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# RELATIONSHIP BETWEEN MERISTEMATIC CHARACTERISTICS,

### YIELD COMPONENTS AND YIELD OF BARLEY (HORDEUM

### VULGARE)

Ву

### James Benjamin Abaka Whyte

#### A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

### MASTER OF SCIENCE

Department of Crop and Soil Sciences

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MY PARENTS

### ABSTRACT

### RELATIONSHIP BETWEEN MERISTEMATIC CHARACTERISTICS, YIELD COMPONENTS AND YIELD OF BARLEY (HORDEUM VULGARE)

By

### James Benjamin Abaka Whyte

Each organ is sequentially developed and although each may be affected by environmental stress and different gene systems, the phenotypic expression of each of the plant organs is closely related to each other. This relationship is brought about in higher plants by the nature of the apical meristem because the size of any plant organ depends on the size of the meristem from which it is developed.

X969-3 followed a different pathway in development than Bl30, which had a development pattern similar to that of the other control varieties. X969-3 thus produced a higher number of seeds per head for its level of X. This property resulted from an initially broader based meristem and a time lapse period between the vegetative stage and the onset of the reproductive stage. Some lines in the progeny inherited this property, together with genes for higher X, contributed by Bl30. This resulted in the production of a higher number of fertile tillers for a given head size or vice versa.

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Evidence is provided to show that 50 to 60% of the relative size of X and Y can be determined by examination of the meristem at Stage 3. The relative growth rate and width of the meristem at Stage 3 have a positive and negative relationship, respectively, in predicting the number of fertile tillers per unit area. Size of the meristem is most important in predicting the number of seeds per head. The width of the meristem has a negative relationship while the length of the meristem establishes a positive relationship in the prediction of the number of seeds per head.

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### INTRODUCTION

Agronomists, as well as other agriculturalists, are already confronted with the problem of providing food for a world population that continues to grow at an accelerated rate. Improvement of crop productivity through plant breeding has been realized by induction and deduction from empirical data. However, much advancement can probably be obtained from the application of fundamental concepts of plant growth and development.

Yield components were described as early as 1923 by Engledow and Wadham, but the importance of yield components as determinants of cereal yield was only fully recognized when put in geometric context. Geometrically, yield is expressed as a volume of a rectangular parallepiped with its components, number of tillers per unit area (X), number of kernels per head (Y) and average kernel weight (Z), as the edges. Yield is subject to change through change in one or more of its components and geometrically, the greatest yield change is obtained with a change in its shortest edge. Heterotic effects in yield result more from the interaction of yield components instead of overdominance through loci interaction. Hamid and Grafius (1978) show that the earlier

developed organs have a profound influence on later formed structures. The order of development of the yield components of barley are number of tillers per unit area, number of seeds per head and seed weight. Genetic control of yield, W, is indirectly channeled through its components, with the earlier formed structures assuming the major part of the control.

The primordia of organs evolve from meristems and the central role of this structure has been pointed out by Sinnott (1921). He stated that, "The size of any given organ depends upon the size of the growing point out of which it has been developed." The interest in using apical meristems of the shoot of flowering plants in studies on morphogenesis may be questioned, since the meristem is small and delicate, practically enclosed in surrounding tissues and consequently very difficult to handle experimentally. However, the conversion of the meristem from the vegetative to the reproductive condition is among the most dramatic examples of a switching of a developmental pathway. The vegetative growth period involves the formation of tillers and leaf primordia. The change of meristem from the vegetative to reproductive stage coincides with the cessation of the formation of tiller buds and leaf. The switching from

vegetative to reproductive phase exerts a direct effect on the relationships between yield components.

The negative correlations between yield components have posed a block to yield improvement of crop plants. In effect, these negative correlations prevent simultaneous maximization of X, Y and Z and thus impose a ceiling on grain yield. Relaxation of these negative correlations can result in great yield increases of such crop plants. Short statured hexaploid wheats, derivatives of Norin 10 cultivar, outyield the standard wheats as a result of relaxation of the negative correlations between the yield components. Grafius <u>et al</u>. (1976) reported the uncoupling of X and Y in barley so that a higher value of Y for a given value of X was possible. This characteristic was carried over into the progeny with resulting increased yields of unselected progeny.

In 1952, Watson stated that leaf size was the main determinant of differences in yield of dry weight objectives of plant breeding. Thorne (1966) concluded that grain yield of cereals was related to photosynthetic area above the flag leaf node. Since grain filling is mainly comprised of carbon derivatives synthesized during photosynthesis, it would be logical to expect higher rates of photosynthesis to result in higher yield. Up

to date, there is very meager evidence to show a direct association between photosynthetic efficiency and differences between cultivars in grain yield. On the other hand, there is a great deal of evidence pointing to the importance of sinks in increasing yield.

The following study was an attempt to relate the relaxation of negative correlations between yield components with events taking place in the primary meristem.

#### LITERATURE REVIEW

Considerable emphasis is currently being placed in a number of breeding programs upon the improvement of plant characteristics with an ultimate increase in grain yield. The task of constructing higher yielding populations of barley (<u>Hordeum vulgare</u> L.) by combinations of lines selected for their agronomic characteristics, disease and insect resistance has been rewarding. Plant breeders are now faced with the challenge of understanding the mechanisms involved in the expression of yield to plan their techniques for breeding higher yielding crops, especially those that may have already reached a plateau.

In barley, the complex trait, yield (W), has three components: the number of tillers per unit area (X), the average number of kernels per head (Y) and the average kernel weight (Z). This biological phenomenon can be expressed geometrically as the volume of a rectangular parallepiped with its components X, Y and Z being the edges. Yield can be changed by changing one or more of the components. Grafius (1956, 1964) presented five theorems to justify the geometric interpretation of yield using its components.

Varieties which maintain their standing in different

plant communities either resist change or adjust favorably to changes in environment. This buffering capability is a result of physiological processes which are ultimately expressed through their structural yield components. If changes occur at random among the three dimensions of the rectangular parallepiped, then the most stable configuration is the cube. However, if changes are not random and one edge is more resistant to change than the others, then some other form of configuration might be more resistant to changes in volume. Any negative change in one edge is compensated for by a positive change in the other edges. The greatest change in volume occurs with changes in the shortest edge.

Removal of epistatic interactions due to the components necessitates the use of geometric approach to express yield. The question of overdominance as a genetic basis for heterosis has raised some academic discussions. The questions of multiplicative interaction between components or edges of the geometric interpretation and interaction at the locus level need to be solved. With respect to yield, the effect does not appear to be interlocus, but interaction between the edges of the geometric figure.

A simple system was used by Grafius (1964) to show

this effect. "Let the various  $A_1$  to  $A_n$  loci interact with the various  $B_1$  to  $B_n$  loci in pairs with summation of effects between pairs, for example,  $A_1B_1 + A_2B_2 + \ldots$ .  $A_nB_n$  where  $A_1$  and  $B_1$  represent loci, not alleles. As a contrasting model, let the sum of all the  $A_1$  effects interact with the sum of the  $B_1$  effects. It is apparent that:

Epistasis in the classic sense shown on the left of the inequality is less than the geometric interaction between the gene systems affecting the individual yield components.

Other forms of interaction are possible since gene action in complex trait need not be restricted to any one type. However, major heterotic effects can be associated with the right hand side of (1).

Duarte and Adams (1963) showed that means of components of leaf area in beans (<u>Phaseolus vulgaris</u>); leaflet number and leaflet area, exhibited dominance effects. However, the leaf area of the  $F_1$  exceeded the total for both parents.

Representing the degree of dominance by a = H/D

where H and D are the non-additive and additive genetic variances, respectively, they showed that leaflet number exhibited complete dominance (a = 1) while leaflet size showed partial dominance (0 < a < 1). Heterosis (a > 1) is observed in the product.

All plants follow a developmental rhythm. Small grain plants such as oats, barley, wheat and millet start by laying down tillers followed by floral initials, stem elongation and cessation of tillering, pollination, filling and maturation of kernels. The phases of tillering, floral initiation and maturation extend over the ontogeny of the plants and are directly related to the components X, Y and Z.

The analysis of crop yield entails the analysis of plant growth. The attainment of the characteristic form and function in a crop plant depends upon a chain of interrelated events which are sequential in time, gene regulated at critical sites and times and subject to modifying influences of the environment. The events do follow an integrated pattern (Adams, 1967). Yield is an example of integration in which the components of seed yield are to some extent interdependent in their development.

Bonnett (1964) describes morphogenesis as "The

development of the shape and arrangement of the parts of the plant, the time and sequence of development of the parts and the histology of the parts as they develop." It is an epigenetic process; one condition leads to another and does so in a channeled and controlled fashion.

In a series of papers, Grafius (1969), Grafius and Thomas (1971) and Thomas <u>et al</u>. (1971 a, b, c) presented the concept of sequential developmental process of yield components. The components of yield in the studies were X, number of heads per unit area; Y, the number of seeds per head; and Z, the average seed weight. The chronological developmental sequence of the components is X to Y to Z. Yield, W, is a multiplicative product of the components, i.e. W=XYZ. A transformation technique was given by Thomas <u>et al</u>. (1971a) to remove the part of variation of a component trait which is contributed by the trait(s) which appears earlier in the development sequence. Plant organs laid down early in the sequence exert more genetic control over variation in W than traits laid down later in the ontogeny.

Rasmusson and Cannel (1970) and Tai (1975) pointed out that yield components in cereal crops are determined at different stages in the ontogeny of the plant and thus are differentially affected by variation in the

environment. This suggests that the three yield components in cereals are affected by independent environmental factors during the same or different periods of plant development.

The formation of yield components in sequence results in a different relationship between a component trait and the environment resources. The development of the first component trait is solely determined by the genetics and the resources available during the early stage of growth. A component trait whose development is subsequent to others is not only influenced by the resources available during its formation, but by the development and conformation of its predecessor. The mechanism for controlling the formation of a yield component is thus increasingly complicated in the chronological developmental sequence.

Correlations exist between yield components. These correlations may be due to genetic linkages, pleiotropy or to physiological developmental relationships. Adams (1967) established the existence of negative correlations between yield components of several crop plants, attributing their occurrences to:

1. Possession of developmental plasticity in plants which enable them to take alternate pathways to attain their final adult forms. Variation in one component is

compensated for by variation in another.

2. Developmental induction. Competition of two plant structures for a common, limited nutrient supply will tend to favor one structure over the other in the amount received.

The concepts proposed by Sinnot (1921, 1960) and Bonnett (1964) on the development of organs in plants as controlled by developmental allometry needs special consideration. Each part and function is so closely related with the rest that the whole plant develops in an orderly fashion toward the growth of a mature individual. Adams (1975) points out the phenomenon of size and numbers as part of the overall allometry in a plant. He showed the significant relationship between number of pods per plant with main stem node number and that of seed size and leaf size in <u>Phaseolus vulgaris</u>. High yield potential is achieved by a balance between 'factors of numbers' (e.g. number of nodes) and factors of size (e. g. stem diameter leaf area).

Grafius (1978) proposed that, "Plasticity is inversely proportional to ontogenetic proximity." Events arising from the same meristem are harder to manipulate than those separated in space and time origin. A second corollary states that size and numbers are

negatively correlated. Fowler and Rasmusson (1969) showed a diminishing correlation between leaves borne on the same culm with increase in distance between the leaves (both in space and time of origin).

Allometric relationships between X, Y and Z might result more from competition than from the effects of common origin. Grafius (1978) called this 'stress matrix' because a correlation matrix is implied on correlations between several traits. Since the correlations are physiological, the stress matrix varies with the environment and the gene pool. Linkage may be present but its effect can be reduced on the assumption that genes for the components are distributed throughout the chromosomes. Allometric relations between traits not arising from the same meristem could also be brought about by the need for structural balance and hormonal stimulation in addition to competition for environmental resources (Grafius, 1978). Adams (1967) reported a much reduced correlation between yield components for space planted versus solid stands for navy beans, Phaseolus vulgaris. Hoen and Andrew (1969) reported near zero correlations for the yield components in corn. Under closer spacing and/or higher yields such correlations increased in intensity (Grafius, 1969).

Grafius <u>et al</u>. (1976) reported the uncoupling of X and Y in barley so that a higher value of Y for a given value of X was possible. The parental materials showed the uncoupling when Y was graphed against X. Variety X969-3 proved to be an outlier in that a larger than expected Y for a given X was observed. This characteristic was carried over into the progeny with resulting increased yields of the unselected progeny over the best parent in one of the backcross populations - after selfing several generations.

Hamid and Grafius (1978) developed the path coefficient diagram in conformity with Sinnott's Law and known developmental relationships. Grafius (1978) updated the pathway. The importance of the trait set early during morphogenesis, namely the number of heads/area (X) is demonstrated.

The plants' reaction to develop any one level of X triggers a chain reaction affecting all latter formed organs as shown by Sinnott's Law. By virtue of its direct association with meristem size, X assumes a pivotal role in determining sizes of plant organs and eventually the determination of economic yield itself. This dependence of X could be modified by external factors such as nutrients (Aspinall, 1961, 1963), water (Wardlaw,

1971), temperature, light intensity and daylength (Cannel, 1969; Friend, 1965) or internally by hormone levels (Leopold, 1949). One must recognize also that the initial control originates in the gene and the magnitude of the stress matrix for the yield components has a bearing on the phenotypic expression. It is an intraplant response evoked by external factors in the environment.

There is a general concensus that from 80-90% of the carbohydrates in grain are obtained from CO<sub>2</sub> fixed after anthesis. Many workers have stressed the importance of photosynthesis in the upper leaf area and ear to grain filling. Such physiological studies are necessary in identifying the photosynthetic sites involved and their relative contribution to post anthesis accumulation of assimilates in the grain. However, the determination of grain yield (W), specifically the observed differences among a set of genotypes normally involved in a breeding program, entails a more complex process and would rarely be resolved merely by the relationship of photosynthetic efficiency and W. In the first place, the expression of the economic yield in cereals is the end product of three major physiological processes, namely, accumulation (of assimilates) translocation and storage. Any one

process could be limiting, and in the set of data presented by Hamid and Grafius (1978) the relationship of average leaf area to differences in grain yield was found to be nonsignificant. Working with similar materials, Grafius and Barnard (1976) attempted to relate leaf canopy, integrated over time, to yield, but found no significant relationship. Berdahl <u>et al</u>. (1972) showed no consistent yield advantage of small over large leaves or vice versa. Evans and Dustone (1970) and Khan and Tsunoda (1970) have observed in cereals that higher yielding cultivars had lower photosynthetic rates.

Size and number of the appropriate components of yield, W, may be more critical than the size or number of the photosynthetic surfaces in causing differences in W genotypes.

As reported by Grafius (1978), Sinnott redirected allometric science in plants by discarding the then current practice of trying to correlate the development of plant organs with the growth and development of the whole plant. Instead, he showed that if one related the size of an organ with the size of the primary meristem from which it arose, many of the ambiguities of the earlier work disappeared.

Sinnott (1921) showed that the fundamental difference

between shapes of gourd <u>Lagenaria</u> <u>vulgaris</u>, Ser is K (the regression coefficient of log length (Y) against width (X) of the earliest ovary primordia). K equals to .8, 1.2 and 2.2 for bottle gourd, hercules club and snake gourd, respectively. However, one can have different shapes due to the length of development time and/or the growth rate with the same K value.

Fruit shape is simply inherited, making the selection of a new K value rather easy but an attempt to manipulate the rate of growth of either width or length independently is less likely to be productive.

The relationship between size of meristem and size of plant organ was first recorded by Sinnott, 1921. Since then, others have noted this relationship for a wide range of crops.

The size of the shoot apex is associated with the size of leaves; species with smaller apices (e.g. ryegrass and clover) have narrow leaf primordia and narrower leaves than those with large apices (e.g. peas and maize) (Aitken, 1967). He deduced that the association of the width of the shoot apex may be an important limiting factor to leaf size and hence, total leaf area. Maltzahn (1957) detected that the primordia of flowers and leaves are considerably longer in a large fruited type in a

Comparative study of size differences in two strains of <u>Cucurbita pepo</u>.

After observing a developmental relationship between the shoot apex and leaf blade width in maize, Abbe <u>et al</u>. (1941) concluded that it is possible to make a direct comparison between the size of the shoot apex and the width of the leaf blade from the earliest stages of development to leaf 12.

Hybrid vigor has been suggested to operate early in the embryonic growth period resulting in larger meristems (Quinby, 1970). The relationship between plant characteristics appear to be more allometric than genetic. Genetic differences in leaf size in barley do exist, but only minimal genetic variance will be associated with variation between areas of leaves on the same culm. Instead, the primary genetic variance will be associated with factors governing the size of the meristem from which the culm, leaves and glumes have arisen.

Publications dealing with the development of the barley spike from germination to maturity are rare. Bonnett (1935) dealt with the development of the barley spike from the earliest stages to complete differentiation. Fisher (1973) showed a marked difference between the morphological development of the spike in short statured

hexaploid wheat (<u>Triticum</u> <u>aestivum</u> L.), a derivative of Norin 10 cultivar and the standard hexaploid wheat. In exploring the origin of the heterotic effect through a comparative quantitative morphogenetical study of the sorghum panicle, Blum (1977) realized that heterosis in the number of grains per basal primary branch could be traced to two major factors:

1. Larger reproductive apex that allowed development of larger basal branch primordia.

2. A 4-day lapse between termination of the acropetal formation of branches and the onset of the basipetal formation of spikelets. The time lapse was utilized in the hybrid for the increase in the basal branch size prior to spikelet initiation.

The control of the genesis of form in plants is thus through three major physiological and structural factors; size of the organ primordia, growth rate of the developing organ and the physical constraints exerted by adjacent primordia or organs.

#### MATERIALS AND METHODS

The material used was derived from two parental lines of barley, X969-3 and B130. A straight cross and two complementary backcrosses were made and grown to the equivalent F4. Twenty random selections were made in each progeny and allowed to self to the equivalent F9.

Six lines from each population plus 68-105-15 (recently released as Bowers) were selected on the basis of contrasting values for their yield components, namely number of tillers per 30 cm (X), number of seeds per head (Y) and average seed weight (Z). Two control varieties 60-215-6 and Larker (C.I. 10648) plus the two parents (X969-3 and B130) were used in the experiment. Meristematic measurements were taken on the selected lines and varieties (parents and controls).

A lattice square design with four replications was used. The plots were four-row plots 0.0254 m apart and 2.4 m long, planted at a rate of 35 g per plot. The study was carried out in Tuscola county, Michigan. Planting date was April 17, 1978.

Meristems were sampled in the following procedure: Four predetermined stages were used as markers at which meristems were to be sampled. The stages include:

1. Vegetative stage.

2. Transition stage showed by the appearance of double ridges on the meristem (Figure I).

3. Reproductive stage characterized by spikelet differentiation.

4. Elongation and further differentiation.

Owing to inaccurate timing, meristems were not sampled for Stage I in the main experiment. The pictures of Stage I in Figure I are from the previous year.

Before any sample was taken at each stage, seedlings within each genotype were visually selected for similar morphological characteristics from the outer two rows of the whole plot. One or two seedlings were uprooted, and their meristems dissected out to determine the developmental stage. Five seedlings were then harvested from the outer two rows, starting from the 31st day after planting. Owing to the large number of seedlings involved, and the rapidity with which they dehydrate, the portions of main tillers containing the meristems were preserved in a solution containing 95% ethyl alcohol, water, glycerine and formaldehyde in proportions of 52%, 38%, 5% and 5%, respectively.

The main tillers were used because they have a greater potential for production within a defined and finite environment than has any other single tiller.

They have the principal benefit of the early water and nutrient uptake by the seminal root system. The early development of the main tiller gives a much longer interval for the development of ear than in later culms and they have far longer period to double ridge formation (Rawson, 1967); and this may be a factor leading to a greater number of spikelets. Similarly, the main culm has a longer period in which to initiate florets.

The five plants were selected to represent the mean of each line or variety. Subsequent sampling was carried out at four day intervals.

The meristems were dissected out and measurements taken using a light microscope equipped with a measuring ocular. Measurements taken include maximum length (L) and maximum width (WD) of the meristems.

The relative growth rate (GR) at Stage 3 was measured as follows. A sample of 10 meristems of the same relative size was obtained from each line. Counts were made of meristems with characteristics similar to B130 (used as standard). The number was expressed as a fraction of the total sample and used as the estimate of the relative growth rate. In making the readings, special attention was paid to the stage of development as estimated by growth of awns and to the expansion of the tip



of the meristem. Meristems in the vegetative stage (similar to X969-3) still retain the cylindrical tip as shown in Figure 3.

Other measurements taken during the plant growth and at maturity include:

1. The average stem diameter (SD) was computed from measurements taken at the base of the head. Use was made of a simple and rapid technique suggested by Evans (1972). A guage as illustrated above was carved out of a thin resilient paper, the size of a standard credit card and graduated markings in millimeters were line along its inner edges. Rapid readings were obtained by inserting the particular part of the plant in the guage.

2. Estimates of seeds per head (Y) were derived from a random sample of twenty heads per plot preceding harvest.

3. The average seed weight (Z) was calculated from a 3 gm sample per plot using an electronic seed counter.

4. The number of tillers per 30 cm (X) was obtained by dividing grain yield per 30 cm of row by the product of seeds per head and the average seed weight.

5. The central two rows of the plot were harvested for grain yield (W).

The correlation and regression analyses were performed using mean values for the selected lines presented in Tables 2, 6 and 7.

The relative contribution of the three yield components, X, Y and Z on yield (W) was estimated using a multiple regression equation with W as dependent variable and X, Y and Z, as independent variables. The analysis is not germaine to the objectives of this study, however, it is reported in the appendix. The yield components, X, Y, and XY were each used as a dependent variable while meristematic measurements at Stage 3 were used as independent variables in a series of multiple regression equations. This was an attempt to break down the yield components into their subcomponents at the meristematic level.

#### RESULTS

The stages used as markers for meristematic measurements are shown in Figures 1 through 4. Using B130 as the standard, the following agronomic characteristics and developmental processes are typical of the individual stages.

Stage 1: Nearly all the leaves and leaf initials that the main stem bears are present at this stage. The leaves range from those fully differentiated at the base of the meristem to leaf primordia just distinguishable as ridges above. Stem development and elongation begin, thus preparing for spike differentiation.

Stage 2: The first indication of spike differentiation is the appearance of double ridges. The ridges are shown as bumps on a rather smooth edge of the meristems (Fig. 1). The pair of ridges are nearly equal in size initially. At a later time, the upper ridge of each pair grows more rapidly and spikelets are formed from them. The lower ridge probably becomes the internode of the rachis (Bonnett, 1935). The ridges are more developed in X969-3 than Bl30.

Stage 3: Spikelet differentiation is indicated. Several stages of spikelet development are shown on the same spike. Spikelet initials are prominent in the





B130

- Figure I. Structural characteristics of barley apical meristem at Stage I. Magnification = 80X
  - d double ridge


Magnification = 60X



Magnification = 60X



central and basal portions while the ridges at the top of the spike show only evidences of spikelet differentiation.

Differentiation of the first structure of the spikelet, the lemma, takes place. Primordia of other spikelet parts differentiate while the awn begins its development as an outgrowth from the lemma. The internodes of the rachis are very short at this stage. Spikelet differentiation proceeds towards the apex, but the last formed spikelets never complete their development. They remain infertile and rudimentary.

Stage 4: There is further differentiation and elongation of the spike to form the mature spike. The degree of elongation determines the spike density (Bonnett, 1935).

Table 1 gives the mean values for the meristematic measurements taken on the varieties, parents and control. Two discernible differences are obvious among the meristems of the varieties. These include their relative sizes and their rate of progress from the vegetative to reproductive stage.

At Stage 2, both the maximum length and width for X969-3 are largest. Bl30, Larker and 60-215-6 follow in a decreasing order. However, at Stage 3, 60-215-6 has

the largest meristem followed by Larker, Bl30 and X969-3. The relative sizes of the meristem at Stage 4 follow the same trend as that of Stage 3, with respect to the four above mentioned varieties.

In comparing the rate of progress from the vegetative to reproductive stages, regarding B130 as possessing the standard rate of progress within the gene pool, it was found that X969-3 (low X) had a lower rate of progress while 60-215-6 (high X) had a higher rate of development. This is shown in Figure 3.

Determination of the rate of progress also showed that differentiation and elongation of the awn coincides with the development of the full set of spikelet initials on the meristem as shown by B130 and 60-215-6 (Fig. 3).

Figure 5 shows a graphical presentation of the above mentioned differences. Two forms of growth pattern are discernible from the graph of length against width.

1. The control varieties follow the same path initially as B130 but differ in their 'take off points'. The take off point (TOP) is that point in development when ratio of length to width increases greatly. B130 and Larker take off from a smaller sized meristem than 60-215-6, the latter having a higher rate of development before the TOP. The rate of elongation is higher in

	L (mm) W (mm)
	L (mm) W (mm)
(standard).	L (mm) W (mm)
B130	Entry Name

Mean values for the maximum length (L) and width (WD) of the primary apical meristem at three different stages (SII, SIII, SIV) relative to

Table 1.

respectively	
3.0,	
and	
3.25	
2.75,	
Stage	
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Larker	•••
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5-6 • • •	
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2962 2962	TALIA

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31

1.516

7.967

.777.

2.323

0.396

1.138

B130

X969

1.289

4.045

.722

1.835

0.465

1.215

1.725

12.675

0.931

2.815

0.357

0.967

60-215-6

LARKER

**1.4**93

7.888

0.818

2.399

0.378

1.153

60-215-6 after the TOP.

2. X969-3, though it starts with a larger meristem virtually skips the elongation process until after four days (Stage 5). This delay results in a greater diameter meristem which is followed by an increase in the elongation process to a rate higher than that of 60-215-6.

Other differences observed between the behavior of X969-3 and the control varieties include the difference in time to reach Stage 2. X969-3 reached Stage 2 four days before the other control varieties, but maintained its vegetative stage shape through Stage 4 before the elongation process started.

Table 2 gives the mean values for the meristematic measurements taken on the selected lines. There were substantial differences in length and width at Stages 3 and 4 among the varieties and lines. These differences are further shown by the variances in Table 3.

The mean values of selected lines, with a peculiar apical meristematic growth pattern, and their parents are given in Table 4. Lines 68-105-17 and 68-105-9 show a similar growth pattern to parent X969-3 while lines 68-104-3 and 68-104-19 show a similar pattern to B130. The others are intermediate. Some start off with the X969-3 growth pattern and end with the B130 pattern of



Figure 5. Maximum length against maximum width of meristem.

Entry NameL (mm)WD (mm)GR68-103-11.290 $.494$ $2.176$ $.780$ $0.1$ 68-103-31.251 $.414$ $2.084$ $.684$ $0.2$ 68-103-81.221 $.414$ $2.084$ $.684$ $0.2$ 68-103-81.221 $.414$ $2.084$ $.684$ $0.2$ 68-103-81.221 $.412$ $1.956$ $.686$ $0.0$ 68-103-161.171 $.412$ $1.956$ $.686$ $0.0$ 68-103-181.325 $.488$ $2.736$ $.898$ $0.9$ 68-103-181.325 $.488$ $2.736$ $.898$ $0.9$ 68-104-31.199 $.382$ $2.394$ $.606$ $0.7$ 68-104+161.286 $.456$ $2.557$ $.892$ $0.8$ 68-104+191.233 $.401$ $2.572$ $.846$ $0.7$ 68-104+201.107 $.407$ $2.915$ $.925$ $0.8$ 68-104+201.107 $.401$ $2.572$ $.846$ $0.7$	WD (mm) (mm) (780 (780 (780 (780 (780 (780 (780 (780	Imm     Imm       1     11.706       4     9.217       4     9.069       6     725       6     5.608       9     8.709       8     13.313       8     17.227       16     733	WD (mm) 1.870 1.872 1.513 1.513 1.513 1.637 1.603 1.603 1.832 1.820	
68-103-1       1.290       .494       2.176       .780       0.1         68-103-3       1.251       .414       2.084       .684       0.2         68-103-8       1.221       .414       2.084       .684       0.2         68-103-8       1.221       .414       2.084       .684       0.2         68-103-16       1.171       .412       1.956       .686       0.0         68-103-17       1.080       .427       2.107       .795       0.4         68-103-18       1.325       .488       2.736       .898       0.9         68-103-18       1.325       .488       2.736       .898       0.9         68-104-3       1.199       .382       2.394       .606       0.7         68-104+10       1.286       .477       2.915       .925       0.8         68-104+16       1.155       .477       2.915       .925       0.8         68-104+19       1.233       .401       2.572       .846       0.7         68-104+20       1.107       .401       2.572       .846       0.7         68-104+20       1.107       .401       2.572       .811       0.5      0		1 11.706 9.217 9.217 9.217 9.217 6.725 6.725 6.725 6.725 8.709 8.709 8.709 8.709 8.13313 16.733	1.870 1.772 1.637 1.513 1.637 1.633 1.603 1.832 1.832	
68-103-3       1.251       .414       2.084       .684       0.2         68-103-8       1.221       .439       2.178       .795       0.4         68-103-16       1.171       .412       1.956       .686       0.0         68-103-17       1.080       .427       2.107       .795       0.4         68-103-17       1.080       .427       2.107       .790       0.6         68-103-18       1.325       .488       2.736       .898       0.9         68-104-3       1.199       .382       2.736       .898       0.9         68-104+16       1.255       .477       2.915       .925       0.8         68-104+16       1.155       .477       2.915       .925       0.8         68-104+18       1.343       .467       2.491       .789       0.7         68-104+20       1.107       .401       2.572       .846       0.7         68-104+20       1.107       .401       2.572       .846       0.7         68-104+20       1.107       .401       2.572       .846       0.7         68-104+20       1.107       .401       2.572       .811       0.5 <td></td> <td>2       9.217         4       9.069         6       5.608         9       8.709         8       13.313         8       17.227         16       7.33</td> <td>1.772 1.637 1.513 1.398 1.603 1.603 1.832 1.820</td> <td></td>		2       9.217         4       9.069         6       5.608         9       8.709         8       13.313         8       17.227         16       7.33	1.772 1.637 1.513 1.398 1.603 1.603 1.832 1.820	
68-103-8       1.221       .439       2.178       .795       0.4         68-103-16       1.171       .412       1.956       .686       0.0         68-103-17       1.080       .427       2.107       .790       0.6         68-103-18       1.325       .488       2.736       .898       0.9         68-103-18       1.325       .488       2.736       .898       0.9         68-104-3       1.199       .382       2.394       .606       0.7         68-104-10       1.286       .477       2.915       .925       0.8         68-104-10       1.286       .477       2.915       .925       0.8         68-104-10       1.233       .401       2.577       .892       0.8         68-104-19       1.233       .401       2.577       .846       0.7         68-104-20       1.107       .407       2.304       .811       0.5	.795 .686 .790 .898 .898 .892 .892 .925 .00 .789 .811	4       9.069         6       5.608         9       8.709         9       13.313         16       17.227         16       7.33	1.637 1.513 1.398 1.603 1.417 1.832 1.820	
68-103-16       1.171       .412       1.956       .686       0.0         68-103-17       1.080       .427       2.107       .790       0.6         68-103-18       1.325       .488       2.736       .898       0.9         68-103-18       1.325       .488       2.736       .898       0.9         68-104-3       1.199       .382       2.394       .606       0.7         68-104-10       1.286       .456       2.557       .892       0.8         68-104-10       1.286       .456       2.557       .892       0.8         68-104+10       1.233       .467       2.915       .925       0.8         68-104+20       1.155       .477       2.915       .925       0.8         68-104+20       1.233       .401       2.577       .846       0.7         68-104+20       1.107       .407       2.304       .811       0.5		6.725 6.725 9.608 8.709 8.709 8.709 8.709 1.738 13.313 8 17.227	1.513 1.398 1.603 1.417 1.832 1.820	
68-103-17       1.080       .427       2.107       .790       0.6         68-103-18       1.325       .488       2.736       .898       0.9         68-103-18       1.325       .488       2.736       .898       0.9         68-104-3       1.199       .382       2.394       .606       0.7         68-104-10       1.286       .456       2.557       .892       0.8         68-104-16       1.155       .477       2.915       .925       0.8         68-104-18       1.343       .467       2.915       .925       0.8         68-104-18       1.343       .401       2.5572       .846       0.7         68-104-20       1.107       .401       2.572       .846       0.7	.790 .898 .892 .925 .789 .811	.6 5.608 9 8.709 7 7.738 8 13.313 8 17.227	1.398 1.603 1.417 1.832 1.820	
68-103-18       1.325       .488       2.736       .898       0.9         68-104-3       1.199       .382       2.394       .606       0.7         68-104-10       1.286       .456       2.557       .892       0.8         68-104-10       1.286       .456       2.557       .892       0.8         68-104-16       1.155       .477       2.915       .925       0.8         68-104-18       1.343       .467       2.915       .925       0.8         68-104-18       1.343       .467       2.491       .789       0.7         68-104-20       1.107       .401       2.572       .846       0.7	.898 .606 .892 .892 .925 .811 .811	.9 8.709 .7 7.738 .8 13.313 .8 17.227 .6 733	1.603 1.417 1.832 1.820	
68-104-3       1.199       .382       2.394       .606       0.7         68-104-10       1.286       .456       2.557       .892       0.8         68-104-16       1.155       .477       2.915       .925       0.8         68-104-16       1.155       .477       2.915       .925       0.8         68-104-18       1.343       .467       2.491       .789       0.7         68-104-19       1.233       .401       2.572       .846       0.7         68-104-20       1.107       .407       2.304       .811       0.5	.606 .892 .925 .789 .811	.7 7.738 .8 13.313 .8 17.227	1.417 1.832 1.820	
68-104-10       1.286       .456       2.557       .892       0.8         68-104-16       1.155       .477       2.915       .925       0.8         68-104-18       1.343       .467       2.491       .789       0.7         68-104-19       1.233       .461       2.572       .846       0.7         68-104-20       1.107       .407       2.572       .846       0.7	.892 .925 .789 .846 .811	.8 13.313 .8 17.227 .7 16.733	1.832 1.820	
68-104-16       1.155       .477       2.915       .925       0.8         68-104-18       1.343       .467       2.491       .789       0.7         68-104-19       1.233       .401       2.572       .846       0.7         68-104-20       1.107       .407       2.304       .811       0.5		.8 17.227 7 16.733	1.820	
68-104-18 1.343 .467 2.491 .789 0.7 68-104-19 1.233 .401 2.572 .846 0.7 68-104-20 1.107 .407 2.304 .811 0.5	.789 0 .846 0 .811 0	7 16.733		
68-104-19 1.233 .401 2.572 .846 0.7 68-104-20 1.107 .407 2.304 .811 0.5	846 0 .811 0		1.804	
68-104-20 1.107 .407 2.304 .811 0.5	811 0	.7 10.600	1.578	
60-10E-2 1 1 E 100 0 100 0 100 0 0		.5 8.617	1.618	
0°10 //8° 2492 2478 /CI.I 2-COT-00	.877 0	.6 10.725	1.755	
68-105-9 1.117 .440 2.023 .767 0.3	.767 0	.3 3.988	1.283	
68-105-15 1.278 .484 2.277 .826 0.5	.826 0	.5 8.938	1.679	
68-105-16 1.180 .421 2.192 .816 1.0	816 1	.0 12.975	1.948	
68-105-17 0.991 .396 1.945 .755 0.1	.755 0	.1 4.925	1.334	
68-105-18 1.242 .472 2.341 .802 0.6	.802 0	.6 9.692	1.662	
68-105-20 1.040 .379 2.236 .859 0.2	.859 0	.2 4.073	1.208	

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Mean values for the maximum length (L) and width (WD) of the primary apical meristem at three different stages (SII, SIII, SIV) relative

Table 2.

growth, and vice versa.

Generally, rates of development of the 104 group of lines (X969-3 x  $B130^2$ ) were more related to B130 (the recurrent parent) while 103 lines (X969-3 x B130) and the 105 lines (X969-3<sup>2</sup> x B130) showed intermediacy between B130 and X969-3.

Meristems from selected lines are shown in Figures 6, 7 and 8. Lines 68-105-9 and 68-105-17 show characteristics similar to X969-3. They have a low number of tillers per 30 cm (X), but produced a higher than expected number of seeds per head (Y). Their meristems in the vegetative phase possess the characteristic cylindrical apex. Their rate of development is low. With a high rate of development, lines 68-104-3 and 68-104-19 have a high number of tillers per 30 cm (X) and produce the expected number of seeds per head (Y). Their awns are well differentiated and the meristems have lost their cylindrical apex. Lines 68-103-8 and 68-105-18 produce a low number of tillers and their expected number of seeds per head. Rate of development is intermediate. About 50% of their meristems show characteristics similar to X969-3 and 50% to Bl30 (standard). Meristem sizes are larger in lines 68-104-3 and 68-104-19 than in lines 68-105-9 and 68-105-17, while lines 68-103-8 and 68-105-18 have intermediate sizes between the

and width (WD) of the primary	(SII, SIII, SIV) relative to	
Aean square values for maximum length (L)	<pre>spical meristem at three different stages 3130 (standard).</pre>	
Table 3.		

		IIS		SIII		SIV	
Source	đf	ц	QM	ц	ДМ	ц	ДM
Varieties	22	.0467**	.0063	.3130**	.0251**	53.1615**	.1526**
Error	66	.0192	.0039	.0610	.0062	4.3512	.0163

\*\* P < .01

Table 4. Mea an ap: Bl:	un values 1 their F 1cal meri 30 (stand	s of sele barents 1 [stem at lard) and	scted lir For maxin three/fo I the rel	ies with num lengt nur stage ative gr	pecul h (L) s (SI owth	iar meris and widt I, SIII, rate at S	stematic g th (WD) of SIV, SV) stage III	<pre>growth pa f the pri relative (GR).</pre>	ttern mary to
Entry Name	S] L (mm)	LI W (mm)	L (mm)	SIII WD (mm)	GR	SIV L (mm)	( mm) (IM	SV L (mm)	( um ) M
68-105-9	1.117	0.440	2.023	0.767	0.3	3.988	1.283	20.800	1.970
68-105-17	166.0	0.396	1.945	0.755	0.1	4.925	1.334	20.625	1.999
68-104-3	1.199	0.382	2.394	0.606	0.7	7.738	1.417	8	1 1 1
68-104-19	1.233	0.401	2.572	0.846	0.7	10.600	1.578	1	
68-103-8	1.221	0.439	2.178	0.795	0.4	9.069	1.637	1 1 1	ļ
68-105-18	1.242	0.472	2.341	0.802	0.6	9.692	1.662	1	1 1 1
68-105-15	1.278	0.484	2.277	0.826	0.5	8.938	1.679	1 1 1	P 10 1
68-103-1	1.290	0.494	2.176	0.780	0.1	11.706	1.870	1 1 1	8 2 8
X969-3	1.215	0.465	1.835	0.722	0.0	4.045	1.289	22.110	2.060
B130	1.138	0.396	2.323	0.777	1.0	7.967	1.516	8	8
LSD(P = .05)	.196	. 088	.349	.111		2.950	.181		
LSD(P = .01)	.261	.117	.465	.148		3.923	.240		
X969-3, 60-2 When Bl30 is	l5-6 and in Stage	Larker a 23.	are in St	ages 2.7	5, 3.	25 and 3.	0, respec	ctively,	

.









two groups above.

Table 5 gives the correlation coefficients between the meristematic measurements. The length and width at any one stage are significantly correlated with each other. Sizes of meristems at Stage 3 are correlated with sizes of meristems at Stage 4 while a significant correlation exists between growth rate and size at Stage 3.

The mean values for the yield components (X, Y, Z), yield (W), number of seeds per unit area (XY) and stem diameter are given in Table 6. There were significant differences between the lines and varieties for the various plant characteristics. The high number of tillers produced by some of the selected lines resulted from the inheritance of the gene system for high tillering contributed by the Bl30 parent. Hamid and Grafius (1978) have demonstrated a positive relationship between SD and Y. The data here support the expected relationship between SD and size of meristem (Table 5).

There is ample evidence for the relationships between X, Y, Z and W in the published literature. There is, however, only fragmentary evidence regarding the relationship of the meristems to the components of yield and the data will be examined from this standpoint. First and crucial to the argument, I show that 50 to 60% of the

relative size of X and Y can be determined by examination of the meristem at Stage 3.

Examination of the growing point at Stage 3 reveals an important phase in the ontogeny of the genotypes. It marks the end of tiller production and the initiation of differentiation of florets. An indication of the potential number of florets per head borne by a genotype is given by the size of the meristem at this stage.

The time required to reach this stage is influenced by the variety and the environment in which it is grown. Different varieties vary in the time required from planting to maturity, however, most of the differences are in the early stages of growth. The time from heading to maturity is the same in all varieties. Excesses or deficiencies of the necessary environmental conditions may shorten or lengthen the time period required to reach Stage 3.

With reference to Table 7, length at Stage 3 is significantly and negatively correlated with number of seeds per head and stem diameter. It, however, has only a negative relationship with number of seeds per unit area (XY) and yield. A genotype with greater length at Stage 3 will produce a small stem diameter, small number of seeds per head, etc.

Width at Stage 3 is positively correlated with

three	rela-	and	
(WD) at	I, SIV)	e three	
width	I, SII	t Stag	
and	m (SI	GR) a	
ih (L)	riste	ate (	
lengt	cal me	owth r	
aximum	ry api	ive gr	
of ma	primar	relati	
<b>Defficients</b>	ges of the	(standard)	(SD).
elation co	erent stag	to Bl30	diameter
Corr	diff	tive	stem
Table 5.			

	LS2	WD2	LS3	WD3	LS4	WD4
WD2	.700**					
LS3	.438	.434				
WD3	.084		.631**			
LS4	.595**	.537*	•666*	.388		
WD4	.655**	.579**	.399	.287	.863**	
R	.367	.297	.732**	.464*	.563*	.428
SD	578**	138	513*		. 643** –	.469*

\*\* P <u><</u> .01 \* P <u><</u> .05

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of	м) ,	
number	plot (	
<b>,</b> (X)	per	
0 Cm	vield	r (SD)
per 30	grain y	iamete
illers	(Z)	stem d
ile t:	'eight	and
fert	eed w	(ХХ)
er of	age s	area
numbe	aver	unit
the	(X)	per
s for	head	seeds
alue	per	of
Mean v	seeds	number
.9		
Table		

Entry Name	X (#).	Т (#)	z (mg)	( dm )	(#)XX	SD (mm)
B130	18.46	60.03	39.00	688.00	1103.89	1.23
X969-3	16.61	64.91	42.50	731.00	1079.90	1.41
60-215-6	24.89	34.43	43.70	596.25	852.81	1.26
LARKER	20.64	51.30	42.40	718.75	1060.06	1.23
68-103-1	16.50	63.19	40.40	665.00	1035.74	1.35
68-103-3	15.83	62.87	39.60	628.75	991.97	1.36
68-103-8	17.41	59.51	44.00	729.00	1035.96	1.32
68-103-16	15.07	60.99	43.00	630.25	915.70	1.46
68-103-17	16.98	64.46	41.70	728.50	1092.38	1.54
68-103-18	17.52	54.43	44.60	680.25	953.07	1.41
68-104-3	25.11	42.65	39.90	682.50	1070.27	1.14
68-104-10	19.33	52.81	43.30	707.75	1021.09	1.25
68-104-16	15.52	58.58	42.00	611.00	910.37	1.29
68-104-18	17.10	59.43	42.00	678.25	1010.80	1.28
68-104-19	20.21	54.01	40.80	711.75	1090.67	1.31
68-104-20	22.29	38.77	41.30	567.75	861.27	1.16
68-105-2	16.51	61.74	41.70	679.50	1020.48	1.45
68-105-9	16.76	61.46	43.90	720.50	1026.81	1.54
68-105-15	17.72	63.72	41.50	750.00	1128.97	1.49
68-105-16	18.54	58.69	42.70	743.25	1089.97	1.34
68-105-17	17.62	66.05	44.00	817.75	1163.08	1.60
68-105-18	14.25	62.91	42.60	609.25	895.46	1.55
68-105-20	14.78	61.62	44.50	647.25	911.21	1.54
LSD (P < .05)	2.10	4.90	1.80	63.27	110.93	0.11
LSD(P < .01)	2.73	6.37	2.30	82.25	144.20	0.14

average seed weight and negatively correlated with the number of tillers per 30 cm though not at high significant levels.

The relative growth rate to Stage 3 is negatively and significantly correlated with number of seeds per head, stem diameter and head size, but positively correlated with number of tillers per 30 cm. A genotype with a relatively higher growth rate establishes a larger number of tillers, however, stem diameter, head size and number of seeds per head are reduced. The retardation in growth rate allows for a bigger head size formation. This is a natural phenomenon. Figure 9 shows the regression of number of seeds per head on length at Stage 3. The regression is significant (P < .05).

The regression of the third stage measurements of width, length and rate of development on dependent variables, number of tillers per 30 cm (X) and number of seeds per head are given in Table 8. The mean square values for the regressions are highly significant ( $P \le .01$ ) and the coefficient of determination ( $R^2 = .5196$  and .6501 for X and Y, respectively) indicate that the variance in the dependent variables can be partially accounted for by the variations in the three independent variables (L3, WD3, GR). Tables 9 and 10 provide the statistics for the

different stages of the primary apical meristem (SII, SIII, SIV) relative to B130 (standard), relative growth rate at Stage III (GR), number of fertile tillers per 30 cm (X), number of seeds per head (Y), average seed weight (Z), number of seeds per unit area (XY), head size (YZ), stem diameter (SD) and yield per unit area (W). Correlation coefficients of maximum length (L) and width (WD) at three Table 7.

	Х	Y	Z	ХХ	ΧZ	SD	3
LS2	.162	357	271	171	.306	578**	301
WD2	279	060.	.007	277	105	138	277
LS3	.180	491**	060	305	.246	513**	336
WD3	331	.152	.404*	192	176	.112	006
LS4	.039	215	294	154	.257	643**	288
WD4	050	033	364	050	.081	504**	215
R	.401*	518**	026	.046	472**	469**	.034

\* P <u><</u> .01

\*\* P < .05





regression.

Aside from the degree of explained variances, there are several other highly interesting observations. In the case of number of seeds per head (Y), the b values are negative, -15.29 and -6.52, for length and relative growth rate, respectively, but positive 53.31, for width. The effects of width and length are significant ( $P \leq .01$ ) while GR has no significant major effect in predicting Y. The  $R^2$  delete values for WD, L and GR are 0.2951, 0.4638 and 0.5949, respectively. This shows that width is most important in predicting Y followed by length. Size of meristem is thus most important in the prediction of number of seeds per head.

The partial regression coefficient for width is significant ( $P \le .01$ ) and negative (-22.35) in the prediction of number of tillers. Relative growth rate and length have a positive contribution to X, however, only the b value for GR is significant ( $P \le .05$ ). R<sup>2</sup> delete values are 0.1887, 0.3610 and 0.5024 for WD, GR and L, respectively. Length of meristem is least important in determining tiller production. Rate of development of width is more important in tiller production. The higher the rate of development of the meristem, the bigger the X value it will have, however, width of meristem will be small.

. Analysis of variance on the multiple regression of number of tillers per	30 cm (X) and number of seeds per head (Y), each as a dependent variable	on the length (L), width (WD) and relative growth rate (GR) at Stage III.	
Table 8,			

Source	đf	Mean Squares X	Т
Regression	£	17.9750**	119.2332**
Error	15	3.3243	12.8373
R <sup>2</sup>		0.5196	0.6501

\*\* P <u><</u> .01

	R <sup>2</sup> deletes	0.5024	0.1887	0.3610	
ariables.	Partial Correlation Coefficient	0.1855	-0.6386	0.4982	
III as independent ve	Significant Level	0.476	0.006	0.042	
rate (GR) at Stage ]	Beta Weight	0.2192	-0.7412	0.5847	
	Variable	LS3	WD 3	R	

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Multiple regression statistics for number of fertile tillers per 30 cm (X) as dependent variable and length (L), width (WD) and relative growth Table 9.

Table 10.	Multiple regression dependent variable a (GR) at Stage III as	statistics for numb nd length (L), widt independent variab	er of seeds per head (Y) h (WD) and relative grow les.	as th rate
Variable	Beta Weight	Significant Level	Partial Correlation Coefficient	R <sup>2</sup> Deletes
г3	-0.7231	0.013	-0.5894	0.4638
WD3	0.7677	0.001	0.7096	0.2951
R	-0.3447	0.145	-0.3689	0.5949

ຑ	Я	
g	vth	
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of	(MD)	•
number	width	ariables
for	(L)	lt va
l statistics	and length (	ıs independer
e regression	nt variable	Stage III a
Multiple	depender	(GR) at
Table 10.		

Number of seeds borne will be small since width has a positive significant relationship with Y.

This is expected in nature because a relatively low growth rate allows for a low number of tillers. This relaxed growth rate encourages the formation of organs (i.e. meristems) with larger width. Since the width determines the length that the organ assumes, a meristem with a larger surface area is produced. A larger number of floral initials are borne resulting in the production of a larger number of seeds per head. This is in conformity with the fact that sizes and numbers of plant organs are negatively correlated (Grafius, 1978).

The development of plant organs in terms of their gross size and number is closely interrelated. This relationship exists even though plants organs are laid down sequentially and each may be affected by different modes of environmental stress. X has a negative influence on stem diameter, number of seeds per head and average seed weight. This influence is exerted through the establishment of a meristem size at Stage 3. The rate of establishment is genetically controlled and has a direct relationship with the number of tillers coded for by the plant. All other traits regarding size and numbers are then evolved toward the attainment of the ultimate character, grain yield.

## DISCUSSION

Yield is determined by the number of fertile tillers per unit area, number of seeds per head and average seed weight.

Tiller production is one of the first developmental processes at the organ level. It has a far reaching effect on the growth and development of organs laid down later in the plant's ontogeny. Generally, one finds a negative correlation between number of tillers and number of seeds per head and this correlation is largely physiologic.

The morphological development of the primary culm of barley from germination to pollination can be divided into three phases as opposed to the two proposed by Bonnett (1935). The phases can be determined approximately by examining the stem and more accurately by examining the apical meristem. During the first phase, the stem internodes do not elongate, leaves and leaf initials differentiate from the growing point, which remains smooth in outline and increases in length. The apical meristem increases in size during the second developmental phase, double ridges appear, spikelet structures and tiller initials differentiate. During the third phase, the

internodes of the stem elongate and further differentiation of spikes occur to complete their development in preparation for pollination. Development of the other fertile tillers follow in rapid succession when the main stem passes into the third phase.

The very early differences in the time of differentiation and rate of spikelet development are reflected in the mature plant characteristics. Although there were no varietal differences in growth until Stage 2, differential growth from just before and after Stage 3 became obvious.

There was a 4-day time lapse, for the transformation of the apical meristem from the appearance of double ridges to the onset of spikelet differentiation, between X969-3 and the other control varieties. The progeny which have a similar growth pattern to X969-3 possess this property.

Spikelet differentiation is retarded in X969-3. This retardation allows for a larger sized meristem formation. An extra surface area is provided for the development of an additional number of seeds per tiller by the variety. Similarly, Lee <u>et al</u>. (1974) and Williams (1975) are of the opinion that a delayed and larger basal branch at the time of spikelet initiation allows for the formation of more spikelets, florets and grains in sorghum.

The interesting thing here is that although the development of the meristem is delayed in X969-3 and in some of the progeny, these plants are not necessarily later in heading. Somehow or other the difference in time is made Those with larger X tended to have smaller diameter up. meristems as well as a faster rate of development. The characteristic size of the meristem at Stage 3 is dependent on the number of tillers coded for by the genotype. Rate of development of the meristem at this stage is a function of meristem size. The larger the meristem the higher the rate of elongation. However, owing to the 4-day time lag X969-3 resulting in the larger sized meristem, its rate of elongation is greater than that of the control variety with the highest tillering within this gene pool.

There is reason to suspect that the larger reproductive apex at T.O.P. in X969-3 traces back to a larger vegetative apex. If so, then the gain in number of seeds per head (Y), may be established in the first developmental phase with all the physiological and practical implications.

This property possessed by variety X969-3 is under direct genetic control because it is carried over into its progeny. Grafius <u>et al</u>. (1976) reported the uncoupling of X and Y in the same variety and showed that this

characteristic was carried over into the progeny with resulting increased yield of the unselected progeny over the best parent.

The production of a large number of seeds per head can be traced to a large meristem size while tiller production involves the relative growth rate of the meristem and the width of the meristem. The greater the growth rate, the larger the number of tillers produced. However, the width of the meristem is small. Number of seeds per head is thus a function of the number of fertile tillers formed.

Plant development is programmed in its heredity which interacts with the environment. This necessitates the formation of the various morphological structures in some integrated form and the control of the balance between plant characteristics involving sizes and numbers is manifested through the growth of the apical meristem.

The number of high yielding lines, originating from the straight cross and the backcross to X969-3 parental line, obtained from the few original randomly selected populations is intriguing. Line 68-105-15 has recently been released as Bowers because of its high yielding potential in trials at many locations in Michigan. There appears to be good reason to suggest that the meristematic

## SUMMARY AND CONCLUSION

Four varieties with varying values in their yield components, but having comparatively similar levels of grain yield, in addition to 19 lines from the straight and two complementary backcrosses between two of the varieties, B130 and X969-3, were used in the experiment.

The development of meristems between Stages 2 and 3 show a switch in the developmental pathway as shown by the relative sizes of the meristems at the two stages. Varieties with relatively large meristem sizes at Stage 2 developed relatively small sized meristems at Stage 3.

Bl30 followed the same developmental pathway as the other control varieties initially, but differed in its take off point. Its rate of development before the take off point was intermediate between 60-215-6 (higher tillering) and X969-3 (lower tillering), a property, which is characteristic of the number of fertile tillers it bears. Some lines produced high number of tillers through the inheritance of the gene system for high tillering contributed by the Bl30 parent. Their head sizes were however, small.

X969-3 followed a different pathway in development than the other varieties resulting in the production of

a higher number of seeds per head for its level of X. This property results from an initially broader based meristem and a time-lapse period between the vegetative stage and the onset of the reproductive stage. Some lines in the progeny inherited this property, together with genes for higher X which resulted in a higher tiller number for a given head size. Apparently, whenever these two occurred together, we get more fertile tillers for a given head size than would have been expected. In other words the negative correlation between X and Y is somewhat relaxed.

The results also showed that variation in X and Y can be significantly accounted for by the variation in size and relative growth rate at Stage 3. Variation in width at Stage 3 and the relative growth are most important in predicting the number of fertile tillers per unit area while width and length at Stage 3 are important in explaining the variation in the number of seeds per head. The relative growth rate has a positive effect in the prediction of the number of fertile tillers per unit area. This results in the formation of small diameter meristems with production of increasing number of fertile tillers accounting for the negative relationship between the diameter of the meristem and number of fertile tillers per unit area. Width maintains the negative relationship in predicting

the number of seeds per head. Its significant positive correlation with the length of the meristem establishes a positive predictive value between the meristem length and the number of seeds per head. With relaxed growth rate, a high number of seeds per head is produced for the number of fertile tillers borne.

From the number of lines with similar meristematic characteristics as X969-3, it was proposed that meristematic properties are controlled by few genes.

## APPENDIX

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Table Al.	Mean acre	values f (BU/AC)	or head for the	size (YZ) selected	, height lines and	(HT) and yie I varieties,	eld in bushels per control and parents.
Entry Name			YZ (gm)		HT (i	in)	BU/AC)
B130			2.34		38.2	25	93.84
X969-3			2.75		33.0	00	99.71
60-215-6			1.50		25.5	00	81.33
LARKER			2.18		38.2	25	98.04
68-103-1			2.54		35.0	00	90.71
68-103-3			2.49		37.2	25	85.76
68-103-8			2.62		41.0	00	99.44
68-103-16			2.62		41.7	75	85.97
68-103-17			2.69		33.7	75	99.37
68-103-18			2.43		36.0	00	92.79
68-104-3			1.70		40.0	00	93.09
68-104-10			2.29		38.0	00	96.54
68-104-16			2.46		38.5	50	83.34
68-104-18			2.50		39.5	50	92.51
68-104-19			2.21		39.7	75	97.08
68-104-20			1.60		37.2	25	77.44
68-105-2			2.57		37.0	00	92.68
68-105-9			2.69		34.7	75	98.28
68-105-15			2.64		36.0	00	102.30
68-105-16			2.51		35.5	50	101.38
68-105-17			2.91		34.0	00	111.54
68-105-18			2.68		38.5	50	83.10
68-105-20			2.74		38.2	25	83.28
LSD(P < .0)	5)		0.18		1.5	52	8.63
LSD (P < .0.	1)		0.23		1.9	97	11.22

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X					ł	•* .384
ХХ					* .540*	.888
ΧZ				037	819	.198
Z			.485*	242	321	.231
Y		.151	.937**	.039	810**	.117
SD	.794**	.430	.861**	.014	639**	.218
	Х	Z	ZX	ХХ	×	м

per	head (Y) and average seed weight	(Z)
Source	đf	Mean Square
Regression	ε	16171.3683**
Error	15	144.7601

Analysis of variance on the mulitiple regression of yield (W) as dependent variable on number of tillers per 30 cm (X), number of seeds

Table A3.

\*\* P < .01

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	on R <sup>2</sup> deletes	.0601	.2868	.6795	
	Partial Correlatic Coefficient	.9769	.9695	.9308	
• •	Significant Level	<0.0005	<0.0005	<0.0005	
independent variåbles.	Beta Weights	1.7190	1.4236	.5674	
<u>.</u>	/ariables	×	Х	2	

Multiple regression statistics for yield per unit area (W) as the dependent variable and the number of fertile tillers per 30 cm(X), number of seeds per head (Y) and average seed weight (Z) as Table A4.

		Åf	Mean Square
	gression	ſ	9011.4317
gression 3 9011.4317	ror	15	5409.4322

Analysis of variance on the multiple regression of number of seeds per unit area (XY) on length (L), width (WD) and relative growth rates (GR) at Stage III. Table A5.

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Variables	Beta Weights	Significant Levels	Partial Correlation Coefficients	R <sup>2</sup> deletes
L3	-0.7293	0.071	-0.4490	0.0605
WD3	-0.0025	0.993	-0.0023	0.2499
Я	0.5814	0.097	0.4158	0.0931

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