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THE PRIMARY SHOOT APICAL MERISTEM, YIELD COMPONENTS AND YIELD OF BARLEY (<u>HORDEUM VULGARE</u>, L. EMEND. LAM.)
I. AN ASSESSMENT OF THE INVOLVEMENT OF PROMOTIVE HORMONES
II. A MATHEMATICAL MODEL FOR YIELD

presented by

James Benjamin Abaka Whyte

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Crop Science

Major professor

Date 11/13/81

THE PRIMARY SHOOT APICAL MERISTEM, YIELD COMPONENTS AND YIELD OF BARLEY (*HORDEUM VULGARE*, L. EMEND. LAM.)

I. AN ASSESSMENT OF THE INVOLVEMENT OF PROMOTIVE HORMONES

II. A MATHEMATICAL MODEL FOR YIELD

By

James Benjamin Abaka Whyte

A DISSERTATION

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

DOCTOR OF PHILOSOPHY
Department of Crop and Soil Sciences
1981

ABSTRACT

THE PRIMARY SHOOT APICAL MERISTEM, YIELD COMPONENTS AND YIELD OF BARLEY (*HORDEUM VULGARE*, L. EMEND. LAM.)

I. AN ASSESSMENT OF THE INVOLVEMENT OF PROMOTIVE HORMONES

II. A MATHEMATICAL MODEL FOR YIELD

By

James Benjamin Abaka Whyte

The study is in three parts. First, an assessment of promotive hormones' involvement in the growth and development of shoot apical meristem in relation with yield components and yield of barley was made. Second, the use of findings as the basis for reconceptualizing the developmental allometry among the yield components and yield. Third, assessment of the reconceptualized model using data for twelve oat varieties planted between 1976 and 1979, inclusive.

Twelve genotypes with differing yield components were used in the experiments. Meristems were sampled at transition, reproduction and elongation stages and measurements taken of their length, width and relative growth rate. Additionally, yield, number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z) were determined. Hormone applications were done at transition stage and two days after.

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James Benjamin Abaka Whyte

Genotypes with larger meristems had lower growth rate, low X, high Y and bigger head size. Applications of the hormones induced changes in the measured characteristics. The magnitudes of the changes depended on the type of hormone applied and genotype under consideration. Indications of existence of equilibrium among the hormones were shown.

The model involved the use of path coefficient analysis to determine the effects of three hypothetically separable independent environmental resources, E_1, E_2 and E_3, to yield through their direct effect on X, Y and Z, respectively. Two sets of environmental components (efficiencies) were estimated from X, Y and Z.

Varietal constants were positive, highest for X followed by Y and then Z. All varieties had similar efficiencies in production of X and Y. Efficiencies for Z production varied. All the varieties and seven of the environments had significant yield predictions.

The relationship between the predicted and observed yields was linear and highly significant.

IN MEMORY OF
MY GRANDMOTHER, NANA EFUA OTUA,
AND FATHER, JOHN KOFI ADOKO WHYTE.

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ACKNOWLEDGEMENTS

My interest in plant breeding, particularly on the subject presented in this study, has been nurtured by the devotion and the example of my mentor, Dr. J.E. Grafius. I mourn his death which came before the completion of this study.

I am indebted to Drs. D.D. Harpstead, M.W. Adams, D. Penner and C. Pollard, members of my guidance committee for their encouragement and constructive inputs into my work as a graduate student.

Dr. R.L. Green, Dean of the College of Urban Development, provided a great deal of support to make possible the successful completion of my graduate studies. I am grateful.

My sincere appreciation goes to Mr. Dimon Wolfe for the unqualified assistance he provided in my field research work. Miss Patti Perkins' assistance with the typing and preparation of the dissertation is acknowledged.

Finally, for their love, untiring encouragement, moral support and the understanding they have always accorded me, I am forever grateful to my FAMILY.

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INTRODUCTION

Yield is a complex trait and in barley, yield has three components; the number of heads per unit area (X), the number of seeds per head (Y) and the seed weight (Z). Changes in yield are obtained through changes in one or more of the components, however, simultaneous maximization of the yield components for yield improvement has not been possible. This is due to the negative associations among the yield components and when these negative correlations are reduced, significant improvements can be obtained. There has been reports of yield improvements induced by the relaxation of the significant negative correlation between the number of heads per unit area and the number of seeds per head.

The level of number of heads produced per unit area has a great effect on the sizes and numbers of the later-formed organs owing to its direct association with the shoot apical meristem size. This association can be modified by external factors such as nutrients, light, water and temperature or possibly through hormonal manipulations.

In altering the yield components and yield through the manipulation of the hormonal levels, other plant characteristics such as height, leaf area, growth rate, head size, tillering, to mention but a few, change. Yield is either reduced or increased, depending on the relationships among the above mentioned plant characteristics with it. This investigation was initiated to assess the involvement of the promotive hormones in the development of the primary shoot apical meristem, yield components and yield of barley genotypes with differing yield components and yield. A second objective was to determine the reactions of these genotypes to application of some hormones.

It is documented that different genotypes perform differently in various environments. The relationship between the performances of the different genotypes in the various environments and some measure of these environments (environmental indices) is frequently linear or nearly so. Using the concept of sequential development of the yield components, the developmental allometry, and the proposition that the yield components of cereal crops are produced at different stages in the ontogeny of plants, a model is presented for yield. This model provides an insight into the genotype-environment interaction involved in the production of each component of yield toward the genotypic yield performances.

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CHAPTER 1

AN ASSESSMENT OF THE INVOLVEMENT OF PROMOTIVE HORMONES

INTRODUCTION

In barley, the complex trait, yield (W) has three components: the number of heads per unit area (X), the number of seeds per head (Y) and the seed weight (Z). The order of development of the yield components are number of heads per unit area to number of seeds per head to seed weight. Geometrically, yield of barley can be expressed as a volume of a rectangular parallelepiped with its components as the edges. Yield changes when one or more of its components change and the greatest change is obtained with a change in its shortest edge (Grafius, 1956; 1964). Hamid and Grafius (1978) showed that the earlier developed yield components have a profound influence on the later developed structures. Thus, the genetic control of yield is indirectly channeled through its components, with the earlier formed structures assuming the major part of the control.

The negative correlations among the yield components of several crop plants as established by Adams (1967) has rendered the maximization of X, Y and Z, simultaneously, impossible. This has resulted in the imposition of a ceiling on grain yield. Relaxation of these negative correlations could result in great yield increases in such crop plants.

Grafius *et al*. (1976) reported such a relaxation in the X and Y relationship in barley. A higher value of Y for a given value of X was obtained, resulting in increased yield of the unselected progeny over the better parent.

The development in a plant of trait X at any one level triggers a chain of reactions which affect all later formed organs as shown by Sinnott's Law (1921). Sinnott stated that, 'The size of any organ depends upon the size of the growing point out of which it has been developed'. By virtue of the direct association between X and meristem size, X assumes a pivotal role in determining sizes of plant organs formed later and eventually the determination of grain yield.

The conversion of the barley apical meristem from the vegetative to the reproductive condition coincides with the cessation of tiller and leaf bud development and the initiation of the floral primordia and then kernel formation. This dramatic switch exerts a direct effect on the relationships among the yield components. The dependence of X on meristem size and the effect that X has on organs formed later in the ontogeny of the plant could be modified by external factors (Aspinall, 1961; 1963; Cannel, 1969; Friend, 1965; Wardlaw, 1971) or internal factors (Leopold, 1949).

Improvement of crop productivity through plant breeding has been mainly achieved through the manipulation of plant

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characteristics to utilize environmental factors with greater efficiency. Physiological and biochemical means of improvement is a more recent objective and is being encouraged, however, the frequency of achievements is quite slow. The physiological and biochemical processes occurring during the development of a plant is so integrated that an equilibrium state is established at all times during growth, differentiation and development. Changing the internal equilibrium alters the final resulting product and the extent of this alteration in relationship to grain yield is dependent on the degree of association between the two.

Attempts have been made to increase yield through hormonal application. Unfortunately, much of the reported results are contradictory. In the quest for altered yield, other plant characteristics such as height, leaf area, stem diameter, growth rate, seed size, tillering, head size, etc., also change. Depending on the association between these changes and yield, yield is either reduced or increased.

The following study seeks to:

1. Investigate the levels and activities of the promotive hormones and to relate the observed differences to:
    a. Growth and development
    b. Yield components
    c. Yield

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2. Synchronize the growth and development of the standard genotypes with that of X969-3 (an outlier) through the manipulation of their endogenous hormonal levels and to determine the effect that such manipulation has on yield components and yield.

LITERATURE REVIEW

All plants follow a developmental rhythm. Small grains such as oats, barley, wheat, millet and sorghum 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 plant and are directly related to the yield components.

Grafius (1969), Grafius and Thomas (1971) and Thomas *et al*. (1971a, b, c) elaborated upon the concept of a sequential developmental process of yield components. The chronological developmental sequence of the yield components of barley is number of heads per unit area (X) to number of kernels per head (Y) to kernel weight (Z). Yield (W) is a multiplicative product of the components, i.e. W=XYZ. Yield is subject to change through change in one or more of its components.

Yield components are determined at different stages in the ontogeny of a plant (Rasmusson and Cannell, 1970) and are differentially affected by variation in the environment (Tai, 1975). This suggests that the three yield components in barley are affected by independent environmental factors during the same or different periods of the plant's development. The formation of yield components in sequence results

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in a different relationship between a component trait and the environmental resources. The development of the first component trait, i.e. number of heads per unit area, is solely determined by genetics and the environmental resources available during the early stage of growth. A component trait which develops subsequent to others is not only influenced by the resources available during its formation, but also by the development and characteristics of its predecessor. The mechanisms for controlling yield components are thus increasingly complicated in the chronological developmental sequence. Thomas *et al*. (1971a) proposed a transformation to factor out the effect on yield of a component trait appearing earlier in the development sequence. Hamid and Grafius (1978) showed that the plant organs laid down early in the sequence exert more genetic control over variation in yield than traits laid down later in the ontogeny.

Adams (1967) showed the existence of negative correlations between the yield components of several crop plants. Correlations among yield components may be due to genetic linkages, pleiotropy or physiological developmental relationships. These negative correlations have posed a block to yield improvement of crop plants. The simultaneous maximization of X, Y, and Z is prevented and as a result a

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ceiling of yield is created. Relaxation of these negative correlations can result in great yield increases of such crop plants. The short statured hexaploid wheats, derivatives of Norin 10 cultivar, outyield the standard wheats as a result of the relaxation of the negative correlations between the yield components. Grafius _et al_. (1976) reported the relaxation of the negative correlation between the number of heads per unit area and number of seeds per head in barley so that a higher value of Y for a given value of X was possible. This characteristic was inherited by some progeny lines with resulting increased yields of its unselected progeny over the best parent in one of the backcross populations - after selfing several generations.

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 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.

The development of organs in plants is controlled by developmental allometry (Sinnott, 1921, 1960; Bonnett, 1964). Each part and function is so closely related with the rest

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that the whole plant develops in an orderly fashion to produce a mature individual. Adams (1975) points out the phenomenon of size and numbers as part of the overall allometry in a plant. He showed significant relationships between number of pods per plant vs. main stem node number and seed size vs. leaf size in *Phaseolus vulgaris*. 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). Size and number of appropriate components of yield (W) may be more critical than the size or number of the photosynthetic surfaces in causing differences in yield of genotypes (Evans and Dustone, 1970; Khan and Tsunoda, 1970; Berdahl *et al*., 1972; Hamid and Grafius, 1978).

The primordia of organs evolve from meristems and the central role of these structures has been pointed out by Sinnott (1921). Sinnott stated that, "The size of any given organ depends upon the size of the growing point out of which it has been developed". An important feature of apical meristems of small cereal grain plants is that they undergo both vegetative and reproductive phases of growth. The vegetative growth period involves the formation of tiller and leaf primordia. The change of meristem from the vegetative to reproductive stage coincides with the cessation

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of the development of tiller buds and leaves and the onset of initiation of reproductive structures. The switch from vegetative to reproductive phase exerts a direct effect on the relationships among the yield components of small cereal grain plants.

The level of X affects all later-formed organs (Hamid and Grafius, 1978). By virtue of its direct negative association with meristem size, X assumes a pivotal role in determining sizes of plant organs and eventually the determination of economic yield itself. The importance of the number of heads per unit area (X) is demonstrated in a path coefficient diagram developed in conformity with Sinnott's Law and known developmental relationships (Hamid and Grafius, 1978; Grafius, 1978).

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 (Abbe _et_ _al_., 1941; Stant, 1954; Aitken, 1967; Quinby, 1970; Fisher, 1973; Blum, 1977; Whyte, 1979). The relationships among plant characteristics appears 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 ass

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associated with factors governing the size of the meristem from which the culm, leaves and glumes have arisen.

Whyte (1979) traced the origin of the relaxation of the negative correlation between X and Y (Grafius *et al*., 1976) to two major factors:

1. An initially broader meristem
2. A 4-day time lapse period between the end of vegetative stage and the onset of the reproductive stage.

Lee *et al*. (1974), Williams (1975), Fisher (1973) and Blum (1977) established similar relationships in detecting the origin of the heterotic effect in the sorghum panicle.

Grafius (1978) introduced a dichotomy to the ideas of Sinnott: allometry associated with organs arising from either (a) the same meristem or (b) different meristems.

Allometric relationships among X, Y and Z might result from competition rather than from the effects of common origin. The stress matrix (Grafius, 1978) established between the components varies with the environment and the gene pool. Linkage may be present but its effect is less important if one assumes that genes for the components are distributed throughout the chromosomes. Allometric relationships among 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

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for environmental resources (Adams, 1967; Hoen and Andrew 1959; Grafius, 1969).

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. A second corollary states that size of the organ and numbers of organs 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). Attempts to select for different leaf sizes on the same culm were futile.

The dependence of X on meristem size and the effect that X has on later-formed plant organs is quite intriguing. This dependence could be modified by external factors such as nutrients (Aspinall, 1961, 1963), water (Wardlaw, 1971), temperature, light intensity and duration (Cannell, 1969; Friend, 1965) or internally by hormone levels (Leopold, 1949).

Five distinct groups of compounds have been characterized as hormones. Auxins, gibberellins and cytokinins are the promotive hormones while abscisic acid is regarded as an inhibitory hormone. Ehtylene, however, acts both as a promotory and an inhibitory hormone. The proportions of the various hormones present appear to affect the growth rate and subsequent differentiation pattern of a tissue in the complete organism. The presence of both promotive and inhibitory hormones permits a precise control of many developmental activities.

Tata (1966) hypothesized that hormone action lies in the control of the mechanisms by which enzymes are made in the cell. The points at which they act include:

1. The genetic information in the cells which determine their ultimate potential.

2. The transcription of messenger RNA (mRNA) from DNA specifying the type of protein to be produced.

3. The machinery for protein synthesis involving the ribosomes, transfer RNA (tRNA) and other regulatory substances.

4. Post-transcriptional processes.

Genes do exist in different states of activity and the state of any particular gene is important for hormonal activation or inactivation.

Evidence indicates that gibberellin is involved in extension growth of plant tissues and has been cited as the mechanism for bolting in rosette plants. Gibberellin treatment of intact plants causes enhanced elongation of existing internodal cells and also increases the number of cells present in each internode principally as a result of an increase in mitosis in the subapical region of the stem.

The magnitude of the stem elongation response to gibberellin varies from species to species and from variety to variety within a species. Jones and Phillips (1966) showed a direct correlation between elongation rate of internodes of different ages and the gibberellin contents of the same internodes. Endogenous gibberellins are present in highest concentration in those regions undergoing most rapid extension growth, providing strong evidence that gibberellin is concerned in normal control of stem extension growth. Radley (1970) found that semi-dwarf wheats contain more endogenous gibberellin-like activity than normal varieties, particularly in their young stage. Application of gibberellic acid markedly stimulates the growth of seedlings of normal varieties but not the dwarf seedling. She, therefore, assumed that a block to the utilization of gibberellin causes the accumulation of the hormone.

The actual role of gibberellin in promoting stem elongation is not known. Experimental evidence show that nucleic acid metabolism is involved in the process. Lang et al. (1967) showed that protein synthesis is required for growth induced by gibberellic acid.

Gibberellic acid (GA_3) causes an increase in activity of two hormones required for the synthesis of lecithin, a major component of cell membranes (Ho and Varner, 1974).

GA_3 causes *de-novo* synthesis of several hydrolytic enzymes in barley aleurone layer. Since RNA synthesis is required for this hormone effect, the synthesis of the enzymes is dependent on the synthesis of their mRNA. Higgins *et al*. (1976) showed a positive correlation between the rate of α-amylase synthesis *in vivo* and the level of translatable mRNA for α-amylase. The hormone is required throughout the period of enzyme synthesis; its removal causes the level of enzyme production to return to that of the aleurone layers not treated with gibberellic acid.

α-amylase production is inhibited by inhibitors of oxidative phosphorylation and protein synthesis. Abscisic acid also antagonizes GA_3-mediated hydrolase synthesis through the prevention of the GA_3 effect on poly(A)-RNA synthesis *in vitro*.

The above evidences suggest that the expression of the gibberellin effect may require the synthesis of enzyme specific RNA molecules during transcription.

Cytokinins or plant cell division factors, are chemical substances which have the ability to induce cytokinesis in cultured plant tissues (Skoog *et al*., 1965). At the same time, cytokinins evoke a number of physiological responses, such as promotion of cell enlargement and delay of leaf senescence, which do not involve cell division (Skoog *et al*., 1970; Kende, 1971). This suggests that the cytokinins might not act directly to trigger the events of cytokinesis, but rather that cytokinesis is a secondary result of some biochemical role played by the hormone in plant cell metabolism.

Fosket and Short (1973) followed changes in protein content and cell proliferation activity after a cytokinin-requiring strain of cultured *Glycine max* tissue was transferred to freshly prepared media which either contained or lacked cytokinin. After two days, no further increase was observed in the absence of cytokinin. Cell population attained during the first six days was a function of the cytokinin concentration of the culture medium.

There is a temperature-dependent lag phase between auxin application and the resulting growth response of oat coleoptile sections (Rayle and Cleland, 1970; Nissl and Zenk, 1969). This lag indicates that auxin does not act directly on growth but on some process which later alters the growth rate (Ray *et al*., 1962). The intermediate process is sensitive to inhibitors of both protein and RNA synthesis (Nooden *et al*., 1963), indicating the necessity of these substances for auxin action. Auxins cause an increase in the synthesis of RNA and protein (Key *et al*., 1964; Trewavas, 1968). This effect is counteracted by antiauxins.

Actinomycin D and 5-fluouracil inhibit RNA synthesis

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without affecting auxin induced growth (Nooden, 1968; Lin and Key, 1967; Ingle et al., 1965). Kinetic studies of the effect of actinomycin D on growth show that there is a 'pile of substances' on which auxin acts but this pile is absent in the absence of auxin (Penny and Galston, 1966). Regardless of when the inhibitor is applied, auxin application induces growth before the effect of the transcription inhibitor is manifested. Thus, mRNA specific for auxin induced growth exist which is translated into protein upon application of auxin. As the mRNA is used up, new mRNA is produced for auxin induced growth to continue and it is this process which is sensitive to actinomycin D.

Auxin brings about cell extension by increasing the cell wall plasticity. This increase takes place in two stages (Penny and Galston, 1966):

1. An early effect which involves loosening and breaking the physical bonds.
2. A later effect which is dependent on RNA and protein synthesis.

The early effect is mediated at least in part by hydrogen ion (H^+) secretion (Hager et al., 1971; Rayle et al., 1972; Rayle, 1973). Hager et al., (1971) stimulated growth through acidification of the cell wall and concluded that auxin may act by activating adenosine triphosphatase which pumps H^+ into the cell wall. Jacobs and Ray (1976) reported a similar inc

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increase in growth rate with auxin and externally applied H^+ and also realized that before the initiation of the enhanced growth rate, there was reduction in pH in both maize and pea. Rayle _et al_. (1970) monitored the changes in cell wall composition as a result of auxin application and proposed two possible modes of action of H^+ whether induced by auxin or externally applied:

1. Chemical hydrolysis of cell wall polymers.
2. Activation of enzymes which are otherwise inactive at the neutral pH.

At present, the major concept of the mode of action of auxins is that they depress certain genes and induce mRNA synthesis. This results in the synthesis of new enzymes, and ultimately the cell wall, allowing cells to expand. Induction of protein synthesis by a chemical effector via transcription and translation of DNA is a time consuming process and is preceded by a characteristic lag phase (Branscomb _et al_., 1968). Nissl _et al_. (1969), however, showed that the lag phase can be gradually shortened to zero and the rate is hormone concentration and temperature dependent.

Publications dealing with the relationship between hormonal contents and activities, meristematic growth and development, yield components and yield of cereals are lacking.

The developmental morphology of the shoot apex of gramineous species is well documented (Bonnett, 1935, 1936, 1937, 1966; Sharman, 1947; Bremer-Reinders, 1958). The spike is a branched system bearing fertile and infertile branches. However, in barley, certain differences are noted when its inflorescence are compared with other members of the graminae. The main shoot axis does not differentiate into a terminal spikelet, primary branches are terminated by an ovary and no glume primordia are formed on the rachis.

In the mature cereal seed, there is already a well-developed shoot with 3 or 4 leaf initials and an apical dome enclosed within the coleoptile. As the plant grows, the apical dome initiates acropetally a succession of primordia of which the first three to ten form leaves. Each primordium unit may later differentiate an elongated internode and an axillary bud (tiller bud). The primordia subsequently initiated on the main shoot develop to form floral parts. In barley (Bonnett, 1966) and wheat (Barnard, 1964), as the primordium develops the leaf initial is more or less completely suppressed and the axillary portion differentiates to form single, many-flowered spikelets (in wheat) or three single flowered spikelets (in barley). The transition from leaf to floral development of the shoot apex is accompanied by changes in the growth rate (Barnard, 1964; Williams, 1964, 1974).

Two distinct phases of growth exist in the rachis of the barley inflorescence (Nicholls and May, 1963): 1. Formation of primordia acropetally accompanied with little or no change in the mean interprimordial distance. Cell number per segment remains relatively constant. Cell length is maximum at the end of this phase.

2. Cessation of primordia formation and elongation of the apex due to an increase in rachis interprimordial length. This is accompanied by increased cell division and the appearance of stamen initials (Nicholls and May, 1963) or awns (Aspinall, 1966; Kirby and Faris, 1970). Evidence is provided (Nicholls and May, 1963; Paleg and Aspinall, 1964; Kirby and Faris, 1970; Evans, 1971; Nicholls, 1974a) that suggests that at least two factors are involved in this growth phase: a factor produced in the inflorescence at floret initial formation and a factor produced during long days. Both of these factors must be present for rapid rachis internode elongation to be initiated. If one of these is missing for genetic or physiological reasons, then rachis internode elongation is delayed.

Also evident during these phases are changes in the apical dome. Increase in size of the apical dome occurs during the vegetative growth period in barley (Fellipe and Dale, 1973; Kirby, 1977) wheat (Williams, 1974) and maize

(Abbe and Phinney, 1951). Maximum dome size occurs when the maximum number of floral primordium has been produced and awns initiated, after which the size of the dome declines (Kirby, 1974a). Most of the spikelets which are initiated during the reduction process die (Kirby, 1977). Changes in dome size appear to be related to the size and number of primordia which are initiated and hence the number of grains in the mature head. The developmentally most advanced spikelet bud is found near the middle of the inflorescence (Sharman 1947; Kirby, 1974a). Sharman (1947) speculated that this pattern might be due to the fact either that each successively initiated spikelet bud starts its development earlier in the history of the node with which it is associated or that it might develop at a greater rate. Kirby (1977) showed that each successive primordium initiated had a higher relative growth rate than the previous one in the basal two-thirds of the apex. There was an increase in length and diameter of each successive primordium initiated until the middle of the head after which there was a decline in diameter and volume. Differences in the growth rate and in the inital sizes of the primordia on the floral apex determine primordium number and the gradient of grain size and spikelet fertility which occurs in the mature head(Kirby, 1974a).

There is no detectable vascular system in the barley inflorescence until after internode elongation has been initiated (Nicholls and May, 1963; Kirby and Rymer, 1974). This implies that the transport of nutrients from the base of the inflorescence to the apical and lateral meristems is by diffusion until the vascular system develops. Under these conditions, the apical meristem ceases activity and dies because the developing lateral spikelets compete more successfully for the available nutrients (Kirby and Faris, 1970). The increase in the relative growth rate in the elongation phase of the barley meristem coincides with the establishment of vascular connections to the spikelet primordia. At this stage it may be supposed that the young head is no longer at a disadvantage in relation to the other organs of the plant. The death of the terminal spikelets may be the result of a high resistance to assimilate transport, leading to starvation because of competition from the basal and mid spikelets of the head which have an established vascular system (Kirby and Rymer, 1974). Growth rate might be regulated hormonally since a high concentration of gibberellin-like substances coincides with the increased growth rate of the shoot apex (Nicholls and May, 1964). Vascularization may be the consequence of this growth rate rather than the cause of it (Kirby and Rymer, 1974).

The initiation of internode elongation has been correlated with peaks in activity of gibberellin-like substances extracted from long-day and cold requiring dicotyledonous rosette plants (Harada and Nitsch, 1959; Lang, 1960; Reinhard and Lang, 1961). It is also induced by applying certain photoperiodic regimes or gibberellic acid in a number of long-day plants (Sach et al., 1959; Baldev and Lang, 1965; Jacqmard, 1968; Liu and Loy, 1976). Increased growth of the apex and floral initiation have been observed when GA_3 is applied to plants growing in short days (Koller et al., 1960; Evans, 1964, 1969; Hurd and Purvis, 1964). Nicholls and May (1964) found a higher concentration of gibberellin-like substances in the apex at the double ridge stage in plants grown in 24-hr light periods compared with plants grown in 8 hr conditions. This is compatible with known biological properties of gibberellic acid, namely, increased cell enlargement in treated plants (Brian, 1961) and increased growth rates of gramineous apices following gibberellic acid application (Purvis, 1960; Banbat and Ochesanu, 1963). Nicholls and May (1964) suggest that at the double ridge stage of development the supply of gibberellin-like substances limits growth of the apex. At the spikelet initial stage, however, a higher concentration of gibberellin-like substances was observed. The difference in concentration of gibberellin-like substances between apices harvested at the stamen-initial stage and those harvested later may reflect a difference in the rate of utilization. There was a greater decrease in gibberellin concentration in 24-hr plants, with higher growth rate, than in 8-hr plants.

The growth and development of the barley spike is inhibited by weekly applications of large amounts of GA_3 (Paleg and Aspinall, 1958) or, if applied only once, abnormal forms of development are observed (Kirby, 1971). Nicholls (1974b) considered that the growth of the apex was dominated by the meristematic activity of three regions:

1. The meristematic region of the apex that is concerned with the elongation of the apical dome above the youngest visible primordium.
2. The meristematic region of the single and double ridge primordia that arise on the flanks of the shoot apex.
3. The internodal meristems in the main axis of the young inflorescence which are involved in its elongation (Nicholls and May, 1964).

A single application of gibberellic acid resulted in enhanced rates of growth of the apex and subadjacent leaf primordia for only a relatively short period in the life cycle of the plant (Nicholls, 1978). The first morphological response to the treatment was an increased dome length, which

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was followed by increased rates of growth and development of subadjacent leaf primordia and basal spikelet primordia. After the period of enhancement, the growth rates of the apices of the treated plants fell to values comparable to those of the control plants. The enhanced growth rates may have resulted either from an effect of GA_3 on diffusivity of nutrients or from an initial effect of GA_3 on the shoot apical meristem. However, any model of the role of GA_3 in the regulation of growth of barley apical meristem must take into account the observed sequence of responses: the apical dome in vegetative shoot apices and both the apical dome and the upper ridges (rachille initials) in the first stages of development of floral shoot apices. A response by the remainder of the apical region follows.

Variations in the light environment have a profound influence on apical development in barley (Aspinall and Paleg, 1963, 1964; Paleg and Aspinall, 1964) but also have many other physiological and morphological effects on plant growth. Some of these effects on vegetative growth are probably mediated through variations in the supply of carbohydrates particularly with changes in light intensity (Friend, Helson and Fisher, 1962). However, many plant responses to light, particularly variations in photoperiod or spectral content, are derived from photomorphogenic pathways such as the

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phytochrome system (Mohr, 1962). The growth of a plant in one light environment will therefore be dependent upon the interaction of several complex controlling mechanisms.

Considerable differences in photoperiodic responses of cereal varieties are recorded (Takahashi and Yasuda, 1960; Griffiths, 1961) and barley varieties have been considered day-neutral (Takahashi and Yasuda, 1960), long-day (Guitards, 1960), or obligate long-day plants (Takahashi and Yasuda, 1960). In comparing the effects of light intensity and photoperiod on 10 barley varieties, Aspinall (1966) found that apical primordium production was linked with floral organogenesis over all photoperiods. Generally, there was an increase in time taken to reach double ridge initiation and stamen initial stages of development through reduction in photoperiod from 24-hr to 8-hr and omission of incandescent light (spectral composition change). The effect was greater on stamen initial production than on double ridges formation, implying that the development following the initiation of double ridges is more susceptible to control by the availability of the products of photosynthesis than is the initiation of double ridges itself. Night interruptions decreased, and omission of the far-red component from the light source increased the time taken to initiate stamens. Thus, stamen initiation is under photoperiodic as well as photosynthetic control. Primordium production was lower the shorter the photoperiod. The author concluded that the relationship between apical development and internode elongation is not fixed and that the physiological mechanism(s) which initiates elongation may not be closely correlated with a particular stage of apical development. Rachis internode elongation occurs under short days (Nicholls, 1974a), perhaps as a result of lack of gibberellin following floret initial appearance (Nicholls, 1978).

The influence of soil moisture tension on plant growth has been examined in many species (Stocker, 1960). Most drought studies on cereals have been made on the later stages of inflorescence development. Milthorpe (1950) and Amer and Williams (1958) showed that immature tissues can tolerate higher intensities of dehydration than more mature tissues with a large proportion of vacuolated cells. Drought conditions interrupt translocation of nutrients from the stem to younger leaves of the shoot apex of tomato plants (Gates 1955a, b, 1957) and delay floral initiation and development (Brown, 1953). In cereals there appears to be a stage between spikelet differentiation and flowering which is particularly sensitive to drought (Zavadskaja and Skazkin, 1960). Stress at this stage induces pollen sterility (Novikov, 1952), a disruption of the reduction division stage of meiosis (Zavadskaja and Skazkin, 1960) or disturbances in spikelet differentiation (Novikov, 1954). The severity of the effects depends on duration of stress, timing of the stress period and environmental conditions during stress (Russell, 1959). Aspinall, Nicholls and May (1964) found a reduction in primordia formation, inflorescence development and apical length with water stress. Generally, a stress before stamen initiation is likely to increase tillering, and marked reductions may occur in internode elongation and grain numbers; after anthesis, effects on elongation and grain number may still occur but grain size is severely decreased. Soil moisture stress tends to affect the organs growing most rapidly and the tendency for the effects of stress to be more severe at the very beginning of a particular growth process supports the notion (May and Milthorpe, 1962) that cell division is likely to be the event most influenced.

The realization of the importance of temperature as a regulator of flowering arose from studies of Gasner in 1918 on the flowering of cultivated cereals (Wareing and Phillips, 1970). Increasing the temperature from 10 to 30°C increases the rate of shoot apex growth and primordium (leaf and floral) production. Floral initiation occurs earlier (Friend _et al_., 1963), as a result of either an increased rate of production of flower-inducing substances or from an increased sensitivity of the meristematic cells to a given level of flower inducing substance. This promotion of flowering by temperature increase seem to be independent of the phytochrome system. Head abnormalities in barley have been found with increasing temperatures (Kirby, 1974b). The abnormalities obtained are similar to shoot-apex of 2,4-D-treated plants (Leaf, 1959; Luxova and Lux, 1964). Rapid changes in the concentrations of growth substances within the plant in response to changes in the environment are known (Osborne, 1972). Differential responses of growth substances to changes in temperature have been reported by Atkin and Barton (1972). Therefore, the abnormalities may be due to temperature-sensitive changes in the auxin metabolism of the plant.

The relative growth of total and leaf dry matter, and lamina development are strongly influenced by plant population (Kirby, 1967, 1969, 1973). These morphological changes come about by plant population differences affecting initiation and growth of the tillers, stem or leaf growth, and the initiation and subsequent growth of the spikelet initials at the shoot apex. The higher the population density, the faster the growth rate. The shoot apex reaches the double ridge stage earlier and this persists throughout the development of the apex. Rate of primordium production is little affected by density, but the duration is markedly affected. Plants grown at high densities had a high con

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concentration of gibberellins in their tissues (Kirby and Faris, 1970). The enhancement of apex development by the higher concentration of gibberellin results in earlier competition for nutrients diffusing through the apex. This leads to starvation of the tip of the apex and earlier death of this region and consequently, fewer spikelets. Differences in the light environment of the plants, either intensity or composition, most probably brings about the differences in the gibberellin content.

Tillering may be divided into three phases. The first involves the initiation of tiller buds and is little affected by the environment (Evans _et al_., 1964). The next phase deals with the appearance of the tillers at an advanced stage. Lastly, the fate of the developing tillers is determined before their heads emerge (Kirby, 1967; Rawson and Donald, 1969). Tiller bud initiation is little affected by plant density, however, some of these buds did not grow or grew and emerged from the subtending leaf sheath. The growth rates of the tillers which grew were not affected by density. Fewer buds developed at higher densities and the morphology of the tillers produced was affected by density (Kirby and Faris, 1972). This suggests that the growth of the tiller bud may be controlled by levels of endogenous gibberellin, while in the final stage, growth after emergence fr

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from the subtending leaf sheath, competition for light appears to be the factor which determines whether a tiller survives to produce a head.

A number of lateral and tiller buds are formed in the axils of the lower leaves of the main stem during the growth and development of the barley plant (Kirby and Faris, 1972). Only a proportion of the tillers produced normally survive to produce grains (Thorne, 1962). The death of some of these tillers probably constitute a wastage of resources. When the tillers are developing they compete for assimilates and minerals, intercept light and affect transpiration (Clifford et al., 1973), thus reducing the size of these shoots and their potential yield (Kirby and Jones, 1977). When the infertile tillers die, some of the minerals and carbon compounds are translocated back to the other fertile shoots, however, a proportion is not available to the surviving parts of the plant (Rawson and Donald, 1969). Donald (1968) thus proposed the 'uniculm' plant type to be the most suitable plant model for the attainment of maximum yield.

Some experiments have been done to investigate the proposition that non-head bearing tillers may be wasteful of plant resources. Tiller removal affects the growth and final size of the main shoot. A higher number of large sized leaves emerge earlier on the main shoot of detillered plants.

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Larger main shoots with heavier grains are produced. When the main shoot is removed, the coleoptile tiller produces more leaves earlier and bear more grains than the coleoptile tiller of the intact plant (Kirby and Jones, 1977). Thus, during the initiation and early growth of the plant, tillers compete with the main shoot for the limited resources, thus reducing the size of the main shoot.

With ample water supply and severe detillering, only a slight grain yield reduction is observed although the total shoot dry weight is reduced. With the same amount of water plants with few tillers tend to have greater grain yield, higher water use efficiency and harvest index than plants allowed to tiller freely. In effect, genotypes which produce few tillers have a high rate of survival and are able to achieve relatively high yields in drought conditions, and their yield potentials are maintained under optimal conditions (Jones and Kirby, 1977).

THEORETICAL PREDICTION OF THE EXISTENCE OF BIOCHEMICAL EQUILIBRIUM IN BIOLOGICAL SYSTEMS.

The analysis used here is adapted from Smith's (1968) mathematical presentation of diffusion along a tube of a substance which ultimately induce a chemical change resulting in changes in growth and development.

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Consider the flow of a substance in solution along a tube with a cross sectional area of a. The concentration x of this solution plotted against s, the distance along the tube is shown in Figure 1. The amount of the substance at a point of the tube is ax, hence for a short length ∂s of the tube, the amount is $ax\partial s$. If A and B are the rates of diffusion from left to right across the two faces of the element, then A-B is the rate at which the substance is increasing in ∂s.

Thus, $\frac{d}{dt}(ax\partial s) = a\partial s \frac{dx}{dt} = A-B.$ .... (1)

The rate of diffusion across a surface is proportional to the surface area of the tube and the concentration gradient at right angles to the surface.

Hence, $A = -a\mu \left(\frac{dx}{ds}\right)$ at s and

$B = -a\mu \left(\frac{dx}{ds}\right)$ at $s + \partial s$

where μ = constant, depending on temperature and the diffusing substance. The minus sign occurs because when $\left(\frac{dx}{ds}\right)$ is positive, diffusion would be from right to left and A and B would be negative.

$$A - B = -a\mu \left[\left(\frac{dx}{ds}\right) \text{ at } s - \left(\frac{dx}{ds}\right) \text{ at } s + \partial s\right]$$

$$= a\mu \left[\partial s \cdot \frac{d^2x}{ds^2} \right]$$

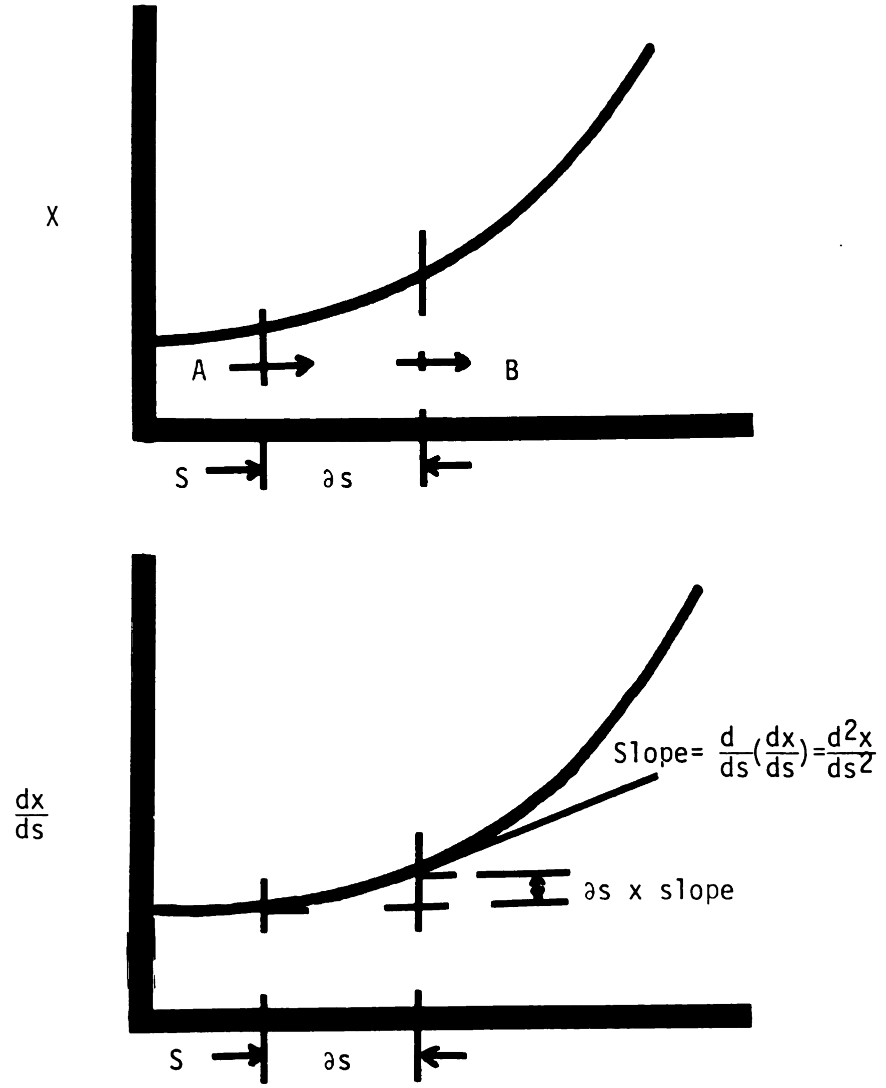

Figure 1. Geometrical derivation of the diffusion equation. (from J. M. Smith, 1968).

Substituting in equation (1), we get

$$\frac{dx}{dt} = \mu \cdot \frac{d^2x}{ds^2}$$

This partial differential describes diffusion along a tube. It indicates that if the graph of x against s is concave upwards, then x is increasing at this point and vice versa.

Consider the effects of diffusion and chemical reaction simultaneously. Let the concentration of two chemical substances A and B be X and Y. Suppose that the substrates from which A and B can be synthesized and degraded, and also the relevant enzymes are present. There will be some values of concentrations X_E and Y_E for which there is a chemical equilibrium. We can represent X and Y as; $X = X_E + x$ and $Y = Y_E + y$

where x and y are measures of concentration departures from their equilibrium values.

Assume our interest is in the changes in X and Y as functions of time and distance along the tube, then,

when $x = y = 0$, $\frac{dx}{dt} = \frac{dy}{dt} = 0$

With small changes from the equilibrium

$$\frac{dx}{dt} = ax + by; \quad \frac{dy}{dt} = cx + dy$$

where a, b, c and d are reaction rates.

If u and v are the rates of diffusion of A and B respectively, and allowing for diffusion along the tube,

then $$\frac{dx}{dt} = ax + by + u\frac{d^2x}{ds^2}$$

$$\frac{dy}{dt} = cx + dy + v\frac{d^2y}{ds^2}$$

We can solve the equations algebraically, but it is more interesting for the present purpose to solve them graphically.

If all values of x and y are zero for all values of s along the tube then at time t=0, $\frac{dx}{dt} = \frac{dy}{dt} = 0$

If this homogenous equilibrium is disturbed, the equilibrium is restored through adjustments of the values of the reaction rates a, b, c and d, and the diffusion rates u and v, so that x and y tend to zero with increasing time.

Certain values of the constants render the equilibrium, unstable. Thus, even when there is an initial homogenous state with $x = y = 0$, a standing wave of concentration of the substances may arise from any small initial disturbance.

Some assumptions ought to be made at this point:

1. If the concentration of A rises above the equilibrium level, rate of synthesis of both A and B rises. a and c are positive.

2. If the concentration of B rises, it leads to

destruction of A. b is negative and d is assumed to be zero.

3. B diffuses faster than A. $v > u$.

Figure 2 a, b, c and d, show what happens when the homogenous equilibrium is disturbed by a small departure in the concentration of A. Fig. 2a, shows a disturbance in the equilibrium. This leads to a further rise in A and B, but B diffuses out further (Fig. 2b). At the point marked by the arrow, y is positive and x is zero, leading to destruction of A (Fig. 2c). This in turn, leads to the destruction of B so that a trough develops on either side of the initial peak (Fig. 2d). These troughs cause the development of other peaks and so on, until a standing wave has been developed whose chemical wavelengths depend on the constants defining the rates of reaction and diffusion.

The wave pattern will be utilized to show the existence of an equilibrium between the promotive hormones which induce growth and development in an orderly manner.

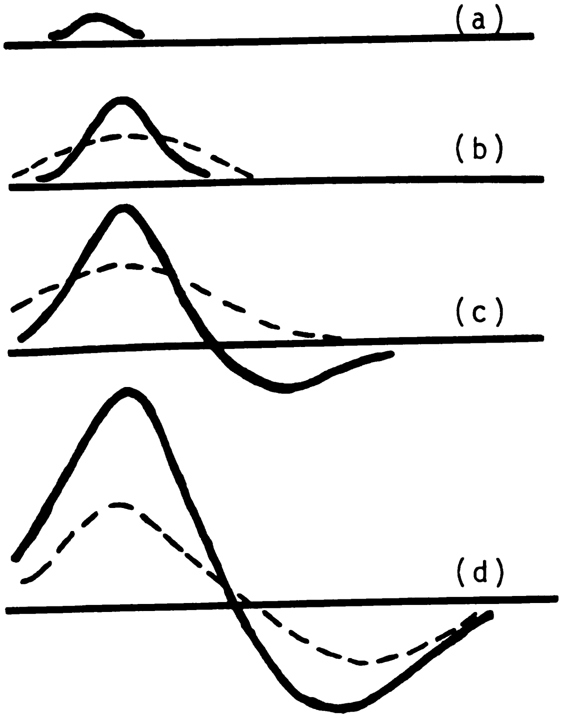

Figure 2. Development of a standing wave.
(from J. M. Smith, 1968).

MATERIALS AND METHODS

The same twelve genotypes of barley were used in all the experiments. They were selected on the basis of differing values in their yield components, namely number of heads per unit area (X), number of seeds per head (Y) and average seed weight (Z).

A rectangular-lattice design with four replications was used. The plots were four-row plots 0.0254m apart and 2.4m long, planted at a rate of 35g per plot. The study was carried out at the Crops Science Research Farm in Ingham county, Michigan. Planting date was May 5, 1980.

INVESTIGATION OF THE LEVELS AND ACTIVITIES OF THE PROMOTIVE HORMONES AND THEIR EFFECTS ON GROWTH AND DEVELOPMENT OF THE PRIMARY SHOOT APICAL MERISTEM, YIELD COMPONENTS AND YIELD OF BARLEY

A. DETERMINATION OF THE GROWTH AND DEVELOPMENT OF THE PRIMARY SHOOT APICAL MERISTEM

Meristems were sampled at three predetermined stages, which were:

1. Transition, identified by the appearance of double ridges.

2. Reproduction characterized by spikelet differentiation.

3. Elongation and further differentiation of meristems.

Before any sample was taken at each stage, seedlings within each genotype were visually selected for similar morphological characteristics from the outer two rows (border rows) of the whole plot. One or two seedlings were uprooted, and their meristems dissected to determine their developmental stage. Five seedlings were then harvested from the outer two rows. The portions of the 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, to prevent structural changes. The five plants were selected to represent the mean of each cultivar. The main culms were used because they have a greater potential for production within a defined and finite environment than has any other single tiller. The meristems were dissected and measurements taken using a light microscope equipped with a measuring ocular. Measurements taken include maximum length (L) and width (WD) of the meristems (Fig. 3).

The relative growth rate (R) of meristems in the reproduction state was determined using the procedure outlined by Whyte (1979)

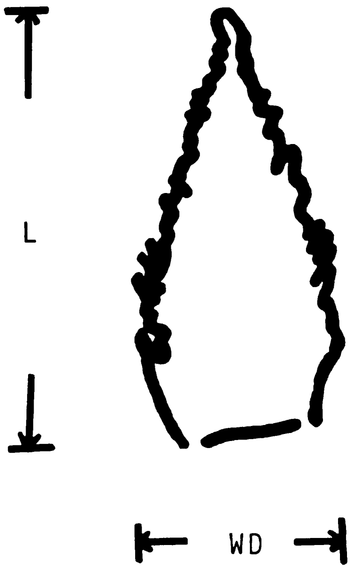

Figure 3.
Diagram of barley shoot apex. The measurements taken of length (L) and width (WD) are shown.

B. ANALYSIS OF THE LEVELS AND ACTIVITIES OF THE ENDOGENOUS PROMOTIVE HORMONES

A sizeable amount of sample was taken from each plot, at each stage, and immediately frozen by placing them in a chest containing dry ice. These were kept in a freezer at -30°C until they were lyophilized. Meristems were dissected from the lyophilized materials and attempts were made to analyze them for their endogenous levels of gibberellin, auxin and cytokinin. These determinations were futile, the reason most likely being the insensivity of the methods employed or the inadequate amounts of meristems obtained from the lyophilized materials.

The object of the endogenous hormonal level determination was to find any existing equilibrium state between the promotive hormones during the reproductive phase. Although the utilized methodology did not reveal the presence of the promotive hormones, a mathematical model (Smith, 1968) will be used to establish the existence of such an equilibrium. The author hopes that a more sensitive procedure will be found in the future, to carry out such types of experiments.

C. MEASUREMENTS OF YIELD COMPONENTS AND YIELD OF BARLEY

Measurements taken during the plant growth and at maturity included height (HT) and heading date (HD) which was calculated from April 30, 1980, when about 75% of plants in each plot had headed. Data for the number of seeds per head (Y) were obtained from a random sample of twenty heads per plot from the border rows just prior to harvest. Yield (W) was obtained from harvesting the central two rows of each plot. The average seed weight (Z) was calculated from a 3g sample per plot using an electronic seed counter to count the number of seeds within the sample. The number of heads per 30cm of row was obtained by dividing one sixteenth of the total weight of grain per plot by the product of seeds per head and kernel weight in grams.

A number of plant characteristics were each used as a dependent variable while measurements taken on the primary shoot apical meristem in the reproduction state of development were used as independent variables in a series of multiple regression analyses. This was an attempt to break down the yield components into their subcomponents at the meristematic level.

Using the path coefficient analysis as outlined by Wright (1921, 1934), the phenotypic correlation were partitioned into their direct and indirect effects as follows:

$\rho_{R(WD)} = a$

$\rho_{RL} = b$

$\rho_{L(WD)} = c$

$\rho_{X(WD)} = d + cf$

$\rho_{XR} = e + bf$

$\rho_{XL} = f + cd + eb$

$\rho_{Y(WD)} = g + ci + jd + cfj$

$\rho_{YR} = h + ej + bi + bfj$

$\rho_{YL} = i + cg + fj + hb + jdc + jeb$

$\rho_{YX} = j + gd + if + he + gcf + ibe + hbf + icd$

$\rho_{Z(WD)} = k + nd + og + mc + ncf + oic + ojd + ojfc$

$\rho_{ZR} = l + mb + oh + ne + oje + nfb + oib + ojbf$

$\rho_{ZL} = m + lb + oi + nf + kc + ogc + ojf + ohb + nbe + ndc + ojeb + ojdc$

$\rho_{ZX} = n + kd + oj + mf + le + kcf + ohe + oif + ogd + mbe + mcd + lbf + ohbf + oicd + oibe + ogcf$

$$\rho_{ZY} = o + nj + kg + mi + lh + neh + nfi + ndg + kdj + mfj + mcg + mbh + lej + nfcg + nfbh + mbej + mcdj + lbfj + kcfj + nebi + ndci + kci + lbi$$

The rationale behind the diagram (Fig. 4) is based on the developmental ontogeny of the plant and Sinnott's law as presented by Hamid and Grafius (1978) and Grafius (1978). Grafius (1978) showed a cause and effect relationship between leaf size and seed size after considering that the lemma and palea are modified floral leaves and hence larger leaves should be associated with relatively larger sizes of the lemma and palea, the determinants of seed size. Since the relative sizes of the lemma and palea derive from the same apical meristem, its substitution by the measured characteristics of the apical meristem in the reproduction state of development becomes more acceptable. A direct connection is thus established between the meristematic characteristics and number of seeds per head and the average seed weight. Nicholls and May (1964) proposed two probable factors contributing to the elongation of the apical meristem during the reproductive stage of growth. The major factor is the net increase in the number of primordia produced and the minor factor being their elongation. I am, therefore, inclined to represent the relationship between

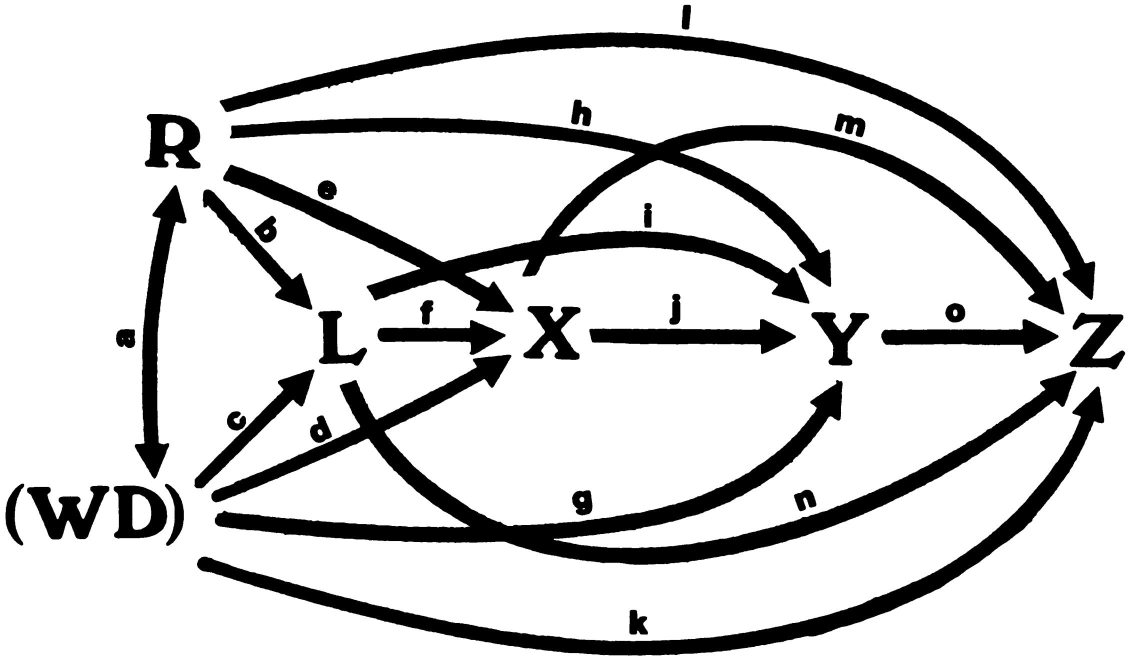

Figure 4. Developmental allometry showing the influence of the primary apical meristem of barley in the reproduction state of development on the yield components: number of heads per unit area (X), number of seeds per head (Y), seed weight (Z); width (WD), length (L) and relative growth rate (R) of the primary apical meristem. Single arrowed lines denote path coefficients and double arrowed lines denote correlation coefficients.

width and relative growth rate by a correlation instead of path. However, both width and relative growth rate are known to predict length, thus, the path representation.

The path coefficients can be obtained by solving the simultaneous equations.

EFFECTS OF MANIPULATION OF THE ENDOGENOUS HORMONAL (PROMOTIVE) LEVELS ON THE GROWTH AND DEVELOPMENT OF THE PRIMARY APICAL MERISTEM, YIELD COMPONENTS AND YIELD OF BARLEY

This experiment consisted of five blocks, each planted with four replications of the twelve cultivars. Each block was randomly assigned to one of five treatments (control, auxin, gibberellin, cytokinin and cycocel).

Solutions of auxin, cytokinin, cycocel, and gibberellin were prepared, using indole acetic acid, kinetin, (2-chloroethyl) dimethyl ammonium chloride and gibberellic acid (GA_3), with concentrations of 3×10^{-6}M, 10^{-4}M, 2.5×10^{-4}M and 10^{-4}M, respectively. Dimethyl sulfoxide (1%) was included as a carrier in all solutions, and plants in the control block were treated with the same concentration of dimethyl sulfoxide.

Using the same procedure as in the first group of experiments, meristems of the genotypes were sampled just before they reached the transition stage. The plot(s) in consideration were then sprayed with its respective hormone solution thereafter.

Two sprayings of each plot were done. The first was carried out when a genotype reached the transition stage and the second done two days later. Sprayings were done in the evening when air movement was minimal. Plants within each plot were sprayed until the hormone solution started dripping, thus allowing for possible root uptake of the hormone especially with regard to the cytokinin application. The site of biosynthesis of cytokinin is the roots (Kende, 1965) and cytokinin application experiments used mostly soil drench (Bokhari and Youngner, 1971).

Meristems of genotypes reaching the reproduction stage were sampled and preserved. Measurements were taken of the maximum length and width of meristems sampled just prior to the transition and at reproduction stages.

Other measurements taken during the plant growth and at maturity included height (HT), heading date (HD) calculated fron April 30, 1981, when about 75% of plants in a plot had headed, number of seeds per head (Y), number of heads per 30 cm (X) and the average kernel weight (Z). Yield (W) was obtained from harvesting the central two rows of each plot.

Some analyses were done after transforming the data in order to express the mean values as the mean percentage change over the control. The formula used for the transformation was:

$$\left(\frac{A_H - Ac}{Ac}\right) \quad 100\%$$

where A_H = mean value for a plant characteristic obtained after a hormone treatment.

Ac = mean value for a plant characteristic obtained from the control plot.

Use was made of the mean percentage change over control values for lengths of meristem to establish the existence of an equilibrium between the promotive hormones and through a reasonable extrapolation, comments were made about the yield components.

RESULTS

A. RELATIONSHIP BETWEEN THE PRIMARY SHOOT APICAL MERISTEM, YIELD COMPONENTS AND YIELD OF BARLEY.

The relative size of the primary shoot apical meristem and its rate of transformation from the vegetative to reproductive development state of the genotypes were significantly different (Table 1). Genotypes X969-3, 68-105-9 and 68-105-17 start with larger meristems but delay the elongation process by four days. This delay results in the formation of a larger sized meristem. They reached the transition state four days in advance of the other genotypes. Bowers barley (68-105-15) has been regarded as an outlier (Grafius _et al_., 1976) but data of Whyte (1979) and the results of the development of meristems presented here do not support the claim.

The mean values for the yield components (X, Y, Z), yield (W) and the other plant characteristics measured are presented in Table 2. There were significant differences between the genotypes for the various characteristics.

Table 3 gives the correlation coefficients between meristematic measurements, yield components and yield. The length and width at stages 1 and 2 are positively and significantly correlated with each other. Width at stage 3

Table 1. Mean values for the maximum length (L) and maximum width (WD) of the primary apical meristems of barley in the transition (Stage 1), reproduction (Stage II) and elongation (Stage IIIA and B) states of development.

	Stage I		Stage II		Stage III A		Stage III B	
Genotypes	L(mm)	(WD)(mm)	L(mm)	(WD)(mm)	L(mm)	(WD)(mm)	L(mm)	(WD)(mm)
BOWERS	2.423	.888	5.583	1.418	30.250	2.375		
X969-3	2.913	.963	4.808	1.418	8.417	2.110	29.418	2.453
B130	2.300	.760	5.083	1.518	19.778	2.278		
60-215-6	2.250	.878	3.773	1.110	18.558	2.000		
DICKSON	2.178	.733	5.083	1.433	27.000	2.378		
LARKER	2.558	.755	4.533	1.383	33.833	2.250		
68-105-9	3.703	1.210	5.000	1.350	8.815	2.038	26.000	2.483
68-105-17	3.078	.850	4.630	1.330	8.845	1.980	27.000	2.268
68-104-3	2.518	.583	5.128	1.150	25.000	2.000		
68-104-19	2.595	.800	5.500	1.483	21.500	2.751		
68-103-8	2.418	.700	4.668	1.500	20.500	2.250		
68-103-18	3.000	.975	5.250	1.500	24.000	2.333		
LSD (α=.05)	.464	.160	.729	.172	4.928	.376		
LSD (α=.05	.616	.213	.978	.231	6.613	.504		

Table 2. Mean values for yield (W), number of seeds per unit area (XY), head size (YZ), number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), height (HT) and heading (HD) of barley.

GENOTYPES	W(g)	XY(#)	YZ(g)	X(#)	Y(#)	Z(mg)	HT(in)	HD(days)
BOWERS	690.25	1434.98	2.174	19.92	72.14	30.16	38.50	27.25
X969-3	744.25	1624.89	2.170	21.58	76.00	28.60	39.25	24.25
B130	710.25	1449.82	1.861	24.09	60.92	30.64	40.00	26.25
60-215-6	503.75	1127.96	0.945	33.42	33.84	27.95	32.25	26.50
DICKSON	502.00	1076.27	1.749	17.94	60.04	29.14	38.25	27.75
LARKER	747.25	1367.03	1.818	25.82	53.15	34.21	40.00	26.00
68-105-9	723.50	1465.61	2.346	19.33	76.07	30.86	40.25	25.25
68-105-17	657.00	1394.78	2.283	18.01	77.57	29.50	38.50	27.75
68-104-3	707.50	1432.43	1.249	35.69	40.39	30.95	39.75	25.50
68-104-19	699.75	1387.44	1.686	25.98	53.57	31.51	41.25	25.00
68-103-8	696.50	1407.21	1.935	22.46	62.61	30.90	41.00	25.50
68-103-18	717.25	1295.35	1.871	24.00	54.10	34.60	39.75	24.00
LSD (α=.05)	66.96	139.07	.178	3.06	6.53	.19	2.90	1.18
LSD (α=.01)	88.92	184.68	.234	4.06	8.68	.25	3.85	1.57

Table 3. Correlation coefficients among the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), height (HT), heading (HD), maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the transition (SI), reproduction (SII) and elongation (SIII) states of development.

	X	Y	Z	XY	YZ	W	HT	HD	L-SI	WD-SI	L-SII	WDSII	L-SIII	WD-SIII
Y	-.885**													
Z	.053	-.128												
XY	-.138	.862**	.089											
YZ	-.876**	.966**	.130	.554										
W	-.073	.369	.580*	.862**	.508									
HT	-.332	.418	.564	.569	.553	.753**								
HD	-.268	.103	-.441	-.456	-.005	-.597*	-.386							
L-SI	-.351	.544	.214	.457	.605*	.478	.306	-.391						
WD-SI	-.427	.492	-.008	.205	.508	.157	-.081	-.290	.775**					
L-SII	-.399	.429	.371	.389	.514	.498	.763**	-.137	.156	-.013				
WD-SII	-.660*	.561	.432	.327	.667*	.480	.779**	-.207	.102	.058	.708**			
L-SIII	-.238	.261	.266	.202	.313	.289	.195	.089	-.002	.061	.295	.182		
WD-SIII	-.575*	.527	.148	.281	.565	.301	.542	-.255	.339	.405	.593*	.675*	.096	
R	.428	-.680*	.101	-.566	-.646*	-.398	-.247	.293	.814**	-.566	-.174	-.093	-.188	-.286

* $P \leq .05$

** $P \leq .01$

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is significantly correlated with length and width at the reproduction stage. Relative growth rate is significantly and negatively correlated with length at the transition stage, head size and number of seeds per head. Width at the reproduction stage is significantly and positively correlated with head size and height but negatively correlated with number of heads per unit area. The relative growth rate of the primary shoot apical meristem and number of heads per unit area are negatively correlated with most of the other measurements taken in the study but positively correlated with each other. Both are negatively and significantly correlated with head size and number of seeds per head. A pattern is established: when the number of heads per unit area increases, the relative growth rate increases while head size decreases due to a decrease in the number of seed per head. The relationship between the relative growth rate with head size and number of seeds per head are plotted in Figure 5 and 6 and the significant regression line reaffirms the inverse relationship. A genotype with a higher number of heads per unit area will grow at a higher rate, however, it will produce a smaller head size and a lower number of seeds per head. Thus, a lower rate of growth results in the production of a larger number of seeds per head and eventually a bigger head size. Even

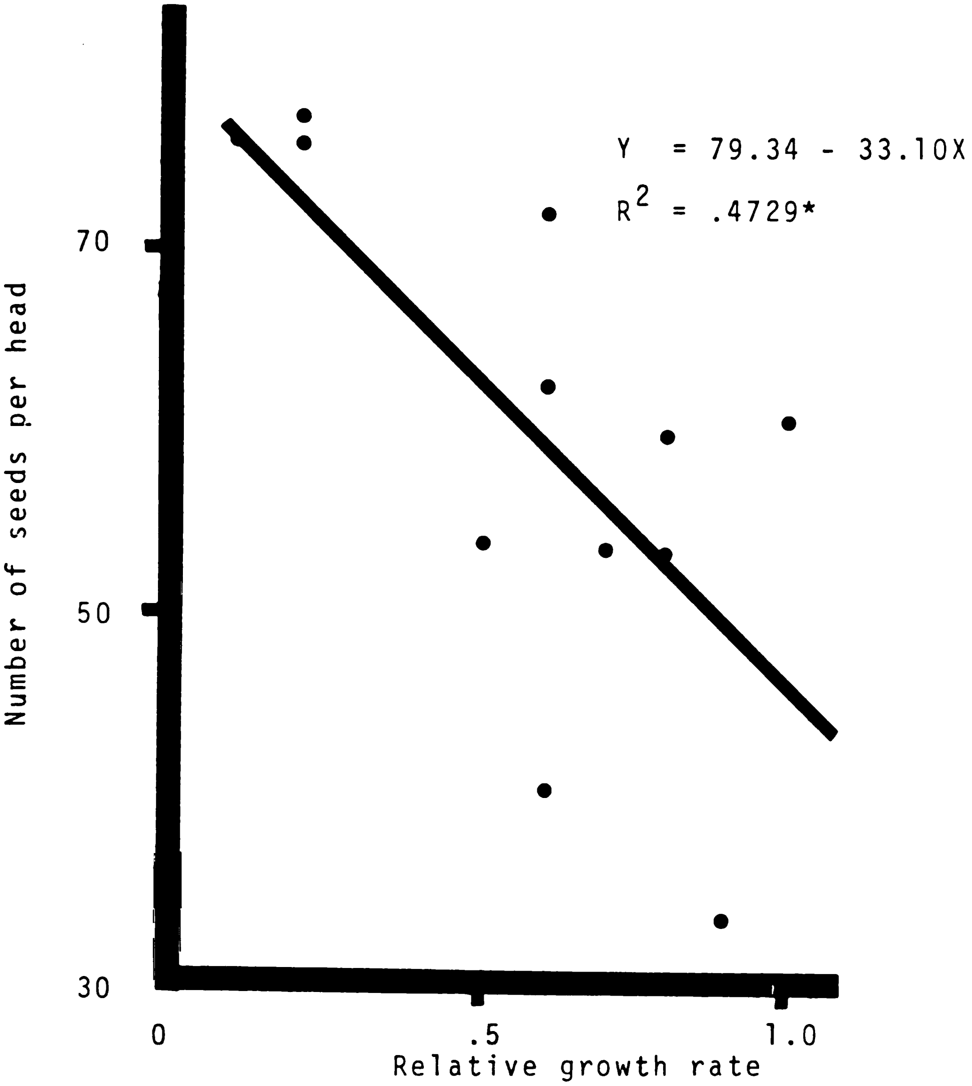

Figure 5. Regression of the number of seeds per head on the relative growth rate of the primary apical meristem of barley in the reproduction state of development.

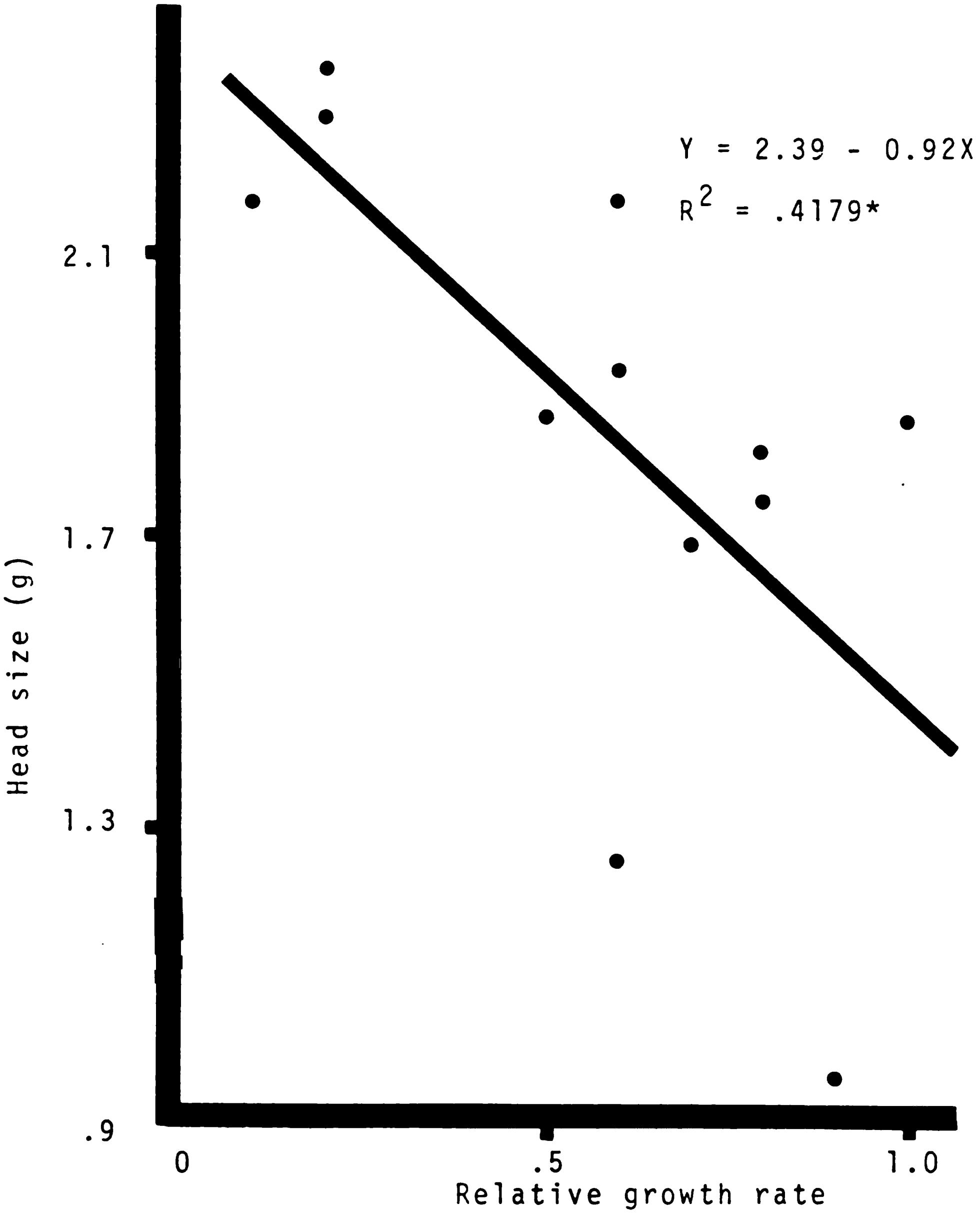

Figure 6. Regression of head size on the relative growth rate of the primary apical meristem of barley in the reproduction state of development.

though the above notion can be generally accepted, one has to wonder whether the relationships arise because of the number of heads per unit area associated with the system or the number of heads per unit area cause such a relationship to arise.

The mean square values for the multiple regression involving length, width, and relative growth rate of the primary shoot apical meristem as independent variables and the dependent variables number of heads per unit area (X), number of seeds per head (Y) and head size (YZ) are significant, as shown in Table 4. The same regression using the dependent variables average seed weight (Z), number of seeds per unit area (XY) and yield (W) showed no significance. The coefficient of determination (R^2 = 0.5959, 0.7156 and 0.7912 for X, Y and YZ, respectively) indicate that the variance in the dependent variables can be accounted for in large part by variation in the three independent variables.

Some interesting observations found in the multiple regression analysis include:

(1) Only the relative growth rate and width of the meristem showed significance in the multiple regression analysis presented.

(2) While the width of the meristem has a positive predictive value, the relative growth rate has a negative

Table 4. Analysis of variance for the multiple regression of the number of heads per unit area (X), number of seeds per head (Y) and head size (YZ), each as a dependent variable on the maximum length (L), maximum width (WD) and the relative growth rate (R) of the primary apical meristem of barley in the reproduction state of development as the independent variables.

Source	df	X	Y	YZ
Regression	3	69.9010	517.6362	.4931
Error	8	17.7766	77.1303	.0488
R^2		0.5959	0.7156	0.7912

* $P \leq .05$
** $P \leq .01$

predictive value for both head size and the number of seeds per head. The reverse is the case with predicting the number of heads per unit area. Width and relative growth rates have negative and positive predictive value, respectively, for the number of heads per unit area (Table 5).

The smaller the width of the primary shoot apical meristem of a genotype, the higher the number of heads it will produce per unit area and the higher its rate of growth. Number of seeds borne per head will be small since width has a positive correlation with Y. A similar picture is obtained when the prediction of either head size or the number of seeds per head is considered. The higher the relative growth rate of the primary shoot apical meristem of a genotype, the lower the number of seeds borne per head or the smaller the head size it will have. The width of the meristem will be small while number of heads produced per unit area will be high since width has a significant negative relationship with X.

B. THE REACTION OF THE PRIMARY SHOOT APICAL MERISTEMS TO APPLIED HORMONES

Mean values for the maximum length and width of the primary shoot apical meristem before the transitional and at the reproduction stages of development are given in Table 6. The 'outliers' had larger sized apical meristems initially,

Table 5. Multiple regression statistics for the number of heads per unit area (X), number of seeds per head (Y) and head size (YZ), each as a dependent variable on the maximum length (L), maximum width (WD) and the relative growth rate (R) of the primary apical meristem of barley in the reproduction state of development as the independent variables df=8. Upper, middle and lower values are the statistics for X, Y and YZ, respectively.

Variable	Partial Regression Coefficient	Beta Weights	Significant Level	Partial Correlation Coefficient	R^2 deletes
L	1.942 -1.609 - .030	.224 -.075 -.045	.507 .789 .843	.238 -.097 -.072	.572 .713 .790
WD	-27.273 48.010 1.642	-.782 .554 .646	.040 .072 .002	-.655 .591 .706	.292 .563 .584
R	7.734 -31.237 - .850	.395 -.642 -.595	.122 .010 .007	.521 -.764 -.788	.445 .317 .449

Table 6. Mean values for maximum length (L) and maximum width (WD) of the primary apical meristem of barley just before the transition (S<I) and in the reproduction (SII) states of development.

	STAGE < I		STAGE II	
GENOTYPES	L(mm)	WD(mm)	L(mm)	WD(mm)
BOWERS	1.825	.688	4.770	1.583
X969-3	2.213	.875	4.825	1.680
B130	1.400	.450	4.750	1.375
60-215-6	1.850	.550	3.583	1.000
DICKSON	1.475	.408	4.210	1.178
LARKER	1.525	.438	4.500	1.500
68-105-9	2.215	.863	4.750	1.443
68-105-17	2.003	.675	4.720	1.500
68-104-3	1.500	.470	4.526	1.150
68-104-19	1.413	.463	4.500	1.350
68-103-8	1.450	.525	5.543	1.378
68-103-18	1.875	.700	5.313	1.375
LSD (α=.05)	.280	.138	.597	.199
LSD (α=.01)	.376	.186	.804	.267

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but few differences were observed in the reproduction state of development. A switch in rate of increase in the size of the meristem is, however, shown.

Table 7 gives the mean percentage change over control, of the maximum length and width of the primary shoot apical meristems in the reproduction state, due to the applications of gibberellin, cycocel, cytokinin and auxin at the transition stage of development. Significant differences exist for both the length and width, suggesting differences in reactions to the applied hormones.

These mean values were plotted as histograms to determine how the reactions to hormone vary with the number of heads per unit area (Figures 7-10). Genotypes are arranged in the histograms in the order of increasing production of number of heads per unit area. The first eight genotypes are considered standard genotypes while the last four are 'outliers'. Bowers is included in the set of outliers to determine whether its reaction is more related to that set or to the set of standard genotypes. Of the eight standard genotypes, Dickson and 60-215-6 produce the least and the highest number of heads per unit area, respectively. There is no significant differences between the 'outliers' for the number of heads produced per unit area while significant differences exist between the standard genotypes for the same trait.

Table 7. Mean values for the percentage change over control for the maximum

Table 7. Mean values for the percentage change over control for the maximum length (ΔL) and maximum width (ΔWD) of the primary apical meristem of barley in the reproduction state of development due to the application of gibberellin (GA_3), cycocel (CCC), cytokinin (Kinetin) and auxin (IAA) at the transition stage of development.

	Δ L				Δ WD			
GENOTYPES	GA_3	CCC	Kinetin	IAA	GA_3	CCC	Kinetin	IAA
BOWERS	-10.48	10.69	2.20	9.22	-17.08	- 1.93	-10.30	2.81
X969-3	8.34	13.11	11.81	12.28	19.35	10.27	1.19	4.00
B130	-18.42	-12.26	- 6.58	15.79	- 1.45	- 3.09	1.64	.36
60-215-6	30.20	12.75	12.41	9.61	52.00	14.75	20.25	8.25
DICKSON	4.93	11.82	7.52	12.83	18.00	9.93	- .47	16.94
LARKER	- 6.50	10.50	7.50	11.11	- 4.33	0	-17.50	- 8.17
68-105-9	31.42	9.21	3.95	15.79	35.14	16.25	8.28	19.37
68-105-17	7.26	5.93	.64	14.78	.83	5.83	5.83	2.83
68-104-3	5.42	31.16	29.03	18.39	- 3.91	22.39	19.78	16.30
68-104-19	- 6.00	11.11	19.44	20.39	2.04	11.11	11.11	10.56
68-103-8	-29.37	-26.66	-13.27	-14.31	- .22	- 7.84	14.84	7.58
68-103-18	-23.96	-15.30	- 8.57	- 5.89	0	6.00	9.09	9.09
LSD (α=.05)		13.57				12.68		
LSD (α=.01)		17.85				16.69		

The lengths of the meristems at the reproduction stage of the standard genotypes producing the least and the two highest numbers of heads per unit area were increased, while those for the other standard varieties were reduced with gibberellin application. Genotypes 68-103-8 and 60-215-6 had the greatest decrease and increase, respectively, in the lengths of their meristems. Of the outliers, the length was reduced in Bowers and increased in the rest, with 68-105-9 having the greatest increase. Application of GA_3 induced significant increase in the width of meristems of Dickson and 60-215-6 but had no effect on the rest of the standard genotypes. With the outliers, width was reduced in Bowers but increased in 68-105-9 and X969-3. No significant change was observed with 68-105-17 (Fig. 7). Thus, the sizes of the apical meristem in the reproduction state were increased in the outliers, with the exception of Bowers, and in the standard genotypes producing the least and highest number of heads per unit area. The other standard genotypes and Bowers had a reduction in the sizes of their apical meristems with gibberellin application.

Interesting trends worthy of note are the changes in the length of the apical meristem due to gibberellin application. Considering just the standard genotypes, there is an increasing reduction in meristem length with increasing

Fig

Percentage change in meristematic

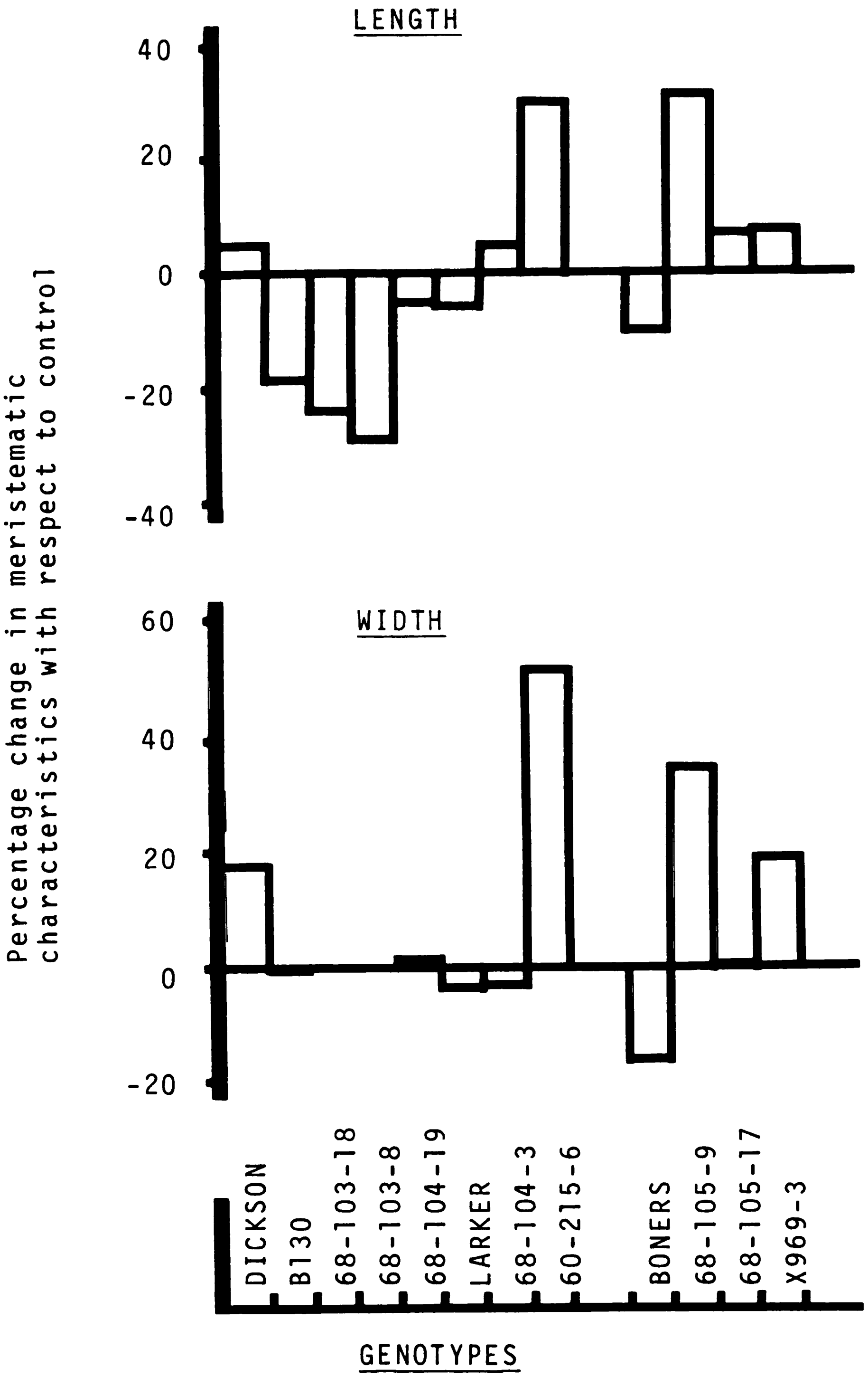


Figure 7. Percentage change in maximum length and maximum width of the primary apical meristem of barley in the reproduction state of development due to gibberellin (GA_3) applica- at the transition stage of development.

number of heads per unit area. However, after the greatest length reduction is achieved, i.e., with 68-103-8, this reduction starts to decrease and eventually the maximum length starts to increase with further increase in the number of heads per unit area. Little can be said about the trend resulting in the changes in length of the apical meristems of the outliers since the number of heads per unit area in these genotypes are not significantly different from each other.

Figure 8 depicts the effect of the application of (2-chloroethyl) dimethyl ammonium chloride (CCC) on the length and width of the primary apical meristem as compared to control for the same genotypes. A similar trend in reaction to GA_3 is shown with the effect of CCC. The genotypes with a relatively high reduction in length due to GA_3 application showed length reductions. These include B130, 68-103-8 and 68-103-18 from the group of standard genotypes and Bowers from the outlier group. The rest of the genotypes showed an increase in length with CCC application. Generally, there was a slight reduction in the reaction of the apical meristem to CCC as compared to GA_3 treated plants. The second highest tillering standard genotype, 68-104-3, had the greatest change in reaction to CCC as compared to GA_3, i.e., from 5% to 30% increase in length. The width was

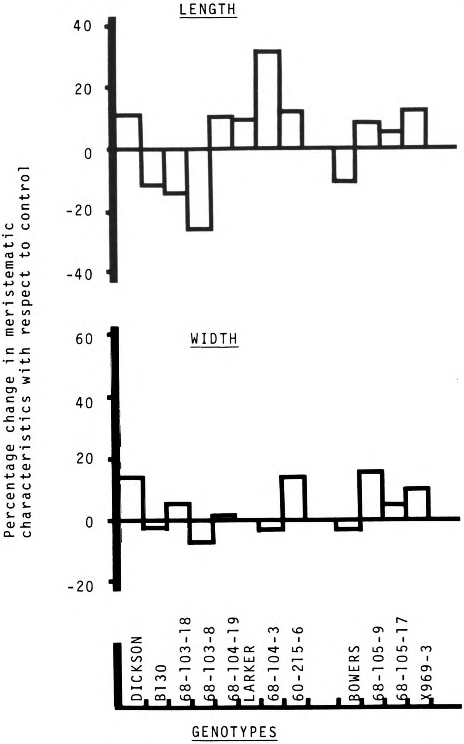


Figure 8. Percentage of change in maximum length and maximum width of the primary apical meristem of barley in the reproduction state of development due to cycocel (CCC) application at the transition stage of development.

increased significantly in Dickson, 60-215-6, 68-105-9 and X969-3, however, these increases were lower than that of the gibberellin-treated plants.

The length of meristem were reduced in the reproduction state for B130, 68-103-8 and 68-103-18 from the application of cytokinin (Kinetin) in comparison to the control. Only X969-3 had a significant increase in length among the outliers with the other three showing almost no change in length. The highest increase was obtained from 68-104-3 followed by 68-104-19 then 60-215-6 (Fig. 9). With the exception of Larker and Bowers, widths of meristems were either increased or remained constant. The greatest increase in width was obtained in 60-215-6 followed by 68-104-9 then 68-103-18 among the standard genotypes. Without considering Larker, width generally increased with increasing heads produced per unit area from Kinetin application.

With auxin (IAA) application (Fig. 10), lengths of the primary shoot apical meristems of all genotypes, with the exception of 68-103-8 and 68-103-18, increased. The 104 lines had the highest increase. The width of the primary apical meristem of Larker showed a decrease while that of the rest of the genotypes showed an increase. Genotype 68-105-9 had the highest width increase with the rest of the outliers showing a relatively small increase which is

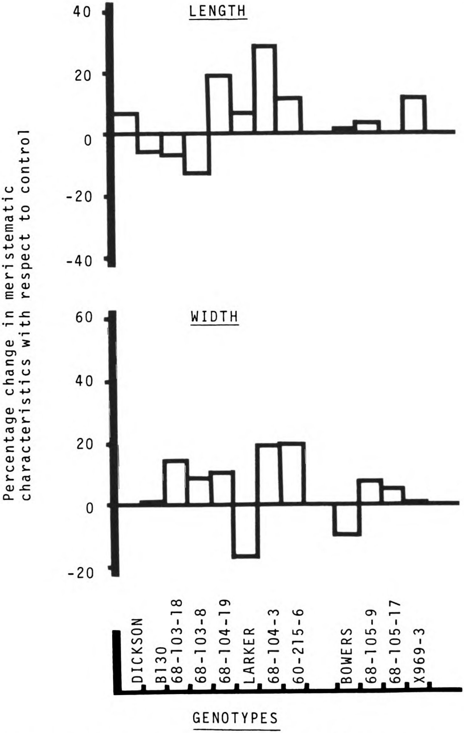


Figure 9. Percentage change in maximum length and maximum width of the primary apical meristem of barley in the reproduction state of development due to cytokinin (Kinetin) application at the transition stage of development.

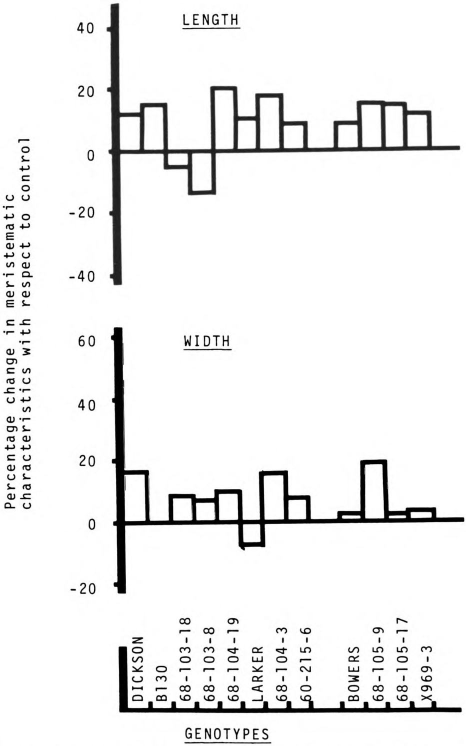


Figure 10. Percentage change in maximum length and maximum width of the primary apical meristem of barley in the reproduction state of development due to auxin (IAA) application at the transition stage of development.

not significantly different from that of the control. The relative width increases of both Dickson and 68-104-3 were the same. A general pattern cannot easily be used to describe the reactions of the genotypes to auxin application with respect to their width changes, however, the length changes show similar reaction patterns to the GA_3, CCC and Kinetin applications.

C. THE REACTION OF YIELD COMPONENTS AND YIELD TO APPLIED HORMONES.

The mean values for number of heads per unit area (X), number of seeds per head (Y), average seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), height (HT) and heading (HD) for the control block are given in Table 8. There were significant differences between the genotypes for all the characteristics mentioned above.

Table 9 gives the correlation coefficients between the plant characteristics measured (control block). X maintains a negative correlation with the characteristics, though not all the correlations were significant. X is significantly and negatively correlated with head size (YZ), number of seeds per head (Y), length (L) and width (WD) of the primary shoot apical meristem at the reproduction stage. Thus, the higher the number of heads produced per unit area by a genotype, the smaller the head size, number of seeds per head

Table 8. Mean values for the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), height (HT) and heading (HD) of barley (Control block).

GENOTYPE	X(#)	Y(#)	Z(mg)	XY(#)	YZ(g)	W(g)	HT(in)	HD(days)
BOWERS	17.25	67.97	30.83	1169.61	2.090	575.75	37.50	27.00
X969-3	19.55	63.89	30.26	1225.16	1.925	591.00	39.00	23.00
B130	18.59	57.52	30.71	1065.84	1.764	524.50	39.75	25.75
60-215-6	30.14	32.96	31.68	955.73	1.036	485.00	28.75	24.50
DICKSON	15.35	63.60	28.39	973.90	1.804	441.50	38.25	27.50
LARKER	20.89	50.67	31.89	1056.40	1.614	539.25	40.00	25.75
68-105-9	18.83	65.83	29.82	1236.56	1.961	590.75	40.00	24.50
68-105-17	18.55	65.30	29.82	1210.48	1.946	575.00	38.50	26.50
68-104-3	27.26	44.52	28.98	1199.89	1.288	555.25	41.75	25.25
68-104-19	20.86	55.81	29.65	1150.30	1.646	546.25	40.50	25.00
68-103-8	19.99	58.34	30.01	1166.53	1.750	559.75	41.75	25.75
68-103-18	19.91	52.79	31.86	1053.19	1.684	538.25	39.50	24.00
LSD (α=.05)	3.95	6.23	.19	134.83	.177	64.74	2.11	.74
LSD (α=.01)	5.31	8.39	.26	181.58	.239	87.18	2.84	1.00

Table 9. Correlation coefficients among the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development, height (HT) and heading (HD) (Control block).

	X	Y	Z	XY	YZ	W	L	HD	HD
Y	-.911**								
Z	.264	-.335							
XY	-.185	.369	.333						
YZ	-.914**	.915**	-.209	.503					
W	-.110	.270	.081	.912**	.465				
L	-.615*	.596*	.154	.373	.662*	.482			
WD	-.662*	.706*	.155	.611*	.816**	.728**	.648*		
HD	-.410	.321	-.358	-.232	.241	-.390	-.092	-.128	
HT	-.479	.510	-.395	.562	.466	.438	.558	.441	.077

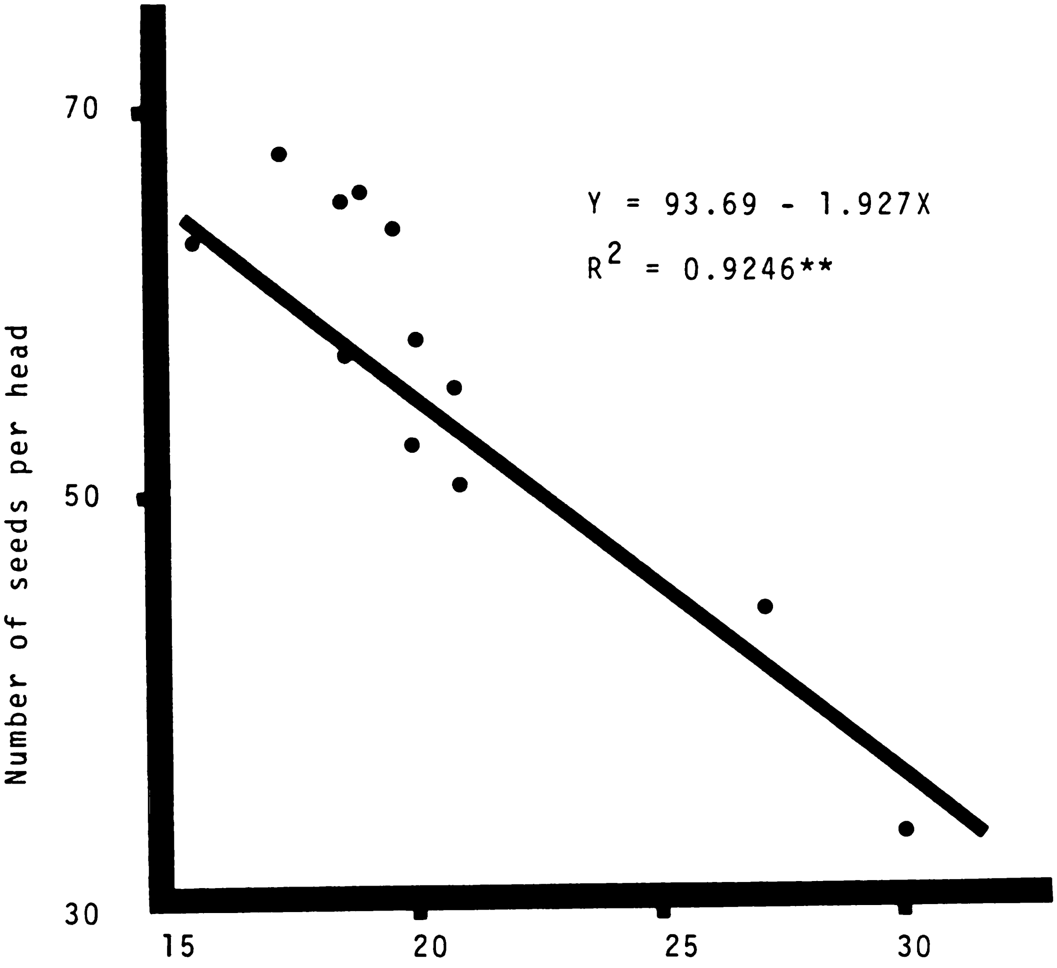
* $P \leq .05$

** $P \leq .01$

and length and width of meristem in the reproduction state. Y is, however, significantly and positively correlated with head size and length (L) and width (WD) of the primary shoot apical meristem at the reproduction stage. The larger the size of meristem at the reproduction stage, the larger the head size, as shown by the significant correlation between (L), (WD) and (YZ), and the higher the number of seeds produced per head. Yield (W) is only significantly correlated with number of seeds per unit area and width of meristem at the reproductive state. Figure 11 shows the regression of number of seeds per head (Y) on number of fertile tillers per unit area (X) using mean values for the standard genotypes. The variation in X accounts for about 92% ($R^2 = 0.9246$) of the variation in Y.

Figure 12 shows the regression of number of seeds per head on the number of heads per unit area for all treatments, i.e. control, gibberellin, cycocel, cytokinin and auxin using the mean values for the standard genotypes. The points were eliminated to avoid confusion on the graph, however, it will be presented presently. There were no significant differences between the regression lines even though changes in both number of seeds per head and number of heads per unit area occurred.

Table 10 gives the correlation coefficients among the



Number of heads per unit area

Figure 11. Regression of the number of seeds per head on the number of heads per unit area of barley (control block).

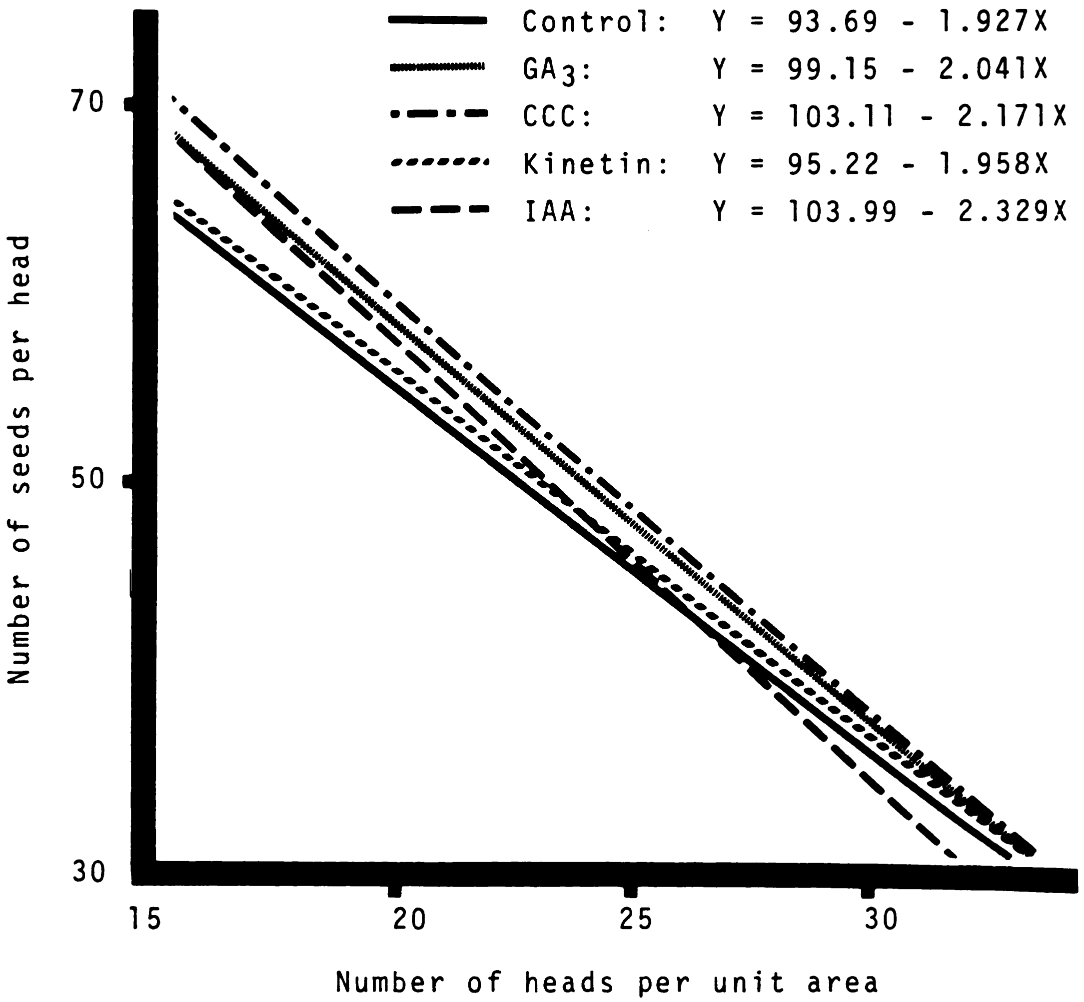


Figure 12. Comparison of regressions of number of seeds per head on number of heads per unit area of barley due to GA_3, CCC, Kinetin and IAA application at the transition stage of development with a control.

Table 10. Correlation coefficients among the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development, height (HT) and heading (HD) resulting from gibberellin (GA_3) application at the transition stage of development.

	X	Y	Z	XY	YZ	W	L	WD	HD
Y	-.935**								
Z	-.346	.227							
XY	-.587*	.697*	-.057						
YZ	-.943**	.976**	.429	.627*					
W	-.586*	.735**	.492	.840**	.783**				
L	-.263	.295	.286	-.027	.365	.134			
WD	-.371	.404	.261	.117	.451	.248	.850**		
HT	-.207	.287	-.269	-.106	.007	-.253	-.346	-.522	
HD	-.526	.573	.300	.681*	.577*	.742**	-.213	-.208	.187

* $P \leq .05$

** $P \leq .01$

plant characteristics of the gibberellin applied block. X is significantly and negatively correlated with Y, XY, YZ and W, while Y is significantly and positively correlated with XY, YZ and W. Z, however, has no significant relationship with any of the plant characteristics measured. Heading is significantly correlated with XY, YZ, Y and W. Thus, the longer the heading date, the higher the values for XY, YZ, Y and W. The maximum length and width of the meristem in the reproduction state have no significant relationship with the other plant characteristics but maintained the significant correlation between themselves.

Figures 13, 17, 21 and 25 show the regressions of number of seeds per head (Y) on the number of fertile tillers per unit area due to hormonal application. The star and circle points are for control and a hormone, respectively, and each genotype has its values joined by the dashed line. This technique is adopted to show the change that the individual genotypes underwent as a result of hormonal application.

With gibberellin application (Fig. 13), changes were obtained in X for genotypes with the least and highest number of heads per unit area, while changes in Y were frequently observed with the outliers and with genotypes producing medium number of heads per unit area of the group

Number of seeds per head

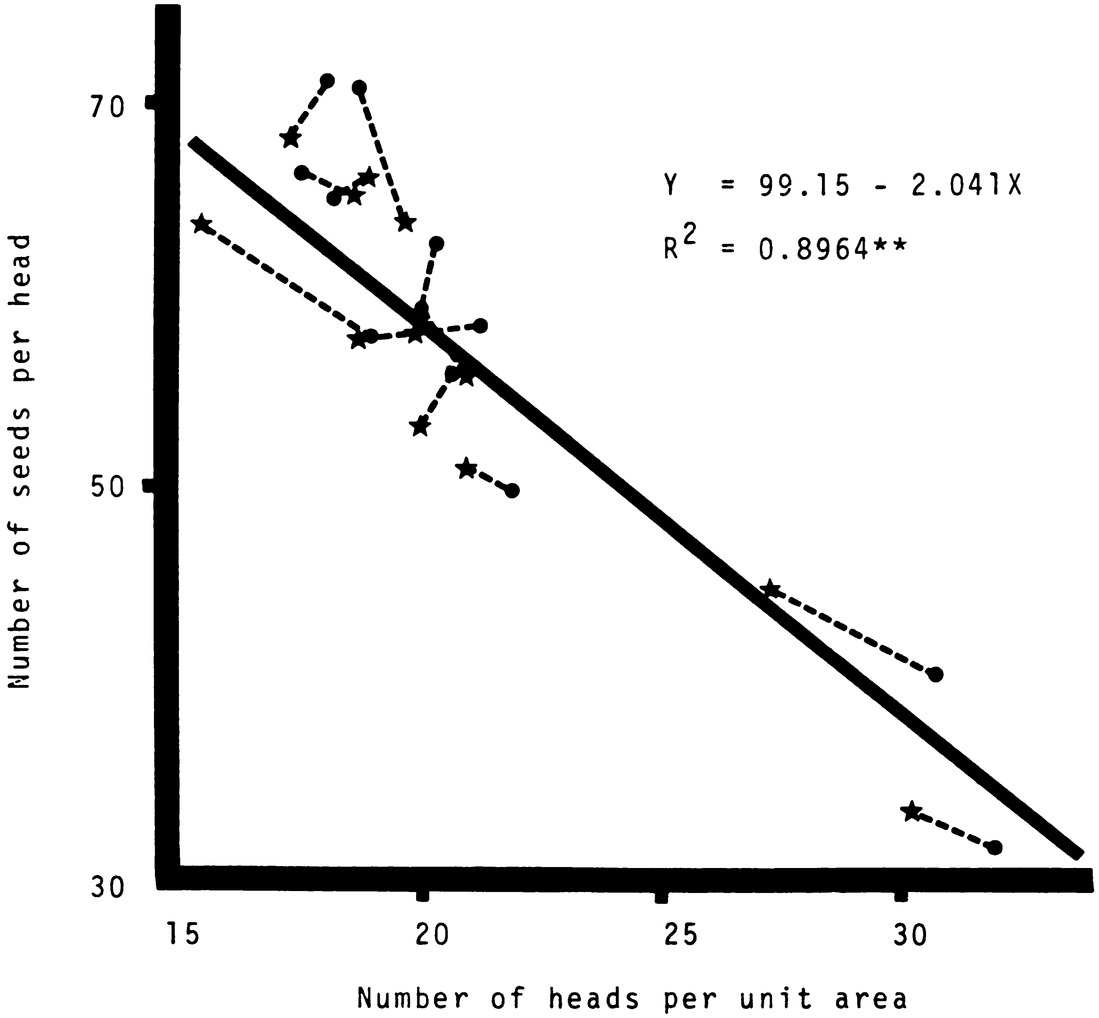


Figure 13. Regression of the number of seeds per head on the number of heads per unit area of barley due to GA_3 application at the transition stage of development. (Stars and circles represent the control and GA_3 applied characteristics, respectively, and individual genotypes are joined by broken lines).

defined as standard genotypes. Associated with these changes, were small changes in Y and X, respectively. Thus, with gibberellin application, the obvious changes in X and Y depended on the tillering capability of the genotype in question.

There were significant differences between the genotypes for the percentage change over control for most of the plant characteristics due to gibberellin application (Table A1). In both the standard genotypes and the outliers, genotypic yield changes declined with increasing number of heads per unit area. Dickson had the highest positive yield change while 60-215-6 had a decrease in yield with gibberellin application. With the outliers, Bowers and X969-3 had the highest and least changes, respectively (Fig. 14).

The histograms of changes in YZ and XY were drawn to determine whether the changes in W was due mainly to changes in head size or number of seeds per unit area. The graph of percentage change over control for YZ show that with increasing number of heads per unit area, head size increases to a point and start decreasing for the standard varieties while the outliers had an increasing change with increasing X. Changes in number of seeds per unit area, however, decreased to about the control mean values with increase in X. The outliers, however, showed an initial decrease and

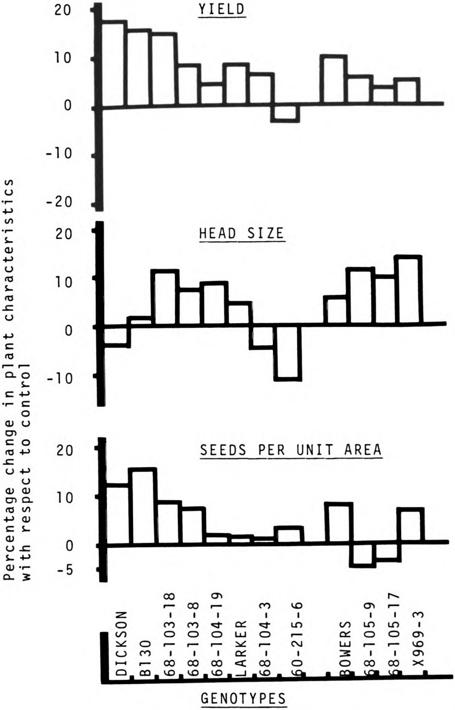


Figure 14. Percentage change in yield, head size and number of seeds per unit area of barley due to GA_3 application at the transition stage of development.

then an increase as fertile tillers production increased (Fig. 14).

Changes in average seed weight showed no trend in the standard varieties but an initial increase and then a decrease was observed with the outliers, as fertile tiller production increased (Fig. 15). The changes shown in X and Y due to gibberellin application are similar to that shown in Figure 13. Genotypes with the least and high X increased the number of heads produced per unit area with slight decreases in the number of seeds produced per head. Genotypes with medium number of heads per unit area produced more seeds per head with small changes in their X.

Heading and height (Fig. 16) were generally reduced in all the genotypes but not at significant levels.

The correlation coefficients obtained from the CCC applied block for the measured plant characteristics are given in Table 11. X maintains its significant negative correlation with Y and YZ while Y has significant positive correlations with XY, YZ and W. Width of meristem in the reproduction state has significant relationships with Y, XY, YZ, W, L and HT. Heading has a significant negative correlation with seed size. Number of seeds per unit area is significantly correlated with head size and yield.

The graph of number of seeds per head on number of fertile tillers per unit area due to the application of CCC

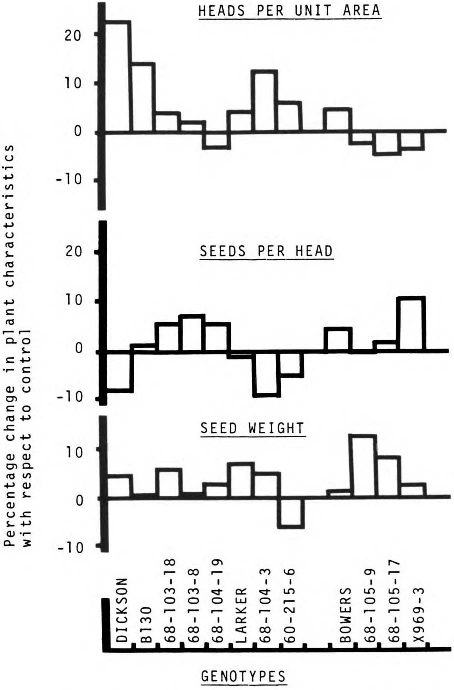


Figure 15. Percentage change in number of heads per unit area, number of seeds per head and seed weight of barley due to GA_3 application at the transition stage of development.

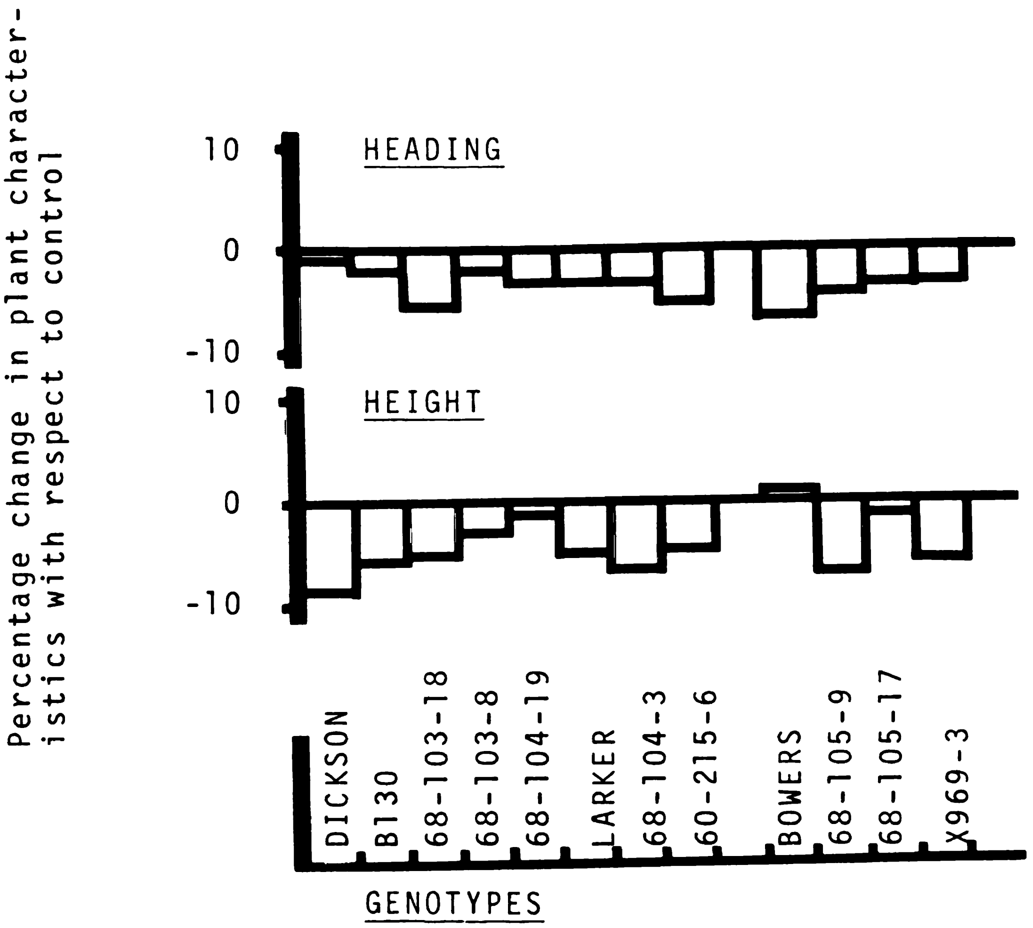


Figure 16. Percentage change in heading and height of barley due to GA_3 application at the transition stage of development.

Table 11. Correlation coefficients among the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development, height (HT) and heading (HD) resulting from cycocel (CCC) application of the transition stage of development.

	X	Y	Z	XY	YZ	W	L	WD	HD
Y	-.895**								
Z	.109	-.080							
XY	-.314	.677*	-.154						
YZ	-.882**	.990**	.060	.659*					
W	-.289	.659*	.139	.957**	-.013				
L	-.399	.543	-.187	.482	.523	.427			
WD	-.514	.748**	-.051	.754**	.745**	.742**	.861**		
HT	-.011	-.203	-.208	-.490	-.240	-.556	-.358	-.614*	
HD	-.503	.468	-.675*	.424	.387	.233	.358	.359	-.151

* $P \leq .05$

** $P \leq .01$

is shown in Fig. 17. There was virtually no change in the points for the genotypes with highest X. B130 has the greatest change in number of heads produced for CCC application followed by Dickson. All other standard genotypes plus the outliers increased their number of seeds produced per head. The highest increase in Y was obtained with 68-103-18 from the standard genotypes and 68-105-17 from the group of outliers. The increase in Y was accompanied with almost no change in X.

There were no established trends for the percentage change over control for yield, head size and number of seeds per unit area (Fig. 18) although significant differences exist between the genotypes (Table A2). Some genotypes had increased yield while others were not changed substantially. The changes in W were due to changes in YZ for 68-103-18 and XY for B130 and Larker. The change in W for Bowers is mainly due to its change in XY while that of the other three outliers were due to YZ.

In determining the yield component prone to change with cycocel application, it was observed that Dickson, B130 and Bowers had relatively higher increases in X while in 68-103-18, 68-105-17, X969-3 and Larker increases in the number of seeds produced per head were obtained. Average seed weight was increased substantially in Dickson and

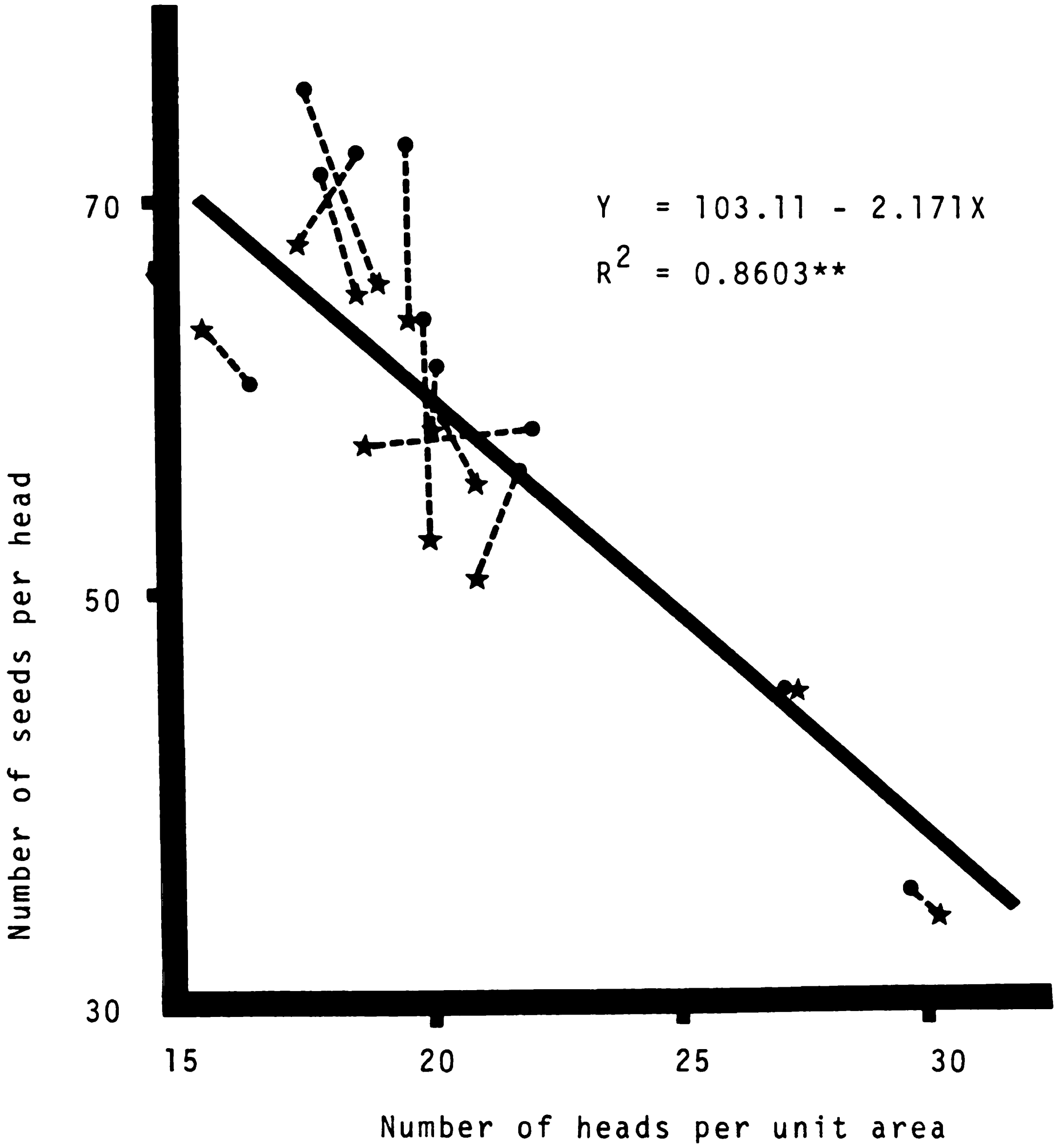


Figure 17. Regression of the number of seeds per head on the number of heads per unit area of barley due to CCC application at the transition stage of development. (Stars and circles represent the control and GA3 applied characteristics, respectively, and individual genotypes are joined by broken lines).

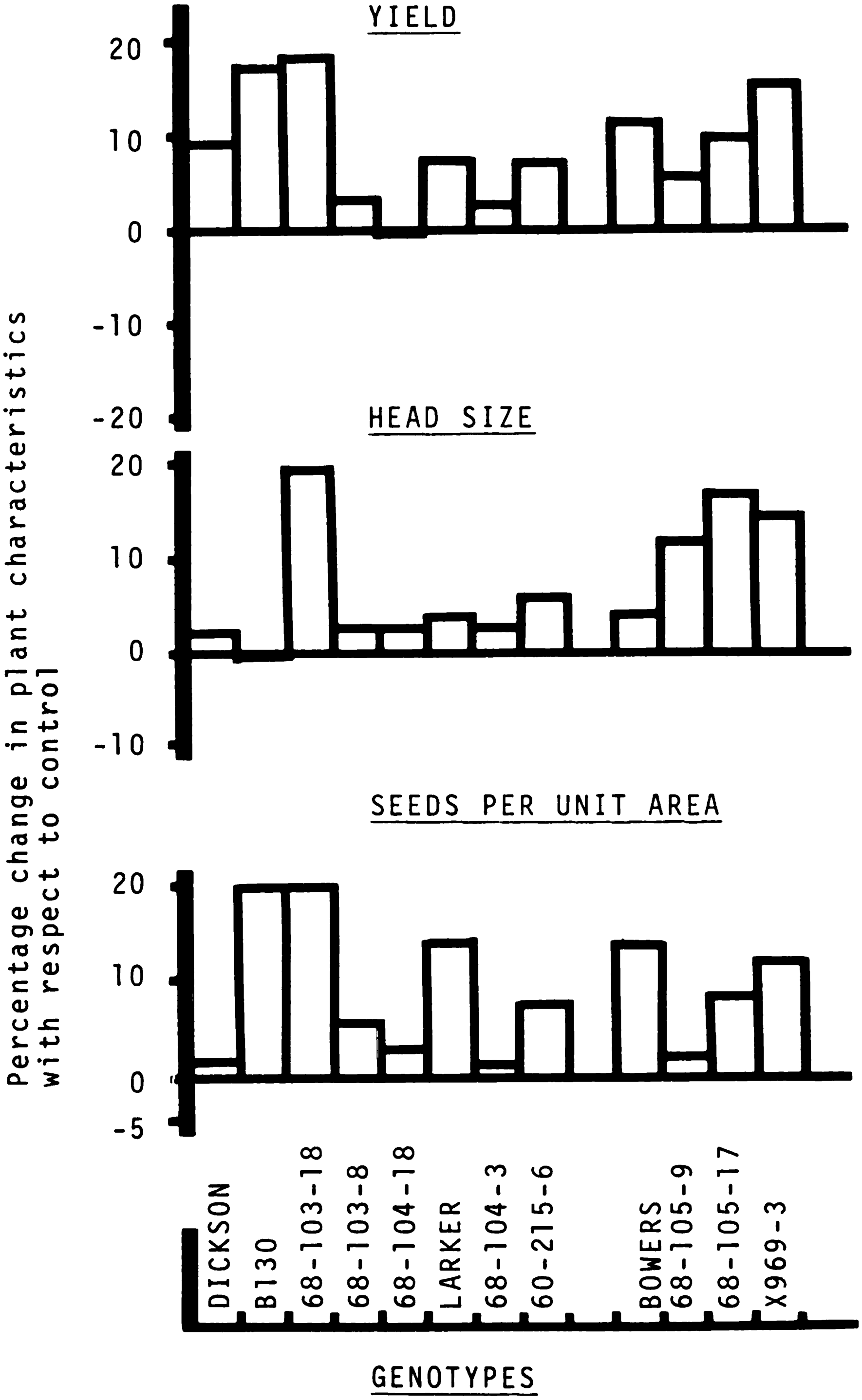


Figure 18. Percentage change in yield, head size and number of seeds per unit area of barley due to CCC application at the transition stage of development.

reduced in Larker (Fig. 19).

Heading was increased in 68-105-9 while height shows not much change as compared to their controls (Fig. 20).

The correlation coefficients among plant characteristics measured from the cytokinin applied experimental block are given in Table 12. Length and width of meristem in the reproduction state are both significantly correlated with XY, W and HT while the width is additionally correlated significantly with Y, YZ and HD. Yield is significantly correlated with XY and HD. X, however, is negatively and significantly correlated with head size and the number of seeds per head.

Cytokinin application tended to change number of heads per unit area, generally, in most of the genotypes used in the experiment. 68-103-18, 68-104-19, Larker and 68-105-17 had virtually no change in both X and Y (Fig. 21).

Only 60-215-6 and 68-105-17 had a reduction in yield relative to the control while the rest had some form of an increase in yield (Fig. 22). X969-3 had the biggest increase in head size while 68-103-18 had the largest increase in the number of seeds per unit area. The manifestation of yield changes in terms of X, Y and Z, varied among the genotypes (Fig. 23). 60-215-6 and X969-3 both had increased Y but decreased X while Dickson, B130,

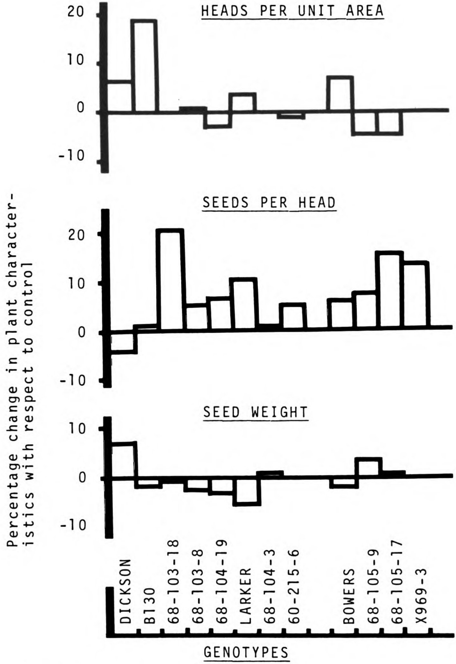


Figure 19. Percentage change in number of heads per unit area, number of seeds per head and seed weight of barley due to CCC application at the transition stage of development.

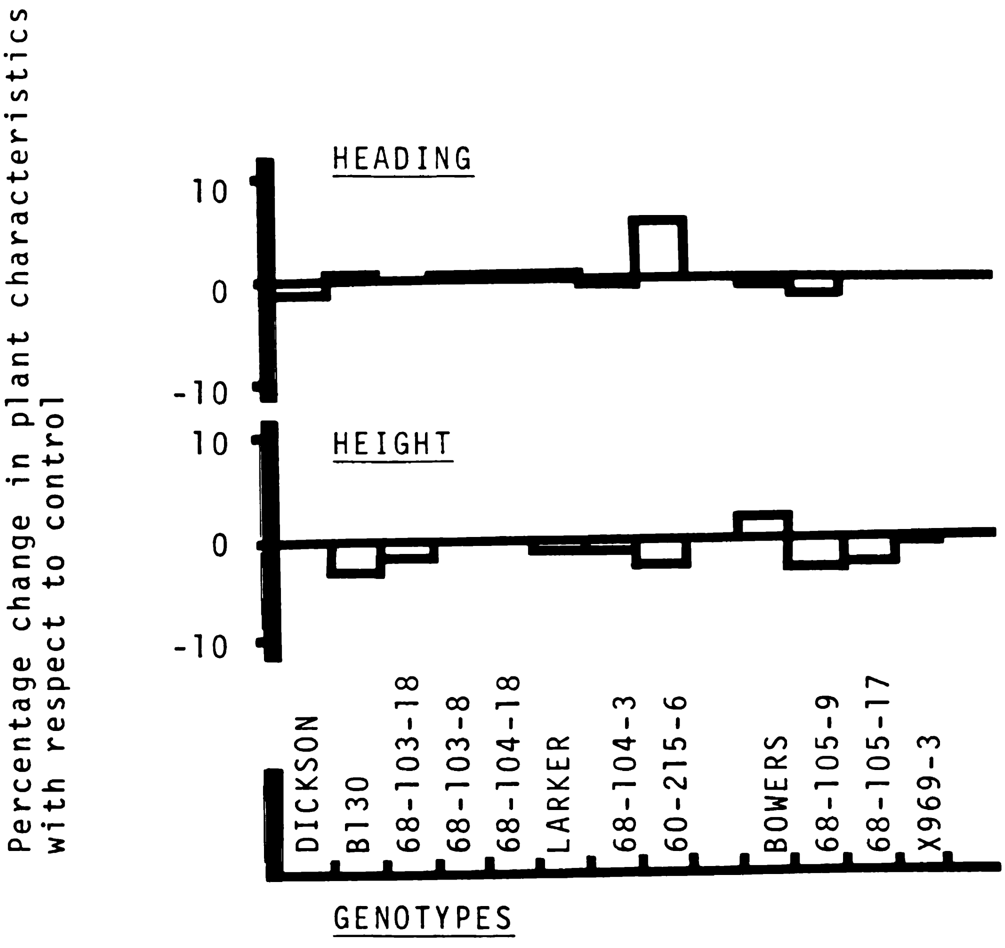


Figure 20. Percentage change in heading and height of barley due to CCC application at the transition stage of development.

Table 12. Correlation coefficients among the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), maximum length (L), and maximum width (WD) of the primary apical meristem of barley in reproduction state of development, height (HT), and heading (HD) resulting from cytokinin (kinetin) application at the transition stage of development.

	X	Y	Z	XY	YZ	W	L	WD	HD
Y	-.885**								
Z	.099	-.335							
XY	-.158	.578*	-.415						
YZ	-.903**	.971**	-.105	.520					
W	-.138	.470	.072	.877**	.530				
L	-.240	.523	-.290	.735**	.500	.654*			
WD	-.341	.660*	-.436	.780**	.590*	.649*	.657*		
HT	-.052	-.163	-.036	-.412	-.192	-.476	-.605*	-.575*	
HD	-.260	.494	-.205	.724**	.489	.692*	.748**	.514	-.273

* $P \leq .05$

** $P \leq .01$

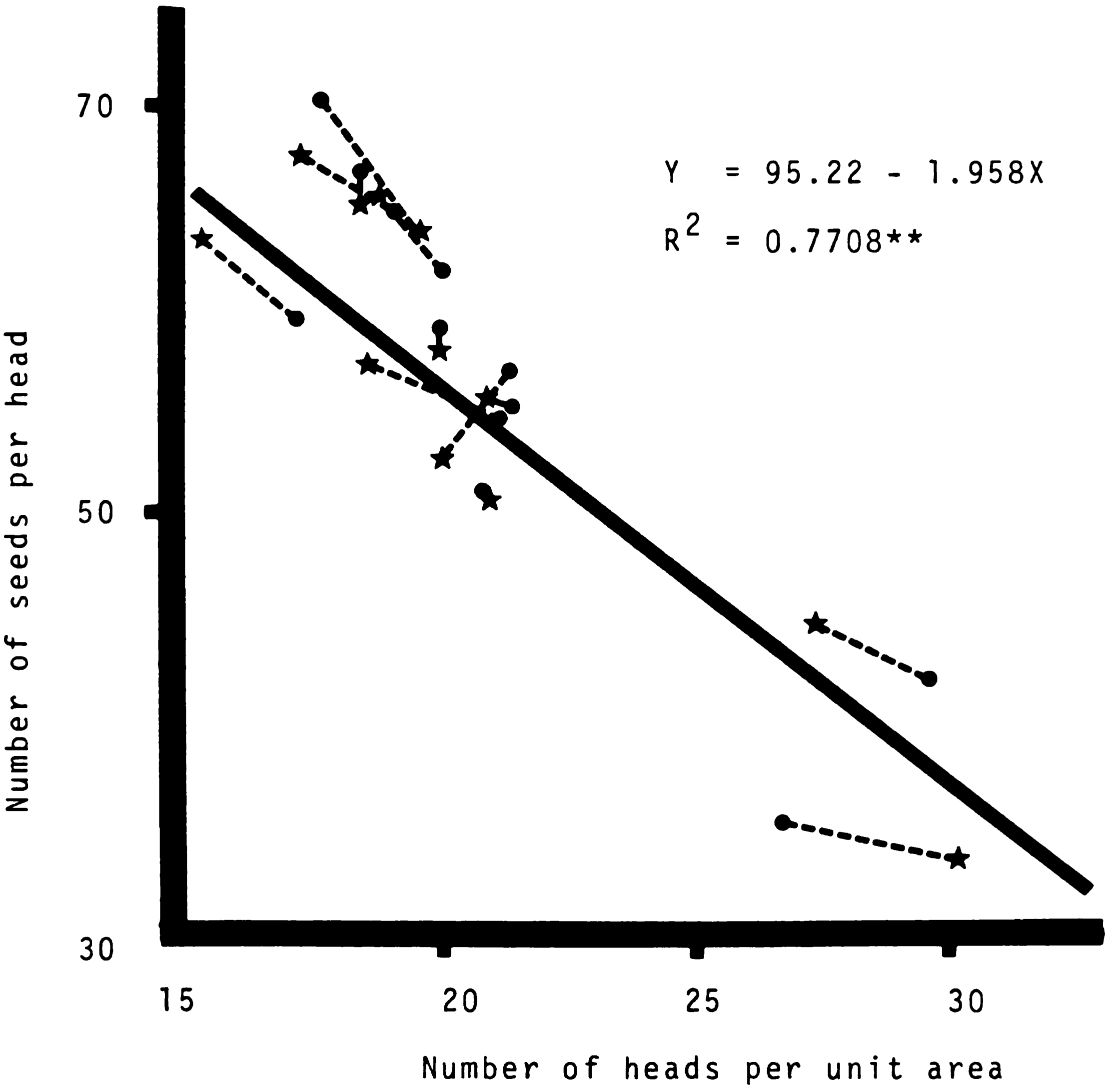


Figure 21. Regression of the number of seeds per head on the number of heads per unit area of barley due to kinetin application of the transition stage of development. (Stars and circles represent the control and GA_3 applied characteristics, respectively, and individual genotypes are joined by broken lines).

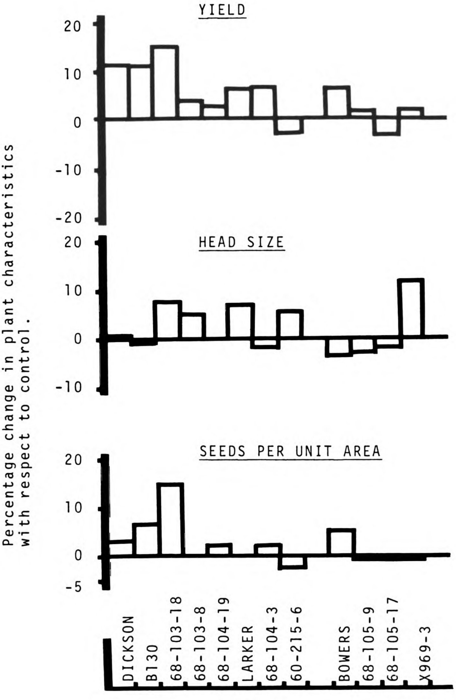


Figure 22. Percentage change in yield, head size and number of seeds per unit area of barley due to kinetin application at the transition stage of development

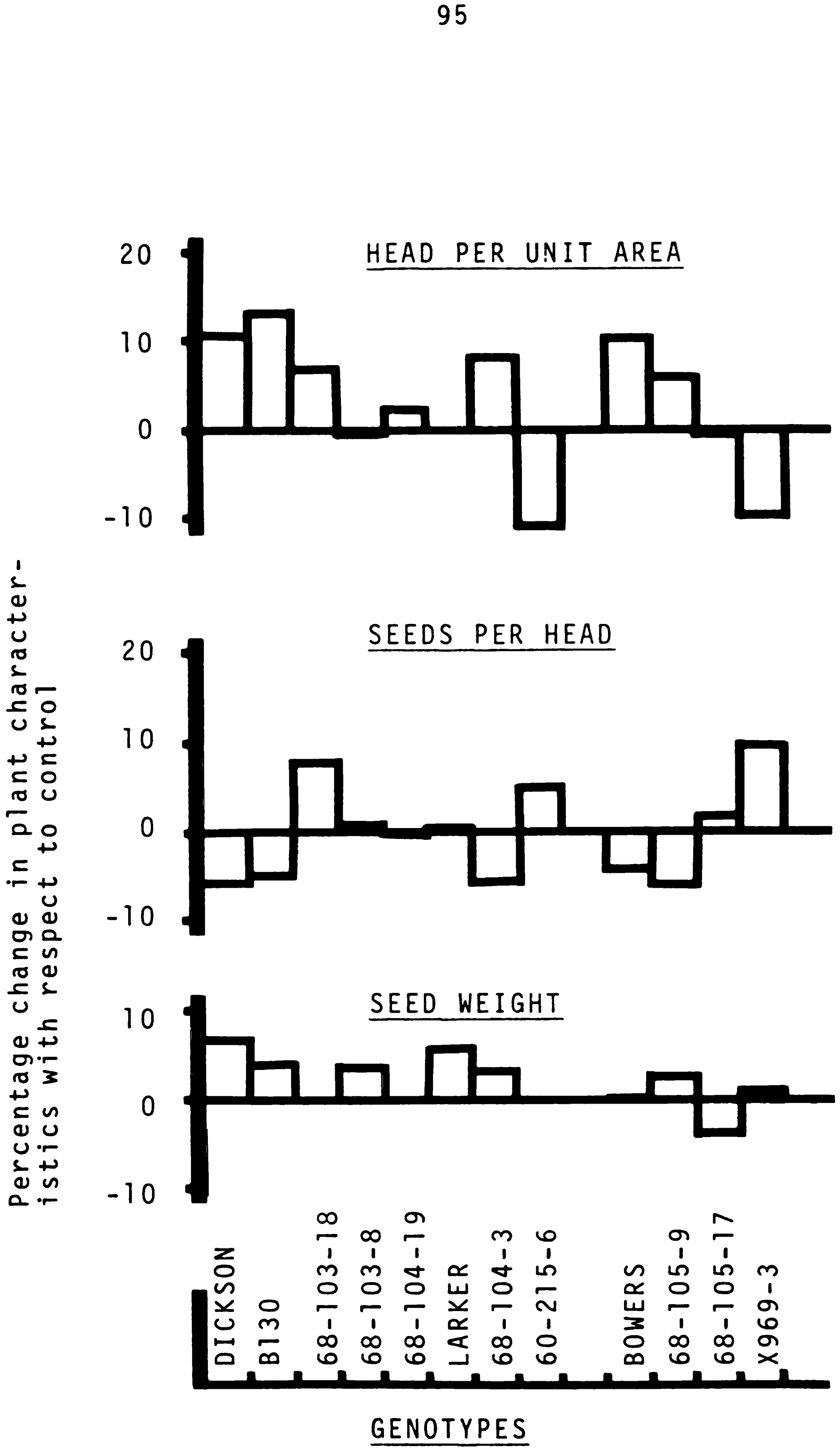


Figure 23. Percentage change in number of heads per unit area, number of seeds per head and seed weight of barley due to kinetin application at the transition stage of development.

68-104-3, Bowers and 68-105-9 showed the opposite effect. Their number of heads per unit area were increased while their number of seeds per head decreased. 68-103-18 increased its number of fertile tillers and number of seeds per head produced. Even though there were slight changes in the average seed weight produced, there was no established trend and the changes were not significantly different from the control. The number of days to heading and height were not changed significantly from controls (Fig. 24).

Significant differences exist between the genotypes for the plant characteristics measured after the cytokinin application (Table A3).

Correlation coefficients among plant characteristics developed after auxin application are presented in Table 13. Y, XY, YZ and W, are significantly and positively intercorrelated with each other. X is significantly and negatively correlated with Y and YZ. Length and width of the primary apical meristem in the reproduction state are significantly correlated with Y, XY, YZ and W, but negatively correlated with X.

Figure 25 shows the effect of auxin application on the regression of Y on X. Changes in both X and Y are observed but larger changes are observed in the number of seeds per head.

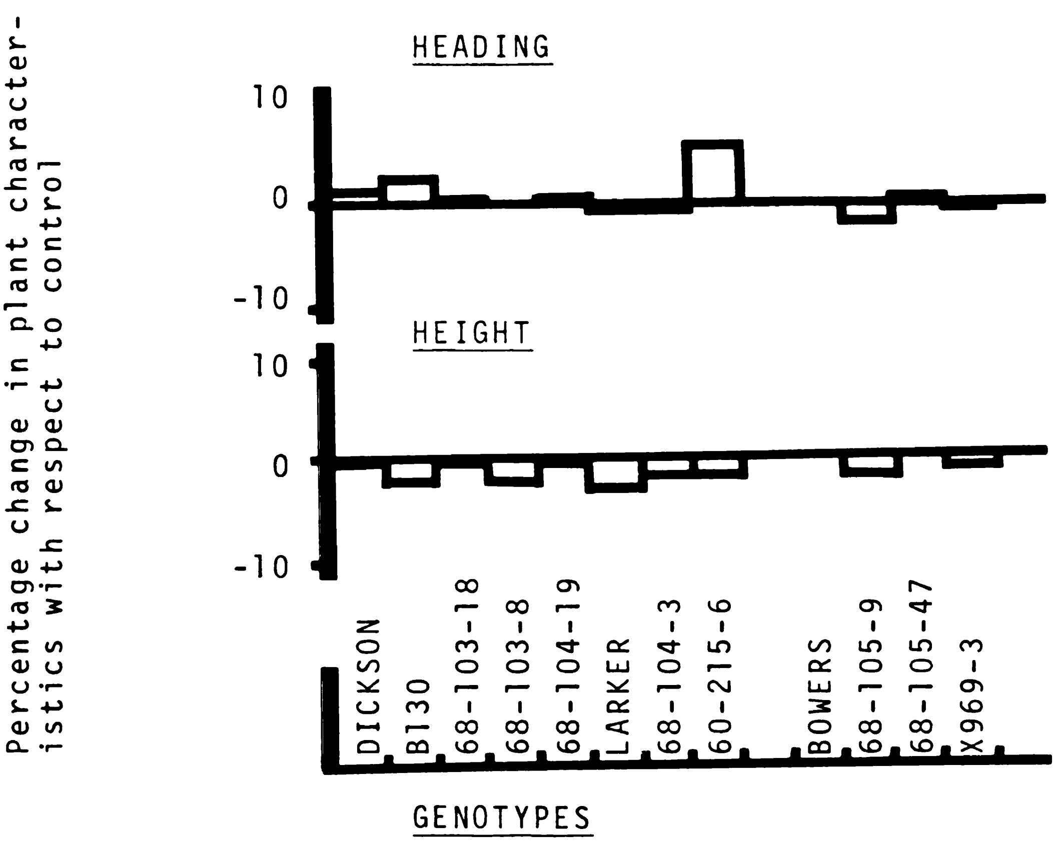


Figure 24. Percentage change in heading and height of barley due to kinetin application at the transition stage of development.

Table 13. Correlation coefficients among the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), number of seeds per unit area (XY), head size (YZ), yield (W), maximum length (L) and maximum width (WD) of the primary apical meristem of barley in reproduction state of development, height (HT) and heading (HD) resulting from auxin (IAA) application at the transition stage of development.

	X	Y	Z	XY	YZ	W	L	WD	HD
Y	-.897**								
Z	-.115	.032							
XY	-.340	.696*	.012						
YZ	-.895**	.974**	.255	.669*					
W	-.361	.641*	.455	.896**	.717**				
L	-.681*	.862**	.016	.826**	.833**	.743**			
WD	-.702*	.888**	.101	.757**	.881**	.725**	.795**		
HT	-.109	-.188	-.069	-.538	-.193	-.515	-.218	-.437	
HD	-.361	.456	-.242	.606*	.381	.432	.437	.496	-.339

* $P \leq .05$

** $P \leq .01$

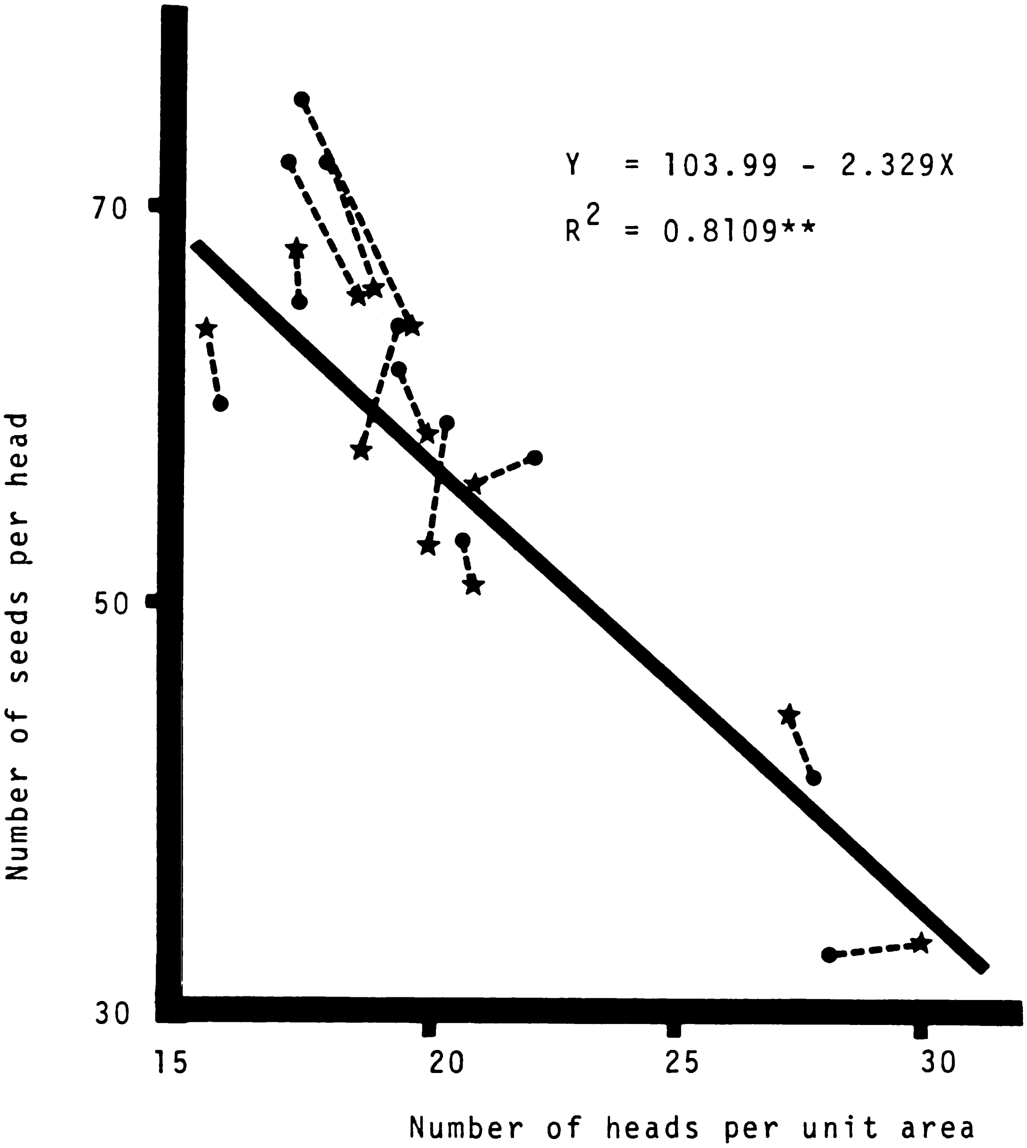


Figure 25. Regression of the number of seeds per head on the number of heads per unit area of barley due to IAA application at the transition stage of development. (Stars and circles represent the control and GA_3 applied characteristics, respectively, and individual genotypes are joined by broken lines).

Significant changes exist between the genotypes for the percentage change over control on most of the measured characteristics (Table A4). The yield changes of the standard genotypes establish a trend when one considers all but 68-103-8 and 68-104-19. Starting with Dickson, there is an increase in the yield changes until genotype 68-103-18 (max. % yield increase) after which there is a reduction in the percentage increase until a reduction in yield is attained with the two genotypes producing high number of heads per unit area. Auxin decreased the yield of Bowers but had no effects on 68-105-9, 68-105-17 and X969-3 (Fig. 26). The trend in the changes in head size among the standard genotypes are similar to that of the yield changes. 68-105-9, 68-105-17 and X969-3, however, had an increase in head size. The number of seeds per unit area show a decreasing trend with increasing number of heads per unit area.

Auxin decreased the number of heads per unit area in 60-215-6, 68-105-9, 68-105-17 and X969-3. The other genotypes were not affected significantly (Fig. 27). Changes in the number of seeds per head were similar to those of yield and head size. Number of seed per head for 68-105-9, 68-105-17 and X969-3 were significantly increased. The average seed weight was generally reduced in almost all the

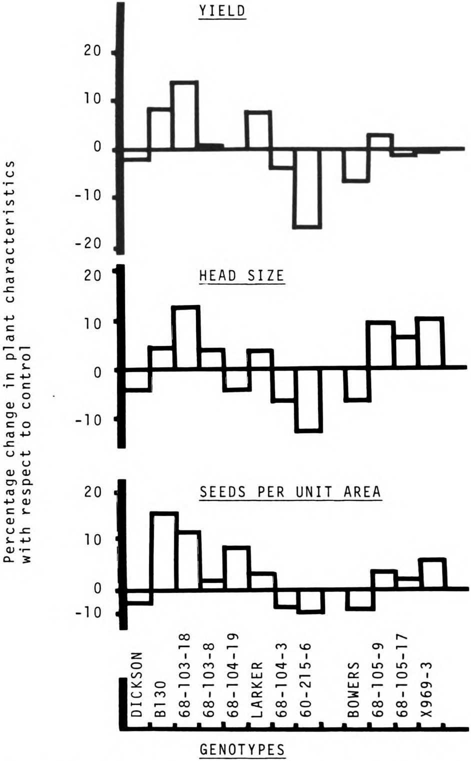


Figure 26. Percentage change in yield, head size and number of seeds per unit area of barley due to IAA application at the transition stage of development.

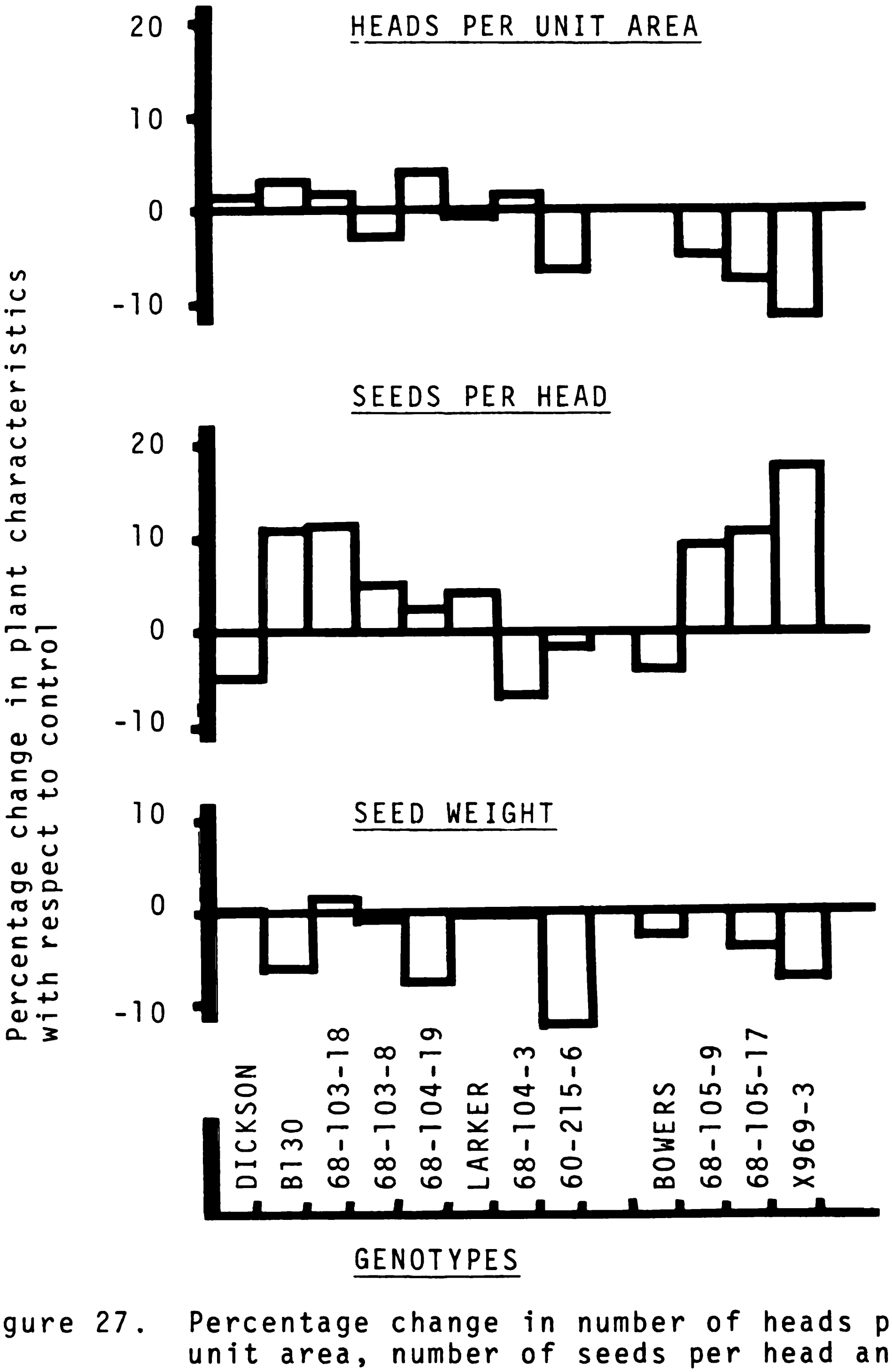


Figure 27. Percentage change in number of heads per unit area, number of seeds per head and seed weight of barley due to IAA application at the transition stage of development.

genotypes with the greatest change observed in 60-215-6 followed by 68-104-19, X969-3 and B130. A clear case of component compensation is shown by the outliers. This phenomenon is also observed in some standard genotypes while the others had no change in X with an increase in Y.

No significant changes were observed in the heading and height graphs (Fig. 28).

The highest change in yield among the genotypes was obtained from cycocel application followed by gibberellin, auxin and cytokinin in that order. Table 14 gives the correlation coefficients among the changes that were observed in the measured plant characteristics. Generally, a positive change in the number of heads per unit area is associated with a negative change in the number of seeds per head or vice versa for all the treatments. Changes in head size are also substantially reduced in all treatments but auxin. The correlation coefficient is low even though it is negative ($\rho=-.259$). Changes in head size are highly correlated with changes in Y in all treatments but cytokinin ($\rho=.221$). XY changes correlate positively and significantly with yield changes (all treatments), changes in X (all treatments but auxin) and head size (auxin alone).

The type of change in the yield components or combinations of them is dependent on the genotype and treatment

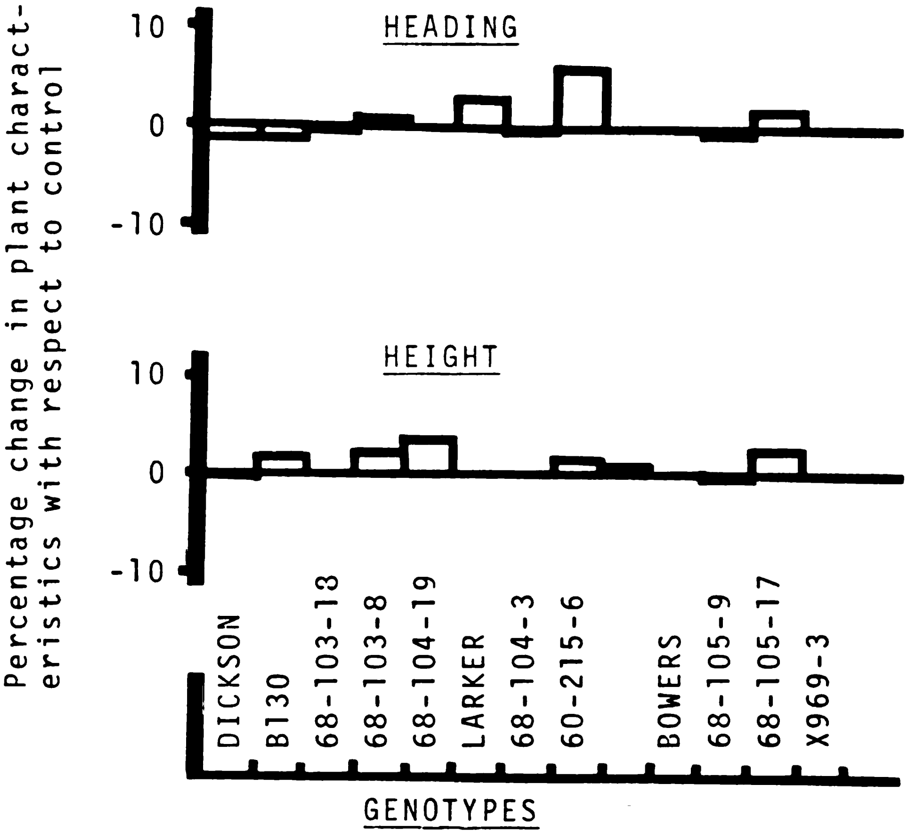


Figure 28. Percentage change in heading and height of barley due to IAA application at the transition stage of development.

Table 14. Correlation coefficients among the percentage change over control for the number of heads per unit area (ΔX), number of seeds per head (ΔY), seed weight (ΔZ), number of seeds per unit area (ΔXY), head size (ΔYZ), yield (ΔW), maximum length (ΔL) and maximum width (ΔWD) of the primary apical meristem of barley in the reproduction state of development due to the application of gibberellin, cycocel, cytokinin and auxin, respectively, at the transition stage of development.

	ΔW	ΔZ	ΔYZ	ΔL	ΔWD	ΔX	ΔXY
ΔZ	.248						
	.048						
	.529						
	.542						
ΔYZ	.222	.544					
	.416	.172					
	.050	.060					
	.803**	.383					
ΔL	-.590*	.084	-.305				
	-.331	.295	-.082				
	-.267	.039	-.127				
	-.257	-.310	-.305				
ΔWD	-.474	-.221	-.367	.783**			
	-.325	.529	.189	.744**			
	-.281	-.277	-.042	.200			
	-.115	.236	-.179	.101			
ΔX	.519	-.225	-.711**	-.133	-.053		
	.493	-.135	-.570	-.282	-.531		
	.719**	.366	-.652*	-.164	-.229		
	.362	.338	-.259	.075	.188		
ΔXY	.718**	-.492	-.194	-.582*	-.245	.633*	
	.842**	-.496	.251	-.451	-.563	.521	
	.819**	.049	-.004	-.347	-.128	.611*	
	.829**	-.017	.680*	-.067	-.273	.238	
ΔY	-.141	.456	.834**	.034	-.027	-.811**	-.443
	.160	.026	.833**	-.100	.069	-.581*	.118
	-.567	-.707**	.221	-.221	.134	-.548	-.212
	.405	.006	.773**	.050	-.073	-.539	.463

* P ≤ .05

** P ≤ .01

under consideration. Genotypes producing low and high number of heads per unit area are prone to changes in X while the genotypes producing medium X have the least resistance to changes in their number of seeds per head.

With auxin treatment, ΔX has high negative correlations with ΔY. ΔXY has significant positive correlations with ΔW, and ΔYZ. Generally, the correlations between XY with X and Y is positive and negative, respectively or vice versa, depending on the significance of the relationship between X and Y. The positive correlations (not significant) between ΔXY with ΔX and ΔY show some relaxation between ΔX and ΔY due to auxin application. A similar observation is shown with the cycocel application even though the correlation between ΔXY with ΔY is low ($\rho = .118$). The effects of gibberellin and cytokinin application follow the normal trend, however, the correlation between ΔXY with ΔY is lower for the cytokinin treatment ($\rho = -.212$) in comparison with the gibberellin treatment ($\rho = -.414$). The above effects are also depicted in the correlation coefficients between ΔX and ΔY ($\rho = -.814$, $-.581$, $-.548$ and $-.539$ for the GA_3, CCC, Kinetin and IAA treatments, respectively).

Removing the outliers causes the effect to show up better. The correlation coefficient between ΔXY with ΔX and ΔY are all positive, however, relaxation of the ΔX and

ΔY relationship is shown in the cycocel (ρ =-.368) and auxin (ρ =.204) treatments. The same relationship show significant negative correlation for both the gibberellin (ρ =-.706**) and cytokinin (ρ =-.630**) treatments (Table 15).

Table 16 presents the mean square values for the multiple regression analysis involving the length and width of the primary apical meristem in the reproduction state of development as the independent variables and plant characteristics measured from GA_3, CCC, Kinetin, IAA and the control plots of the second group of experiments as dependent variables. No significant prediction was obtained for all characteristics resulting from the GA_3 treatment. Seed weight was not significant for the regressions in all the treatments. Additionally, no significant relationships were obtained for XY (control), X(CCC and Kinetin) and YZ (Kinetin). The coefficient of determination for the significant characteristics were generally higher in the IAA treatment, followed by CCC, Kinetin and Control in that order. The width of the meristem is shown to be the more important independent characteristic in the prediction of the plant characteristics (Tables A5-A8) in all the treatments.

Table 15. Correlation coefficients among the percentage change over control for the number of heads per unit area (ΔX), number of seeds per head (ΔY), seed weight (ΔZ), number of seeds per unit area (ΔXY), head size (ΔYZ), yield (ΔW), maximum length (ΔL) and maximum width (ΔWD) of the primary apical meristem of barley in the reproduction state of development due to application of gibberellin, cycocel, cytokinin and auxin, respectively, for the standard genotypes.

	ΔW	ΔZ	ΔYZ	ΔL	ΔWD	ΔX	ΔXY
ΔZ	.630* .111 .303 .567						
ΔYZ	.397 .451 -.087 .939**	.524 -.054 -.249 .579*					
ΔL	-.609* -.450 -.390 -.292	-.489 .295 -.058 -.348	-.875** -.247 -.487 -.559				
ΔWD	-.554 -.311 -.410 -.303	-.806** .448 -.616* .130	-.713** .106 -.212 -.424	.784** .850** .212 .068			
ΔX	.529 .618* .854** .623*	.105 .107 .424 .328	-.566 -.410 -.585* .321	.253 -.298 -.101 .430	.132 -.477 -.246 .181		
ΔXY	.757** .840** .848** .831**	-.029 -.444 -.247 .016	.092 .427 .042 .723**	-.395 -.555 -.377 -.082	-.065 -.519 -.092 -.437	.571 .508 .639* .573	
ΔY	.120 .318 -.190 .780*	.038 -.586* -.699* .035	.870** .838** .865** .834**	.768** -.372 -.371 -.426	-.389 -.183 .157 -.595*	-.706** -.368 -.630* .204	.147 .598* .190 .904**

* $P \leq .05$
** $P \leq .01$

Table 16. Analysis of variance for the multiple regression of the number of heads per unit area (X), number of seeds per head (Y), seed weight (Z), head size (YZ), number of seeds per unit area (XY) and yield (W), each as a dependent variable on the maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development as the independent variables due to gibberellin, cycocel, cytokinin and auxin application, at the transition stage of development.

	Source	df	X	Y	Z	XY	YZ	W
Control	Regression	2	43.56*	254.91**			.3376**	5603.95**
	Error	9	11.17	49.94	ns	ns	.0326	1106.20
	R^2		.4643	.5314			.6969	.5296
GA_3	Regression	2						
	Error	9	ns	ns	ns	ns	ns	ns
	R^2							
CCC	Regression	2	ns	471.91**	ns	52383.23***	.4478**	13371.84***
	Error	9		69.81		5574.04	.0637	1129.25
	R^2			.6003		.6762	.6098	.7249
Kinetin	Regression	2	ns	255.08*	ns	40395.97***	ns	6111.35**
	Error	9		69.47		3554.91		1295.43
	R^2			.4493		.7163		.5118
IAA	Regression	2	47.29**	750.60**	ns	61888.58***	.6364***	13631.63**
	Error	9	9.16	28.35		5639.88	.0303	2006.35
	R^2		.5342	.8547		.7092	.8236	.6016

* $P \leq .10$ ** $P \leq .05$ *** $P \leq .01$

DISCUSSION

Tiller formation is one of the first developmental processes that occur at the organ level. Once formed, the growth and development of organs laid down later in the plants' ontogeny are established. The higher the number of tillers produced by a genotype, the smaller the size of head it produces. Culm diameter, leaf size and number of seeds per head are reduced (Grafius *et al*., 1976; Hamid and Grafius, 1978, Whyte 1979). The relative alteration in the average seed weight is dependent largely on environmental factors although the potential seed size is normally determined by the genetics of the genotype in question (Grafius, 1978).

The apparent effect of tillering on the growth and development of organs produced later in the ontogeny of the plant resides in the relationship that tillers have with the shoot meristem. Meristems are localized regions of mitotically active cells which are of diverse morphology, a reflection of their mitotic activity, and location (Sussex, 1963). Some function continuously throughout the life of the plant (shoot apical meristem of annual plants), others are persistent but seasonally intermittent (terminal and lateral meristems of perennials) while others are transitory and temporary such as the leaf apical meristem. From the time of its initiation each meristem is stable, however, changes occur within the meristem and its products. Some of these changes are gradual, such as the ontogenetic size change in a meristem. Others are sudden as in the conversion of a vegetative shoot meristem into a flower meristem.

In cereal plants, the above ground organs evolve from the shoot apical meristem. The main shoot is developed with the apical dome initiating acropetally a succession of primordia to form its leaves. Each primordium unit later differentiate an elongated internode and/or a tiller bud and subsequently tillers and main shoot develop floral primordia.

The results presented here and by Whyte (1979) show the nature of the relationship between tiller production and the size of the primary apical shoot meristem. The higher the number of tillers produced by a genotype, the smaller is the size of the primary shoot apical meristem it produces. Since organs arise from meristems, it is reasonable to expect inter-organ associations to be highly correlated. The correlation coefficients of stem diameter with head size and number of seeds per head are .861** and .794**, respectively (Whyte, 1979) and culm diameter with leaf area and head size are .806** and .798*, respectively

(Hamid, 1976). As pointed out by Adams (1975) and Grafius (1978), high yield potentials are achieved through a balance between factors of numbers (e.g., number of nodes, number of tillers) and factors of size (e.g., stem diameter, leaf area, head size, pod size). A balance is therefore established between the number of tillers per unit area with culm size, leaf area and head size through the relationship that the number of tillers and meristem size have with each other.

The early differences in time of differentiation and rate of spikelet development are reflected in the mature plant characteristics. There was a 4-day delay for the transformation of the primary apical meristem from the appearance of double ridges to the onset of spikelet differentiation, among X969-3, 68-105-9, 68-105-17 and the other genotypes. This delay allows for a larger sized meristem to form. An extra surface is provided for the development of additional whorls of seeds given the number of tillers they produce per unit area. Lee *et al*. (1974), Williams (1975) and Blum (1977) found that a delayed and larger basal branch at the time of spikelet initiation allowed for the formation of more spikelets, florets and grains in sorghum. Although the development of the meristem is delayed in the three genotypes, the difference in time is compensated for by having greater rate of development once the full set of floral primordia is established. Equivalent heading dates are realized. Whyte (1979) suspected that the larger reproductive apex at the initiation of elongation in X969-3 and the progeny lines with similar behavior could be traced back to the larger vegetative apex. In effect the gain in the number of seeds per head may be established in the first developmental phase with all the physiological and practical implications.

The path coefficients between the meristematic characteristics at the reproductive state of growth with the number of seeds per head and the average seed weight confirm the above consideration (Figure A1). The width of the apical meristem has its greatest influence on its length and number of heads per unit area. Its relationship to length (L) and number of heads per unit area (X) are, respectively, positive and negative. Both length and relative growth rate (R) are, however, positive determinants of X. Width of the meristem (WD) has a positive influence on the number of seeds per head (Y) while R, L and WD have negative influence on Y. Y, L, R and WD are all negatively related to seed weight (Z). X, Y and L are, however, more important determinants of Z relative to R and WD.

The analysis of variance of the number of heads per unit area, number of seeds per head and head size using the maximum length, maximum width and the relative growth rate at the reproductive state of development show that a significant portion of the variation in the dependent variables can be accounted for by the variation in the three components. The coefficient of determination for X, Y and YZ are .5959, .7156 and .7912, respectively. As stated earlier, the salient feature of the multiple regression statistics show that the higher the number of tillers produced by a genotype, the smaller will be the width of the meristems produced, however, the relative growth rate of meristem will be higher. Number of seeds borne per head will be small since width has a positive correlation with Y.

From the above, one can deduce that a genotype with a low growth rate produces a lower number of heads per unit area. A further relaxation of growth rate encourages the formation of organs (i.e., meristems) with larger width. Since the width determines the length that the organ assumes, an apical meristem with a large surface area is produced. A higher number of floral initials are borne resulting in the production of a higher number of seeds per head and eventually, a bigger sized head. This confirms the fact that sizes and numbers of plant organs are negatively correlated (Grafius, 1978).

Leopold (1949) contended that the relationship between the size of meristems and plant organs could be modified by changing the internal hormonal content. This led to research into attempts to change plant characteristics and hopefully, yield through hormonal application. The applications were done without much regard to the time best suited for its effectiveness. There were applications through seed soaking, spraying at one leaf stage and at bolting, to mention but a few. Often a few genotypes without varying yield components, if ever considered, were used resulting in inconsistent results.

Much is realized when one considers the effects that hormones have on the characteristics of meristems, the determinants of organ size and numbers, when the applications are done at the right stage, given the objective of the study. Whyte (1979) showed that about 52% and 65% of variation in X and Y, respectively, could be accounted for by the variation in length, width and the relative growth rate of the primary apical meristem at the reproductive state of development. A similar determination is presented in the data (60%, 71% and 79% of the variation in X, Y and YZ, respectively, is accounted for by the same independent variables).

The application of GA_3, CCC, Kinetin and IAA induced changes in both the maximum width and maximum length of the primary apical meristem at the reproduction stage of development. The magnitude of these changes depended on the type of hormone applied and the genotype under consideration. Basically, length measurements were changed to a greater extent than the width measurements. GA_3 induced the greatest changes in the length, followed in decreasing order by CCC, Kinetin and IAA. The length of meristems of the genotypes with the least and highest X were increased while those of the genotypes with medium X were decreased in all the treatments. Only the least and highest tillering genotypes had significant width increases with the GA_3 and CCC application. Kinetin and IAA however, were more general in their induction of width changes among the genotypes. The differences in reaction of the meristems to the applied hormones is expected because at the stage of development when the applications were carried out, the maximum width of the genotype was about attained leaving only the length to be subjected to greater changes.

Let us consider the meristem as the initial point at which seedlings react to applied hormones. Since length is more prone to change, any disturbance in the internal equilibrium will be observed in the length changes, graphically shown as a wave pattern.

This relationship is shown by changes in length of the apical meristem due to disturbances caused by the applications of GA_3, CCC, Kinetine and IAA. The establishment of these wave patterns show that the promotive hormones are present in equilibrium with each other for normal growth and development of the plant. Gibberellin has been documented as being the hormone involved in the increase in length of barley meristem in the reproduction state. This is not necessarily the totality since it is now being shown that the other two promotive hormones are involved in the growth and developmental processes. Any disturbance in the hormonal equilibrium results in a series of changes which is ultimately expressed in either an increase or a decrease in the size (length) of the meristem. One is cautioned to think that only the promotive hormones regulate growth and development of the meristem, but that the inhibitory hormones also play a large role in the regulatory processes. Gibberellin, however, induces its effect on a wider range of genotypes followed, in a decreasing order, by cycocel, cytokinin and auxin. The largest length reduction was observed with 68-103-8 in all the treatments, however, the largest length increase varied between 68-104-3 and 60-215-6, depending on the treatment. The effectiveness of utilizing any of the promotive hormones for inducing changes in the meristem of a genotype is thus dependent on the genotype and the hormone in question. The stage of development at which application is done is very critical because induction of activity of the genetic constituents does not occur haphazardly, but in an orderly fashion coupled with the short range of time during which hormones act.

Some changes were observed in the outliers but because of the insignificant differences in the number of heads they produce per unit area, I am bound to view the changes as genotype-specific.

Yield changes were observed as a result of application of the promotive hormones. The changes were due to the changes in meristematic sizes. Even though the meristematic changes followed some wave pattern, not all the changes in the yield components and yield followed the same trend. However, the type of change also depended on the hormone applied and the genotype in consideration.

The change in yield due to GA_3 application decreased with increasing tillering. A clear case of component compensation is shown in changes observed in the number of heads per unit area and the number of seeds per head. Genotypes with the least and high number of heads per unit area had the greatest changes in X while the genotypes producing medium number of heads per unit area were more prone to changing their head size. Changes in the average seed weight was generally between +5 and -5%.

CCC induced yield changes followed a similar trend as that of the GA_3 application, however, these changes are not consistent. B130 and Dickson had the greatest change in X while the other genotypes had virtually no change. Most of the changes in yield of the medium tiller producing genotypes came from changes in the number of seeds per head. The high tillering genotypes had no change in both X and Y.

Yield changes with cytokinin application were not consistent with any trend, however, changes in X were obtained with the high and low tillering genotypes while the medium tillering genotypes had virtually no changes. 60-215-6 decreased its tillering and increase its head size.

With IAA application, there was an initial increase in yield changes to a maximum (with 68-103-8) followed by reductions with increasing tillering. 60-215-6, the highest tillering genotype used in the study, had the greatest yield reduction. The yield changes were due to changes in Y, primarily. The changes induced with IAA application are similar to that induced with CCC with a slight difference. The major change in the yield were due to changes in Y, however with auxin application, slight changes in X were obtained in addition.

The length and width of the meristem were used as independent variables in multiple regression analyses involving X, Y, Z, XY, YZ and W as dependent variable for each of the treatments. None of the predictions involving the gibberellin application were significant. This is due to the lack of change in the width measurements in comparison with the other treatments. Width has been shown to be a more important component in the prediction of the yield components.

One of the objectives of the study was to change the number of seeds per head keeping the level of number of heads per unit area constant. In addition to changing Y, changes in X were observed in the data presented. These changes were found to be negatively correlated, however, the magnitude of the relationship is relaxed with the CCC and IAA application.

The above observation raises the question whether the significant negative correlation between X and Y is due to the number of tillers associated with the system or X causes such a relationship to arise. As it is generally known, there is an initial well-developed shoot with 3 or 4 leaf initials and an apical dome enclosed within the coleoptile of a mature seed. As the plant grows, a succession of primordia are initiated, which later differentiate an elongated internode and/or a tiller bud. The tillers and main shoot later differentiate floral parts.

This led to the proposition of the sequential developmental processes by Grafius (1969). Technically, one sees no flaw with this reasoning, however, we have to caution ourselves and critically examine the relationship.

Consider the flow chart shown in Figure 29. The primary meristem differentiates a tiller bud which grows into a tiller and later differentiates floral parts. The question to ask at this point is when is the head size (number of florets per head) really established? Two obvious answers arise from the diagram.

1. At the point of differentiation of the tiller meristem.
2. At a later developmental stage of growth.

The later answer is bound to be the dominant one because signs of differentiation are depicted. The first answer is favored for the following reasons:

1. Developmental ontogeny has both a space and time reference and events arising from a common primary origin can be removed in time and thus experience some relaxation of the correlation as shown by Fowler and Rasmusson (1969). The correlation between the area of leaves on the same culm of barley diminished as the distance between leaves (both in space and time of origin) increased. Attempts would have been futile to select for different leaf sizes on the

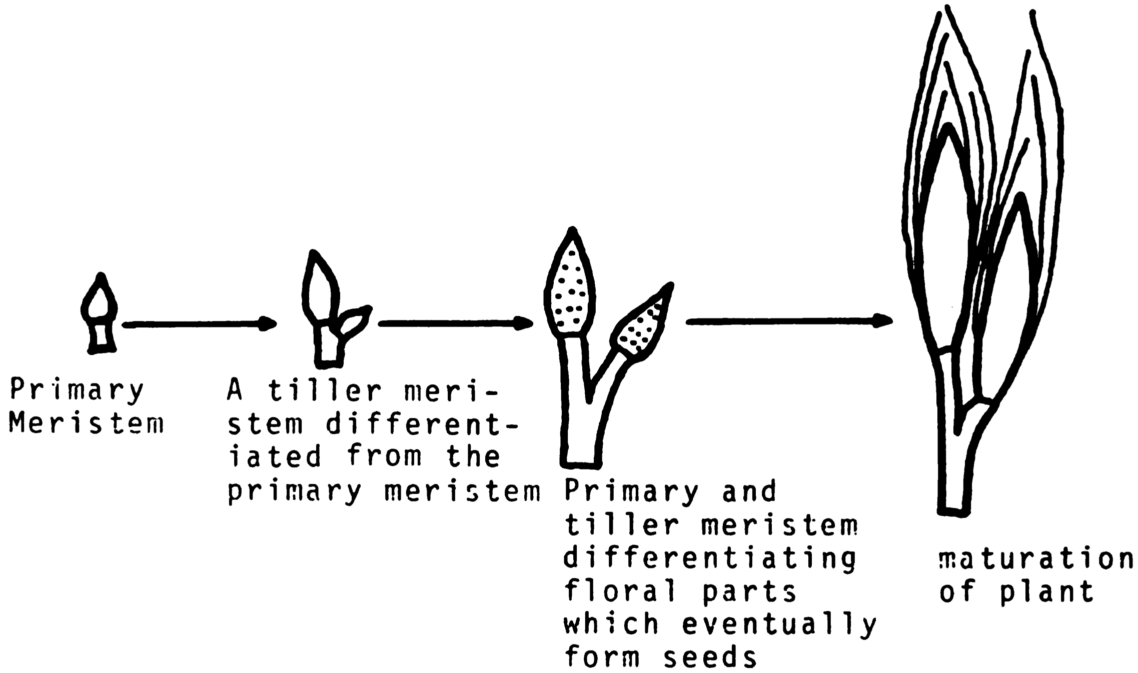


Figure 29. Diagrammatic representation of sequence of events during the growth and development of the apical meristems.

same culm. This is so because they arise from the same meristem and changing one factor leads to a similar change in another factor in close proximity because of the high positive correlation. 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. One can accept not coming across any literature on the relationship between individual tillers and their respective head sizes but one can reason through the leaf area work quoted above that a similar situation is bound to occur between X and Y. The primary and tiller meristems differentiate the floral parts and as a result changing either X or Y will tend to change Y or X in the reverse manner. Breeders are unable to use X or Y as a breeding objective since they arise from the same meristem and any determination to increase one yield component (either X or Y) will be accompanied by a decrease in the other component (i.e. Y or X). On the other hand, seed weight does not present similar problems since developmentally, it is farther removed in both space and time from the common origin of the primary apical meristem; additionally, they arise from different meristems.

2. The hormonal applications were done with the objective of changing Y, however, changes in X were also observed. The observed changes were negatively correlated. Z was not affected by the changes in X and Y.

3. The influence of the length, width and relative growth rate of the meristem on X and Y are almost the same showing that the number of heads per unit area and the number of seeds per head have a common origin at the meristematic level.

4. The magnitude of the paths between X and Y with Z are almost the same but with different signs. This is

interpretted as the result of the initial significant negative relationship established between X and Y.

5. This further reinforces my prediction (Whyte, 1979) that the larger reproductive apex at the initiation of elongation could be traced back to a larger vegetative apex and that any gain in the number of seeds per head may be established in the first developmental phase with all the physiological and practical implications.

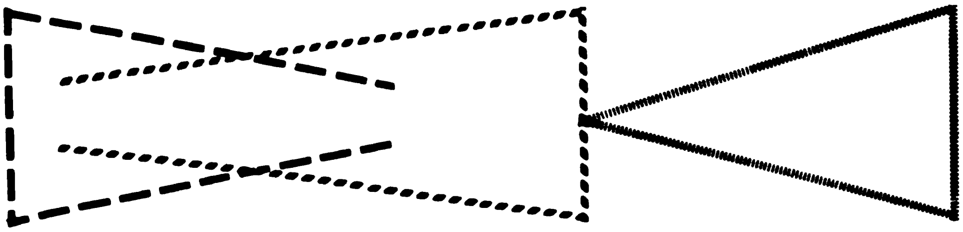
6. The relative efficiencies for the production of X and Y were similar while that for Z production varied as will be shown in Chapter 2.

In no way is competition for nutrients discounted. It strengthens the relationship between X and Y.

On the basis of the foregoing findings and reasonings, we may reconceptualize, diagrammatically, the sequential developmental process of yield components as shown in Figure 30.

There has been some assertion that the sequence of yield component formation overlap (Tai, 1975) but the magnitude of this overlapping is traditionally thought to be minimal.

A 95% confidence belt around the regression of Y on X for the control block (Fig. 31) show that the hormonal application induced certain changes in some standard



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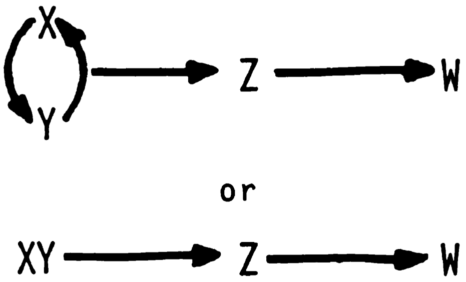

Figure 30. Diagrammatic representation of the sequential development of the yield components and yield of barley.

varieties rendering them outliers. An 'outlier' is defined as any genotype which does not fall within the 95% confidence belt (variance of a predicted value) established around the regression of Y on X for the control block (Fig. A2). No single hormone induced changes great enough to render all the genotypes as outliers. The yield component changes varied among the genotypes which, by the definition, could be described as outliers. Drastic positive changes in X were attained in B130 with GA_3 and CCC treatments with virtually no change in Y. 68-103-8 (GA_3 and CCC treatments), 68-103-18(CCC treatment) changed basically their number of seeds per unit area while B130 and 68-104-19 (IAA treatment) changed both their X and Y before attaining the outlier status.

SUMMARY AND CONCLUSION

The present investigation was undertaken to assess the involvement of the promotive hormones in the development of the primary shoot apical meristem in relation with the production of the yield components and yield of barley.

The results showed that the outliers reached the transition stage four days in advance of the standard varieties, however, the elongation of their meristems were delayed by four days. The sizes of the meristems of the outliers were larger than those for the standard genotypes. A switch in the rate of development was observed in the growth of meristems. Genotypes with higher rate of growth at the transition stage had a lower growth rate after the reproduction stage of development.

The coefficient of determination (R^2 = .5959, .7156 and .7912 for X, Y and YZ, respectively) indicate that the variance in the dependent variables X, Y and YZ, can be accounted for in large part by variation in the meristematic measurements used as the independent variables in the multiple regression analyses performed.

Thus, it was thought that a genotype with a low growth rate at the reproduction stage of development produced a low number of heads per unit area. Further relaxation of the growth rate encouraged the formation of organs, i.e., meristems with larger width. Since width determined the length that the organ assumed, a larger sized meristem is obtained. A higher number whorls of floral initials are borne on the meristem resulting in the production of a higher number of seeds per head and a bigger head size.

The determination of the endogenous promotive hormone levels and activities was not successful due to the inadequate amount of sample available and the insensitivity of the method applied.

Application of GA_3, CCC, Kinetin and IAA induced changes in both the length and width of the primary apical meristems at the reproduction stage of development. The lengths were changed to a larger extent than the width, however, the magnitude of these changes depended on the type of hormone applied and the genotype in question.

Wave patterns were shown by the histograms of percentage change over control for lengths of the primary shoot apical meristem vrs. genotypes arranged in the order of increasing number of heads per unit area in all treatments. This indicated that the promotive hormones are in equilibrium with each other for normal growth and development of the plant. The involvement of the inhibitory hormones was not discounted. The wave pattern was observed more in the changes in lengths of the apical meristems. This was expected because at the stage of development when the applications were carried out, the maximum width of the genotype was about attained leaving only the length to be subjected to greater changes caused by the disturbances created in the internal equilibrium.

Yield changes were observed as a result of application of the promotive hormones. These changes were due to changes in the sizes of the meristems. Even though the meristematic changes followed some wave pattern, not all the changes in the yield components and yield followed the same trend. The type of change also depended on the hormone applied and the genotype under consideration. Changes in X or Y or both were induced in some standard genotypes to render them 'outliers'. No single hormone induced changes great enough to render all the genotypes as outliers. Width was found to be the most important of the meristematic measurements in the prediction of the yield components and yield.

An interesting finding was the significant negative correlations between the changes in the number of heads per unit area and the changes in the number of seeds per head in all the treatments. The intent here was to increase the number of seeds per head keeping the number of heads per unit area constant. Removing the outliers tended to show an effect of relaxation between changes in X and Y in the CCC and IAA treatments.

All the above findings prompted the raising of the question as to whether the significant negative correlation between X and Y is due to the number of fertile tillers associated with the system of growth and development or X causes such a relationship to arise as it is traditionally observed. Evidence in favor of the negative correlation between X and Y arising from the number of fertile tillers associated with the system of growth and development was advanced. This led to the proposition of reconceptualization of the sequential developmental process of the yield components and yield.

APPENDICES

Table A1. Mean percentage change over control for yield (ΔW), number of seeds per unit area (ΔXY), head size (ΔYZ), number of heads per unit area (ΔX), number of seeds per head (ΔY), seed weight (ΔZ), height (ΔHT) and heading (ΔHD) of barley due to gibberellin application at the transition stage of development.

GENOTYPES	ΔW	ΔXY	ΔYZ	ΔX	ΔY	ΔZ	ΔHT	ΔHD
BOWERS	10.51	8.61	5.92	4.56	4.54	1.38	1.33	-7.41
X969-3	10.36	7.19	13.90	-4.67	10.73	2.40	-6.41	-4.35
B130	16.21	15.96	2.11	14.14	1.45	.56	-6.29	-2.91
60-215-6	- 3.56	3.56	-11.56	5.94	- 5.90	-6.80	-5.22	-6.12
DICKSON	18.06	12.66	- 4.45	23.08	- 8.69	4.65	-9.15	-1.82
LARKER	8.95	1.97	4.79	4.13	- 2.04	6.92	-5.63	-3.88
68-105-9	6.14	-5.07	11.49	-3.17	- .97	12.56	-7.50	-5.10
68-105-17	4.04	3.91	9.97	-5.49	1.70	8.12	-1.95	-4.76
68-104-3	6.89	1.50	- 5.18	12.48	- 9.90	5.07	-7.19	-3.96
68-104-19	4.90	2.43	8.98	-3.96	5.82	2.75	-1.85	-4.00
68-103-8	8.89	7.75	7.71	1.98	7.21	.95	-3.59	-3.88
68-103-18	15.19	9.03	11.64	3.68	5.77	5.78	-5.70	-6.25
LSD (α=.05)	11.81	11.36	10.90	14.47	12.63	7.38	4.71	1.96
LSD (α=.01)	15.55	14.95	14.34	19.04	16.62	9.71	6.20	2.58

Table A2. Mean percentage change over control for yield (ΔW), number of seeds per unit area (ΔXY), head size (ΔYZ), number of heads per unit area (ΔX), number of seeds per head (ΔY), seed weight (ΔZ), height (ΔHT) and heading (ΔHD) of barley due to cycocel application at the transition stage of development.

GENOTYPE	ΔW	ΔXY	ΔYZ	ΔX	ΔY	ΔZ	ΔHT	ΔHD
BOWERS	11.77	14.32	4.19	7.18	6.57	-2.28	2.00	- .93
X969-3	15.91	14.91	14.74	- .43	13.91	.40	-1.28	0
B130	17.64	20.40	- .86	19.00	1.38	-2.10	-3.77	.97
60-215-6	7.47	7.76	6.30	-1.72	5.65	- .28	-3.48	6.12
DICKSON	9.57	1.89	2.48	6.57	-4.64	7.45	0	-1.82
LARKER	7.79	14.41	4.09	3.75	10.93	-5.90	-1.88	.97
68-105-9	5.88	2.31	12.00	-5.31	8.07	3.89	-3.75	-2.04
68-105-17	10.09	8.64	17.16	-5.32	16.20	.96	-3.25	0
68-104-3	3.11	1.62	2.97	- .67	1.42	1.24	-1.80	- .99
68-104-19	- .92	3.21	2.90	-3.59	6.96	-3.65	0	1.00
68-103-8	3.53	6.04	2.79	.74	5.68	-2.75	0	.97
68-103-18	18.81	20.54	19.66	- .08	21.32	-1.20	-2.53	0
LSD (α=.05)	11.81	11.36	10.90	14.47	12.63	7.38	4.71	1.96
LSD (α=.01)	15.55	14.95	14.34	19.04	16.62	9.71	6.20	2.58

Table A3. Mean percentage change over control for yield (ΔW), number of seeds per unit area (ΔXY), head size (ΔYZ), number of heads per unit area (ΔX), number of seeds per head (ΔY), seed weight (ΔZ), height (ΔHT) and heading (ΔHD) of barley due to cytokinin application at the transition stage of development.

	ΔW	ΔXY	ΔYZ	ΔX	ΔY	ΔZ	ΔHT	ΔHD
BOWERS	6.38	5.91	-3.95	10.46	-4.46	.61	0	0
X969-3	2.28	.42	12.08	-10.01	10.11	1.32	.64	-1.09
B130	11.44	7.35	-1.36	13.50	-5.22	4.57	-2.52	2.91
60-215-6	-3.20	-2.55	5.94	-11.34	5.44	- .08	1.74	6.12
DICKSON	11.72	4.01	1.03	10.92	-6.05	7.29	- .65	-1.82
LARKER	6.77	.60	7.26	- .07	.79	6.26	-3.13	- .97
68-105-9	2.16	- .33	-3.49	6.23	-6.29	3.07	-1.88	-2.04
68-105-17	-3.56	.45	-2.17	- .99	2.21	-4.20	0	.95
68-104-3	6.93	2.97	-2.27	8.41	-6.03	3.64	-1.80	- .99
68-104-19	3.02	3.02	.02	2.45	- .78	.56	.62	1.00
68-103-8	4.20	- .02	5.50	- .84	1.34	4.23	-2.40	0
68-103-18	15.19	15.58	7.93	7.16	8.17	- .21	- .63	1.04
LSD (α=.05)	11.81	11.36	10.90	14.47	12.63	7.38	4.71	1.96
LSD (α=.01)	15.55	14.95	14.34	19.04	16.62	9.71	6.20	2.58

Table A4. Mean percentage change over control for yield (ΔW), number of seeds per unit area (ΔXY), head size (ΔYZ), number of heads per unit area (ΔX), number of seeds per head (ΔY), seed weight (ΔZ), height (ΔHT) and heading (ΔHD) of barley due to auxin application at the transition stage of development.

	ΔW	ΔXY	ΔYZ	ΔX	ΔY	ΔZ	ΔHT	ΔHD
BOWERS	- 7.08	-4.70	-7.06	.45	-4.23	- 2.78	1.33	0
X969-3	- 1.31	5.90	10.19	-11.48	18.12	- 7.12	2.56	-1.36
B130	8.63	15.85	4.80	3.65	11.42	- 6.02	1.89	1.94
60-215-6	-16.75	-5.31	-13.25	- 6.75	-2.12	-12.10	1.74	6.12
DICKSON	- 2.49	-3.34	- 4.66	1.98	-5.41	.65	- .65	-1.82
LARKER	2.92	3.48	4.01	- 1.18	4.66	- .51	0	2.91
68-105-9	3.22	3.76	9.45	- 5.25	9.69	- .20	0	-1.02
68-105-17	- 1.70	2.06	6.69	- 7.69	10.98	- 3.79	- .65	1.90
68-104-3	- 4.41	-4.50	- 7.03	1.97	-6.94	.66	0	- .99
68-104-19	.09	8.84	- 4.77	4.69	2.96	- 7.80	3.70	0
68-103-8	1.03	2.14	4.36	- 3.19	5.51	- 1.09	2.40	.97
68-103-18	14.17	11.94	13.20	2.18	11.73	2.07	- .63	-1.04
LSD (α=.05)	11.81	11.36	10.90	14.47	12.63	7.38	4.71	1.96
LSD (α=.01)	15.55	14.95	14.34	19.04	16.62	9.71	6.20	2.58

Table A5. Multiple regression statistics for the number of heads per unit area (ΔX), number of seeds per head (ΔY), head size (ΔYZ) and yield (ΔW), each as a dependent variable on the maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development as the independent variables. The statistics are in the order of X, Y, YZ and W, respectively (Control Block).

Variable	Partial Regression Coefficient	Beta Weights	Significant Level	Partial Correlation Coefficient	R^2 deletes
L	-2.768	-.365	.283	-.355	.387
	4.076	.238	.448	.256	.499
	.125	.229	.367	.302	.666
	1.438	.018	.954	.020	.529
WD	-8.317	-.385	.260	-.372	.378
	26.938	.552	.098	.523	.355
	1.037	.668	.022	.679	.438
	164.116	.716	.041	.622	.232

Table A6. Multiple regression statistics for the number of seeds per head (Y), number of seeds per unit area (XY), head size (YZ) and yield (W), each as a dependent variable on the maximum length (L) and maximum width of the primary apical meristem of barley in the reproduction state of development as the independent variables. The statistics are in the order of Y, XY, YZ and W, respectively (cycocel block).

Variable	Partial Regression Coefficient	Beta Weights	Significant Level	Partial Correlation Coefficient	R^2 deletes
L	- 9.658	-.394	.367	-.302	.560
	-157.419	-.647	.111	-.500	.568
	- .345	-.461	.290	-.351	.555
	- 97.508	-.821	.041	-.623	.550
WD	69.216	1.088	.028	.658	.295
	828.019	1.311	.007	.760	.232
	2.220	1.412	.021	.681	.273
	446.730	1.449	.002	.814	.182

Table A7. Multiple regression statistics for the number of seeds per head (Y), number of seeds per unit area (XY) and yield (W), each as a dependent variable on the maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development as the independent variables. The statistics are in the order of Y,XY and W, respectively (cytokinin block).

Variable	Partial Regression Coefficient	Beta Weights	Significant Level	Partial Correlation Coefficient	R^2 deletes
L	4.284	.158	.641	.159	.435
	99.237	.368	.152	.462	.639
	49.604	.400	.228	.396	.421
WD	33.811	.555	.125	.491	.274
	338.257	.558	.042	.620	.540
	107.726	.386	.243	.384	.427

Table A8. Multiple regression statistics for the number of heads per unit area (X), number of seeds per head (Y), number of seeds per unit area (XY), head size (YZ) and yield (W), each as a dependent variable, on the maximum length (L) and maximum width (WD) of the primary apical meristem of barley in the reproduction state of development as the independent variables. The statistics are in order of X, Y, XY, YZ, and W, respectively (auxin block).

Variable	Partial Regression Coefficient	Beta Weights	Significant Level	Partial Correlation Coefficient	R^2 deletes
L	- 2.817	-.334	.396	-.285	.493
	11.235	.423	.074	.559	.789
	161.359	.610	.070	.566	.572
	.283	.360	.154	.461	.776
	61.062	.453	.224	.399	.526
WD	- 9.609	-.436	.274	-.362	.464
	38.251	.552	.027	.660	.743
	187.819	.272	.383	.292	.682
	1.224	.595	.030	.612	.693
	128.668	.365	.320	.331	.552

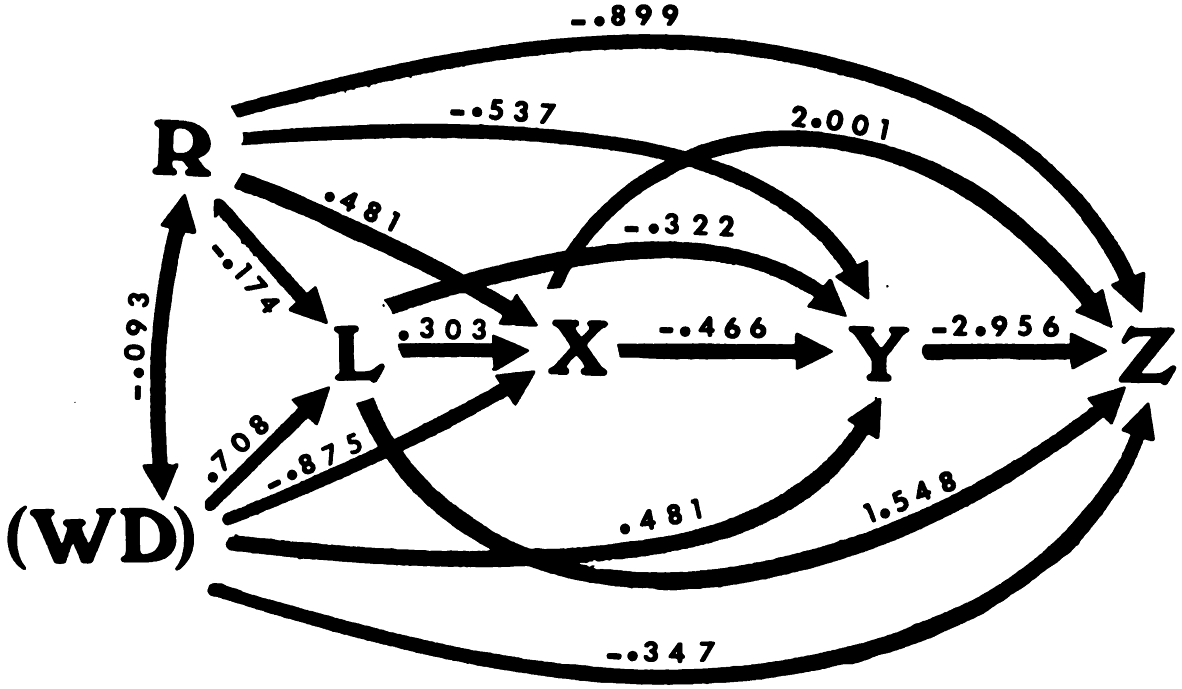

Figure A1 Developmental allometry showing the influence of the primary apical meristem of barley in the reproduction state of development on the yield components: number of heads per unit area (X), number of seeds per head (Y), seed weight (Z); width (WD), length (L) and relative growth rate (R) of the primary apical meristem. Single arrowed lines denote path coefficients and double arrowed lines denote correlation coefficients.

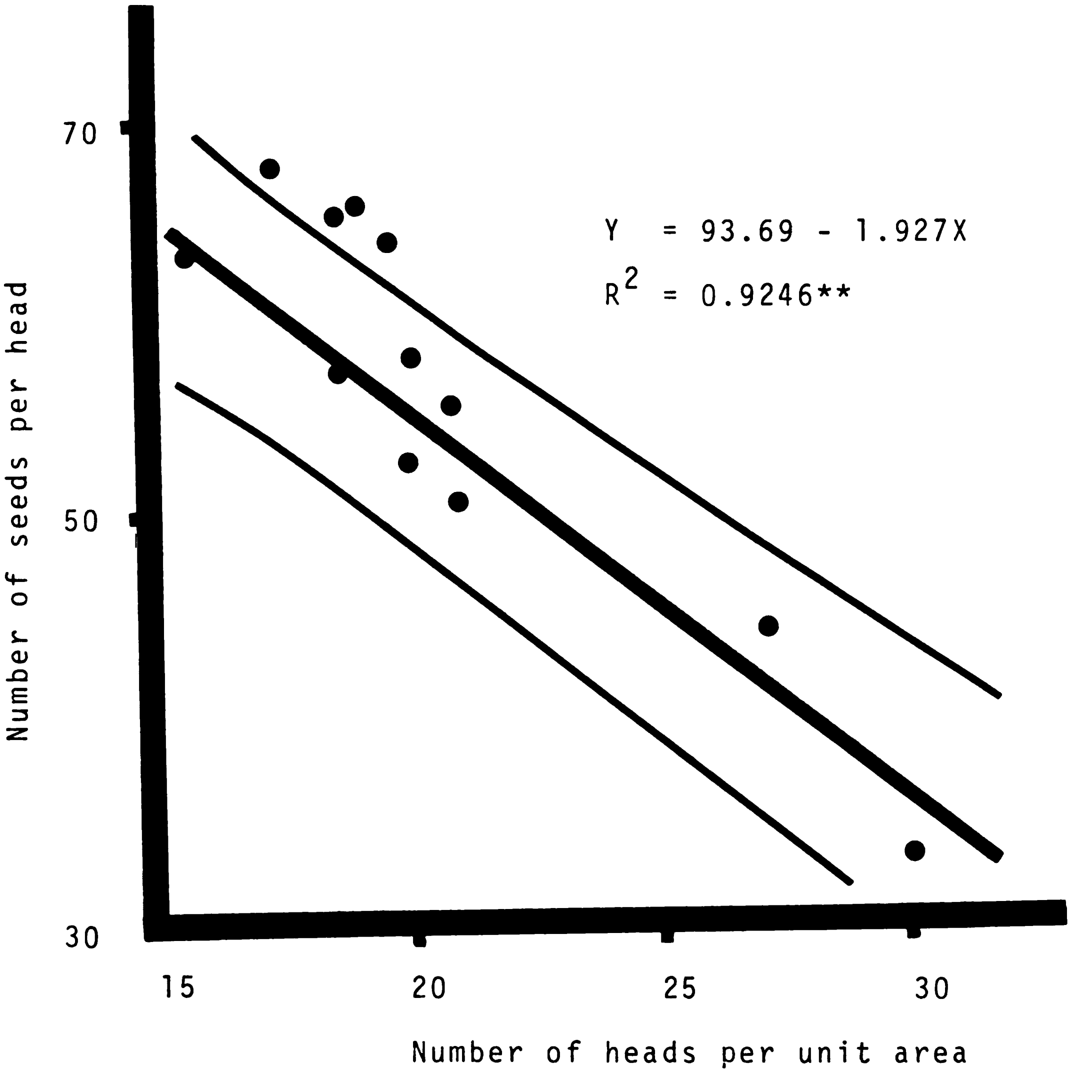

Figure A2. Regression of the number of seeds per head on the number of heads per unit area (control block) with its 95% confidence belt (variance of a predicted value).

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CHAPTER 2

A MATHEMATICAL MODEL FOR YIELD

INTRODUCTION

Performance of different genotypes vary in different environments because of the existence of genotype-environment interactions. The relationship between the performance of different genotypes in various environments and some measure of these environments is frequently linear or nearly so (Finlay and Wilkinson, 1963; Perkins and Jinks, 1968; Breese, 1969; Baker, 1969).

Some articles are available which review and compare different methods of genotype-environment analysis (Freeman, 1973; Moll and Stuber, 1974; Hill, 1975). Different methods have been proposed to measure the stability of genotypes tested over a range of environments. These include multivariate statistical analysis (Freeman, 1973; Hill, 1975), principal component analysis (Perkins, 1972) pattern analysis (Byth *et al*., 1976), cluster analysis (Lin and Thompson, 1975) sequential developmental analysis (Tai, 1975, 1979; Nelson, 1981) and independent measures of environmental factors (Fripp, 1972; Perkins, 1972; Wood, 1976). Much attention is drawn to the factors which contribute to the interaction of the genotype with the environment.

Using the concept of sequential development of yield components (Grafius, 1969; Grafius and Thomas, 1971; Thomas *et al*., 1971a, b, c), the developmental allometry (Hamid and Grafius, 1978) in cereal crops, and the proposition that yield components of cereal crops are determined at different stages in the ontogeny of plants (Rasmusson and Cannell, 1970), Tai (1975, 1979) and Nelson (1981) proposed a yield equation expressed in standard deviation units. Tai's (1975) equation is composed of a mean genotype effect, three multiplicative terms of the genotype-environment interaction and an error deviate. The three interaction factors are composed of three genotypic components, each representing the efficiency of a genotype to utilize a standard deviation unit input, in one of the three environmental components towards the formation of the final yield. Nelson (1981) proposed a modification of Tai's equation by substituting the grand mean and grand standard deviation (over genotypes and year sites) for Tai's genotype-specific values. He, however, used the same type of calculations to arrive at a similar yield equation. Some erroneous reasoning is presented in the equations so I intend to propose a new mathematical model for yield, still based on the concept of sequential development of yield components, in addition to the regression method of determining genotype-environment interaction.

THEORETICAL CONSIDERATION

The justification for this model is to offer a modified form of the models proposed by Tai (1975, 1979) and Nelson (1981). Use is made of the regression and path coefficient analytical methods for determining the genotype-environment interaction.

The environmental resource is still assumed hypothetically to be separable into three independent groups, each used during the formation of one each of the yield components. The cause-effect diagram for the developmental ontogeny of cereal crop plants (Nelson, 1981) is presented in Figure 1. The method of path coefficient analysis (Wright 1921, 1934) is applied to the diagram to determine the relationship between the three groups of resources and yield.

Let ρXY, ρXZ, ρXW, ρYW, and ρZW be the correlation coefficients between the yield components and yield and a_1, a_2, a_3, a_4, a_5, and a_6 be their corresponding path coefficients. Equating the two coefficients, we get:

$$\rho_{XY} = a_1$$

$$\rho_{XZ} = a_2 + a_1 a_3$$

$$\rho_{YZ} = a_3 + a_1 a_2$$

$$\rho_{XW} = a_4 + a_1 a_5 + a_2 a_6 + a_1 a_3 a_6$$

$$\rho_{YW} = a_5 + a_1 a_4 + a_3 a_6 + a_1 a_2 a_6$$

$$\rho_{ZW} = a_6 + a_2 a_4 + a_3 a_5 + a_1 a_3 a_4 + a_1 a_2 a_5 \quad \text{......(1)}$$

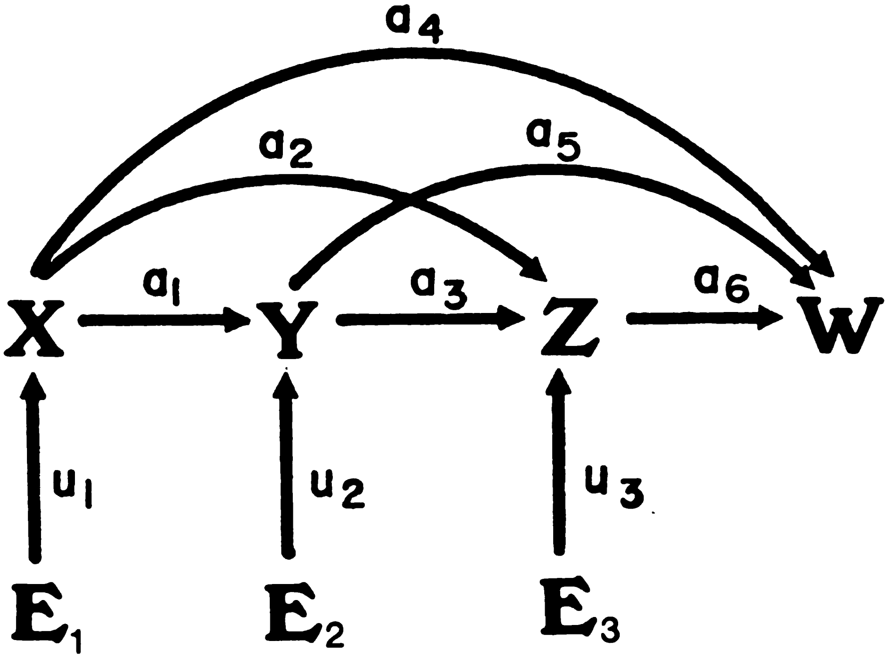


Figure 1. A causation diagram showing the developmental relationships between yield and the yield components: yield (W), number of heads per unit area (X), number of seeds per head (Y) and average seed weight (Z). The lower case letters on the various single-arrow paths are path coefficients. E_1, E_2 and E_3 indicate the independent groups of environmental resources.

The six path coefficients can be obtained by solving the simultaneous equations. The path coefficients from E_1, E_2 and E_3 to X, Y and Z, respectively, can be determined using the regression analysis proposed by Finlay and Wilkinson (1963), Breese (1969) and Baker (1969).

Suppose the performance of m genotypes is measured in n environments then the number of heads per unit area X_{ijk} of the kth replicate of the ith genotype in the jth environment can be represented by:

$$X_{ijk} = \mu + g_i + e_j + d_{ij} + \varepsilon_{ijk} \text{ ....(2)}$$

where

μ = the overall mean

g_i = the mean effect of the ith genotype

e_j = the mean effect of the jth environment

d_{ij} = the effect due to the interaction of the ith genotype in the jth environment.

ε_{ijk} = normal random variable, mean 0, variance $\sigma 2$.

A mixed model is assumed with a fixed number of genotypes and a random sample of environments with r replication.

In calculating the regression of X's of the separate genotypes on the mean number of heads of all the genotypes, the d_{ij} in equation 2 is regressed on e_j thus;

$$d_{ij} = \beta_i e_j + \partial_{ij} \text{ .... (3)}$$

Where β_i is the linear regression coefficient for the ith genotype and ∂_{ij} is a deviation.

Using equation 3, equation 2 can be rewritten as

$$X_{ijk} = \mu + g_i + (1 + \beta_i)e_j + \partial_{ij} + \varepsilon_{ijk} \text{ ......} \quad (4)$$

The analysis of variance for the above equation is given in Table 1.

Using the EMS_2, each of the genotype-environment interaction terms can be compared with the residual experimental error, and the heterogeneity of regression further compared with the deviations. This is to determine whether the regression accounts for a significantly large part of the observed interaction, a procedure similar to the joint regression analysis procedure.

A modification of Tai's (1975, 1979) and Nelson's (1981) procedures for determination of the paths between the independent environments and the yield components is presented.

If one wishes to measure the amount of impact of one variable on another, a standardized coefficient will serve the purpose because the method of path coefficients is essentially based on the degree of determination of the variance of the dependent variable by others (Li, 1975).

Let σ_p^2 be the variance in X of the genotypes within all the environments

and σ_E^2 the environmental variance for X

Then, $\dfrac{\sigma_E^2}{\sigma_p^2} =$ proportion of population variance contributed by the environment.

Table 1. Analysis of variance table for two-factor mixed model study.

Source	df	SS	EMS$_1$(Genotype measured by $\bar{x}$)	EMS$_2$(Genotype measured by $\bar{x} \div \beta e$*)
Genotype	m-1	$\sum_{i} X_{i..}^2/rn - \sum X_{...}^2/rnm$	$\sigma^2 + r\sigma^2 GE + rm\sigma^2_G$	$\sigma^2 + r\sigma^2_d + rm\sigma^2_a$
Environment	n-1	$\sum_{j} X_{.j.}^2/rm - \sum X_{...}^2/rnm$	$\sigma^2 + rm\sigma^2_E$	$\sigma^2 + rm\sigma^2_E$
Genotype x Environment	(m-1)(n-1)	$\sum_{i}\sum_{j} X_{ij.}^2/r - \sum_{i} X_{i..}^2/rn$ $- \sum X_{.j.}^2/rm + \sum X_{...}^2/rnm$	$\sigma^2 + r\sigma^2_{GE}$	
Heterogeneity (b)	m-1			$\sigma^2 + r\sigma^2_d + rn\sigma^2_b$
Dev. from regression(d)	(m-1)(n-2)			$\sigma^2 + r\sigma^2_d$
Error	mn(r-1)	$\sum_{ijk}\sum\sum X_{ijk}^2 - \sum\sum_{ij.}^2/r$ $\sum_{ijk}\sum\sum X_{ijk}^2 - \sum X_{...}^2/rmn$	σ^2	σ^2

*$\bar{x}$ = population mean, βe = linear regression on environmental measure. The convention will be adopted where $X_{ij.}$ refers to a total over the suffix replaced by a dot.

This measures the square of the path from E_1 to X.

Thus, $$\frac{\sigma_E^2}{\sigma_p^2} = U_1^2$$

$$U_1 = \left[\frac{\sigma_E^2}{\sigma_p^2}\right]^{\frac{1}{2}} \quad \ldots\ldots\ldots\ldots\ldots(5)$$

The mode of production of the yield components as presented in the earlier chapter allow similar analyses to be used to determine the path coefficients between E_2 and E_3 to Y and Z, respectively. Removing the effects of variation of component traits appearing earlier in the developmental sequence to yield, as presented by Thomas et al. (1971a) is not critical.

If W_1, r_1, r_2 and r_3 represent yield and the three independent groups of environmental resources measured in standard deviation units, a relationship is obtained;

$$W = V_1'r_1 + V_2'r_2 + V_3'r_3 + e$$

in which V_1', V_2' and V_3' are the path coefficients from E_1, E_2 and E_3 to yield (W), respectively, and e is the residual effect. The three path coefficients can be solved as follows:

$$V_1' = U_1\ (a_4 + a_1a_5 + a_2a_6 + a_1a_3a_6) = U_1\rho_{(XW)}$$

$$V_2' = U_2(a_3a_6 + a_5)$$

$$V_3' = U_3a_6 \quad \ldots\ldots\ldots\ldots (6)$$

In testing m genotypes over n environments, the yield of the ith genotype in the jth environment can be expressed generally as follows;

$$\frac{W_{ij} - W_{..}}{\sigma_{W..}} = a + \frac{X_{ij} - X_{i.}}{\sigma_{Xi.}} V'_{1i} r_{1j} + \frac{Y_{ij} - Y_{i.}}{\sigma_{Yi.}} V'_{2i} r_{2j} + \frac{Z_{ij} - Z_{i.}}{\sigma_{zi.}} V'_{3i} r_{3j} + e \quad \ldots\ldots\ldots\ldots (7)$$

The above equation can be rewritten as:

$$W_{ij} = a + K_1 V'_{1i} r_{1j} + K_2 V'_{2i} r_{2j} + K_3 V'_{3i} r_{3j} + e \quad \ldots\ldots (8)$$

where W_{ij} = yield of ith genotype in jth environment standardized over population mean and variance.

a = constant

K_1 = genotypic number of heads per unit area (X) standardized over genotypic mean and variance.

K_2 = genotypic number of seeds per head (Y) standardized over genotypic mean and variance.

K_3 = genotypic seed weight (Z) standardized over genotypic mean and variance.

All other variables have the same meaning as given earlier.

The formula represents a new mathematical model for the observed standardized yield, W_{ij}, of a genotype in an environment. It is composed of a constant, three multiplication terms of genotype-environment interaction effect and an error deviate. The interaction effects are made of the standardized genotypic yield components (K_1, K_2, K_3), constant genotypic components (V'_{1i}, V'_{2i}, V'_{3i}) and environmental components (r_{1j}, r_{2j}, r_{3j}). Two forms of environmental components can be obtained from X, Y and Z. The first set of components gives the efficiency of a genotype to use any of the three environmental components to produce any of the yield components. The other set gives the efficiency by which genotypes utilize the three environmental components in any environment.

MATERIALS AND METHODS

Data from twelve varieties of oats (Table 2) grown between the years 1976 and 1979, inclusive, will be used in testing the proposed model. Thirteen sets of data collected by the late Dr. John E. Grafius, were available for the analysis in the present study. These were taken as representing thirteen 'environments' and Table 3 gives more information about them.

Planting was the same in all the environments. The plots were four-row plots, 0.0254 m apart and 2.4 m long, planted at a rate of 30 g per plot. Each plot was replicated four times in any environment.

All the varieties were reasonably well adapted to Michigan and exhibit a wide range of various traits.

Data for seeds per head (Y) were obtained from a random sample of twenty heads per plot just prior to harvest. The average seed weight (Z) was calculated from a 3 g sample per plot using an electronic seed counter to count the number of seeds within the sample. The number of heads per 30 cm of row was obtained by dividing one sixteenth of the total weight of grain per plot by the product of seeds per head and kernel weight in grams.

Simple correlation coefficients between the yield components and yield for each of the twelve varieties were

Table 2. Names of the oat varieties.

Menominee*

Korwood*

Mackinaw*

Orbit

Ausable*

Mariner*

Clintland 64 (Cld 64)

Dal

Portal

Wright

Garry

Noble

*Michigan Lines

Table 3. Description of the thirteen environments.

Environment no.	Site	Year	Planting Date
1	Ingham County	1977	March 14
2	Tuscola County	1977	March 13
3	Kalamazoo County	1977	March 13
4	Lenawee County	1977	March 11
5	Ingham County	1978	
6	Tuscola County	1978	
7	Kalamazoo County	1978	
8	Lenawee County	1978	
9	Tuscola County	1979	March 19
10	Kalamazoo County	1979	March 16
11	Lenawee County	1979	March 23
12	Tuscola County	1976	April 6
13	Lenawee County	1976	April 5

calculated. The six correlation coefficients were used in (1) to obtain estimates of the six path coefficients a_1 to a_6 for each variety. The constant varietal components of the genotype-environment interaction were calculated using the path coefficients and the U's.

Varietal yield components and yield were regressed on population yield components and yield to determine the variation between yield components and yield under varying environments for each of the varieties.

Using standardized varietal mean yield (over population mean and standard deviation), standardized yield components (over varietal mean and standard deviation) and the constant varietal component of the genotype-environment (GE) interaction, the three environmental components of the GE interactions of each of the thirteen environments were estimated in standard deviation units by the method of least squares. In determining the environmental component of the GE interaction for each of the twelve genotypes, the constant in equation was eliminated. This was done to force the regression line through the origin and to determine the coefficient of determination of the GE interaction by the three GE components of the equation.

RESULTS

The correlation coefficients among the yield components and yield for each of the twelve varieties are shown in Table 4. The correlations between the number of heads per unit area (X) and yield (W) are positive and significant ($P \leq .01$) for all the varieties. That between X and the number of seeds per head (Y) are negative for all the varieties but Noble and Mackinaw, however, none is significant. Significant positive correlations exist between Y and seed weight (Z) for Mariner and Noble. W has a positive and significant correlations with Y for six varieties (Portal, Noble, Mariner, Dal, Cld 64, Mackinaw) and with Z, for Korwood and Portal.

Table 5 presents the path coefficients between yield components and yield. The number of heads per unit area is the largest determinant of yield for all the varieties. This is followed, in a decreasing order, by number of seeds per head and seed weight. Wright has the largest a_4 value and the least a_5 value. Garry and Menominee have the highest a_5 and a_6 values, respectively. The least a_4 and a_6 values were obtained for Portal and Orbit, respectively.

The mean square values (Table 6) show that significant differences exist between the marginal means for varieties,

Table 4. Correlation coefficients among yield (W), number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z) for each of the varieties.

	X vrs			Y vrs		Z vrs
Variety	Y	Z	W	Z	W	W
Menominee	-.211	.006	.801***	-.199	.343	.143
Korwood	-.196	.113	.824***	.456	.359	.499*
Wright	-.416	-.145	.851***	.409	.069	.202
Garry	-.205	-.336	.775***	.132	.422	-.065
Portal	-.127	.262	.723***	.375	.568**	.583**
Noble	.014	-.354	.788***	.480*	.593**	.129
Ausable	-.147	-.024	.734***	.179	.383	.232
Mariner	-.135	-.065	.725***	.490*	.551**	.391
Orbit	-.261	-.031	.838***	.313	.275	.192
Dal	-.136	-.379	.774***	.350	.478*	.054
Cld 64	.130	-.026	.864**	.333	.591**	.254
Mackinaw	.111	.166	.872***	.008	.557**	.216

* $P \leq .10$

** $P \leq .05$

*** $P \leq .01$

Table 5. Path coefficients between the yield components and yield for each of the varieties.

Variety	a_1	a_2	a_3	a_4	a_5	a_6
Menominee	-.211	-.038	-.207	.923	.588	.254
Korwood	-.196	.231	.501	.890	.453	.104
Wright	-.416	.030	.421	1.058	.437	.164
Garry	-.205	-.323	-.066	1.022	.632	.252
Portal	-.127	.315	.415	.758	.605	.155
Noble	.014	-.361	.485	.850	.487	.196
Ausable	-.147	.002	.179	.822	.567	.151
Mariner	-.135	.001	.490	.793	.580	.159
Orbit	-.261	.055	.327	.970	.509	.062
Dal	-.136	-.337	.304	.933	.572	.212
CLD 64	.130	-.070	.342	.810	.443	.127
Mackinaw	.111	.167	-.011	.851	.461	.071

Table 6. Mean square values for yield (W), number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z) of 12 varieties tested over 13 environments.

Source	df	W	X	Y	Z
Varieties	11	94839.68**	67.42**	1677.60**	.000391**
Environment	12	884248.66**	479.56**	2702.04**	.000078**
Varieties + Environment	132	6748.05**	7.96**	107.59**	.000005**
Error	468	3147.73	4.72	69.59	.000002

** $P \leq .01$

environment and the interaction between varieties and environment for all the characteristics under consideration. Tables 7 and 8 give the mean values for yield, number of heads per unit area, number of seeds per head and seed weight for the varieties and environments, respectively, arranged in a decreasing order. Cld 64, Mackinaw, Noble and Cld 64 have the least mean values for W, X, Y and Z, respectively. Menominee, Noble, Garry and Orbit have the highest mean values for the above mentioned characteristics, respectively. Generally, varieties with a low mean X values had high Y values or vice versa. Menominee, the highest yielding variety of the set used in the experiment, had relatively high values for both number of heads per unit area and number of seeds per head. It had medium seed weight. Cld 64 had relatively low values for all the measured characteristics.

Environments 13 and 4 were the worst in supporting the production of the yield components and yield. Some forms of negative associations are observed between the environments for the production of X and Y, however, these are not as obvious as represented by the varietal mean values. Environments 1 and 9 are examples. This is the result of the low insignificant negative correlations between the number of heads per unit area and the number of seeds per

Table 7. Arrangement of the varieties in the order of increasing mean values for yield (W), number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z).

W		X		Y		Z	
Genotype	Mean value	Genotype	Mean value	Genotype	Mean value	Genotype	Mean value
Cld 64	463.88	Mackinaw	13.32	Noble	61.81	Cld 64	.02813
Dal	495.62	Portal	14.56	Orbit	62.87	Wright	.02865
Wright	496.48	Garry	14.67	Cld 64	67.57	Mariner	.02893
Partial	524.02	Cld 64	15.20	Wright	68.20	Dal	.02910
Noble	537.00	Ausable	15.30	Dal	69.99	Portal	.02931
Mackinaw	543.81	Dal	15.31	Mackinaw	70.43	Menominee	.03003
Mariner	555.02	Korwood	15.68	Ausable	71.70	Garry	.03034
Ausable	558.50	Mariner	16.05	Mariner	74.25	Korwood	.03034
Garry	570.23	Wright	16.07	Korwood	75.02	Noble	.03075
Korwood	573.27	Orbit	16.12	Menominee	76.14	Ausable	.03214
Orbit	588.37	Menominee	16.88	Portal	76.52	Mackinaw	.03616
Menominee	613.42	Noble	17.71	Garry	81.00	Orbit	.03635
LSD (α=.05)	77.76		3.01		11.56		.0019
LSD (α=.01)	102.33		3.96		15.22		.0024

Table 8. Arrangement of the environments in the order of increasing mean values for yield (W), number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z).

W		X		Y		Z	
Env. No.	Mean Value	Env No.	Mean Value	Env. No.	Mean Value	Env. No.	Mean Value
13	258.88	13	10.34	13	54.77	4	.02899
4	321.10	4	10.71	1	64.72	2	.02900
12	452.79	12	12.21	9	65.35	13	.02948
11	456.63	11	12.93	4	66.62	3	.02973
8	530.40	10	14.67	11	67.38	12	.03047
6	575.02	8	15.34	8	70.61	6	.03085
10	580.25	6	16.15	6	72.93	8	.03095
9	603.48	7	17.27	2	73.06	5	.03132
1	611.13	5	17.68	5	74.81	7	.03146
2	636.79	9	18.04	3	76.42	10	.03155
5	651.98	1	18.75	12	77.39	1	.03186
3	676.92	3	19.17	10	80.22	9	.03235
7	704.31	2	19.17	7	82.48	11	.03307
LSD(α=.05)	77.76		3.01		11.56		.0019
LSD(α=.01)	102.33		3.96		15.22		.0024

head for all the varieties. Other contributing factors are the differences in reaction of the varieties to differing environments for the measured characteristics as shown in the Appendix (Figures A1 to A4).

Highly significant linear regressions exist between the measured genotypic characteristics and their respective environmental indices. An environmental index is the mean for a characteristic of all the varieties within the environment as used for the regression model for studying genotype-environment interaction (Finlay and Wilkinson, 1963; Breese, 1969). The regressions accounted for most of the variation in the variety-environment interaction for the yield components and yield of all the varieties. Although the regressions were highly significant ($P \leq .01$) in almost all the determinations, there were relative differences in the genotypic R^2 values for seed weight.

Figure 2 shows the regressions of genotypic mean yield on the environmental yield indices for five of the varieties used in the study. Menominee's performance is above the environmental mean yields while Cld 64's performance is below. Wright performs well in the relatively poor growing conditions and poorly in the good environment. The reverse is the case with Mackinaw. It performs poorly in the poor environment but better than average in the good environment.

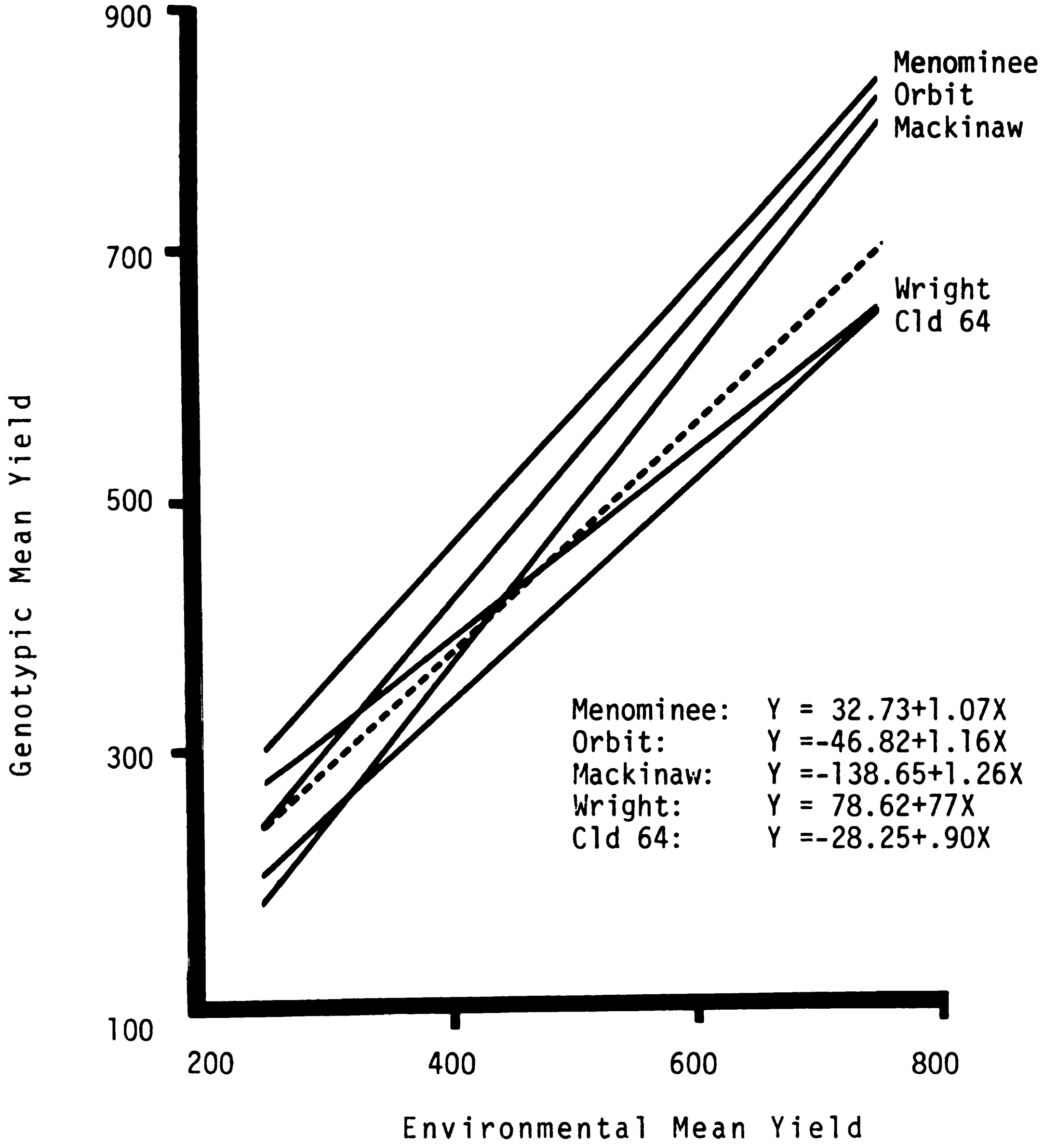


Figure 2. Yield response of Mackinaw, Orbit, Wright, Cld 64 and Menominee to thirteen varying environments in Michigan, 1976-1979.

The performance of Orbit is above average in the good environment, however, it has a mean yield equal to the environment mean yield of the relatively poor growing conditions.

The performances of Cld 64 and Mackinaw were below the average genotypic performances while Menominee and Wright had above average production of number of heads per unit area in all the environments (Fig. 3). Orbit produced more heads per unit area than the genotypic averages under the good environmental conditions but produced less than the average X in the poor environments.

The regressions of the genotypic mean Y values on the environmental indices are shown in Figure 4. Menominee has a better performance than average in all the environments while Cld 64 and Orbit have poor performances in all environments. Mackinaw produces a lesser number of seeds per head than average in the poor environments while more seeds per head than average are produced in the better environments. Wright produces a higher and lower than average Y in relatively poor and good environments, respectively.

Orbit and Mackinaw have heavier seeds while Menominee, Wright and Cld 64 have lighter seeds than average in all environments (Fig. 5).

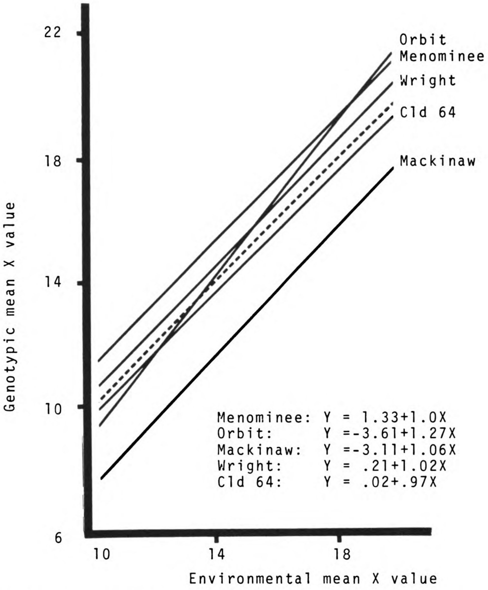


Figure 3. Response for the number of heads per unit area of Mackinaw, Orbit, Wright, Cld 64 and Menominee to thirteen varying environments in Michigan, 1976-1979.

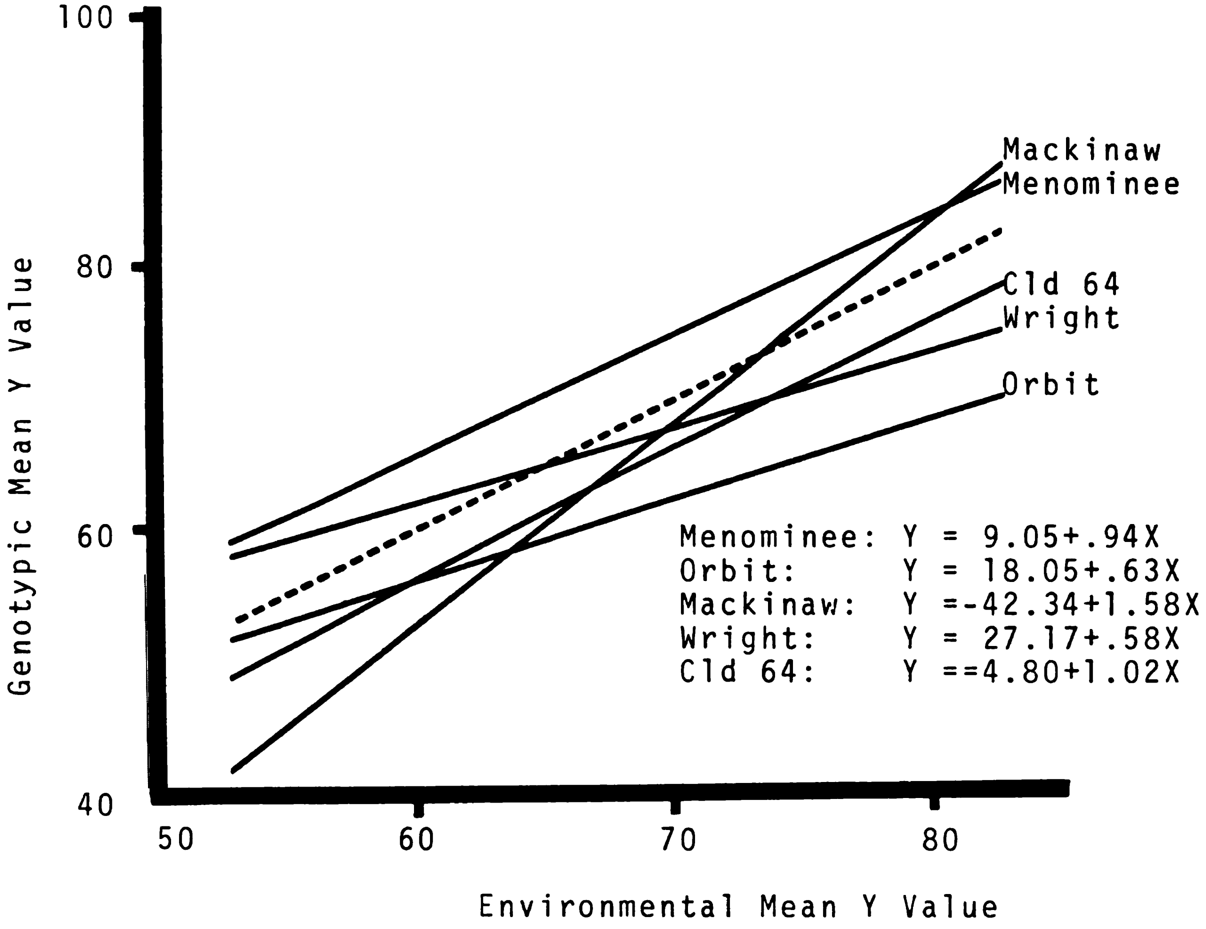


Figure 4. Response for the number of seeds per head of Mackinaw, Orbit, Wright, Cld 64 and Menominee to thirteen varying environments in Michigan, 1976-1979.

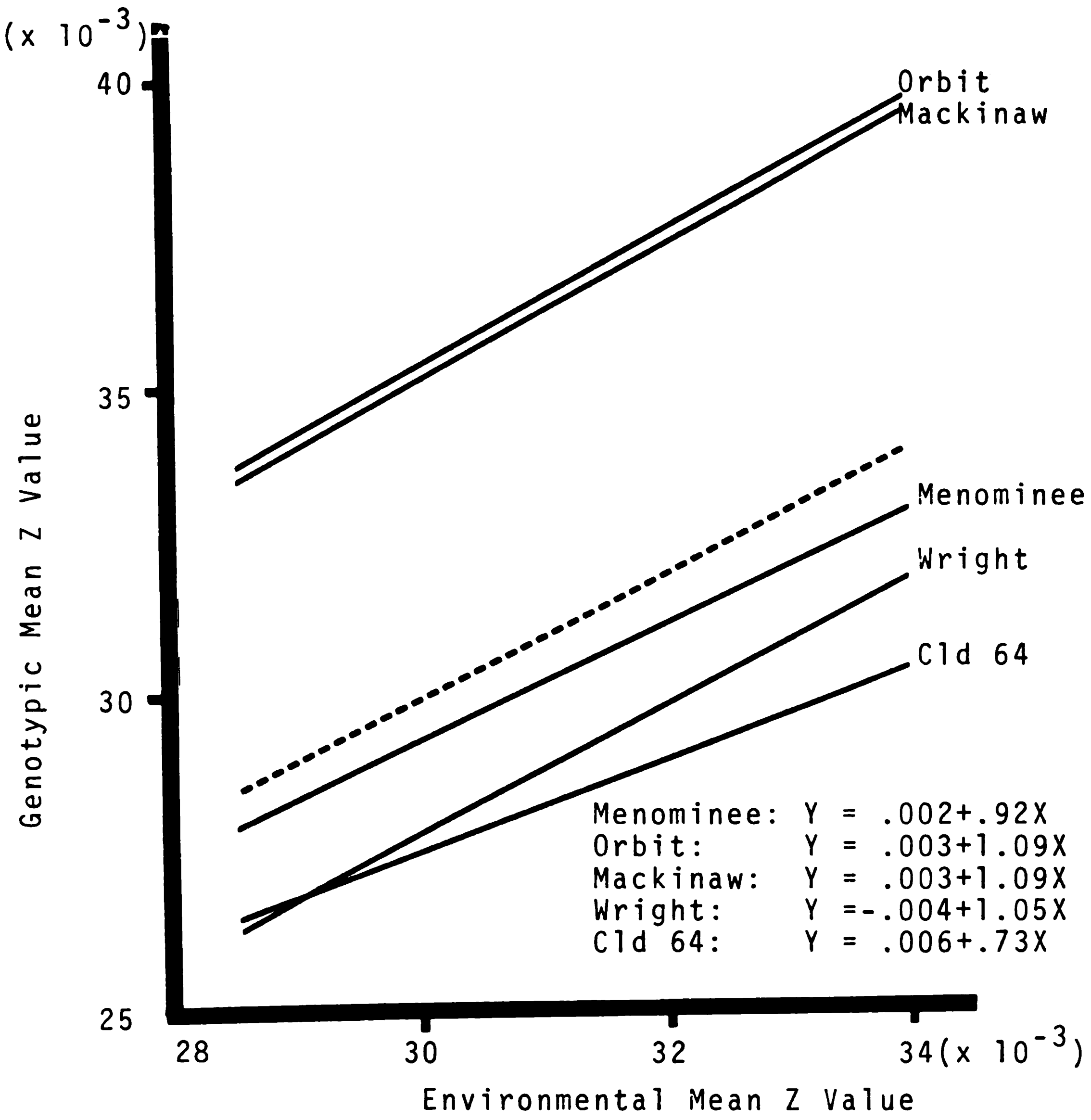


Figure 5. Seed weight response of Mackinaw, Orbit, Wright, Cld 64 and Menominee to thirteen varying environments in Michigan, 1976-1979.

One ought to be careful about these kinds of comparisons since they seem to reflect adversely upon certain varieties. We must remember that the particular sample of varieties used in such analysis determines the mean and departures from the mean slope and one variety may not actually be worse than many other varieties if the sample were different.

Component compensation between X and Y is not shown to any great extent in Figures 2 and 3. Performances of Orbit and Wright in relationship to X and Y show some signs of compensation. The signs of compensation shown by the two varieties results from the relative high but insignificant negative correlations between their X and Y. Orbit and Mackinaw have the highest response to environment for seed filling.

The path coefficients between E_1 and X, E_2 and Y and E_3 and Z are .7949, .5915 and .3849, respectively. Environment thus play its largest role in the production of heads followed by seeds per head and seed weight.

Estimates of the genotypic constants of the genotype environment interaction are given in Table 9. The estimates were positive for all the varieties. The constants were highest for number of heads per unit area followed by number of seeds per head and seed weight. V_1' values were generally about twice the values of V_2'. The V_3' values were

Table 9. Estimates of the varietal constant component of the variety-environment interaction.

Variety	V_1'	V_2'	V_3'
Menominee	.6367	.3167	.0978
Korwood	.6550	.2988	.0400
Wright	.6765	.3006	.0651
Garry	.6160	.3640	.0970
Portal	.5747	.3959	.0697
Noble	.6234	.3443	.0754
Ausable	.5835	.3514	.0581
Mariner	.5763	.3892	.0612
Orbit	.6661	.3131	.0239
Dal	.6153	.3765	.0816
Cld 64	.6868	.2877	.0489
Mackinaw	.6932	.2722	.0273

$V_1' = .7949\ \rho(XW)$

$V_2' = .5915\ (a_3 a_6 + a_5)$

$V_3' = .3849\ a_6$

characteristically variety-specific. They varied between 3.6% of V_1' (Orbit) to 15.7% of V_1' (Garry).

The correlation coefficients between the varietal mean yield components and estimates of the varietal constants are given in Table 10. V_1' has negative correlations with V_2' and V_3', however, only its correlation with V_2' is significant ($P \leq .01$). An insignificant positive correlation exist between V_2' and V_3'. The genotypic mean seed weight has a highly significant ($P \leq .05$) negative correlation with V_3' values.

Table 11 gives estimates of the environmental components of the genotype-environment interaction for the twelve varieties. All the varieties have relatively similar efficiencies in utilizing a standard unit of each of the environments E_1 and E_2 to produce their number of heads per unit area and the number of seeds per head. Relative efficiencies for the production of seed weight varies. Orbit and Mackinaw have the highest efficiencies, 5.661 and 4.961, respectively, in utilizing environment E_3 to produce their seed weight characteristics. Garry has the least efficiency (1.916) in seed weight production through the utilization of E_3.

The coefficient of determination for the multiple regression analysis involving yield, as the dependent variable, and the three multiplicative terms of genotype-environment interaction, as independent variables, are

Table 10. Correlation coefficients among varietal mean number of heads per unit area (X_i), number of seeds per head (Y_i), seed weight (Z_i) and estimates of the varietal constants (V_1', V_2', V_3') of the variety-environment interaction.

	X_i	Y_i	Z_i	V_1'	V_2'
V_1'	-.120	-.420	.329		
V_2'	.086	.355	-.382	-.936**	
V_3'	.341	.433	-.600*	-.441	.486

* $P \leq .05$

** $P \leq .01$

Table 11. Estimates of the environmental components of the variety-environment interaction for the varieties.

Variety	r_1	r_2	r_3	R^2
Menominee	1.491	1.736	2.643	.755**
Korwood	1.470	1.432	4.736	.959**
Garry	1.409	1.585	1.916	.949**
Portal	1.212	1.283	2.731	.965**
Noble	1.266	1.433	2.853	.990**
Ausable	1.381	1.837	3.529	.973**
Mariner	1.375	1.115	3.220	.983**
Orbit	1.478	1.420	5.661	.913**
Dal	1.189	1.104	2.634	.789**
Cld 64	1.024	1.516	2.530	.604**
Mackinaw	1.336	1.519	4.961	.981**
Wright	1.155	1.455	2.906	.794**

** $P \leq .01$

highly significant ($P \leq .01$). This shows that each genotype has an unique developmental processes whereby the environments E_1, E_2 and E_3 are utilized in the production of its yield components and yield. The R^2 values are obtained after forcing the regression line to pass through the origin (the constant in the yield equations was eliminated). Thus a high proportion of the variations in the yields of a variety within the tested environments is accounted for by the variety's interaction with the environment.

Estimates of the environmental components of the genotype-environment interaction of the thirteen environments are presented in Table 12. Seven of the environments had significant yield predictions for the genotypes. This is interpreted as due to the similar behaviors of all the varieties within these environments. The proportion of variation among the yields of all the varieties in the seven environments accounted for by the genotype-environment interactions varied between about 55% (environment 6) and 82% (environment 5).

The r values presented in Table 12 give the requirements of the varieties from E_1, E_2 and E_3 for the production of a standard unit of each of the yield components X, Y, and Z, respectively. The contribution of E_1, E_2 and E_3 to the production of X, Y, and Z, respectively, and their significance varied among the seven environments. E_1 was

Table 12. Estimates of the environmental components of the variety-environment interaction for the environments.

Environment no.	r_1	r_2	r_3	R^2
1	2.019***	2.875*	7.904	.770***
2	- .218	.018	.348	.034
3	.151	.685	5.252	.090
4	.782**	.784	1.428	.417
5	1.878***	2.683	.537	.824***
6	2.004**	1.562	9.412**	.551*
7	.767	1.173	-8.661*	.489
8	2.283***	1.236	3.361	.725**
9	2.075***	5.669***	5.461**	.737***
10	.721	.972	- .866	.235
11	1.493**	2.173**	5.585	.685**
12	1.329	1.191	7.003	.367
13	1.667***	.889**	1.181	.788***

* $P \leq .10$

** $P \leq .05$

*** $P \leq .01$

significant in all the predictions. E_2 was significant for yield predictions in environments 1, 9, 11, and 13, while E_3 was significant in varietal yield predictions in environments 6, 7, 9 and 11. Thus in environment 1, about 2, 3, and 8 units of E_1, E_2 and E_3, respectively, are required for the production of standard units of X, Y, and Z, respectively. The contributions of the genotype-environment interactions for production of X and Y are significant in the prediction of yield of all the genotypes within environment 1. Genotype-environment interaction for Z production is not significant in the yield prediction. An interpretation can now be given to the r values and the significance of the genotype-environment for each of the yield components in the prediction of yield.

Figure 6 shows the regression of the predicted yield on the observed yield when the model presented in equation 8 was applied to the data for the twelve varieties in all the thirteen environments. The R^2 for the highly significant ($P \leq .01$) multiple regression equation is .8901. Thus about 89% of the variation in the observed yields can be accounted for by the predicted yield made primarily from the genotype-environment interactions involved in the production of the yield components. The analysis of variance and multiple regression statistics for the regression are presented in Tables A1 and A2, respectively. All

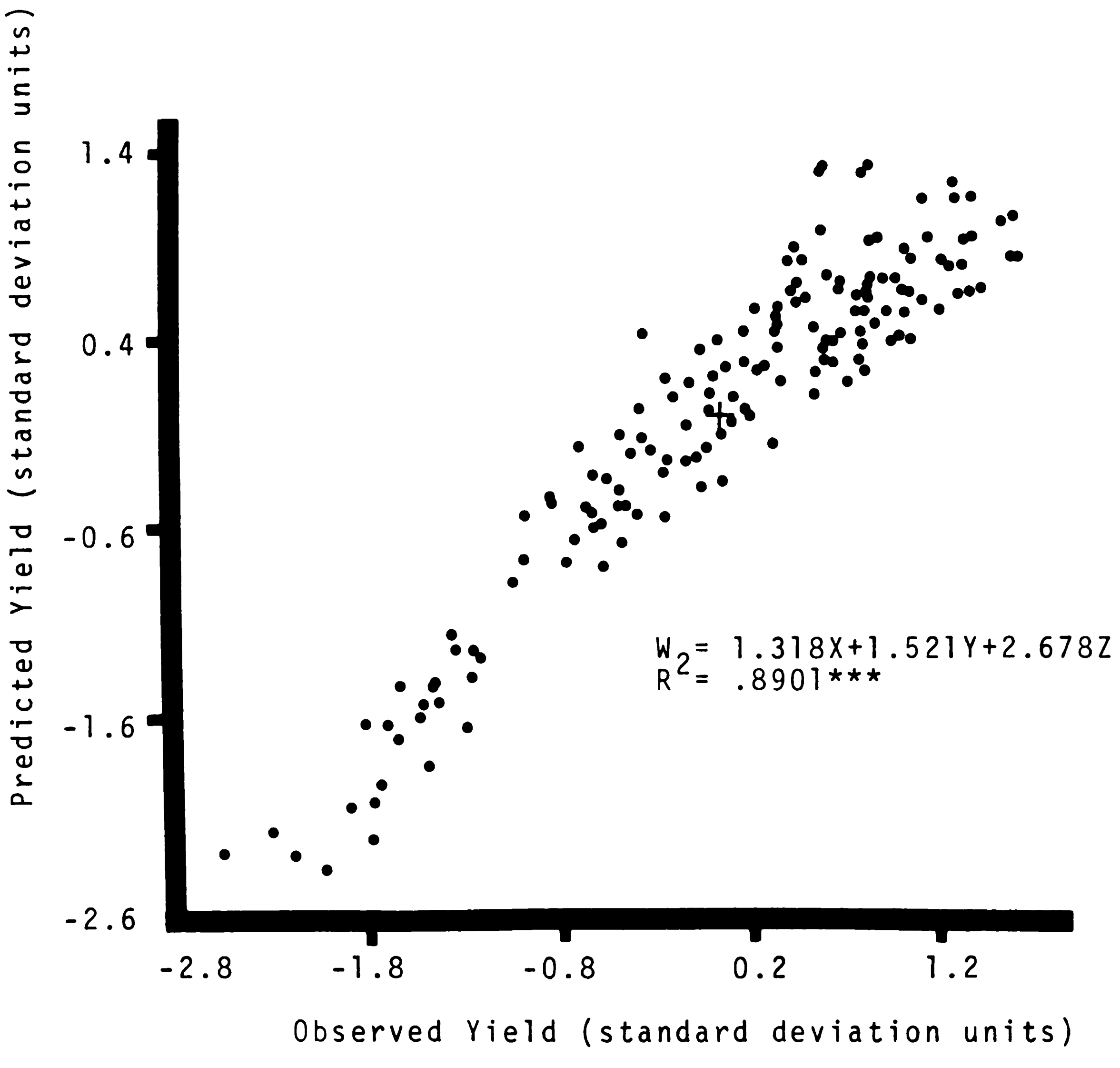


Figure 6. Regression of predicted yield on observed yield.

the independent characteristics were significant, however, X had the largest predictive value followed, in a decreasing order by Y and then Z.

The regression of the residuals on the predicted yield show a horizontal band (Figure 7) showing no ambiquities associated with the model.

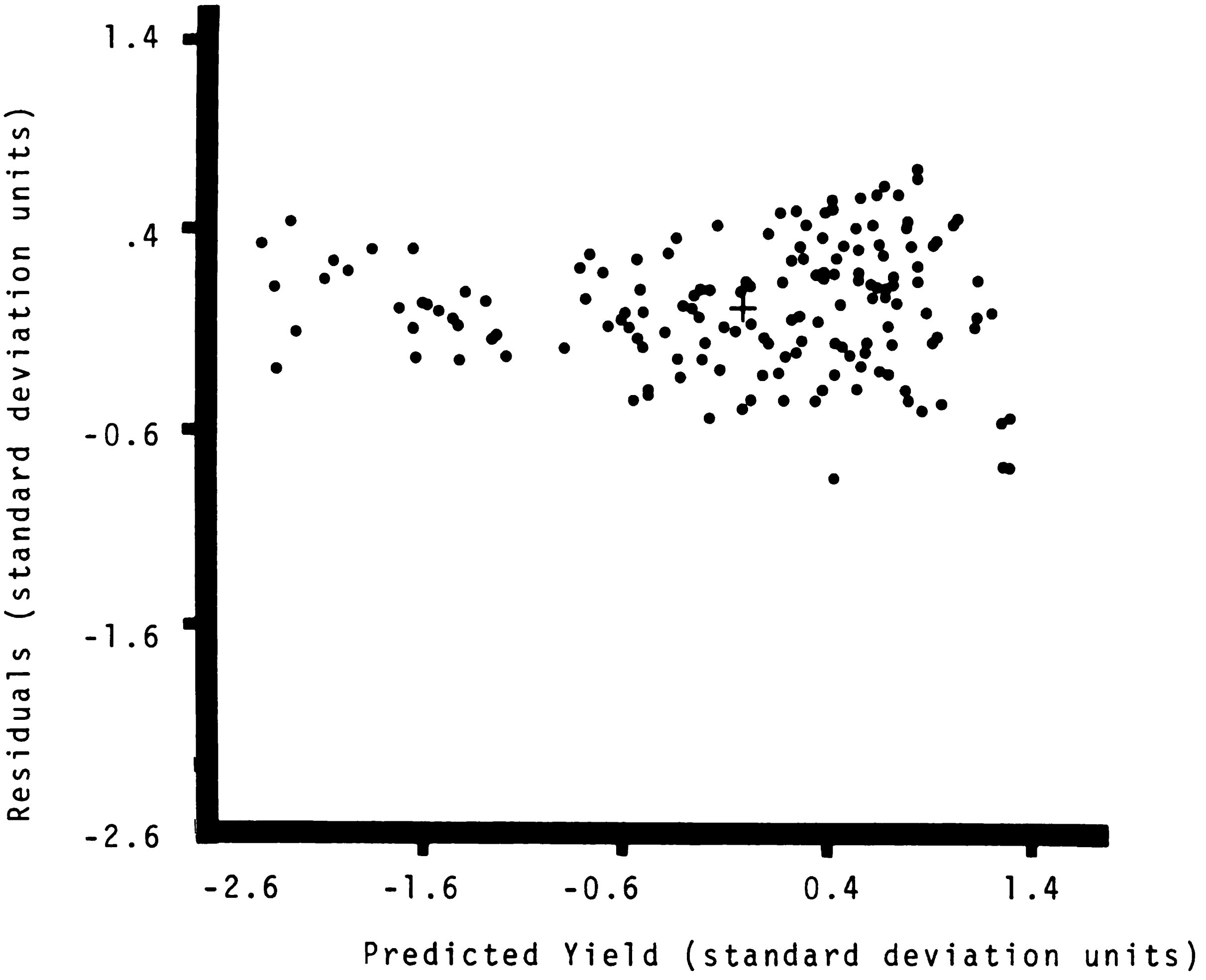


Figure 7. Regression of residuals on predicted yield.

DISCUSSION

The basic assumption in the present analysis is that three independent environmental components, E_1, E_2 and E_3 were involved in the production of the yield components X, Y, and Z, respectively. Based on the concept of sequential development of the yield components, the effect of each of the environmental components on yield was determined for each genotype and expressed as the genotypic constants (V_1', V_2', V_3'). The constants are in effect the path coefficients between the three independent environmental components and yield.

Hamid and Grafius (1978) showed that plant organs established earlier in the developmental ontogeny of small cereal grains crops have a great effect on the later developed organs. Thomas *et al*.(1971a) provided a method for eliminating the variation of an earlier established yield component on the development of later organs. The adjusted yield component values so obtained are independent of each other. Using these adjusted values for the determination of the path coefficients between the yield components and yield eliminates any dependency between them.

Tai (1975, 1979) and Nelson (1981), used similar methods for the determination of the path coefficients between the independent environmental components, E_1, E_2, and E_3 and X, Y, Z, respectively. Their determination signifies that X, the first developed yield component, is determined solely by the environment. This is inflationary because the variation within the performances of genotypes is not only determined by the environment but, additionally, by genotypic variation and the interaction between a genotype and environment. Consideration to the three sources of variations need to be taken into account in imposing restrictions or making assumptions in the formulation of a model for any plant characteristic. Using the method provided for the determination of the path coefficients between E_1, E_2, and E_3 with X, Y and Z, respectively, the author was able to remove the effects of the inflations associated with the determinations used by Tai (1975) and Nelson (1981). The effects of E_1 is largest in the production of its respective yield component (i.e., X) followed by E_2 and then E_3 in the production of Y and Z, respectively, as shown by their u values.

Another inherent error in the series of equation used to determine the path coefficients from E_2 and E_3 to Y and Z, respectively, is observed. The equations are valid if one is dealing with only the yield components. Environmental indices have been constructed using the mean values of all genotypes in each environment as in the regression model for genotype-environment interaction determinations. Generally, much of the variability in the measured characteristic (yield) of genotypes is accounted for by the linear functions of the environmental indices. Using the measurable traits (i.e., yield components) to depict the independent environmental components (E_2 and E_3) becomes erroneous because the relationships between the yield components is not indicative of the correlation between any of the environmental components. Different genotypes behave differently in various environments. The significant negative correlation coefficient between X and Y between different genotypes in an environment was purely physiologic as shown in Chapter 1. Additionally, the effects of the independent environmental components on the yield components is decreased with the later developed components. Environments play their largest role in the development of plant structures established earlier in the ontogeny of small cereal grain crops. Plant structures established later are genotypically controlled. Caution has to be taken in calculating environmental effects as presented by Tai (1975) and Nelson (1981).

Two measures of phenotypic stability of genotypes have been used when genotypic characteristics are regressed on their respective environmental indices. Since the mean slope is given by the regression of the environmental indices on itself, b=1. Thus genotypes with regression coefficients significantly higher or lower than one are regarded as having a low or high degree of stability, respectively (Finlay and Wilkinson, 1963; Perkins and Jinks, 1968). Eberhart and Russel (1966) and Breese (1969) proposed a second measure obtained by combining the environment and genotype-environment terms in the analysis of variance and testing for the heterogeneity (deviations from regression) of the regressions. They realized that regressing genotypic means on the environmental indices leads to inexact tests of significance however, using the deviations as a measure of phenotypic stability.

These determinations have been criticized on statistical grounds (Freeman and Perkins, 1971). Fripp (1972) showed that biases introduced by the use of the indices does not affect the ranking of the genotypes according to the magnitude of their regression coefficients or to the proportion of genotype-environment interaction accounted for by the heterogeneity of these regressions when compared with results of analysis of regression against various independent but biological measures. Freeman and Perkins (1971) outlined methods for characterizing environments without using the same individuals to determine both the environmental effects and genotype-environment interactions.

When the linear regression accounts for a significantly large part of the genotype-environment interaction, reliable predictions are obtained (Bucio-Alanis, Perkins and Jinks, 1969). If only a small portion of the variation is accounted for, other forms of analysis are used because the analysis will have no predictive value.

The genotypic stability for all the measured characteristics can be determined using their respective regression coefficients since significant portions of the genotype-environment interactions are accounted for in the genotypes for all the characteristics. These observations suggest some genuine underlying linear relationships between the performances of genotypes in different environments. The dispersion of the regression lines for Z presents an interesting observation which needs further enquiry.

The genotype-environment significantly accounted for between 60% (Cld 64) and 99% (Noble) of the variation in yield of the genotypes (after removing the constant from the model). Addition of the constant increased the R^2 values above .980 in all the genotypes. This shows that each variety behaves similarly in all environments. Estimates of the environmental components of the genotype-environment interaction show that the genotypes have virtually similar efficiencies in the production of their number of heads per unit area and number of seeds per head. The slight differences might be due to the additional environment required for the transformation from the vegetative to reproductive growth state and further differentiation of the floral parts. Efficiencies for seed weight production seem to be subjected to much environmental effects as shown by the varying values for r_3 among the genotypes. Orbit and Mackinaw have the highest capacity (5.661 and 4.961, respectively) in utilizing the variation in the environment for their Z production while Garry has the least capacity (1.916) for the same process. A genotype is herein defined as stable when it produces a unit of the yield components from a unit each of the independent environmental components E_1, E_2, and E_3. Cld 64, Dal and Garry are the most stable genotypes relative to the other genotypes used in the study for the production of X, Y, and Z, respectively. Menominee, Ausable and Orbit are the least stable of the genotypes for the production of X, Y, and Z, respectively. When all the yield components are considered together, Garry emerges as the most stable among the genotypes under test, the test having been conducted in a given set of environments.

The coefficient of determination of the observed yield by the predicted yield varied between 3.4% (environment 2) and 82% (environment 5) for the thirteen environments. Seven of the environments had significant yield predictions for the genotypes. This is explained by the similarity of behavior of the genotypes within those environments. The independent environmental requirements for the production of the yield components varied greatly from one environment to another. In defining environmental stability as that from which genotypes (behaving similarly) require one standard unit of each of E_1, E_2 and E_3 to produce one standard unit of X, Y, and Z, environment 13 is characterized as being the most stable environment of the studied environments. This environment is the worst of the lot.

Certain effects which are normally covered in the linear regression method of determining genotype-environment interactions are depicted when this multiple regression model is used. Variation between genotypes exist in more than one dimension.

The highly significant ($P \leq .01$) linear relationship between the predicted yield and the observed yield, the horizontal band obtained by the regression of residuals on the predicted yield and the magnitude of the coefficient of determination ($R^2 = .8901$) render the model useable for yield prediction. The basic phenomenon used in the formulation of the model is the sequential development of the yield components as outlined by Hamid and Grafius (1978) and Grafius (1978).

SUMMARY AND CONCLUSION

A modified form of models proposed by Tai (1975, 1979) and Nelson (1981) is offered making use of the regression and path coefficient methods for determining the genotype-environment interaction. Basically, the model involves the use of path coefficient analysis (Wright, 1921, 1934) to determine the effect of three hypothetically separable independent groups of environmental resources to yield through their direct effect on one each of the yield components. The direct effects are calculated from the proportion of environmental variance in the population variance for each of the yield components.

The model is composed of a constant, three multiplicative terms of genotype-environment interaction effect and an error deviate. The interaction effects are made of the standardized genotypic yield components, constant genotypic components and environmental components. Two sets of environmental components are obtained from X, Y and Z. The first gives the efficiency of a genotype to use any of the three environmental components to produce any of the yield component. The other set gives the efficiency by which genotypes utilize the three environmental components in any environment.

Data from twelve varieties of oats grown between the years 1976 and 1979, inclusive, was used in testing the proposed model. There were thirteen environments in all. The data included yield, number of heads per unit area, number of seeds per head and seed weight. The necessary analyses were performed to obtain values for the different variables of the model from which the two sets of environmental components were estimated. In determining the environmental component of the genotype-environment interaction for each of the twelve varieties. the constant in the equation was eliminated.

The analysis of variance showed the existence of significant differences between the marginal means for the varieties, environments and their interaction for all the characteristics. Highly significant linear regressions exist between the measured varietal characteristics and their respective environmental indices, however, there were relative differences in the varietal R^2 values for seed weight. Environment was detected as playing its largest role in the production of number of heads per unit area followed, in a decreasing order, by number of seeds per head and then seed weight.

Estimates of the varietal constants were positive for all the varieties. The highest group of values was associated with the number of heads produced per unit area followed by number of seeds per head and then seed weight.

All the varieties had relatively similar efficiencies in utilizing a standard unit of each of the environments E_1 and E_2 to produce their X and Y. Efficiencies for seed weight production varied among the varieties. There was evidence to show that each variety had unique developmental processes whereby the environments E_1, E_2 and E_3 were utilized in the production of its yield components and yield.

Seven of the eleven environments tested had significant yield predictions for the genotypes. This was interpretted as the result of the overlapping of the unique developmental processes possessed by the varieties. The contribution of E_1, E_2 and E_3 to the production of X, Y and Z, respectively, and their significance varied among the seven environments.

The regression of the predicted yield on the observed yield using all the data was highly significant ($P \leq .01$). The coefficient of variation for the multiple regression equation was .8901.

A horizontal band was obtained when the residuals were regressed on the predicted yield showing the absence of ambiquities in the model.

Certain effects which are normally covered in the linear regression method of determining genotype-environment interactions are exposed using this model. Variation is shown to exist in more than one dimension between genotypes.

APPENDICES

Table A1. Analysis of variance for the prediction of the observed yield (dependent variable) by the three multiplicative terms of variety-environment interaction (independent variables) involving the production of the number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z), respectively.

Source	df	SS	MS	F	S19
Total	155	139.0362			
Regression	3	123.7622	41.2541	410.5416	<.0005
Error	152	15.2740	.1004		
		R^2 = .8901			

Table A2. Multiple regression statistics for the prediction of the observed yield (dependent variable) by the three multiplicative terms of variety-environment interaction (independent variables) involving the production of number of heads per unit area (X), number of seeds per head (Y) and seed weight (Z), respectively.

Variable	Regression Coefficient	Beta Weight	Significance	Partial Correlation Coefficient	R^2 deletes
Const.	- .002	.942	<.0005	-.0059	.8901
X	1.319	.7625	<.0005	.9137	.3347
Y	1.521	.4004	<.0005	.7634	.7367
Z	2.683	.1479	<.0005	.4055	.8685

Figure A1. Regression equations and graphs for the yield response of the twelve varieties to thirteen varying environments in Michigan, 1976-1979.

Varietal Letter	Varietal Name	Regression Equation	R^2
A	Menominee	$Y = 32.725+1.069X$	.9659**
B	Orbit	$Y =-46.820+1.164X$	.9725**
C	Korwood	$Y =-86.045+1.214X$	.9507**
D	Mackinaw	$Y =-138.653+1.257X$	.9684**
E	Garry	$Y = 51.298+.956X$	.9062**
F	Ausable	$Y = 32.100+.969X$	.9783**
G	Portal	$Y =-6.506+.977X$	.9556**
H	Noble	$Y = 19.240+.953X$	.8916**
I	Mariner	$Y = 17.214+.985X$	.9773**
J	Wright	$Y = 78.621+.769X$	.8967**
K	Cld 64	$Y =-28.247+.906X$	.8602**
L	Dal	$Y = 75.623+.773X$	.9411**

** $P \leq .01$

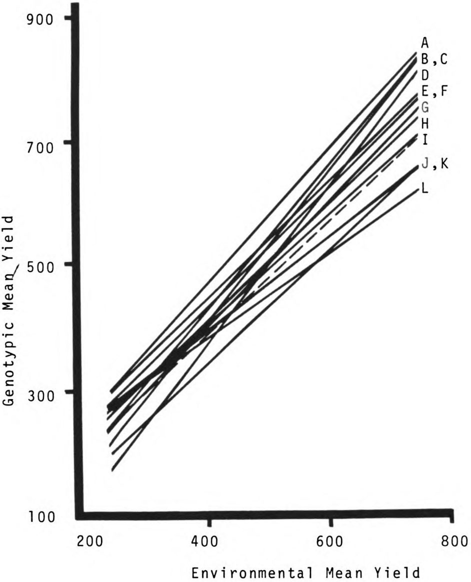

A
B, C
D
E, F
G
H
I
J, K
L
900
700
500
300
100
200
400
600
800
Genotypic Mean Yield
Environmental Mean Yield

Figure A2. Regression equations and graphs for the response for the number of heads per unit area of the twelve varieties to thirteen varying environments in Michigan, 1976-1979.

Varietal Letter	Varietal Name	Regression Equation	R^2
A	Menominee	$Y = 1.325+.999X$	.8840**
B	Orbit	$Y =-3.607+1.266X$	.9457**
C	Korwood	$Y =-3.709+1.244X$	.9309**
D	Mackinaw	$Y =-3.105+1.055X$	.8824**
E	Garry	$Y =-.039+.945X$	.8729**
F	Ausable	$Y = .998+.919X$	.8211**
G	Portal	$Y = 2.911+.748X$	.8736**
H	Noble	$Y = 2.371+.985X$	.7328**
I	Mariner	$Y = .704+.985X$	.9334**
J	Wright	$Y = .214+1.018X$	.7680**
K	Cld 64	$Y = .024+.974X$	.7791**
L	Dal	$Y = 1.919+.860X$	.8974**

$^{**}P \leq .01$

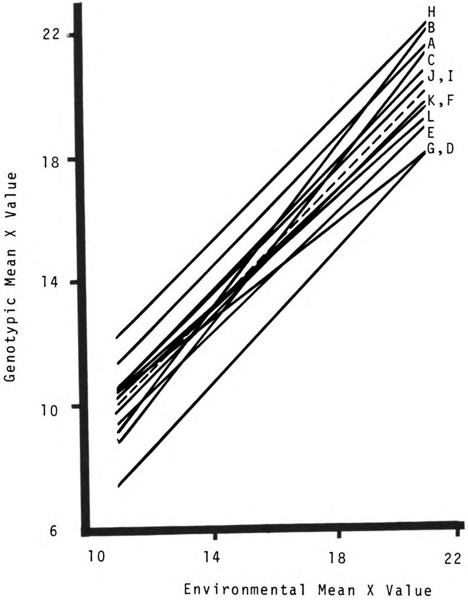

Genotypic Mean X Value
22
18
14
10
6
10
14
18
22
Environmental Mean X Value
H
B
A
C
J,I
K,F
L
E
G,D

Figure A3. Regression equations and graphs for the response for the number of seeds per head of the twelve varieties to thirteen varying environments in Michigan, 1976-1979.

Varietal Letter	Varietal Name	Regression Equation	R^2
A	Menominee	Y = 9.051+.941X	.6551**
B	Orbit	Y = 18.093+.628X	.5742**
C	Korwood	Y = 10.437+.910X	.6982**
D	Mackinaw	Y =-42.339+1.582X	.8693**
E	Garry	Y =-19.845+1.415X	.8090**
F	Ausable	Y =-15.965+1.230X	.7788**
G	Portal	Y =-23.420+1.402X	.9268**
H	Noble	Y = 9.619+.732X	.6074**
I	Mariner	Y = 10.291+.897X	.8904**
J	Wright	Y = 27.166+.576X	.4326*
K	Cld 64	Y =-4.799+1.015X	.7007**
L	Dal	Y = 21.262+.683X	.7682**

* $P \leq .05$

** $P \leq .01$

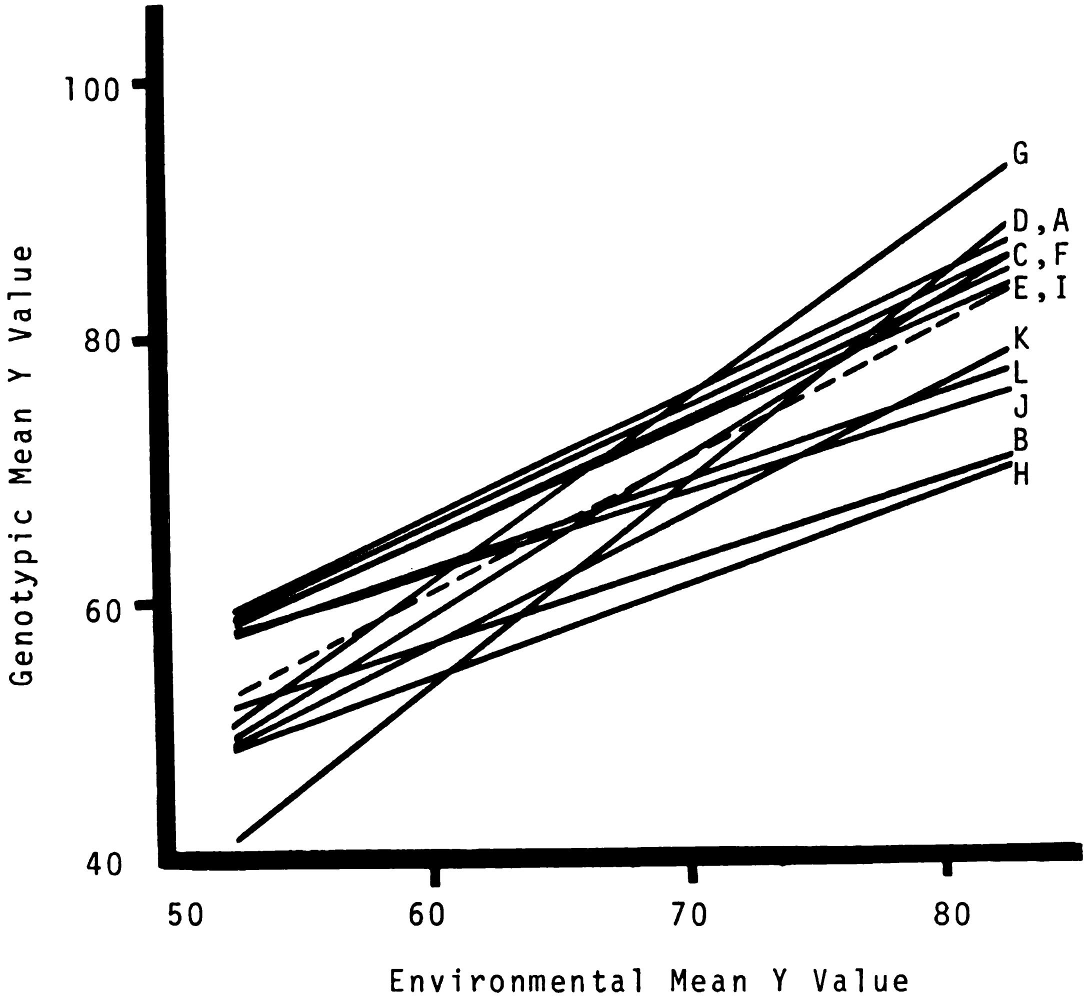
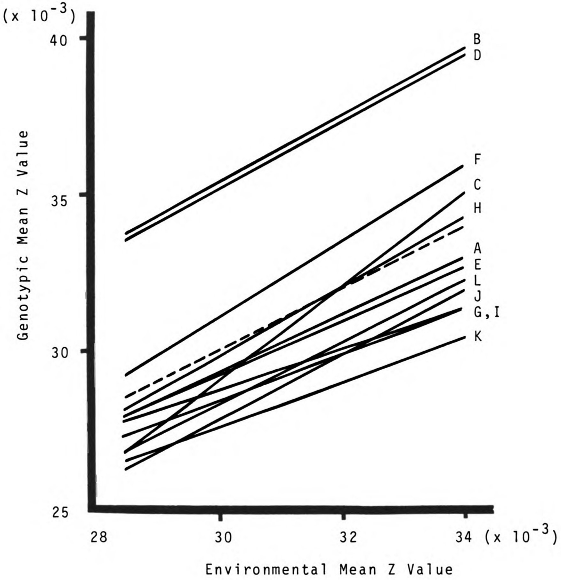

Genotypic Mean Y Value
100
80
60
40
50
60
70
80
Environmental Mean Y Value
G
D,A
C,F
E,I
K
L
J
B
H

Figure A4. Regression equations and graphs for the seed weight response of the twelve varieties to thirteen varying environments in Michigan, 1976-1979.

Varietal Letter	Varietal Name	Regression Equation	R^2
A	Menominee	$Y = .0018+.9160X$	.4652**
B	Orbit	$Y = .0026+1.0927X$	.6607**
C	Korwood	$Y =-.0158+1.4948X$	.7782**
D	Mackinaw	$Y = .0026+1.0861X$	.6086**
E	Garry	$Y = .0064+.7748X$	.5144**
F	Ausable	$Y =-.0059+1.2317X$	.8405**
G	Portal	$Y = .0084+.6771X$	.4455*
H	Noble	$Y =-.0039+1.1229X$	.5378**
I	Mariner	$Y = .0058+.7498X$	.5378**
J	Wright	$Y =-.0038+1.0514X$	.7153**
K	Cld 64	$Y = .0057+.7263X$	.5720**
L	Dal	$Y =-.0011+.9783X$	.6434**

* $P \leq .05$

** $P \leq .01$


(x 10^{-3})
40
35
30
25
Genotypic Mean Z Value
28
30
32
34 (x 10^{-3})
Environmental Mean Z Value
B
D
F
C
H
A
E
L
J
G,I
K

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