PARENTAL SELECTION BY AN OBJECTIVE IDEAL IN WINTER BARLEY

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ABSTRACT

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by Cecil D. Nickell

Twelve parents were selected and combined using the vector method to produce nineteen crosses. A subjective ideal based upon the knowledge of the population of lines and the environment was used to pick the best parents in 1960-61. The 1964 season was quite different from the 1960-61 season and the best parents chosen in 1964 were not the same ones selected in 1960-61. Also, correlations between the values of the component traits of yield and malting were zero or negative, further indicating the independence between seasons.

Through the use of a set of indicator lines, the environmental differences between seasons were overcome. Multiple regression equations were calculated using the values of the indicator lines and the values of the subjective ideal for a given year to determine the beta weights for each indicator. With betas averaged for five years and the current year's data for the indicator lines, an objective ideal was produced. This new ideal did pick the best lines for both 1960-61 and for 1964.

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By

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INTRODUCTION

The plant breeder is faced with a large number of complexities which include the genetics of the plant and a dynamic environment. Progress in breeding programs is dependent upon solving these complexities. The plant breeder works with an organism which has a basic genetic make up, but the extent to which this basic unit manifests itself is dependent upon the ever changing environment. The complete control of this dynamic entity, environment, is impossible with our present knowledge. The next best opportunity to solve the problem of selection in a changing environment appears to lie in developing sets of biological indicators that can be used as a base for prediction.

A primary phase of a plant breeder's work revolves around selecting parents and combining them in such a manner to produce better varieties. The more traits that a breeder works with the more complex the selection of parents becomes.

Grafius (4, 5) proposed a vector method for selecting and combining parents for maximum progress. The same author proposed that parents could be selected using a large number of traits and that the parental means could be used as a predictor for combining the parents. A practical ideal must be set up for successful use of the vector method. Parents then can be chosen in such a way that the progeny means of the unselected bulks will approach this ideal as closely as possible. Present information indicates that the progeny means can be predicted for any given year but there is as yet no provision for increasing the reliability of prediction between years. Now, if large seasonal variations in the ideal do occur, how can a plant breeder feel sure that the ideal he uses in one particular year will pick the best parents for another environment or season? Seasons are variable and some method of selecting an ideal is needed which will answer the question, "What are the best parents, not only for this year, but for five years hence?"

It will be the primary objective of this thesis to establish a method which will extend the vector method to include seasonal variation.

LITERATURE

Heritable traits can be classified as complex or simple. Simple traits are usually controlled by a small number of genes and are usually highly heritable. Complex traits are controlled by a large number of genes between which interactions may occur to compound the heritability of the trait resulting in relatively low predictability.

Grafius (3, 4, 5) defines yield as being a complex trait made up of (X) heads per unit area, (Y) kernels per head, and (Z) kernel weight in oats and barley. It was shown in space planting that X, Y, and Z were independent of each other. Grafius (5) points out that in the development of a plant, a rhythmic process is followed. Small grain developmental patterns consist of the laying down of tillers, floral initiation, stem elongation, cessation of tillering, pollination and lastly, the filling and maturing of the seed. Therefore, X, Y, and Z are directly related to the life span of the plant. When competition for the existing environment ensues, the correlations become negative between X, Y, and Z. The relative values of these correlations will depend upon the particular year. Grafius (4), using X, Y, and Z in spring barley, found evidence of additivity for the three traits. Grafius (4), Leudders (7) and Whitehouse (12), using components, also found that the parents could be used in the prediction of yield.

Smith (9) and Grafius (4) indicate that malting quality as a complex trait could be broken down into components of the chemical behavior and morphology of the seeds. Smith (9) used six characters: malt extract, wort nitrogen, malt nitrogen, diastatic power, beta-amylase and alpha-amylase as malting quality components. Evidence of additivity for many traits was found in eleven crosses of spring X winter barley crosses. Grafius (4) using spring barley found additivity in the malting quality characters of kernel weight, plumpness, malt extract, wort nitrogen, malt nitrogen, diastatic power, and alpha-amylase.

Grafius (4, 5), and Grafius and Adams (6) proposed that a vector method could be used to select and combine parents to produce populations which would closely approximate an ideal even when using a large set of traits. Assumptions were made that no epistasis existed, or if it did, that it was due to component interaction which could be removed by the use of components and that the vectors were all approximately the same length. A vector was used to describe a variety made up of the large number of traits. An ideal was defined as a practical optimum based upon the population performance and the environment. The ideal was <u>subjectively</u> picked each year for use as a measuring stick for assigning over-all worth to the potential parents.

Correlation values were calculated between the lines and the ideal in order to determine which parents to pick and combine. The vector method is dependent upon picking parents and using the parental means in making the prediction of the crosses.

Grafius (2, 3) found that heterosis could be explained by a multiplicative interaction. For example, yield may be increased by having a small increase in one or more of the components. Whitehouse (12) demonstrated additivity for yield components but found epistatic interaction for yield. Duarte and Adams (1), using leaflet area and leaflet number, showed extreme overdominance for leaf area but no over dominance in the components. Williams and Gilbert (14) also found that heterosis in a complex trait could be a consequence of multiplicative interaction among the components which are additive or which could show dominance, completely or partially.

Powers (8) reported a case of heterosis in yield of tomato fruit due to intra- and inter-allelic interactions between components of the fruit. Breaking the complex trait down into components simplified the mode of heterosis.

METHODS AND MATERIALS

Parents were selected using the vector method (4, 6) from thirty-one lines based upon the averaged data of the 1960 and 1961 seasons. Malting quality was analyzed by Dr. A. D. Dickson of the U.S.D.A. Barley and Malt Laboratory at Madison, Wisconsin. Agronomic data were collected in the field and combined with the quality data to constitute twenty characters which were used to select the parents. Nineteen crosses were made in the field in 1962 using twelve parents. The F_1 seed was planted in the greenhouse in the fall of 1962. The F_2 bulked seed was planted in the field in early spring of 1963 to allow for vernalization and seed production. The bulked F_3 seed was planted in the fall of 1963 in replicated plots, eighteen feet long and four rows wide (four feet) with the parents planted in adjacent plots. In the summer of 1964 the plots were cut back to twelve feet with the two middle rows being harvested for yield (W). Heads per three feet(X) were counted, once, in each of the two middle rows. Seed weight (Z) was determined by counting the seeds in a three gram sample. Seeds per head (Y) were calculated by the following formula:

$$Y = \frac{W}{8(X)(Z)}$$

W = Yield in grams.

X = Heads per area multiplied by 8 to make 24 sq feet.

Z = Seed weight in gm.

Disease ratings were made in the field, one being good and six poor. Lodging and winter survival are reported in percentages. Height was measured in inches from base of the head to ground level. Heading date was recorded when approximately one-half of plants were headed (head emerging from the sheath). Malt quality was evaluated on the basis of the quality analysis by Dr. A. D. Dickson.

Transformed data were used in Table 2 for the correlation of progeny with midparents. The data for all the traits are in different units, and therefore the following equation was used to transform the data into common positive units.

$$X_i' = C + \frac{X_i - \overline{X_i}}{\sigma X_i} \qquad [1]$$

C = A constant which is added to give a positive transformed value.

X_i' = The value of the transformed data.

X_i = The observed value of the trait.

$\overline{X_i}$ = The mean value of the trait

$$4.917 = 5.00 + \left(\frac{21.5 - 21.76}{1.82}\right)$$

The standard partial regression coefficients (β) in Table 4 for each trait were obtained by the following equation:

$$\hat{U} = \bar{U} + \beta_W \frac{\sigma_U}{\sigma_W} r_W [\Delta W_{X,Y,Z}] + \ldots + \beta_{Ht} \frac{\sigma_U}{\sigma_{Ht}} r_{Ht}[\Delta Ht] \qquad [2]$$

U = Over-all worth of the line.

β = Standard partial regression coefficient.

σ_U = Standard deviation of over-all worth score.

σ_W, σ_{Mq} = Standard deviation of the trait in question.

r = Correlation of trait between the years.

ΔW, Δmq. . . = Difference between observed value of trait and the mean of the trait.

The β's in [2] represent the weight given each complex trait and this weight is to be further apportioned among components of the complex trait. For example, the weights for the components of the complex traits W and Mq are derived from multiple regression equations as in [3] and [4].

$$\hat{W} = \bar{W} + \beta_X \frac{\sigma_W}{\sigma_X} r_X[\Delta X] + \beta_Y \frac{\sigma_W}{\sigma_Y} r_Y[\Delta Y] + \beta_Z \frac{\sigma_W}{\sigma_Z} r_Z[\Delta Z] \qquad [3]$$

W = Yield of the line.

β_i = Standard partial regression coefficient.

r_i = Correlation between the same trait in different years.

ΔX, ΔY, ΔZ = Difference between observed and mean value.

$$\hat{Mq} = \overline{Mq} + \beta_Z \frac{\sigma_{Mq}}{\sigma_Z} r_Z[\Delta Z] + \ldots + \beta_\alpha \frac{\sigma_{Mq}}{\sigma_\alpha} r_\alpha[\Delta\alpha] \quad [4]$$

Mq = Malt quality score.

β_i = Standard partial regression coefficient.

r_i = Correlation between the values of the traits between years.

$\Delta Z, \ldots, \Delta\alpha$ = Difference between observed and mean values.

The final equation is found by expanding [2] to include the components of the complex traits as in [2a].

$$\hat{U} = \overline{U} + \beta_W[\beta_X \frac{\sigma_W}{\sigma_X} r_X(\Delta X) + \ldots + \beta_Z \frac{\sigma_W}{\sigma_Z} r_Z(\Delta Z)]$$
$$+ \beta_{Mq} [\beta_Z \frac{\sigma_{Mq}}{\sigma_Z} r_Z(\Delta Z) + \ldots + \beta_\alpha \frac{\sigma_{Mq}}{\sigma_\alpha} r_\alpha(\Delta\alpha)]$$
$$+ \beta_{TWT} \frac{\sigma_U}{\sigma_{TWT}} r_{TWT}(\Delta TWT) + \ldots + \beta_{Ht} \frac{\sigma_U}{\sigma_{Ht}} r_{Ht}(\Delta Ht) \quad [2a]$$

$$X_i = 1.00 + \frac{|\beta_i|}{\sigma_i} r_i \Delta X_i \quad [5]$$

$$X_j = 1.00 + \frac{|\beta_i \beta_j|}{\sigma_j} r_j \Delta X_j \quad [6]$$

β_i = Beta weight obtained in equation [2] for the complex traits.

β_j = Beta weight obtained in equation [3] or [4] for the component trait.

σ = Standard deviation.

r_i or r_j = Correlation between the same complex or component trait in different years.

ΔX_i or ΔX_j = Difference of the observed value and the mean value.

The reason for this rather long discussion involving weighting lies in the need to establish some means of converting all data to the same units while at the same time recognizing that some traits are more important than others. The basic charade here is to obtain subjective weighting first and then convert all data to common units by subtracting the mean and dividing by the standard deviation. This gives an array with a mean of zero and a variance of one. A constant is added to avoid negative numbers.

RESULTS

Data are presented in Table 1 for the progeny mean and midparental mean of each character measured. Also listed are the F_3 bulk cross means in percentage of the midparental mean. The values for yield demonstrate heterosis as determined by percentage increase over the midparent. The t-test was highly significant. The average yield of the bulk progenies exceeded the average of the highest parents by 2.2% further indicating heterosis for yield. High seed weight was dominant, being equal to the average of the high parents in the crosses. Seeds per head showed partial dominance. Early heading data was dominant with the average of the bulks being equal to the average of the early parents. Per cent plump, under malt quality, exceeds the midparent mean by 35.5%, which is highly significant with the t-test. The value for plumpness also exceeded the average of the highest parents by 11.7%. Both malt extract and beta-amylase show highly significant difference from the midparent, Table 1.

Table 2 contains the correlation coefficients of the bulk progeny means versus the calculated midparent. Since the data were in different units for the various traits within each cross, the data were transformed as described in equation [1]. In all but one cross the r values were

TABLE 1.--The comparison of the unselected progeny means with the midparental mean. The per cent increase of the progeny mean over the midparental mean was calculated by dividing the progeny mean of each trait by the corresponding mean of the midparents for the same trait and multipling by 100 to give a percentage.

Trait	Mean of Crosses	Midparental	% Increase Over Midparent
Yield (W) Bus/acre	85.5	79.9	107.3**
Heads per unit area (X) N°	177.6	181.0	98.1
Kernel weight (Z) mg.	33.6	31.5	106.6**
Kernel per head (Y) N°	21.8	21.1	103.1
Test Weight (TWT) lbs./bu.	47.5	46.3	102.6**
Survival (So) %	84.2	85.1	98.9
Heading date (Hd) May	19.3	20.9	108.3**
Mildew (ML) Score	2.3	2.0	87.0
Lodging (LD) %	3.5	3.8	108.9
Height (HT) in.	35.4	36.0	98.3**
Barley Nitrogen (BN) %	2.20	2.21	99.5
Plumpness (P) %	29.4	21.7	135.5**
Color score (C)	19.1	20.2	94.6
Malt Extract (XT) %	73.8	73.3	100.8**
Wort Nitrogen (WN) %	.706	.684	103.2*
WN/MN	32.7	31.7	103.2
Diastase (DP) %	188	182	103.3
β-amylase (β)	611	582	105.8**
α-amylase (α) units	45.2	43.3	104.4

* significantly different as determined by t-test
** highly significant as tested by t-test

TABLE 2.--Correlation of the bulk progeny with the midparental values using transformed data. The data were transformed by equation [1]. This converts all data to the same units, having a mean of 5.0 and a variance of one.

Cross Number	n	d.f. (n-3)	r	z	(n-3)z
62-431	20	17	.525*	.570	
-432	20	17	.393	.416	
-433	20	17	.380	.400	
-434	20	17	.388	.410	
-435	20	17	.585**	.668	
-436	20	17	.645**	.766	
-437	20	17	-.155	-.157	
-439	20	17	.465*	.504	
-440	20	17	.297	.307	
-441	20	17	.245	.251	
-442	20	17	.481*	.525	
-443	20	17	.699**	.866	
-444	20	17	.253	.260	
-445	20	17	.474*	.527	
-446	20	17	.321	.334	
-447	20	17	.548*	.612	
-448	20	17	.776**	1.042	
-449	20	17	.175	.177	
-450	20	17	.688**	.845	
Total		323			158.491
Average			.455**	.491	

* significant at 5% level
** highly significant at 1% level

positive with ten crosses showing significance at either the 1% or 5% levels. The average correlation coefficient of the set of crosses was highly significant at the 1 per cent level with an r = .455.

The parent-progeny correlations are listed in Table 3. The r values for seeds per head and seed weight which are

TABLE 3.--The correlation of the bulk progeny values for each trait with midparental values. Raw data were used since correlations were run between the values of each trait which are in the same units.

Trait	n	d.f. n-2	r
Yield	19	17	.3776
heads per unit area	19	17	.0973
seeds per head	19	17	.4748*
seed weight	19	17	.6849**
Test Weight	19	17	.2887
Survival	19	17	.1550
Heading Date	19	17	.2709
Mildew	19	17	.6116**
Lodging	19	17	.4288
Height	19	17	.3834
Barley Nitrogen	19	17	.7334**
Plumpness	19	17	.4224
Color Score	19	17	.3059
Malt Extract	19	17	.5330*
Wort Nitrogen	19	17	.7205**
WN/MN	19	17	.4231
Diastase	19	17	.8422**
β-amylase	19	17	.8117**
α-amylase	19	17	.3567

* significant at 5% level
** highly significant at 1% level

part of yield are significant and highly significant, respectively. The malt quality components are all .3 or above indicating positive correlation with the midparent. Barley nitrogen, malt extract, wort nitrogen, diastase, and beta-amylase are significantly correlated with the parental means. The weakest correlation is for X and for survival. Presumably there is a severe interaction between winter survival and tillering.

Table 4 contains the beta weights (standard partial regression coefficients) occurring from year to year for the individual traits. Equation [2] was used to calculate the beta weights for complex traits that make up the over-all score. Equation [3] was used to calculate the betas for the components of malting quality using equation [4].

The listed beta weights indicate the changes from year to year due to the environment. It should be pointed out that the absolute values of the betas indicate the importance of the trait in the particular year. Comparing 1960 with 1964, malting quality had approximately the same emphasis. The importance of lodging, however, changed drastically due to far less lodging in 1964.

As mentioned before, the ideal for any particular year is based upon the population's performance in a given environment. To determine if the performance of progeny in 1964 can be related to the predictions made in 1960-61, three lines were picked as indicators of the season. Using these three lines and the ideal picked for 1964, a multiple regression equation was calculated.

$$\underline{\hat{I}} = \bar{I} + \beta_A \frac{\sigma_I}{\sigma_A} \Delta\underline{A} + \beta_B \frac{\sigma_I}{\sigma_B} \Delta\underline{B} + \beta_C \frac{\sigma_I}{\sigma_C} \Delta\underline{C} \qquad [7]$$

$\underline{\hat{I}}$ = Established ideal for the particular year and is a multivariate vector. The ideal vector is made up of component traits of yield and malting quality and simply inherited traits such as height and disease reaction. Since all the traits that make up the ideal are in different units they are transformed to a common base by equations [5] and [6].

TABLE 4.--Comparison of beta weights (standard partial regression coefficients) between 5-year data for each trait used in the selection of parents. The first two major subdivisions of the table are for the complex traits, malting quality and yield. The third major subdivision is for over-all score which includes malt quality and yield. The absolute magnitude of the β's indicate the importance of a trait in any year.

Trait	1960	1961	1960-61	1962	1963	1964
Malt quality						
Kernel weight	-.3342	.0487	.0212	-.2253	-.1347	.1220
Plumpness	.1455	-.5670	-.3382	-.1897	-.4562	-.2361
Color Score	.0738	.0135	-.0145	-.0829	-.3251	-.0034
Malt Extract	-.5506	-.0181	-.3133	-.0794	-.7418	-.3536
Wort Nitrogen	-.3795	.2341	-.0744	.1198	-.2481	-.1704
Malt Nitrogen	-.3211	.4409	.3474	.1773	.0005	.4304
Diastase	-.1925	-.6898	-.6346	-.8205	-.4316	-1.0981
α-amylase	-.4493	-.2299	-.2033	-.3149	.2607	.3832
Yield						
Heads/area	.8035		.8387	.3626		.6023
Seeds/head	.9808		.9776	1.2017		.8979
Kernel weight	.5864		.3559	.1977		.2766
Over-all Score						
Malt quality	.9082	.4959	.4930	.3719	.7973	.9494
Yield	-.1835	-.2771	-.3779	-.6069	-.3557	-.3369
Test Weight	-.0386	-.1117	-.0610	-.1475	-.1820	-.0261
Survival	.1516	-.3676	-.1677	.0148	-.1499	-.0374
Heading Date	.0721	.0807	-.0294	.1032		.2005
Mildew	.2418	.3418	.1773	-.0822		.1430
Lodging	.5203		.2866	.2486		.0074
Height	-.0593	.0671		-.1767	-.0307	.0076

$\beta_A, \beta_B, \beta_C$ = The standard partial regression coefficients which govern the amount contributed to the ideal by the indicator line A (410-1), line B (414-80), and line C (Hudson).

$\underline{\hat{I}}$ = Standard deviation of the ideal. It is important to note that σ_I refers to variation within the ideal.

$\sigma_A, \sigma_B, \sigma_C$ = Standard deviation of the biological indicators. These statistics refer to variation within vectors $\underline{A}$, $\underline{B}$, and $\underline{C}$.

$\Delta_{\underline{A}}, \Delta_{\underline{B}}, \Delta_{\underline{C}}$ = Difference from the mean of a line and the observed value of a given trait. $\underline{A}$ is a vector made up of many traits as are $\underline{B}$ and $\underline{C}$. It is assumed that $\Delta\underline{A} = (\underline{A} - \bar{A}) = (\underline{A} - 1)$ since $\bar{A}$ = the mean magnitude of vector $\underline{A}$ which is assumed to be an estimate of 1.

A num~~b~~erical example using data calculated by equations [5] and [6] is used in equation [7] as follows:

$$1.06 = 1.03+\beta_A\left(\frac{.048}{.048}\right)(.99-1.00)+\beta_B\left(\frac{.048}{.065}\right)(.98-1.04)+\beta_C\left(\frac{.048}{.045}\right)(.90-.98)$$

$$1.09 = 1.03+\beta_A\left(\frac{.048}{.048}\right)(.94-1.00)+\beta_B\left(\frac{.048}{.065}\right)(.99-1.04)+\beta_C\left(\frac{.048}{.045}\right)(.97-.98)$$

$$1.13 = 1.03+\beta_A\left(\frac{.048}{.048}\right)(1.06-1.00)+\beta_B\left(\frac{.048}{.065}\right)(1.06-1.04)+\beta_C\left(\frac{.048}{.045}\right)(.97-.98)$$

$$\vdots$$

The above example explains how the beta-weights are calculated in Table 5. Using the beta-weights calculated in equation [7] and the three lines in the 1960-61 population, a new ideal was calculated.

TABLE 5.--Comparison of beta weights using three indicator lines over five years. The average betas at the bottom of the table are averaged by using a weighting method. Nineteen traits were used to calculate the betas for 1960, 1962, and 1964 data; fourteen traits were used in the calculation of the betas in 1961 and 1963. Therefore, the betas for 1960, 1962, and 1964 were all multiplied by 19; the betas in 1961 and 1963 were multiplied by 14 and all added together and divided by 85 (the total number of traits for the five years).

Year	Indicator lines 410-1	 414-80	 Hudson
1960	.6534	.0728	.2890
1961	-.1086	.2720	-.4293
1962	.2444	-.3596	.7505
1963	.1861	.7235	-.3816
1964	.0972	.1942	-.0148
Average	.2350	.1310	.1021

The new ideals in Table 6, based upon the average beta weights and three indicators, were calculated using the following equation:

$$\underline{\hat{I}} = \bar{I} + \beta_A \frac{\sigma_I}{\sigma_A} (\underline{A}-\bar{A}) + \beta_B \frac{\sigma_I}{\sigma_B}(\underline{B}-\bar{B}) + \beta_C \frac{\sigma_I}{\sigma_C}(\underline{C}-\bar{C}) \qquad [8]$$

Equation [8] is based on data standardized by the equations [5] and [6] so that each trait has a mean of 1, a variance of 1, and a standard deviation of 1. This includes the proposed ideal. Therefore, equation [8] reduces to:

TABLE 6.--The three indicator lines and the three ideals for the average 1960 and 1961 data. (I_{av} = the objective ideal based upon the average betas, I_{64} = ideal produced based upon 1964 betas and I_{60-61} = ideal picked subjectively for 1960-1961.)

Trait	Indicator Lines			Ideals		
	410-1	414-80	Hudson	I_{60-61}	I_{av}	I_{64}
Yield						
Heads/area	163.0	176.0	170.0	168.0	163.8	163.3
Seeds/head	23.4	21.2	20.3	22.8	22.1	22.1
Kernel weight	32.4	32.2	31.0	35.0	32.2	32.7
Malt Quality						
Barley nitrogen	2.05	2.09	2.08	1.90	2.07	2.07
Kernel weight	32.4	32.2	31.0	35.0	32.2	32.7
Plumpness	35.6	44.0	41.2	60.0	42.7	44.0
Color score	24.0	29.0	27.5	30.0	26.3	27.4
Malt extract	76.4	76.3	75.0	77.4	75.7	75.6
Wort nitrogen	.655	.685	.673	.700	.644	.638
Malt nitrogen	2.00	2.08	2.04	1.84	2.00	2.00
Diastase	192	206	180	200	184	183
Beta amylase	624	682	577	670	616	618
Alpha amylase	42.4	42.7	41.4	45.0	40.7	40.3
Survival						
Survival wet	60.0	60.0	40.0	80.0	55.4	56.7
Survival dry	90.0	95.0	90.0	90.0	89.6	89.5
Heading date	28.0	29.0	30.0	30.0	29.8	30.1
Mildew	1.0	6.0	3.0	2.0	3.2	3.8
Lodging	00.0	72.0	00.0	20.0	19.8	28.1
Height	39.0	39.0	36.0	38.0	38.0	38.0
Test weight	51.2	51.6	49.3	49.4	49.8	49.7

$$\underline{\hat{I}} = 1.00 + b_A(\underline{A}-\bar{A}) + b_B(\underline{B}-\bar{B}) + b_c(\underline{C}-\bar{C}) \quad [9]$$

I = Is estimated to be 1.

b_A = Is estimated to be equal to $\beta_A \frac{\sigma_T}{\sigma_A} = \beta_A$

A, B, C = Is the standardized value for the particular trait.

$$a = 1.00 - \beta_A(\bar{A}) - \beta_B(\bar{B}) - \beta_C(\bar{C}) \quad [10]$$

a = Constant value based upon the averaged betas and the mean of standardized values, which is approximately 1.00.

$$a = 1.00 - \beta_A - \beta_B - \beta_C \quad [11]$$

The following is a numerical example of equation [11].

$$0.5319 = 1 - 0.2350\ (1) - 0.1310\ (1) - 0.1021\ (1),$$

$$0.7234 = 1 - 0.0972\ (1) - 0.1942\ (1) + 0.0148\ (1).$$

Equation [11] is the simplified form of equation [10]. The values for the constant "a" for the average betas is 0.5319 and 0.7234 for the 1964 betas. Using equation [11], equation [9] may be reduced to:

$$\underline{\hat{I}} = a + b_A(\underline{A}) + b_B(\underline{B}) + b_C(\underline{C}) \quad [12]$$

a = Constant calculated in equation [11].

$\underline{A}$, $\underline{B}$, $\underline{C}$ = Vectors in standardized units of the traits for each of the indicators.

b_A, b_B, b_C = Is estimated to equal to $\beta_A \frac{\sigma_I}{\sigma_A} = \beta_A$

$\underline{\hat{I}}$ = The new ideal vector.

Using equation [12], the new ideal can be calculated as follows using the averaged betas and data which was transformed by equations [5] and [6].

Z 0.53 + (0.24 x 0.99) + (0.13 x 0.98) + (0.10 x 0.90) = 0.98

P 0.53 + (0.24 x 0.94) + (0.13 x 0.99) + (0.10 x 0.98) = 0.98

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The values for the new ideal are in standardized units must be converted to raw values which may be used to assign over-all worths to the lines. In this case the data are converted by following the reverse procedure to that used in weighting.

$$X_i = \frac{\sigma_X}{|\beta_i| r_i} (X_i' - 1.00) + \bar{X}_i \qquad [13]$$

$$X_j = \frac{\sigma_X}{|\beta_i \beta_j| r_j} (X_j' - 1.00) + \bar{X}_j \qquad [14]$$

β_i = Beta weight for complex trait.

β_j = Beta weight for component traits.

X_i = Value of trait i.

$\bar{X}_i$ = Mean of the trait i.

X_j' = Transformed value of the component trait.

X_i' = Transformed value of the complex trait.

r_{Xi} = Correlations of the values for each trait between years.

Using equations [13] and [14], the raw values are calculated as indicated below.

Z 32.2 = 36.20 (0.9845 - 1.0000) + 32.8

P 42.3 = 166.70 (0.9829 - 1.0000) + 45.1

XT 75.7 = 15.87 (1.0197 - 1.0000) + 75.4

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The values in Table 7 indicate that the ideal constructed by using the average betas and indicator lines picked a composite of the parents selected by the subjective ideal for 1960-61 and the ideal produced by the 1964 betas. The subjective ideal was picked by observing the population and the environment. The ideal based on the 1964 betas was calculated by using the 1960-61 values for the indicator lines and the betas calculated for 1964.

Table 8 lists the correlation coefficients of 1960 versus 1961 and 1960 versus 1964. In 1960 the winter survival was as high as in 1964, but note the r value for winter survival is .4593, which is positive although not significant. Also, none of the correlation coefficients for the components of malt quality and yield were significant, in fact they were approximately zero. A total of 31 lines was used in the correlations for 1960 versus 1964 and only 16 lines were used in 1960 versus 1964 comparison. This may account for part of the difference. But the main cause of lack of agreement is the variation in environment. Different sets of genes are being called into play in 1960 and in 1964.

TABLE 7.--Correlations of all lines with the three ideals. There was a total of 31 lines of which 12 were used as parents. Comparisons with I_{60-61} and with I_{64} indicates poor agreement. The average ideal, however, picks the better lines in both years.

Lines	I_{60-61}	I_{av}	I_{64}
Hudson	-.1540	.5444 b	.0305
403-12	.0319	.2670	-.1673
410-1 a	.4679 b	.6841 b	-.0564
410-2 a	.4144 b	.7232 b	.0676
410-3 a	.6064 b	.6333 b	-.0223
410-8 a	.6040 b	.2560	-.2206
410-11	.5567 b	.3699 b	-.1123
411-1	.3734	.5761 b	.2039
411-4 a	.3656	.0109	-.3339
411-8	.1240	-.7353	-.5875
411-9	-.3754	-.2897	-.2534
411-11	-.2456	-.4236	.1073
411-12 a	.7649 b	-.1094	-.4693
409-3	-.0672	-.3039	.1129
417-5	.2944	.0619	.0367
414-7	-.4336	-.0073	.3931 b
414-16	.2159	-.3857	-.4781
414-17 a	.4482 b	-.3056	-.3005
414-18 a	-.3747	-.2340	-.0207
414-19	-.1309	-.2912	-.3914
414-20	-.4012	-.3522	-.0782
414-21 a	.1345	-.2508	-.6135
414-23	-.1258	.2662	.1178
414-29	-.0990	.1549	.0502
414-31	-.5619	-.4255	-.2945
414-33	.2510	-.0933	-.1016
414-40	-.6178	-.4848	-.0642
414-41	-.4766	-.0723	.2656
414-60 a	.0474	.4071 b	.6030 b
414-75	-.2496	.2784	.4204 b
414-80 a	-.1933	.3070 b	.9329 b
I_{60-61}		.2284	-.0141
I_{av}			.5829

a lines used in the nineteen crosses

b lines with favorable correlations with the ideal

TABLE 8.--Correlations between the same trait between years. Thirty-one lines were used to calculate the r values between 1960 and 1961 for each trait and sixteen lines were used in the correlation of each between 1960 and 1964.

Trait	1960 vs 1961	1960 vs 1964
Yield	.3914*	.0740
Heads/area		-.3809
Kernels/head		-.0233
Kernel weight		.0047
Malt Quality	.3038	.2585
Barley nitrogen	.0735	-.2523
Kernel weight	.4978**	.0047
Plumpness	.4152*	.1956
Color score	-.0099	.4035
Malt extract	.4843**	-.0846
Wort nitrogen	.6297**	-.0134
Malt nitrogen	.0453	-.1555
Diastase	.0963	.0730
Beta-amylase	.0406	.0730
Alpha amylase	.7288**	.4002
Test Weight	.5338**	.5626*
Survival	-.2835	.4593
Heading date	.5614**	.3925
Mildew	.6836**	.2568
Height	.4811**	.4316
Lodging		.2268
Over-all worth	.5677**	.4909

* significant at 5%

** highly significant at 1%

DISCUSSION

Figures 1 and 2 present a pictorial representation of the steps involved in the vector method and the extension to compensate for seasonal variation by the use of an objective ideal. Figure 1 contains, the procedure in the vector method which has been established previously (4, 5, 6,). Figure 2 contains the new extension to the vector method. It outlines the procedures used in determining the average betas for the indicator lines and the use of these average betas with the current years data of the indicator lines to produce an average. The average ideal has been shown to pick parents that will perform as expected five years hence. These two figures present a brief review of exact procedures described before in the results and discussion of this thesis.

Standardizing the Ideal Through Biological Indicators

The weight for any particular trait in the vector method will vary from year to year depending upon the environment. For example, in 1960 winter kill was low and, obviously, less emphasis was put on winter hardiness. Malt quality was emphasized in all years as indicated in Table 4. The same is true for certain agronomic traits such as kernels per head. In contrast, the betas for heading date are all quite weak.

Comparing the beta weights for the individual traits for 1960-61 average data, from which the parents for this experiment were selected, and the 1964 betas, all are similar except more emphasis was placed on malt quality in 1964. Emphasis on lodging was low in 1964 and high in 1960-61, causing a difference in emphasis in selection.

Correlations between the component characters in 1960 and 1964 were, in general, zero or negative. Winter hardiness was similar between the years, but in 1964, drouthy conditions existed which compounds the picture. Correlations between the characters in 1960 and 1961 were in general positive, but the r value of winter hardiness was -.28. Winter survival was higher in 1960 and extreme winter kill occurred in 1961. A question arises, if there is no association between 1960 and 1964, how can selection pressure be effective when different sets of genes are being called into play each season? As presented in Table 7, the objective ideal does pick the best parents. The average beta weights level out the fluctuations between seasons in such a manner that predictable results are obtained.

The vector method has as a goal the production of unselected bulk progeny whose means approach an ideal. Usually, a subjective ideal is determined each year based

Original data for n lines and m complex traits

Score each line as to its overall worth
(U) on a 1-5 scale with 1 = good

Line	Traits							
	W	Mq	Ld	So	Ht	...	Hd	U
1	92.6	2.8	10	50	30		28	3.8
2	109.1	2.0	20	70	32		30	1.5
3	108.2	3.0	20	60	29		26	2.8
.								
.								
.								
n								

Calculate multiple regression with U as the independent variable.
Also calculate regression for complex traits W and Mq.

$$\hat{U} = \bar{U} + \beta_W \frac{\sigma_u}{\sigma_W} r_W \, \Delta W + \ . \ . \ . + \beta_{Hd} \frac{\sigma_u}{\sigma_{Hd}} r_{Hd} \, \Delta Hd$$

$$\hat{W} = \bar{W} + \beta_X \frac{\sigma_W}{\sigma_X} r_X \, \Delta X + \ . \ . \ . + \beta_Z \frac{\sigma_W}{\sigma_Z} r_Z \, \Delta Z$$

$$\hat{Mq} = \bar{Mq} + \beta_p \frac{\sigma_{Mq}}{\sigma_p} r_p \, \Delta p + \ . \ . \ . + \beta_\alpha \frac{\sigma_{Mq}}{\sigma_\alpha} r_\alpha \, \Delta \alpha$$

Weight all original data either by

$$X_i' = 1.00 + |\beta_i| \frac{X-\bar{X}}{\sigma_{X_i}} r_{X_i} \quad \text{or}$$

$$X_j' = 1.00 + |\beta_i \beta_j| \frac{X-\bar{X}}{\sigma_{X_j}} r_{X_j}, \ \text{depending}$$

on whether or not X is a complex or a component trait, respectively.

$$W' = 1.00 + |.1835| \left(\frac{92.6-98.0}{4.38}\right). 36$$

$$X' = 1.00 + |.1835 \ .9808| \left(\frac{165.0-170.0}{10.30}\right) .50$$

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Rotate the table 90° and run correlations after inserting the subjective ideal. Complex traits are omitted if their components are used.

Traits	Lines					
	1	2	3	...	n	Ideal
x	.9570	1.0320	.9990			
y	.9070	1.0600	1.0140			
z	.9670	.[illegible]	.9780			
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.						

FIGURE 1.--A brief pictorial representation of the vector method which has been established previously by Grafius (5).

Correlations can be used to pick parents, however the ideal may change from one year to next due to environmental fluctuations. To minimize this effect, biological indicators can be grown each year and an ideal constructed from them by the equation

$$\hat{\underline{I}} = \bar{I} + \beta_A \frac{\sigma_I}{\sigma_A} (\underline{A}-\bar{A}) + \beta_B \frac{\sigma_I}{\sigma_B} (\underline{B}-\bar{B}) + \beta_C \frac{\sigma_I}{\sigma_C} (\underline{C}-\bar{C})$$

If β_A, β_B, and β_C are known, $\hat{I}$ can be calculated for any year. But to do this, vectors $\underline{A}$ thru $\underline{C}$ must be in standard measure. Convert the data for each trait by

$$X'_i = 1.00 + |\beta_i| \frac{X-\bar{X}}{\sigma_X} r_X \text{ or } X'_j = 1.00 + |\beta_i \beta_j| \frac{X-\bar{X}}{\sigma_X} r_X$$

Calculate $\hat{\underline{I}}$ from converted data

Biological Indicators

	A	B	C	Ideal
X	1.017	1.090	1.060	1.045
Y	1.060	.958	.916	1.032
Z	.989	.983	.895	1.061
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The β values for several years may be averaged algebraically. These average values can operate in current years from the biological indicators to give an average ideal. However $\underline{A}$ thru $\underline{C}$ are vectors and the data should be converted to standard measure.

$$X'_i = 1.00 + |\beta_i| \frac{X-\bar{X}}{\sigma_X} r_X \quad \text{or} \quad X'_j = 1.00 + |\beta_i \beta_j| \frac{X-\bar{X}}{\sigma_X} r_X$$

The new ideal is then calculated using average betas and current data.

$$\hat{I} = a + b_A (\underline{A}) + b_B (\underline{B}) + b_C(\underline{C})$$

The above data may be changed back to original units by the reverse process.

$$X = \frac{\sigma_X}{|\beta_i| r_X} (X'_i - 1.00) + \bar{X} \quad \text{or} \quad X = \frac{\sigma_X}{|\beta_i \beta_j|\, r_X} (X_j - 1.00) + \bar{X}$$

FIGURE 2.--A pictorial representation of the extension to the vector method. The procedures are outlined for the determination of the average betas. Using these average betas and the data of the current year for the indicator lines, a new objective ideal is constructed.

upon the knowledge of the population and the environment. Evidence was presented indicating that the subjective ideal is only good in the year in which it was established. This can be attributed to environmental changes between seasons and the response of the population to these environmental changes. Even though the parents are selected by this ideal, they will only perform as expected in the year of selection, not in other environments. Using several lines which are good indicators of the environmental changes, an ideal can be calculated as stated previously in this thesis. The ideal will fluctuate with the season due to the environmental changes. This ideal will pick parents which will perform over several sets of environments. The selected parents can then be combined as described by Grafius (5) using the vector method which will produce unselected bulks having a mean performance approaching an ideal based on the indicator lines. With the ability to select parents and combine them to produce the best crosses in the future, the selection of lines from the unselected bulks after a few generations of selfing becomes simplified.

Since the emphasis on particular traits can change between years, a long time average is desirable in order to give any predictability to parental means in the vector method. Five years data were collected and used to calculate the average beta weights. Between the time of crossing and the time the performance trials on the unselected bulks are complete, another three years will have passed. Using the ideal based on the current data for three indicators and the average betas, the best bulks can be selected and selections made from within these crosses. Two to three years will ordinarily pass by until replicated performance trials have been conducted on the selected lines. Further selection of the outstanding lines can be made again based upon the average betas and the current data from three indicator lines. One would, of course, use the actual average performance data too. But in addition to this average data there are average data for a ten to eleven year period collected on the parents which will also help in selection of the new varieties.

To simplify the picture, the following outline gives the steps in a breeding program which used the vector method and the objective ideal:

1. Data are collected for two or three years on a population of potential parents. Each year indicator lines are grown with the population. An ideal is picked each year subjectively to evaluate the lines. Beta weights are determine for each year for each of the indicators and average the betas for the three years.

2. Using the average betas and the current data from indicator lines, an ideal is calculated by which parents are selected and combined to produce unselected bulks.

3. Grow the parents and the unselected bulks in plot trials for two or three years until homozygosity is approached within the crosses.

4. Again determine the average betas for the parents. The data now spans six years. Calculate the ideal and select the best unselected bulks.

5. Make selections from the best bulks. Grow the parents and bulks until the selected lines can be tested.

6. Using the average betas and the current data from the indicator lines, the objective ideal is determined and will be used to select the best lines.

It may be feasible to use two or three years data to pick the parents in spring cereals with the calculated ideal, which would shorten the cycle by three years. This would allow collection of data on the parents for eight years.

With the great potential of hybrid cereals, the use of the objective ideal will become more important. In the case of hybridization, dominance will be experienced; but since the ideal will pick parents which will perform better over several environments, the hybrids should also show maximum adaptation. The vector method along with the objective ideal and estimates of dominance can be used to construct hybrids which will approach an ideal and will thus eliminate many unnecessary crosses.

Comparison of Progeny with Calculated Midparents

The average yield of the bulk progenies exceeded the midparental value by 7.3% in the F_3 generation and exceeded that of the average high parents by 2.2%. Since yield is broken down in components, X (heads per unit area), Y (seeds per head), and Z (seed weight), and the product of X, Y, and Z equals yield, then if any one or more of the components exceed their midparent, the multiplication of the dominant effects may give heterosis. In this case, X = 98.1%, Y = 103.1% and Z = 106.6%. These are all in per cent of the midparent and the product X, Y, and Z equals 107.8%. As shown, even with the reduction in one component and an increase in the other two, heterosis does exist if measured as an increase over the midparental values. The increase in the components may be due to dominance even though these components exhibit additivity as indicated in Table 3 where seeds per head and seed weight are shown to be significantly correlated with the midparent.

Interaction between traits presents a third source of possible deviation from the midparent. Heads per unit area decreased by two per cent between the progeny and mid-parent means. At the same time, heading date become earlier than the midparent. Now the development of a biological organism is such that the various stages follow one another in a certain sequence. Tillers are put down until such time that floral initials start to form. Floral initiation tapers off when elongation starts.

Since an earlier heading date leaves less time for tiller formation, the bulk progenies being earlier should also have fewer tillers. Time then influences tillering, and eventually affects kernel weight and kernels per head as explained by Grafius (5).

Per cent plump exceeded the midparent by thirty-five per cent and exceeded the average highest parent by 11.7%. Seed weight and plumpness are highly correlated with an r = .83. With the earlier heading date perhaps more energy was left to produce larger seeds? Plumpness increase, even though it exceeded the average of the highest parent, may be due to the early heading date. An argument may arise about the difference of just two days in heading date, but a statistical difference does exist and the early heading date does coincide with the reduced tillering and greater kernel weight. With the reduced tiller number and earlier heading date, the rainfall was great enough to boost the extra filling of the seeds.

Malt extract is closely associated with seed size and plumpness. All three traits show a statistically highly significant difference from the midparent. Extract difference can be explained by increased seed weight and plumpness since significant difference occurred in both traits.

It is not surprising that in the F_3 generation such differences exist between the midparent and progeny. Heterozygosis exists in these early generations and since we are working with normally self pollinating organism, originating from lines which are homozygous,even modest degrees of heterozygosis may be noted.

When comparisons were made between individual characters of the bulks and midparents, high correlations were found. Correlations for seeds per head and extract were significant at the 5% level; and for seed weight, disease reaction, barley nitrogen, wort nitrogen, diastase and beta-amylase were highly significant. Even with significant differences from the midparent, kernel weight still was highly correlated with the midparent. Heads per unit area was independent of the midparental values, which may be due to the difference in heading date and possibly to differences in winter hardiness.

Since heading date notes were taken on unselected bulks, any early lines in the population will tend to cause the observer to give an earlier reading than may really be true. Survival may have some effect on heading date, but with the small difference in survival, no definite conclusion can be made. Also, survival may be broken into components which may be more additive than the complex trait winter survival (4).

The components of malt quality all are positively correlated with the midparents. Barley nitrogen, extract, wort nitrogen diastase, and beta-amylase all are staticti-cally significantly correlated. In general, additivity was experienced in the malt quality characters.

When comparisons were made between the bulk progeny and the midparents, ten of the nineteen crosses were significantly or high significantly correlated. Table 2 shows only one bulk with a negative correlation value with the midparents. The average correlation value for the nineteen lines as calculated, using Z transformation in Snedecore (10), giving r = .455 ~~.536~~ which was highly significant.

SUMMARY

A method is presented in which an ideal may be calculated by using average standard partial regression coefficients averaged for five years and the current data from three biological indicator lines. It was also established that this ideal would pick lines which would perform well under several environments. The new objective ideal coupled with the vector method will give a more accurate evaluation to the predictability of the crosses and also will lend itself to better selection of parents. The new ideal will compensate for seasonal variation automatically through the indicator lines. The objective ideal will pick the best parents, and also will help in the selection of the best unselected bulks and finally will help in the selection of lines from these bulks.

Additivity was demonstrated in general for all component traits of malting quality and yield even though dominance was demonstrated in the component traits and heterosis for yield. Yield increase can attributed to multiplicative interaction of the components X, Y, and Z. These bulks were in the F_3 generation, and enough heterozygosity was still present to account for the dominance and heterosis.

LITERATURE CITED

1. Duarte, R. A., and Adams, M. W. 1963. Component interaction in relation to expression of a complex trait in a field bean cross. Crop Science 3:185-186.

2. Grafius, J. E. 1956. Components of yield in oats. A geometrical interpretation. Agron. Jour. 48:419-423.

3. ______. 1959. Heterosis in Barley. Agron. Jour. 51:551-554.

4. ______. 1964. A geometry for plant breeding. Crop Science 4:241-146.

5. ______. 1965. A geometry of plant breeding. Research Bull. 7 Michigan State University Ag. Exp. Station.

6. ______, and Adams, M. W. 1960. Eugenics in crops Agron. Jour. 52:519-523.

7. Leudders, V. D. 1960. An analysis of the components of yield in 18 oat crosses. M. S. Thesis, Michigan State University.

8. Powers, L. Gene. 1952. Recombination and heterosis. Heterosis. Edited by John W. Gowen. Iowa State College Press.

9. Smith, D. H. 1963. Relationship of winter habit and malting quality in winter x spring barley crosses. Ph. D. Thesis, Michigan State University.

10. Snedecor, G. W. 1946. Statistical Methods. Iowa State College Press.

11. Thompson, J. B., and R. N. H. Whitehouse. 1962. Studies on the breeding of self pollinating cereals. 4. Environment and the inheritance of quality in spring wheats. Euphytica 11:181-196.

12. Whitehouse, R. N. H., Thompson, J. B., and Dovalle Ribeiro, M. A. M. 1958. Studies on the breeding of self pollinating cereals. 2. The use of a diallel cross analysis in yield production. Euphytica 7:147-169.

13. Williams, W. 1959. Heterosis and the genetics of complex characters. Nature 184:527-530.

14. ______, and Gilbert, N. 1960. Heterosis in the tomato. Heredity 14:133-149.