

A QUANTITATIVE GENETIC STUDY IN WINTER OATS

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CHAPTER I

INTRODUCTION

Breeding programs vary greatly in detail but with few exceptions all are concerned with two major phases: 1) development of genetically variable material, and 2) selection within this material. Accomplishments consist of creating and identifying better genotypes than existed before. The latter phase is met with much difficulty in quantitative characters, one of the chief difficulties being the confounding effects of the environment.

One of the approaches that plant breeders have taken in recent years to attain greater efficiency in breeding operations involves the use of quantitative genetic theory. A basic objective of quantitative genetics is to characterize populations in statistical terms so as to permit accurate predictions of population behavior under the influence of selection. Although much information has been published in most crop areas, there have been few efforts to adequately characterize and interpret these data. It is felt by some workers that a more general recognition and utilization of quantitative genetic theory should result in greater efficiency of breeding operations.

The following report is a biometrical study of several quantitative characters in winter oats. Subject matter is divided into three parts: genetic and environmental variation, heritability, and genotypic and phenotypic correlations. The research is reported by chapters in a form

and style that is consistent with the requirements of scientific journals in the author's field. This style was adopted with the belief that the experimental data can be presented more precisely and interpreted more efficiently.

CHAPTER II

MATERIALS AND METHODS

The following three populations of F_3 and F_4 lines were studied:

Population 1 -- 50 lines from a cross of Cimarron (P_B) with Stw 594363 (P_A), an Arlington x Wintok selection.

Population 2 -- 56 lines from a cross of Cimarron (P_B) with C.I. 7500 (P_C), a Wintok Selection x Hairy Culberson selection.

Population 3 -- 80 lines from a cross of Bronco (P_D) with Stw 594363 (P_A).

The four parents used in the three populations are winter oats that are adapted to Oklahoma conditions. Cimarron and Bronco are commercial varieties grown extensively in Oklahoma, while Stw 594363 and C.I. 7500 are pure line selections that have been grown in experiment station nurseries for several years. The general characteristics of each of these parents are shown in Table I.

Each line of the populations traced to the seed of a randomly selected F_2 plant. Seed from each bulk harvested F_3 plant row was used to plant the F_4 progeny rows. The F_3 lines were grown in 1965 at Stillwater and Altus, Oklahoma, while the F_4 's were grown in 1966 at Stillwater, Woodward, and Cherokee, Oklahoma. Stillwater and Woodward will be referred to as locations 1 and 2, respectively, in this report; tests at the other locations were destroyed by adverse weather condi-

TABLE I
 PARENT AND LINE MEANS FOR SEVEN CHARACTERS FROM THREE POPULATIONS
 OF WINTER OATS GROWN IN THREE ENVIRONMENTS

Character	Populations								
	1			2			3		
	P _A	P _B	Line	P _B	P _C	Line	P _A	P _D	Line
Days to Heading ^a	35.5	31.4	34.0	30.4	45.9	36.8	35.0	44.6	39.5
Plant Height (cm)	75.9	67.2	71.9	62.7 ^b	75.9 ^b	68.1 ^b	73.9 ^b	83.3 ^b	81.2 ^b
Straw Strength ^c	5.81	3.81	4.36	3.36 ^b	3.46 ^b	4.40 ^b	5.84 ^b	3.65 ^b	4.55 ^b
Panicle Number/Ft.	38.5	44.2	44.9	45.7	48.5	49.8	39.2	45.6	42.8
Seeds/Panicle	37.4	24.1	30.5	24.1	17.2	22.1	36.2	26.4	32.6
Seed Weight (cg)	2.07	2.30	2.11	2.16	2.23	2.18	2.01	2.14	1.95
Grain Yield/Ft. (g)	29.8	24.8	28.8	24.0	18.1	23.5	28.0	23.8	26.5

^aDays to heading from April 1.

^bMean of two environments only.

^cMeasured by snap test scores from 1 to 10 (strength increases with numerical value).

tions. Lines within each population were planted in a randomized complete block design with two replications. Each parent of the cross was included four times at random in each replication. Plot size was a single row five feet in length at location 1 in 1965 and location 2 in 1966 and ten feet at location 1 in 1966, all with one foot spacing between rows. The harvested plot sizes for the three field trials, respectively, were two, three, and eight feet. Seeding rate was about 15 seeds per foot in 1965 and 24 seeds per foot in 1966 at each location. Stands were good in all tests.

Observations were made on the following characters at all field trials except where noted:

Date headed -- the date when 75% of the heads in a plot were completely emerged from the boot. These dates were converted to number of days from April 1 to heading for statistical analysis.

Plant height -- the average distance in centimeters from ground level to panicle tips within each plot. Measurements were not taken in populations 2 and 3 at location 2 in 1966.

Straw strength -- measured by the "snap test" as described by Murphy et al. (33). Snap test scores from 1 to 10 (score increases with straw strength) were assigned to each plot 25 days after heading. Culms from about one foot of row were pressed toward the alley and allowed to return to the upright position. Force of displacement and rapidity of return were used as a basis for scoring. Populations 2 and 3 at location 1 in 1966 were not scored.

Grain yield -- the weight of grain recorded in grams produced by each plot. The weights were converted to a square foot basis

prior to statistical analysis.

Number of panicles -- the number of fertile panicles harvested from each plot for yield determinations. These values were converted to a square foot basis before statistical analysis.

Seed weight -- the weight to the nearest .01 gram of two 100 kernel samples from each plot. Average seed weight in centigrams per seed was used in analyzing and reporting the data.

Number of seeds per panicle -- computed using the formula: grain yield per square foot ÷ number of panicles per square foot x weight per seed.

The general statistical procedures followed for analyzing the variability of the material grown in this study have been given by Comstock and Robinson (7). Analysis of the data was based on the assumption that performance as measured in any of the characters considered was composed as indicated in the following equation:

$$X_{ijklm} = u + p_i + l_j + y_k + r_{jkm} + (ly)_{jk} + (pl)_{ij} + (py)_{ik} + (ply)_{ijk} + e_{ijklm}$$

where X_{ijklm} is the measured value for the plot specified by subscripts,

u is the population mean,

p_i is the genetic effect of the i th line,

l_j is the effect of the j th location,

y_k is the effect of the k th year,

r_{jkm} is the effect of the m th replication at the j th location in the k th year, and

e_{ijklm} is a composite of remaining effects (including plot error, sampling error and error of measurement).

Combination of symbols refer to effects of interaction between factors indicated by the single symbols. For example, $(pl)_{ij}$ is the effect resulting from the interaction between genotypes of the i th line and environments of the j th location. Population variances are symbolized by σ^2 and their subscript indicates their source. For example, σ_{pl}^2 will signify variance of effects arising from interaction of lines (genotypes) with locations.

It is of prime importance to note that the genotypic effect, p , reflects the genotypic value of a line as an average for the population of environments of which the locations and years in which the data were obtained were considered to be a sample. It follows that σ_p^2 is genetic variance (among lines) in average merit with respect to that population of environments. The special significance of σ_p^2 arises from the fact that in practical breeding programs it is the average genotypic value over the range of environments encountered in a region in successive years with which the breeder is concerned.

The data from each individual field trial were examined individually and in various combinations by analysis of variance. Combined analysis involved 1) data for two years at one location, 2) data for two locations in one year, and 3) data for the three field trials. Data for the three populations were handled separately throughout. The form of the analysis of variance and associated mean square expectations are presented in Table II. Note from Sections A and B of the table that estimates of σ_p^2 are confounded with interaction variances and in Sections A, B, and C that all interaction variances are confounded but at different degrees.

The best estimates of the various components were substituted in

TABLE II
FORM OF VARIANCE ANALYSIS AND
MEAN SQUARE EXPECTATIONS

	d.f.	Mean Square Expectation
A. Analysis for data from one location in one year.		
Replications	r-1	
Lines	p-1	$\sigma_e^2 + r(\sigma_{ply}^2 + \sigma_{pl}^2 + \sigma_{py}^2 + \sigma_p^2)$
Error	(r-1)(p-1)	σ_e^2
B. Analysis for data from two locations in one year. ^a		
Locations	l-1	
Replication in locations	l(r-1)	
Lines	p-1	$\sigma_e^2 + r(\sigma_{ply}^2 + \sigma_{pl}^2) + rl(\sigma_{py}^2 + \sigma_p^2)$
Lines x locations	(l-1)(p-1)	$\sigma_e^2 + r(\sigma_{ply}^2 + \sigma_{pl}^2)$
Error	l(r-1)(p-1)	σ_e^2
C. Analysis for data from three environments.		
Environments	n-1	
Replications in environments	n(r-1)	
Lines	p-1	$\sigma_e^2 + r(\sigma_{ply}^2 + \sigma_{pl}^2 + \sigma_{py}^2) + rno_p^2$
Lines x environments	(n-1)(p-1)	$\sigma_e^2 + r(\sigma_{ply}^2 + \sigma_{pl}^2 + \sigma_{py}^2)$
Error	n(r-1)(p-1)	σ_e^2

^aAnalysis of data from two years in one location has a similar form with interaction effects of years and locations being reversed in the mean square expectation.

the formula $\frac{o_p^2}{o_{ph}^2}$ to estimate heritability (H) for differences among line means, where o_{ph}^2 was the phenotypic variance.

For the single experiments:

$$H = \frac{(o_p^2 + o_{pl}^2 + o_{py}^2 + o_{ply}^2)}{o_p^2 + o_{pl}^2 + o_{py}^2 + o_{ply}^2 + \frac{o_e^2}{r}}$$

For two locations in one year:

$$H = \frac{(o_p^2 + o_{py}^2)}{(o_p^2 + o_{py}^2) + \frac{(o_{pl}^2 + o_{ply}^2)}{l} + \frac{o_e^2}{rl}}$$

For two years in one location a similar formula to the one above would be used with interactions involving o_{l1}^2 and o_{ly}^2 interchanged.

For three environments (disregarding locations and years):

$$H = \frac{o_p^2}{o_p^2 + \frac{(o_{pl}^2 + o_{py}^2 + o_{ply}^2)}{n} + \frac{o_e^2}{rn}}$$

Genetic coefficients of variation (GCV) were derived from the formula $\frac{o_p}{\bar{x}} \times 100$ where o_p is the genetic standard deviation and \bar{x} is the population mean. The values estimating genetic variance, o_p^2 , were the same as the numerator of the heritability formulas above.

Expected genetic advance (G_s) was derived from the formula $G_s = k o_{ph} H$ where k is the selection differential expressed in phenotypic standard deviations and is given the value of 1.76, the expected value for a normally distributed population where ten percent of the lines are selected. o_{ph} and H took the values estimated in formulas above.

Heritabilities were also estimated by the parent-progeny regression method as follows: $H = b_{yx}$ where b is the regression coefficient, y is the F_4 line means and x is the F_3 line means. Standard unit heritabili-

ties were also derived by the regression method as reported by Frey and Horner (12) where the regression was identical to correlation coefficient on the original data.

Covariance components were estimated from covariance analyses in an analogous manner to the variance components computed from the analyses of variance. Genotypic correlations were computed from the genetic variances and covariances as follows:

$$\text{Genotypic correlation } (r_p) = \frac{o_{p_1 p_2}}{\sqrt{o_{p_1}^2 o_{p_2}^2}}$$

where $o_{p_1 p_2}$ is the genetic covariance component for two traits, and $o_{p_1}^2$ and $o_{p_2}^2$ are the respective genetic variance components. Phenotypic correlations were estimated in the following manner:

$$\text{Phenotypic correlation } (r_{ph}) = \frac{M_{12}}{\sqrt{M_{11} M_{22}}}$$

where M_{12} is the mean product for lines and M_{11} and M_{22} are the mean squares for lines for the two characters under consideration.

The expected change in one character as a result of selecting for another was estimated in the following manner:

$$\text{Expected change in unselected character} = \frac{k o_{p_1 p_2}}{\sqrt{o_{ph}^2}}$$

where the values in the numerator are as described above and o_{ph}^2 is the phenotypic variance of the selected character.

CHAPTER III

GENETIC AND ENVIRONMENTAL VARIABILITY

One of the major goals in plant breeding programs has been to improve the efficiency of selection. Since selection is based on phenotype, not genotype, and the correlation between the two is often low for quantitative characters, progress may be slow and disappointing. In order to improve selection efficiency and to accelerate genetic progress, the breeder in recent years has made attempts to partition phenotypic variation into its component parts, i.e., genetic and non-genetic variation, and to arrive at the relative magnitudes of these components.

Some of the advantages of knowing the magnitude of genetic variation have been discussed by Comstock and Moll (6). They pointed out that: 1) over-estimation of genetic variance would in some cases lead to investment of time and effort not justified by the real potential for improvement of genetic stocks employed, 2) optimum procedures may vary significantly depending on the magnitude of genetic variance, and 3) there is danger that sound breeding programs may be abandoned prematurely or unwisely because of results that are disappointing relative to unwarranted expectations based on erroneous estimates of genetic variance. These authors further suggested that estimates for every genetic population are not necessary since inferences can be made from a limited number of good estimates to similar material.

Comstock and Robinson (7) made a point of the fact that variance

resulting from interaction of genotype and environment is frequently a source of upward bias in estimates of genetic variance. They proposed the use of a components of variance method using random environments of years and locations to arrive at more precise estimates. This method has since been used extensively in corn and to a lesser degree in several self-pollinated crops; cotton (31), barley (11), soybeans (22), lespedeza (17), tobacco (24,30), millet (3), and oats (19,35,39).

Genotype x environment interactions are attributed to differential response of genotypes to different environmental conditions. There is rather general agreement that these interactions have an important bearing on the breeding of better varieties since varieties must be produced that perform well in a range of locations and years. Allard and Bradshaw (1) divided environmental variations into two sorts, predictable and unpredictable. Genotype x location interactions are associated with the former variations while genotype x year and genotype x year x location are associated with the latter. The year-to-year variations cannot be predicted in advance; therefore, the breeder can hardly aim his program at developing varieties for these circumstances. Although location-to-location variations occur, they are somewhat predictable and varieties can be developed to reduce their effects.

The importance of genotype x environment interactions for certain characters in soybeans was reported by Johnson et al. (22). These interactions were much higher for yield than for other important characters. A reduction of 71% of genetic variability was seen in one population when locations and years were considered in the analysis as compared to only a single test. Hanson et al. (17) again pointed out the effect of large interactions and showed that a misleading estimate of genetic

variance for yield in lespedeza would have been obtained from a single test. In this study the genotype x year interactions were relatively large, indicating the importance of testing in different years.

The significance of variety x location interactions in oat variety tests was illustrated by Horner and Frey (20). They proposed that the state of Iowa be divided into subregions to minimize the magnitude of these interactions. Frey (8) also reported in another oat experiment that strain x location interactions were higher for yield than for the various yield components. He constructed an example to show that a strain x environment interaction may exist for yield even though these interactions for the yield components were zero. High variety x year x location interactions were reported in Kansas by Liang et al. (27) in oat varieties grown in five years and five locations. First order interactions were small and nonsignificant. Bolton et al. (2) reported high variety x year x location interactions for oat varieties grown in two years at Stillwater and Woodward, Oklahoma, for number of seed per panicle, seed weight, and grain yield. Variety x year interactions were the highest interactions for number of tillers, height, and maturity. A variety x location interaction was not large except for number of tillers.

Burton (4) and Johnson et al. (22) suggested the use of the genetic coefficient of variation in studying genetic variability in segregating populations. The latter reported that this statistic may facilitate comparisons of genetic variability in different populations and with different characters. Estimates of genetic coefficients of variability were made by Wallace et al. (39) in F_3 and F_4 generation material from a cross of Letoria x Fulwin oats. Average estimates for the two years

were 13.0, 5.2, 15.3, and 6.8 % for yield, seed weight, number of seeds per panicle, and height, respectively.

The purpose of the research reported in this chapter was to study the genetic and environmental variation in several characters of winter oats.

Experimental Results

Means for parents and lines grown in 1965 and 1966 field trials for the seven characters are presented in Table I. As might be expected with quantitative characters most line means were intermediate to the parent means. Differences between parents were largest for date headed in populations 2 and 3, straw strength in populations 1 and 3, and seeds per panicle in all three populations. Smallest differences existed between parents for seed weight, panicle number, and height for all populations. It is significant to note an average difference of 4, 16, and 10 days to heading for the parents of populations 1, 2, and 3, respectively, and the difference in line means since maturity differences may contribute to high genotype x environment interactions and differences in populations if stress periods occur. These stresses will affect maturity groups differently depending on their timing in relation to the physiological stage of the plants.

Estimates of variance components from individual field trials for the seven characters are shown in Table III. The estimates of genetic variance, σ_p^2 , were generally two to three times smaller than error variance, σ_e^2 . For heading date σ_p^2 was much larger than σ_e^2 in all populations and field trials. In a few isolated cases for other characters the two variance components were of similar magnitude but most estimates

TABLE III
ESTIMATES OF COMPONENTS OF VARIANCE FROM INDIVIDUAL FIELD TRIALS

Character	Population	1965, Loc. 1		1966, Loc. 1		1966, Loc. 2		Average	
		σ_p^2	σ_e^2	σ_p^2	σ_e^2	σ_p^2	σ_e^2	σ_p^2	σ_e^2
Date Headed	1	3.07	.31	8.20	2.55	4.45	1.11	5.24	1.32
	2	5.33	.59	6.96	2.11	6.04	.97	6.11	1.22
	3	6.52	.78	6.24	1.40	5.26	1.48	6.01	1.22
Straw Strength	1	.755	.515	.171	.783	.101	.869	.342	.722
	2	.614	.436	----	----	.898	.987	.756 ^a	.712 ^a
	3	.548	.377	----	----	.184	1.530	.366 ^a	1.219 ^a
Plant Height	1	4.08	12.36	7.22	11.77	3.68	19.50	4.99	14.54
	2	22.70	15.13	5.90	19.36	----	----	14.30 ^a	17.25 ^a
	3	8.01	16.17	8.34	16.13	----	----	8.18 ^a	16.15 ^a
Panicule Number	1	11.96	37.84	16.89	24.40	14.44	26.56	14.43	29.60
	2	27.91	39.61	28.85	49.06	33.09	37.81	29.95	42.16
	3	17.32	29.63	22.75	16.74	17.77	39.75	19.28	28.70
Seeds/Panicle	1	6.94	16.67	10.93	12.25	5.65	19.02	7.84	15.98
	2	15.10	10.79	4.08	16.65	5.75	13.42	8.31	13.62
	3	18.95	29.39	22.46	22.15	19.54	24.05	20.32	25.20
Seed Weight	1	.0204	.0231	.0064	.0238	.0128	.0283	.0132	.0251
	2	.0188	.0179	.0222	.0211	.0225	.0306	.0212	.0232
	3	.0311	.0257	.0267	.0229	.0133	.0288	.0237	.0258
Grain Yield	1	8.85	40.99	6.82	6.18	.63	25.47	5.43	24.21
	2	11.43	16.86	3.70	11.40	6.94	17.76	7.36	15.34
	3	4.44	23.33	3.15	13.70	10.55	28.02	6.05	21.87

^aAverage of two environments only.

were inconsistent between populations and field trials. With the exception of yield in populations 1 and 3 in the 1965 trial and population 1 at location 2 in 1966, all estimates of σ_p^2 were significantly different from zero as measured by the F test at the five percent level of probability and most were significant at the one percent level.

It is apparent from the data in Table IV that most genetic estimates were biased upward as a result of genotypic x environment interactions. Genetic variance estimates for most characters except heading date were relatively small when these interactions were removed. Since only one location was used in 1965, estimates of genotype x location and genotype x year interactions were confounded with the second order interaction, genotype x year x location, and direct effect of individual interactions could not be assessed. Estimates of genetic variance were also confounded with one of the first order interactions when two environments were combined but in theory should have been relatively free of interaction effects when the three environments were combined. Interaction variance estimates for characters when locations only and when years only were combined were usually dissimilar; when all three environments were combined the interaction estimate was generally not the highest estimate, but rather somewhat intermediate. These differences in methods of derivation of interactions and also in populations were partially responsible for variable genetic variance estimates. In about two-thirds of the cases in the three different combined analyses, the genetic variance estimates were similar or higher in order of magnitude to those of interaction variances. Heading date of all populations, panicle number of populations 2 and 3, and seed weight and yield of population 2 exhibited the greatest ratios of genetic variance to inter-

TABLE IV
ESTIMATES OF COMPONENTS OF VARIANCE FROM COMBINED ANALYSES

Character	Population	Variance estimated													
		by σ^2_p				by $\sigma^2_1^a$				by σ^2_e					
		2 Loc 2 Yrs	1 Loc 2 Yrs	2 Loc 1 Yr	1 Loc ^b 1 Yr	2 Loc 2 Yrs	1 Loc 2 Yrs	2 Loc 1 Yr	2 Loc 2 Yrs	1 Loc 2 Yrs	2 Loc 1 Yr	1 Loc ^b 1 Yr			
		σ^2_p	σ^2_{pl}	σ^2_{py}	σ^2_{ply}	σ^2_{pl}	σ^2_{py}	σ^2_{ply}	σ^2_{pl}	σ^2_{py}	σ^2_{ply}				
Date Headed	1	4.44	4.60	5.45	5.24	.74**	.76**	.78**	1.17	1.28	1.60	1.32			
	2	5.98	5.97	6.65	6.11	.40**	.42**	.26	1.13	1.17	1.39	1.22			
	3	3.89	3.44	5.14	6.01	1.79**	2.68**	.13	1.23	1.08	1.46	1.22			
Straw Strength	1	.0743	.2827	.0000 ^c	.3420	.2963**	.1969*	.2559*	.8216	.7295	.9748	.7220			
Plant Height	1	2.64	1.34	3.84	4.99	1.03	2.72	.00	14.34	12.61	15.33	14.54			
	2	-----	10.74	-----	14.30	-----	2.92*	-----	-----	17.95	-----	17.29			
	3	-----	5.36	-----	8.18	-----	3.32	-----	-----	17.52	-----	16.15			
Panicle Number	1	3.92	3.78	0.00	14.43	10.37**	7.78	16.70**	29.66	33.81	25.57	29.60			
	2	31.52	33.81	32.56	29.95	6.09	2.44	7.89*	41.23	42.03	42.04	42.16			
	3	13.96	13.04	16.72	19.28	5.42*	8.35**	3.69	30.10	21.33	30.33	28.70			
Seeds/Panicle	1	2.92	6.72	1.04	7.84	5.98**	1.90**	8.85**	14.77	13.83	13.60	15.98			
	2	4.77	4.06	4.57	8.31	4.73**	6.42**	1.59	14.01	14.00	15.63	13.62			
	3	7.05	4.00	19.02	20.32	13.37**	17.68**	2.13	23.29	24.88	20.24	25.20			
Seed Weight	1	.0057	.0060	.0013	.0132	.0074**	.0066*	.0081*	.0234	.0202	.0236	.0251			
	2	.0128	.0107	.0130	.0212	.0070**	.0079**	.0074**	.0269	.0206	.0314	.0232			
	3	.0020	.0000	.0110	.0237	.0204	.0330	.0071*	.0229	.0234	.0215	.0258			
Grain Yield	1	3.17	4.90	0.00	5.43	2.57*	2.79	4.85**	22.32	23.77	12.99	24.21			
	2	4.32	5.35	4.73	7.36	3.64*	2.76	1.49	16.39	14.90	16.15	15.34			
	3	1.11	2.20	2.74	6.05	5.12**	1.85	4.39*	20.20	16.70	18.34	21.87			

^a σ^2_1 is interaction variance.

^b Three-single test average.

^c All negative variance estimates were considered to be zero.

*Exceeds the 5% level of significance.

**Exceeds the 1% level of significance.

action variance. Heading date of population 3 showed a high genotype x year interaction.

Genetic coefficient of variation estimates for single environments ranged from 3 to 22 % with seeds per panicle, straw strength, and panicle number yielding the largest values and plant height, seed weight, and heading date the lowest (Table V). Since line means for most characters remained relatively constant between environments, the same general relationships that existed between populations and field trials for a character in the genetic variance estimates above were again exhibited. However, relationships between characters changed. Estimates of GCV for most traits were reduced considerably when genotype x environment interactions were removed (Table VI). These ranged from 0 to 14 %. The characters of population 2 were affected least by interactions and yielded higher genetic coefficients of variability than characters for populations 1 and 3.

Discussion

Accurate estimates of the components of variance are helpful to the breeder in evaluating breeding programs and in determining the best procedures for selection and testing. Not only should a breeder know if a population possesses sufficient genetic variability to justify working with it, but he should also be aware of the danger of mistaking variance resulting from interactions of genotype x environment for usable genetic variance. This danger would most likely occur when evaluation of breeding material was carried on only at a central breeding station.

It is evident from the data presented in this experiment that for most characters studied, an erroneous estimate of genetic variance would

TABLE V
GENETIC COEFFICIENTS OF VARIATION FOR INDIVIDUAL FIELD TRIALS

Character	Population	1965, Loc 1	1966, Loc 1	1966, Loc 2	3-Test Average
Date Headed	1	5.20	8.21	6.34	6.58
	2	6.47	6.82	6.83	6.71
	3	6.70	5.95	5.97	6.21
Straw Strength	1	19.53	9.86	7.16	12.18
	2	21.24	-----	20.16	20.70 ^a
	3	22.10	-----	7.48	14.79 ^a
Plant Height	1	2.72	4.34	2.41	3.16
	2	6.38	3.94	-----	5.16 ^a
	3	3.31	3.76	-----	3.54 ^a
Panicle Number	1	8.05	9.58	7.74	8.50
	2	11.57	10.97	10.53	11.00
	3	10.10	11.55	9.18	10.30
Seeds/Panicle	1	8.19	12.70	7.12	9.34
	2	17.71	10.83	9.35	12.63
	3	11.78	15.31	14.96	14.02
Seed Weight	1	5.89	4.10	5.69	5.23
	2	6.28	6.76	6.93	6.66
	3	9.19	7.61	6.47	7.76
Grain Yield	1	9.05	12.20	2.48	7.91
	2	15.69	9.88	8.94	11.50
	3	7.37	6.65	13.45	9.16

^aAverage of two environments only.

TABLE VI
GENETIC COEFFICIENTS OF VARIATION FROM COMBINED ANALYSES

Character	Population	2 Loc	1 Loc	2 Loc	1 Loc ^a
		2 Yrs	2 Yrs	1 Yr	1 Yr
Date Headed	1	6.23	6.27	6.89	6.58
	2	6.62	6.55	6.86	6.71
	3	5.00	4.65	5.64	6.21
Straw Strength	1	6.13	12.23	0.00	12.18
Plant Height	1	2.27	1.69	2.79	3.16
	2	----	4.87	----	5.16
	3	----	2.85	----	3.54
Panicle Number	1	4.52	4.56	0.00	8.50
	2	11.09	12.25	10.75	11.00
	3	8.67	8.81	9.28	10.30
Seeds/Panicle	1	5.58	8.75	3.42	9.34
	2	9.59	10.12	9.85	12.63
	3	8.10	5.79	14.22	14.02
Seed Weight	1	3.58	3.56	1.84	5.23
	2	5.22	4.74	5.28	6.66
	3	2.32	0.00	5.40	7.76
Grain Yield	1	6.35	8.09	0.00	7.91
	2	8.89	11.53	8.95	11.50
	3	3.96	5.29	6.48	9.16

^aThree single test average.

have been obtained from data collected at a single field trial. With the exception of heading date for the three populations and panicle number in populations 2 and 3, the genetic estimates were reduced by 40 to 90 % when the average of single tests were compared to average performance over the three environments in a combined analysis.

The ratio of genetic variance to environmental variance estimates were very high for heading date regardless of the method of analysis, indicating that this trait is quite stable under different environmental conditions. The reason for this stability probably traces to its relatively simple inheritance. Jensen (21), in reviewing the inheritance of maturity in oats, reported estimates ranging from one to three major genes controlling its effect. Data from this study would suggest that little would be gained from a breeding standpoint by observing this trait in different years and locations.

In the six more complexly inherited characters there appeared to be differences in populations for genetic variance. Population 2 yielded higher estimates for all characters studied (except seeds per panicle) and estimates for the various methods were more consistent than for populations 1 and 3. From a genetic standpoint, it seems likely that population 2 has the best potential for genetic improvement. However, from a practical standpoint, it should be noted that the mean yield of the population was the lowest of the three and, therefore, may not necessarily produce the highest yielding segregates when all three populations are considered.

Although good estimates of genotype x location interaction were not available, the very small genetic variances for the three yield components, yield, and straw strength of population 1 at the two 1966 locations

indicated that this interaction was important. The high interactions from the two divergent locations seemed to be related to maturity. Differential response of genotypes to the two locations was presumably a result of moisture stress at location 2 at a time when later maturing lines were adversely affected. This relationship was also quite evident in the parents as they responded differently to the two environments in 1966. The same reasoning can be used to explain high genotype x year interactions for seed weight and seeds per panicle of populations 2 and 3, and panicle number for population 3 for the two years at location 1. This differential response again was shown by the parents, as the early parent was favored in 1965 because of drought stress during the critical heading period, while in 1966 moisture arrived at a time that benefited the late maturing parent.

The environments represented in this study were a very small sample of years and locations in the state. It is likely that interactions as presented above would result in large genotype x year x location interactions when a larger number of random years and locations are used. Miller et al. (31) and Jones et al. (24) stated that second order interactions are important because each individual experiment is unique and the environmental conditions differentiating these experiments are not necessarily related to the year or the location grouping. The importance of genotype x year x location interaction in self-pollinated crops was discussed by Matzinger (29) in his review of experimental estimates in several crops. It was suggested that second order interactions were usually of greater significance than first order interactions, especially where genetic material is grown in a limited area of adaptation. Results from Liang (27) in Kansas and Bolton (2) in Oklahoma supported

this report with oat variety tests by showing high genotype x year x location interactions and non-significant genotype x location values for yield. Bolton also reported high second order interactions for number of seeds per panicle and seed weight.

Genetic variances for yield are of primary interest to the breeder since his breeding procedures depend somewhat on their magnitude. The values for population 3 were exceptionally small and suggest that selection under these experimental conditions would be futile. Opportunities for increasing yield in populations 1 and 2 appear promising although estimates of σ_p^2 were not large. In these two populations, the interaction variance was generally smaller than σ_p^2 which suggests that interactions were not the primary factor for low estimates of σ_p^2 . Two additional factors could contribute to small σ_p^2 ; namely, 1) lack of genetic diversity in the parents, thus little real genetic variance in the cross, and 2) inadequate precision in the experiment for measuring the components of variance for this trait.

Selection is most effective when genetic variance is at a maximum. It is known that genetic variances are increased when crosses are made between parents that differ greatly in the character under study. It has been suggested by Robinson (37) that we may have reached secondary peaks in many crops for certain characters and that greater effort should be given to bringing in wider diversity and a broader base to the germ plasm. Breeders have been somewhat reluctant to bring in new germ plasm in many crops because of the undesirable characteristics associated with unadapted material. Unless they have reached a plateau, they may be justified in using adapted breeding stocks. High genetic variability for yield does not imply that these populations will nec-

essarily produce high yielding segregates.

It is likely that lack of precision played a primary role in low genetic variance estimates for yield. Frey (8) reported that a larger number of replications and larger sized plots are required to estimate yield than other characters in oats because of the large error variance associated with the yield estimates. This concept has had general acceptance in most crop plants whether yield is measured as vegetation or grain. In the present study differences in yield at the one percent level of significance were not detected in single tests in 1965 for populations 1 and 3 nor at location 2 in 1966 of population 1. In this connection it should be noted that magnitudes of genetic variance per se have little meaning unless accompanied by estimates of error variance. This is illustrated by the genetic coefficients of variation for heading date and yield. While their values were of comparable magnitude, the former character showed highly significant estimates of genetic variance and would doubtless respond rapidly to selection. The basic difference in data for these two characters in this study lies in the precision of the tests. A coefficient of variability of about 3% existed for heading data as compared to 17% for yield.

When the genetic variance for the yield components were placed on a mean basis (GCV), the values for seeds per panicle and panicles per foot were quite large while seed weight values were small. Similar relationships, although higher in magnitude, were reported by Wallace et al. (39) in a winter oat cross. These results suggest that there is opportunity to increase the former two traits at a rate much higher than seed weight. This has significance in that yield components, if associated with yield, may be effective selection criteria for yield improve-

ment. Frey (8) suggested that fewer replications and smaller plot size could be used to evaluate good yielding lines by yield component analysis. This author also reported that variety x location interactions for the yield components were lower than those for yield. The data from this study show higher interaction variances with respect to the mean of the population for the yield components than for yield. However, if more precision is required for measuring genetic variance for yield than for the yield components, determinations of yield components may offer some help in selection experiments.

Summary and Conclusions

Estimates of genetic and environmental variances were studied for seven characters in three F_3 and F_4 oat populations. Tests were conducted at one location in 1965 and two locations in 1966 and data were analyzed for various combinations of environments. Genetic variance estimates were reduced from 40 to 90% for all characters except heading date in the three populations and panicle number in populations 2 and 3 when genotype x environment interactions were removed. Heading date was the most stable character studied and can probably be evaluated in a single field trial.

Genotype x year and genotype x location interactions appeared important for different characters and different populations. It was suggested that these interactions would result in large genotype x year x location interactions. The results indicated that caution should be exercised in making inferences from limited genetic studies to oats in general because of the difference in the variance components between populations. Some of the difference in populations was attributed to

maturity differences.

Data indicated that there was opportunity for improving yield in populations 1 and 2. It was suggested that more precision may be required in order to maximize yield improvement in oats. Genetic coefficient of variability estimates were high for seeds per panicle and panicle number and small for seed weight and height.

CHAPTER IV

HERITABILITY

One of the most important properties of a quantitative character is its heritability which is defined by Knight (26) as the portion of the observed variance for which difference in heredity is responsible. This statistic shows the relationship of genetic and non-genetic variances. Aside from showing this relationship, heritability has another important function; namely, its predictive role, expressing the reliability of the phenotypic value as a guide to breeding value. Only the phenotype of individuals is directly measured, but the genotype determines their influence on the next generation. Therefore, if a breeder selects on the basis of phenotype, his success can be predicted on the knowledge of the ratio of genotypic to phenotypic values, i.e. heritability.

Lush (28) made a distinction between narrow and broad sense heritability, the former being the ratio of additive genetic variance to total variance while the latter is the ratio of total genetic to total variance. It was suggested by Sprague (38) that this distinction is of considerable theoretical importance, but in practice may be of limited value because of the large standard errors associated with the estimates.

While the theory of heritability is quite old and relatively simple, it is common knowledge among breeders that caution must be practiced in its application to plant material. Discrepancies arise in its use

between breeders, characters, and crops. Sprague (38) cautioned that heritability is not a stable population parameter but varies with the precision with which the environmental variance is measured. It was pointed out by Hanson (18) that the nature of the genetic variance, the selection unit considered, and the inference population will affect the heritability statement made for a character. Because of these factors, it is evident that estimates must be properly defined in order to have utility and significance to the plant breeder.

Recent studies of a number of characters in different crops have been directed toward estimation of heritability. Several workers (3, 25, 36) have utilized heritability formulas that estimate genetic and environmental variances from F_2 and F_1 , backcross, and/or pure line data, respectively. Others (17, 19, 35, 39) have used estimates derived from components of variance analysis while still others (12, 13, 19, 32, 35) have used parent-progeny regressions. Johnson et al. (22) point out that these methods do not necessarily measure the same thing unless all gene effects are additive.

Variance and regression heritabilities were estimated in F_4 and F_4 - F_5 barley lines, respectively, by Frey and Horner (11). The latter method gave lower estimates due to an upward bias of the variance heritabilities by genotype x environment interaction. The variance method heritabilities used in predicting gains did agree quite well with actual gains, however.

A limited number of heritability studies in oats have been reported. Broad sense heritabilities in the F_2 generation of oat crosses where environmental variance was estimated with parental lines were made by Petr and Frey (36). Values of 61, 87, 74, 33, and 53 % were estimated

for plant height, heading date, spikelets per panicle, panicles per plant, and grain yield, respectively. Jones and Frey (25) estimated broad and narrow sense values in F_2 and F_5 generations for four oat characters using pure lines as estimates of environmental variance and available formulas to obtain coefficients of additive and dominant gene action. They showed that broad and narrow sense heritabilities were closer in the F_5 than the F_2 generation which indicated reduction of non-additive gene action from selfing. These workers suggested that broad sense heritabilities were useful in advanced generation material. Narrow sense values reported from F_5 data were 70, 64, 55, and 30 % for heading date, plant height, kernel weight, and yield, respectively. Pawlisch and Shands (35) reported moderately high heritability estimates by the variance method in an oat cross for height (69%), maturity date (70%), and yield (69%), and high values for heading date (89%) from F_3 and F_4 generation lines grown in different years.

A standard unit regression method for estimating heritability based on a regression coefficient utilizing phenotypic measures expressed as standard deviates was proposed by Frey and Horner (12). The approach has merit only in that heritability estimates are never greater than 1.0 and at least some of the genotype x environment interaction bias due to scale is removed. Values of 62, 63, and 68 % were reported for F_2 - F_3 , F_3 - F_4 , and F_4 - F_5 comparisons, respectively, for plant height in oats. An average of 36% standard unit heritability was reported by Murphy and Frey (32) in 12 oat crosses for groat weight using F_2 and F_3 data. Groat length was more highly heritable with 51%.

A limited number of heritability studies involving straw strength have been reported in oats. The standard unit regression and components

of variance methods were employed by Hess and Shands (19) to measure heritability in several crosses of oats for snap test scores in the F_3 and F_4 generations. Agreement between methods was generally good and values of 69 to 98 % for the variance method and 75 to 98 % for the regression method were reported. These workers also made predictions of genetic advance of 53 and 26 % of the mean from F_3 lines of crosses grown in 1960 and 1964, respectively. Standard unit heritability estimates for straw strength as measured by the CL_r method were reported at 15% in F_3 - F_4 comparison in 12 oat crosses by Frey and Norden (13).

In a study of the oat cross, Letoria x Fulwin, Wallace et al. (39) suggested that as much as 15 to 18 % genetic gain in yield could be accomplished by selecting five percent of the superior lines. Their estimates were derived from variance and covariance analyses of F_3 and F_4 generation material.

The purpose of this investigation was to estimate heritabilities for seven quantitative characters of three oat populations using the variance and regression methods of analysis and to make genetic advance predictions from these estimates.

Experimental Results

Heritabilities for various plant characters in the three populations of winter oats were first calculated separately by the variance method from single experiments and these heritabilities are given in Table VII. Estimates were generally high with the highest values being for heading date and somewhat lower values for the remaining six characters. Variations were found between environments and between populations. Since only error variances were removed from the phenotypic variances, herit-

TABLE VII

HERITABILITY ESTIMATES USING THE COMPONENTS OF VARIANCE METHOD
FROM INDIVIDUAL FIELD TRIALS (IN PERCENT)

Character	Population	1965 Loc 1	1966 Loc 1	1966 Loc 2	3-Test Average
Date Headed	1	95	91	92	93
	2	95	91	95	94
	3	94	93	92	93
Straw Strength	1	75	40	26	47
	2	74	--	73	74 ^a
	3	74	--	27	51 ^a
Plant Height	1	40	65	36	47
	2	75	48	--	61 ^a
	3	50	61	--	56 ^a
Panicle Number	1	39	68	62	56
	2	59	64	72	65
	3	47	80	57	61
Seeds/Panicle	1	45	73	47	55
	2	74	42	56	57
	3	56	75	71	67
Seed Weight	1	64	45	58	56
	2	68	76	69	71
	3	71	78	58	69
Grain Yield	1	30	77	7	38
	2	58	49	54	54
	3	27	41	53	40

^aAverage of two environments only.

abilities of this type tend to relate differences in precision of the experiments as much as heritable differences.

Table VIII presents heritabilities calculated from the components of variance and regression methods for different sets of environments. Different estimates of σ_p^2 were used in the variance method as the selection unit ranged from three environments to a single field trial. Estimates for σ_p^2 in heritabilities for the first four columns of Table VIII were σ_p^2 , $\sigma_p^2 + \sigma_{pl}^2$, $\sigma_p^2 + \sigma_{py}^2$, and $\sigma_p^2 + \sigma_{pl}^2 + \sigma_{py}^2 + \sigma_{ply}^2$, respectively. Interactions from genotype x year tended to affect the estimates of populations 2 and 3, while genotype x location interactions seemed the more important in population 1. The estimate calculated from the combination of data from three environments should represent the best estimate of heritability from the components of variance method since a larger number of environments were sampled and the estimates are expected to have less bias due to genotype x environment interactions.

Heritabilities from the regression analyses were computed from F_4 line means onto F_3 line means for two different sets of environments. Estimates are reported in Table VIII in actual values and in standard units. It is usually assumed that the best estimate of heritability by the regression method occurs when the two generations are grown in different years and at different locations each year. This has the advantage of removing some of the genotype x location and genotype x year interactions that may exist. Regressions in actual value and standard units were similar enough to indicate that bias caused by genotype x environment interaction associated with the contraction or expansion of the phenotypic scale was not serious. Some of the high values were reduced and some of the low values were raised by the standard unit

TABLE VIII
HERITABILITY ESTIMATES FROM COMBINED ANALYSES (IN PERCENT)

Character	Population	Method of Estimation							
		Variance				Regression		S. U. Regression	
		2 Loc ^a 2 Yrs	1 Loc 2 Yrs	2 Loc 1 Yr	1 Loc ^b 1 Yr	2 Loc ^c 2 Yrs	1 Loc 2 Yrs	2 Loc ^c 2 Yrs	1 Loc 2 Yrs
Date Headed	1	91	87	87	93	101	142	79	86
	2	95	88	93	94	95	106	86	87
	3	83	68	92	93	45	50	50	52
Straw Strength	1	24	50	00	47	2	28	2	41
	2	--	--	--	61	52	--	39	--
	3	--	--	--	56	8	--	6	--
Plant Height	1	49	23	51	47	27	13	25	13
	2	--	64	--	61	--	36	--	50
	3	--	47	--	56	--	33	--	31
Panicle Number	1	32	23	00	56	30	12	30	13
	2	78	74	68	65	59	71	53	60
	3	67	58	64	61	38	41	34	41
Seeds/Panicle	1	40	60	12	55	7	44	6	43
	2	53	38	49	57	22	20	27	24
	3	46	21	76	67	-6	12	-6	12
Seed Weight	1	47	42	12	56	31	19	32	29
	2	65	27	53	71	53	39	43	37
	3	16	00	55	69	-1	-10	00	-3
Grain Yield	1	41	40	00	38	18	17	29	29
	2	52	51	50	54	15	27	16	36
	3	18	38	29	40	-10	13	-9	17

^aCombined analysis from three environments (Loc 1, 1965 and Loc 2 and 3, 1966).

^bThree single test average.

^cRegression of F₄ line means from Loc 2 on F₃ line means from Loc 1.

method but the changes were generally not serious.

The only distinct character relative to heritability was heading date. Values for this character tended to be high for all populations and methods of determination. Population 3 estimates were reduced substantially when genotype x year interactions were removed. The remaining six characters showed few trends between populations or between methods of analysis. For the yield components and yield, the values tended to be in a descending order of panicle number, seed weight, seeds per panicle, and grain yield. Panicle number was the only one of these four characters that was relatively consistent for all populations. Population differences were apparent with population 2 exhibiting highest values for most characters, followed by population 1. Population 3 was lowest in most characters especially with estimates from the regression method where negative values were obtained for yield, seed weight, and seeds per panicle. Correspondingly low estimates for yield and seed weight were found with the variance analysis.

Genetic advance estimates using heritability values from Tables VII and VIII were calculated individually for the three single experiments, the variance analysis of combined data from the three environments, and the standard unit regressions (Table IX). These estimates reported on a mean basis were selected to represent differences in experimental units and methods of calculating heritability. The relationships of expected gain for characters and populations showed the same general trend seen in the heritability estimates. One significant deviation was the difference in magnitude in the estimates for heading date as compared to the other characters. For example, expected gain for panicle number was greater than heading date. This resulted from a considerably

TABLE IX
 EXPECTED GENETIC ADVANCE IN PERCENT OF THE MEAN USING DIFFERENT HERITABILITY ESTIMATES,
 AND ACTUAL GAIN FROM A SIMULATED SELECTION EXPERIMENT IN 1965

Character	Population	Method of Estimation					SU Regr. 1965, Loc 1 1966, Loc 2	Actual Gain 1966 Loc 1 & 2
		1965	1966	Variance		Combined ^a Data		
		Loc 1	Loc 1	1966 Loc 2	3-Test Average			
Date Headed	1	9	14	11	11	10	7	10
	2	11	11	12	11	11	10	11
	3	12	10	11	11	8	6	6
Straw Strength	1	30	11	6	16	5	1	12
	2	32	--	30	31	21 ^b	17	16 ^c
	3	34	--	7	21	10 ^b	3	5 ^c
Plant Height	1	3	6	3	5	3	2	3
	2	10	5	--	8	7 ^b	7	4 ^c
	3	4	5	--	5	3 ^b	3	6 ^c
Panicle Number	1	9	14	11	11	5	7	4
	2	16	15	16	16	17	14	13
	3	12	18	12	14	13	9	11
Seeds/Panicle	1	9	19	9	12	6	1	2
	2	27	12	12	17	12	10	8
	3	16	23	22	20	10	0	1
Seed Weight	1	8	5	8	7	4	4	2
	2	9	10	10	10	7	6	10
	3	14	12	9	12	2	0	3
Grain Yield	1	9	19	1	10	7	8	3
	2	21	12	12	15	11	6	7
	3	7	8	17	11	3	0	0

^aCombined analysis from three environments (Loc 1, 1965, and Loc 1 and 2, 1966).

^bEstimates from two environments only.

^cEstimates from one location only

greater phenotypic variation in panicle number than in heading date for the three populations. Since phenotypic standard deviation is a component of the genetic advance formula, the size of these values is important.

In order to compare expected genetic advance with actual genetic gain, a simulated selection experiment was carried out on the 1965 F_3 test. Actual gains in percent of the mean for the selected ten percent of the lines grown in two locations in 1966 are given in the last column of Table IX. Predicted and actual gains were similar for heading date and panicle number in populations 1 and 2, height in populations 1 and 3, and seed weight in population 2. Otherwise the predicted gains were overestimated from two to several times.

Discussion

The concept of heritability is quite simple as it relates the amount of total variability in an individual or population of individuals that is caused by heredity. However, the application of the statistic to plant breeding is not so simple since restrictions are often placed on the definition. For example, heritability statements may be qualified with narrow and broad sense terms or with different experimental units used to obtain the measurement. Both of these restrictions affect the magnitude and meaning of the estimate.

Heritability from the variance method reported in this study would by definition be in the broad sense as no attempt was made to partition out the additive genetic variance. The significance of broad and narrow sense values are not clearly understood in most self-pollinated crops since reliable estimates of the components of genetic variance are not

available. Jones and Frey (25) and Petr and Frey (36) reported that dominance was important in F_2 generation oats for some characters including yield. They suggested that broad and narrow sense heritability estimates would be quite different in the F_2 generation but the difference would dissipate in later generations. The validity of these estimates, like most estimates in self-pollinated crops, is questioned because of inadequate designs to account for effects of epistasis, linkage, genotype x environment interactions, and in the case of oats hexaploid inheritance on the methods employed for estimation. Some workers (29,38) suggest that genetic variance in self-pollinated species is primarily of an additive nature and, consequently, the difference in broad and narrow sense values is rather academic. Even if dominance is important in F_1 and F_2 generations, it rapidly dissipates in the selfing process to only $1/4$, $1/16$, and $1/64$ of the original in the F_3 , F_4 , and F_5 generations, respectively, and may be of little consequence. It was further suggested by Sprague (38) that narrow sense estimates in practice may be of limited significance because of the high standard errors associated with variance estimates.

The parent-progeny regression technique is generally considered to yield heritability estimates in the narrow sense. Since estimates in this study were lower when this method was used, one might be tempted to speculate that the difference resulted from non-additive gene action. However, too much emphasis should not be placed on this reasoning since other causes could be responsible for these differences. For example, replication effects were not removed from the regression computations but were excluded from the variance analysis estimates. Also the selection unit for the regression heritabilities was the F_3 test while that

of the variance heritabilities was the F_3 and F_4 tests. More information is needed relative to the significance of non-additive genetic variance in self-pollinated crops since their effects have implications concerning early generation selection.

Hanson (18) discussed the possibility of standardizing the experimental and selection units for a crop so that heritability might have a consistent definition for a crop and a character of a specific crop. He suggested that an acceptable standard selection unit in soybeans would consist of measurements on a plot basis with two replications within two environments. The selection unit designed for the present study in winter oats was plot means with two replications within two years and at two locations each year. This experimental unit seemed to be a "workable" unit for oat breeders for early generation selection if small plots are used. However, one location was lost in 1965 and the selection unit reverted to two and three location-year environments. Heritability estimates presented in Table VIII suggest that any two of the environments that had a common year or location would not suffice as a selection unit since genotype x year interactions were important for certain characters and populations while genotype x location interactions were important for different characters and populations. It is doubtful if two or three environments could adequately sample the diverse environmental conditions in Oklahoma. If genotype x year x location interaction is a primary factor in overestimating genetic variance, and consequently heritability as was suggested in Chapter III, more years and locations are necessary in order to reduce this interaction effect. However, it should be pointed out in this connection that the best possible estimate is not necessarily the goal of the breeder since he is usually limited by

economic factors as to the number of environments he can sample.

It is interesting to note that heritability estimates by the variance method for single environments and the three combined environments were quite similar in many instances. One might argue that the difference in heritabilities for these two different selection units were not great enough to justify the additional environments. However, the fact that the two estimates are of a similar magnitude should not suggest that they measure the same thing; in fact, only on rare occasions would they be expected to do so. Progeny variance from a single test (Table IV) contains interaction variances in addition to genetic variance, the variance referred to in the definition of heritability, whereas progeny variance obtained from means of genotypes evaluated over two or more locations and years has an estimate of the interaction variances removed from it. Therefore, the data in the first case do not provide an estimate of heritability according to its definition but rather an estimate of the ratio of genetic variance plus interaction variance to phenotypic variance. Because the estimate of progeny variance is expected to be higher in single tests, it stands to reason that heritability estimates would be proportionally higher. However, this is not necessarily the case as can be shown for seeds per panicle in population 2. The genetic variance estimate was reduced about 50% from a single test to the combination of three tests, whereas heritability changed very little. This relationship occurs because phenotypic variance is also reduced when mean variances are measured over several environments. The cause of this reduction should become apparent when the derivation of phenotypic variance $\sigma_{ph}^2 = \sigma_p^2 + \frac{\sigma_i^2}{n} + \frac{\sigma_e^2}{rn}$ is considered where the estimate is on a mean basis rather than a plot basis. Unless σ_p^2 is very minor in

relation to the other variance components, the change in heritability would not be expected to be great.

Indications from this study that heading date is the easiest character of the seven under consideration to select for are in agreement with previous reports (25,35,36). High heritability is generally expected in characters having rather simple inheritance as is the case for maturity. Stability in this character has significance in that the breeder can select for any maturity range in a population and be confident in obtaining his expectations. In addition, the results from the selection experiment show that evaluation and/or selection can be effectively performed in a single field trial since for this character the phenotype is a good indicator of the genotype.

Data for plant height and straw strength were not recorded for all tests in populations 2 and 3; therefore, some of the effects of genotype x environment interaction were lacking. It appeared from the results available that plant height might respond at a low-to-moderate rate from selection. One of the factors that was responsible for these low response predictions was the small amount of variability in the populations. This in turn probably resulted from the narrow range for height between the parents of the three crosses. Straw strength heritability and genetic advance estimates were not encouraging except for population 2. The results of Hess and Shands (19) were much more promising in spring oats as their values were higher and more consistent for snap scores than for actual lodging values. Since the snap test is a subjective rating of straw strength, it is likely that additional human errors in classification affected the estimates. In addition, it is known that straw strength is very sensitive to environmental stresses that often

occur sometime during the spring. More work is needed for evaluating the potential of the snap test as a method of selecting for straw strength; differential lodging does not occur with regularity and when lodging occurs evaluation in single row plots is difficult.

Yield is the character of major economic importance and therefore was of particular interest in this study. It is generally recognized that yield is quite variable and usually less heritable than other characters. Results from this study relate the erratic nature of yield estimates from one selection unit to another and from one procedure to another which suggests that testing techniques need to be refined. Coefficients of variability of about 17% were found which is usually considered too high for yield determination. In fact, Burton (2) reported that eight percent is too large since 21 replications would be required for a yield of five percent to be considered significant at the five percent level of probability. It has been suggested that larger plot size and/or more replications are required for precise measurements of yield.

Despite the inconsistencies mentioned above, selection from populations 1 and 2 for yield appear promising. By accepting the combined variance analysis of three environments as a good estimate, one would expect to improve the mean of the population from 7 and 11 % by selecting the superior 10% of the lines in the population. These expectations, if realized, would exceed the yield of the best parent in the two crosses by five to eight percent. This is particularly encouraging for at least three reasons. First, the chance of recovering a line in the selected group that exceeds the mean of this group would appear very likely. Second, another cycle of selection can be initiated by selecting

within lines of the selected group. Since the lines were F_2 derived, one would expect a considerable amount of genetic variability to persist. Third, the superior lines can be intercrossed in different combinations and a new cycle begun with the hope of accumulating more favorable genes into a single genotype. This system of improvement was suggested by Palmer (34) in a discussion of progressive improvement in self-pollinated crops and would seem to have considerable merit.

Oat breeders are interested in predictive values of yield components because of their potential utility in selecting indirectly for yield if associations with yield are strong enough to permit the use of this scheme. Heritability and genetic advance estimates from the variance analysis indicate that progress from selecting the three yield components would be similar to that of yield. These results are not in agreement with those in earlier reports (8,9). However, if the more conservative estimates of the regression method are considered, panicle number and seeds per panicle in two populations and seed weight in one population yielded higher selective values than yield. Over all populations and methods of estimations, panicle number gave the highest and most consistent results of the yield components and yield. Because the character did not appear to be as sensitive to environmental change, panicle number deserves consideration as an indicator for yield.

Data from this investigation revealed that genetic populations differed with respect to their genetic parameter estimates. Therefore, inferences from single population data to all genetic material should be made with caution. Additional population studies should be made to determine if the results from these populations are representative of the genetic stocks used in this region. If populations differ as much

as these and inferences cannot be made to the species in general, the breeder would be compelled to study every population individually to determine the most efficient breeding procedures. Obviously, this would not be practical in a plant breeding program.

Summary and Conclusions

Estimates of heritability and genetic advance were obtained for seven quantitative characters of three oat crosses. Selection units consisted of single tests (F_3 lines in 1965 and F_4 lines at two locations in 1966) and various combinations of the three single tests. Components of variance and regression analyses were used to estimate heritability and these estimates were used to arrive at expected genetic advance.

Standard unit heritability estimates were consistently lower than variance heritabilities under similar test conditions. It could not be determined from this study if these differences were the result of bias from non-additive genetic variances.

It was suggested that a selection unit of measurements on line means in two replications in at least two years and two locations would be desirable for early generation selection experiments in winter oats. Fewer environments seemed inadequate for precise estimates because of the normally diverse environmental conditions in this area.

Heritability estimates from single experiments were generally high but biased upward by genotype x environment interactions. Heading date was the most stable character studied and yielded the highest and most consistent values for all tests. Panicle number was affected by interaction variances but produced the highest and most consistent heritabil-

ities next to heading date. Most of the characters, excluding heading date, were variable between populations and between methods of estimation. There appeared to be little difference in yield and yield components in magnitude of heritability by the variance method. However, with the standard unit method, panicle number and seed weight for two populations and seeds per panicle for one population were much higher than yield estimates.

In a simulated selection experiment in the 1965 test, expected genetic advance and actual gain in the two tests in 1966 were similar for heading date and panicle number in two populations and seed weight in one population. All other estimates of expected gain were inflated considerably.

Populations differed with respect to their potential for improvement. Genetic improvement should be much easier to accomplish in population 2, closely followed by population 1, where yield improvements superior to the high parent would be expected. Population 3 did not appear to merit additional work. Because of population differences it appeared that caution should be practiced in making inferences from one genetic population to another.

CHAPTER V

GENOTYPIC AND PHENOTYPIC CORRELATIONS

The plant breeder is not only interested in variability of populations but also in the relationship of characters. These relationships may be useful in planning the breeding programs by suggesting the most efficient procedures to employ. Not only do correlations provide basic information about the species with which a breeder works, but they also provide indications on the difficulties of combining certain characters and whether certain unimportant characters may be helpful in selecting for other important characters.

Correlation coefficients have been used for some time to measure the relationship of various plant characters. However, few of these studies in oats have dealt with segregating populations. Garber and Quisenberry (14) in 1948 reported negative correlations (about $-.30$) between heading date and number of culms in an oat cross. Frey (10) concluded that although seed weight and yield were positively correlated in six crosses of oats, in general, the addition of seed weight as a selection criterion decreased the gain in yield.

Burton (4) suggested the use of genotypic correlations in studying associations in plant characters. While correlation coefficients show the relationship between two or more variables, they do not show how much of the measured relationship is heritable in segregating generations.

High genotypic correlations among 15 F_2 populations of oats for plant height with heading date, spikelets per plant, and yield were reported by Petr and Frey (36). Grain yield was most closely associated with plant height, number of spikelets per panicle, and number of panicles per plant. The authors also reported little relationship between yield and heading date. Similar associations for height with yield and heading date, and heading date with yield were found by Pawlisch and Shands (35).

Wallace et al. (39) used phenotypic and genotypic correlations to study relationships of characters in the F_3 and F_4 generations of an oat cross. Yield was highly associated with height, number of seed per plant, and number of seed per panicle. Number of culms per plant and weight per seed generally gave low genotypic and phenotypic correlations with other characters studied. Plant height yielded high positive values with number of seed per plant and number of seed per panicle. For the most part, phenotypic and genotypic correlations for any pair of traits seemed to be of comparable magnitude. The authors found no indication that a selection index based on characters studied would have enough advantage over selection only on yield to be of practical significance.

Associations of straw strength measurements in oats have been studied by various workers. High associations have been shown for the snap test and lodging percent, cL_r and lodging percent, and snap test and cL_r tests (15,16,19,33). Frey and Norden (13) also reported a highly significant negative association between cL_r and height while Hess and Shands (19) found high negative correlations between snap test scores and height in all crosses except those involving one particular parent.

The objective of this study was to determine the association of seven characters in three populations of winter oats with the use of

phenotypic and genotypic correlations and to consider their implications to plant breeding.

Experimental Results

Correlations for the seven characters of three winter oat crosses for each of three test sites are shown in Table X. In general, genotypic and phenotypic correlations agreed in sign and magnitude. Correlations between test sites were not consistent which indicates the differential response of characters to different macro-environments. Likewise, populations responded differently to the individual environments which might be expected where maturity ranges are different between populations.

Table XI presents genotypic and phenotypic correlations from data that was combined for the three environments in 1965 and 1966. Several genotypic correlations were very large in comparison to phenotypic values and occasionally exceeded 1.0. Phenotypic values of characters from different populations agreed well but genotypic values for several associations were quite different. The significance of these differences is difficult to evaluate since an acceptable means of testing genotypic correlations has not been developed.

Largest positive correlations from the combined data resulted from seeds per panicle and yield while the highest negative values resulted from seeds per panicle and panicle number, panicle number and seed weight and heading date and yield (populations 1 and 3).

Since correlations between heading date and yield, and seeds per panicle and yield were generally favorable to the breeder, estimates of expected progress in improving yield by selecting for heading date and

TABLE X

GENOTYPIC AND PHENOTYPIC CORRELATIONS FROM INDIVIDUAL FIELD TRIALS FOR SEVEN CHARACTERS IN
THREE OAT CROSSES (GENOTYPIC AND PHENOTYPIC CORRELATIONS ON
RIGHT AND LEFT SIDE OF DIAGONAL, RESPECTIVELY)

Character	Population	Test ^a	Character																										
			Heading Date			Straw Strength			Plant Height			Panicle Number			Seeds/Panicle			Seed Weight			Grain Yield								
			1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3						
Heading Date	1					-.56	-.20	.34	.74	-.07	.39	-.61	.44	-.51	-.30	-.33	.75	.05	.69	-.53	-.81	.19	-.97						
	2					-.53	-----	.09	.48	.33	-----	.03	.26	-.19	.07	-.52	-.03	-.11	.43	-.21	.04	-.07	-.48						
	3					-.69	-----	-.03	.49	.81	-----	-.02	.44	-.03	.46	-.67	-.87	-.64	.42	.39	-.15	-.29	-.74						
Straw Strength	1		-.48	-.38	.17				-.04	.01	.60	-.55	-.09	-.16	.94	.28	.37	.25	-.17	.04	.51	-.54	.28						
	2		-.46	-----	.07				-.09	-----	-----	-.60	-----	-.05	.26	-----	.04	.44	-----	-.03	.02	-----	-.02						
	3		-.63	-----	-.07				.00	-----	-----	-.23	-----	-.54	-.01	-----	.20	.31	-----	-.43	.20	-----	-.40						
Plant Height	1		.46	-.14	.26	-.03	-.02	.33				-.61	-.19	-.35	-.11	.89	.53	.03	.19	.02	-.61	.89	.53						
	2		.40	.20	-----	-.22	-----	-----				-.14	-.18	-----	.60	.19	-----	.17	.02	-----	.61	.19	-----						
	3		.36	.57	-----	-.01	-----	-----				-.49	-.03	-----	.77	-.34	-----	-.21	.41	-----	.35	-.34	-----						
Panicle Number	1		-.38	.37	-.38	-.16	-.54	-.13	-.22	-.19	-.17				-.78	-.45	-.92	-.52	.17	.10	.15	.32	.14						
	2		.02	.24	-.17	-.38	-----	-.02	-.21	-.16	-----				-.35	-.22	-.59	-.52	-.33	-.39	.19	.68	.29						
	3		-.03	.38	.02	-.06	-----	-.42	-.38	-.01	-----				-.69	-.79	-.19	.06	.25	-.07	.31	.15	.38						
Seeds/Panicle	1		-.24	-.31	.47	.55	.12	.22	.20	.71	.52	-.36	-.49	-.62				.14	-.30	-.28	.40	.64	-.75						
	2		-.03	-.38	-.03	.23	-----	.02	.56	.36	-----	-.31	-.41	-.50				-.13	-.79	-.03	.79	.51	.37						
	3		.30	-.62	-.75	-.01	-----	.04	.62	-.08	-----	-.54	-.70	-.21				-.60	-.65	-.47	.12	.36	.74						
Seed Weight	1		.01	.45	-.44	.10	-.09	.01	.21	.07	.23	-.16	.15	.02	.20	-.33	-.25				.71	.14	1.29						
	2		-.10	.35	-.19	.29	-----	-.13	.09	.08	-----	-.31	-.10	-.25	-.11	-.47	-.16				-.12	-.46	.28						
	3		-.54	.35	.24	.30	-----	-.27	-.07	.32	-----	-.04	.18	.04	-.34	-.54	-.22				.33	-.19	.15						
Grain Yield	1		-.45	.14	-.22	.29	-.32	.06	.09	.71	.52	.48	.33	.30	.52	.57	.26	.48	.16	.48									
	2		.00	-.07	-.39	.07	-----	-.06	.44	.36	-----	.29	.39	.67	.75	.58	.41	.04	-.16	.29									
	3		-.13	-.27	-.55	.18	-----	-.35	.29	-.08	-----	.32	.16	.38	.37	.46	.70	.35	-.04	.23									

^aField test 1, 2, and 3 are 1965 Loc 1, 1966 Loc 1, and 1966 Loc 2, respectively.

TABLE XI
 GENOTYPIC AND PHENOTYPIC CORRELATIONS FOR SEVEN CHARACTERS IN THREE OAT
 CROSSES FROM COMBINED DATA OF THREE ENVIRONMENTS (GENOTYPIC AND
 PHENOTYPIC CORRELATIONS ON RIGHT AND LEFT SIDE OF
 DIAGONAL, RESPECTIVELY)

Character	Population	Character						
		Heading Date	Straw Strength	Plant Height	Panicle Number	Seeds/Panicle	Seed weight	Grain Yield
Heading Date	1		-.56	.42	-.63	.18	-.11	-.51
	2		----	----	.07	-.12	-.03	-.19
	3		----	----	.01	-.46	-.28	-.99
Straw Strength	1	-.29		.48	-.17	.45	.69	.55
Plant Height	1	.24	.17		-.11	.83	.72	.99
Panicle Number	1	-.27	-.19	-.21		-.44	-1.55	-.49
	2	.05	----	----		-.50	-.60	.31
	3	.05	----	----		-.75	-.82	-.08
Seeds/Panicle	1	.07	.32	.60	-.48		1.05	1.15
	2	-.31	----	----	-.46		.14	.59
	3	-.35	----	----	-.55		.33	.91
Seed weight	1	-.06	.19	.34	-.43	.25		.43
	2	-.03	----	----	-.74	-.08		-.05
	3	-.07	----	----	-.17	-.23		-1.01
Grain Yield	1	-.28	.19	.53	.17	.64	.43	
	2	-.17	----	----	.31	.58	.06	
	3	-.42	----	----	.23	.56	.07	

seeds per panicle were calculated. The estimates expressed in percentage of the progress expected from selecting yield itself for populations 1, 2, and 3, respectively, were as follows: heading date -- 75, 22, and 235; seeds per panicle -- 114, 58, and 145. High estimates of efficiency in population 3 resulted because of the low heritability of yield and relatively high values for heading date and seeds per panicle.

Discussion

It is apparent from data reported in Table X that character associations are influenced greatly by environmental conditions. For example, high negative correlations were found between heading date and yield for population 1 in two environments, whereas, a positive association was found in the third. This and other similar examples relate to a breeder how hazardous it may be to place confidence in character associations from single experiments.

Genotypic correlation coefficients provide a measure of the genotypic associations between characters. When the coefficients are obtained from data collected over several environments, the bias due to genotype x environment interactions is reduced. Therefore, if the environments are representative of the area, these correlations give a truer estimate of genetic associations which may aid in breeding programs.

Genetic correlations greater than 1.0 might cause one to question the value of this statistic. To date, not enough is known about these genetic estimates to arrive at a procedure to test their significance. According to Burton (3), R. F. Comstock, who proposed the use of these correlations, suggested that more experience is needed before a satis-

factory error term for genotypic correlations can be found. It can be noted that where unrealistic genotypic values occurred or where large discrepancies between phenotypic and genotypic values were observed the magnitude of genetic variance of at least one of the characters involved was usually very low. This suggests that genotypic correlations have limited utility where genetic variance estimates are small.

The correlations between characters normally considered in oat breeding programs indicate that character associations are generally favorable to the breeder (Table XI). In the past, breeding trends have been aimed at developing oat varieties possessing high grain yield, early maturity, lodging resistance, short plant height, and large kernels. The only character which might be difficult to combine with other desirable characters would be short plant type. Several workers (35,36, 39) have also reported high positive associations between height and yield, and height and maturity. If these relationships are general in oats the breeder must be cautious in screening early generation stocks for short types since this would tend to reduce the probabilities of finding high yielding genotypes.

For years breeders have measured associations between plant characters in an attempt to find characters that may be useful indicators of the important traits under consideration. The yield components have attracted much interest since it seems logical that one or more of them could be a good indicator of yield. Frey (8,9) suggested that yield components may be more effective as selection criteria since selection for yield requires larger plot size, more replications, and more years and locations of testing. Similar findings were reported by Johnson et al. (22) in soybeans. Indications from this study were that seeds

per panicle may offer some aid in selection for yield. Genetic associations were high for these characters but heritability of seeds per panicle did not appear higher than that of yield. These results indicated that selection for seeds per panicle would be more efficient than selection for yield itself in populations 1 and 3 but only about one-half as efficient in population 2. If seeds per panicle can be measured with more precision than yield from small plots and with less genotype x environment interaction effects, this character may have utility as a yield indicator.

Heading date in this study fulfilled the requirement for an acceptable indicator for yield. The character is highly heritable and was negatively correlated with yield. Should this relationship prove general for oats in this region, populations could be screened at one location in one year for days to heading and then evaluated in more extensive tests. This procedure would have the advantage of utilizing much larger populations. It should be emphasized that these results represent estimates from a very small sample of environments and may not be repeatable under a different set of conditions. The association between heading date and yield has generally been reported low or highly variable while that of seeds per panicle has generally been established as high and positive (35,36,39). Therefore, implications about heading date and possibly seeds per panicles should be treated with caution until similar studies in this area of production are carried out to confirm the results of this work.

Summary and Conclusions

Genotypic and phenotypic correlations were obtained for seven char-

acters of three winter oat crosses grown in three field trials. The following results were obtained:

1. Correlations from single experiments should be used with caution since characters exhibited differential responses to different environments.

2. Genotypic and phenotypic correlations from single experiments were of similar sign and magnitude which suggested that genotypic correlations may add little information under these conditions.

3. Genotypic correlations from data involving several environments differ from phenotypic correlations when genotype x environmental interactions are important. Unknown sources of bias and/or low genetic variances caused genotypic values to be greater than 1.0.

4. Yield was most closely correlated with seeds per panicle (+), plant height (+), and heading date (-). Coefficients of yield with other characters were lower and inconsistent. Panicle number showed generally high negative values with seed weight and seeds per panicle. Plant height and date headed were positively correlated. Phenotypic correlations were generally similar between populations for the character but genotypic values were variable for some comparisons.

5. Genetic barriers appeared to be non-existent for the combination of desirable characteristics except where plant height was involved. Consequently, caution should be practiced in discarding early generation lines on the basis of plant height.

6. Indications are that seeds per panicle and heading date may be efficient indicators of yield. However, additional studies are needed to support this possibility.

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