Genetic and environmental yield, yield component, and morphological responses of six heading date isotypes to Titan barley (Hordeum vulgare) grown in 15 environments
by Virgil William Smail

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Agronomy
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Abstract:
Six Titan isolines differing in increments of heading date spanning a 13-day period were grown in 15 environments using commercial planting rates and 1 environment planted at a 1 plant/30 cm^2 rate.

Yield, spikes/30 cm^2, kernels/spike, and kernel weights, as well as 10 other morphological traits, were measured at each environment.

Three methods of analysis were utilized to interpret different aspects of the effect of maturity isolines on the development allometry of the plant as expressed through yield and yield component responses. Using a two-dimensional version of the parallelipiped analysis it was noted that whether space planted or drilled the isolines exhibited strong yield component differences. In the space planted environment no yield component compensation was observed resulting in marked yield differences. The mean response over 15 environments of the yield trial showed marked yield component compensation and no significant yield differences. A regression analysis of each isoline with mean performance over each environment revealed strong isoline x environment interactions for the three yield components and minimal interactions for yield responses among the isolines. Path coefficient analysis revealed that across environments and isolines, tillers per unit area, and seeds per spike had the highest direct effect on yields. Kernel weights showed a moderate but consistent effect. Across environments and within isolines (environmentally induced variation), tillers per unit area and kernel weights had the highest direct effect on yield of the isolines. By utilizing three methods of analysis not only was it possible to determine a pattern of isoline yield and yield component responses caused by the differences in planting dates between environments, but it was also possible to gain a clearer understanding of the plants' developmental allometry in different environments. The consistently high correlation response between kernels per spike and isotype heading data at all environments, as well as the pattern of path coefficients imply that the kernels per spike response is the yield component controlling the response in tillering, kernel development and yield. A physiological control mechanism placing a priority on nutrient and water allocation to developing heads, over developing tillers, was suggested.

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VIRGIL WILLIAM SMAIL

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Approved:

Robert J. Eslick
Chairperson, Graduate Committee

Hayden Ferguson
Head, Major Department

Michael Malone
Graduate Dean

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ABSTRACT

Six Titan isolines differing in increments of heading date spanning a 13-day period were grown in 15 environments using commercial planting rates and 1 environment planted at a 1 plant/30 cm^2 rate. Yield, spikes/30 cm^2, kernels/spike, and kernel weights, as well as 10 other morphological traits, were measured at each environment. Three methods of analysis were utilized to interpret different aspects of the effect of maturity isolines on the development allometry of the plant as expressed through yield and yield component responses. Using a two-dimensional version of the parallelipiped analysis it was noted that whether space planted or drilled the isolines exhibited strong yield component differences. In the space planted environment no yield component compensation was observed resulting in marked yield differences. The mean response over 15 environments of the yield trial showed marked yield component compensation and no significant yield differences. A regression analysis of each isoline with mean performance over each environment revealed strong isoline x environment interactions for the three yield components and minimal interactions for yield responses among the isolines. Path coefficient analysis revealed that across environments and isolines, tillers per unit area, and seeds per spike had the highest direct effect on yields. Kernel weights showed a moderate but consistent effect. Across environments and within isolines (environmentally induced variation), tillers per unit area and kernel weights had the highest direct effect on yield of the isolines. By utilizing three methods of analysis not only was it possible to determine a pattern of isoline yield and yield component responses caused by the differences in planting dates between environments, but it was also possible to gain a clearer understanding of the plants' developmental allometry in different environments. The consistently high correlation response between kernels per spike and isotype heading data at all environments, as well as the pattern of path coefficients imply that the kernels per spike response is the yield component controlling the response in tillering, kernel development and yield. A physiological control mechanism placing a priority on nutrient and water allocation to developing heads, over developing tillers, was suggested.

INTRODUCTION

Barley is second only to winter wheat in acreage planted in Montana. The heading date of a barley variety is crucial to its adaptation to the short, cool, growing seasons found in Montana. Early heading dates allow barley to escape natural growth hazards such as hail, insects, disease and drought. Late heading dates allow barley to maximize yield responses with longer growing seasons and irrigation. Consequently a thorough understanding of the effects of different heading dates on the yield response of barley in numerous environments is crucial to efficient selection of high yielding varieties.

The major hindrance to determining the effect of genetic heading dates on barley growth is the confounding factor of basic genotypic differences influencing the heading date response differences in varieties studied. Isogenic analysis isolates the one factor of heading date differences and allows the clarification of the effects of this trait on the yield, yield component, and quality component responses of barley.

An isogenic series of Titan barley covering a 13 day heading date range planted in 15 environments was used to determine the following:

1) Plant morphological and yield component responses pleiotropic to the genetic heading dates.
2) The effect of environmental versus genetic heading date differences on yield, yield components and quality component responses.
3) The yield component characters most strongly controlling heading date induced yield responses.
4) Those yield component and quality component characters which can be selected to improve performance given a specific heading date, and to determine the optimum environment for the selection of those traits.

LITERATURE REVIEW

Genetics of Heading Date Control

The maturation rate of barley is highly heritable, however heading date has been shown to be simply, or complexly inherited. It is also sensitive to environmental fluctuations, especially temperature and photoperiods (Nilan, 1964). Many investigators have concluded that the complexities involved in heading response cannot be investigated using the traditional biometrical tools, such as diallel analysis, genotypic vs phenotypic analysis of variance, and additive vs dominant components of variation alone (Aspinall, 1965; Bell, 1939; Paroda and Hayes, 1971; Takahashi and Yasuda, 1971). Environmental and physiological interactions involved in determining the heading date response must also be considered (Bell, 1939).

Spring barley is considered as a "long day" plant since its heading time is accelerated by long days. However, heading of winter types is retarded by long days until vernalization is complete. In vernalized winter habit barleys and in spring habit barleys, the plants' genetically controlled heading response is determined by its sensitivity to photoperiods and thermal conditions (Takahashi and Yasuda, 1971).

The vernalization response is controlled by three interacting loci expressing epistasis and incomplete dominance, thus creating six levels of growth habit, depending upon the combinations of the genes $\underline{sh_1}$, $\underline{sh_2}$, and $\underline{sh_3}$. To avoid confounding photoperiodic response with growth habit

responses in genetic analyses, spring habit cultivars or totally vernalized winter habit cultivars should be used (Takahaski and Yasuda, 1971).

Genetic sensitivities to photoperiods cause marked differences in time to heading among spring or vernalized winter barleys when grown under differentially shortened photoperiods (Takahaski and Yasuda, 1971). These responses allow varieties to be classified as day-length neutral, day-length sensitive, or as intermediate in sensitivity. Day-length neutral plants are insensitive to short photoperiods, and head in the same ranking with other day-neutral varieties, regardless of the photoperiod. The rank of heading responses between day-length sensitive varieties can change drastically depending upon the photoperiod (Bell, 1939; Takahashi and Yasuda, 1960 and 1971). Sensitivity to short photoperiods was shown to be a sensitivity to long dark periods (Borthwick et al., 1971; Paleg and Aspinall, 1966), by an application at night of far-red light, producing responses similar to long photoperiods. In totally vernalized barley, wheat and oats, longer photoperiods and higher temperatures (up to about 25C) increase the phasic rate of development of the plants (Aspinall, 1966; Borthwick et al., 1971; Klaimi and Qualset, 1973 (in wheat), 1974; Riddell and Gries, 1958; Takahashi and Yasuda, 1960). The sensitivity of a cultivar to short photoperiod is a cultivar x photoperiod (environment) interaction. Most genetic studies fail to consider and differentiate this

interaction which confounds interpretation of measured heritabilities.

Insensitivity to long photoperiods is manifested by cultivars which when grown under long day conditions (providing a specific minimum photoperiod) always head earlier than other varieties, regardless of the photoperiod. The ranking between these cultivars are always constant, and the insensitivity is highly heritable. This trait is found in all combinations with the other physiological characters both confounding, and enhancing the heading date responses of a cultivar. Thus, any attempts at isolating the genetic inheritance of a particular cultivar must insure that these physiological factors are not affecting the results (Takahashi and Yasuda, 1971).

The chromosome locations of two genes ea5 (ea_k) and ea7 (ea_c) imparting long day photoperiod sensitivity with short day insensitivity, have been found by Yasuda (1977) and Ramage and Suneson (1958), respectively. The ea_k (recessive) gene first reported in the early two-rowed variety Kinai, was shown to be allelic with the early gene, ea_c, mutagenically induced in the Bonus mutant, Mari, and was assigned to chromosome 5 (Favret and Frecha, 1967; Gustafson et al., 1974; Yasuda, 1977). The gene ea_c was originally located in segregates of chemically mutated California Mariot kernels (Ramage and Suneson, 1958). It is a monofactorial recessive located on chromosome 6

(Burnham, 1970). Other earliness genes have been investigated, but their linkage associations have not been determined.

The inheritance of heading date in barley involves both dominant and recessive genes controlling early and late heading responses, and is simply to complexly inherited depending upon the number of genes controlling the trait (Fischer, 1975; Frey, 1954; Johnson and Eunis, 1964; Nilan, 1964; Smith, 1951). In most of these studies, the only control of photoperiod was similar planting dates for the separation generations of testing, at the same location. Consequently, the actual heading response may be even more complex than implied. Winter habit as well as physiological factors may be interacting in such a way that expression of many genes affecting heading date were masked by the environment (Bell, 1939; Aspinall, 1966).

Several studies have examined the photoperiodic sensitivity of specific varieties by exposing those varieties to different photoperiods (Aspinall, 1966; Ramage et al., 1964; Takahashi and Yasuda, 1971; Tingle et al., 1970; Yasuda, 1977). A general reduction in days to heading when exposed to longer photoperiods was reported as a common occurrence in spring grains, while the change in rank of relative heading dates among cultivars when exposed to different photoperiods serves as an indicator of sensitivity.

PHOTOPERIOD MANIPULATION

Bell (1939) planted several barley cultivars on different dates ranging from February 14 to April 1 over a seven-year period and observed differences in days to spike emergence. The days from sowing to spike emergence universally decreased with exposure to the longer photoperiods found in March than in April. Although earlier plantings generally meant a longer time from sowing to spike emergence, the differences in planting times were not correlated to the ranking of spike emergence between varieties. Those varieties with the shortest time to spike emergence were capable of the greatest reduction in the developmental period to spike emergence. The more slowly developing varieties had less reduction in this period in the later sowings. The consistently earlier heading date of the early cultivars implies a degree of photoperiod insensitivity.

One major problem with this type of planting date study is the largely uncontrolled environment, i.e., temperature, moisture availability at different developmental stages, etc. Due to these many uncontrolled differences in planting dates, little else can be deduced from these studies due to the cultivar x environment interaction. Efforts should be made to control as many variables in the environment as possible to reduce intra-cultivar variability between environments (Went, 1953).

Guitard (1960) and later Faris and Guitard (1969) attempted to surmount the problem of variable environmental conditions by investigating the controlled influence of temperature (12.8 to 23.9C) and photoperiods (8, 16, 24 hr.) in all combinations on the response of spring barleys in the following three stages of growth: Stage I - seeding to internode elongation, Stage II - internode elongation to heading, Stage III - heading to maturity. The cultivars used were Olli (photoperiod insensitive) and Vantage (photoperiod sensitive).

High positive correlations of number of leaves, stem length, spike length, and number of fertile florets per spike to days to heading were reported for both Olli and Vantage. A close association between number of tillers and duration of tillering was also reported.

The responses were explained on the basis of an altered duration of each successive stage of development due to the photoperiod and temperature treatment. Thus, causing a change in the degree of development, as well as the number and size of organs established in each developmental stage. The plant responses were conditioned by photoperiod both prior to and during the developmental stages. There were two exceptions--the number of kernels per spike was influenced by photoperiod during, but not following stage II, and the duration of tiller initiation and total number of tillers were influenced only prior to stage II (Faris and Guitard, 1969). The observed correlations and patterns of responses caused by the differing periods of

development may be due to the developmental allometry of a developing plant (Hamid and Grafius, 1978).

YIELD COMPONENT COMPENSATION

Yield components are used to evaluate and understand the complex character of yield. The three yield components in barley are (X) spikes per unit area, (Y) kernels per spike, and (Z) kernel weight. The heritabilities of each of the components should be higher than the usually low heritability of yield itself, since fewer genes control each component than control yield. Yield is essentially a product of these genes and the genotype x environment interaction of the different yield components (Woodworth, 1931).

Compensating patterns of genotype x environment interactions have prevented the understanding of yield components. Grafius (1956) proposed an intuitive interpretation of yield component compensation utilizing parallelipids (cubic volumes). Yield is considered as the volume, and the three yield components consist of the sides of the parallelipipid. The dimensional components are calculated as a ratio of the mean nursery response of each component, allowing different parallelipids to be compared. The shapes illustrate the relative contribution of each component to yield (volume) at a particular environment for a given cultivar. The conversion of each component to a ratio of the mean allows the yield components of all cultivars in a trial or

experiment to be converted to a common unit (1.00) and are thus easily compared (Grafius, 1956, 1957, 1964).

The compensatory pattern of yield component responses creates a predictable pattern of negative phenotypic correlations between the components. These negative correlations have been one of the key impediments to progress in yield selection studies, since compensation minimizes yield differences and effectiveness of selection (Abo-Elenein et al., 1975; Adams, 1967; Atkins, 1964; Carleton and Foote, 1968; Dixit, 1973; Frey and Horner, 1955; Grafius, 1956, 1957, 1964; Grafius and Okoli, 1974; Pandey and Torrie, 1973; Rasmussen and Cannell, 1970; Solanki and Bakshi, 1973; Woodworth, 1931; Yap and Harvey, 1972). Adams (1967) postulated that these correlations could be caused by genetically independent components developing in a sequential pattern that are free to vary in response to either a limited but constant input or an oscillating input of nutrients, such that supply becomes limiting at the most critical stages (periods of greatest demand) in the developmental sequence. This theory is based upon the assumption that a genotypic correlation may occur with direct genetic linkage, pleiotropy, or allometric relationships between the sequentially developed traits.

The negative correlations between yield components in field beans, and other crops, seem to be independent of direct genetic control, since no relationships are observed between components of space planted

plants exposed to minimal inter-plant competition for nutrients. With direct genetic control, the correlations would remain strong under most environmental circumstances. Also, pleiotropy would be expressed uniformally in the responses of yield components under various environmental conditions (Grafius, 1972; Thomas et al., 1970a).

In barley the effectiveness of component selection may differ substantially in different populations and may actually lead to reductions in yield. Selection for high and low number of spikes have been accompanied by positive responses in kernel weights and negative responses in kernels/spike in different types of populations. Since these two traits increase or decrease together with selection of the other traits, it has been suggested that either genetic linkages exist between the first and last components (Rasmussen and Cannell, 1970), or that developmental allometry is controlling these relationships (Hamid and Grafius, 1978; Grafius, 1978).

The effectiveness of component selection for yield improvement is dependent upon two factors: 1) the yield components must be highly heritable; 2) strong positive associations must exist between yield and the component selected (Rasmussen and Cannell, 1970). The heritability of a yield component is partially determined by the position in the developmental chain at which a component response is established (Adams, 1967; Grafius, 1969; Rasmussen and Cannell, 1970; Thomas et al., 1970a). For example, as postulated by Rasmussen and Cannell (1970),

spikes per plant is the first in the development sequence and typically has the greatest environmental variation and the lowest measured heritabilities. This tendency reverses as each successive component in a chain of development is considered, thus kernel weights express the strongest genetic control, and vary the least over environments.

Thomas et al. (1970b), hypothesized that the strength of the correlations between yield components was a direct response of the degree of stress caused by interplant, intraplant, and intracomponent nutrient competition. By adjusting all of the genetic correlations to zero and analyzing the differences between the correlated values and the values with correlations removed as an estimate of stress, he showed that the direct effect of the genotype on the kernel weight response is minimal. However, the genotype x environment interaction had a strong effect on the kernel weight responses. In direct conflict to Rasmussen and Cannell (1970), he showed that the adjusted genotypic response of kernel weights was the most variable over environments and, therefore, expressed less genetic control than kernels per spike. It was concluded that if the characters are strongly correlated, then the calculated genetic control over later characters is merely a reflection, through stresses, of the degree of genetic control over previous characters. Therefore, the degree of true genetic control diminishes as characters further along the sequential developmental path are affected by the responses of the preceding traits (Thomas et al., 1970a;

Grafius and Thomas, 1970; Hamid and Grafius, 1978; Grafius, 1978). A yield component or other morphological trait competes more severely with itself than with any other trait, probably due to identical periods of development with other plants in a row. Depending on the resources available and the competition created, each environment will create a specific pattern of yield component response.

Plant growth and development have evolved around a sequentially integrated system which is dynamic throughout the entire ontogeny of the plant (Grafius, 1978). Thus, the early developed organs profoundly affect the later developed components. The developmental responses of the yield components, as well as other organs, are intertwined through the contraints set by the relative growth of a part of the plant on that of the whole plant (allometry) (Hamid and Grafius, 1978; Tai, 1974).

Allometric control resides in the restrictions of new cell production, limited to the meristematic tissues. Since primorida of every organ evolve from meristematic tissue and since "the size of any given organ depends upon the size of the growing point out of which it has been developed" (Sinnott, 1921), then any factor affecting the size of a meristem will, in turn, affect the size of <u>all</u> organs developing from that meristem (Hamid and Grafius, 1978). Path-coefficient analysis data support this theory of developmental allometry.

Path coefficient analysis (Dewey and Lu, 1959; Malhotra and Jain, 1972; Omar et al., 1966; Pandey and Torrie, 1973; Tai, 1975; Grafius, 1978) has caused yield component analysis to become a valuable method of analysis. It is accurate because it isolates both the direct and indirect effects found in a correlation between two characters. In all path diagrams, the structure must be logical and defensible (Wright, 1921, 1934). The rationale used by Hamid and Grafius (1978) to establish their specific diagram is:

> In the small grains, the proliferation of tillers is one of the first developmental processes at the organ level. The above-ground organs evolve from the shoot meristem and each of these organs is sequentially laid down, beginning with establishment of the main stem, followed by proliferation of the tiller primordia and subsequent development of other plant structures such as the leaf, the culm, and the floral primordia.

The establishment of tiller number (X) triggers a chain of reactions determining in part, the sizes of subsequent plant organs and thus eventually determining the economic yield itself. Tiller response can be affected by many external and internal forces such as nutrients, light intensity, day length, and hormonal levels (Hamid and Grafius, 1978; Grafius, 1978; Tewari, 1976).

Considerable intercultivar variation has been reported for genotypic, phenotypic, and environmental correlation coefficients, as well as path-coefficients, of yield and yield components (Abo-Elenein and Moris, 1975; Dashora et al., 1977; Morsi and Abo-Elenien, 1975; Nasr et al., 1974a,b; Riggs and Hayter, 1975; Seth and Singh, 1978; Solanki

and Bashki, 1973; Tewari, 1976). The number of tillers, grains and 1000 kernel weights were found to be positively associated with grain yield both at the genotypic and phenotypic level. Negative correlations have been observed between yield and non-component traits such as days to flowering and ear-length. The number of tillers per unit area expresses a strong direct and indirect effect on yield and the other yield components and is a major factor controlling the correlations between these other characters and yield (Solanki and Bashki, 1973). Breeding early, high tillering cultivars with large kernels should lead to increases in yield level (Grafius and Barnard, 1976; Solanki and Bashki, 1973).

Tewari (1976) reported that the expression of the yield component responses and ultimately the yield of 60 barley cultivars was affected by plant maturation rate, spike length, grain number, plant height, 1000 grain weight, number of ears, internode number, and fodder yield, depending upon the environment. Spike length, the kernel weight and grain number had the greatest effect on yield. In a separate study (Sethi and Singh, 1978) forage yield of barley was also highly correlated with heading date in 28 cultivars. Regression analysis of heading date, plant height, tillers/plant, and green-forage yield to dry matter production accounted for 92% of the variability in dry forage production. These studies indicate that yield components are not passive products in the pathway determining grain yield, but instead,

exert strong influences on yield through the source-sink, transport relationships (Grafius, 1972).

ISOGENIC ANALYSIS

Numerous investigators have studied yield component responses under varying external conditions, such as photoperiod and temperature regimes (Aspinall, 1961; Aspinall and Paleg, 1963; Bell, 1939; guitard, 1960; Nicholls, 1974; Nicholls and May, 1963; Paleg and Aspinall, 1966; Takahashi and Yasuda, 1960; etc.) by stress from nutrient and water deficiencies (Aspinall, 1961; Aspinall et al., 1964) and soil temperature regimes (Day and Thompson, 1975). Relatively few, however, have used yield component responses to explain the internal patterns of component development affected by external environmental manipulation (Campbell and Mead, 1968; Downs et al., 1959; Faris and Guitard, 1969; Griffith, 1961; Guitard, 1969; and Hough, 1975), due to the difficulty in allowing just one or a few genetically controlled physiological traits to vary at a time. Isogenic analysis is one method of accomplishing this. Atkins and Manglesdorf (1942) first described the use of isogenic lines, and more recent authors (Eslick and Hockett, 1974; Faris, 1974; and Ferguson, 1974) have expanded the use of isogenic lines.

Studies of full-awn and half-awn isogenic lines have revealed that half-awned types produced the highest yields, except under the highest

yielding conditions, when full-awned types yield the most. It was postulated that under conditions of stress, differences in competition for substrate at the time of awn initiation and early growth affected the development of florets and tillers (Schaller et al., 1972).

Faris (1974) studied four isogenic awn types (full awn, half-awn, quarter-awn, and no awn) for fertile spikes/unit area and per plant, kernels/spike, kernel weight, and yield. The pattern of yield component responses revealed that the presence of the awn indirectly influenced kernel size and yield by affecting the number of spikes and florets which developed during the early phases of growth, thus creating a greater drain of nutrients in an awned isotype compared to an awnless isotype. The longer the awn the greater the demand, resulting in a reduced number of florets per spike and a reduced number of fertile tillers.

PHYSIOLOGIC CONTROL OF TILLERING

Numerous early studies on the control mechanisms of tillering (Watson, 1936; Leopold, 1947; Aspinall, 1961) failed to reveal a complete picture of tillering control (Kirby and Jones, 1977). Mineral nutrients and water availability influence tillering (Kirby and Jones, 1977), but the primary control factors are believed to lie in hormonal systems of apical dominance in the cereal plant (Kirby and Jones, 1977). In monocotyledons, auxin controls the distribution of nutrients, and

axillary bud growth is governed by the resulting nutrient availability (Aspinall, 1961, 1963; Kirby, 1977; Kirby and Jones, 1977; Seiler et al., 1974). The control system is not simple, since the tillers rapidly produce adventitious roots and become largely independent of vascular connections with the remaining plant (Kirby and Faris, 1972). Also, any system of nutrient distribution involves competition between a number of individual tillers for the total nutrient supply (Kirby and Jones, 1977).

Aspinall (1961, 1963) concluded that the rate and patterns of tillering is largely controlled by nutrient supply, and that any shceme of internal control of tiller elongation by an apical dominance system must account for the modification of control with changes in nutrient supply. With nutrient stress, the apice and not the tiller bud senesced; therefore, the tiller buds are believed to have more tolerance to nutrient and water stresses (Aspinall, 1963; Kirby, 1977), allowing the plant to break out of its nontillering period by the reapplication of nutrients and water during the period of head development (Kirby, 1977). Thus barley is not limited in the number of tillers due to size alone, but also is limited by nutrient levels.

The initial period of rapid tillering of barley is followed by a reduced rate of tillering which corresponds to the beginning of spike development in plants grown with unlimited nutrients. The rate of

tillering was reestablished after spike development. Inhibitory levels of available water cause fluctuations in tillering rate, which may be due to the cyclic activation of new tillers caused by the decrease in nutrient demands of newly headed tillers (Aspinall, 1961). Since the flush of tillering occurs between the formation of the spike and spike emergence, then the highest nutrient demand must occur during spike development, preventing the elongating of the new tillers and consequently little competition must originate from the developing kernels, thus supporting, in part, the theories of Adams (1967) and Hamid and Grafius (1978), on the developmental allometry of barley.

The effects of soil moisture stress on barley growth has also shown that organs growing most rapidly at the time of stress are the most easily stressed. Tillering, reduced during stress periods, is enhanced with the reapplication of water, up to anthesis. This effect is greatest the earlier the stress is applied, implying a continued development of tiller buds during the drought or stress period without consequent elongation. It was also shown that water stress applied before spike initiation is likely to influence only tillering (Aspinall et al., 1965).

Kernels per spike are seriously affected by stress applied prior to anthesis, probably by reducing the number of spikelets initiated. Stress at anthesis and shortly thereafter, results in shrivelled

kernels. However, as grain development proceeds, kernels became progressively less sensitive to drought (Aspinall et al., 1965).

An analysis of the contribution of component tillers to yield (Cannell, 1969a) in three spring barley varieties under different nitrogen levels and plant densities has shown that after the main tiller, the most important tiller was that developing in the axil of the first true leaf, followed by the coleoptile node tiller, and the tiller in the axil of the second true leaf. Secondary and tertiary tillers were rare and contributed little to yield. Survival and contribution to yield of the plants were highest for the main tiller. Differences in grain yields were not obtained under the different plant densities, but this is not unusual in barley grown under field conditions (Watson, 1958; Kirby, 1967; Stoskopf and Reinbergs, 1965; Frey, 1959 a&b). The varieties attained these similar yield levels through different response patterns in the yield components. Due to the variable patterns of tiller formation, it was concluded that tillering is an important compensatory mechanism in yield determination, although in Northwest field conditions most plants develop only one or two tillers (Cannell, 1969a; Stoskopf and Reinbergs, 1965).

Several studies on the effect of changing plant density on tiller morphology and development (Kirby, 1967, 1969; Kirby and Faris, 1972; Leakey, 1971) have shown that as plant densities increase, yield changes little, but the response differences in tillering is great,

while smaller response differences are reported for kernels per spike and kernel weight.

The formation of tiller buds up to the third leaf stage of growth are not affected by plant density. Interplant competition becomes evident only after the fourth tiller bud has started to develop, which corresponds to the stage at which spike primordia are differentiated. Since changes in density treatments have little effect upon the above general patterns, it would seem that the initiation of tiller buds is largely under internal control of the plant (Kirby and Faris, 1972).

Dissection has revealed that the tiller bud either grows and emerges from the leaf sheath, or it does not begin elongation, suggesting on "on-off" mechanism governed by a threshold effect of nutrient level, light, and gibberellic acid concentration. It was also shown that during early tiller growth, competition does not operate by a previously formed stronger shoot depriving a late formed weaker shoot (Kirby and Faris, 1972). This response has been termed "cooperative interaction." Instead, the later formed tillers seem to deprive the more mature tillers of nutrients causing a reduction in their tiller size (Kirby and Jones, 1977).

The determination of whether a growing tiller will develop a spike does, however, appear to be controlled by direct competition between tillers for light (Kirby and Faris, 1972; Kirby and Jones, 1977; Leakey, 1971) and nutrients (Aspinall, 1961; Cannell, 1968; Kirby and

Jones, 1977). Subsequent tillering is stopped under field conditions at the time of spike initiation (Aspinall, 1961 and Cannell, 1968), due to the increase in nutrient demand from the developing spikelet primordia, and the elongating tiller leaf sheaths and internodes (Kirby and Faris, 1972; Leakey, 1971).

CONTROL OF SPIKE DEVELOPMENT

One of the first studies on the morphological development of the spike was reported by Bonnett (1935, 1966) which concluded that tiller development can be divided into two phases of growth response of the stem and of the shoot. In the first phase, the tiller internodes remain short, the tiller meristem produces only leaf primordia, and the undifferentiated portions of the spike apex begins to elongate. The second phase begins by the elongation of the tiller internodes and the differentiation of double ridges on the shoot, signaling the development of the spike. As the internodes continue to elongate, the spike and its parts differentiate and develop in the order of spikelet primordia, empty glumes, lemma, palea, stamens, awns, and finally pistil. Since the barley spike is indeterminant in growth, some response to the environment can be made in the number of fertile spikelets at the tip of the spike (Gallagher et al., 1975, 1976; Kirby and Faris, 1972). During this period of spikelet development the vascular elements are established but no connection to spikelet primordia are formed (Kirby and Rymer, 1974).

The spike elongation phase starts at the awn primordia stage and terminates immediately prior to spike emergence. The spikelet primordia continue to develop until the terminal primordia senesces, halting subsequent development, probably due to shortage of nutrients, water or light (Kirby and Faris, 1972). Spike elongation begins with an increase in concentration of gibberellic acid (Nicholls and May, 1963), the connection of vascular bundles of the rachis to the kernels, and the differentiation of the previously established procambium primordia (Kirby and Rymer, 1974). The association of the development of the vascular tissue with the high concentration of gibberellic acid leaves the question of control in some doubt, but is hypothesized that the growth rate may be regulated hormonally and vascularization may be a consequence of this growth, rather than the cause of it (Kirby, 1977; Kirby and Rymer, 1974).

KERNEL DEVELOPMENT

Harlan (1920) detailed much of the developmental morphology of Hannchen kernels. When the kernel is first developing, the growth is largely in the pericarp. The tissues surrounding the embryo sac and the ovary walls develop rapidly into the caryopsis. The size of the kernel is dependent upon age and position on the spike. The age of the kernel on the spike depends on the time of flowering which varies on the spike. The first florets to flower are located centrally on the

spike; the last to fertilize are at the extremities of the spike (Harlan, 1920).

Moisture loss in the kernels is correlated to kernel weight (Martini et al., 1923; Harlan and Anthony, 1920, 1921; Harlan and Pope, 1923; Gallagher et al., 1976). A core of vascular tissue in the spikelet terminates in the ovary in four vascular bundles, indicating that assimilates from the rest of the plant can easily be translocated to the developing kernel (Kirby and Rymer, 1974).

After spike emergence the spike and tiller (leaves and culm) both deposit assimilates in the grain (Watson and Norman, 1932). Carbohydrates and nitrogen compounds are transported and assimilated independently of each other. Carbohydrate contribution by photosynthesis in the green parts above the flag leaf node reportedly amount to more than 85% of the total grain weight causing high correlations between grain yield and areas of green parts above the flag node (Simpson, 1967; Yap and Harvey, 1972). Leaf areas, peduncle area, and spike area have all been shown to positively affect grain yield (Yap and Harvey, 1972).

In a study of awned versus awnless isogenic lines of barley, the net photosynthesis per spike of the awnless and deawned types were similar. The awned type had a 40% increase in photosynthetic capacity over the awnless isotype. Net photosynthesis of the head was only 30-40% that of the flag leaf, but only 20% of the flag leaf assimilate was translocated to the spike. Assuming all of the assimilates

photosynthesized in the spike remain there, it was concluded that for both isogenic types (short and long awn), 34% of the total assimilate to the head were contributed by the flag leaf and 66% by the spike itself (Teare et al., 1972; Faris, 1974; Johnson et al., 1975; Yap and Harvey, 1972).

Awn dry weight rather than number or length, best describe the photosynthetic tissue present (Johnson et al., 1975). An increased amount of awn tissue resulted in greater rates of net photosynthesis, dark respiration, and transpiration per spike. Awns also varied in their peak photosynthetic activity, some reaching their peak at the start of kernel filling, some at the end of kernel development. All awns remained photosynthetically active throughout kernel development. Kernel weights were reportedly linearly related to awn length. Increased awn length was also associated with reduced number of spikes and florets per spike.

Conflicting studies have reported that in the earlier phases of grain filling, the flag leaf sheath and spike itself are the main sources for new assimilates used in filling the developing grain. From 30-40% of the final grain weight is provided by movement of material from the stem and leaves which can lose ½ of their weight during the period of grain filling (Biscoe et al., 1974; Gallagher et al., 1975; Yoshida, 1972). In light of this, it was postulated that if a crop variety is able to draw on large amounts of material assimilated prior

to anthesis and translocated from the stem under adverse conditions for grain filling, it would have a definite advantage over a variety which cannot (Gallagher et al., 1975, 1976).

Although premature cessation of growth of tillers and spike growth can be induced by moderate water stress, the rate of grain growth (dry weight) in the early stages of development can be reduced only by severe water stress (Aspinall, 1965). Water stress affects the growth and final morphology of the mature kernel in three ways: 1) continued water stress over a long period reduces grain growth; 2) severe water stresses cause an early cessation of growth; and 3) severe water stress causes loss of dry matter in the final stages of ripening.

Due to the large effect variable environments express on kernel weights, heritability estimates have varied depending on the varieties used, the environmental and seasonal conditions, and the method of calculation (Brothakur and Poehlman, 1970; Fiuzat and Atkings, 1953; Murty and Sethi, 1961).

ROOT DEVELOPMENT

The larger the crop yield, the more thoroughly is the available soil moisture utilized in those soil layers permeated by the roots, and the greater the depth at which a barley crop must secure its requisite moisture (Conrad, 1937).

Plant densities have a large effect on both root growth and the percentage of water moisture utilized by the crop (Kirby and Rackham, 1971). As plant density increases from 50 to 800 plants/m^2 the root and shoot dry weights increase. Most barley roots are above 30 cm with 10% of the roots occuring below 1 meter. However, barley roots often penetrate to 132 cm, and often constitute up to 2% of the soil weight at the four-foot level (Kirby and Rackham, 1971; Kirby, 1967).

Root system development may be controlled by a highly coordinated hormonal regulating mechanism (Crossett et al., 1975). In heterogeneous soil environments, the development of a particular branch in a root system depends not only upon the conditions in its immediate surroundings, but also upon the growth of the remainder of the root system. The compensatory response can vary considerably depending upon the extent and type of alteration of growth (Crossett et al., 1975). Brachytic isogenic lines of Betzes (short stature barleys) have root systems that are genetically reduced in their depth of penetration, resulting in an increased percentage of residual soil moisture (Ries, 1977), at different soil depths.

GENERAL MATERIALS AND METHODS

Five maturity Titan isotypes and Titan (Table 1) were evaluated in yield trials in 14 environments and in space planting conditions in one environment. Physiological, morphological and agronomic traits as well as yield components and quality components were evaluated in each environment. The specific inheritance of the heading dates in this material is not known, but it is suspected to mono- or bifactorial.

Table 1. Parental constitution of Titan isogenic series varying in heading date

Abbreviation	Pedigree	Heading Type
(E)	Munsing x 7 Titan Gatway x 7 Titan	Composited Early
(D)	B570 x 7 Titan Munsing x 7 Titan Gatway x 7 Titan	Composited Derived Normal
(T)	Titan	Normal
(M)	Munsing x 7 Titan	Medium Late
(L)	B570 x 7 Titan	Late
(V)	Munsing x 7 Titan	Very Late

The 14 yield trials were planted in randomized complete blocks with four replications in bordered four row 3 meter long plots, with 1.5 m^2 harvest area per plot. The seeding rate was 1 gm/30 cm for six

irrigated trials and .7 gm/30 cm for the eight dryland yield trials. The space planted nursery the seeding rate was 1 kernel/30 cm. Uniform fertilizer applications were based upon soil analysis at each location.

The statistical analyses utilized in these experiments varies somewhat from trait to trait. The traits of the mutant isotypes were compared by means of an "F-test" and when applicable, a Duncan's New Multiple Range test was used to compare responses among isotypes over the 14 yield trial environments (Steele and Torie, 1960; Snedecor and Cochran, 1967). Regression, correlation (Grafius, 1978; Pederson et al., 1978) and path-coefficient analysis (Hamid and Grafius, 1978) were applied when appropriate, and finally, a modified trisected version of Grafius' (1956) parallelipiped method was used to enhance comparison between the yield component responses of the isotypes. The remaining traits were summarized by converting each value to a percentage of the mean of all the isotypes at each environment and presented as a bar graph, to facilitate intertrait and interenvironment comparisons.

In the statewide regression analysis the mean response of all the isotypes is expressed as the unit line, and the individual regression line is an indication of the individual isotype response in relation to the unit line, and mean response

YIELD TRIAL - MEASUREMENT OF TRAITS

1. The yield, measured in grain weight per harvested area, is converted to quintels per hectare by the following equation:

Harvested Weights x .06728 = quintels/hectare.

2. Test weights (kg/hectalitre) were calculated utilizing the "Ohaus Test Weight Scale" and .946 liter volumes.

3. Heading dates were recorded as days after January 1 when the first floret of the main tiller reached the flag leaf blade on 50 percent of the plants.

4. Plant height (cm) was measured from the crown to the top floret at hard dough stage.

5. The seed sizing was accomplished by use of a mechanical shaker equipped with 2.381 x 19.05 mm and 2.182 x 14.05 mm slotted seives. The samples were shaken for three minutes. The seed remaining on the larger seive were recorded as "plump;" seed remaining on the smaller seive were recorded as "medium;" and the fraction passing through both seives were considered "thins." The percentages of each fraction to the whole were recorded.

6. Protein percent of the grain was obtained from the "Neotec Grain Quality Analyzer" (McNeal et al., 1978).

7. Kernel Weight (gms/1000 kernels) was obtained by counting the number of kernels in a 33.33 gm sample of grain and converting that count to a grams per thousand kernel basis.

8. The yield components, tiller/30 cm^2 and kernels/spike, were estimated by utilizing the procedure presented by Hamid and Grafius (1978), using ten random heads per plot, collected at each environment.

Kernel weights calculated from the yield harvests were utilized as the third yield component.

9. Percent shattering was determined as the average number of missing kernels on ten spikes.

SOIL MOISTURE REMOVAL

Soil sample from each plot, 30 cm increments to 180 cm (when possible), were taken near the center of each four row plot at Bozeman and Fort Ellis, 1977. Percent moisture for each sample was gravimetrically calculated based on wet weight and oven dried weight (100°C for 48 hours). An analysis of variance was calculated on each 30 cm level and Duncans Multiple Range test was used for mean separation when applicable. Correlations between soil moisture at each depth and the yield components, yield and heading dates were calculated.

SPACE PLANTED NURSERY

The space planted trial was planted in a randomized complete block design with two replications. The main tiller of each of ten plants per plot, selected at random, were analyzed for the following characteristics: chlorophyll content of N-1 leaf, area, width, and length of the "N" to the "N-4" leaf blades; spike length (cm); awn length (cm); number of kernels per spike (counted); rachis internode number and length; and tiller internode lengths of N to N-4 internode.

The following determinations were made on the complete plant: total number of tillers; total yield in grams; percent plump and percent thin kernels; and percent protein in the kernels.

The main tiller of each of the selected plants was defined as the first tiller to extend its spike from the boot. These tillers were labelled and excised at the base at 40% kernel moisture (kernel development was at a maximum, but lower leaf senescence had not occurred). The tillers were placed in an ice bath and data collected immediately for the before-mentioned traits. The chlorophyll readings were taken from the first leaf below the flag leaf with an Ennis and Associated hand held chlorophyll meter (no reference).

The main tiller leaves (n=flag leaf to N-4 leaf) were excised at the leaf auricle. The area of each excised leaf blade was measured with a "Hayashi Denko" automatic leaf area meter and the length and the width (at the widest point) were recorded (cm).

Main culm internode length was measured from the basal node to the top of the N-1 node and then from the top of each node to the top of the succeedingly lower node.

The spike was excised at the basal internode, and the length of the rachis to the topmost kernel attachment was recorded, as was the length from the last kernel to the top of the longest awn. The kernels and rachis nodes were then counted. The mean of 10 rachis internodes

lengths was then calculated and recorded, to eliminate dwarfing effects at the end of the spike.

Harvest of the selected plants occurred at approximately 14% kernel moisture. The total number of tillers were counted and total yield of the ten plants was determined. The harvested seed was then analyzed for test weight, seed size, kernel weights, and percent protein following the same procedure previously described.

All of the collected data was analyzed for significant varietal effects with a standard analysis of variance (Steele and Torie, 1960). Duncan's New Multiple Ranges Test for mean separations were calculated when appropriate. Regression, correlation (Grafius, 1978; Pederson et al., 1978) and path-coefficient analyses (Hamid and Grafius, 1978) were used on all of the data. The responses were summarized in a trisected parallelipiped analysis to facilitate comparisons between different traits (Grafius, 1956).

RESULTS AND DISCUSSION

HEADING DATE, YIELD, AND YIELD COMPONENTS ANALYSIS OF VARIANCE

The analysis of variance (summarized in Table 2) of isotype heading dates in each environment shows that there were significant differences in isotypic heading dates detected at each location (Table 2). Duncan's Multiple Range test applied to the mean isotypic heading date responses over all yield trial environments (Table 2) revealed no differences between Titan and the derived Titan; but that the other maturity isotypes were different from each other and Titan (Figure 1). Heading date differences among isotypes were detected in the space planted nursery (Table 3, Figure 2).

The analysis of variance of the mean yield responses from 15 environments revealed no significant isotypic effects (Table 2, Figure 1), however, there were significant isotypic responses for each of the yield components, indicating component compensation. The pattern of compensation illustrated by the mean trisected parallelipiped reveals that early heading isotypes produced more tillers/30 cm^2, fewer kernels per spike and higher kernel weights (Figure 1).

There was little range in the mean kernel weight responses when compared to other traits (Figure 1). This is in agreement with Grafius (1956) and Thomas et al. (1970a) also found that variation in kernel weight responses are normally quite stable. The spikes/30 cm^2 and the