AN ANALYSIS OF THE COMPONENTS OF YIELD IN 18 OAT CROSSES

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By

VIRGIL D. LUEDDERS

AN ABSTRACT

Submitted to the College of Agriculture of Michigan State
University of Agriculture and Applied Science
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ABSTRACT

VIRGIL LUEDDERS

The yields of oat parents and progenies of crosses were analyzed by the yield components method. The results obtained were similar to those of barley. The 3 components of yield, heads per plant (X), seeds per head (Y), and kernel weight (Z), were found to be affected by different gene systems.

Due to homeostasis, the variance of the F_2 was less than that of the mid-parent in several instances. The higher yielding crosses can be predicted utilizing the yield components of the mid-parents, thereby eliminating the necessity for making all of the possible crosses.

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INTRODUCTION

Yield is a quantitative character and is the result of the actions and interactions of many genes throughout the life of the plant. Since yield is the end product of this complex process, it is more meaningful to analyse it by resolving it into its simpler parts, the components of yield.

In the case of small grains and specifically oats, these components of yield are the number of heads per plant (X), the number of seeds per head (Y), and the average weight per kernel (Z). The product of these three components is the total yield per plant ($X \cdot Y \cdot Z = W$). This product may be represented geometrically as the volume of a rectangular parallelepiped with the edges X, Y, and Z. If the edges of this figure are not correlated, then different gene systems are affecting them and yield is an artifact.

The volume of the parallelepiped, or yield, can be increased most easily and rapidly by increasing the shortest edge. Therefore, it should be possible to get the greatest increase in the yield of a variety by crossing so as to increase the smallest component (lengthen the shortest edge of the parallelepiped), e.g., increase the number of kernels per head in a variety that has a large number of tillers and high kernel weight so as to get the highest or maximum yield possible.

If it is possible to reduce the yield-depressing effect of the limiting factor or component of yield, then it should be feasible to

choose parents (2 or more) that have high values for one or more of these components and by the appropriate breeding techniques incorporate them into one line which would have distinctly superior yield capabilities. The use of components should make the prediction of progeny expectations more accurate and reliable, and help to change the status of plant breeding from an art to that of an exact science.

Oats and barley are both self-fertilized and have a primary chromosome number of $N = 7$, but the cultivated oat is a hexaploid whereas the cultivated barley is a diploid. Hence, one might expect cultivated oats to have gene systems built up in evolutionary time which take advantage of the hexaploid condition. Intra-allelic interaction can exist in true breeding hexaploids if autosyndesis occurs, as it does in oats. Thus heterosis could be due to both inter- and intra-allelic interactions. The fraction of heterotic effects due to the interaction of additive by additive effects and the intra-allelic interaction, due to gene action between homologous chromosomes of the three genomes, is potentially fixable in the true-breeding form. If the latter is of great importance, it should interfere with the prediction of progeny values from mid-parental values.

The analyses and discussion in this paper are based on the following statements: the yield components method of analysis indicates why one yield might be higher than another; the components of yield are assumed to be independent; the same types of analyses can be used on both oats and barley, with the exception that if intra-allelic interaction is important it will interfere with yield prediction;

it is possible to select parents which will give high-yielding progeny when crossed, and these results are assumed to be predictable; and the F_2 is more variable than the parents.

REVIEW OF LITERATURE

The concept of analysing the components of yield is not new but has not been used extensively. Frankel (3) found that the main increase in yield is achieved by overcoming the limiting factors whose effects can be distinguished with a fair degree of certainty, rather than by assembling productivity genes, although this process may accompany the former process. As the components of yield in wheat, he used: ears per plant, grains per ear, and weight of grain; these could conceivably be further resolved but this resolution would reach a practicable end point.

In a study of factors affecting the yield of barley, Kohls (12) pointed out that yield was positively correlated with the number of kernels per plant, number of heads per plant and weight per kernel. This is not at all surprising since these are the components of yield.

The yield components of cotton; bolls per plant, seed cotton per boll, seeds per boll, lint per seed, etc., have been analysed by Hutchinson (10), who found that one is increased at the expense of the others. Manning (18) got yield increases utilizing only the 3 major components of yield of cotton, namely, bolls per plant, seeds per boll, and lint per seed.

Dewey and Lu (2) analysed the components of crested wheatgrass seed production, using as the components: seed size, spikelets per spike, fertility or seeds per spikelet and plant size. They neglected to take one important measurement, namely spikes per plant. Fertility

and plant size were the most important components, whereas the seed size varied less and therefore caused less change in yield than did the other components. This relationship of seed size to yield is inherent in the concept of yield.

Immer (11) used heads per plant, seeds per head and weight per seed to measure the extent of heterosis in a number of barley crosses and their progenies.

Grafius (5) used a geometrical interpretation to analyse the components of yield in oats, uniquely demonstrating the relationship with the model of a rectangular parallelepiped, with the number of panicles per unit area (X), the average number of kernels per panicle (Y), and the average kernel weight (Z) as the three edges and the total yield (W) as the volume. This approach was also used in his analysis of barley yields (6), except that in this case X is the number of heads per plant. Yield is shown to be an artifact. The F_2 variance is separated into its environmental and genetic portions, with the genetic variance further partitioned into additive, non-additive and interaction or epistatic effects.

By means of an elegant regression model Whitehouse <u>et al</u> (21) drew conclusions similar to those of Grafius concerning the components of yield, but failed to designate yield as an artifact.

MATERIALS AND METHODS

The material consisted of harvested seeds in envelopes, with the number of heads per plant and the cross and plant number recorded on the envelope. These included the 20 parents (20 different spring oat varieties), the F_2 of 18 crosses, and the F_3 of 3 of these crosses. The crosses were Ajax by 7 of these varieties and Craig by the other 11 varieties.

The 18 crosses were made by Grafius, who also planted and harvested the F_2, the F_3, and all of the parental varieties in 1956. These parents and progeny were space-planted 12 inches apart in the row with 12 inches between the rows in a randomized block experiment. Two replications were used. An attempt was made to have 19 plants per plot but in most cases there were missing plants which were replaced with filler plants. The actual numbers of plants harvested and subsequently analyzed are reported in Table 1.

RESULTS

The data for the parents, F_2's, and F_3's are given in Table 1. The average F_2 values exceed the parental means for X, Y, Z and naturally also for W. The average F_3 value for X is significantly less, but the Y and Z values are not significantly different from the average of the F_2 means for the same 3 crosses. The comparison of these values indicates dominance for X and lack of or at least a low order of dominance for Y and Z.

Table 1

Heads Per Plant (X), Seeds Per Head (Y), Kernel Weights (Z), and Yields Per Plant (W), for the Oat Parents and Progeny

Parents	No. of Plants	X	Y	Z	W
		No.	No.	Centigrams	Grams
Cherokee	75	10.688	40.378	2.721	11.609
Ajax	126	13.984	64.140	2.464	21.800
Clinton	19	11.263	53.032	2.411	15.042
Clintland	43	8.814	52.828	2.519	12.323
Mo-0-205	33	11.546	53.997	2.203	12.397
Clintafe	20	11.650	61.410	2.010	15.120
Sauk	57	10.035	52.237	2.346	12.462
Clarion	52	9.096	50.346	2.388	11.635
Craig	137	9.380	43.820	2.469	10.110
Shelby	99	14.515	42.054	2.447	14.929
Victory	36	14.000	46.333	2.486	16.047
Beaver	28	11.607	60.846	2.678	19.048
Garry	38	9.263	48.587	2.440	10.963
Vanguard	47	16.636	45.613	2.291	18.628
Abegweit	15	14.467	56.046	2.687	21.867
Rodney	25	11.720	47.812	2.796	13.576
Erban	36	14.416	48.778	2.617	18.572
Jackson	24	10.750	54.779	2.625	15.363
Simcoe	23	10.393	56.744	2.691	16.861
Shefford	37	15.162	36.267	2.960	16.646
Average of All Parents		11.969	50.752	2.512	15.250
LSD 5% Between Parents		2.522	7.567	.238	3.982

Table 1 (continued)

F_2's	No. of Plants	X No.	Y No.	Z Centi-grams	W Grams
Ajax X Cherokee	174	12.977	48.384	2.523	16.221
Ajax X Clinton	67	11.298	59.880	2.406	16.672
Ajax X Mo-0-205	86	13.430	63.498	2.415	20.955
Ajax X Clintafe	117	13.684	68.609*	2.314	21.384
Ajax X Clintland	118	11.034	63.432	2.534*	18.039
Ajax X Sauk	157	11.784	61.482	2.393	17.515
Ajax X Clarion	156	11.654	60.263	2.490*	17.569
Craig X Shelby	132	12.712	44.439*	2.704*	15.151*
Craig X Victory	79	13.127	50.276*	2.438	16.042
Craig X Beaver	69	11.899*	53.901	2.726*	17.238
Craig X Garry	58	10.483*	54.633*	2.591*	15.272*
Craig X Vanguard	89	11.989	44.904	2.339	13.569
Craig X Abegweit	23	12.347	47.813	2.778*	16.517
Craig X Rodney	101	10.614	50.308*	2.678	14.874*
Craig X Erban	28	12.536	47.757	2.664*	16.197
Craig X Jackson	72	10.875*	56.885*	2.650*	16.245*
Craig X Simcoe	109	12.982*	59.720*	2.722*	21.016*
Craig X Shefford	98	12.051	45.754*	2.832	16.063
Average of All F_2's		12.082	54.552	2.567	17.030
LSD 5% Between F_2's		1.936	5.758	.039	3.032
F_3's					
Ajax X Cherokee	878	11.478	52.421	2.608	15.932
Ajax X Clintafe	373	12.724	64.915*	2.130	17.580
Craig X Garry	202	10.129*	55.632*	2.424	14.086*
Average of All F_3's		11.444	57.656	2.387	15.866
LSD 5% Between F_3's		1.065	4.892	.087	2.013
LSD 5% Between F_2 and F_3		1.105	3.778	.0467	1.820

*Indicates F_2 and F_3 values are greater than the value of the high parent; does not imply significance.

Figure 1 compares the F_2 with the mid-parent. The graphs for Y and Z are approximately linear but the graph for W does not fit a straight line. However, this is as expected since W is the product of X, Y, and Z and it is perhaps naive to expect volumes to graph as straight lines. Table 2 shows the correlation coefficients for these comparisons. The values are remarkably similar to those obtained by Grafius (6) for barley. When the barley F_1 is compared with the mid-parent: $r_x = .48$, $r_y = .88^{**}$, $r_z = .75^{**}$, and $r_w = .45$.

Table 2

Correlation Coefficients for the F_2 Means vs. Mid-Parent for Heads Per Plant, Seeds Per Head, Kernel Weights, and Total Yields Per Plant

Character Correlated	d.f.	F_2 vs. Mid-Parent
Heads per plant, X	16	.499*
Seeds per head, Y	16	.884**
Kernel weight, Z	16	.844**
Yield per plant, W	16	.525*

$^*P < .05$ $^{**}P < .01$

The correlation coefficients showing the relationship between X, Y, and Z are found in Table 3. In the parental population for the average r only X and Y are significantly correlated (positive) whereas X vs. Z and Y vs. Z show a non-significant correlation, indicating zero relationship or independence. The significant Chi square values

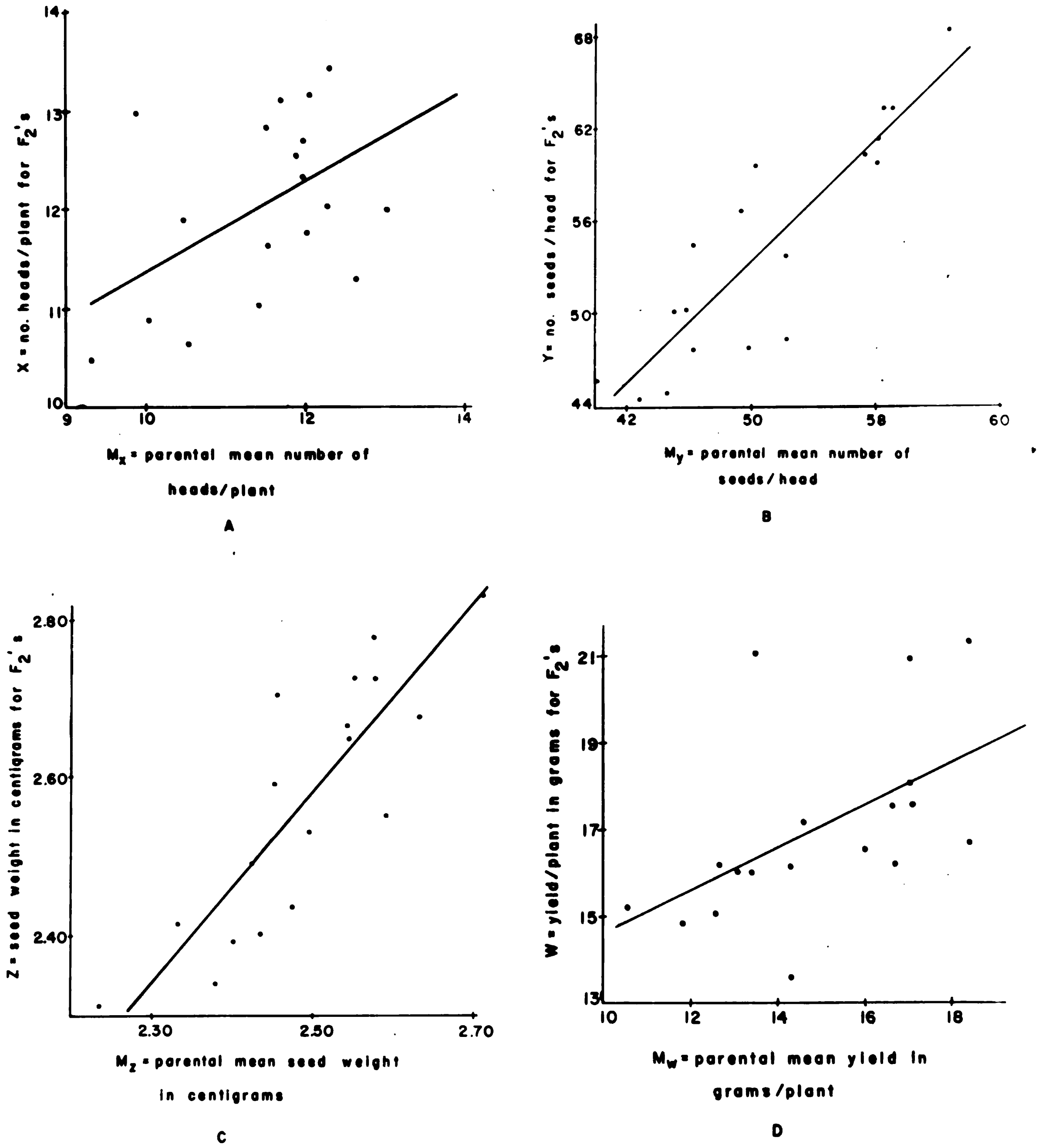

Figure 1. Graphs of F_2's on the Mid-Parents (M). A, Number of Heads Per Plant (X); B, Number of Seeds Per Head (Y); C, Average Kernel Weight in Centigrams (Z); and D, Total Yield Per Plant (W).

at the bottom of Table 3 indicate that the population of parents is not homogeneous for any of the 3 traits, X, Y, and Z. Thus the correlations may be due to either chance associations of genes or linked gene systems for the 3 components in some cases and random associations in the others. For example, if there were alleles for differential response to high and low nitrogen in all 3 gene systems, then in the coupling association one would expect to get a positive correlation coefficient; a negative correlation from the repulsion association; and a zero correlation coefficient in the case of random distribution of these factors for X, for Y, and for Z. All 3 types of correlation coefficients (positive, negative and zero) occur, although it must be admitted that significant negative values are not frequent.

An overall average correlation coefficient, while not strictly valid because of the heterogeneity of the populations, indicates that only X and Y are associated as an average condition. Even here the association is weak, although it is highly significant statistically. The fact that zero and negative as well as positive correlation coefficients occur in the population of parents indicates that there are two separate gene systems for X and Y, rather than one gene system controlling both of them. However, this does not rule out the existence of a third system, such as genes for heading date, which could possibly regulate both the X and Y systems by a triggering mechanism. For example, the early onset of shoot development could effectively control both the size of head and the number of tillers.

In the F_2 and F_3, X vs. Y again shows a small but statistically significant positive correlation and here the Y vs. Z correlation is also statistically significant and negative but it is so small that it is of little biological interest.

Table 3

Correlation Coefficients showing the Relationship of X (Heads Per Plant), Y (Seeds Per Head), and Z (Kernel Weights) for the Parents, F_2's and F_3's

Generation	d.f.	X vs. Y r	X vs. Z r	Y vs. Z r
Parents				
Cherokee	72	.121	-.024	-.319
Ajax	123	.073	.131	.106
Clinton	16	.456	-.001	-.208
Clintland	40	.251	.021	.182
Mo-0-205	30	.500*	.134	-.169
Clintafe	17	.765**	-.277	-.386
Sauk	54	.374**	-.272*	-.250
Clarion	49	.343*	-.059	.180
Craig	134	.315**	-.152	-.300**
Shelby	96	.333**	-.111	-.191
Victory	33	.148	-.262	.252
Beaver	25	.037	.031	.334
Garry	35	.060	-.036	-.134
Vanguard	44	.515**	.397**	.273
Abegweit	12	.431	-.148	-.303
Rodney	22	-.170	.000	.381
Erban	33	.043	.181	.185
Jackson	21	.132	-.261	-.214
Simcoe	20	.535*	.650**	.508*
Shefford	34	.118	.088	.239
Average r		.257**	-.050	-.036
		$\chi^2 = 37.43$	$\chi^2 = 36.01$	$\chi^2 = 50.00$
		$P < .01$	$P = .02-.01$	$P < .01$

Table 3 (continued)

Generation	d.f.	X vs. Y r	X vs. Z r	Y vs. Z r
F_2				
Ajax X Cherokee	171	.212**	.170*	-.209**
Ajax X Clinton	64	.389*	.010	-.220
Ajax X Mo-O-205	83	.204	.012	.000
Ajax X Clintafe	114	-.028	-.196	-.176
Ajax X Clintland	115	.028	-.002	.178
Ajax X Sauk	154	.291**	.025	-.009
Ajax X Clarion	153	.325**	-.261**	-.174*
Craig X Shelby	129	.089	-.066	-.333**
Craig X Victory	76	.312**	-.028	-.423**
Craig X Beaver	66	.106	-.010	-.453**
Craig X Garry	55	.416**	.165	.123
Craig X Vanguard	86	.413**	-.002	-.087
Craig X Abegweit	20	.168	-.136	-.125
Craig X Rodney	98	.352**	.259**	.057
Craig X Erban	25	.209	-.187	-.033
Craig X Jackson	69	.021	.002	-.074
Craig X Simcoe	106	.179	-.008	-.274**
Craig X Shefford	95	.502**	-.436**	-.202*
Average r		.235**	-.034	-.146**
		$\chi^2 = 42.27$	$\chi^2 = 50.00$	$\chi^2 = 49.58$
		$P < .01$	$P < .01$	$P < .01$
F_3				
Ajax X Cherokee	875	.247	-.088	-.103
Ajax X Clintafe	370	.145	.061	-.002
Craig X Garry	199	.346	.103	-.115
Average r		.236**	-.002	-.079**
		$\chi^2 = 6.27$	$\chi^2 = 10.3$	$\chi^2 = 2.95$
		P.= 05–.02	$P < .01$	P=.30–.20

*P < .05 **P < .01

The Y vs. Z negative correlation is too small to interpret biologically since it explains less than 1% of the variation. Statistical significance is possible because of the very large number of degrees of freedom. The positive correlation between tiller number and the number of kernels is difficult to explain satisfactorily and was completely unexpected. It was expected that as the number of tillers increased the number of kernels per head would decrease. This line of reasoning is supported by Labanauskas and Dungan (13), who found that the tillers declined in yield from the first one formed to the last, the main stem yielding much more than the individual tillers. However, the total yield of 5 tillers was more than twice as much as that of the principal stem.

Table 4 shows the estimates of the genetic and environmental variances for the different crosses. Some of these values for genetic variance are negative, indicating that the parents are more variable than the F_2's, but this is diametrically opposed to the genetical model. These discrepancies may have been due to chance because of small numbers or to homeostasis.

Developmental homeostasis seems to be the more likely explanation to this puzzle. On the average, the F_2 means are greater than the mid-parental means for X, Y, and Z. The variance of an F_2 is $1/2\ D + 1/4\ H + E_1$, where D is the additive genetic variance, H is the non-additive genetic variance, and E is the environmental variance; whereas the variance of the parents is entirely E or environmental.

Table 4

Estimates of Genetic and Environmental Variances Based on F_2 and Parental Plants for 18 Oat Crosses Where the Genetic Variance is equal to the Variance of the F_2—the Mean Variance of the Parents

Cross	X	Y	Z	W
Ajax X Cherokee	16.3866	183.05	.070901	47.7864
	12.8515	166.71	.052434	39.6843
	3.5351	16.34	.018467	8.1021
Ajax X Clinton	8.0137	252.62	.044750	37.7437
	23.4394	221.57	.028700	84.6464
	-15.4257	31.05	.016050	-46.9027
Ajax X Mo-0-205	12.0313	212.81	.042637	61.6114
	12.2948	204.41	.060877	45.2525
	-.2635	8.40	-.018240	16.3589
Ajax X Clintafe	24.7652	250.80	.060465	69.5397
	10.3646	269.46	.039178	45.8021
	14.4006	-18.66	.021287	23.7376
Ajax X Clintland	11.5431	199.87	.073656	45.7700
	10.6182	209.12	.036246	40.5394
	.9249	-9.25	.037410	5.2306
Ajax X Sauk	9.3090	230.46	.078714	46.4152
	10.4586	196.33	.050845	44.2029
	-1.1496	34.13	.027869	2.2123
Ajax X Clarion	11.6573	235.49	.067244	50.9990
	19.2227	214.54	.050061	59.5420
	-7.5654	20.95	.017183	-8.5430
Craig X Shelby	21.7885	186.97	.083494	52.3569
	13.7236	143.13	.038087	25.2994
	8.0649	43.84	.045407	27.0575

Table 4 (continued)

Cross	X	Y	Z	W
Craig X Victory	19.1067	228.89	.052019	57.8630
	10.9708	151.55	.062692	23.3197
	8.1359	77.34	-.010673	34.5433
Craig X Beaver	15.3881	173.18	.089267	42.3673
	7.7433	187.17	.049587	29.9330
	7.6448	-13.99	.039680	12.4343
Craig X Garry	11.6919	407.55	.048971	55.4756
	13.6503	216.92	.046504	26.6756
	-1.9584	190.63	.002467	28.8000
Craig X Vanguard	22.8249	262.67	.066033	58.0452
	28.3081	187.89	.049792	60.0623
	-5.4832	74.78	.016241	-2.0171
Craig X Abegwit	13.4795	195.63	.033464	49.9637
	10.5354	159.65	.041658	23.0662
	2.9441	35.98	-.008194	26.8975
Craig X Rodney	10.4354	308.79	.066983	44.1283
	13.7188	260.92	.060028	23.7082
	-3.2834	47.87	.006955	20.4201
Craig X Erban	18.6247	223.43	.061180	59.8652
	12.0568	143.34	.046427	29.9107
	6.5679	80.09	.014753	29.9545
Craig X Jackson	9.3591	126.21	.047450	32.0780
	14.5121	191.09	.060096	34.4556
	-5.1530	-64.88	-.012646	-2.3776

Table 4 (continued)

Cross	X	Y	Z	W
Craig X Simcoe	8.9838	235.95	.050892	52.0959
	10.8083	189.08	.060798	32.8236
	-1.8245	45.87	-.009906	19.2723
Craig X Shefford	10.7755	144.80	.086944	45.8933
	15.0968	160.00	.057901	40.1484
	-4.3213	-15.20	.029003	5.7449
Average σ^2_G	0.3217	32.516	.012950	11.1625

Hence the F_2 variance should exceed that of the parents. If the means of the F_2 were less than that of the mid-parent, then theoretically it would be possible for the variance of the mid-parent to exceed that of the F_2, since the size of the mean and of the variance is correlated. However, the F_2 means are larger than the mid-parental means, and in addition the heritabilities for X, Y, and Z are .499*, .884**, and .844**, respectively. These heritabilities are shown in Table 2, where the correlation coefficients are equal to the standard partial regression coefficients of the F_2 on the mid-parent. Heritability values of this magnitude indicate large values of D in relation to H and E. Therefore, the inescapable conclusion is that the F_2 varied less than the model predicted it would.

Adams and Shank (1), Lewis (15, 16, 17), Lerner (14), among others, have proposed that this is exactly what would be expected if the hybrids are better buffered or better canalized in their development than the homozygote. Adams and Shank found that inbred lines of corn were more variable than hybrids and also noted differences in buffering among inbreds and among hybrids at the same level of heterozygosity. Thus, though the homeostasis observed was highly related (approximately 80%) to the expected levels of heterozygosity in the hybrids, intrinsic heterozygosity was not a sufficient explanation of homeostasis in maize.

Lewis (17), working with 2 species of tomatoes and their reciprocal crosses, found that the hybrids were much more stable (lower variance of height) than the parents when grown under several combinations of light intensity and temperature. Therefore in a variable environment the heterozygote A_1A_2 seems to be more stable and superior to either A_1A_1 or A_2A_2. This apparently is true in oats as well as in corn and tomatoes.

The comparison of the means of the oat parents, the F_2, and the F_3 is given in Table 5. These include only those parents and F_2's that are represented in the F_3 and therefore, these means are not the same as those found in Table 1. The dominance relationships between the F_1, F_2, and F_3 of oats are compared to the F_1 and F_2 of barley (data from Grafius, 6). The dominance in oats was estimated from the values of the F_2, assuming that the dominance is reduced by 1/2 in each generation.

Table 5

Means of the oat F_3's Compared with Their Respective F_2's and Parents

	X	Y	Z	XYZ = W
	Number	Number	Milligrams	Grams
Parents	11.49	53.75	2.428	15.23
F_2	12.38	57.21	2.476	17.63
F_3	11.44	57.66	2.387	15.87

Table 6

The Dominance Relations of the Oat F_1, F_2, and F_3 Compared to the Barley F_1 and F_2 of Grafius (6)

	Means Expressed as Percentage of the Mid-Parent			
	X	Y	Z	XYZ = W
Barley F_1	126.25	107.82	103.50	141.00
Barley F_2	119.48	103.91	102.00	126.64
Oat F_1 (est.)	116.28	113.40	104.18	137.37
Oat F_2	108.14	106.70	102.09	117.80
Oat F_3	100.32	108.03	98.19	106.40

Both the oats and barley show dominance for X, although the degree of dominance for barley is higher than for oats. This difference could be due to sampling, or to actual response differences in the 2 crops. In barley, dominance for Y decreased by exactly 1/2 from the F_1 to the F_2, but the dominance in oats apparently increased slightly from the F_2 to the F_3, instead of decreasing to approximately 103.35 as expected. This discrepancy is probably due to sampling error. For Z, both oats and barley exhibit a very low order of or a complete lack of dominance. Thus here again oats and barley behave similarly, which is not unexpected since the components of yield seem to be affected by similar gene systems in both species.

DISCUSSION

Perhaps the most interesting finding in these analyses is the fact that the hexaploid oat and the diploid barley react in a similar manner. The correlation coefficients for X, Y, and Z for the progeny versus the mid-parents are almost identical for the two species. This indicates that the major forces of heterosis are epistatic in nature and result from the interaction of additive X additive, additive X non-additive, and non-additive X non-additive rather than dominance or overdominance. Furthermore, the hexaploid does not exhibit an intrinsic type of heterosis due to heterozygosity. The dominance values for the F_2 did not exceed 8.2% for any component, which indicates that it is mainly an additive system of gene action.

Most of the genetic variances were positive as expected but several of them were negative. These negative variances would perhaps not have been so surprising if one had been actively thinking about homeostasis at the time. Homeostasis seems to be a logical and good biological explanation or interpretation for this phenomenon, which may be more common or ubiquitous and more closely related to heterosis than is ordinarily suspected. It was suggested that these negative genetic variances may have been due to the presence of several different genotypes in the original parental varieties but since these were purelined before crossing this is probably not part of the cause.

The dominance relationships appear to be quite similar for oats and barley. The values in Table 6 are averages for the dominances

of the 3 crosses, and there were differences in the degree of dominance between the crosses. The environment and genotype interact to produce various effects and Lewis proposes that dominance is also affected, especially by temperature. Lewis (15) grew tomato plants under high and low temperatures and found that the dominance of genes affecting low flower number is almost complete in the high expression environment and absent in the low expression environment. Thus in oats and barley the different genotypes could possibly have different dominance responses (for the same trait) to the environment.

The heritabilities for X, Y, and Z are .50, .88 and .84, respectively, so that selection should be quite effective, especially for Y and Z. This selection is usually thought of as being applied to the progeny, but can also be used to choose the parents to be crossed.

The regression of the F_2 on the mid-parents shows that it is possible to predict Y and Z on the basis of the mid-parent. In the case of X, the prediction is not as precise although the regression coefficient is significant. If X, Y, and Z can be predicted, then the approximate yield can also be predicted.

If the variety means are expressed as percentages of the overall mean, then the relative magnitude of the expected yields for the various crosses can be calculated. This is done by estimating the relative values of X, Y, and Z for the mid-parents. Thus the product of $\hat{X}\cdot\hat{Y}\cdot\hat{Z}$ will be the relative magnitude of the expected yield. The

hats over the letters indicate estimated values. These are obtained by using the method of Grafius and Wiebe (8), namely, $\hat{X} = \bar{X} + \Delta Xh^2$, where $\hat{X}$ is the estimated value of X, $\bar{X}$ is the population mean for X, ΔX is the deviation from the overall mean $(\bar{X} - X)$, and h^2 is the heritability. Therefore the crosses to be actually made would be those with relatively high $\hat{X}\cdot\hat{Y}\cdot\hat{Z}$ values for the specific mid-parents. These would be expected to produce higher yielding progeny than those crosses involving the parents with a low $\hat{X}\cdot\hat{Y}\cdot\hat{Z}$ value.

The above calculations were made for the 20 parents used in this experiment, and these results compared to the F_2 can be used as evidence for the validity of the method. The estimated or expected order of the F_2 yields involving the common parent Ajax are: Clinton > Clintafe>Mo-0-205>Clintland>Sauk>Cherokee>Clarion. The actual observed order is Clintafe>Mo-0-205>Clintland>Clarion>Sauk>Clinton> Cherokee. The Clinton cross was a distinct miss but the others are in good order. No special significance is attached to the one aberrant case which could well be due to the small sample (19 plants). There were 11 crosses involving Craig as the common parent. The 5 of 11 crosses that were predicted to have the highest yield were the same 5 that did show the highest yields in the F_2, although the order is not the same. However, here the order may not be important because only one of the 5 values is significantly different from the rest and it ranked first instead of fourth as expected.

Thus it is possible to eliminate those crosses which will not result in high yielding progeny and the breeder can concentrate his

efforts to crossing only those parents which have a higher probability of producing high yielding progeny. Since the heritability for the number of heads is lower, selection for X may not be as successful as that for Y and Z.

Frey (4) agrees that yield component analyses can be used to select parental combinations and to predict high yielding segregates, however he does not give any method for selection or prediction. Fadrhons (9) found that the most productive forms of small grains were derived from crosses of those with good tillering capacity and many grains per ear by those with many grains per ear and high 1000-grain weight.

Whitehouse _et_ _al_. (21) are skeptical about this, and believe that attempts to raise yield by combining large grains and numerous grains per spikelet would very likely reach a biological limit so that some other character, perhaps ear number, would be reduced. Because of this limitation there is very little prospect of discerning which pairs of varieties will combine advantageously without actually making the crosses. However the progeny do outyield the parents, even the high parents in some cases, so that if some biological limit does exist, it apparently has not been reached as yet, and it could more than likely be some other character (perhaps straw strength) as well as one of the yield components.

Table 7 compares the means of the mid-parents and the F_2, the difference between them, and also the means, standard errors, t-values

and the significance of the differences. The data in this table were used to construct Figure 1, and the correlation coefficients found in Table 2 are the ones presented in this table.

Table 7

Means of the Mid-Parents and the F_2's, Their Correlation, The Difference Between Them (F_2-P_m), and the Means, Standard Errors, and t-Values of the Differences for Number of Heads (X), Seeds Per Head (Y), Seed Weight in Centigrams (Z), and Total Yield (W)

	X			Y		
	Mid-Parent	F_2	F_2-P_m	P_m	F_2	F_2-P_m
Ajax X Cherokee	12.095	12.977	.882	52.259	48.384	-3.875
Ajax X Clinton	12.624	11.298	-1.326	58.086	59.880	1.794
Ajax X Clintland	11.399	11.034	-.365	58.484	63.432	4.948
Ajax X Mo-0-205	12.265	13.430	1.165	59.069	63.498	4.429
Ajax X Clintafe	12.817	13.684	.867	62.775	68.609	5.834
Ajax X Sauk	12.010	11.784	-.226	58.189	61.482	3.293
Ajax X Clarion	11.540	11.654	.114	57.243	60.263	3.020
Craig X Shelby	11.948	12.712	.764	42.937	44.439	1.502
Craig X Victory	11.690	13.127	1.437	45.077	50.276	5.199
Craig X Beaver	10.494	11.899	1.405	52.333	53.901	1.568
Craig X Garry	9.322	10.483	1.161	46.204	54.633	8.429
Craig X Vanguard	13.008	11.989	-1.019	44.717	44.904	.187
Craig X Abegweit	11.924	12.347	.423	49.933	47.813	-2.120
Craig X Rodney	10.550	10.614	.064	45.816	50.308	4.492
Craig X Erban	11.898	12.536	.638	46.299	47.757	1.458
Craig X Jackson	10.065	10.875	.810	49.299	56.885	7.586
Craig X Simcoe	9.887	12.982	3.095	50.282	59.720	9.438
Craig X Shefford	12.270	12.051	-.219	40.048	45.754	5.754
Means	11.545	12.082	.537	51.058	54.552	3.494
Correlation	.499*			.884**		
Standard Errors			±.239			±1.177
t-Values			2.244*			2.968**

Table 7 (continued)

	Z			W		
	Mid-Parent	F_2	F_2-P_m	P_m	F_2	F_2-P_m
Ajax X Cherokee	2.593	2.523	-.070	16.705	16.221	-.484
Ajax X Clinton	2.438	2.406	-.032	18.421	16.672	-1.749
Ajax X Clintland	2.497	2.534	.037	17.062	18.039	.977
Ajax X Mo-0-205	2.334	2.415	.081	17.099	20.955	3.896
Ajax X Clintafe	2.237	2.314	.077	18.460	21.384	2.924
Ajax X Sauk	2.405	2.393	-.012	17.131	17.515	.384
Ajax X Clarion	2.426	2.490	.064	16.718	17.569	.851
Craig X Shelby	2.458	2.704	.246	12.520	15.151	2.631
Craig X Victory	2.478	2.438	-.050	13.079	16.042	2.963
Craig X Beaver	2.574	2.726	.152	14.579	17.238	2.659
Craig X Garry	2.455	2.591	.136	10.537	15.272	4.735
Craig X Vanguard	2.380	2.339	-.041	14.369	13.569	-.800
Craig X Abegweit	2.578	2.778	.200	15.989	16.517	.528
Craig X Rodney	2.633	2.678	.045	11.843	14.874	3.031
Craig X Erban	2.543	2.664	.121	14.341	16.197	1.856
Craig X Jackson	2.547	2.650	.103	12.737	16.245	3.508
Craig X Simcoe	2.580	2.722	.142	13.486	21.016	7.530
Craig X Shefford	2.715	2.832	.117	13.378	16.063	2.685
Means	2.493	2.567	.073	14.914	17.030	2.118
Correlations	.844**			.525*		
Standard Errors			±.021			±.521
t-Values			3.481**			7.804**

*P <.05 **P<.01

SUMMARY AND CONCLUSIONS

The average F_2 values exceeded the parental means for all 3 of the yield components and also for total yield. The mid-parent vs. F_2 correlations were all positive and significant, and approximately the same magnitude as those observed for barley. The significant Chi squares indicate that the populations were not homogeneous. The occurrence of negative, zero, and positive correlations for X vs. Y, X vs. Z, and Y vs. Z in the parental and F_2 generations indicates that separate gene systems are affecting each of the 3 components.

Most of the genetic variances were positive, however some of them were negative; this phenomenon is believed to be the result of developmental homeostasis. Both oats and barley show dominance for X, a low order of dominance for Y, and lack of dominance for Z. The heritabilities are high for Y and Z and intermediate for X, thus increasing the confidence with which one can select favorable parental combinations for crossing and predicting the approximate relative results by the yield components method.

It is concluded that: the yield components method of analysis is the best now available and may be used on both oats and barley; the 3 components of yield are affected by 3 essentially independent gene systems; in general, the F_2 is more variable than the parents, but with homeostasis the F_2 may be less variable than the parents; and, a breeder can select high-yielding parental combinations and predict the relative results by the use of the components method.

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