THE INTERACTION OF GENOTYPE WITH NIGHT TEMPERATURE AND LENGTH OF DAY IN BARLEY

By

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AN ABSTRACT

Submitted to the College of Agriculture of Michigan
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ABSTRACT

One hundred and fifty varieties of Manchurian barley were planted in the field in 1956 and 1957. There were two dates of planting each year. Varietal behavior was observed from date of heading, height of plants, and number and weight of seeds. On the basis of the data, an attempt was made to study the interaction of genotype and night temperature and genotype and seasonal change in the amount of daylight.

Varietal behavior was analyzed by vector analysis. Vector diagrams considering each of the characteristics observed were presented. The diagrams were obtained by letting r^2 for a set of bivariate data be equal to the cosine of an angle θ between two vectors for each characteristic studied. The two vectors having a common origin formed a plane which was interpreted as a plane of force. The relative varietal behavior was shown to be determined in part by the force in the plane.

Varietal interaction was observed when number and weight of seeds were considered. It was concluded that these interactions were due to night temperature. Genotype interaction was observed when date of heading data were plotted, and it was concluded that the interaction was due to night temperature and daylength. In the diagram analyzing height of plants a possible genotype-daylength interaction was indicated, but the degree of determination of the generating vector was so low, that no conclusion could be made.

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INTRODUCTION

One of the most limiting factors for barley production in Michigan appears to be night temperature. The exact mechanism involved is not known, but it may be related to a respiration response. In any event, even under the most favorable moisture and fertility relationships, yields of over 60 bushels per acre are extremely rare. These low yields may be due in part to pathogens, but the main difficulty seems to be the inability of the present varieties to produce well in a high night-temperature environment. Frequently, such varieties are used by plant breeders in their work.

In any breeding program, the first consideration, after the objectives have been determined, is to find sources of germ plasm. This thesis is an attempt to survey some 150 varieties of Manchurian barley from the world collection to find out if a night temperature interaction exists and if so, to pick out some parents for a breeding program.

At this point the question may be raised concerning the source of material. "Why Manchuria? Why not Abyssinia or some other higher temperature location?" Unfortunately, barley is a winter crop or a high altitude spring crop near the equator. Plant exploration and introduction with night temperatures in mind would undoubtedly be of great help at this point.

REVIEW OF LITERATURE

Effects of given levels of night temperature on the growth of various plants have been demonstrated empirically. Roberts and Struckmeyer (5)* observed the effects of night temperature upon such photoperiodic responses of higher plants as elongation of the stem, length of time to flowering, extent of flowering, and seed set. They observed various plants grown at 55° and 70° F. night temperatures with half of each lot being placed under long day conditions and half under short day. The behavior of different plants under a given daylength varied greatly with variation in night temperature. Furthermore, it was very apparent that some varieties within a species showed a marked adaptation to varying night temperatures.

Boswell (1) studied the influence of night temperature upon the growth and yield of garden peas and observed that, the higher the night temperature, up to a certain point, the more rapid the growth rate. Wiggans (8) observed a steady decrease in the number of days from sowing to heading and from sowing to maturity of oats with successive planting dates in spring. He based his conclusions on several years' data and disregarded effects of daylength changes because these changes were constant from year to year.

Gregory (3) studied performance of barley and observed that net assimilation rate was positively correlated with mean day temperature and negatively correlated with mean night

* Numbers in parentheses refer to "Literature cited."

temperature. His interpretation of these results was that high night temperatures increased respiration less and so reduced net assimilation rate, whereas high day temperatures increased NAR by increasing the rate of photosynthesis.

Watson (7) determined mean net assimilation rate of several species of crops growing in the same area over the same period of the year. Differences were found that were consistent from year to year. Significant differences were found between wheat and barley, barley and sugar beet, potato and sugar beet.

Whereas extensive empirical results concerning effects of high night temperature on various plants are available and some work has been done in an attempt to explain, on a physiological basis, interspecific variation due to high night temperature, very little attention has been given intervarietal variation.

Genotype-night temperature interaction has not been extensively studied, although it has been observed by Roberts and Struckmeyer (5) that some varieties within a species show a marked adaptation to widely differing conditions.

McKinney and Sando (4) studied earliness and seasonal growth habit in wheat as influenced by temperature and photoperiodism. They showed that segregating populations from certain crosses did not give constant segregating ratios for earliness under all conditions of temperature and daylength, and concluded that temperature-daylength response characteristics were determined by internal mechanisms regulated genetically.

Grafius (2) studied the genotype-night temperature interaction in oat and barley varieties. The genotype-night temperature interaction appeared to conform to the equation $Y = c\ 10^{kt}$, based on the hypothesis that relative yields of various genotypes responded to average night temperatures in a manner similar to the compound interest curve. Although the genotype-night temperature interaction was not proved, there was a strong indication that such an interaction existed.

THEORETICAL CONSIDERATIONS

The correlation coefficient "r" is a numerical expression of relationship between variables in a bivariate population. Every set of paired data is identified by two regression lines which are commonly represented by their slopes, b_{12}, b_{21}. It has been already shown that $r = \sqrt{b_{12} \cdot b_{21}}$, or $r^2 = b_{12} \cdot b_{21}$ (6).

In Figure 1, two regression lines with slopes b_{12} and b_{21} are represented. θ is the angle of the regression line b_{12} and β is the angle of b_{21}.

Now, since $r^2 = b_{12} \cdot b_{21}$, $r^2 = \tan\theta \cdot \tan\beta = \frac{AB}{AO} \cdot \frac{AO}{AC} = \frac{AB}{AC}$.

If Figure 1 is repeated and now segment AC is represented by vector $\bar{a}$ (Figure 2) and if a vector $\bar{b}$, equal in length to vector $\bar{a}$, is so constructed that a perpendicular dropped from Q to AC meets AC at B, an angle α is generated.

Now, since $r^2 = \frac{AB}{AC}$, $r^2 = \frac{\bar{b}\ \cos\alpha}{\bar{a}}$, and since $\bar{a} = \bar{b}$, then $r^2 = \cos\alpha$.

Thus, an $\cos^{-1}\alpha$ is associated with the bivariate population. This angle is unique for the two regression lines which have been derived from the paired data of a given population. Therefore, the relationship between any two sets of paired data may be represented by an angle α such that the squared correlation coefficient is equal to $\cos\alpha_a$.

Knowing that any r^2 is the cosine of a corresponding angle α, a new method of analysis of correlated data using vector analysis is indicated (Grafius and Kiesling, unpublished).

The method allows the biologist to assign planes of force and to measure the degree of determination of other sets by these planes and ultimately to estimate individual varietal responses. For example, it is apparent that two non-parallel vectors with a common origin form a plane. Suppose one has two sets of the same barley varieties grown at two different night temperatures. These can be represented as two vectors with a common origin having $\cos^{-1} \alpha = r^2$. If the differences between the two sets are mainly due to night temperature, then the two vectors form a night temperature plane. Other vectors compared with this plane will cast shadows on the plane which are, in reality, resultants. The angle θ between one of the coplanar vectors, for example, $\bar{a}$, and the resultant, determines the temperature effect. The squared coefficient between the resultant and the generating vector represents the degree of determination by the resultant forces in the plane of the generating vector. The geometry is such that when the generating veeter is not influenced by the plane, no shadow is cast on the plane.

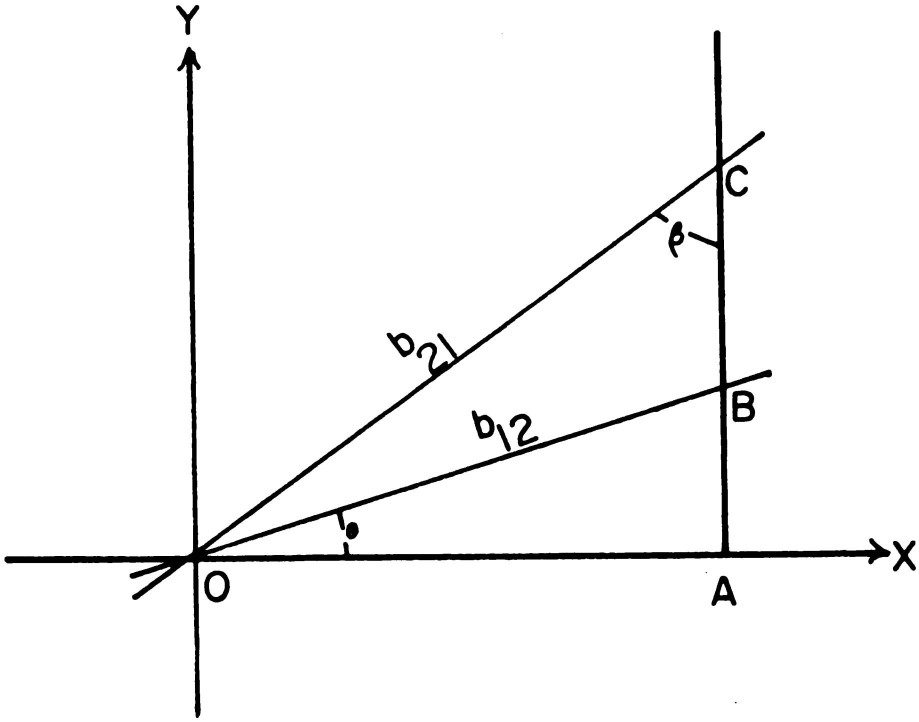

Figure 1. Regression lines OB and OC with slopes b_{12} and b_{21} respectively.

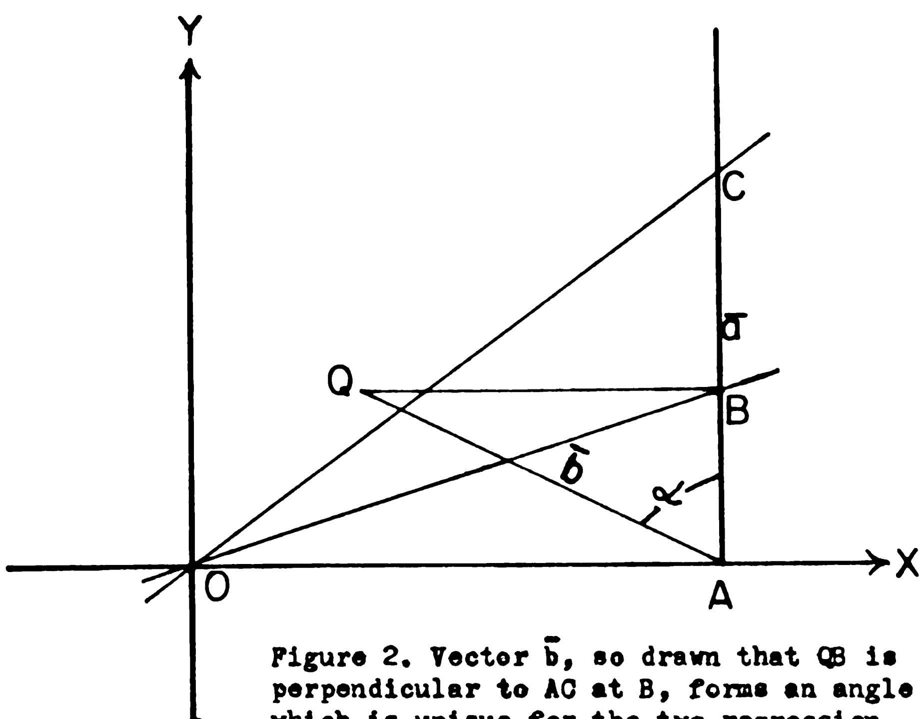

Figure 2. Vector $\bar{b}$, so drawn that QB is perpendicular to AC at B, forms an angle which <u>is</u> unique for the two regression lines $\overline{OB}$ and $\overline{OC}$, where AC = $\bar{a}$ ± $\bar{b}$.

MATERIALS AND METHODS

Four hundred and thirty varieties of Manchurian barley from the World Collection were planted in the field in the summer of 1956 and used in the study of genotype-night temperature interaction. Two and a half grams, or about 100 seeds, of each variety were planted by hand, in five foot rows one foot apart; the seeds were placed, approximately, at 3/4 inch intervals. There was one replication and two dates of planting, April 24 and May 22. Notes were taken for each planting on heading date, average height, weight, and number of kernels of 10 heads. The number of kernels was computed by determining the weight of 100 seeds and then dividing this number into the weight of all the seeds from 10 heads. The height of each variety was taken to be the mean of 9 measurements of that variety two weeks after heading. Measurements were made from the base of the plant to the base of the head. A given variety was considered "headed-out" when 75% of the heads in the row were extruding from the boot.

In the summer of 1957 a similar procedure was followed with 150 varieties being selected at random from the 430 varieties used in 1956. All subsequent calculations and analyses are based on the data for the 150 varieties for both 1956 and 1957. Planting procedures and observations were similar to those of 1956. The two dates of planting were April 30 and June 2.

The plots used both in 1956 and 1957 were of uniform fertility and were well drained. Mildew was prevalent in both 1956 and 1957 and was controlled by dusting the plants with sulfur, thus, keeping the effects of disease at a very low level. Aphids were controlled by a malathion spray.

RESULTS

Table 1 presents degree-nights for each one of the two growing seasons, both early and late planting. Degree-nights is a cumulative total of degrees above 60° F. for the period, two weeks after planting date to two weeks after average heading date of all the varieties in a set. Sixty degrees was considered a critical point on the basis of observations in the greenhouse. It is admittedly an arbitrary point.

Table 1: Degree-nights for the two growing seasons

Season	Degree Nights
Early-1956[1]	112
Late-1956	110
Early-1957	88
Late-1957	129

Correlation coefficients were calculated for the observations for all possible combinations of the growing seasons. These, along with corresponding values for r^2 and corresponding angles, are presented in Table 2.

Two varieties, O.I. 4266 and O.I. 4426, did not head out in the Late-1957 planting. They headed out in Early-1957 and

[1] Early-1956 refers to April 24, 1956 planting. Late-1956 refers to May 22, 1956 planting. Early-1957 refers to April 30, 1957 planting, and Late-1957 refers to June 2, 1957 planting.

Table 2 : Values of r, r^2, and angle θ for combinations of Early-1956, Late-1956, Early-1957, and Late-1957

Variates		Date of Heading	Height	Weight of Seeds	Number of Seeds
	r	0.406**	0.637**	0.569**	0.690**
E'56 vs. L'56	r^2	0.1648	0.4058	0.3238	0.4761
	θ	80.5°	66.1°	71.1°	61.6°
	r	0.627**	0.432**	0.687**	0.825**
E'57 vs. L'57	r^2	0.3931	0.1866	0.4719	0.6806
	θ	66.8°	79.3°	61.9°	47.1°
	r	0.411**	-0.139	0.597**	0.812**
E'56 vs. L'57	r^2	0.1689	0.0193	0.3564	0.6593
	θ	80.3°	88.9°	69.1°	48.8°
	r	0.308**	0.510**	0.799**	0.789**
E'56 vs. E'57	r^2	0.0949	0.2601	0.6384	0.6225
	θ	84.6°	74.9°	50.3°	51.5°
	r	0.557**	0.084	0.586**	0.697**
E'57 vs. L'56	r^2	0.3102	0.0071	0.3434	0.4858
	θ	71.9°	89.6°	69.9°	60.9°
	r	0.504**	0.246**	0.471**	0.704**
L'56 vs. L'57	r^2	0.2540	0.0605	0.2218	0.4956
	θ	75.3°	86.5°	77.2°	60.3°

**r significant at 1% level

in both plantings of 1956. The data from these varieties were not included in the computation of correlation coefficients because it appeared that they did not belong to the population under study since their reaction to conditions of the Late-1957 season was totally different from the reaction of all the other varieties.

It now becomes possible to analyze the results by means of vector analysis. In order to exemplify the procedure, complete analysis will be carried out. In this instance, the weight of seeds is the character under study.

The first step in vector analysis is to set up a plane of force. From Table 1 it can be observed that Early-1957 and Late-1957 differ by 41 degree-nights. Rainfall and fertility appeared adequate for both sets, and diseases were controlled. The main difference between the two sets appeared to be the period in which each was grown. Both length of day and night temperature were major variables. For some plant characteristics one was more important; for others the reverse was true. In Figure 3 a plane is set up, using as vectors Early-1957 and Late-1957. The angle formed by the two vectors is obtained from Table 2.

Early-1956 and Late-1956 are two other vectors which are associated with this plane. Each one of them casts a shadow, or a resultant, on the plane. The position of each of the resultants is determined from the angle θ which it forms with both of the coplanar vectors.

Assume that $\bar{a}$ (Early-1957) is a vector; θ for Early-1956 is then determined by using the information presented in Figure 4. The angles and the corresponding cosines are obtained from Table 2.

Referring to Figure 4 and by use of spherical trigonometry: $\cos A = \dfrac{\cos \alpha - (\cos \beta)(\cos \gamma)}{\sin \beta \cdot \sin \gamma}$

$$= \frac{0.3564 - (0.6384)(0.4719)}{(0.8821)\ (0.7694)} = 0.0812.$$

Then, $\cot \theta = \dfrac{\cot \gamma}{\cos A} = 10.2241$, $\theta = 5.6°$. Resultant b', then, lies in the plane AOD and is 5.6° away from $\bar{a}$, Figure 3. The position of c' can be determined by a similar procedure.

The behavior of varieties in this plane can be observed by representing the response of each variety by a smooth curve, Figure 3.

The curves are drawn according to the following procedure: the points on the coplanar vector are obtained from the data and plotted as percent of the mean for each set; the points on the resultants are calculated on the basis of the angle θ and the angle β of the coplanar vectors.

The point on b' is calculated as follows:

$$b' = \frac{\bar{a} \cos \theta_{b'}}{\cos \theta_{b'} + \cos(\beta - \theta_{b'})} + \frac{\bar{d} \cos(\beta - \theta_{b'})}{\cos \theta_{b'} + \cos(\beta - \theta_{b'})}$$

Values for $\bar{a}$ and $\bar{d}$ are represented as percent of the mean.

The point on c' is similarly calculated by using $\theta_{c'}$ in this case. Calculation of points on b' and c' is presented in Table 3.

Figure 3, then, shows the pattern of behavior of five given varieties. The diagram, first of all, shows that the vector $\bar{a}$ and resultants b' and c' are markedly removed from vector $\bar{d}$. On the basis of the degree-nights (Table 1), this would be expected if the AOD plane in Figure 3 were due to night temperature. Late-1957 was warm as compared to Early-1956,

Table 3: Calculation of points on resultants b' and c' where
$b' = 0.6421\bar{a} + 0.3579\bar{d}$ and $c' = 0.6076\bar{a} + 0.3923\bar{d}$.
Data are weight of seeds in percent of mean.

C.I.	$\bar{a}$ (% of Mean)	$\bar{d}$ (% of Mean)	$\bar{a}$ x 0.6421	$\bar{d}$ x 0.3579	b'	$\bar{a}$ x 0.6076	$\bar{d}$ x 0.3923	c'
1397	99	98	63.6	35.1	98.7	60.2	38.4	98.6
4827	117	98	75.1	35.1	110.2	71.1	38.4	109.5
4410	96	93	66.6	33.3	94.9	58.3	36.5	94.8
4490	101	79	64.8	28.3	93.1	61.4	31.0	92.4
4527	86	135	55.2	48.3	103.5	52.3	53.0	105.3

Late-1956, and Early-1957. It may be argued that daylength,[1/] rather than night temperature, produced the response. This hypothesis will have to be refuted on the basis of the position of Late-1956 resultant. If daylength were the force involved, Late-1956 would have to be closely associated with Late-1957.

The varieties show a marked interaction as they shift across the plane. The interaction is observed not only in the changing behavior of a given variety as it moves across the plane, but also in the different arrangement of varieties relative to one another in Late-1957 as compared with Early-1957. This interaction is highly significant as shown by the F value in Table 4.

Table 4: F values of (varieties x date of planting) interaction for 1957. Varietal behavior is represented on basis of date of planting, height, weight of seeds, and number of seeds.

Observation	F
Date of Planting	1.61**
Height	1.83**
Weight of Seeds	19.77**
Number of Seeds	1.21

**Significant at 1% level

Varieties were studied, in Figure 5, on the basis of number of seeds. The plane again appears to be a night-temperature plane determined by Early-1957 and Late-1957. Resultants

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[1/] "Daylength" refers to seasonal changes of period of daylight and not photoperiodism <u>per se</u>.

b' and c' are also given. It can be noticed that the position of the resultants is halfway between the two vectors. This arrangement, while demonstrating effect of night temperature, also indicates that the relationship between night temperature and Θ may or may not be linear. It is not linear in Figure 3, but appears to be linear in Figure 5.

Figure 6 is a diagram based on height of plants. The vectors again are Early-1957 and Late-1957; however, this plane can not be considered a night-temperature plane. Rather, it appears to be a daylength plane, because, were it a temperature plane, Late-1956 would not be associated closely with Late-1957. Table 1 shows that the two seasons were distinctly different as far as degree nights was concerned. However, on the basis of daylength, the two seasons were similar, and this is brought out in the diagram. Early-1956 and Early-1957 were also similar in daylength, and the diagram bears that out also. It can thus be inferred that height of plants should be considered a genotype-daylength, rather than a genotype-night temperature interaction.

Heading dates were treated next, and in Figure 7 a varietal interaction can be observed. An interaction of genotype and night temperature and daylength is strongly indicated. This can be borne out when the "degree-nights" data is studied.

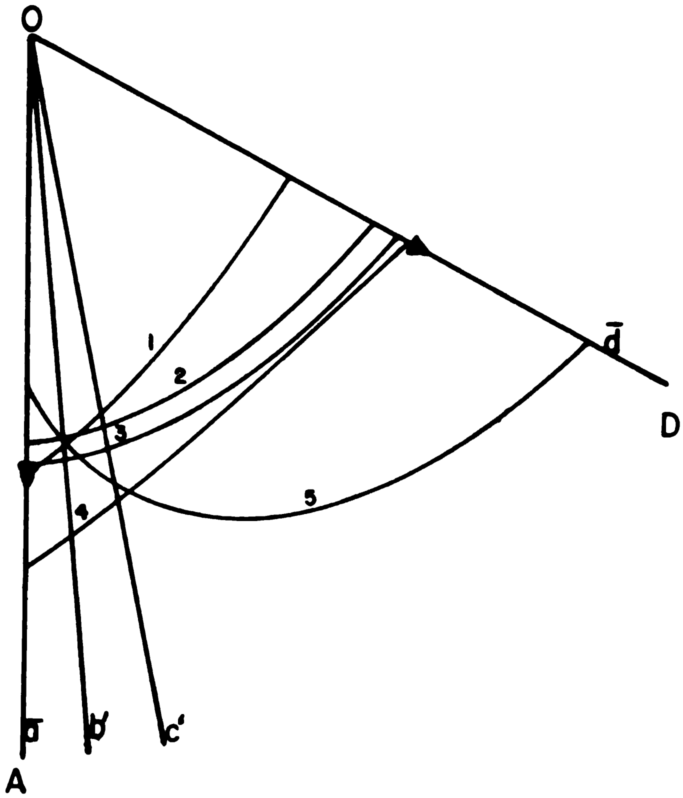

Figure 3. Diagram of varietal behavior on the basis of weight of seeds. Plane AOD is determined by ā (E,'57) and d̄ (L,'57). b' and c' are resultants. b' is generated by E,'56, c' by L,'56. Arrowheads are at 100. Smooth curves represent varietal behavior:
1 - C.I. 4490, 2 - C.I. 4410,
3 - C.I. 1397, 4 - C.I. 4827,
5 - C.I. 4527.

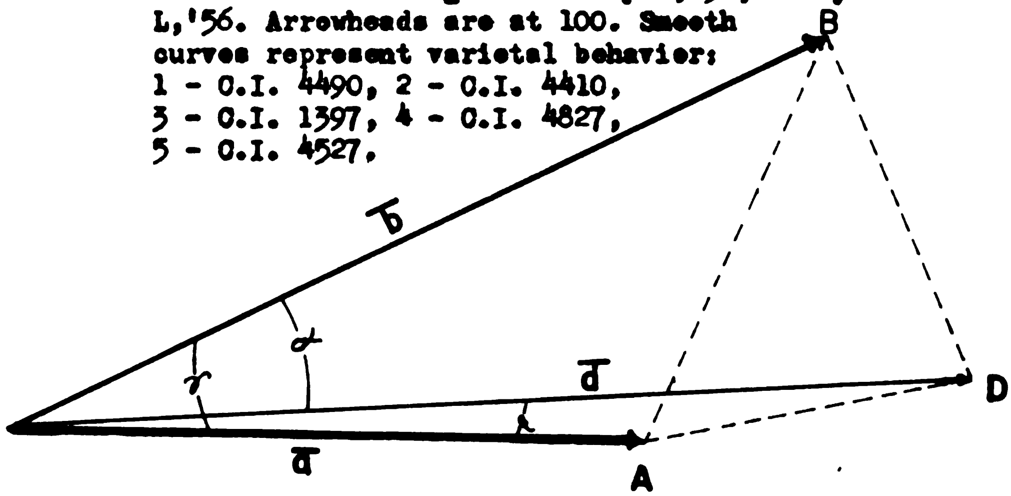

Figure 4. Plane AOD determined by vectors OA (Early 1957) and OD (Late 1957). OB (Early 1956) is the vector which generates a resultant in the plane. Angles between vectors are represented by α , β , γ .

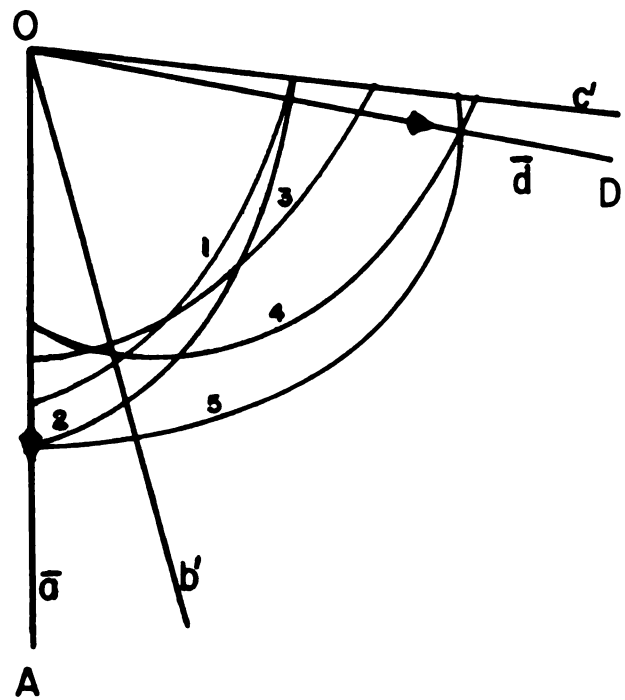

Figure 6. Diagram of varietal behavior on the basis of height of plants. Plane AOD is determined by $\bar{a}$ (E, '57) and $\bar{d}$ (L, '57). b' and c' are resultants. b' is generated by E, '56, c' by L, '56. Arrowheads are at 100. Smooth curves represent varietal behavior: 1 - C.I. 4550, 2 - C.I. 4781, 3 - C.I. 4527-1, 4 - C.I. 4819, 5 - C.I. 4271.

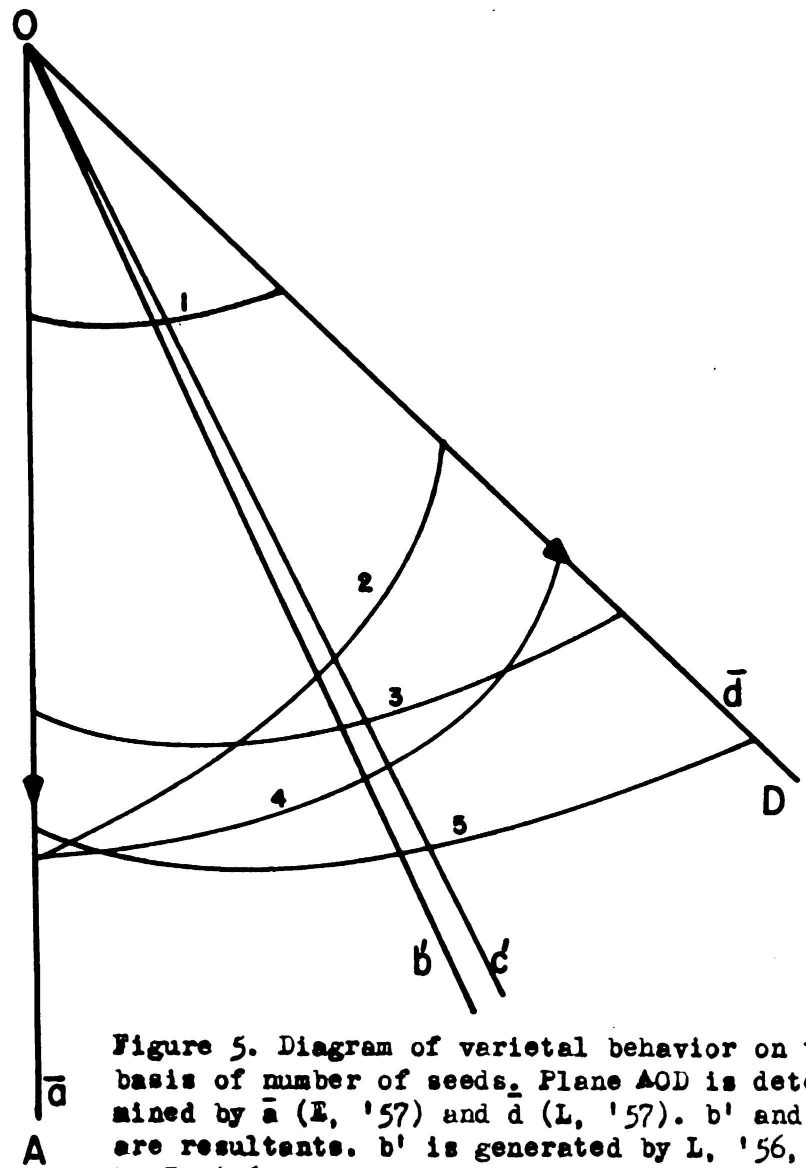

Figure 5. Diagram of varietal behavior on the basis of number of seeds. Plane AOD is determined by $\bar{a}$ (E, '57) and $\bar{d}$ (L, '57). b' and c' are resultants. b' is generated by L, '56, c' by E, '56. Arrowheads are at 100. Smooth curves represent varietal behavior: 1 - C.I. 4263, 2 - C.I. 4573-1, 3 - C.I. 4513, 5 - C.I. 4797.

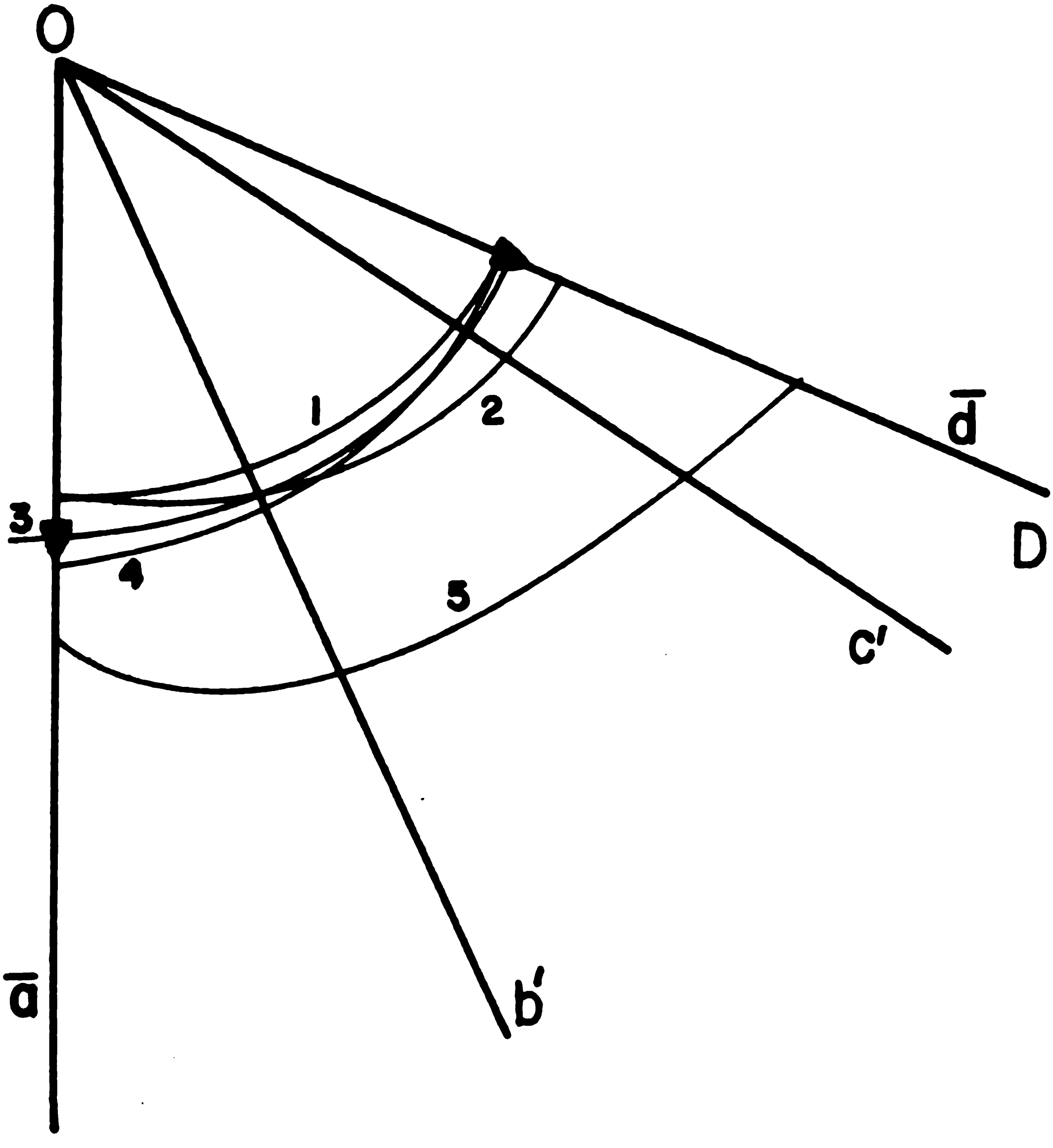

Figure 7. Diagram of varietal behavior on the basis of date of heading. Plane AOD is determined by vectors $\bar{a}$ (E,'57) and $\bar{d}$ (L,'57). b' and c' are resultants. b' is generated by Late '56, c' by Early '56. Arrowheads are at 100. Varietal behavior is represented by smooth curves 1 - O.I. 4490, 2 - O.I. 4423-1, 3 - O.I. 4767, 4 - O.I. 4445, 5 - O.I. 4732.

DISCUSSION

Table 5 presents degrees of determination of the generating vector by the plane AOD where A is Early-1957 and D is Late-1957. These values were obtained by use of Wright's (8) path coefficients. This value is equal to the squared correlation coefficient between the generating vector and the resultant.

Table 5: Degree of determination of generating vector $\bar{v}$ by the forces in the plane Early-1957 and Late-1957

$\bar{v}$	Date of Heading	Height	Weight	Number
Early-1956	0.58	0.42	0.64	0.70
Late-1956	0.35	0.06	0.35	0.54

It can observed that, with the exception of height for Late-1956, the degrees of determination are rather high. This indicates that the resultants in the plane play a large role in determining the generating vectors. The condition of height, Late-1956, however, cannot be understood. One may assume that that vector is only weakly determined by forces in the plane AOD.

It becomes necessary, therefore, to emphasize a very important point, namely, the proper interpretation of the plane; this is the only arbitrary step in vector analysis. Given any amount of data, anyone analyzing the data by vector analysis must obtain identical diagrams and identical curves representing varietal behavior. However, the interpretation of the plane, i.e., the assignation or identification of the forces in the plane which produce the observed effect is a matter which is left to the judgment of the biologist. The biologist must weigh and consider carefully the conditions under which the plants were grown, and he must also study each diagram before he assigns forces to a plane.

Figure 3 shows genotypic interaction as observed on the basis of weight of seeds. The plane is determined by vectors, Early-1957 and Late-1957. On the basis of the following reasons it appears justifiable to assume that this plane is a night-temperature plane. Table 1 shows that Early-1957 and Late-1957 differed considerably in night temperature. If it is argued that seasonal change of amount of daylight could be the main variable, a further study of the diagram will reveal that that is unlikely. Were this the force determining the vectors generating b' and c', the resultant c', which is generated by Late-1956, would have to lie close to Late-1957 because both of those planting dates were characterized by similar daylength. It is then probable that a genotype-night temperature interaction was observed when weight of seeds was the characteristic studied.

The plane of Figure 5 also has been interpreted as a night-temperature plane. This plane also is determined by Early-1957 and Late-1957, the two seasons differing in night temperature. As pointed out earlier, the position of the resultants b' and c' follows from Table 1 and exhibits a linear-type response of genotypes to increase in night temperature, taking number of seeds as a varietal characteristic.

Varietal behavior on the basis of height is diagrammed in Figure 6. As pointed out earlier, the plane, although formed by Early-1957 and Late-1957, does not appear to be a temperature plane, but a daylength plane. This inference was made after the diagram was studied, and it seemed probable that the arrangement of the resultants was mainly due to daylength. However, the degree of determination, as shown in Table 5, is so low that no conclusions can be drawn.

The plane in Figure 7 is also determined by Early-1957 and Late-1957. The degrees of determination of Early-1956 and Late-1956 are fairly high, indicating that the positions of the resultants are indeed controlled by the planar force; hence if this relationship is not due to chance, then one must assume that both daylength and night temperature are involved. If one assumes that warm temperatures for long nights produce the same effect as hot temperatures for short nights, then Early-1956 and Late-1957 should be similar. Conversely, if warm temperatures for short nights and cool temperatures for long nights produce the same effects, then Late-1956 and Early-1957 should be similar. Figure 7 bears this out.

This again illustrates the importance of the interpretation of the plane. In the case of Figures 3, 5, and 7, the interpretation of the plane in each seems plausible. Fertility, disease, insects, and availability of water were the same for all varieties. Daylength and night temperature were the only known major variables in environment. On the basis of the "degree-nights" data and the diagrams, forces were assigned accordingly to the planes and the genotype interaction then explained.

It has been possible, then, by means of vector analysis, to observe genotype-night temperature interaction in the case of weight and number of seeds. In the case of date of heading, the genotype interacted with both night temperature and daylength. It should be again pointed out that due to the low degree of determination, the interaction of varieties on the basis of height cannot be explained. This analysis reveals the interaction by demonstrating the pattern of behavior of the varieties throughout the two growing seasons and four planting dates. It should be kept in mind that each diagram is based strictly on the data because the figures and the angles follow directly from the observations of the plant material. Hence, each diagram is not in the least arbitrary and is unique for the data used.

SUMMARY

One hundred and fifty varieties of Manchurian barley were used in a study of genotype-night temperature interaction. Correlation coefficients were computed from the data, and these were used in analysis of varietal behavior. The varieties were analyzed by vector analysis. The vector diagrams for weight of seeds and number of seeds were interpreted as planes of force, that force being night temperature. The diagram considering height of plants was considered to be a daylength plane on the basis of the description of the environment. The diagram for date of heading is interpreted as a plane of two forces: night temperature and daylength.

On the basis of the behavior of the varieties given as smooth curves in each diagram, genotype interaction is observed in each. In the diagram analyzing weight and number of seeds, a strong indication of genotype-night temperature interaction is observed. A possible genotype-daylength interaction may be indicated in the diagram analyzing height of varieties. However, because of the low degree of determination of the generating vector, that conclusion is not fully justifiable. The diagram concerned with date of heading strongly indicates varietal interaction with both night temperature and daylength.

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