†]	210.09 **	12.34 **	4.71	3.85
1983 ST F_1	307.29 **	9.17 *	4.88	10.07
1983 LA F_1	571.72 **	19.87 **	6.56	6.07
1983 ST F_2	227.79 **	6.61 *	3.65	10.82
1983 LA F_2	185.29 **	5.17 ns	3.16	
FLAD				
1983 ST F_1	124035.80 **	9828.49 **	3319.08	2.65
1983 LA F_1	187929.91 **	18801.63 **	7826.14	2.34
1983 ST F_2	76440.78 **	3015.87 ns	2116.31	
1983 LA F_2	42706.35 **	2114.17 ns	1889.91	
GRAIN YIELD				
1982 ST F_1	209.57 **	113.42 **	23.06	.29
1983 ST F_1	245.70 **	49.42 *	27.60	1.43
1983 LA F_1	175.52 **	192.94 **	59.37	.12
1983 ST F_2	22213.66 **	9108.89 **	2499.21	.43
1983 LA F_2	24954.55 **	2340.02 ns	2196.89	

df for component mean squares: Rep = 5, GCA = 8, SCA = 27, Error = 175, Total = 215.

*,** Significant at the 0.05 and 0.01 levels, respectively.

[†] ST = Stillwater, LA = Lahoma, F_1 = F_1 generation, F_2 = F_2 generation.

Table 3. General combining ability effects for flag leaf area (FLA) of a nine parent diallel cross in 1982 and 1983.

	F_1 generation			F_2 generation	
	Stillwater		Lahoma	Stillwater	Lahoma
Parent	1982	1983	1983	1983	1983
NR391-76	2.05	2.91	4.47	4.47	3.42
Sadovo 1	3.79	2.34	5.01	3.06	3.44
Burgas 2	.94	3.43	2.17	2.88	3.18
Priboy	.39	1.30	2.39	2.17	1.43
TAM W-101	.63	-.57	-.93	-1.02	-1.52
OK754615A	-.80	-.65	-.92	-1.45	-1.63
Payne	-3.57	-1.15	-2.93	-1.24	-.72
Plainsman V	-2.32	-3.18	-4.99	-4.91	-4.34
Triumph 64	-1.11	-3.82	-4.28	-3.95	-3.25
S.E.	1.16	1.18	1.87	1.02	.95
C.V.	11.60	8.80	9.34	7.90	7.66

Table 4. General combining ability effects for flag leaf area duration (FLAD) of a nine parent diallel cross in 1983.

	F_1 generation		F_2 generation	
Parent	Stillwater	Lahoma	Stillwater	Lahoma
NR391-76	23.73	70.06	44.12	38.19
Sadovo 1	23.75	100.65	63.34	51.47
Burgas 2	92.90	9.88	63.40	36.56
Priboy	40.17	69.48	58.07	50.36
TAM W-101	-24.58	-22.40	-13.48	-49.55
OK754615A	-17.99	-34.19	-39.65	-20.56
Payne	11.56	-32.91	-12.19	-6.59
Plainsman V	-77.13	-71.13	-97.32	-63.72
Triumph 64	-72.42	-89.45	-66.31	-36.17
S.E.	30.79	47.29	24.59	23.23
C.V.	10.82	16.53	9.03	9.93

Table 5. General combining ability effects for grain yield of a nine parent diallel cross in 1982 and 1983.

	F_1 generation			F_2 generation	
	Stillwater		Lahoma	Stillwater	Lahoma
Parent	1982	1983	1983	1983	1983
NR391-76	-2.00	-1.85	1.02	7.04	6.10
Sadovo 1	-2.08	-3.89	-3.13	-8.77	-17.29
Burgas 2	-1.10	5.06	-3.34	-43.63	-65.57
Priboy	-.24	-1.01	1.80	37.32	2.57
TAM W-101	3.69	.84	-.79	-34.15	-24.76
OK754615A	1.15	.61	2.42	44.89	33.57
Payne	-2.27	.63	.30	-3.34	46.10
Plainsman V	-.36	-.37	1.13	-30.06	29.81
Triumph 64	3.19	-.01	.59	30.70	-10.52
S.E.	2.75	2.81	4.12	26.72	25.05
C.V.	29.87	21.71	25.45	11.63	8.66

Table 6. Estimates of general and specific combining ability variances for flag leaf area (FLA) and grain yield associated with each parent for the F_1 generation at Stillwater in 1982 and 1983 and at Lahoma in 1983.

	Stillwater				Lahoma	
	1982		1983		1983	
Parent	$\hat{\sigma}^2$gca†	$\hat{\sigma}^2$sca‡	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca
FLA						
NR391-76	4.10	.93	8.37	.61	19.84	1.01
Burgas 2	.78	2.27	11.67	.87	4.57	4.47
Sadovo 1	14.26	1.03	5.38	1.15	24.96	1.95
Priboy	.05	.78	1.59	.47	5.57	-.11
OK754615A	.54	.62	.32	.52	.71	.81
TAM W-101	.30	-.17	.23	.36	.73	1.90
Payne	12.64	3.41	1.22	.79	8.45	4.72
Plainsman V	5.28	.35	14.42	-.09	24.76	1.40
Triumph 64	1.13	.53	14.49	.89	18.18	.83
$\hat{\sigma}^2$	.79		.81		1.09	

Table 6. Continued.

	Stillwater				Lahoma	
	1982		1983		1983	
Parent	$\hat{\sigma}^2$gca†	$\hat{\sigma}^2$sca‡	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca
<u>Grain yield</u>						
NR391-76	3.51	8.86	2.84	6.67	-.22	14.45
Burgas 2	.72	23.11	25.02	6.27	9.90	42.56
Sadovo 1	3.84	8.38	14.55	4.68	8.54	3.10
Priboy	-.43	17.59	.44	1.97	1.98	29.71
OK754615A	.83	6.16	-.21	1.64	4.60	4.14
TAM W-101	13.12	5.26	.13	-.16	-.64	14.07
Payne	4.66	35.29	-.18	7.54	-1.17	53.41
Plainsman V	-.36	1.86	-.44	.59	.02	1.69
Triumph 64	9.69	9.72	-.58	-1.10	-.91	8.52
$\hat{\sigma}^2$	3.84		4.60		9.90	

† $\hat{\sigma}^2_{gca} = \hat{g}_i^2 - (8/63)\hat{\sigma}^2$.

‡ $\hat{\sigma}^2_{sca} = (1/7)\sum_j s_{ij}^2 - (6/7)\hat{\sigma}^2$.

Table 7. Estimates of general and specific combining ability variances for flag leaf area (FLA) and grain yield associated with each parent for the F_2 generation at Stillwater and Lahoma in 1983.

	Stillwater		Lahoma		Stillwater		Lahoma	
Parent	$\hat{\sigma}^2_{gca}$†	$\hat{\sigma}^2_{sca}$‡	$\hat{\sigma}^2_{gca}$	$\hat{\sigma}^2_{sca}$	$\hat{\sigma}^2_{gca}$	$\hat{\sigma}^2_{sca}$	$\hat{\sigma}^2_{gca}$	$\hat{\sigma}^2_{sca}$
<u>FLA</u>					<u>Grain yield</u>			
NR391-76	19.83	1.68	11.57	.88	-56.23	255.59	-55.78	-372.53
Burgas 2	8.14	.41	9.98	1.52	1797.79	5234.82	4206.43	534.18
Sadovo 1	9.21	1.82	11.70	.08	-28.88	1162.76	205.95	-224.24
Priboy	4.56	1.05	1.92	-.49	1286.99	253.00	-86.39	-541.85
OK754615A	1.95	.22	2.53	1.07	1909.32	191.02	1033.96	-40.80
TAM W-101	.89	1.78	2.18	-.15	1060.43	975.98	520.07	80.74
Payne	-1.39	4.60	.39	.32	-94.63	6173.22	2032.22	579.39
Plainsman V	23.96	1.28	18.71	1.12	797.81	458.16	795.65	495.14
Triumph 64	15.45	.71	10.43	.74	836.70	2277.51	17.68	-213.74
$\hat{\sigma}^2$	1.22		1.05		833.07		732.30	

† $\hat{\sigma}^2_{gca} = \hat{g}_i^2 - (8/63)\hat{\sigma}^2$.

‡ $\hat{\sigma}^2_{sca} = (1/7)\sum_j s_{ij}^2 - (6/7)\hat{\sigma}^2$.

Table 8. Estimates of general and specific combining ability variances for flag leaf area duration (FLAD) associated with each parent for the F_1 and F_2 generations at Stillwater and Lahoma in 1983.

	F_1 generation				F_2 generation			
	Stillwater		Lahoma		Stillwater		Lahoma	
Parent	$\hat{\sigma}^2$gca†	$\hat{\sigma}^2$sca‡	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca	$\hat{\sigma}^2$gca	$\hat{\sigma}^2$sca
NR391-76	397.48	838.53	4838.15	513.84	1856.99	51.32	1378.51	29.88
Burgas 2	8464.78	214.14	27.36	5604.82	3929.98	-183.64	1256.66	568.62
Sadovo 1	396.06	1198.75	10060.17	1446.54	3922.38	748.18	2569.19	42.76
Priboy	1448.00	835.95	4757.22	314.94	3282.55	984.97	2456.16	-390.49
OK754615A	158.01	35.46	1098.71	2227.82	1482.54	218.30	342.74	-212.15
TAM W-101	158.01	-756.29	431.51	1255.30	92.13	492.08	2375.23	381.05
Payne	-32.00	1216.75	1012.82	5706.01	59.02	16.06	-36.54	419.48
Plainsman V	5783.41	-649.92	4989.23	1350.76	9381.60	-18.98	3980.27	-1885.50
Triumph 64	5079.03	-359.10	7931.05	1494.69	4307.44	4.89	1228.30	-137.06
$\hat{\sigma}^2$	553.18		1304.36		705.44		629.73	

† $\hat{\sigma}^2 gca = \hat{g}_i^2 - (8/63)\hat{\sigma}^2$.

‡ $\hat{\sigma}^2 sca = (1/7)\sum_j s_{ij}^2 - (6/7)\hat{\sigma}^2$.

Table 9. Specific combining ability estimates for flag leaf area (FLA) from the F_1 generation of a nine parent diallel cross at Stillwater in 1982 and 1983 and at Lahoma in 1983.

	NR391-76	Burgas 2	Sadovo 1	Priboy	OK754615A	TAM W-101	Payne	Plainsman V	Triumph 64
NR391-76		1.47†	-1.34	.82	.69	-1.50	1.52	-.53	-1.13
		1.04	1.22	.95	-1.12	-.05	.13	-.08	-2.08
		1.56	1.13	.00	-.76	-1.29	1.99	-1.01	-1.62
Burgas 2			.41	.95	-.59	.85	-3.91	.20	1.01
			-1.33	1.05	2.12	-.63	-.74	-1.21	-.31
			.42	.91	-.11	2.20	-5.45	.46	.02
Sadovo 1				-1.07	2.09	-.15	1.55	-1.45	-.04
				-1.76	-.37	-.30	2.12	-.72	1.13
				-1.57	1.73	-.89	2.48	-2.33	-.96
Priboy					-1.08	-.01	-1.75	.37	1.77
					.51	.69	-1.26	.51	-.69
					-.57	-.11	.12	1.44	-.22
OK754615A						.13	.59	-.32	-1.52
						-1.04	-.23	.82	-.69
						-1.75	.30	2.07	-.91
TAM W-101							.60	-.25	.33
							-1.32	1.09	1.55
							.70	-1.47	2.61
Payne								2.10	-.70
								-.10	1.39
								-.19	.05
Plainsman V									.27
									-.31
									1.04
Triumph 64									

S.E. common parent = 2.84†
2.89
3.35

S.E. no common parent = 2.59†
2.64
3.06

† Top value for 1982 Stillwater, middle value for 1983 Stillwater, and bottom value for 1983 Lahoma.

Table 10. Specific combining ability estimates for flag leaf area (FLA) from the F_2 generation of a nine parent diallel cross at Stillwater and Lahoma in 1983.

	NR391-76	Burgas 2	Sadovo 1	Priboy	OK754615A	TAM W-101	Payne	Plainsman V	Triumph 64
NR391-76		1.86† 2.70	2.80 .53	-.24 -.26	.40 .18	-1.97 -1.29	-.43 .53	-.64 -1.21	-1.77 -1.19
Burgas 2			-1.75 -.54	.93 .34	.81 .33	-.25 -.84	-.10 1.51	-.06 -1.75	-1.45 -1.76
Sadovo 1				-1.97 .22	-.74 .04	-.31 .93	2.07 -1.93	-.51 -.09	.42 1.28
Priboy					-1.60 -1.07	2.36 .56	-.56 .75	1.19 -.58	-.11 .48
OK754615A						-1.36 .10	.20 -1.03	1.60 3.00	.69 -1.56
TAM W-101							1.13 -.44	-1.04 -.24	1.44 1.21
Payne								-1.81 -.04	-.49 .64
Plainsman V									1.27 .90
Triumph 64									

S.E. common parent = 2.50†
2.33

S.E. no common parent = 2.28
2.12

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† Top value from Stillwater, bottom value from Lahoma.

Table 11. Specific combining ability estimates for flag leaf area duration (FLAD) from the F_1 generation of a nine parent diallel cross at Stillwater and Lahoma in 1983.

	NR391-76	Burgas 2	Sadovo 1	Priboy	OK754615A	TAM W-101	Payne	Plainsman V	Triumph 64
NR391-76		26.28† 7.56	19.47 -10.78	79.52 -35.78	-52.57 7.56	-5.80 -28.97	-.19 66.01	-8.04 -12.63	-58.66 7.03
Burgas 2			-53.46 6.69	-36.13 55.62	59.66 -45.66	13.88 62.85	-23.40 -171.63	.17 53.04	13.04 31.53
Sadovo 1				-52.13 -18.05	-22.78 53.66	.12 -26.82	95.65 76.20	-9.37 -52.30	22.50 -28.59
Priboy					-1.95 -7.54	20.95 -.81	-46.98 -15.78	19.75 22.76	17.02 -.42
OK754615A						-10.14 -17.49	27.63 51.10	13.55 50.09	-13.38 -91.71
TAM W-101							-33.19 11.10	23.86 -55.46	-9.67 55.60
Payne								-44.30 -24.53	24.77 7.52
Plainsman V									4.39 19.04
Triumph 64									

S.E. common parent = 75.43†
115.83

S.E. no common parent = 68.86†
105.74

† Top value from Stillwater, bottom value from Lahoma.

Table 12. Specific combining ability estimates for flag leaf area duration (FLAD) from the F_2 generation of a nine parent diallel cross at Stillwater and Lahoma in 1983.

	NR391-76	Burgas 2	Sadovo 1	Priboy	OK754615A	TAM W-101	Payne	Plainsman V	Triumph 64
NR391-76		28.44[†] 51.07	50.77 -16.56	-20.68 2.06	-7.95 5.40	-9.89 -6.65	-10.59 7.86	-10.01 -25.64	-20.09 -17.56
Burgas 2			-22.25 -30.10	-17.41 -17.93	21.23 14.18	-.32 -23.80	-6.24 47.70	18.82 -24.68	-22.28 -16.44
Sadovo 1				-53.76 -14.94	-32.87 6.94	2.25 38.71	36.09 -3.68	-11.63 -11.65	31.38 31.28
Priboy					-31.02 -14.18	74.95 10.43	9.18 20.56	12.53 14.74	26.20 -.74
OK754615A						-30.00 8.89	26.41 -18.13	35.43 24.92	18.76 -28.02
TAM W-101							7.60	-20.73 12.34	-23.86 20.04
Payne								-38.38 2.08	-24.07 3.56
Plainsman V									13.97 7.89
Triumph 64									

S.E. common parent = 60.23[†]
56.91

S.E. no common parent = 54.99[†]
51.95

[†] Top value from Stillwater, bottom value from Lahoma.

Table 13. Specific combining ability estimates for grain yield from the F_1 generation of a nine parent diallel cross at Stillwater in 1982 and 1983 and at Lahoma in 1983.

	NR391-76	Burgas 2	Sadovo 1	Priboy	OK754615A	TAM W-101	Payne	Plainsman V	Triumph 64
NR391-76		-2.47†	-2.83	1.01	2.10	-3.39	6.53	1.83	-2.59
		1.09	-5.96	.99	-3.63	.47	4.19	.52	2.33
		-3.12	-3.17	-7.60	6.12	1.67	5.74	2.41	-2.05
Burgas 2			-2.89	4.44	-.13	3.85	-10.20	2.22	5.18
			-1.03	-3.91	1.47	.57	-4.89	4.95	1.76
			-1.81	8.43	1.64	5.69	-15.07	1.10	3.14
Sadovo 1				3.25	.85	-1.68	6.61	-.64	-2.68
				-.13	-.08	2.02	4.40	.23	.54
				-1.12	1.10	-2.86	7.38	1.38	-.91
Priboy					-4.49	1.49	-7.89	-2.64	4.82
					3.04	3.14	-2.15	-1.15	.16
					-1.17	-2.45	-7.55	3.79	7.67
OK754615A						2.92	3.37	-.04	-4.58
						-2.48	2.57	-1.27	.38
						-3.07	.67	.67	-5.95
TAM W-101							1.68	-3.90	-.77
							-.34	-1.51	-1.86
							7.71	-6.29	-.41
Payne								1.22	-1.32
								-1.13	-2.65
								-.21	1.33
Plainsman V									1.94
									-.65
									-2.83
Triumph 64									

S.E. common parent = 6.29†
6.88
10.09

S.E. no common parent = 5.74†
6.28
9.21

† Top value from Stillwater in 1982, middle value from Stillwater in 1983, bottom value from Lahoma in 1983.

Table 14. Specific combining ability estimates for grain yield from the F_2 generation of a nine parent diallel cross at Stillwater and at Lahoma in 1983.

	NR391-76	Burgas 2	Sadovo 1	Priboy	OK754615A	TAM W-101	Payne	Plainsman V	Triumph 64
NR391-76		36.67† 22.98	-55.19 -3.31	17.05 -10.38	-10.52 -20.17	30.19 13.50	-.95 4.31	-30.24 -19.07	13.00 12.60
Burgas 2			7.48 -10.31	-18.29 7.50	14.14 -22.83	76.19 39.17	-178.29 -63.36	40.76 35.93	21.33 -9.07
Sadovo 1				55.52 11.21	-.71 -29.45	-24.00 14.21	60.86 32.02	7.24 -21.02	-51.19 6.64
Priboy					-38.14 1.69	-19.10 5.69	25.10 -6.17	2.48 5.12	-24.62 -14.21
OK754615A						-44.33 -13.98	8.86 24.50	38.91 40.12	31.81 20.12
TAM W-101							2.57 -37.50	20.62 -34.88	-42.14 13.79
Payne								-24.86 34.93	106.71 11.26
Plainsman V									-54.91 -41.12
Triumph 64									

S.E. common parent = 65.46†
61.37

S.E. no common parent = 59.75
56.02

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† Top value from Stillwater, bottom value from Lahoma.

Table 15. Phenotypic correlations among entry means for the F_1 generation of a nine parent diallel cross at Stillwater in 1982 and 1983 and at Lahoma in 1983.

	Flag leaf area	Flag leaf duration	Flag leaf area duration	Grain yield	Tiller number	Kernels/ spike	Kernel weight	Plant height	Heading date
Flag leaf area		--† -.009 -.150	-- .899** .916**	.041 .289 -.156	-.035 .038 -.311*	.230 .542** .315*	.417** .286 .073	.162 .186 -.069	-.226 .511** .321*
Flag leaf duration			-- .424** .252	-- .603** .567**	-- .488** .380**	-- .075 .086	-- .474** .127	-- .290 .172	-- -.338* -.237
Flag leaf area duration				-- .536** .079	-- .256 .144	-- .519** .326*	-- .472** .137	-- .303* .024	-- .345* .216
Grain yield					.869** .689** .653**	-.273 .154 .197	.527** .798** .213	.465** .525** .341*	-.417** -.040 -.354*
Tiller number						-.367* -.249 -.321*	.217 .550** -.053	.212 .312* -.008	-.368* -.191 -.475**
Kernels/spike							-.309* -.139 -.408**	.068 .265 .112	.060 .347* .407**
Kernel weight								.566** .526** .311*	-.304* -.128 -.311*
Plant height									-.206 .035 -.165
Heading date									

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above from Stillwater 1982, middle value from Stillwater 1983, and bottom value from Lahoma 1983.

Table 16. Phenotypic correlations among entry means for the F_2 generation of a nine parent diallel cross at Stillwater and Lahoma in 1983.

	Flag leaf area	Flag leaf duration	Flag leaf area duration	Grain yield	Tiller number	Kernels/ spike	Kernel weight	Plant height	Heading date
Flag leaf area		-.384**† -.342*	.927** .906**	.006 -.362*	-.288 -.523**	.074 .146	.255 .153	.079 .224	.493** .637**
Flag leaf duration			-.015 .081	.076 .365*	.084 .131	-.209 -.103	.223 .383**	.044 .155	-.601** -.553**
Flag leaf area duration				.041 -.215	-.274 -.474**	-.011 .095	.384** .329*	.110 .313*	.291 .439**
Grain yield					.561** .372*	.338* .414**	.386** -.187	.453** .012	.034 -.049
Tiller number						-.263 -.515**	.061 -.152	.144 -.294*	.084 -.229
Kernels/spike							-.356* -.532**	.072 .196	.125 .411**
Kernel weight								.345* .224	-.111 -.412**
Plant height									-.042 .130
Heading date									

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Value above from Stillwater, value below from Lahoma.

VITA 2

Dolores Wynn Mornhinweg

Candidate for the Degree of

Doctor of Philosophy

Thesis: HERITABILITY AND COMBINING ABILITY OF FLAG LEAF AREA AND FLAG LEAF AREA DURATION AND THEIR RELATIONSHIP TO GRAIN YIELD IN WINTER WHEAT

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