AN ANALYSIS OF A NEGATIVE RESPONSE TO SELECTION FOR HIGH YIELD IN WINTER BARLEY, HORDEUM VULGARE

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ABSTRACT

AN ANALYSIS OF A NEGATIVE RESPONSE TO SELECTION FOR HIGH YIELD IN WINTER BARLEY, HORDEUM VULGARE

by Cecil D. Nickell

A winter barley population composed of 387 lines in the F_5 generation was grown in 1966 from which 136 strains were selected with a mean yield of 123.3 per cent of the check variety. The same selected population was grown in 1967 producing a mean yield of 90.7 per cent of the check variety.

The "apparent" negative response to selection was analyzed with respect to yield components; heads per unit area (X), seeds per head (Y), and seed weight (Z). Twice as many heads were produced in 1967 as compared to 1966, but fewer seeds per head and smaller seeds were produced in 1967 than in 1966. The inverse relationship between the components is explained by "component compensation."

The inter-annual correlations for the yield components were slightly positive, while the value for yield was slightly negative.

The overriding effect of the environment on the genetic processes and extreme compensation between yield components were postulated to cause the low inter-annual correlations.

An "universal" surface was created by plotting seed weight, seed number per area, and yield in three-dimensions. Mathematically and biologically, only one surface can be formed upon which all seed bearing crops can be placed. Each seed crop has an unique position upon the surface. The swarm of points on the "universal" surface created by the data collected in both 1966 and 1967 can be thought of as representing a portion of the total evolutionary highway for barley.

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By

Cecil D. Nickell

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INTRODUCTION

Selection, practiced under a dynamic environment, provides the plant breeder with many frustrations. Qualitative characters are usually affected only in a minor way by the environment, allowing the plant breeder to make selection progress. On the other hand, quantitative traits are polygenic and are subject to many alterations by the environment. During recent years, there has been a tendency to partition the more complex quantitative traits into simpler components. Certain complex characters often may be thought of as artifacts made up on actions and interactions of their components. Presumably, the heritability of these complex characters is lower, in general than for the components.

Yield in winter barley is defined as the product of, in order of development, heads per unit area (X), seeds per head (Y), and seed weight (Z). Genetically, these traits are assumed to be independent, but they do interact with each other and with the environment. Even though the heritability is frequently high for the components, they are assumed to be quantitative characters. Selection, even for components of the complex trait, yield, may produce some very unusual and undesirable results.

A population of winter barley lines was created by making nineteen crosses with the goal of producing high yielding progeny of good malting quality. Selection pressure was placed on yield with special emphasis on larger seeds and higher tiller number. The expected selected population mean in 1967 should have fallen between the selected and unselected population means of 1966, (Figure 1 and 2) when the check variety mean is used as a reference point.

If the check variety is used as a constant point, the "apparent" genetic gain is negative. To the plant breeder, a negative response to selection is quite undesirable.

It is the intent of this thesis to analyze and explain why such results should have been experienced for yield under two environments.

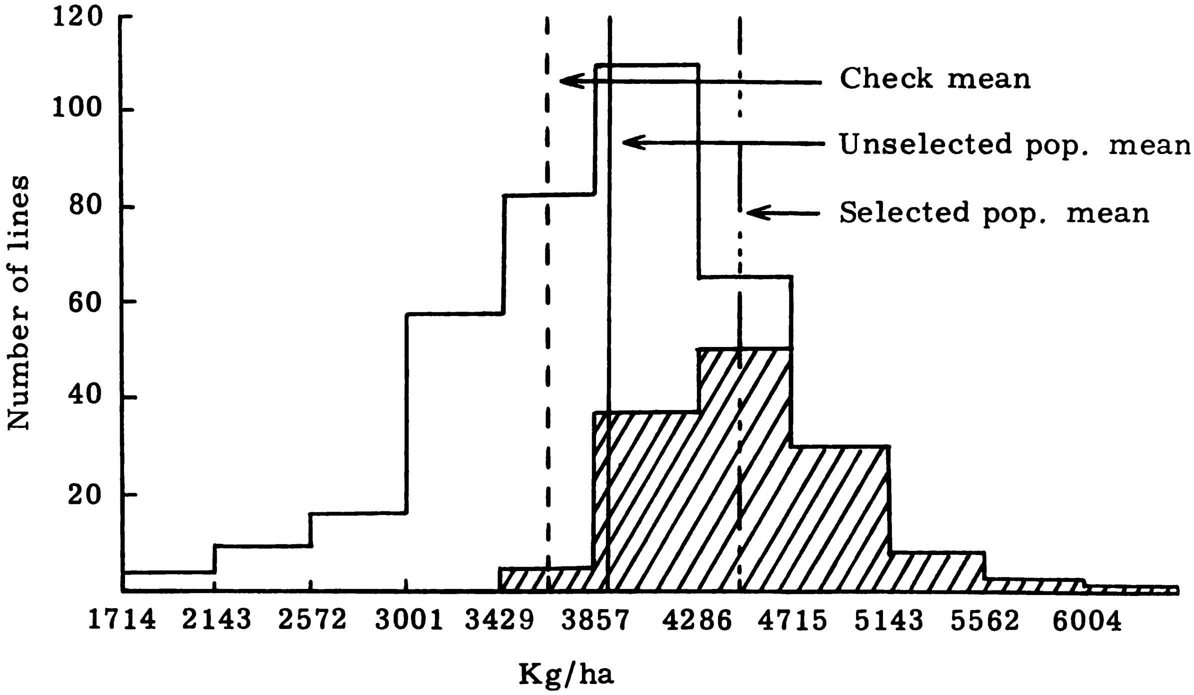


FIGURE 1. -- The distribution of 387 winter barley lines against yield categories for 1966. The cross-hatched area represents the distribution of the 136 selected lines in 1966. The broken line represents the yield of the check variety, Hudson, in 1966.

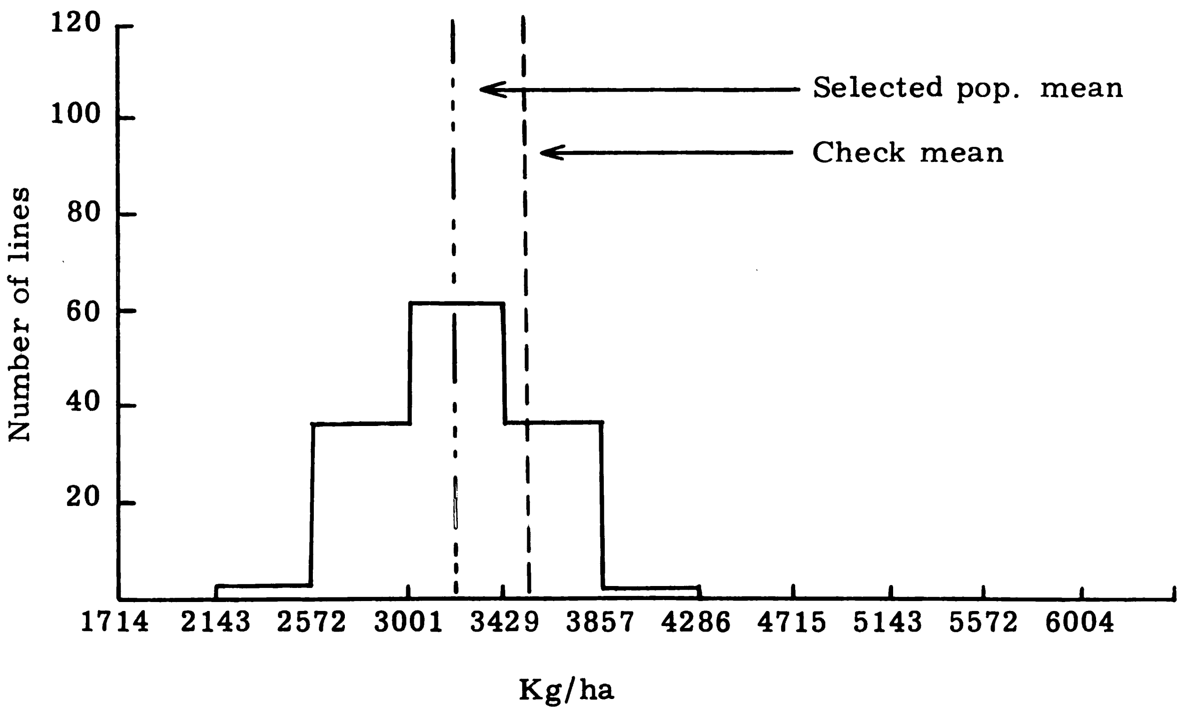


FIGURE 2. -- The distribution of selected lines grown in 1967 against yield categories.

LITERATURE

Yield in oats has been defined by Grafius (7) as a geometrical construct, namely, a parallelopiped with the yield components as the edges: panicles per unit area (X), kernels per panicle (Y), and kernel weight (Z). The longest edge is the most subject to change and the changes in edges or components tend to counterbalance.

In cotton, Hutchinson (9) defined bolls per plant, seed cotton per boll, seeds per boll, and lint per seed as yield components. Selection was more effective for certain components than others and some of the characters were affected greatly by the environment. He was one of the first individuals to show that the increase of one character could be associated with the decrease of another, which was called "physiological incompatabilities."

Whitehouse et al. (16) described the yield components of wheat as weight per kernel, kernel per spike, spikelets per ear, and ears per plant. Complete independence between these components was indicated by correlation analysis.

Olsson (14) reported a tendency toward a decrease in seed weight in Brassica and Sinapis with an increase in the number of seeds per pod, and selection for low seed number produced a decrease in fertility.

Archibong (2) found that competitive stresses in navy beans caused significant changes in the yield component interrelationships. Pod number per plant was more subject to change than seed weight or seed number per pod.

Adams (1) found negative correlations between yield components in field beans. He found that within these components low to zero correlations would occur in space plantings and negative correlations would occur in close-interval plantings. Inter-plant competition for metabolites was suggested as the mechanism for component compensation.

Johnson et al. (10) found a highly negative association between seed number per plant and seed weight both in phenotypic and genotypic correlations in soybeans. A negative association was also found between pod number per plant and seed weight.

Bal et al. (3) reported an association of heavy seeds in barley with small heads, after natural selection, again presenting the idea of negative association between yield components.

Kambal et al. (11) reported negative associations between yield components in hybrid grain sorghum but these were absent in the parent population and, in fact, a highly positive correlation existed between seeds per head and seed weight.

Other authors have published on the negative interrelationship of yield components: corn (Leng (12)), several grass species (Van Keuren (18)), tomatoes (Williams (17)), and crested wheatgrass (Dewey and Lu (4)).

METHODS AND MATERIALS

In 1962, twelve winter barley lines were selected as parents to start the second cycle of a recurrent selection program. These lines were presumed to be essentially homozygous since they were in the F_8 generation. Selection was based upon several characteristics which included yield, seed weight, seeds per head, heads per unit area, disease reaction and nine malting quality traits. Combinations of parental lines were selected using the vector approach as described by Grafius (8). Nineteen crosses were made in 1962 and each cross maintained in bulk through the F_3 generation, and agronomic and malting data were collected. Eleven crosses were selected based on superior malting and agronomic performance. Five hundred heads from each cross were picked at random and planted in head hills in the fall of 1964. Severe cold injury occurred during the winter reducing the number of head hills from 5, 500 to approximately 2, 500. In the summer of 1965, 387 hills were selected using the criteria of plant vigor, disease resistance, seed size and tiller number. These selections were planted in the fall of 1965 in single rod-row plots with check plots of either Hudson, Wong, or

Dicktoo winter barley planted every eleventh plot. Winter kill occurred early in 1966 resulting in an average survival of 56%. In the summer of 1966, 136 lines were chosen, with selection being based upon yield data, winter survival, seed weight, protein analysis, and seed number per unit area.

Replicated plots were planted in the fall of 1966 with Hudson and Wong as checks. Data were collected in 1967 on yield, seed weight, seed number per unit area, and disease reaction. No winter kill was observed in 1967.

RESULTS

Yield data from the population of 387 winter barley lines harvested in 1966 are summarized in Figure 1. The mean of the total population of 387 lines was 3903.6 Kg/ha (91.08 bu/acre). The selected population mean yield was 4490.0 Kg/ha (104.78 bu/acre). The same 136 selected lines were grown in 1967 with Hudson as the check variety. The mean yield (Figure 2) of the population was 3206.0 Kg/ha (74.8 bu/acre) and the Hudson mean was 3535.0 Kg/ha (82.5 bu/acre). A decrease of 1284.9 Kg/ha (30 bu/acre) occurred in the selected population mean comparing the 1966 and 1967 results. The check variety change was only 107.2 Kg/ha (2.5 bu/acre) lower in 1967. Two check varieties were used in both years, Hudson and Wong, and each responded the same in the two years; therefore, Hudson will be used as the check variety throughout the results.

Figure 3 and 4 provide a summary of seeds per 0.9 meter of linear row obtained from both the selected and unselected population in 1966 and 1967. The mean for the unselected population was 3850 seeds/.9m compared to 4292 seeds/.9m for the selected population in 1966. The check variety produced 4015 seeds/.9m which

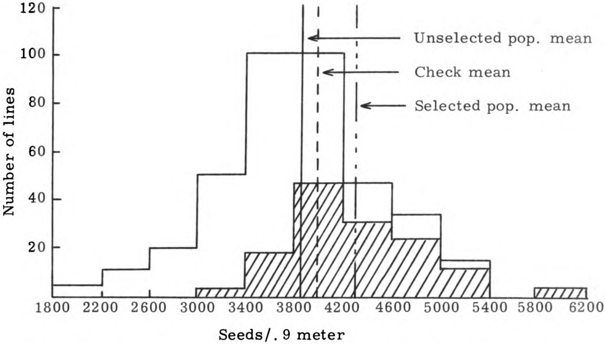


FIGURE 3. -- The distribution of 387 winter barley lines against seed number categories for 1966. The cross-hatched area represents the distribution of the 136 selected lines grown in 1966. The broken line represents the yield of a check, Hudson, in 1966.

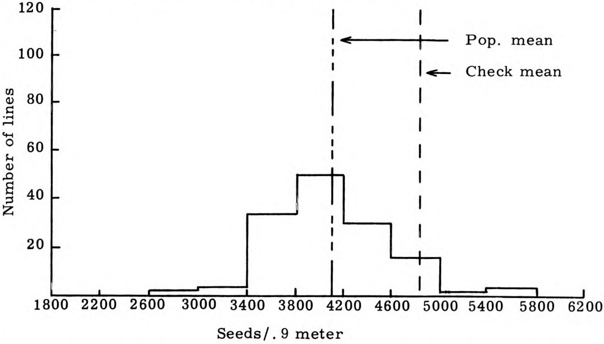


FIGURE 4. -- The distribution of the selected lines in 1967 against seed number categories, with Hudson as a check.

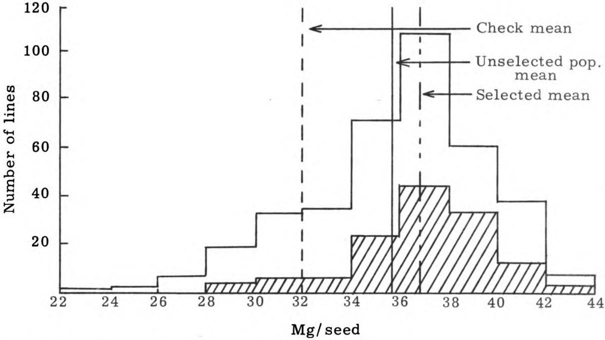


FIGURE 5. -- The distribution of 387 lines against seed weight categories for 1966. The cross-hatched area represents the distribution of the 136 selected lines. The broken line represents the seed weight of the check, Hudson, in 1966.

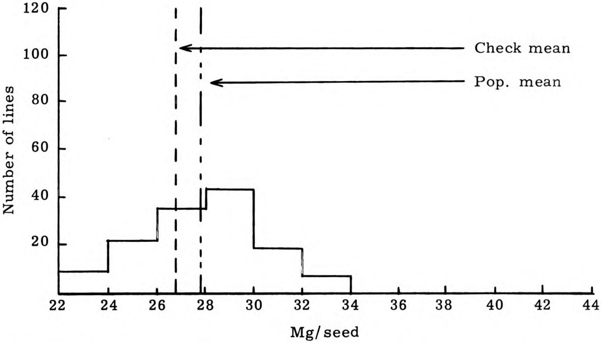


FIGURE 6. -- The distribution of the 136 selected lines grown in 1967 against seed weight categories. The broken line represents the check, Hudson, in 1967.

was above the unselected population mean and below the selected population mean. In 1967, the 136 lines produced an average of 4101.3 seeds/.9m and the check variety 4843.1 seeds/.9m. Between years the selected population mean was reduced only 191 seeds/.9m but the check variety increased 842.8 seeds/.9m.

Figure 5 summarizes the distribution of seed weight in 1966 for the total population. The unselected population mean was 35.7 mg/seed compared to 36.6 mg/seed for the selected group. Figure 6 presents the distribution for seed weight of the selected population in 1967. The mean seed weight decreased 9 milligrams per seed below the 1966 mean. The check variety was depressed from 32.0 to 26.8 milligrams per seed in 1967.

Seeds-per-head was determined on a limited number of lines by selecting 5 heads at random from each plot and counting the seeds.

Table 1 provides a summary of these results obtained on 139 lines in the unselected population and 51 of the selected group. The selected group mean did exceed the unselected population mean for all the components and also for yield. The number of heads per .9m doubled in 1967 over 1966. At the same time seed weight and seed number per head was reduced. Seeds per .9m decreased approximately 390 seeds. Yield was greatly depressed in this limited set of lines as it was in the total selected population.

TABLE 1.--Comparison of yield component means between the selected and unselected population, and between the selected population grown in 1966 and 1967. The unselected population contains 139 lines, and the selected group is made up of 51 lines.

Trait	Unselected	Selected	
	1966	1966	1967
Heads per .9 meter (X)	91.3	100.9	199.5
Seeds per head (Y)	42.6	43.8	20.2
Seed weight mg/seed (Z)	37.1	37.4	28.5
Seeds per .9 meter (XY)	3889.4	4419.4	4029.9
Yield (W = XYZ) Kg/ha	4122.7	4721.0	3266.6
Bu/acre	96.2	110.2	76.5

Phenotypic correlations were calculated between yield components for the unselected and selected populations (Table 2). Both the pooled and unpooled values between tiller number and seed number per head were highly negative in both populations and in both years. A negative relationship was found between tiller number and seed weight in both years and populations, but was statistically significant only in the selected population for 1966, when based upon the unpooled data. The correlation of seed weight with seed number per head was zero in 1966. However, in 1967, a highly significant negative relationship was found. Seed number per unit area was highly negatively correlated with seed weight in both years and in both populations.

TABLE 2. -- Correlations between yield and yield components calculated from the data collected in 1966 and 1967. (The top line represents the pooled coefficients over 11 crosses and the bottom line the unpooled correlation coefficients.)

	r_{xy}	r_{xz}	r_{zy}	[1] r_{nz}
Unselected population				
387 lines				-.34**
				-.28**
139 lines	-.44**	-.32**	.12	-.34**
	-.72**	-.16	-.02	-.41**
Selected population				
1966				
136 lines				-.55**
				-.58**
51 lines	-.77**	-.35*	.16	-.56**
	-.71**	-.38*	.05	-.59**
1967				
136 lines	-.60**	-.18*	-.23**	-.46**
	-.46**	-.12	-.37**	-.50**
51 lines	-.56**	-.07	-.27	-.45**
	-.34*	.04	-.35*	-.49**

[1] n = xy (seeds per .9 meter of linear row)

Correlations were calculated between years for each of the yield components and yield (Table 3). The between-years association for yield was zero, as was the case for tiller number and seeds per head. A positive correlation was found for seed weight in the 136 lines in the selected population but it was low in magnitude.

TABLE 3.--Inter-annual correlations of yield components and yield based upon data collected in 1966 and 1967.

	r_{xx}	r_{yy}	r_{zz}	[1] r_{nn}	r_{ww}
Selected population					
136 lines			.24*	.16	.05
			.36**	.20*	-.12
51 lines	.10	.22	.29*		.05
	.03	.14	.22		.06

[1] n = xy (seeds per .9 meter linear row)

Figure 7 is a multi-page representation of seed weight versus yield where each page represents one particular level of seed number. In order to obtain this graph, the data were stratified according to seed number using levels of seeds per .9 meter, with levels differing by 400 seeds.

The equation for the regression line on each plane and the corresponding correlation coefficient are presented in Table 4.

FIGURE 7. -- Regression of yield [illegible] weight at various levels of seed number [illegible] winter barley.

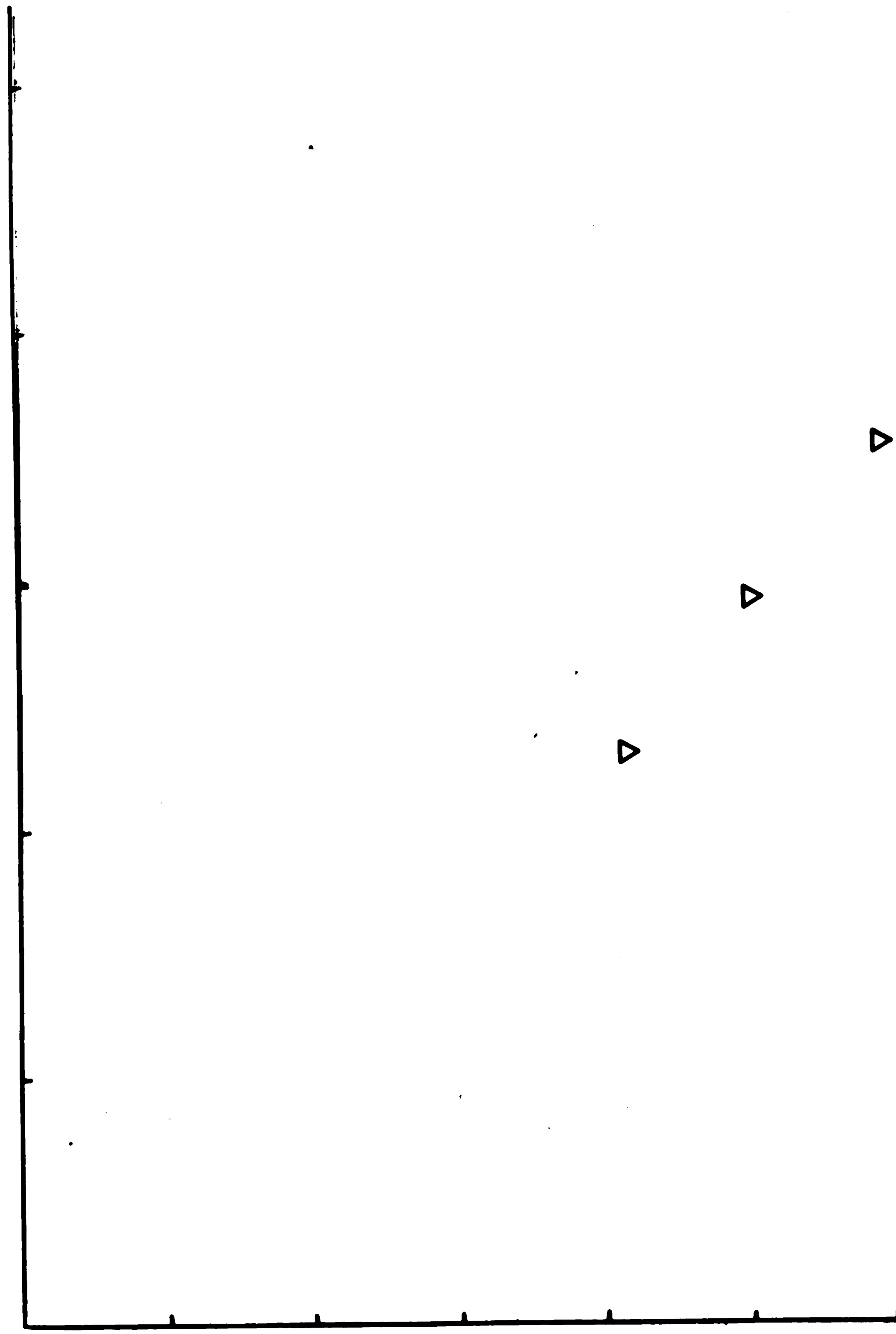


FIGURE 7. -- Regression of yield upon seed weight at various levels of seed number per square meter in winter barley.

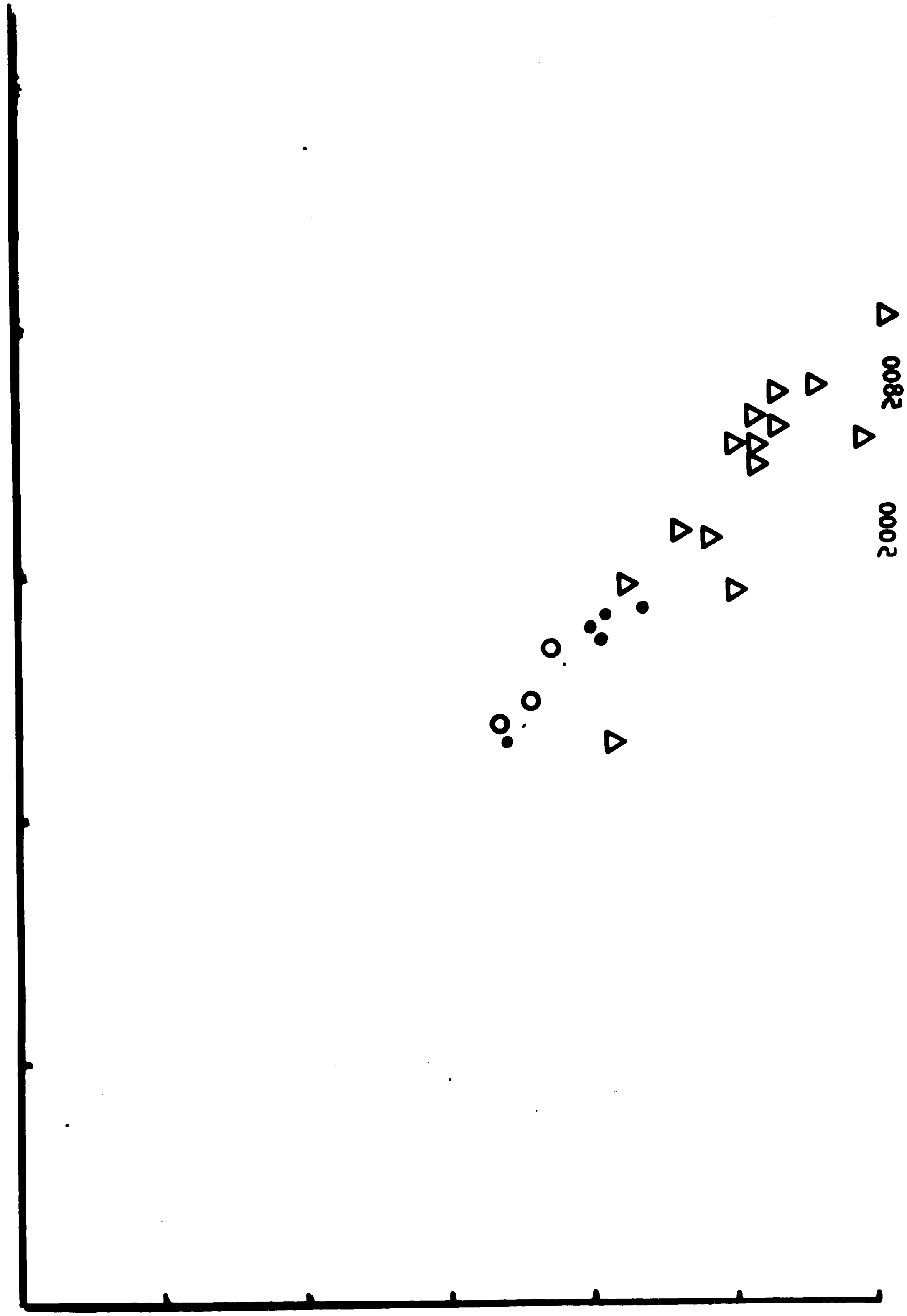
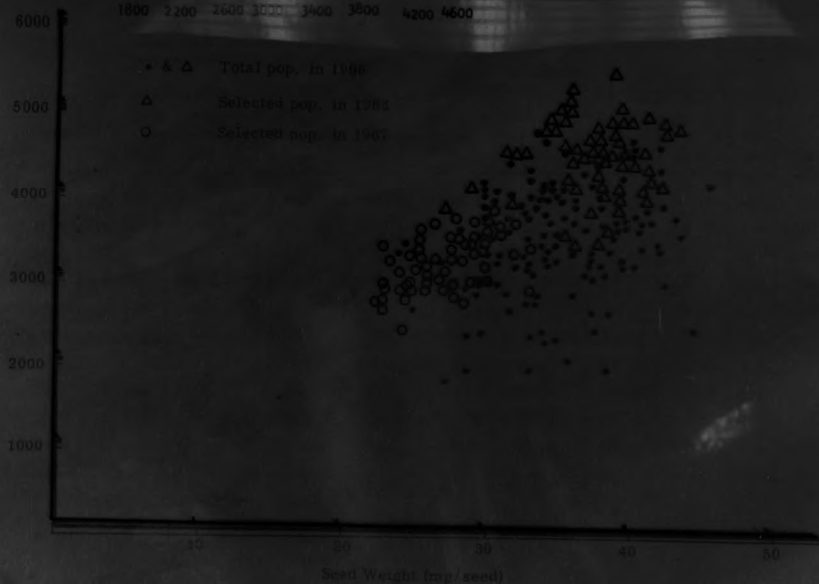
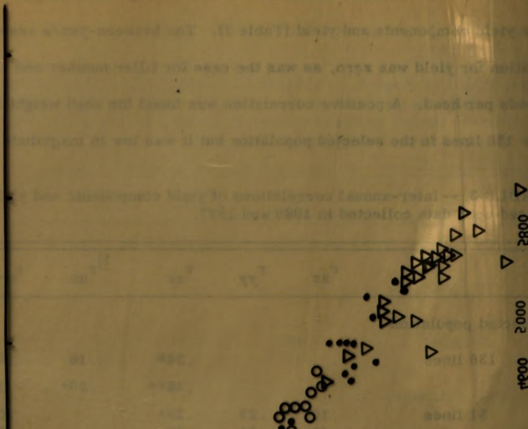


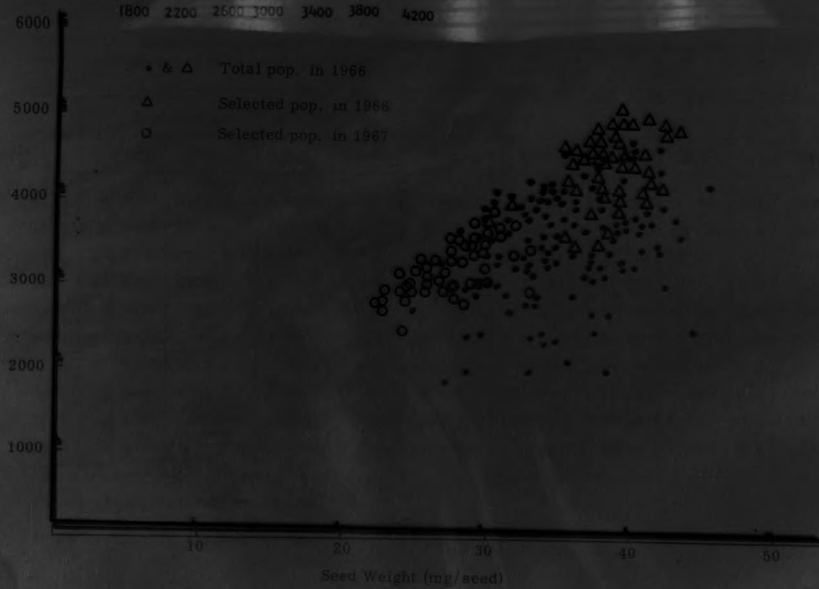
FIGURE 7. -- Regression of yield upon seed weight at various levels of seed number per .9 meter in winter barley.





5800
5000

FIGURE 7.--Regression of yield upon seed weight at various levels of seed number per .9 meter in winter barley.



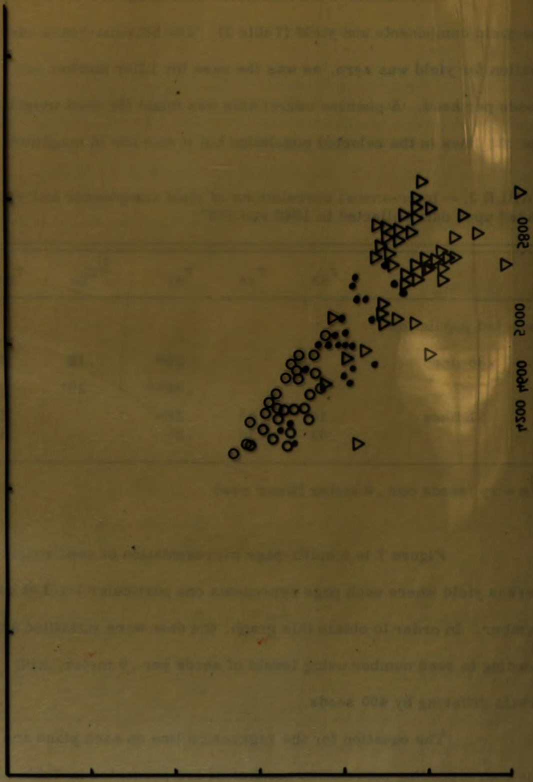

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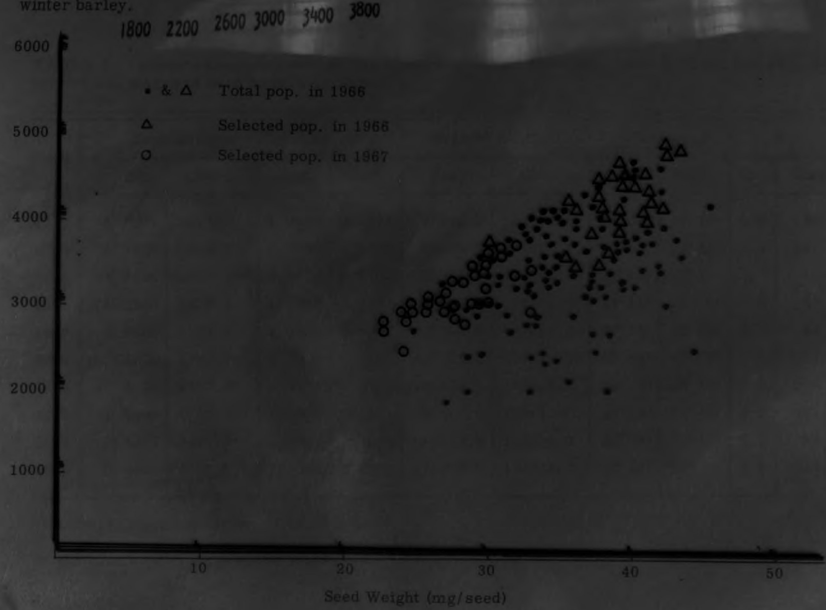
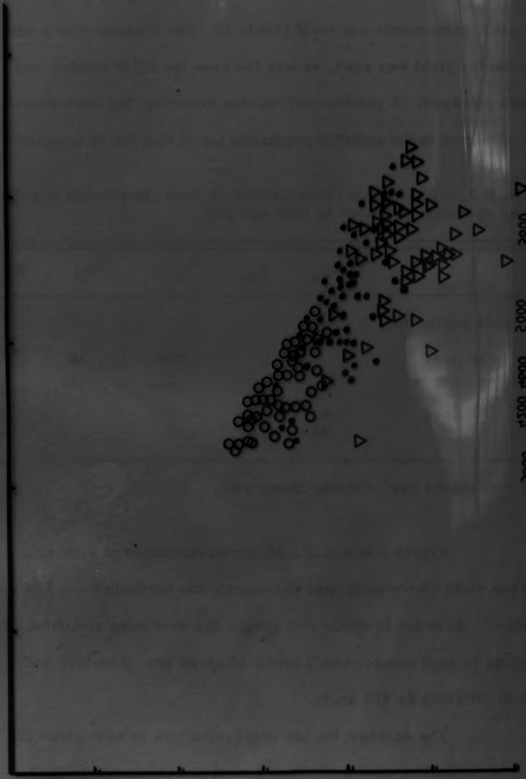
FIGURE 7.--Regression of yield upon seed weight at various levels of seed number per .9 meter in winter barley.





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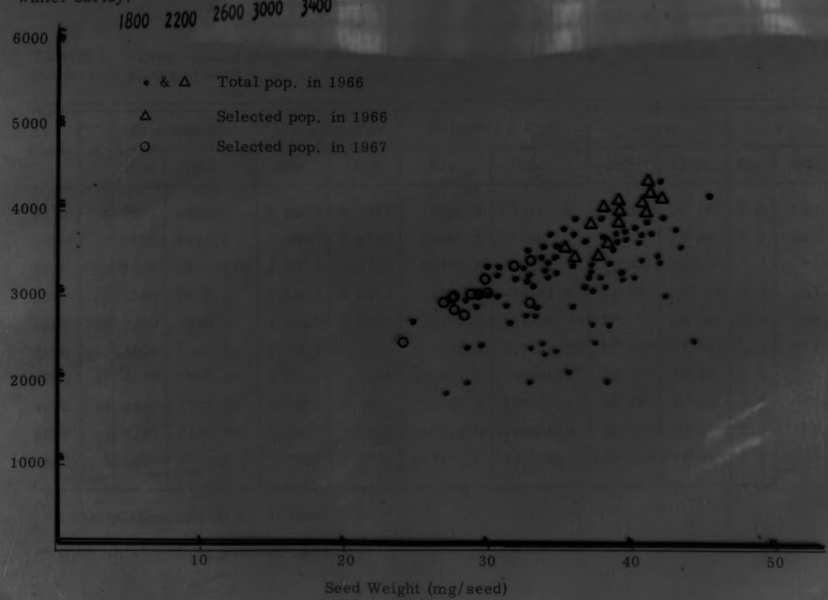
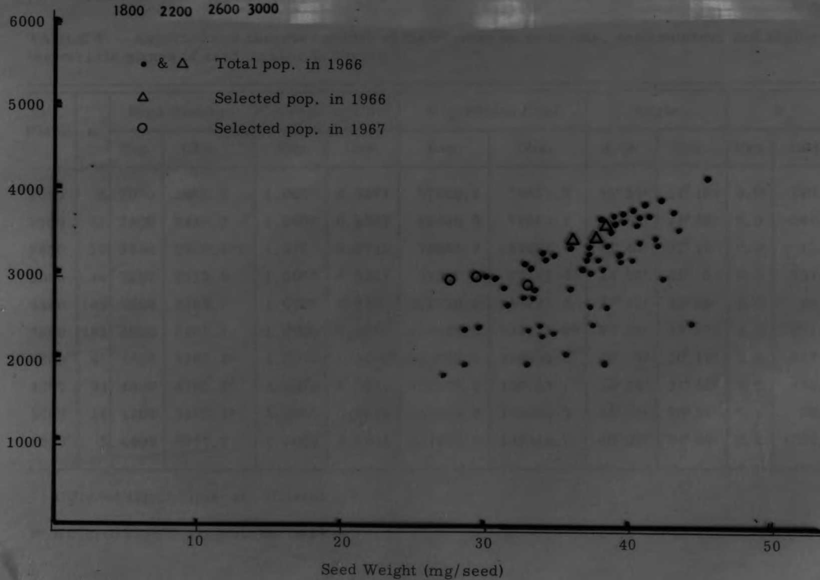



3400
3800
4200
4600
5000
5800

FIGURE 7. -- Regression of yield upon seed weight at various levels of seed number per .9 meter in winter barley.



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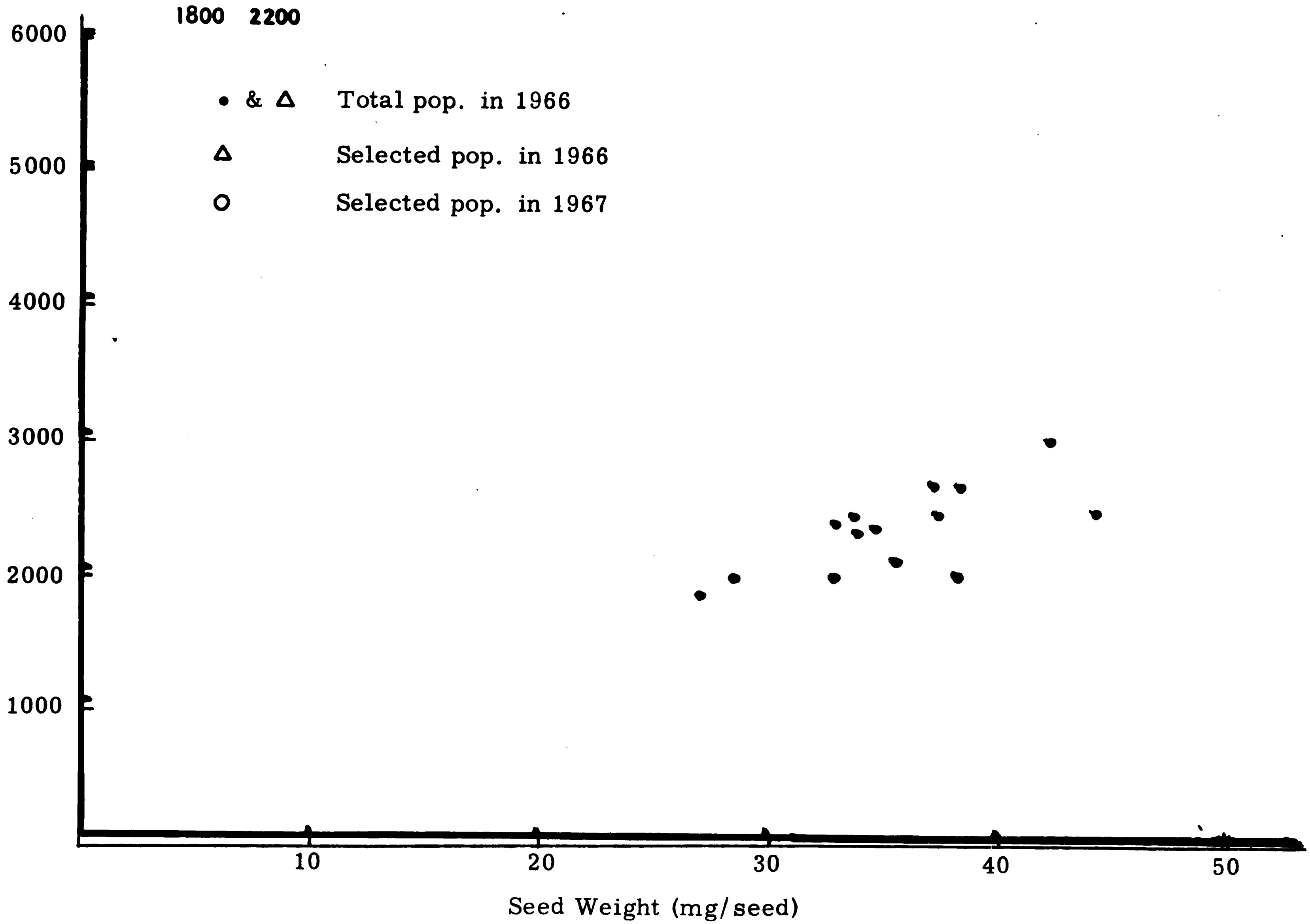

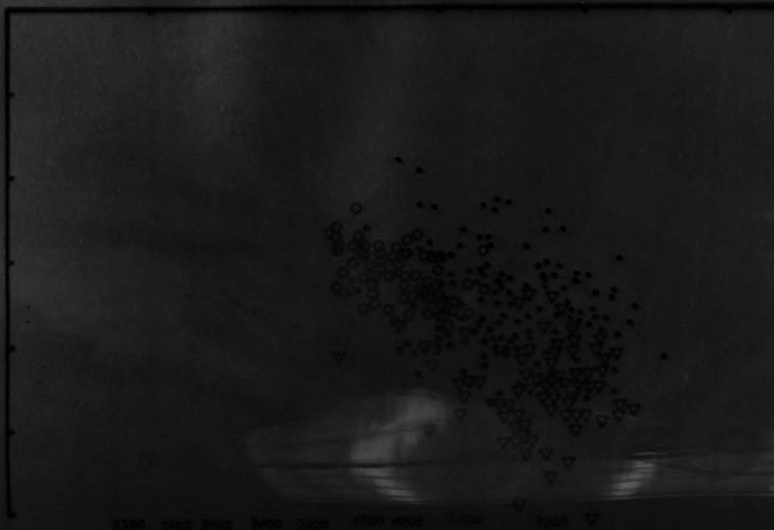

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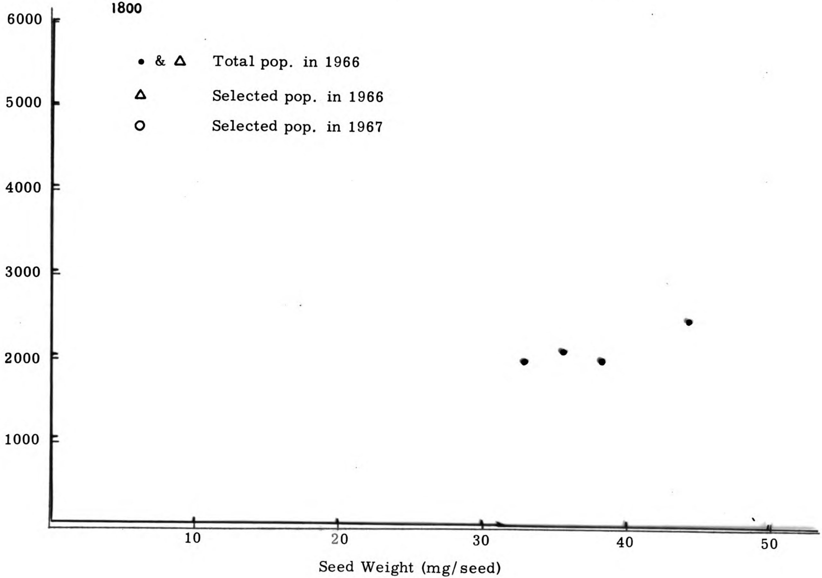

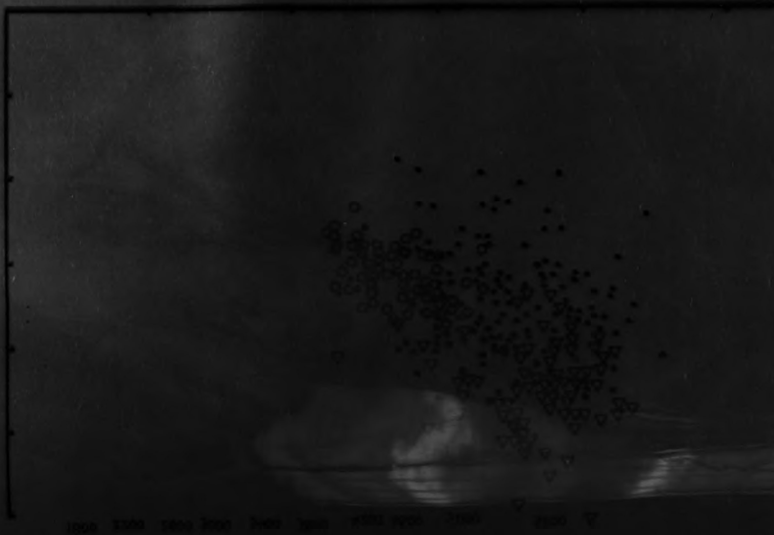

FIGURE 7.--Regression of yield upon seed weight at various levels of seed number per .9 meter in winter barley.

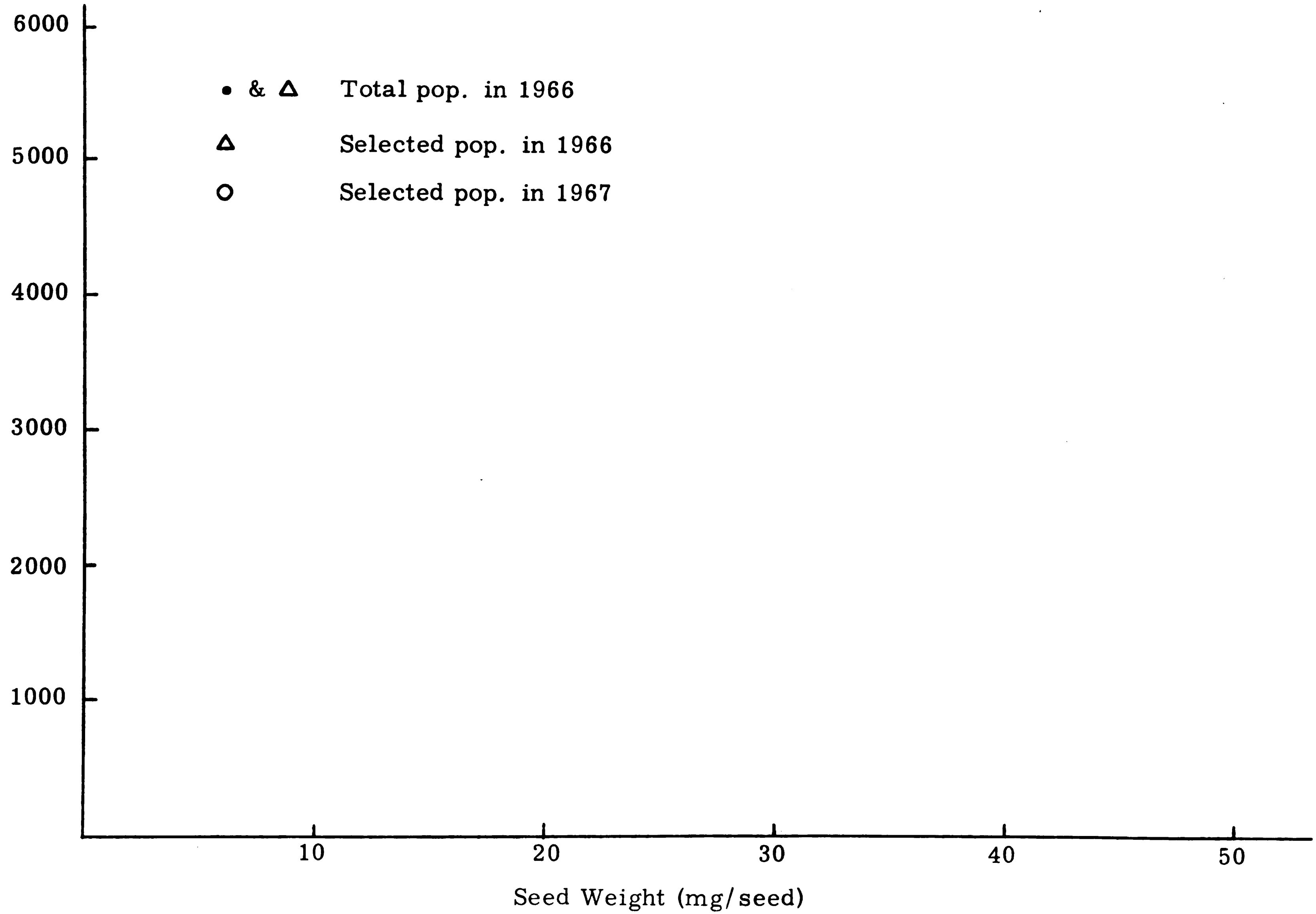

TABLE 4. -- Expected and observed values of the regression equations, seed number, and angles in the various planes of seed number in Figure 7.

Plane	n	Seed Number		Correlation Coef.		Regression Coef.		Angle		b_o	
		Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
1800	4	2000	2064.0	1.0000	0.8827	57065.2	39459.8	15° 36'	11° 10'	0.0	720.8
2200	12	2400	2420.0	1.0000	0.9382	68480.0	79683.1	18° 54'	21° 43'	0.0	-368.3
2600	20	2800	2869.4**	1.0000	0.9762	79894.8	82082.7	21° 48'	22° 19'	0.0	11.8
3000	49	3200	3222.8	1.0000	0.8851	91305.2	77141.4*	24° 32'	21° 5'	0.0	553.6*
3400	100	3600	3596.9	1.0000	0.9435	102720.0	105222.8	27° 12'	26° 55'	0.0	44.6
3800	101	4000	3983.7	1.0000	0.9366	114134.8	106121.9*	29° 44'	27° 57'	0.0	271.5
4200	47	4400	4362.2*	1.0000	0.9492	125545.2	116695.8	32° 7'	30° 16'	0.0	277.1
4600	34	4800	4765.3*	1.0000	0.9837	136960.0	138563.3	34° 24'	34° 43'	0.0	-81.9
5000	16	5200	5175.1*	1.0000	0.9818	148374.8	146850.3	36° 35'	36° 17'	0.0	36.4
5800	3	6000	6097.7	1.0000	0.9994	171200.0	138314.7	40° 34'	34° 40'	0.0	1025.1

* Differed significantly at .05 level

** Differed significantly at .01 level

The correlation coefficients all closely approach unity. The regression coefficient gradually changes from plane to plane, consequently the angle (θ) also changes. Theta, θ, is the angle between the regression line and the axis upon which seed weight is plotted. The greater the seed number the greater the slope. Only one regression equation deviated significantly from the expected value, zero, of b_o. The correlations within each plane were all above 0.88, with the majority above 0.93. By plotting the data for 1966 and for the selected population in 1967, across levels of seed number, a surface is formed.

Figure 8 provides a graphic representation showing relationships of the position of the progeny on a certain plane in 1966 and their position in 1967. A quantum as used in Figure 8 represents 400 seeds per .9 meter. The change in quanta represents the increase or decrease in seed number between years for the population.

Figure 9 provides the same type of graph presented in Figure 8, but represents the position of the progeny on a certain plane in 1966 and their position in 1967 when paired at random.

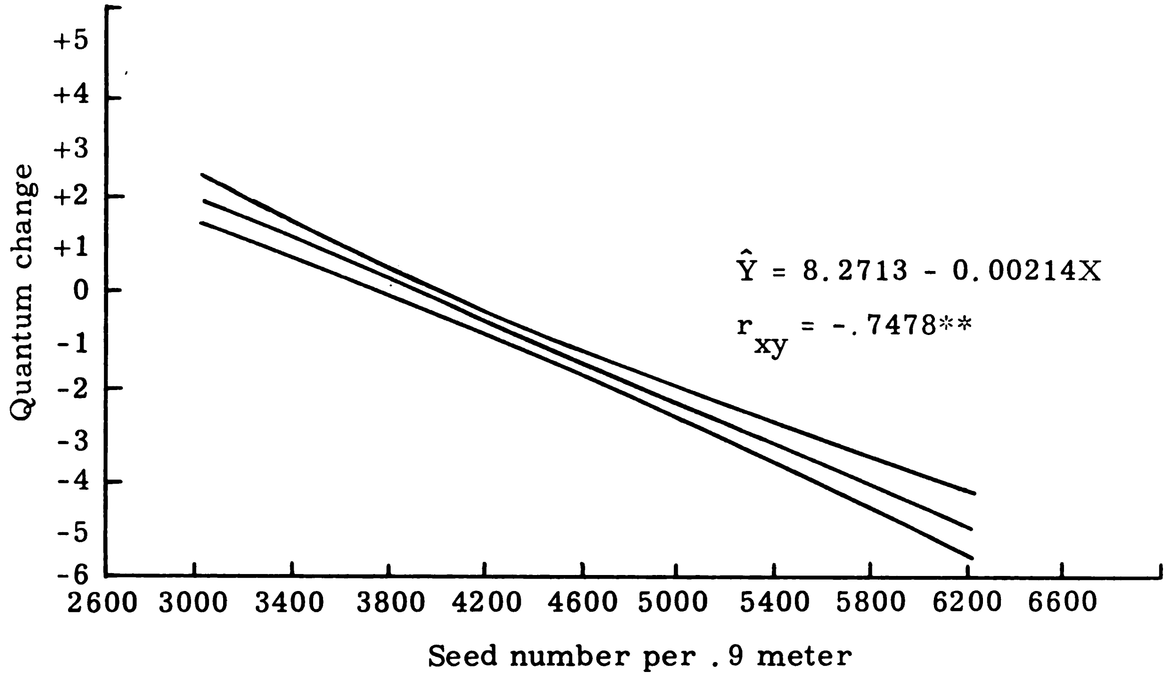

FIGURE 8. -- The regression of quantum change between the data of 1966 and that of 1967 for seed number per .9 meter for 136 lines of winter barley, with 95% confidence bands.

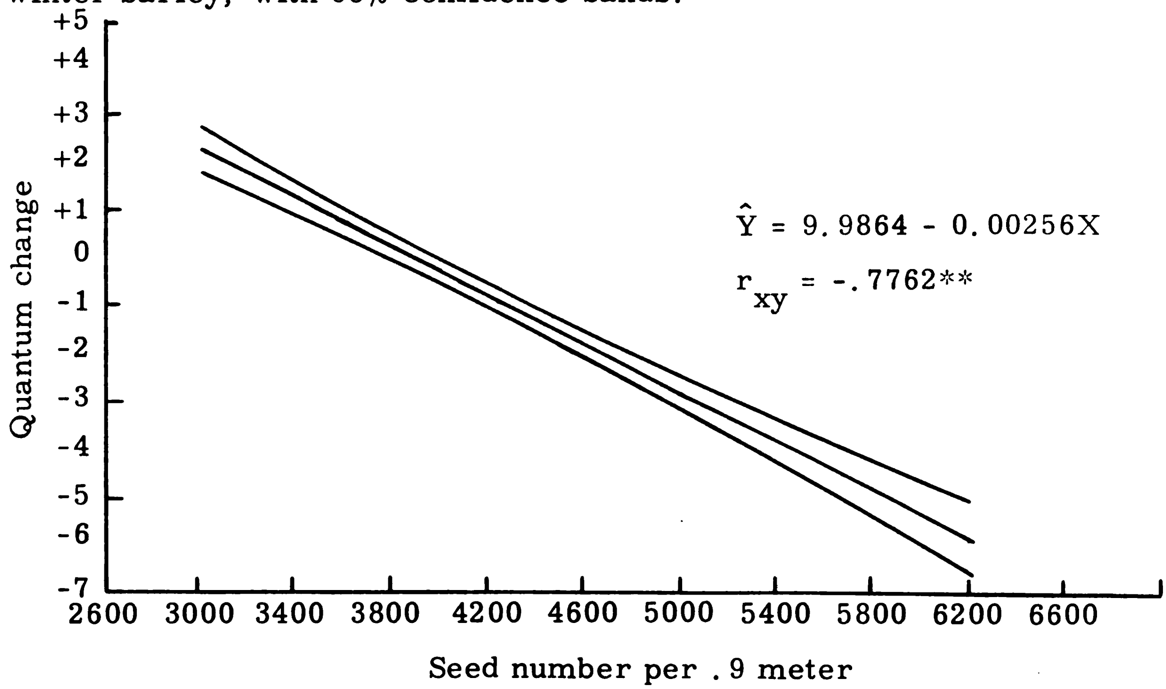

FIGURE 9. -- The regression of quantum change between the data of 1966 and 1967 for seed number per .9 meter paired at random, with 95% confidence bands.

DISCUSSION

Component Inter-relationships

Yield is the economic end product of a barley plant's life cycle, and may be represented as a geometric construct of three components: X, heads per unit area, Y, seeds per head, and Z, seed weight. These components develop in a sequential manner during the growing season. Winter barley is planted in September in Michigan and matures the following July (Figure 10).

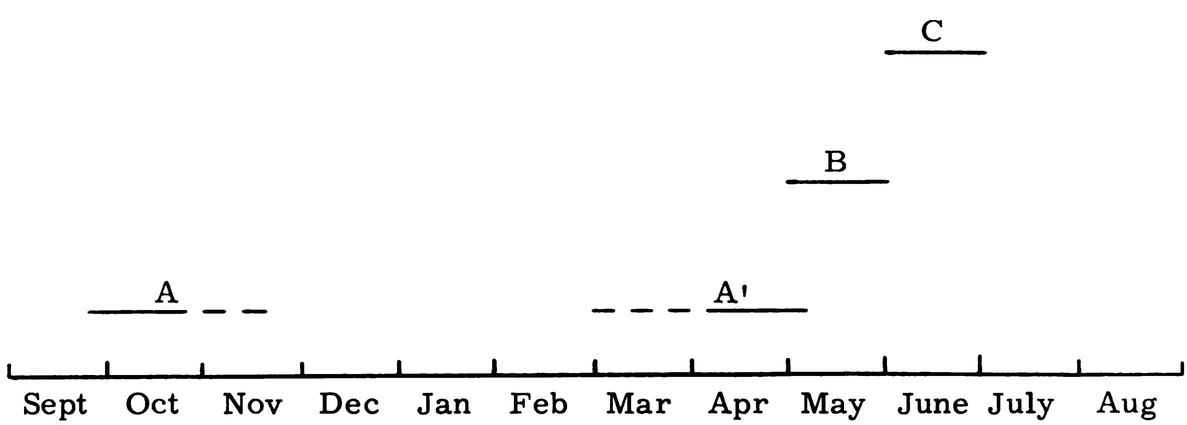

FIGURE 10. -- A representation of development over the growing season of the winter barley plant in Michigan.

Tiller initiation (A) and elongation (A') occurs in September and October and from March to May. Head formation (B) occurs from the first week of May to the last week of May. Fertilization (C) occurs the last week of May and the first week of June, with seed filling occurring the second and third weeks of June.

The barley plant may produce several hundred tillers, but the number which are actually produced depends upon temperature, moisture, light, and the genetics of the plant. With adequate water, nitrogen, and light, tillers may be produced to a point at which the plant may be unable to use added nutrients. The inability of the plant to use added nutrients may be genetic or due to a limiting endogenous nutritional resource required for their utilization. During April and early May, the tillering process depends upon the soil for water and minerals and the leaves for photosynthetic metabolites and growth factors. A primordial spike may be developed at the apex of each tiller bud. The size of the primordial spike determines the number of potential spikelets and, ultimately, seeds per head. If the amount of available nutrients were constant, the amount allocated to each tiller would be less with several tillers than with few. Because of the lower nutrient supply per tiller bud, smaller spike primordia would be formed, resulting in smaller heads. This appeared to be the case in 1967. Twice as many tillers were produced in 1967 as in 1966, and smaller heads were formed in 1967 than in 1966. With so many tillers per unit area, the available nutrients per tiller were reduced causing smaller heads. In 1966, tiller-number per area reduced because of winter injury, allowing for a larger nutrient supply per tiller and hence bigger heads.

With few tillers, the vascular system of each tiller could possess greater capacity for carrying essential nutrients. These tillers would be larger in diameter, allowing the development of greater vascular transport capacity.

In cereals, approximately 70 to 80 per cent of the total carbohydrates in the seed are produced by the flag leaf, stem, and awns. Therefore, with larger heads, the photosynthetic area of these parts would be larger.

With the compensatory effect within years due to environmental effects, it is understandable that reduced relationships might exist between seasons for yield components. The environment in 1966 produced optimum conditions for that particular set of components for yield. Tiller number was extremely low, allowing the plant to over-extend Y, seed number/head, and with an unlimited supply of nutrients at seed filling time, yield per plant was high. In 1967, component X was extremely over-extended and a resource limit resulted, induced by within plant competition and the environment, causing small heads and small seeds.

Selection for increased head production and increased seed weight was successful, but their expression was overshadowed by component compensation in one or the other seasons. The genetic potential of the selected population to produce big seeds was demonstrated in 1966, while the genetic potential to produce many heads was expressed in 1967. Although the selection advance for yield was apparently negative, the plants still possess the genetic potential of producing high yields if compensatory interactions were removed.

In order to take advantage of the plant's potential to produce many tillers, large heads and heavy seeds, some solutions are suggested. An optimum number of tillers could be determined at which varieties can be grown to insure high yields. For example, in the population grown in 1967: if in the spring the plant population could have been thinned to 70% of the original stand, large heads and large seeds might have been formed as was experienced in 1966. The question arises as to how the environment could be bypassed to provide artificial man-made compensation. A solution might be the application of high levels of fertility to produce many tillers, big heads and/or big seeds. Irrigation coupled with high fertility would provide an opportunity to select for varietal response to these factors and, presumably to improve yield. Also, selection of individuals which may possess high levels of photosynthetic efficiency would, along with adequate water and fertility, provide high nutritional levels preventing metabolic limits from restricting component development in barley. These solutions may sound simple but are really complex in nature. Only a better understanding of the genetic interrelationship of the factors affecting yield and genetic-environment relationship will provide, hopefully, better guidelines for making lasting selection gains.

Universal Surface

Figure 7 was developed in order to visualize more clearly the relationship of seed weight with yield. The two-dimensional relationship of seed weight with yield produced a correlation of .3162, but by stratifying according to the third dimension, seed number, a highly positive association, was seen at once within each seed-number plane.

If the seed-number planes of Figure 7 are arranged in a three-dimensional spatial configuration, each plane stacked upon another, from low seed number to high seed number planes, somewhat like the spacing of individual slats of a venetian shade, then the data will form a surface in three-dimensional space. The surface is a continuous belt extending from a region of low seed number to a region of high seed number, marked along the way by strains occupying co-ordinate points determined by their seed number and seed weight values. The surface is sloping throughout and seemingly uplifted at a middle region, reflecting the somewhat better performance of the adaptive intermediates. Mathematically and biologically only one surface exists with this relationship. Yield is the product of seed number and seed weight. The deltas represent the selected population grown in 1966, the dots represent the lines which were not selected, and the circles represent the response of the selected population to the environment of 1967. This method of plotting data provides a way of observing the effect of the environment upon yield components and yield. The swarm of points for barley will expand and move it in the reference space--on the universal surface--depending upon the response of the components to the environment.

The dimensions and position of the barley swarm upon the surface will also change due to selection pressure placed upon the population by man. If genetic changes are made in seed weight or seed number which alter the boundaries, the swarm will assume a new position laterally or linearly on the surface.

Theoretically, if the surface were extended to infinity for seed number, seed weight would approach zero because of the negative association of seed number and seed weight, hence yield would approach zero. At the other extreme, when seed number approaches zero, seed weight would become large, but yield would again approach zero.

The array of points which form the surface could be thought of as part of the evolutionary surface for barley. If one assumes that Hordeum vulgare has arisen from the inter-crossing of Hordeum agriocrithon, a six-row barley, and Hordeum spontaneum, a two-row barley, it would appear that directional selection by the environment and by man has been toward larger seeded and higher yielding varieties. The wild species of barley have small seeds, which are produced in great numbers. Man has selected for heavy seeds and high yields, but due to the negative association of seed number with seed weight, a compensatory genetic shift has occurred toward fewer seeds.

In a compensatory situation, the genotypes most likely to produce heavier seeds are those that produce on the average fewer tillers. Consequently, by deliberately selecting for heavier seeds, man has been selecting for fewer tillers and hence fewer seeds.

If larger values of seed number were added as planes, they would contain the wild species of barley such as Hordeum jubatum, bulbosum, pusillum and murinum, to name a few. By adding smaller seed numbered planes, the two-row barleys can be placed on the surface.

This "universal" surface is the only possible one upon which all species of the seed crops can be placed for this particular relationship. Each seed crop will produce its own "swarm" on the surface. When the environment affects any one of the components it is reflected by movement of the points on the surface.

Where upon the universal surface should selection be practiced to make the most fruitful progress? If the phenotypic correlations between seasons are highly positive, selection should be practiced on the planes which have high seed number and large seeds, resulting in high yield. In this case, the lines would be expected to repeat their relative performance year after year. On the other hand, if the environment overrides the genetic expression of the lines through inducing component compensation, then genetic gain by selection strictly on the component basis is more difficult.

The inter-annual correlation is a measure of repeatability of performance between years and in the present case this value for seed number was quite low (.2023). A method--a graphical plot--is shown in Figure 8 which demonstrates the inter-year relationship of seed number. The seed number scale for 1966 is marked on the horizontal axis. On the vertical axis is scaled the number of "quanta" by which a line changed in 1967 (a "quantum," in the sense used, refers to a 400-seed shift, either in a plus or minus direction, from its seed number in 1966). For example, strain A produced 3,000 seeds per .9 meter in 1966. If in 1967, strain A produced 3,400 seeds per .9 meter, it would have changed upward by one "quantum."

As may be observed in Figure 8, there is a marked tendency for lines of low seed number in 1966 to produce more seeds in 1967, and for lines of high seed number in 1966 to produce fewer seeds in 1967. The regression of "quanta" shift in 1967 upon seed number position in 1966 was negative and highly significant.

There were two possible interpretations of this result. In the first, it could be postulated that the genotypes are responding differentially to an environmental factor for which the two years are markedly distinct. This factor must cause the low seed-numbered line in 1966 to produce a high number of seeds in 1967, and vice versa. Genotype-environmental interactions of this type are rare in plant biology. In the present case, no single environmental factor capable of affecting the observed responses is apparent. The lines of barley studied were previously unselected for any differential responses, and their very number is so large that numerous failures of differential response would have been expected to show up. None did. Furthermore, if an inversion of performance for 1966 and 1967 had occurred, the inter-annual correlation should have been negative. It was, in fact, slightly positive.

A second interpretation may also be given. If mostly random processes are operating between years rather than directed (genetic) processes, then the data will conform to a graph like Figure 8. Figure 9 was obtained by taking the value of each line in 1966 and pairing it at random with a value from the 1967 data array, and plotting in the same manner as was used in Figure 8. On the basis of probability alone, it is obvious that a line on the low end of the 1966 data array would--if random processes predominate--end up in 1967 at a point higher on the scale. And, similarly, a line high in 1966 would end up lower in 1967.

The second interpretation is supported by the low inter-annual correlation and, without other evidence supporting a specific genotype-environment interaction, suggests an overriding effect on seed number genes of random varieties imposed by the environment.

SUMMARY

The best-planned selection procedures can produce some unusual and undesirable results. Even so, logical interpretations must exist for these responses.

Negative associations between yield components exist due primarily to inter-plant and intra-plant competition which has been termed "component compensation" by Adams (1).

The low inter-annual relationships of yield components, even though larger in magnitude than for yield, are due to the over-riding effects of the environment upon the genetic systems, and to extremes in component compensation within the two environments.

A pictorial representation of the evolution of barley was presented, based upon yield and its components. The surface that is formed can be called "universal" since only one surface is possible for all seed crop plants. The effect of the environment on the components can also be represented upon this surface.

Evidence was presented that optima exist for yield components and their inter-relationship in order that maximum yields can be reached. Selections in one environment for these optima do not mean necessarily that under another environment the same production performance will be obtained.

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