



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 cm² rate.

Yield, spikes/30 cm², 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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GENETIC AND ENVIRONMENTAL YIELD, YIELD COMPONENT, AND
MORPHOLOGICAL RESPONSES OF SIX HEADING DATE ISOTYPES
OF TITAN BARLEY (HORDEUM VULGARE) GROWN IN
15 ENVIRONMENTS

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

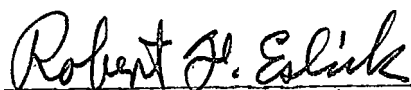
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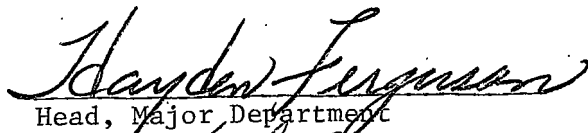
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TABLE OF CONTENTS

	<u>Page</u>
VITA , ...	ii
ACKNOWLEDGMENT	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	viii
ABSTRACT	xii
INTRODUCTION	1
LITERATURE REVIEW	2
Genetics of Heading Date Control	2
Photoperiod Manipulation	6
Yield Component Compensation	8
Isogenic Analysis	15
Physiological Control of Tillering	16
Control of Spike Development	21
Kernel Development	22
Root Development	25
GENERAL MATERIALS AND METHODS	27
Yield Trial-Measurement of Traits	28
Soil Moisture Removal	30
Space Planted Nursery	30
RESULTS AND DISCUSSION	33
Heading Date, Yield, and Yield Components	33
- Analysis of Variance	33
- Statewide Regression Analysis	45
- Correlated Genetic Responses of Characters	55
- Genetic Path Analysis	80
- Environmental Correlation	90
- Environmental Path Analysis	93
Morphological Traits	97
Soil Water Extraction Experiment	117

	<u>Page</u>
Percent Shattering	121
Source Seed Analysis	122
CONCLUSIONS	126
REFERENCES	132

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1 Parental constitution of Titan isogenic series varying in heading date	27
2 Analysis of Variance for yield and yield components on six isotypes of Titan grown in 15 environments	34
3 Heading dates of Titan isotypes relative to Titan	37
4 Analysis of variance for yield, yield components and correlations with heading date for six heading date isotypes of Titan grown in one space planted nursery	39
5 Correlation matrix between heading date, yield and the yield components for each isotype averaged over all environments (N=6) (Genetic Variation)	60
6 Correlation values between heading dates and yield and yield component responses in each environment	61
7 Correlation matrix between mean heading date, yield and yield components for six Titan maturity isotypes grown in space planted conditions (Bozeman, 1977)	65
8 Analysis of variance for morphological traits and correlations with heading date for six heading date isotypes of Titans grown in one space planted nursery	74
9 Path coefficient analysis of the responses of 6 Titan maturity isogenic lines averaged over 15 environments	82
10 Path coefficient analysis of the average responses of 6 Titan maturity lines grown in a space planted nursery	84

<u>Table</u>	<u>Page</u>
11 Path coefficient analysis of mean isogenic responses in each environment (genetic variation)	85
12 Correlation matrix between heading date, yield and yield components studied for each environment averaged over all isotypes (environmental variation)	91
13 Path coefficient analysis of mean environmental responses for each maturity isogene and the correlation of each component and yield to the environmental heading date (environmental variation)	94
14 Analysis of variance for morphological traits measured on six isotypes of Titan in 15 environments	98
15 Correlation matrix between all traits studied for each isotype averaged over all environments (N=6) (genetic variation)	104
16 Correlation matrix between mean trait responses for six Titan maturity isotypes grown in space planted conditions (Bozeman, 1977) (N=9)	112
17 Correlation matrix between all traits studied for each environment averaged over all isotypes (environmental variation)	113

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Trisected parallelipiped, mean percentage analysis, and Duncan's Multiple Range Test comparing the mean yield, yield component and quality component responses of six Titan heading date isotypes over 15 environments, ordered according to heading dates	36
2	Space planted trisected, parallelipiped, mean percentage analysis, and Duncan's Multiple Range Test comparing the yield, yield components and morphological traits of six Titan heading date isotypes, ordered according to heading date	38
3	Trisected parallelipiped and Duncan's Multiple Range Test comparing the yield and yield component compensation of six Titan heading date isotypes, ordered according to heading dates at each environment	41
4	Regression analysis showing heading date responses of six Titan maturity isotypes over 10 environments	48
5	Regression analysis showing number of spikes/30 cm ² of six Titan maturity isotypes over all environments	49
6	Regression analysis showing number of kernels per spike response of six Titan maturity isotypes over all environments	50
7	Regression analysis showing weight of 1000 kernels of six Titan maturity isotypes over all environments	51
8	Regression analysis showing yield response of six Titan maturity isotypes over all environments	54

<u>Figure</u>		<u>Page</u>
9	Comparison of days from planting to heading with the planting date at nine environments for each maturity isotype of Titan (Only nine of fourteen environments supplied both planting dates and heading date information)	57
10	Monthly rainfall (cm) and evaporation rate (cm) compared to the estimated plant growth cycle as conditioned by planting dates at Bozeman, 1976	58
11	Correlation of heading date to each component response for all isotypes at each environment, ordered according to the heading date of the environment	63
12	Mean percentage analysis and Duncan's Multiple Range Test for leaf area, length, width and main culm internode length of space planted nursery, ordered according to heading date of the isotypes	76
13	Path coefficient diagram showing interrelationships between the mean yield components and yield of six maturity isogenes grown in 15 environments	81
14	Path coefficients calculated on the genetic response across each environment and presented as a percentage of the total direct effects on yield, ranked according to the mean heading date at each environment (Only those environments with recorded heading dates were included)	87
15	Correlation of heading date to each yield component for each isotype across all environments, and ranked according to mean heading date for each isotype (environmental variation)	92

FigurePage

- 16 Path coefficient analysis calculated on the mean environmental responses of each heading date isotype presented as a percent of the total direct effects on yield, ranked according to the mean yield of the isotypes (Environmental Variation) 95
- 17 Mean percentage analysis and Duncan's Multiple Range Test comparing the pattern and range of quality component responses of six Titan heading date isotypes ordered according to heading dates, at each environment 100
- 18 Regression analysis showing test weight (kg/hl) responses of six Titan heading date isotypes over all environments 107
- 19 Regression analysis showing percent thin (through 5.5/64 in.) kernels of six Titan maturity isotypes over all environments 108
- 20 Regression analysis showing percent plump kernels of six Titan maturity isotypes over all environments 109
- 21 Regression analysis showing plant height (cm) responses of six Titan heading date isotypes over all environments 110
- 22 Regression analysis showing responses of percent protein in the kernels of six Titan heading date isotypes over all environments 115
- 23 Residual soil moisture remaining at each soil depth (x 30 cm) following harvest at a dryland (Ft. Ellis) and an irrigated (Bozeman) environment 118
- 24 Correlations of heading dates, spikes/30 cm², kernels/spike, kernel weights and yield to residual soil moisture at each soil depth in Bozeman, 1977 120

<u>Figure</u>		<u>Page</u>
25	Regression analysis showing percent shattering of six Titan heading date isotypes over all environments	123
26	Mean Percentage analysis histogram and Duncan's Multiple Range Test comparing the mean kernel weights, and number of kernels and weight of 11 gram planting volume for the source seeds of the environmental yield trials	125

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 cm² rate. Yield, spikes/30 cm², 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 sh₁, sh₂, and sh₃. To avoid confounding photoperiodic response with growth habit

responses in genetic analyses, spring habit cultivars or totally vernalized winter habit cultivars should be used (Takahashi 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 (Takahashi 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 25°C) 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 - seedling 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 parallelipeds (cubic volumes). Yield is considered as the volume, and the three yield components consist of the sides of the parallelipiped. The dimensional components are calculated as a ratio of the mean nursery response of each component, allowing different parallelipeds 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 uniformly 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 constraints 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 primordia 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 all 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 intercultur 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 scheme 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 apices 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; Leahey, 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 $\frac{1}{2}$ 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/m² the root and shoot dry weights increase. Most barley roots are above 30 cm with 10% of the roots occurring 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 Gateway x 7 Titan	Composited Early
(D)	B570 x 7 Titan Munsing x 7 Titan Gateway 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 m² 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 sieves. The samples were shaken for three minutes. The seed remaining on the larger sieve were recorded as "plump;" seed remaining on the smaller sieve were recorded as "medium;" and the fraction passing through both sieves 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 cm² 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 succeeding 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 parallelepiped reveals that early heading isotypes produced more tillers/30 cm², 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 cm² and the

Table 2. Analysis of Variance for yield and yield components on six isotypes of Titan grown in 15 environments.

Environment		Head Date	Spikes/ 30CM ²	Kernels/ Spike	Kernel Wt./1000	Yield
7601	VAR. M.S.	68.3**	89.7**	208.1**	12.1**	55.1
	ERROR M.S.	.7	5.6	8.1	1.2	21.6
	$\bar{X}$	185.2	21.0	49.5	33.4	36.8
7605	VAR. M.S.	94.8**	45.2**	69.0**	4.8**	11.3
	ERROR M.S.	.4	9.5	4.7	.2	36.8
	$\bar{X}$	176.5	25.8	33.5	35.8	35.1
7607	VAR. M.S.		8.9	111.5**	33.9**	24.6
	ERROR M.S.	No Data	8.9]	7.5	.2	13.9
	$\bar{X}$		23.3	42.2	33.0	33.7
7701	VAR. M.S.	137.0**	144.9**	255.7**	8.3**	141.0**
	ERROR M.S.	1.1	18.1	40.4	1.7	17.7
	$\bar{X}$	177.5	20.3	41.2	33.6	32.4
7707	VAR. M.S.	98.6**			8.4**	47.9**
	ERROR M.S.	.1	No Data	No Data	.6	4.1
	$\bar{X}$	168.7			35.3	31.6
7709	VAR. M.S.		624.5**	158.6**	4.0	180.8
	ERROR M.S.	No Data	185.9	30.0	2.9	84.8
	$\bar{X}$		17.3	37.3	33.8	29.6
7606	VAR. M.S.	83.7**	99.3*	241.0**	35.8**	9.5
	ERROR M.S.	1.9	22.5	29.2	2.5	17.9
	$\bar{X}$	183.5	19.7	39.3	32.3	29.4
7708	VAR. M.S.		59.3*	14.7	13.2**	40.7**
	ERROR M.S.	No Data	17.7	11.1	.4	4.5
	$\bar{X}$		17.3	48.2	31.8	27.8
7705	VAR. M.S.	64.4**	.9	116.9**	6.3**	23.3
	ERROR M.S.	.5	7.1	11.8	.3	12.0
	$\bar{X}$	170.5	11.7	40.7	34.6	26.2
7706	VAR. M.S.	88.2**	6.0	113.4**	17.3**	10.5
	ERROR M.S.	.5	11.0	56.0	1.8	24.2
	$\bar{X}$	173.5	11.7	51.2	33.2	23.3
7602	VAR. M.S.		12.8	97.0**	4.8*	23.4
	ERROR M.S.	No Data	7.2	11.7	1.3	14.1
	$\bar{X}$		12.7	48.3	32.2	21.4

*, **Significant at the P=.05, P=.01 level, respectively for the "F-Test."
Environments are coded as in Figures 2 and 6.

Table 2. (Cont'd.)

Environment		Head Date	Spikes 30cm ²	Kernels/ Spike	Kernel Wt/1000	Yield
7608	VAR. M.S.	68.4**	3.2*	26.4	7.9	6.8
	ERROR M.S.	.6	.9	11.7	3.7	3.1
	X	164.3	11.2	47.5	34.9	20.2
7702	VAR. M.S.	39.8**	.1*	43.9	20.2**	11.8
	ERROR M.S.	1.4	2.3	32.7	.3	8.3
	X	193.7	9.7	52.8	30.4	13.5
7711	VAR. M.S.	161.5**	15.0**	62.6**	16.4**	51.6**
	ERROR M.S.	.2	2.3	11.9	.7	6.2
	X	189.0	9.5	49.3	33.2	17.5
7609	VAR. M.S.		479.4	87.5**	.02	89.6**
	ERROR M.S.	No Date	181.8	9.9	.04	13.9
	X		34.3	47.0	25.4	17.1
MEAN OF	ERROR M.S.	.740	34.34	19.76	1.20	17.16
ENVIRON. X		178.2	17.9	44.9	32.9	26.7
	D.F.	50	65	65	70	70

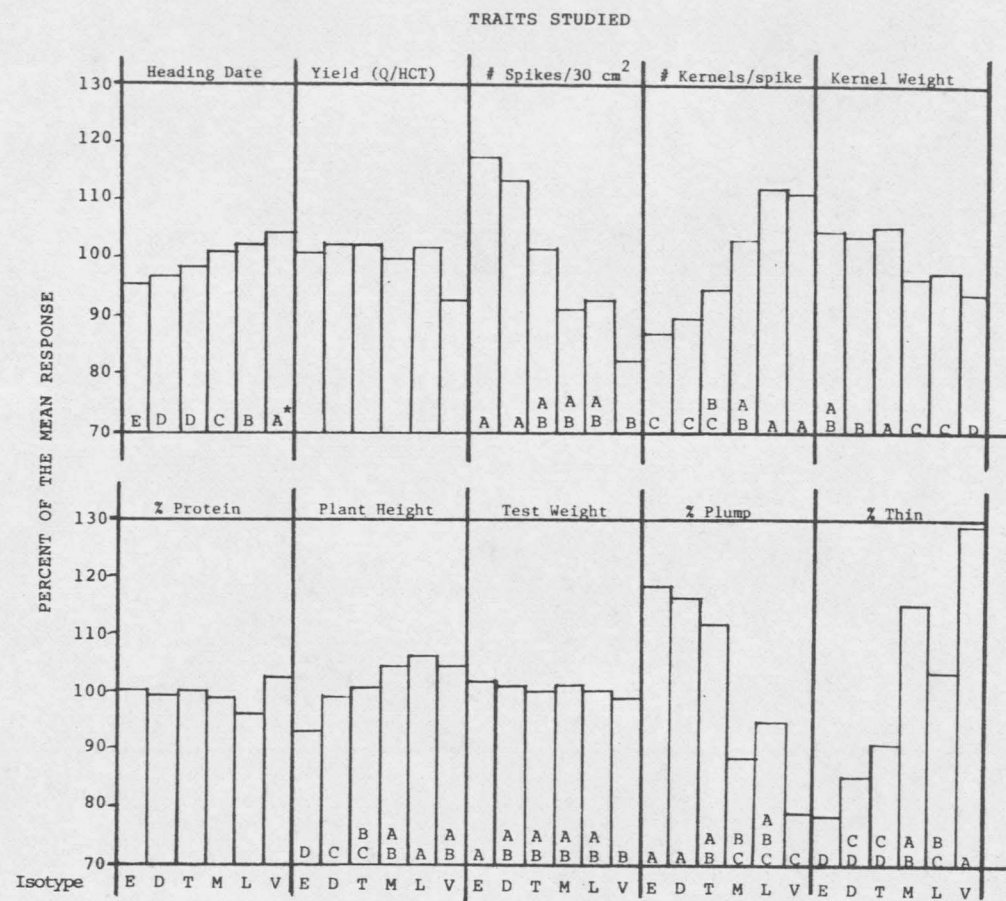


Figure 1. Trisected parallelipiped, mean percentage analysis, and Duncan's Multiple Range Test* comparing the mean yield, yield component and quality component responses of six Titan heading date isotypes over 15 environments, ordered according to heading dates.

*Separate letters denote significantly different means. Similar letters denote non-significant differences ($P = .05$).

Table 3. Heading dates of Titan isotypes relative to Titan.

Maturity code	Maturity type	Relative Heading date-days
E	Early	-3.1 E
D	Derived	-0.7 D
T	Titan	0 D
M	Medium late	+4.2 C
L	Late	+6.3 B
V	Very late	+8.3 A

*Separate letters denote significant differences, $p=.05$.

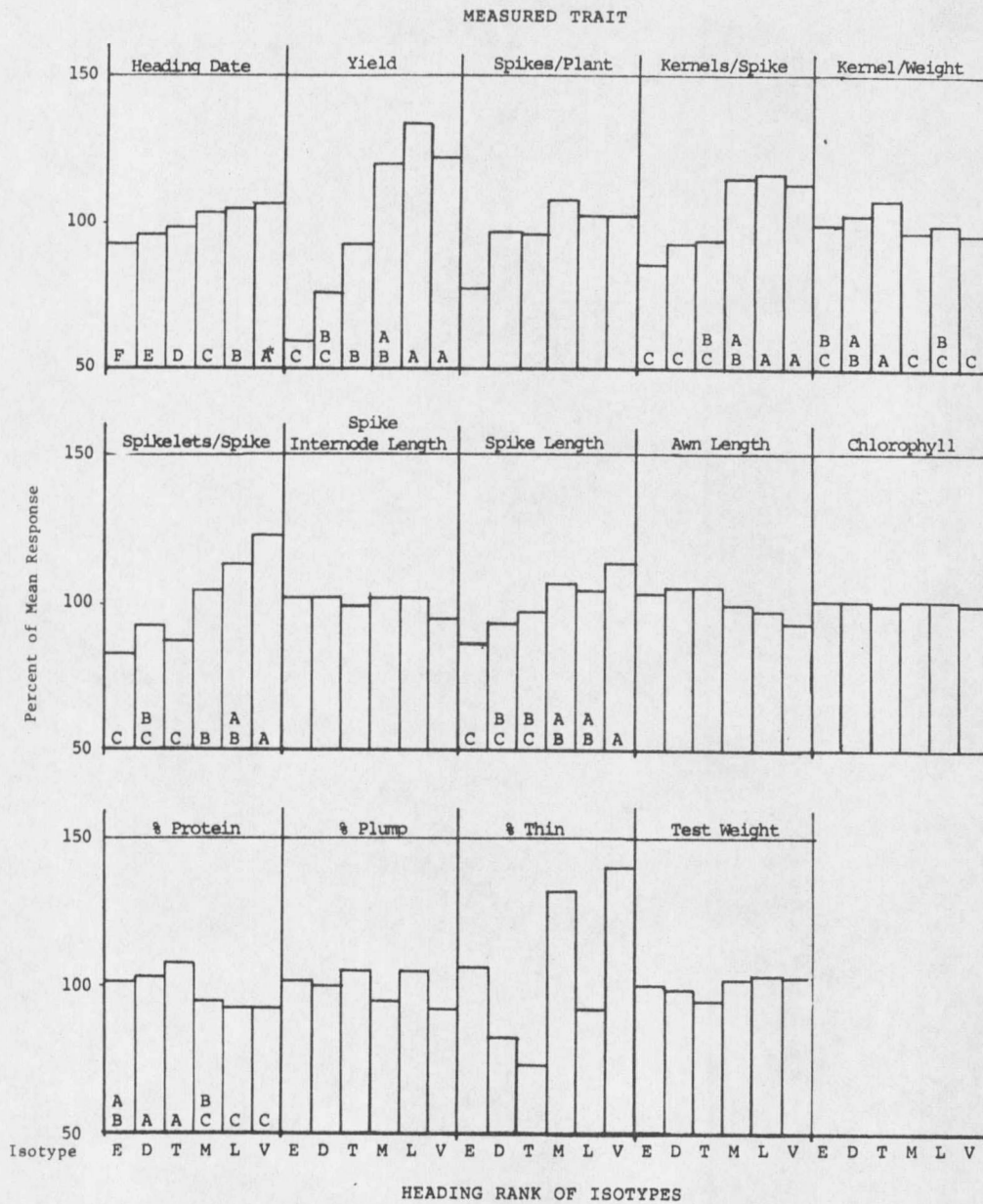


Figure 2. Space planted trisected, parallelipiped, mean percentage analysis, and Duncan's Multiple Range Test* comparing the yield, yield components and morphological traits of six Titan heading date isotypes ordered according to heading date.

*Separate letters denote significantly different means. Similar or no letters denote non-significant differences ($P = .05$).

Table 4. Analysis of variance for yield, yield components and correlations with heading date for six heading date isotypes of Titan grown in one space planted nursery.

CHARACTERISTIC MEASURED	VARIETY	ERROR		REGRESSION	CORRELATION
	MEAN	SQUARE	MEAN	b_{yx}	r
	SQUARE	DF = 8	$\bar{x}$	TO HEADING DATE:	
HEADING DATE, days after 1/1	467.50**	27.99	17.6	1.00	1.00
YIELD, gms/10 plants	528.40**	52.50	49.88	2.61	.94**
SPIKES/ PLANT, No.	294.10	212.81	26.27	.71	.75*
KERNELS/ SPIKE, No.	2391.62**	175.88	65.66	2.01	.97**
KERNEL WEIGHT, mg	6.70**	1.00	42.12	-.15	-.48

*, **Significant at $P=.05$, $P=.01$, respectively.

kernels per spike responses reveal a greater range in response among the isotypes. The fact that the late isotype heading date was intermediate (although not significantly different) to the other two late isotypes (Table 3), both of which had the lower yield responses and lower values, for each yield component over 14 environments, indicates the possibility of associated genetic linkages favoring adaptation. The separate environmental responses, however, did not always follow these same mean patterns, as revealed by the Duncan's Multiple Range test applied to the responses at each environment (Figure 3).

Of the environments studied, 9 of 14, 10 of 14 and 12 of 15, resulted in significant isotype effects for the spikes per 30 cm², kernels per spike, and kernel weight responses, respectively. In contrast to this, only 5 of 15 environments had significant isotype yield responses, illustrating the greater latitude of response between the maturity isotypes for the yield components than was observed for yield (Table 3). With the exception of spikes/plant, the space planted nursery had significant differences for yield and the yield components (Table 5, Figure 2).

The trisected parallelepiped for each environment reveals that the order of yield responses between the maturity isotypes is not consistent from environment to environment (Figure 3), implying that a specific heading date response may be advantageous in one environment, but not in another.

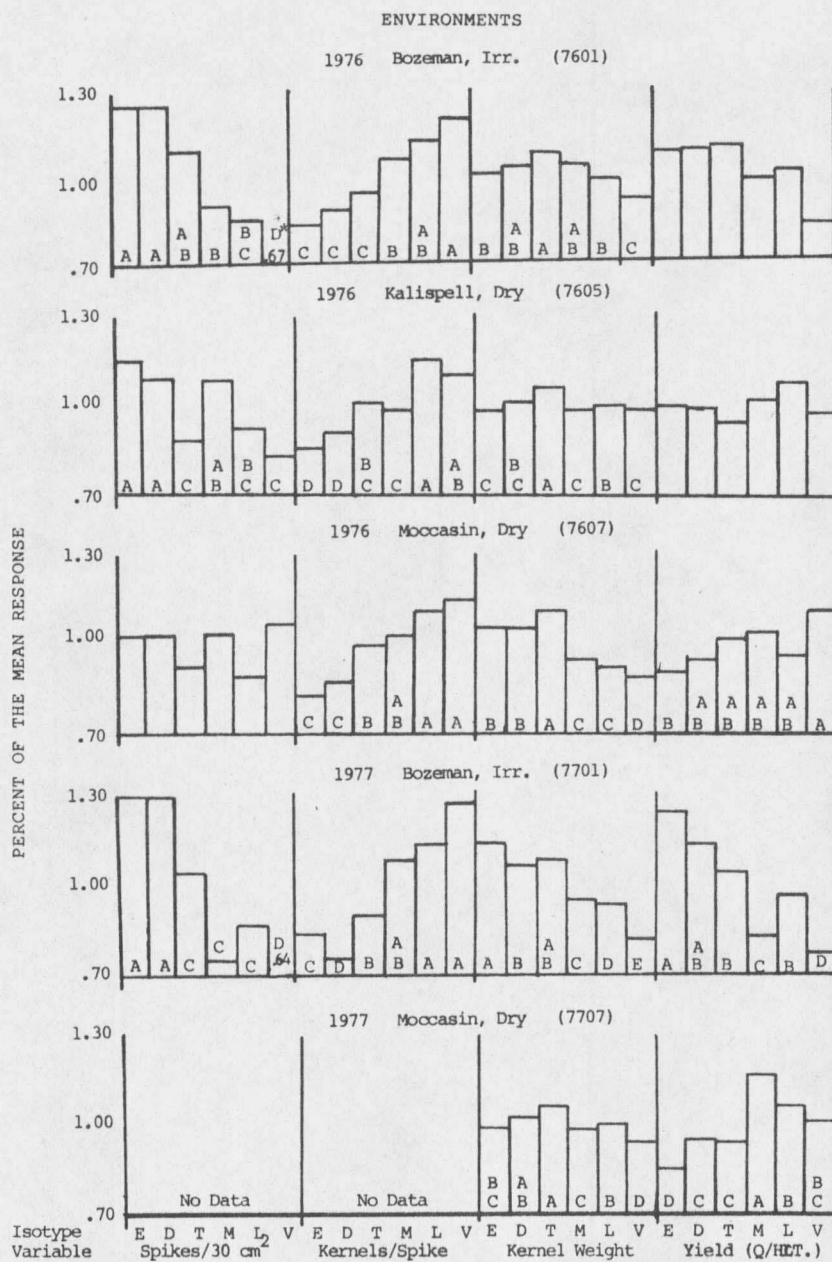


Figure 3. Trisected parallelepiped and Duncan's Multiple Range Test* comparing the yield and yield component compensation of six Titan heading date isotypes ordered according to heading dates at each environment.

*Separate letters denote significantly different means. Similar or no letters denote non-significant differences ($P = .05$).

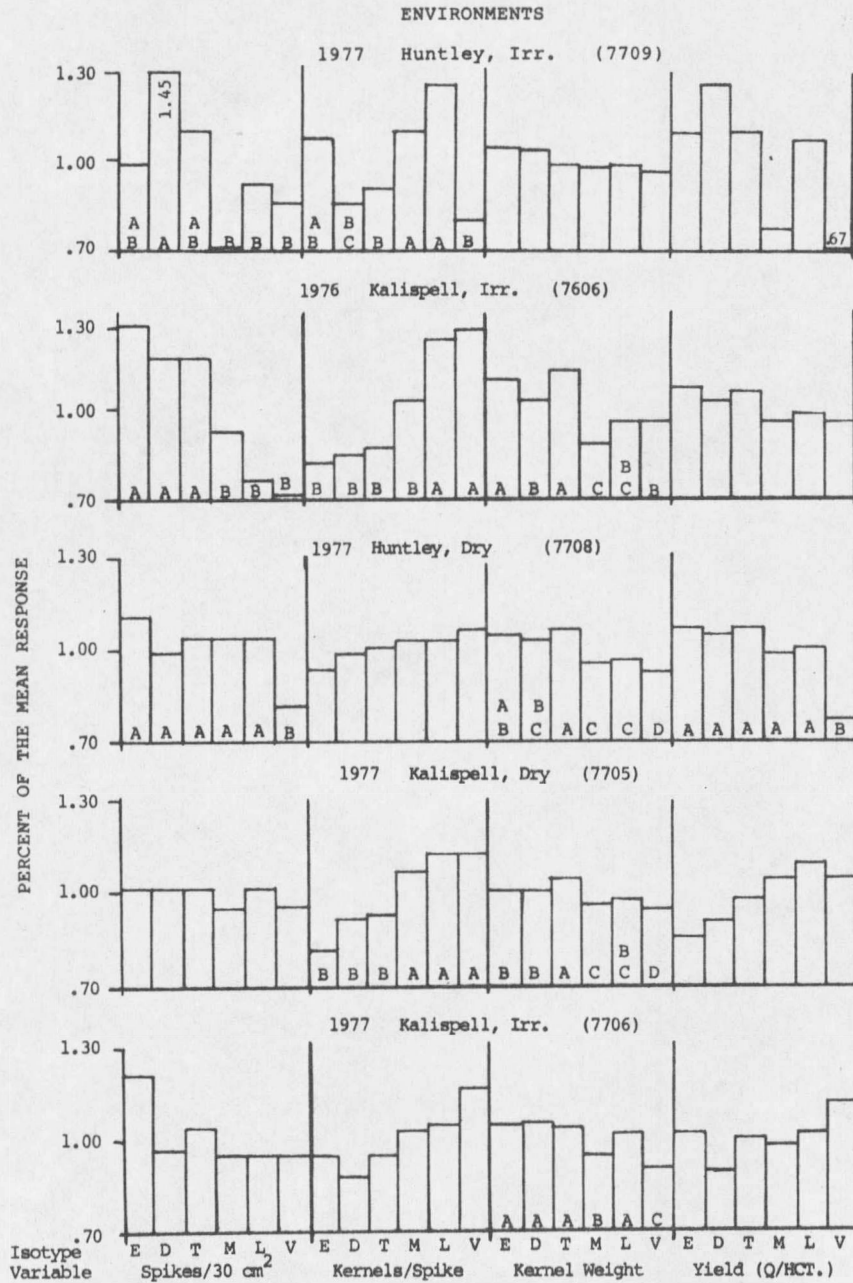


Figure 3. (Continued)

ENVIRONMENTS

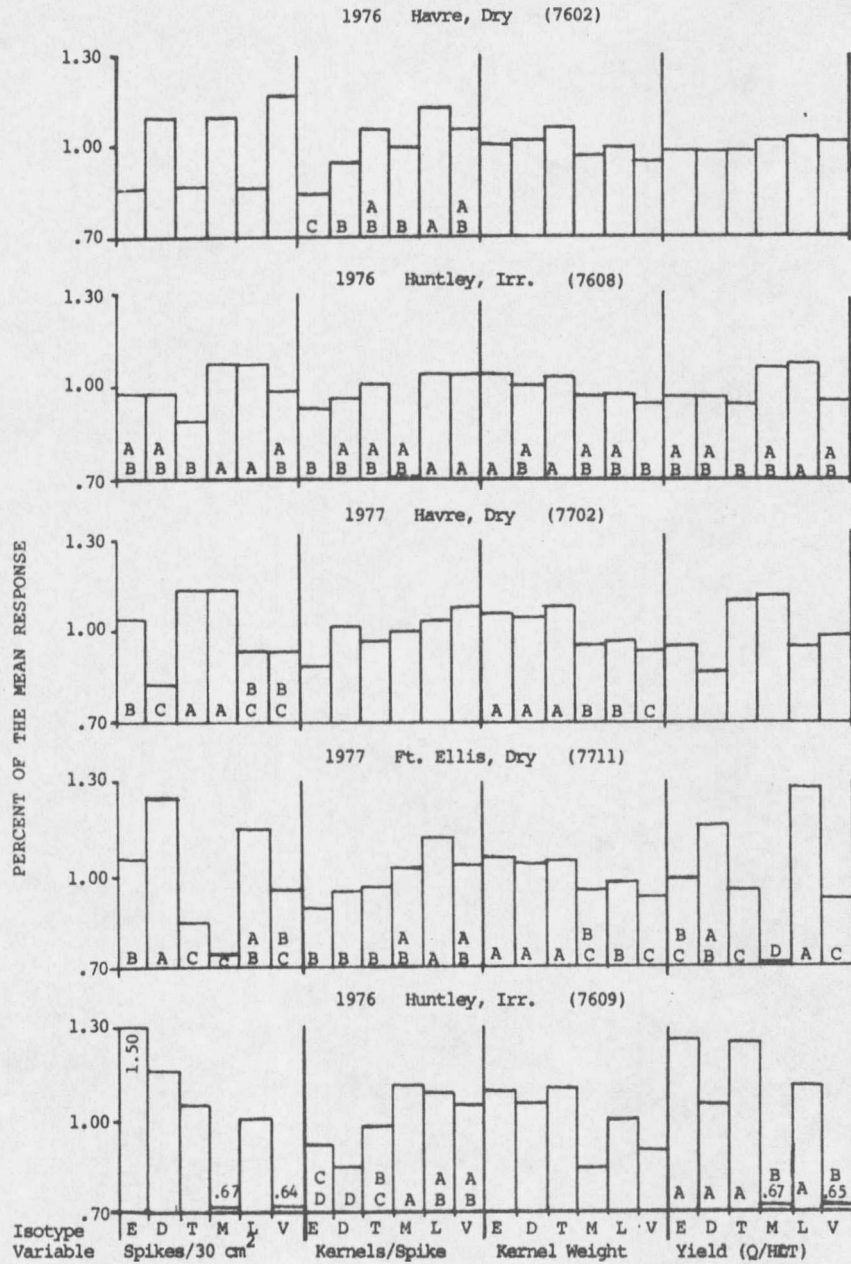


Figure 3. (Continued)

The differences in yield response at Huntley (7609), can be explained by a serious infestation of grasshoppers in August and September, causing an approximated 1/3 yield loss. The kernel weight responses indicate that the grasshoppers differentially preferred the later heading isotypes. Conclusions drawn from responses at this environment should consider this added factor. Discrepancies from the mean response patterns occur in five of the nine and eight of the twelve nurseries producing significant spikes/30 cm² and kernel weight responses (Figure 3), in contrast to one of the ten environments producing significant kernels per spike responses (Figure 3). Five of the eight discrepancies for kernel weights were due to Titan producing disproportionately higher kernel weights (Figure 3). This pattern of discrepancies reveals that tillers/30 cm² and kernel weights are not as environmentally stable as kernels per spike. The pattern of increasing kernels per spike with later heading dates for the isotypes was stable among environments, including the space planted environment (Table 4, Figure 2). The yield values from the space planted nursery should be considered in terms of simple units of yield per 10 plants. They cannot be compared to the drill-stripped nurseries in absolute values, but comparisons of the pattern of responses between the drilled and the space planted nurseries are valid and illustrative of differences in plant responses in a stressed environment compared to a non-stressed environment.

Significant isotypic differences for the same characteristics were found in the space planted nursery as were represented in the 15 yield trial environments except for number of spikes per plant (Table 2 and 4). The pattern of the yield component responses for spikes per plant was opposite of that observed in the mean response for the 15 environments (Figure 1). The significant yield differences found in the space planted nursery are probably due to the complementation of yield component responses as contrasted to the compensation in the drilled plantings (Figure 1 and 2).

STATEWIDE REGRESSION ANALYSIS

The slope of the regression line (b_{yx}) is indicative of the relative performance of the isotype's yield response over the different yielding environments (Finlay and Wilkinson, 1963; Pederson et al., 1978). If the slope is significantly different from unit slope, then an interaction associated with the mean response is implied between that isotype and the environments studied, although a non-associated interaction may occur between an individual isotype and any single environment. These non-associated interactions are not analyzed or discussed.

To discuss the regression analysis it is of value to define "performance" as those responses measured by b_{yx} and the position on the graph as determined by the mean. The coefficient of determination, r^2 ,

is a measure of the "stability" of the performance, a low r^2 indicating non-associated responses.

The coefficient of determination is related to slope by the relationship, $\sqrt{r^2} = b_{yx} \cdot \frac{S_x}{S_y}$ (Snedechor and Cochran, 1967). Therefore, an increase in stability (r^2) for a variety or isotype can be obtained by three methods. The first is to increase the slope (b_{yx}), retaining the same S_x and S_y . The second and third methods are to raise the standard deviation of the independent variable (S_x) or lower the standard deviation of the dependent variable (S_y), with b_{yx} remaining constant. Given sufficient entries in a nursery, selection for either the first or third methods will not change the standard deviation associated with the mean of nursery means (S_x).

If the slope is adjusted to approach the unit slope by selection for higher performance in low isotype performance regions, then it is possible that the mean isotypic response over all environments will be increased. For most traits, when the mean is increased the genetic maximum response is approached for a given environment. The upper range of the normal distributions are consequently limited, reducing the standard deviation (S_y). Thus, the coefficient of determination (r^2) can be increased by simultaneously increasing b_{yx} (if it is initially less than unity) and consequently increasing the mean response and therefore decreasing the standard deviation of the dependent variable (S_y). If initial slope is greater than unity, the reduction in

the standard deviation must over compensate for the reduction in the resulting slope.

The regression slopes (b_{yx}) for heading dates are shown not to be significantly different from the unit slope (Figure 4). Thus, regardless of the environment, as defined by the mean heading date, the isotypes headed consistently earlier or later. There were no associated isotype x environment interactions between the mean heading dates of the isotypic series. The early derived, medium late, and very late isotypes all showed a significant spikes/30 cm² response deviation from the mean environmental response (Figure 5). The two earliest isotypes responded proportionately more to conditions that favored tillering than Titan and the medium late, and very late responded less than Titan. The high coefficient of determination obtained for each isotype implies that the response of these isotypes was largely explained by the mean response at each environment and that the isotypic variety x environment interactions is quite predictable. Spikes/30 cm² had the greatest number of isotype x environment interactions of the yield components supporting the observations based upon the previous three types of analysis that this trait's pattern of response was not consistent among environments. Also, the pattern of interaction reveals that environments producing the fewest number of spikes/30 cm² express the least degree of differences among the isotypes, and those environments

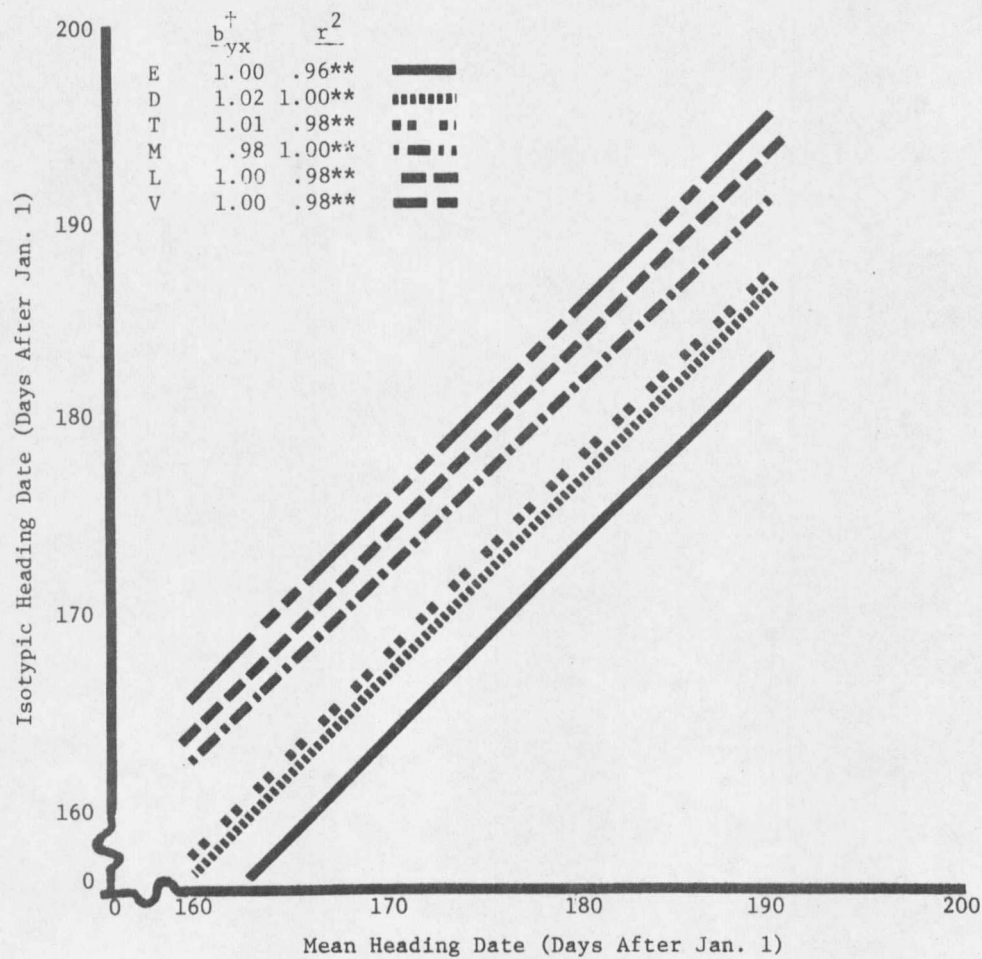


Figure 4 . Regression analysis showing heading date responses of six Titan maturity isotypes over 10 environments. *,** Significant at $p = .05$, $p = .01$, respectively. $\dagger$ t-test showing $H_0: b = 1.00$.

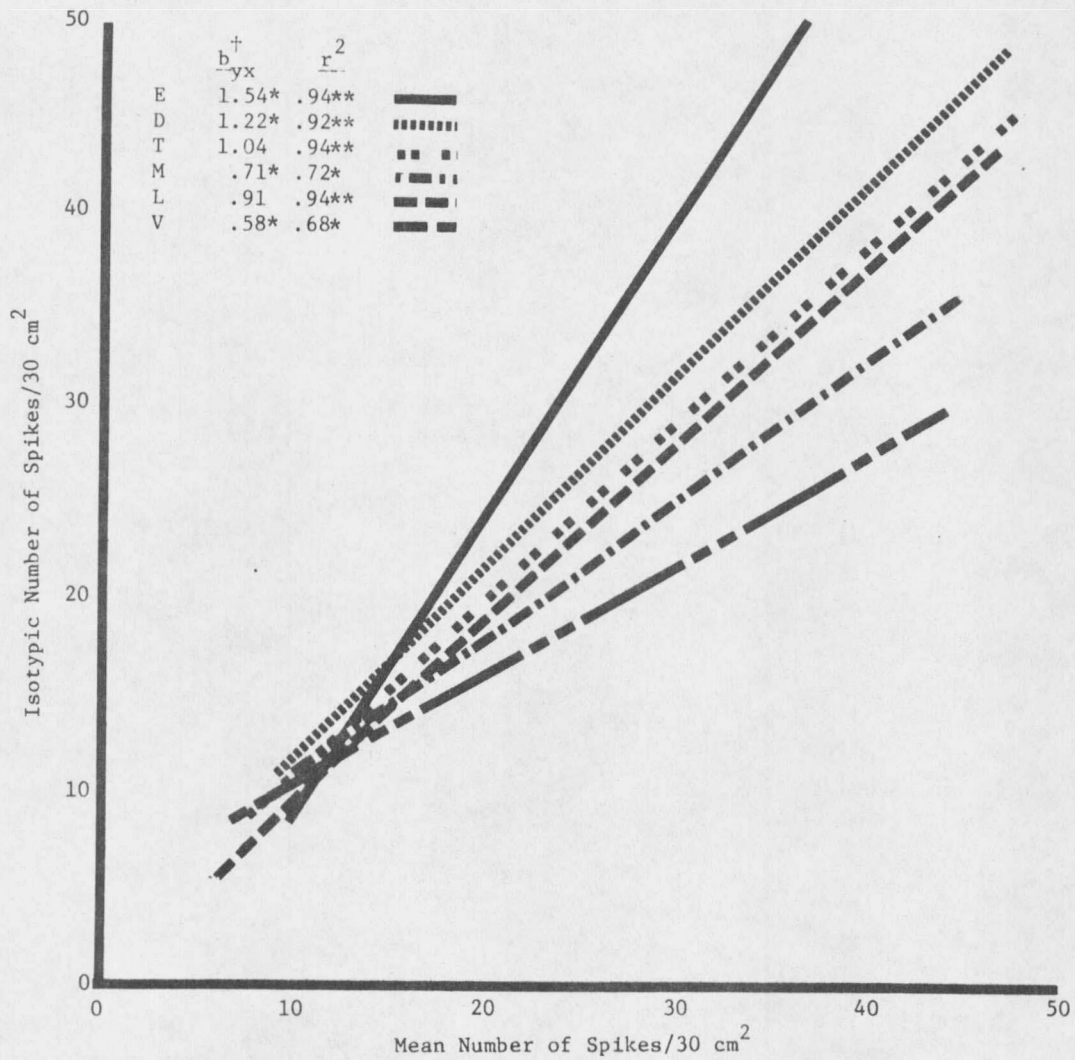


Figure 5. Regression analysis showing number of spikes/30 cm² of six Titan maturity isotypes over 14 environments. *,** Significant at $p = .05$, $p = .01$, respectively; † t-test showing $H_0: b = 1.00$.

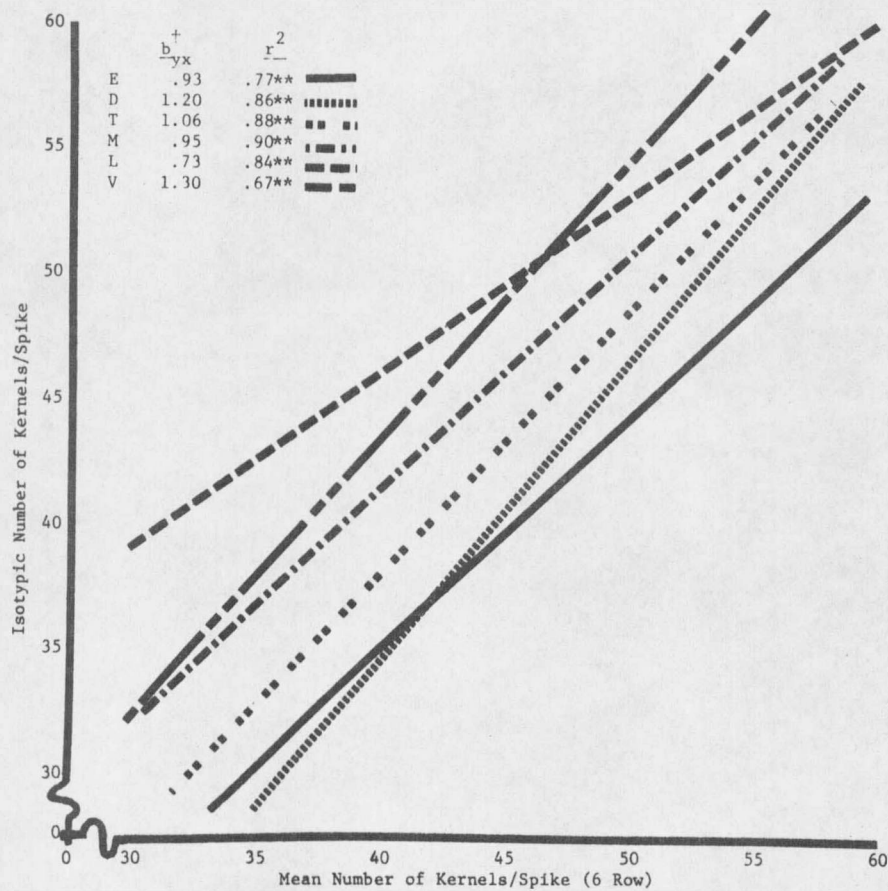


Figure 6. Regression analysis showing number of kernels per spike response of six Titan maturity isotypes over 14 environments. *,** Significant at $p = .05$, $p = .01$, respectively; $\dagger$ -t-test showing $H_0: b = 1.00$.

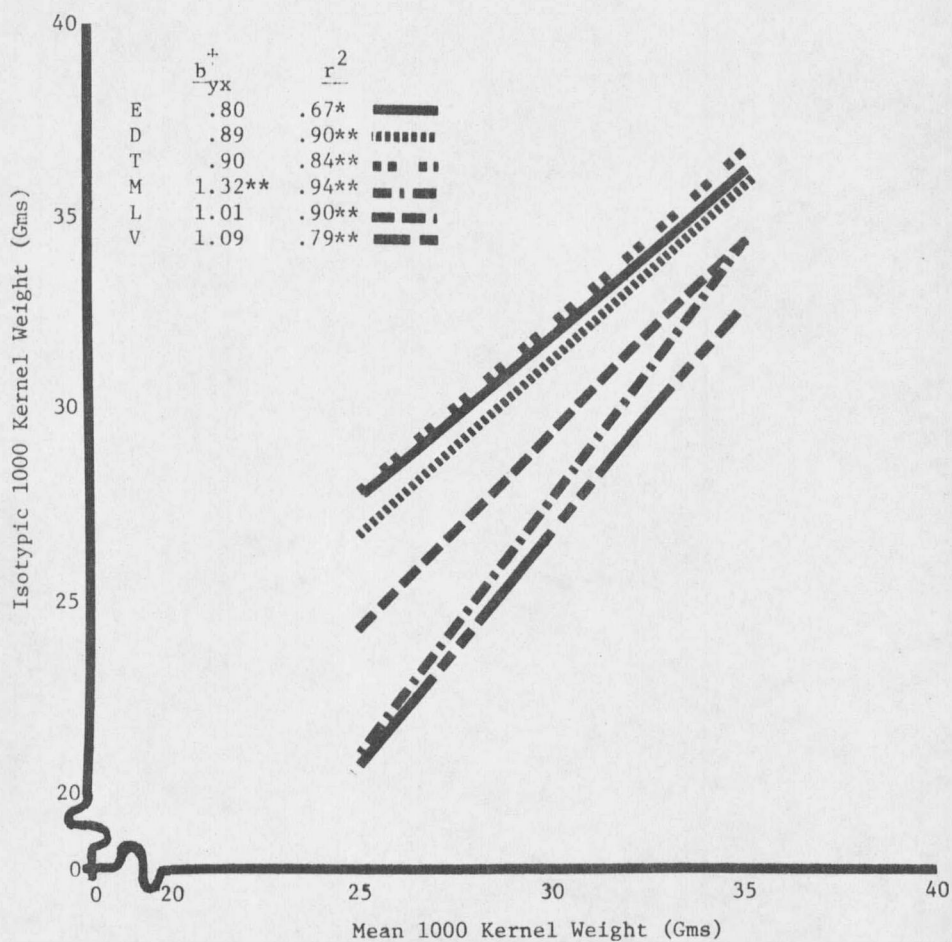


Figure 7. Regression analysis showing weight of 1000 kernels of six Titan maturity isotypes over 14 environments. *,** significant at $p = .05$, $p = .01$; respectively. $\dagger$ - t-test showing $H_0: b = 1.00$.

producing the highest number of spikes/30 cm² produce the greatest differences (Figure 5).

The consistent pattern of increased kernels per spike with an increased heading date (Figure 6) for each environment is revealed in five of six slopes showing non-significance from the unit slope (Figure 6). Late Titan had a significant associated isotype x environment interaction, which was due to the production of more kernels per spike in low response environments than occurred with the other isotypes. It seems that the spike development of the late isotype is favored over the earlier isotypes to a degree not consistent with simple pleiotropic increases in heading dates alone, indicating possible genetic linkages as previously discussed. The significant coefficients of determination (r^2) imply a good degree of predictability in the interaction responses of the isotypes relative to the overall gene pool response (Figure 6, Pederson et al., 1978).

Only the medium late isotype had a significant associated isotype x environment interaction for kernel weights (Figure 7). The magnitude of differences among the isotypes seemed to be less in high kernel weight environments and greater in low kernel weight environments, which are early planted as contrasted to late planted environments (Figure 7) (see correlation analysis). High kernel weights were obtained in the early planted nurseries because they tended to not run out of moisture as quickly.

No significant isotype x environment interactions for yield were detected (Figure 8). The fact that the yield components responses had significant associated interactions implies a compensating pattern between the components eliminating any associated yield isotype x environment interactions. This superficially implies that heading dates are not a vital criteria for yield performance in Montana. However, in the five environments producing significant yield differences, whether the early or later isotype yielded more depended upon the environment in question (for example, in locations 7701 and 7707 the early type went from highest to the lowest yielding type, Figure 3). This inconsistency in performance is not due to associated environmental interactions as shown by the regression slopes. Instead, it was due to the associated interactions of the yield components failing to respond in a compensating manner at a specific environment. This is demonstrated the lower r^2 measuring associated yield stability which tends to be more reduced for the early, medium late, and the very late isotype than for Titan, derived or the late isotype. This lack of stability of the yield response is partially determined by the reduced stability of the yield component responses as shown by the lower coefficients of determination (Figures 5, 6, 7). If the yield performance could be increased by adjusting the early isotype yield slope closer to unity, then the yield stability of the early isotype could be improved. To do this would require the adjustment of the tillers and the kernel weights.

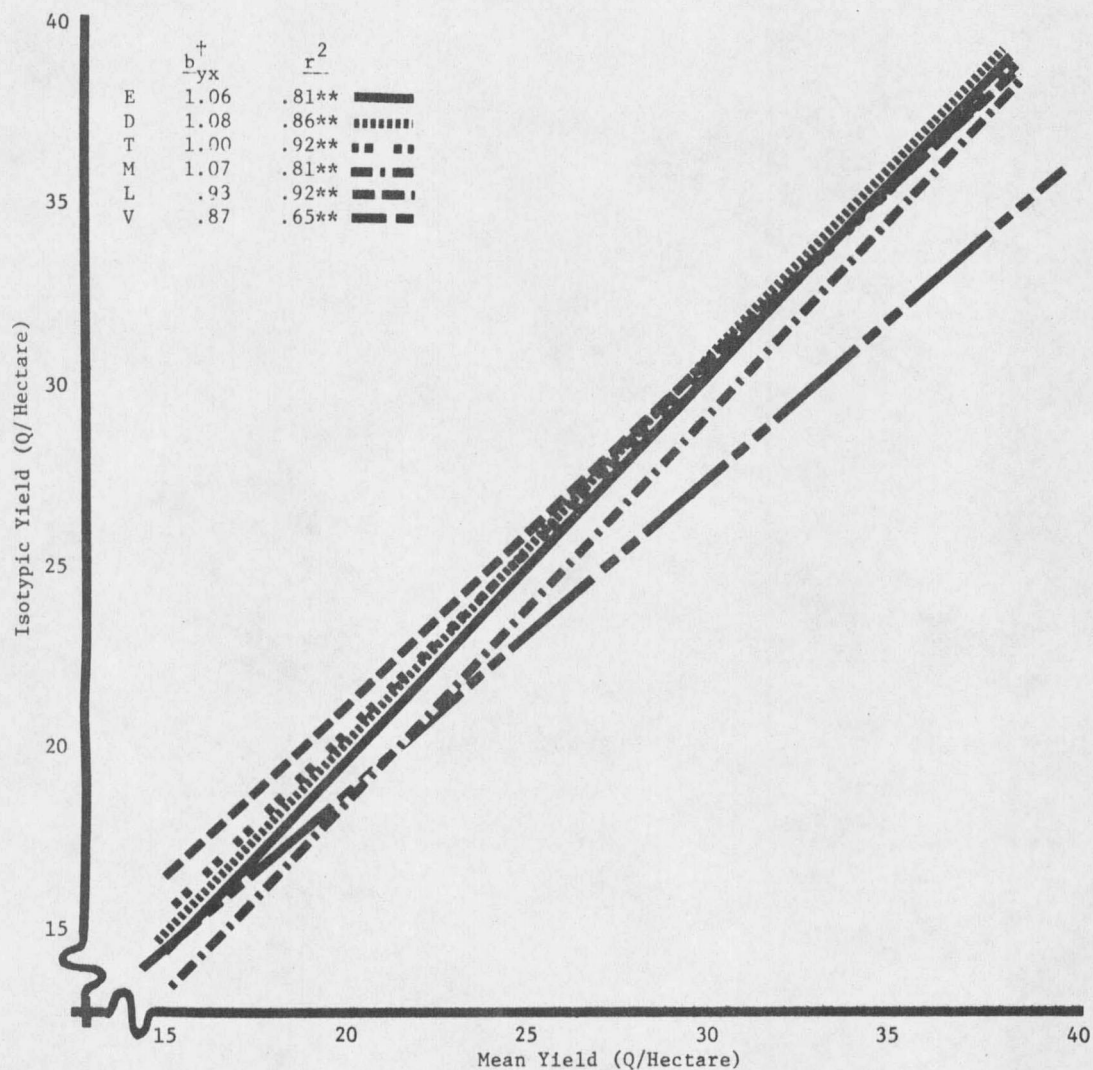


Figure 8. Regression analysis showing yield response of six Titan maturity isotypes over 14 environments. *,** significant at $p = .05$, $p = .01$, respectively. $\dagger$ - t-test showing $H_0: b = 1.00$.

slopes to the unit slope. Selection for high tillers in a low tiller environment (stressed?) and selection for high kernel weights in a high kernel weight environment (non-stressed) should adjust the slopes. This could cause better yield stability for the early isotypes in high yielding environments, enabling more consistent predictions of yield responses in a greater number of environments.

If general yield improvement through selection of cultivars were to be attempted, then the regression analysis implies that selection for tillers in high tillering environments, and for kernels in low kernel weight environments would be most effective due to the maximum differences occurring between the isotypes in these environments. The constantly large differences in kernels per spike performance over all environments implies that kernels per spike can be selected for in most of the environments studied.

CORRELATED GENETIC RESPONSES OF CHARACTERS

The principle criteria which determined the mean heading date in the environments studied was the date of planting (Figure 9). The correlation between planting date and mean heading date is significant and positive ($r=.91^{**}$). When plotted against the planting date of an environment (days after Jan. 1, Figure 9) the days from planting to heading become progressively shorter with later planting dates ($r=-.47$). The reduced period in growth is attributable to an increase in daylength

and a concurrent increase in mean daily temperature. The plants responded by shortening their vegetative stage, and the duration of the tiller and head development stages. This is consistent with greenhouse and growth chamber studies investigating photoperiod and temperature control on barley growth (Aspinall, 1966; Bell, 1939; Borthwick et al., 1971; Faris and Guitard, 1969; and Favret, 1975). It could be postulated that if a desirable heading date were known to bring the barley to heading on that date, for each week delay in planting beyond a certain date an isotype or cultivar of similar daylength sensitivity with a specific number of days earlier in heading could be planted, especially if yield responses can be stabilized. This would allow the grower to more accurately predetermine his harvest period and yield level.

In semi-arid climates the heading date and maturation rate of a crop will determine to a large degree the amount of residual soil moisture available at each successive developmental stage. In Montana, most of the plant available soil moisture is supplied by April, May, and June precipitation. High evaporation during the growing season and large water requirements of the crop (Figure 10) depletes the soil moisture beyond the replenishment supplied by precipitation during the latter part of the growing season, eventually causing drought stress. Generally, early planted or early maturing crops will have more plant available water than a late planted or late heading crop, given a

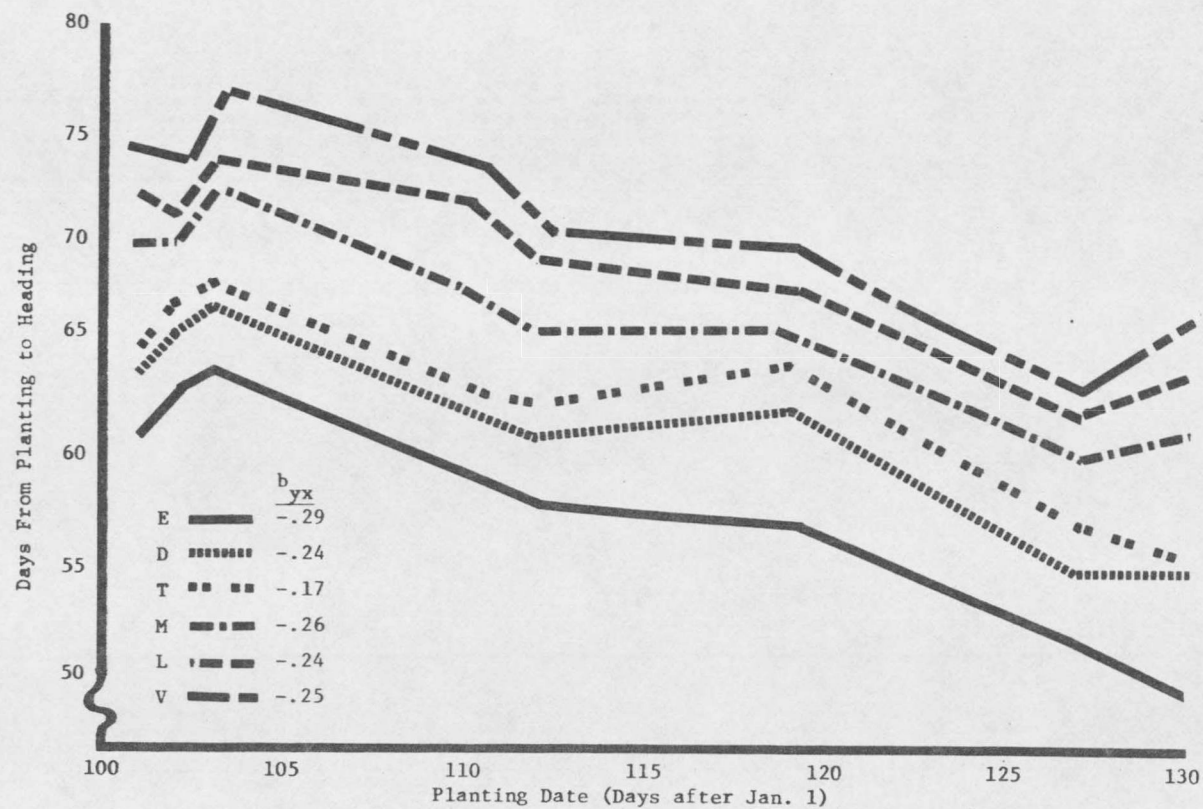


Figure 9. Comparison of days from planting to heading with the planting date at nine environments for each maturity isotype of Titan.

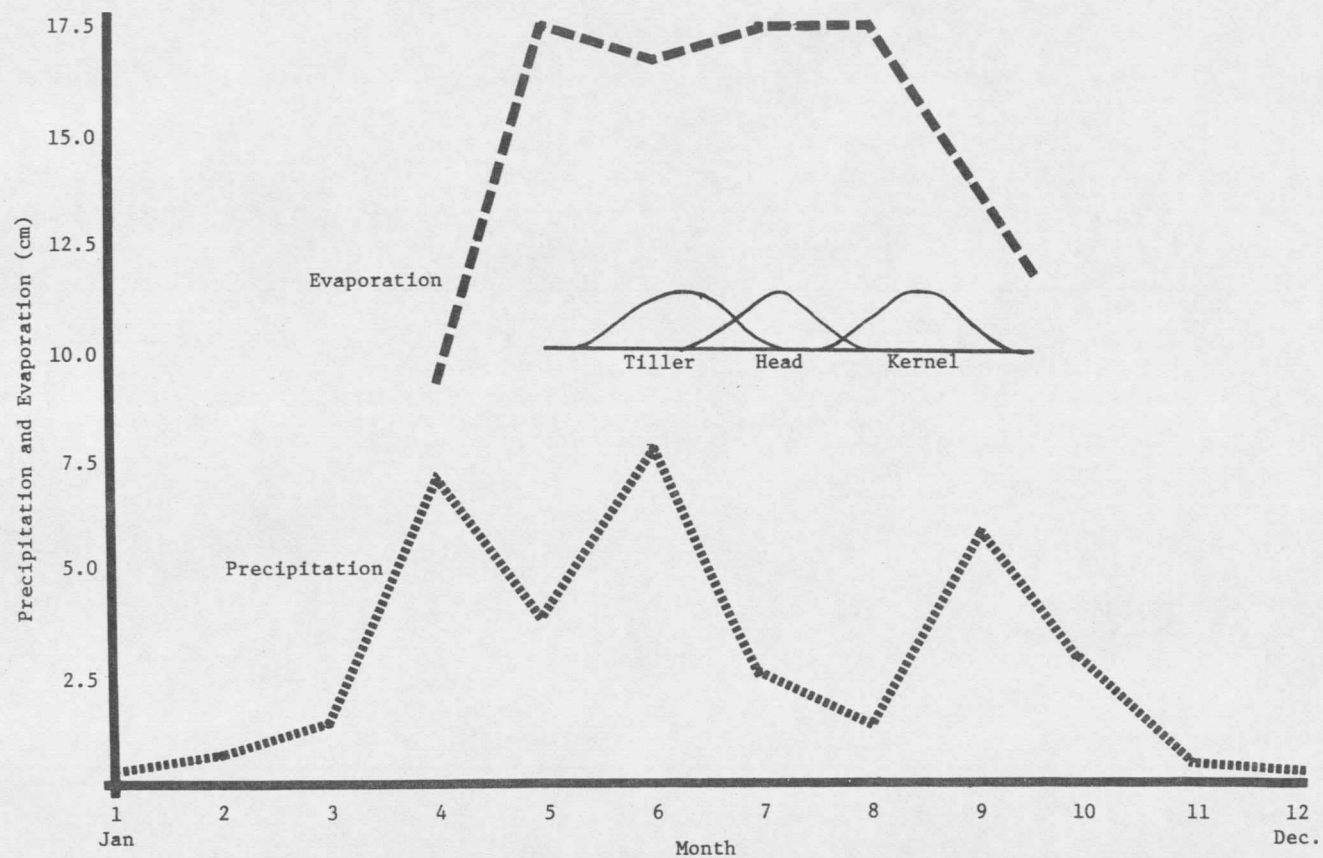


Figure 10. Monthly rainfall (cm) and evaporation rate (cm) compared to the estimated plant growth cycle as conditioned by planting dates at Bozeman, 1976.

specific developmental stage. This fact, and the altered rates of development, will be the primary forces affecting agronomic, morphological and yield component responses of plants differing in planting dates, or genetic heading dates. Due to the uniform environmental responses of the Titan heading date isotypes, it is possible to compare genetic with environmentally induced influences on plant growth responses without confounding the results with associated isotype x environment interactions for heading date responses.

When the mean response patterns due to genetic variations are correlated (Table 4), a large number of significant correlations are observed between heading dates, yield and the yield components. Mean heading date response is positively correlated to kernels per spike, and negatively correlated to spikes/ 30 cm², kernel weight. The correlation values between the yield components are all dependent upon their respective correlations to heading dates (Table 5). Consequently, spikes/30 cm² are negatively correlated to kernels per spike and positively correlated to kernel weights, etc. Kernels per spike and kernel weights are negatively correlated, in the classic compensating pattern. Mean genetic correlation shows spikes/30 cm² also being positively correlated to percent shattering, percent plump, and negatively correlated to plant height and percent thin. The pattern of negative and positive correlations between kernels per spike and the

Table 5. Correlation matrix between heading date, yield and the yield components for each isotype averaged over all environments (N=6). (Genetic Variation).

	Yield	Heading Date	Tillers/ 30 cm ²	Kernels Spike	Kernel Weight
YIELD	1.00				
HEAD DATE	-.58	1.00			
SPIKES/ 30 cm ²	.67	-.95**	1.00		
KERNELS/ SPIKE	-.46	.97**	-.93**	1.00	
KERNEL WEIGHT	.78	-.88*	.83*	-.82*	1.00

*, **Significant at the P=.05, P=.01 level, respectively.

Table 6. Correlation values between heading dates and yield and yield component responses in each environment.

Environ- ments §	Spikes/30 cm ²	Kernels/ Spike	Correlations To	
			Kernel Weights	Yield
.7601	0.96**	.99**	-.63	-.83*
.7605	-.69	.89*	-.23	.28
.7607	-.04	.96**	-.90*	-.37
.7701	-.90*	.92**	-.98**	-.77
.7709	-.52	.05	-.53	-.11
.7606	-.99**	.95**	-.83*	-.55
.7708	-.66	.96**	-.75	-.82*
.7705	-.66	.98**	-.89*	-.90*
.7706	-.76	.88*	-.62	.76
.7602	.46	.80	-.79	.42
.7608	.46	.90*	-.54	.34
.7702	-.15	.88*	-.92**	.23
.7711	-.20	.89*	-.92**	-.26
.7609	-.87	.81*	-.94**	-.52
MEAN	-.95*	.97**	-.88*	-.58
SPACE PLANTED	+.75	.93**	-.33	.89*

*, **Significant to the P=.05, P=.01 level, significantly.

§Environments are coded as in Figure 3.

other traits is opposite that observed for spikes/30 cm², and identical to the other traits positively correlated to heading dates.

Genetically induced correlations at each environment (Table 6) reveal that spikes/30 cm² is not consistently correlated to the environmentally stable heading date response. Thus, although the mean genetic responses did produce significant correlations, individual environments did not necessarily produce the same degree or type of correlations, further illustrating the environmental plasticity of spikes/30 cm response. Figure 11 reveals this pattern graphically. The same strong correlation values between heading date and kernels per spike (y) are found in almost every environment (Table 6 and Figure 11), supporting the responses portrayed in the parallelepiped histograms and the pattern of significant mean separations produced by the Duncan's Multiple Ranges test (Figure 3).

The correlations between kernel weights (z) and heading dates at each of the environments shows this factor to be variable between environments (Table 6). The correlations between kernel weights and other traits measured in the space planted nursery were not as strong as in the stress conditions, due to the moderate kernel weight response (Table 7).

In contrast to the strong genetic correlations alone, the mean genetic yield response was not significantly correlated to mean heading

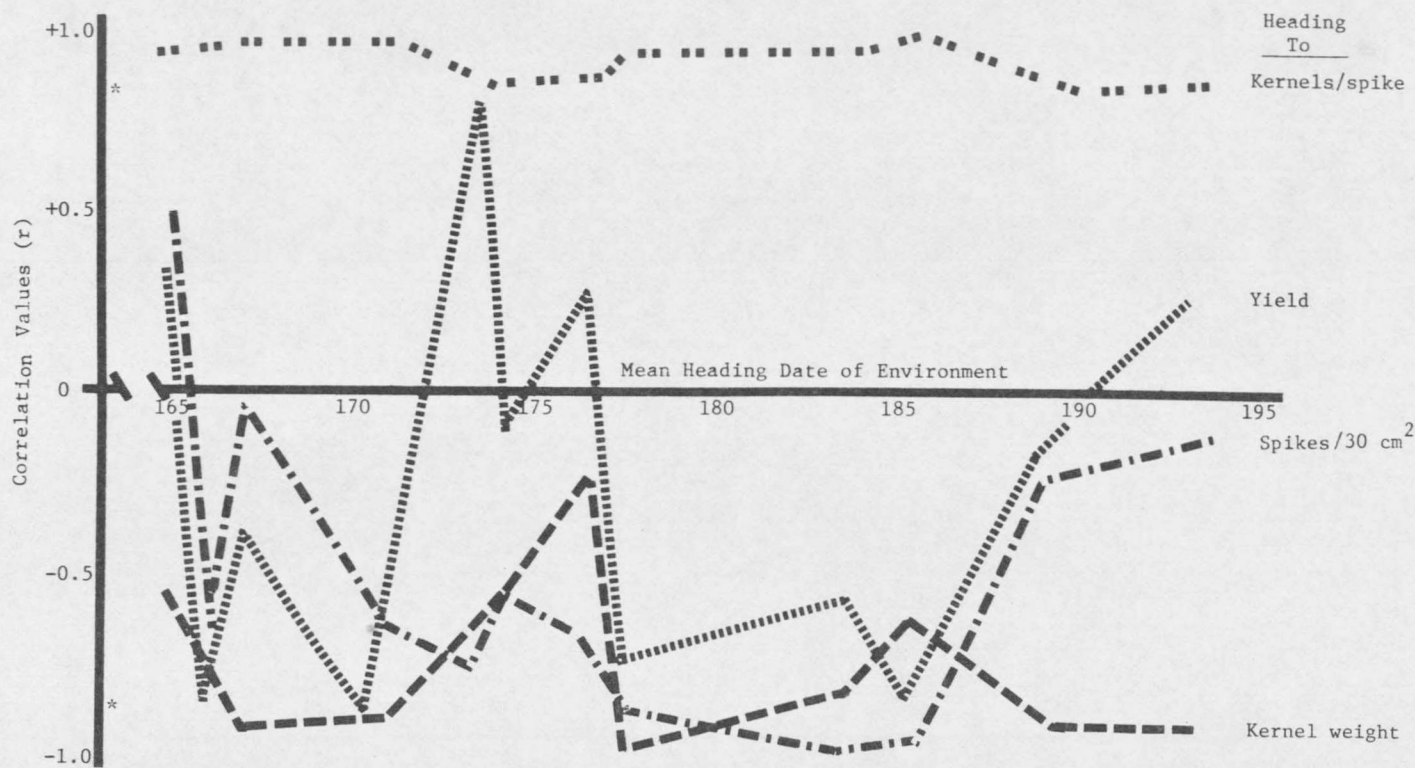


Figure 11. Correlation of heading date to each component response for all isotypes at each environment (ordered according to the heading date of the environment).
*, significant at the P=.05 level.

dates, probably due to compensating components. In only three of the fourteen environments studied did significant correlations between heading date and yield (w) occur. In the two environments producing negative correlations, the yield response approximated the kernel weight response, and the kernels per spike response was relatively flat between the isotypes, as shown by the trisected parallelepiped (Figure 3). In the environment producing the positive yield correlation to heading date (7705), the yield response closely approximated the kernels per spike response and the response pattern of the two remaining components was uniform, illustrating that the component controlling yield can vary among environments. The space planted nursery produced a positive heading date to yield correlation, due to an apparent complementation among the components (Figure 2, Table 7), as well as a large kernels per spike response.

The pattern of plant available water in Montana, shown in Figure 10, can explain most of the observed genotypic correlations to heading dates and the consequent correlations and response patterns of most of the traits studied. The strength of the genetically induced correlations between the first two yield components typically are an indication of the degree of stress under which a plant is placed early in the growth period of the plant (Grafius, 1978; Thomas et al., 1970). The strong correlations found can be assumed to serve as a direct measure of the degree of competition between the different components or the

Table 7. Correlation matrix between mean heading date, yield, and yield components for six Titan maturity isotypes grown in space planted conditions (Bozeman, 1977). (N=9)

	Heading Date	Yield	Spikes/ Plant	Kernels/ Spike	Kernel Weight
HEAD DATE	1.00				
YIELD	.89**	1.00			
TILLERS	.75*	.70*	1.00		
KERNEL/ SPIKE	.93**	.89**	.58	1.00	
KERNEL WEIGHT	-.33	-.33	-.12	-.42	1.00

*, **Significant at $P=.05$, $P=.01$ level, respectively.

degree of pleiotropy with genetic heading date as measured by the consistency of the correlations from environment to environment.

A trait such as tillers/30 cm² which produces a large range of correlation values with heading dates across environments (Table 6), is indicative of a trait which allows a cultivar to interact with a particular environment. On the other hand, the isotypes in question could not interact strongly with the environment through kernels per spike (Table 8, Figures 6&11). Instead, the number of kernels per spike for each isotype is primarily established (relative to the environmental mean response) by the length of the preheading stage, thus implying a pleiotropic, morphological change due to the genetic extension of the vegetative period. Other traits being controlled by this form of pleiotropy exhibit similar consistent correlations, and environmental stability. These traits to be discussed later are plant height, and possibly leaf area, leaf length, leaf width, and spikelets per spike. Other studies have reported similar conclusions (Stoskopf and Reinbergs, 1966; Frey, 1959, a&b with oats) pertaining to the degree of plasticity of the various yield components.

The spikes/30 cm² mean genetic correlation with heading date ($r = -.94^{**}$, Table 5) can be rationalized as being due to an increased moisture supply available to the isotypes which develop quickly. Several investigators have noted the strong control water availability has on tiller development (Aspinall, 1961, 1963; Cannell, 1969a). On the

other hand, it can be questioned whether the water availability difference between an isotype that heads 13 days earlier than another isotype would be great enough to explain the observed differences in mean isotypic tiller response (Figure 1). Since the tiller response of the space planted nursery is positively correlated with heading dates, which is the reverse of that observed in the average stressed yield trial (Figure 2 versus Figure 1), it would seem that simply by spacing out the plants at a rate of 1 per 30 centimeters, the competition for space and presumably water was reduced to the point to allow late heading plants to take advantage of the longer vegetative period and establish significantly more tillers per plant (Table 7). Considering the magnitude of response differences, it can be assumed that a 14 day period of added evaporation and transpiration (Figure 10) found in drill stripped rows, can reduce the plant available soil water to the point of limiting tiller development in the later heading isotypes, and preventing them from developing additional tillers, which they are potentially capable of doing.

The consistent genetic correlations of kernels per spike to heading date at each environment (Table 6) indicates a hormonal control of the allocation of available water and nutrients to the different plant organs. The observed trend is that as the plant genetically heads later in the season, it develops more kernels per spike, both under drill strip and space planted conditions ($r=.97^{**}$; $r=.93^{**}$). If

available water differences were a limiting factor for spike development between the isotypes, then either a negative correlation or variable correlations to heading dates, as observed with tillering, would be expected under the variable drill stripped conditions. However, the correlations between heading dates and each of the components (Table 6) for each environment make it immediately obvious that although tiller correlation values are quite variable among environments, the kernel per spike response is very stable and positive, implying that water and nutrients are limiting for tiller establishment but not for spike development. This consistency is reflected in the low environmental correlation value between heading date and kernels per spike ($r=.33$) implying little environmental response.

If component compensation is due to "number being inversely proportional to size" as postulated by Grafius (1978), then the kernels per spike correlation to heading date should approximate the opposite trend of the tillers/30 cm² to heading date correlations at each environment since heading dates are constant. This doesn't happen, therefore negating this postulate, at least within the confines of tiller establishment and head development, which overlap in the growth cycle of a barley plant (Adams, 1967; Bonnett, 1966; Grafius, 1956, Figure 10). The spike differentiation is started just prior to commencement of tiller internode elongation of the spike bearing tiller. Once a few of the tillers have started elongation, all of the tillers follow soon

after (Cannell, 1969a). The period of head development is thus restricted from slightly before the period of initial tiller elongation to flowering (Bonnett, 1966). The developing plants with genetically different heading dates germinate and establish tillers during the same initial growth stages, theoretically establishing the same number of initial tillers. The late isotypes, however, started internode elongation slightly later and completed the cycle for spike development up to fourteen days later than the earliest heading isotypes. The longer the time a plant has to elongate and establish spikelet nodes, the longer will be the primary spike meristem provided adequate substrates. Thus, the early heading isotype will have a shorter spike meristem and fewer spikelets per spike than the later isotypes, regardless of the environment, as long as the heading date differences are maintained and sufficient metabolites are supplied through a hypothesized hormonal preferential allocation control system.

Investigations have noted that previously established tiller buds can be made to elongate given a reapplication of water, and that intra-organ competition for nutrients is greater than interorgan competition during the development of that organ (Aspinall, 1961, 1963; Cannell, 1969; Gallagher et al., 1975 a&b; Kirby and Jones, 1972, 1977). Thus, in the stressed environment earlier isotypes initially may have established and elongated the same number of tillers (or even fewer tillers) than the later isotypes, the inherent development of smaller spikes

causes a reduced water and nutrient demand within a tiller, resulting in a reduced total soil water utilization during that period making more water available for later tiller development than is found in the later heading isotypes, allowing the early isotypes to elongate and develop more tillers. The late isotype, on the other hand, with more spikelets/spike, required more initial water and nutrients per spike and tiller, increasing the demand for water and nutrients, reducing the number of tiller-buds able to elongate once initial spike development has terminated and preferential substrate allocation has relaxed.

The positive heading date to tillering correlation observed in the space planted nursery (Table 7) is due to the lack of stress allowing the later heading isotypes to establish and elongate more tiller buds than the early isotypes which are genetically restricted in growth period. Tillers in a non-stressed environmental condition thus do not compensate strongly with the spike development, as has been observed in most yield component studies (Adams, 1967; Grafius, 1956, 1972, 1976), and under a nonstressed environment, spikes/30 cm² are pleiotropically controlled by heading dates, since water is not limiting, and developmental periods can be expressed. It seems that although superficially the isotypic yield components are compensating in the classic manner described by Grafius (1954, 1978) and Adams (1967), the genetic control of the compensating pattern does not appear to lie in the tiller response, instead it lies in the development of more kernels per spike,

inherent with a genetically lengthened growth period and controlled by a substrate allocation system. As postulated, systems preferentially allocating nutrients to the developing spikes could account for the consistently strong, positive correlations between heading dates and kernels per spike. A hormonal mode of nutrient allocation to spikes has been suggested to exist in barley by several investigators (Kirby and Faris, 1972; Kirby and Jones, 1977). The tiller response appears to be the environmentally controlled compensating component in this series of Titan isotypes as in other varieties (Kirby and Jones, 1977; Stoskopf and Reinberg, 1966).

Kernel weights are more responsive to environmental variation than kernels per spike, but less responsive than tillering, as is shown by the range of correlation values to heading date and the parallelepiped (Figure 11, Table 6). The control of the kernel weight response in relation to the "number of kernel" components needs consideration. Mean genetically induced responses (Figure 1) imply that the reduced range of response may be due to the apparent compensatory pattern in the other two traits, creating an equal number of kernels per unit area between isotypes as suggested by Thomas et al. (1970a). This does not seem to be the case. In environments having a poor compensatory response (i.e., 7705, 7706, 7608, etc.) the kernel weight response is still uniform, although there are obviously more kernels per unit area in the later isotypes (Figure 3). Instead of a compensatory response

causing uniform kernel weight, it seems that the uniformity could be due to the simple factor of a physical restriction on kernel size caused by the palea and lemma (Grafius, 1978).

The genetic controls for the size of the palea and lemma are purported to be linked to the environmental feedback systems which control the number of kernels per unit area (Grafius et al., 1976). However, being the final component, it can be assumed that most of a plant's active response to the environment has already been established, thus causing the genotype x environment interaction of the kernel weights to be more stable, as shown in the statewide regression (Figure 7). If priority is placed on developing spikes by hormonal mechanisms controlling allocation of nutrients and water to the developing spikelets, including the palea and lemma (Kirby and Faris, 1972; Kirby and Jones, 1977), then nutrient dependent restrictions on maximum kernel size should be reduced.

Grafius (1978) maintains that the size of the palea and lemma will be determined in part by the size of the leaf meristem, since paleas and lemmas are developed from altered leaf meristem. If a plant has larger leaves, it should, consequently, produce larger palea and lemma and a larger potential kernel size (Hamid and Grafius, 1978). However, the potential maximum may not be reached due to environmental stresses. Thus, kernel development is potentially controlled from two sources, the palea and lemma size and the nutrient and water availability. If

this is the case, then in a minimum stressed situation, genetic control of kernel size differences will be maximized (Grafius, 1978).

Leaf length and area are partially determined by rate of plant growth and duration of growth period. Leaf blade measurements were collected on the space planted nursery. Leaf area responses for all of the leaves on a main culm (N=flag leaf to N-4) of an isotype produced significant isotypic differences (Table 8). Isotype leaf area correlation and regression values with isotypic heading date, as summarized in Table 8, are all significant and positive. An increase in days to heading is directly associated with an increased leaf area for each and every leaf on the main culm of the plant (Table 8).

This increase in area can be a result of a longer leaf, a wider leaf or both. At each leaf position on the main culm, the isotypes expressed significant isotypic differences in length and width (Figure 12), implying that both factors contributed to leaf area. The correlations between mean leaf length at each position and the heading date of the isotype were constantly strong, positive, and highly significant. The leaf width to heading date correlations were non-significant for the nth or flag leaf, but the correlations were significantly positive for the remaining lower leaves, n-1 to n-4 (Table 8 and Figure 12).

The leaf area response is probably pleiotropic with the increased growth period by the same reasoning applied to plant heights, spikes, and other pleiotropic morphological traits. Similar conclusions were

Table 8. Analysis of variance for morphological traits and correlations with heading date for six heading date isotypes of Titan grown in one space planted nursery.

CHARACTERISTIC MEASURED	VARIETY		ERROR		REGRESSION	CORRELATION
	MEAN	SQUARE	MEAN	MEAN	b_{yx}	r
	SQUARE	DF = 8	$\bar{x}$	TO HEADING DATE:		
SPIKELETS/ SPIKE, No.	210.88**	23.22	23.78	.62		.98
RACHIS INTER- NODE LENGTH, cm	.42	.32	.79	-.00		.52
SPIKE LENGTH, cm	16.75**	2.09	9.02	.16		.98**
AWN LENGTH, cm	4.98	3.15	10.15	-.75		.06
PROTEIN, %	1.70**	.20	16.59	-.13		-.74*
PLUMP, %	47.80	22.40	78.36	-.33		-.35
THIN, %	5.60	3.80	5.14	.10		.31
TEST WEIGHT, Q / HLT	3.90	3.20	62.92	.10		.36
LEAF AREA, cm ²						
N	342.14**	13.91	16.94	.77		.96
N-1	967.15**	16.59	30.55	1.29		.99
N-2	1668.62**	37.88	30.44	1.71		.98
N-3	1122.91**	28.89	24.84	1.42		.96
N-4	162.13**	14.69	19.91	.68		.95

(Table Continued)

Table 8 . (Continued)

		ERROR			
	VARIETY	MEAN		REGRESSION	CORRELATION
CHARACTERISTIC	MEAN	SQUARE	MEAN	b_{yx}	r
MEASURED	SQUARE	DF = 8	$\bar{x}$	TO HEADING DATE:	
LEAF LENGTH, mm					
N	99.40**	12.11	16.60	.41	.99
N-1	239.41**	4.71	24.23	.60	.94
N-2	344.47**	14.84	25.53	.74	.95
N-3	390.33**	11.79	23.72	.81	.95
N-4	171.66**	17.12	22.60	.72	.98
LEAF WIDTH, mm					
N	.76**	.04	1.48	.03	.88
N-1	.72**	.07	1.85	.03	.98
N-2	1.21**	.11	1.69	.05	.99
N-3	1.13**	.05	1.38	.05	.99
N-4	.14**	.02	1.18	.02	.92
INTERNODE LENGTHS, mm					
N	36.28	26.93	38.73	.16	.80
N-1	19.45**	2.89	22.75	.08	.51
N-2	10.61**	3.44	13.58	.08	.73
N-3	13.01*	3.20	9.83	.16	.96
N-4	2.34	4.19	7.66	.06	.47

*, ** Significant at P = .01 and P = .05 level, respectively.

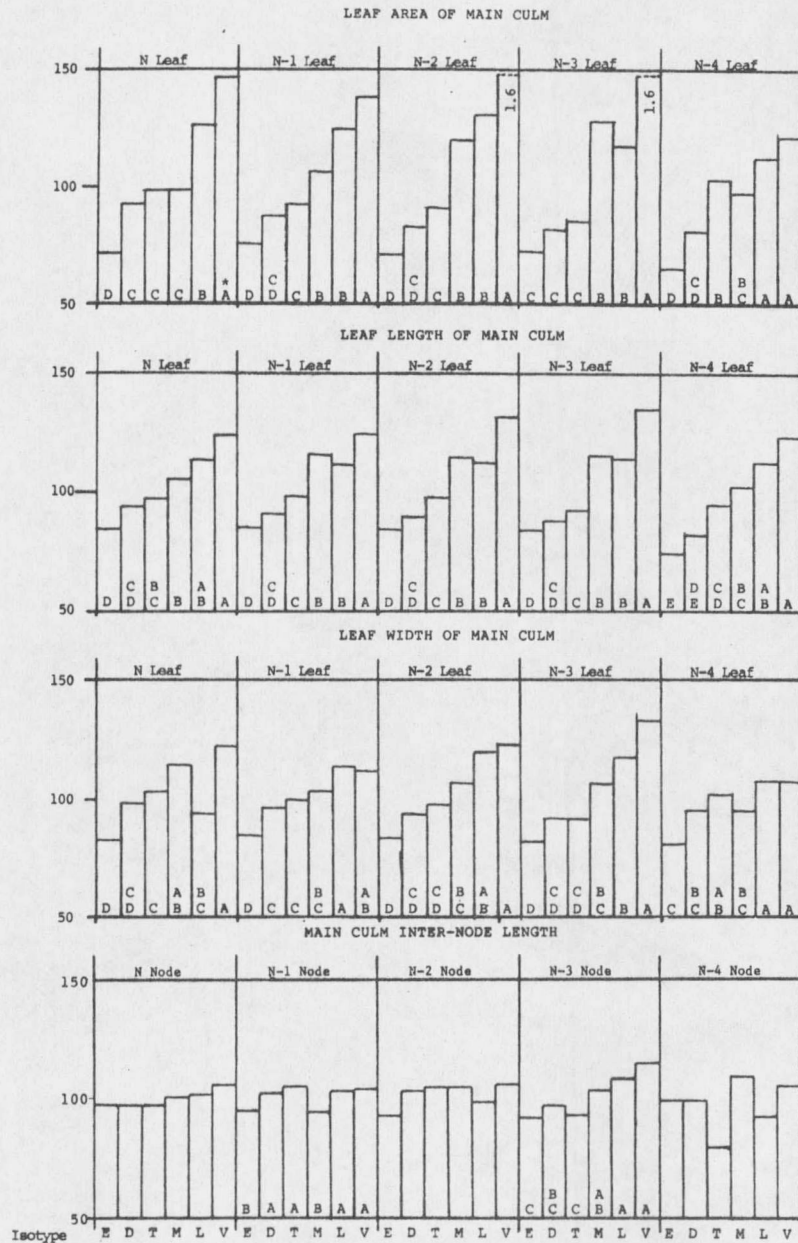


Figure 12. Mean percentage analysis and Duncan's Multiple Range Test* for leaf area, length, width and main culm inter-node length of space planted nursery, ordered according to heading date of the isotype.

*Separate letters denote significantly different means. Similar or no letters denote non-significant differences ($P = .05$).

reported by Dixit (1973). If Grafius's (1978) postulated⁵ are valid, then under the space planted conditions those plants with the largest leaves should also produce the heaviest and largest kernels. The kernel weight and percent plump correlations with heading should, therefore, approximate the heading date to leaf area correlations (Figure 2 versus 12, Tables 4 versus 8).

This does not occur. The observed low correlations could be due to stressed conditions preventing the maximum potential plumpness and kernel weight from being reached. However, the mean kernel weights and percent plump (42.2 grams/1000 kernels; 78.4 percent plump kernels; Table 4), are much higher than all but one of the yield trial environmental means, implying that maximum kernel weights were approached in the space planted nursery. Therefore, it can be assumed that these observations tend to refute Grafius's postulated control due to leaf and culm size and his first corollary.

The correlation between head length and heading date was also strong ($r=.98^{**}$). Rachis internode length could contribute significantly to the head length response; however, the analysis of variance for rachis internode length revealed non-significant isotype effects, which is reflected in the low correlation between the rachis internode length and the isotypic heading responses ($r=.52$) and the flat slope ($b_{yx}=-.00$, Table 8). It appears that the increased number of kernels/spike, and spike length was due to an increased number of spikelets/

spike associated with genetically delayed heading dates, allowing the spike to eventually establish a greater number of spikelets and kernels. This response is supported by observations made by Bonnett (1967) in barley.

In support of the patterns observed in the space planted conditions, those yield trial environments which produced the weakest heading date to spikes/30 cm² correlations, also produced the weakest tillers to kernels per spike correlations (Table 3), and are consequently (according to Thomas et al., 1970; and Grafius, 1978) the least stressed environments. These non-stressed environments also produced weak heading date to kernel weight correlations. If Grafius's 1978 postulates were true, these correlations should have been the highest.

An alternate hypothesis is that the genetic maximum could be identical between the isotypes, since they are theoretically isogenic for all traits except heading date. The main criteria controlling the differences in kernel weight response between these isotypes in stressed environments would be heading date and the related hypothesis of greater water availability. Thus, only the early isotype could develop kernels to their genetic maximum set by the palea and lemma.

This would seem to be in direct conflict with the findings of Hamid and Grafius (1978), Grafius and Thomas (1976), and Grafius (1978), which states that the initial responses of the first two components are the primary factors controlling the kernel weight response (Grafius and

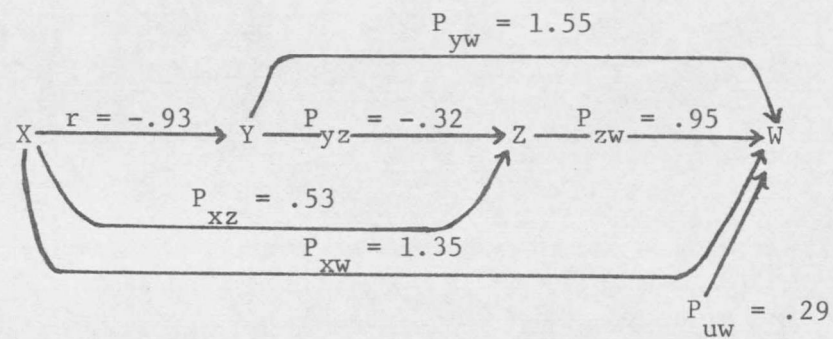
Thomas, 1976). Data presented here implies that if a hormonally induced allocation control system is present in barley, then with a moderate degree of stress, the plant will still develop palea and lemma of the same size as it would under minimal stress. Water limitations during grain filling will still prevent the kernels from reaching that maximum (Grafius, 1978). Thus, it is postulated that the response of the first two components will affect the kernel weight response, not by physiological allometry, but by nutritionally (moisture) preventing it from reaching its maximum genetic potential. This genetic potential will be equal, given a similar genotypic constitution, and is not due to leaf area differences.

Kernel weights were positively correlated to awn lengths and percent protein, and negatively correlated to percent thin kernels and test weights in the space planted nursery (Table 7). It is possible then that under non-stressed conditions the awn length will affect the kernel weight since evapotranspiration through the awn will not be environmentally limited, and thus the genetic awn length differences will manifest an effect. Other research has reported that major differences in awn mass are a major determinate of kernel weight (Faris, 1974; Johnson et al., 1975). Awns would also affect the protein deposition in the kernel due to an increased photosynthate source. However, due to the observed small differences in awn length, it is assumed that awns are a minor factor in determining kernel weights in this material.

GENETIC PATH ANALYSIS

When analyzing the pattern of path coefficients calculated on mean isotypic responses due to genetic heading date differences, we find a high positive direct effect of spikes/30 cm² ($P_{xw}=1.35$), kernels per spike ($P_{yw}=1.56$), and kernel weight ($P_{zw}=.95$) on the mean yield response over 14 environments (Table 9, Figure 13). Spikes/30 cm² has a positive direct effect on yield, but also a very strong negative indirect effect on yield through its direct effect on kernels per spike ($r=-.93$) (Table 9). This indirect effect through kernels per spike ($p=1.46$) explains the low value of the simple mean genetic correlation between tillers/30 cm² and yield ($r=.67$) (Table 5), and is a measure of the degree of component compensation occurring across the isotypes. A similar pattern is found in analyzing the effect of kernels per spike on yield. The direct effect is strong ($p=1.56$) but the effect is again reduced by the strong negative indirect effect ($p=-1.25$) kernels per spike has on yield caused by the compensatory tillering response (Table 9).

In considering whether tillers affect kernels per spike or vice versa, the restrictions of the original pathdiagram must be considered (Figure 13). That the true biological pattern is the one presented in the diagram, is dependent upon the concept of Sinnott's law, and the developmental allometry of a barley plant (Hamid and Grafius, 1978; and Grafius, 1978) which has already been partially negated.



X = spikes/30 cm²
 Y = kernels/spike
 Z = gms/1000 kernels
 W = yield (Q/HA)
 U = unexplained variation

Figure 13. Path coefficient diagram showing interrelationships between the mean yield components and yield of six maturity isogenes grown in 15 environments.

TABLE 9: Path coefficient analysis of the responses of 6 Titan maturity isogenic lines averaged over 15 environments.

<u>Spikes/30 cm² to Yield</u>	
Direct effect	1.35
Indirect via kernels/spike	-1.46
Indirect via weight/1000 kernels	.50
Indirect via kernels/spike+weight/1000 kernels	.28
Simple r	.64
<u>Kernels/Spike to Yield</u>	
Direct effect	1.56
Indirect via spikes/30 cm ²	-1.26
Indirect via weight/1000 kernels	-.30
Indirect via tillers+weight/1000 kernels	-.47
Simple r	-.46
<u>Weight/1000 Kernels to Yield</u>	
Direct effect	.95
Indirect via spikes/30 cm ²	.72
Indirect via kernels/spike	-.49
Indirect via spikes/30 cm ² +yield+kernels/spike	.40
Indirect via spikes/30 cm ² +kernels/spike+yield	-.78
Simple r	.78
<u>Spikes/30 cm² to Kernels/Spike</u>	
Direct effect = simple r	-.93
<u>Spikes/30 cm² to Weight/1000 Kernels</u>	
Direct effect	.53
Indirect via Kernels/Spike	.30
Simple r	.83
<u>Kernels/Spike to Weight/1000 Kernels</u>	
Direct effect	-.32
Indirect via spikes/30 cm ²	-.50
Simple r	-.82
Unexplained	.29

Both effects are accounted for in the pathdiagram. The direct effect of kernel weight on yield is reduced both by the indirect effect of kernels per spike on yield, and by tillers/30 cm² and kernels per spike (number of kernels/unit area) on yield (see Table 9). Thus, the mean effect of kernel weights on yield are reduced by the compensatory effects of tillers/30 cm² and kernels/spike on kernel weights. This is theoretically caused by the differences in available moisture due to different heading dates between the isotypes.

Path analysis of the non-stressed environments reveals that tillers per plant have a small direct effect on yield, and a stronger but still insignificant relationship with kernels per spike ($r=.58$) (Tables 10 and 7). The correlation between tillers/plant and yield is enhanced by the indirect effect of tillers on kernels per spike which expresses the strongest direct effect on yield. Kernel weights have a minimal effect on yield primarily due to the negative direct effect that kernels per spike has on kernel weight, and the uniform kernel weight responses.

An examination of the patterns of cause and effect through path analysis at each environment can give an important indication of what specific environmental factors are affecting the mean responses, the correlations, as well as the direct and indirect effects at an environment. Path coefficients (Table 11) from one analysis (environment or isotype) cannot be compared with those from another analysis since path

TABLE 10: Path coefficient analysis of the average responses of 6 Titan maturity lines grown in a space planted nursery.

<u>Tiller Number/Plant to Yield</u>	
Direct effect	.28
Indirect via Kernels/spike	.42
Indirect via weight/1000 kernels	.00
<u>Indirect via kernels/spike+weight/1000 kernels</u>	<u>-.00</u>
Simple r	.70
 <u>Kernels/Spike to Yield</u>	
Direct effect	.73
Indirect via tillers/plant	.16
Indirect via weight/1000 kernels	-.01
<u>Indirect via tillers+weight/1000 kernels</u>	<u>.00</u>
Simple r	.89
 <u>Weight/1000 Kernels to Yield</u>	
Direct effect	.01
Indirect via tillers/plant	.05
Indirect via kernels/spike	-.3
Indirect via tillers/plant+yield+kernels/spike	.07
<u>Indirect via tillers/plant+kernels/spike+yield</u>	<u>-.08</u>
Simple r	-.33
 <u>Tillers/plant to Kernels/spike</u>	
Direct effect = simple r	.58
 <u>Tillers/plant to Weight/1000 Kernels</u>	
Direct effect	.17
Indirect via Kernels/spike	-.30
Simple r	-.12
 <u>Kernels/spike to Weight/1000 Kernels</u>	
Direct effect	-.52
Indirect via tillers/plant	.10
Simple r	-.42
 Unexplained	 .15

Table 11. Path coefficient analysis of mean isogenic responses in each environment (genetic variation).

ENVIRON- MENTS §	P A T H W A Y						
	X - W	Y - W	Z - W	X - Y	Y - Z	X - Z	U - W
.7601	1.15	.61	.50	-.99	-.03	.66	.21
.7605	1.84	1.87	-.21	-.84	-.80	-1.08	.29
.7607	.81	1.59	.84	-.21	-.87	-.34	.02
.7701	1.19	1.00	.79	-.94	-.83	.12	.04
.7709	.98	.54	.13	-.44	.42	.69	.25
.7606	3.07	2.33	.14	-.99	2.79	3.53	.17
.7708	.59	.03	.52	-.75	-.75	.07	.23
.7705	-.04	1.12	.31	-.62	-.22	.60	.13
.7706	.49	1.24	.22	-.39	-.88	.06	.22
.7602	.79	.48	-.10	.06	.08	-.55	.08
.7608	1.12	.48	.51	.17	-.62	-.45	.22
.7702	1.15	.48	.09	-.49	-.89	-.30	.12
.7711	.80	.61	.46	-.08	-.72	.25	.20
.7609	.36	.46	.99	-.77	-.25	.67	.12
MEAN	1.36	1.56	.94	-.93	-.32	.53	.29
SPACE PLANTED	.28	.73	.01	.58	-.52	.17	.15

§Environments are coded as in Tables

coefficients are an indication of relative strengths when compared to other path coefficients in the same analysis. The values from one analysis thus have no bearing on the relative values expressed in a second analysis (Table 11). To solve this problem, the direct effects on yield including the unknown portion (P_{uw}) were converted to a percentage of the sum total effects on yield. The total of all the

percentages must be equal to 100% and are thus placed on an equal unit with all other path analyses. The results of this method is in effect similar to the result of placing all of the mean responses on a percent of the mean, it allows an indication of the magnitude of the response, as well as allowing a direct comparison from trait to trait regardless of experimental units.

When the path coefficients are converted to a percentage of the total direct effects on yield, they reveal that the magnitude of the direct effect of tillers on yield and kernels per spike on yield are about equal when analyzed for genetic variation at each environment (Figure 14). The direct effects of kernel weights are lower, but still contribute roughly 20% of the direct effects controlling yield. The unknown portion contributes a very small percentage (>7%) to the yield response implying that most of the plants morphological and physiological responses which affect yield are accounted for by the yield components.

When the adjusted path-coefficients for each environment were plotted against yield, no definite pattern was recognizable. However, when plotted against the mean heading date of each respective environment, a pattern did evolve (Figure 14). Those environments which were planted from Julian days 166 to 174 produced a component pattern with kernels per spike response generally expressing the greatest effect on yield. Tillers/30 cm² had the greatest effect on yield in the

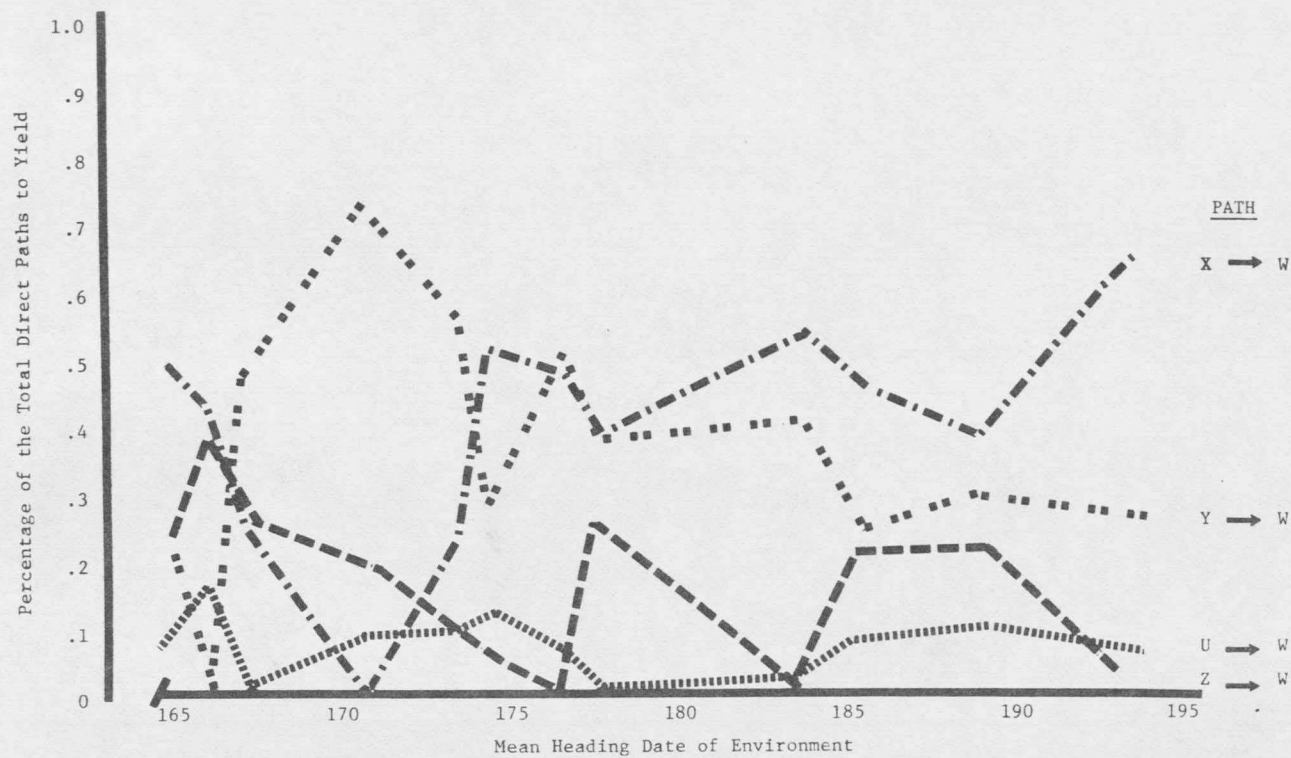


Figure 14. Path coefficients calculated on the genetic response across each environment and presented as a percentage of the total direct effects on yield, ranked according to the mean heading date at each environment.

environments planted after Julian day 176. Kernel weights typically affected the yield response less than the other components, however, in the very early planted environments they had a larger effect on yield.

These patterns again reveal that the degree of stress dominates the strength of the correlations found between the yield components. However, the patterns also show that the genetic yield control is not necessarily with the tillering response. Instead, as shown previously, it is in the establishment of kernels per spike, which is partially dependent upon the genetic heading date, as revealed by the following rationale: The early planting dates (Figure 9) increase the vegetative period from planting to heading; this increased period from planting to heading partially negates the effect of differences in heading dates in the early season, thus, the later heading isotype will have sufficient water to initiate retillering in these environments; whereas in the later planted environments, it is usually only the early isotypes with their shortened growth period and spikes that can reinitiate tillering. This phenomenon should reduce the differences in tiller response between the isotypes. The kernel per spike response, being uniform in different environments, as shown by several other authors (Frey, 1959 a&b in oats; Stoskopf and Reinbergs, 1966; Kirby and Faris, 1972; Kirby and Jones, 1977 in barley), will remain the same. The controlling factor on yield in these early planted environments will therefore be the kernels per spike response, assuming the typically uniform response in

kernel weights. Consequently, the response of kernels per spike to yield is strongest in the three environments heading from 167 to 174 days after January 1 (Figure 14).

This response pattern is reflected in the parallelipiped (Figure 3) for these environments (7608, 7705, 7708). These environments produced relatively "flat" responses of kernels per spike as shown in the parallelipiped for those environments; however, the correlation with heading dates were still strong ($r=.90^{**}$, $r=.96^{**}$, respectively, Table 5). This flat kernel per spike response is probably due to the lengthened vegetative stage in all isotypes, due to early planting, allowing the early isotypes to establish longer spike meristems in relation to the later heading isotypes, therefore reducing the range of responses. The effect on yield was still evident, however. The aberrant tillering response of Titán and the very late heading isotype were reflected in the yield response, thus explaining the moderately strong effect of tillering on yield, in these two environments.

Changes in factors expressing the maximum direct effect on yield were also reported by Tewari (1976). In a low rainfall year heading dates contributed very significantly to yield, through the direct effects of heading dates on plant heights, 1000 kernel weight, internode number, and fodder yield. Whereas, in the following high rainfall year, heading date expressed a low direct effect on yield. These patterns directly support the findings reported here.

ENVIRONMENTAL CORRELATION

The mean isotypic responses for a trait were correlated against the other traits across all environments, measuring environmental variation of the isotypes (Table 10). The resultant environmental correlation matrix (Table 12) illustrates that kernel weights are positively correlated to yield and percent plump and negatively correlated to heading date. Therefore, there is a tendency for a high yielding environment to produce high kernel weights and plump seeds. Recalling that heading differences between environments is dependent upon planting dates, this implies that the earlier seeded environments produce the heaviest and plumpest kernels, which further supports the theory of available water determining kernel size and weight. No significant, environmentall induced relationships between spikes/30 cm² and any trait (Table 12) were detectable.

Environments where mean high number of kernels per spike were produced, tended to produce low yields ($r=-.60^*$), reduced shattering ($r=-.73^{**}$) and fewer plump seeds ($r=-.66^{**}$), all implying a delayed maturation in that type of environment. In general, these correlation patterns reveal that environmentally induced heading dates produce significant correlations with the morphological traits and yield component traits these correlations are similar to genetic heading date correlations.

Table 12. Correlation matrix between heading date, yield and yield components studied for each environment averaged over all isotypes. (Environmental Variation).

	YIELD	HEADING DATE	TILLERS/ 30 cm ²	KERNELS SPIKE	KERNEL WEIGHT
YIELD	1.00				
HEADING DATE	-.16	1.00			
TILLERS/ 30 CM ²	.38	-.12	1.00		
KERNELS/ SPIKE	-.59	.33	-.46	1.00	
KERNEL WEIGHT	.53	-.79**	-.41	-.41	1.00

*, **Significant at P = .05, P = .01 level, respectively. (Degrass of Freedom Varies)

The comparison of correlation values between the heading date and the yield and the yield components of each isotype in each environment taken across all environments reveals three definite patterns (Figure 15). Heading date is significantly, and negatively correlated to the kernel weight response for each isotype revealing that early planted environments produce heavier kernels regardless of the genetic heading date of the isotype. The pattern of correlations between heading date and yield closely follows that between heading date and the tillers/30 cm² of an isotype (Figure 15; Table 3), implying that a close cause and effect relationship exists between tillers/30 cm² and yield. Although

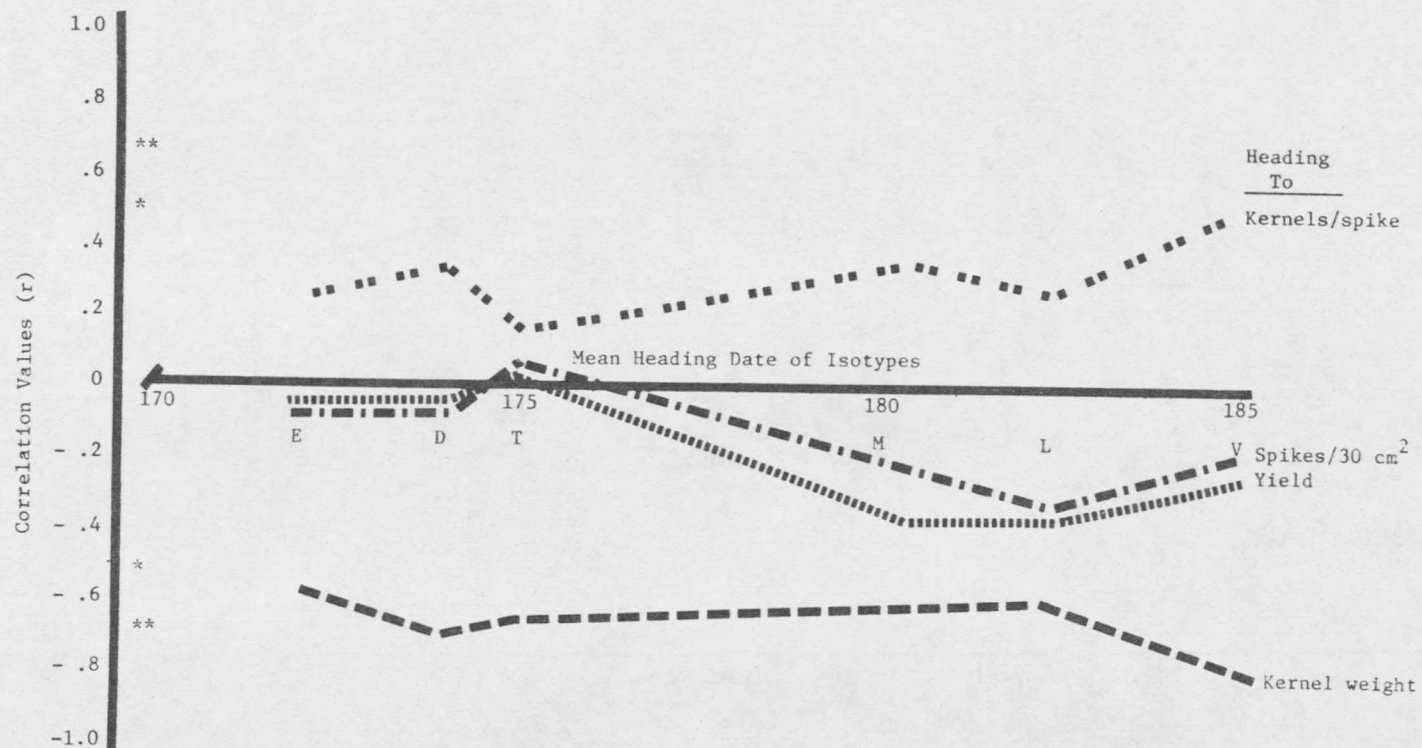


Figure 15. Correlation of heading date to each yield component for each isotype across all environments, and ordered according to mean heading date for each isotype (environmental variation).
*, ** significant at the $p = .05$, $p = 0.1$ levels, respectively.

they are not environmentally correlated, it appears that the tiller response determines the environmental yield response, supporting the genetic path analysis that tillers strongly affect the yield response. The correlation values between heading date and kernels per spike for each isotype is stronger than those for yield and tillers/30 cm², but the values are still non-significant (Table 13). The correlation of the correlations of these two traits to heading date is highly significant ($r=.95^{**}$, $DF=4$).

ENVIRONMENTAL PATH ANALYSIS

When path coefficients are calculated using the correlation matrix based on environmental variation for each isotype (Table 12), we find a different pattern of cause and effect (Table 13) than that observed in the genetic analysis (Table 6). The pattern of path-coefficients converted to a percentage of the total direct effects on the yield of the isotype (Figure 16) reveals that tillers/30 cm² have a moderate effect on the mean yield response over all environments for each isotype as implied previously. Also, kernel weights express an equally strong effect on yield as tillers/30 cm². Since heading (planting) dates affect kernel weights (Figure 15), then planting dates seem to be affecting yield through kernel weight responses. In this analysis, however, the moderate effect of the unknown portion indicating that strong isotype x environment interactions are also affecting yields,

Table 13. Path coefficient analysis of mean environmental responses for each maturity isogene and the correlation of each component and yield to the environmental heading date (Environmental Variation). ‡

ISOGENE	P A T H W A Y							HEADING DATE		" r "	TO:
	X - W	Y - W	Z - W	X - Y	Y - Z	X - Z	U - W				
EARLY	.70	-.05	.70	-.33	-.56	-.63	.64	-.09	.24	-.58	-.05
DERIVED	.91	.21	.85	-.67	-.96	-.98	.53	-.06	.34	-.69*	-.07
TITAN	.72	-.03	.62	-.44	-.70	-.66	.61	.05	.19	-.65*	.02
MUNSING L	.74	.16	.78	-.50	-.61	-.42	.42	-.20	.36	-.61*	-.33
B570-L	+.47	-.17	.68	-.46	-.70	-.73	.49	-.31	.28	-.60	-.35
MUNSING, VL	.79	.70	.90	-.43	-.63	-.32	.63	-.22	.44	-.74	-.21

‡ In those environments in which the heading dates were not obtained, the mean environmental heading date was used in the correlation.

*, ** Significant to the P = .05, P = .01 level, respectively.

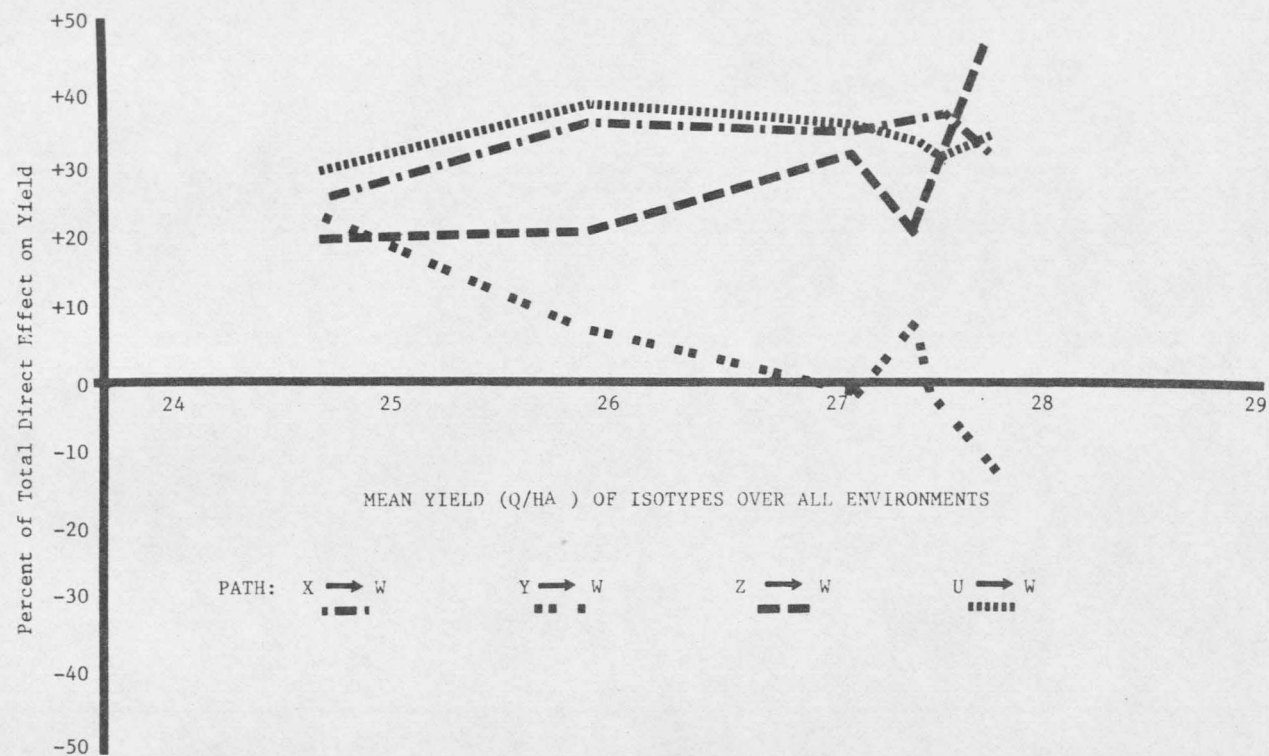


Figure 16. Path coefficient analysis calculated on the mean environmental responses of each heading date isotype presented as a percent of the total direct effects on yield, ranked according to the mean yield of the isotypes (Environmental Variation).

makes it difficult to estimate the major controlling factors due to environmental variation. The effect of kernels per spike on yield seems to increase with decreased yield of the isotypes, indicating a reduced tiller and kernel weight response. Thus, as the ability of the isotypes to respond in an environment with a large tillering response, or a large kernel weight response, decreases, then the hormonally controlled relatively stable kernels per spike development expresses a greater effect on the yield response in those low yielding environments. The factor causing low yields could be late planting, but the environmental correlation does not necessarily show this to be true. This pattern of direct effects further supports the theory that genotype expresses the primary control of kernels per spike, which are consequently environmentally stable, and that the other two traits are the components causing the isotype x environment interactions of yield (Figure 8), supporting Stoskopf and Reinbergs' (1966) findings. The fact that spikes/30 cm² and kernel weight are the most responsive yield components to environmental variation explains the reason for their comparatively large control over the yield response when environmental conditions are varied and genotypes are constant (Figure 16).

The large unknown effect is due, in part, to the large degree of associated and non-associated isotype x environment interaction of tillers and kernel weights which is not all accounted for in the mean analysis of each isotype or in the statewide regression analysis

(Figures 5 and 7). The large unknown portion does cause some problems in interpretation of cause and effects, since approximately 1/3 of the yield response pattern is due to this unexplained effect. The general trends do, however, support the belief that kernels per spike are relatively tightly controlled by a specific genotype, and therefore, the genotype x environment interactions of that genotype are caused by the tiller and kernel weights' isotype x environment interactions.

MORPHOLOGICAL TRAITS

The responses of the morphological traits directly support the assumptions of pleiotropic versus environmental associations between heading dates and the yield component responses. The postulate of water stresses being induced by genetic and environmental heading date differences are also directly supported by morphological responses, when these responses are analyzed for genetic and environmental variation.

The analysis of variance on test weights, plant heights, percent protein, percent plump kernels, and percent thin kernels revealed that 9 of 15, 8 of 12, 10 of 15, 13 of 14 and 10 of 14 environments studied produced significant isotypic effects (Table 14). Results from the Duncans Multiple Ranges test (Figure 17) at each of these environments shows that, in general, the late heading isotypes test weights were significantly different from the early heading isotypes' test weights.

Table 14. Analysis of Variance for Morphological Traits measured on Six Isotypes of Titan in 15 Environments.

Environments	Test (KG/HL) Weight	Plant Weight	Protein Percent	Plump Percent	Thin Percent
7601 VAR. M.S.	2.2	104.5**	1.5**	196.0*	27.1
7601 ERROR M.S.	3.5	5.3	.1	46.9	17.7
7601 $\bar{X}$	62.4	89.2	12.59	53.5	15.7
7605 VAR. M.S.	3.8	169.0**	2.0	5.3	3.2
7605 ERROR M.S.	2.1	11.6	.8	2.9	1.4
7605 $\bar{X}$	64.6	99.7	15.72	81.9	5.1
7607 VAR. M.S.	1.8	No Data	.3	1311.4**	942.6**
7607 ERROR M.S.	1.0		.3	6.8	8.4
7607 $\bar{X}$	65.1		12.05	33.0	28.8
7701 VAR. M.S.	27.4**	104.4**	1.8**	1903.0**	976.6**
7701 ERROR M.S.	2.7	4.9	.2	47.5	27.9
7701 $\bar{X}$	67.1	117.2	17.11	56.1	18.8
7707 VAR. M.S.	6.0*	58.5*	1.4**	317.9**	48.3**
7707 ERROR M.S.	1.9	11.0	.1	10.8	2.7
7707 $\bar{X}$	67.1	77.0	15.30	52.9	9.2
7709 VAR. M.S.	6.1	No Data	1.0*	131.4**	83.5
7709 ERROR M.S.	4.3		.3	46.9	36.0
7709 $\bar{X}$	64.9		16.28	58.3	16.7
7606 VAR. M.S.	17.3**	116.0**	1.8**	418.3**	161.7**
7606 ERROR M.S.	1.5	18.0	.2	69.7	28.1
7606 $\bar{X}$	63.7	110.3	16.80	60.9	16.8
7708 VAR. M.S.	13.9**	No Data	1.5**	823.1**	1028.1**
7708 ERROR M.S.	.9		.2	8.9	19.5
7708 $\bar{X}$	66.1		13.83	24.6	34.8
7705 VAR. M.S.	10.3**	23.0	.6	90.0**	13.5**
7705 ERROR M.S.	2.0	8.4	.8	19.2	1.8
7705 $\bar{X}$	67.0	84.2	15.23	68.1	6.2
7706 VAR. M.S.	2.7**	11.7	1.6**	No Data	No Data
7706 ERROR M.S.	.4	4.9	.3		
7706 $\bar{X}$	50.6	111.5	17.36		

*, **Significant at the $P = .05$, $P = .01$ level, respectively for the "F-test."

Environments are coded as in Tables

Table 14 (Cont'd.)

Environments		Test (KG/HL) Weight	Plant Weight	Protein Percent	Plump Percent	Thin Percent
7602	VAR. M.S.	3.0*	86.1*	1.3**	86.0**	33.1
	ERROR M.S.	.7	19.0	.2	11.1	14.5
	$\bar{X}$	68.6	62.8	9.69	29.9	23.7
7608	VAR. M.S.	5.6	216.0**	.7*	281.9**	5.4*
	ERROR M.S.	2.4	25.4	.2	9.1	1.2
	$\bar{X}$	70.2	81.7	13.23	57.1	8.5
7702	VAR. M.S.	14.2**	11.9	.7	690.4**	845.9**
	ERROR M.S.	1.7	14.3	.3	4.8	14.0
	$\bar{X}$	64.0	43.3	15.44	31.0	32.6
7711	VAR. M.S.	2.0	62.2*	.8	984.1**	153.3**
	ERROR M.S.	1.1	20.0	.4	21.4	3.4
	$\bar{X}$	63.5	85.3	13.15	58.7	10.4
7609	VAR. M.S.	24.1**		1.5**	29.9**	67.0**
	ERROR M.D.	1.5		.2	.8	6.3
	$\bar{X}$	58.1	No Data	13.27	25.4	7.2
Mean of ERROR M.S.		1.847	13.07	.3066	23.54	13.58
ENVIRON. $\bar{X}$		64.2	87.5	14.49	49.40	16.70
D.F.		70	50	70	65	65

*, **Significant at the $P = .05$, $P = .01$ level, respectively for the "F-test."

Environments are coded as in Tables

ENVIRONMENTS

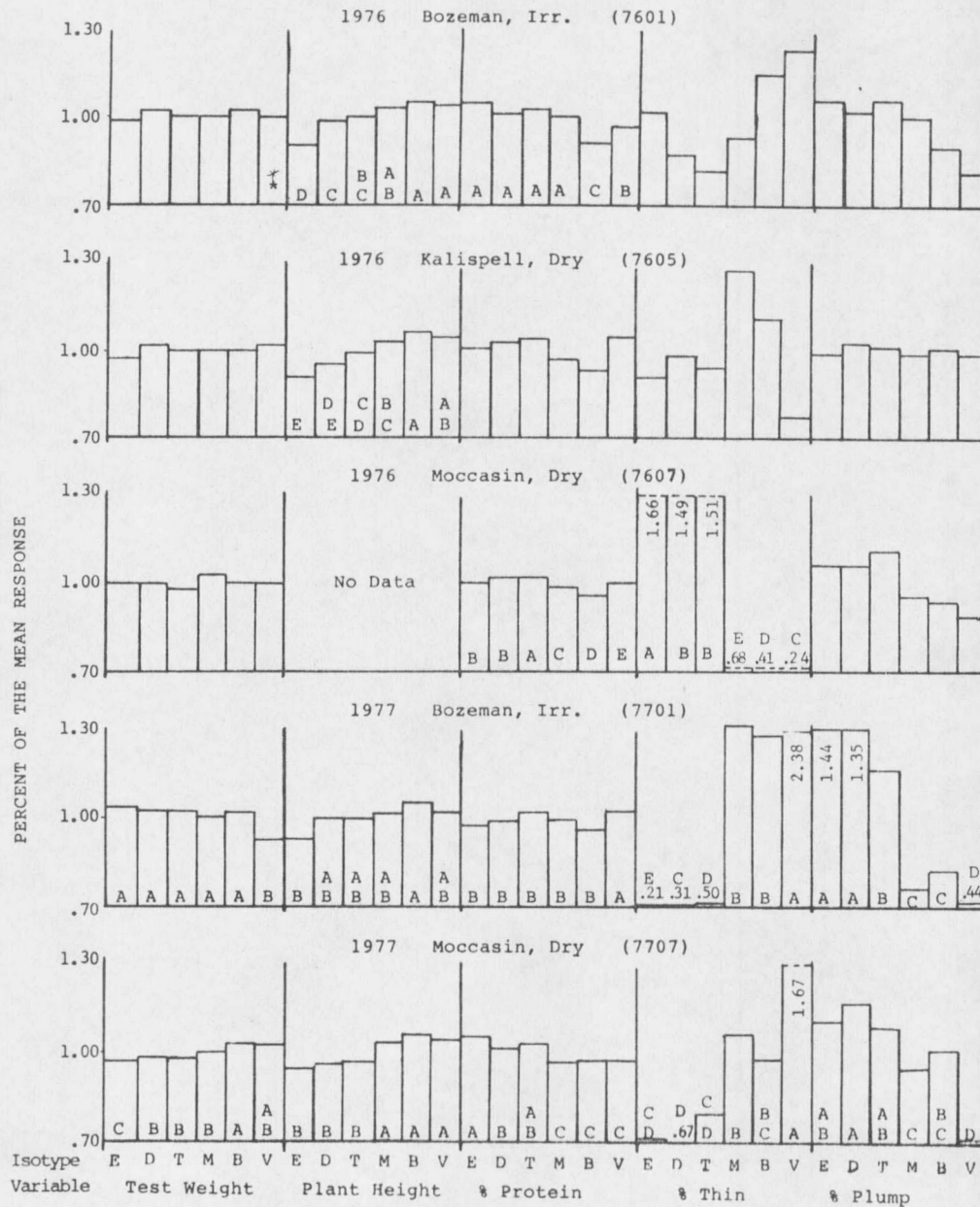
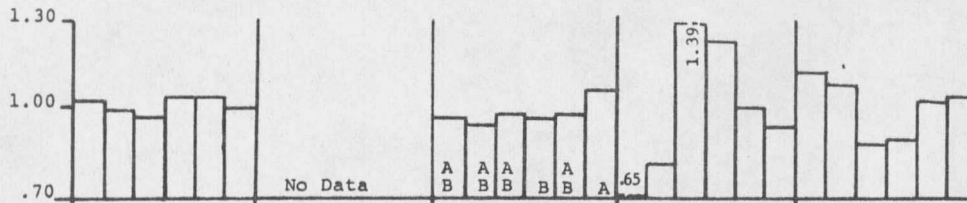


Figure 17. Mean percentage analysis and Duncan's Multiple Range Test* comparing the pattern and range of quality component responses of six Titan heading date isotypes ordered according to heading dates, at each environment.

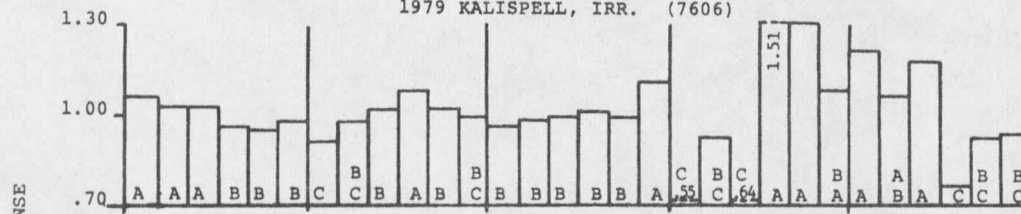
*Separate letters denote significantly different means. Similar or no letters denote non-significant differences (P = .05).

ENVIRONMENTS

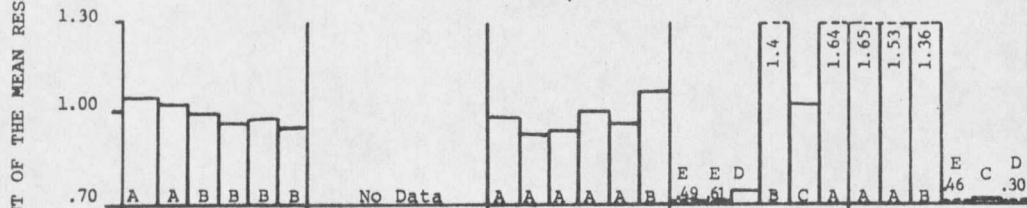
1977 HUNTLEY, IRR. (7709)



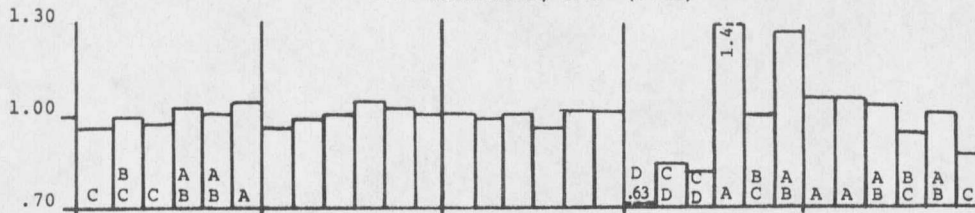
1979 KALISPELL, IRR. (7606)



1977 HUNTLEY, DRY (7708)



1977 KALISPELL, DRY (7705)



1977 KALISPELL, IRR. (7706)

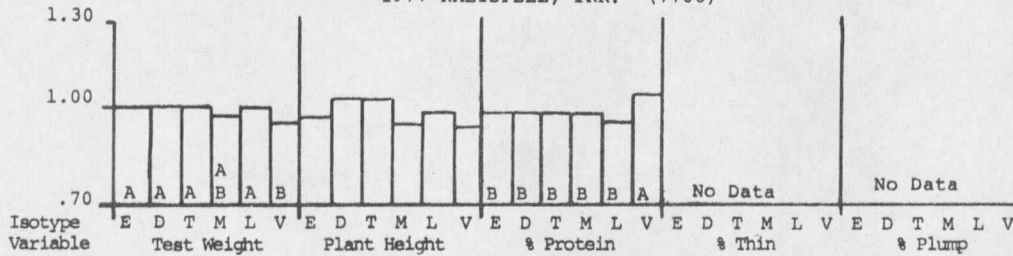
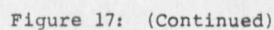


Figure 17: (Continued)



There was a relatively small range of response in test weights among the isotypes, and an examination of the mean percentage analysis (Figure 17) reveals that the response pattern between isotypes was variable between environments. The pattern of significant mean differences for plant heights (Figure 17) revealed that the extreme types (i.e., early being the shortest and very late being the tallest) were significantly different at most environments. The mean isotypes response over all environments (Figure 1) showed a gradual increase in height with a delayed heading date and was positively correlated to heading dates (Table 15). The pattern of plant height responses between isotypes is uniform across environments (Figure 17). However, the magnitude and range of responses varied between environments, as they did for kernels per spike (Figure 3).

The Duncans Multiple Range test on percent protein reveals that in general only a few of the six isotypes were significantly different from the other isotypes in each environment. The range of response in percent protein was smaller than the other morphological traits, as shown by the mean percentage analysis (Figure 17). The pattern of response was not consistent between environments, and the mean response over all environments showed nonsignificant differences in an analysis of variance test (Table 12). In the space planted environment (Table 8 and Figure 2) the early isotype produced a highly significant protein response.

Table 15. Correlation matrix between all traits studied for each isotype averaged over all environments (N=6). (Genetic Variation).

	YIELD	HEADING DATE	TILLERS/ 30 cm ²	KERNELS SPIKE	KERNEL WEIGHT	TEST WEIGHT	PLANT HEIGHT	% SHATTER	% THIN	% PLUMP
TEST WEIGHT	.86*	-.64	.79	-.55	.61	1.00				
PLANT HEIGHT	-.32	.92**	-.89*	.92**	-.70	-.30	1.00			
% SHATTERING	.48	-.94**	.82*	-.90*	.89*	.44	-.89*	1.00		
% THIN	-.82*	.92**	-.96**	.86*	-.92**	-.84*	.80	-.83*	1.00	
% PLUMP	.79	-.94**	.95**	-.89*	.96**	.75	-.80	.87*	-.99**	1.00
% PROTEIN	-.57	-.03	-.08	-.15	-.13	-.64	-.31	.20	.24	-.15

*, **Significant at the P = .05, P = .01 level, respectively.

Due to sampling techniques, the overall plant height was not studied in the space planted nursery. However, the main tiller internode lengths were measured. The heading date isotypes had significantly different main culm internode length for the n-1 and n-3 internodes (Table 8). The internode length to heading date correlations were significant ($r=.92^{**}$) only for the n-3 internode, and in this environment may be considered to be the principal determinant of plant height (Table 8). The nonstressed environment also produced significant isotype effects in the leaf area, leaf length and leaf width for the flag leaf to the n-4 leaf of the main culm (Figure 12 and Table 8).

The range of percent thin kernels response among isotypes at most environments is extremely large (Figure 17), and the pattern is not consistent from one environment to the next. The Duncans Multiple Ranges test (Figure 17) reveals significant differences among most isotypes at the eleven environments (Table 14) with significant results.

In general, the mean percent plump response was divided into the early and late heading isotypes. The three late heading isotypes were usually found to be significantly different from each other with Duncans Multiple Range analysis (Figure 1 and Figure 17). The later heading isotypes also produced the lowest mean number of plump kernels, as is shown in the overall mean percentage analysis (Figure 1). The mean percentage also reveals that the range of responses between the isotypes at each environment were smaller than those produced in the

percent thin response, although the relative range across isotypes was still much larger than most of the other measured traits (Figure 17).

It appears that in the range of environments studied that test weights, percent protein and percent thin kernels did not display an environmentally consistent pattern of results, although there were significant differences found for each of these traits in most of the environments. Plant height and percent plump did, however, produce consistent patterns of significant responses across all environments.

These observations are indirectly supported by the statewide regression analysis. Although test weights, plant heights, percent plump, and percent thin all failed to produce detectable associated isotype x environment interactions, the patterns displayed by the intersecting regression lines implies that, test weights response differences were largest in low test weight environments (Figure 18) and percent thin response differences were largest in high percent thin environments (Figure 19) (high stresses?). In contrast to these patterns of intersecting slopes, percent plump and plant height responses generally produced parallel lines, with the ranking of responses maintained across all environments (Figures 20 and 21), implying pleiotropic responses for plant height and percent plump kernels with genetic heading dates. The fact that the genetic correlations between mean heading dates, percent plump and kernel weights is quite high when averaged over 14 yield trial environments (Table 15) and low in a space

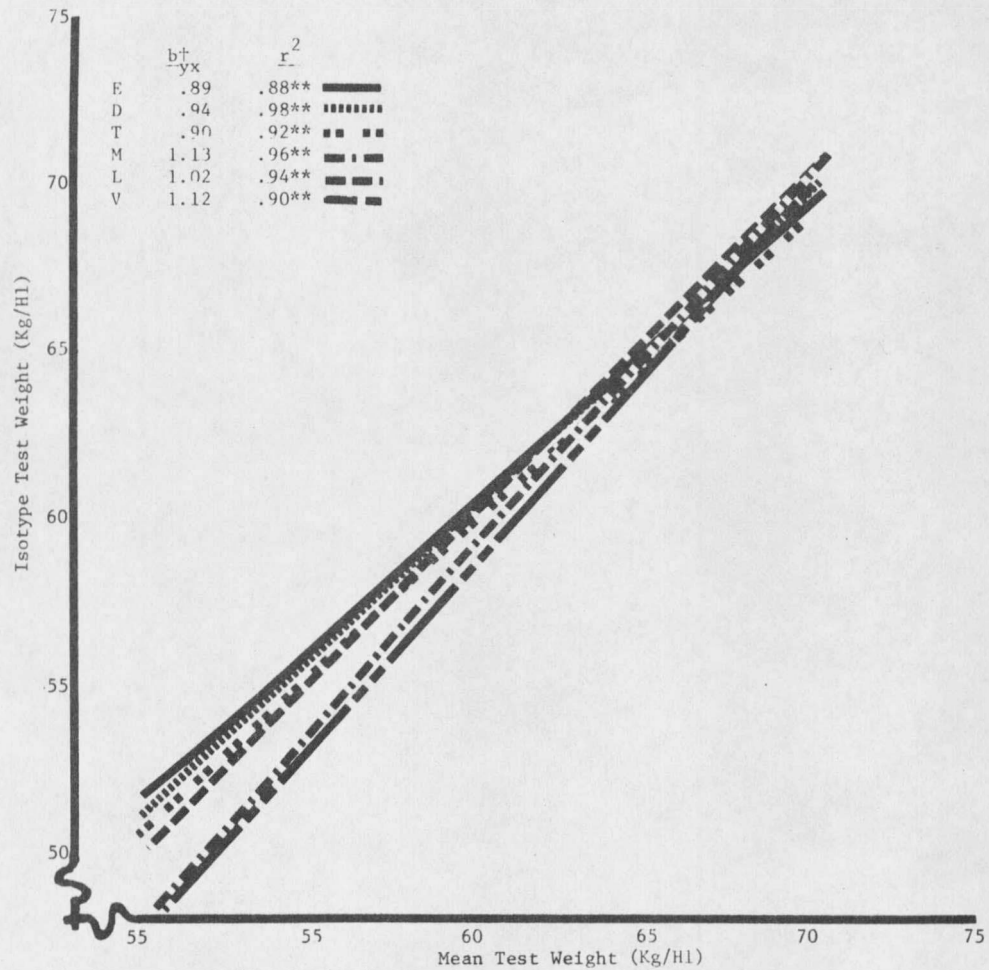


Figure 18. Regression analysis showing test weight (kg/hl) responses of six Titan heading date isotypes over 14 environments. *,** Significant at $p = .05$, $p = .01$, respectively: $\dagger$ -t-test showing $H_0: b = 1.00$.

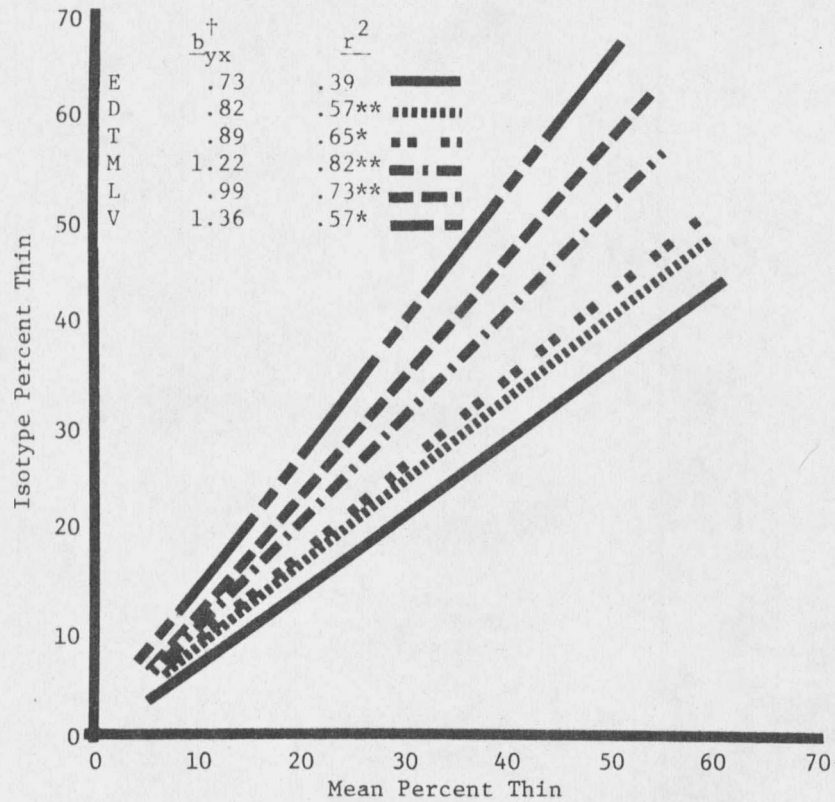


Figure 19. Regression analysis showing percent thin (through 5.5/64 m) kernels of six Titan maturity isotypes over 14 environments. *,** Significant at $p = .05$, $p = .01$, respectively. $\dagger$ t-test showing $H_0: b = 1.00$.

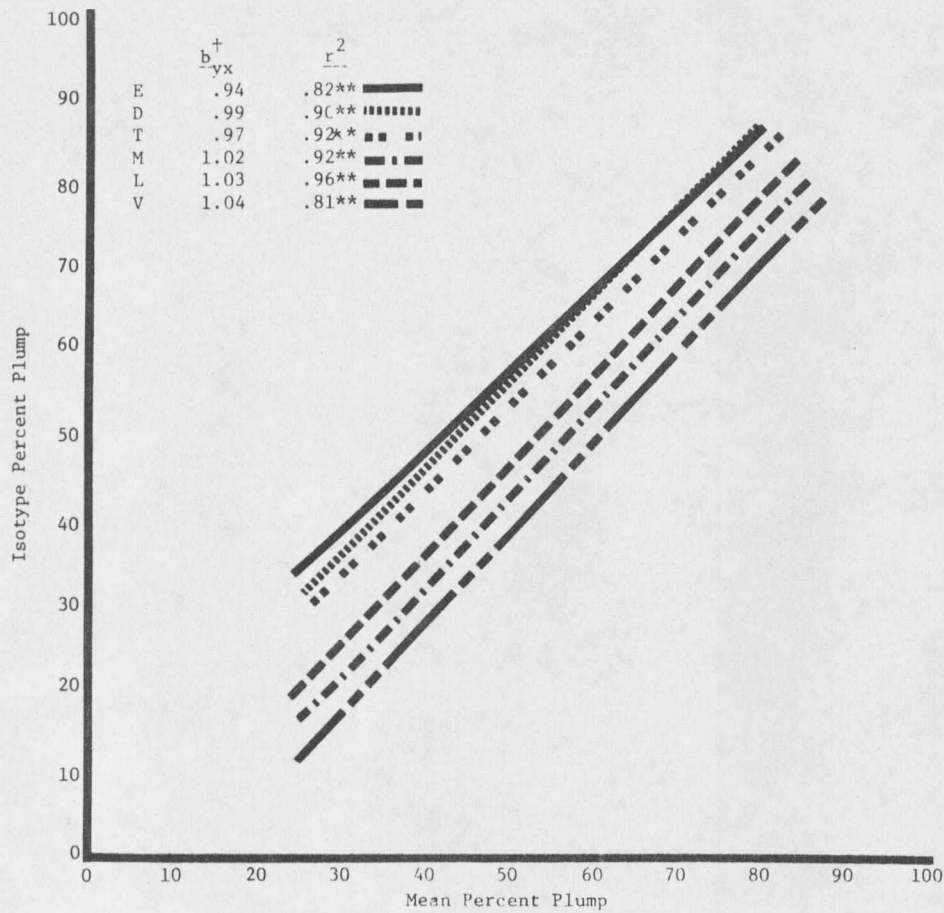


Figure 20. Regression analysis showing percent plump kernels of six Titan maturity isotypes over 14 environments. *, ** Significant at $p = .05$, $p = .01$, respectively; + - t-test showing $H_0: b = 1.00$.

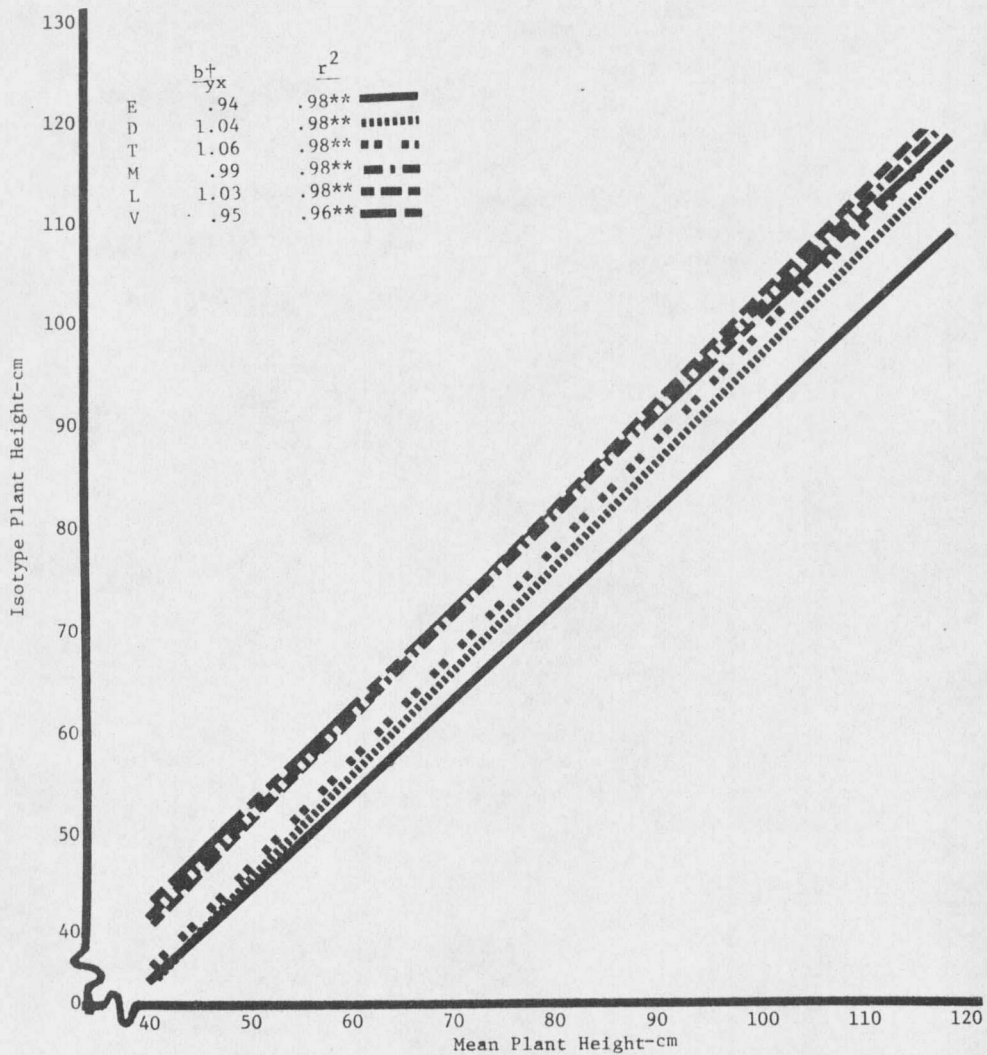


Figure 21. Regression analysis showing plant height (cm) responses of six Titan heading date isotypes over 14 environments. *, ** Significant at $p = .05$, $p = .01$, respectively. † - t-test showing $H_0: b = 1.00$.

planted nursery (Table 16) implies that these quality components are related to heading dates' influence on moisture stresses. On the other hand, the high correlations between plant height and heading dates in the yield trials (Table 15) and the main tiller internode length and heading date in the space planted nursery (Table 16) implies that plant heights are due to genetic pleiotropy with heading dates, as reported by Dixit (1973), and therefore soil moisture differences don't express a strong interisotypic effect.

Percent plump and thin kernel responses, therefore, seem to be dependent upon the relative environmental differences created by genetically different heading dates, specifically water availability differences. Whereas plant heights seem to be due to genetically altered duration of growth. This is supported in part by the observation that environmentally induced heading dates are significantly correlated to percent thin kernels, and not to plant heights or kernels per spike (Table 17). The later planted environments produced thinner kernels, probably due to depleted soil moisture during kernel filling and due to late tillers, not establishing full kernel weights. Kernel weight responses were also negatively correlated to genetic as well as an environmentally induced heading date differences ($r = -.88^*$ and $r = -.79^{**}$), for the same reason.

The lack of any significant genetic correlations between percent protein and the other traits in the yield trial environments and the

Table 16. Correlation matrix between mean trait responses for six Titan maturity isotypes grown in space planted conditions (Bozeman, 1977). (N=9)

	HEADING DATE	YIELD	SPIKES/ PLANT	KERNELS/ SPIKE	KERNEL WEIGHT	# SPIKELETS	RACHIS NODE LENGTH	SPIKE LENGTH	AWN LENGTH	% PROTEIN	% PLUMP	% THIN	TEST WEIGHT
LENGTH	.03	.25	.34	.04	-.24	-.05	1.00						
SPIKE LENGTH	.94**	.94**	.63	.96**	-.35	.96**	.19	1.00					
AWN LENGTH	-.56	-.56	-.04	-.78*	.67**	-.75*	.11	-.70*	1.00				
% PROTEIN	-.74*	.72*	-.47	-.79*	.84**	-.84**	-.10	-.73*	.78*	1.00			
% PLUMP	-.35	-.35	-.34	-.40	.73	-.46	.05	-.39	.43	.59	1.00		
% THIN	.31	.31	.33	.31	-.76*	.37	.09	.28	-.33	-.58	-.90**	1.00	
TEST WEIGHT	.36	.18	.25	.30	-.84**	.43	-.39	.21	-.41	-.77*	-.47	.57	1.00

*, **Significant at P = .05, P = .01 level, respectively.

Table 17. Correlation matrix between all traits studied for each environment averaged over all isotypes. (Environmental Variation).

	YIELD	HEADING DATE	TILLERS/ 30 cm ²	KERNELS SPIKE	KERNEL WEIGHT	TEST WEIGHT	PLANT HEIGHT	% SHATTER	% THIN	% PLUMP	% PROTEIN
TEST WEIGHT	.16	-.21	-.16	-.29	.38	1.00					
PLANT HEIGHT	.51	-.29	.55	-.52	.40	-.38	1.00				
% SHATTERING	.44	-.48	.50	-.73**	.46	.12	.39	1.00			
% THIN	.01	.70*	-.28	.40	-.24	.11	-.49	-.39	1.00		
% PLUMP	.40	-.46	-.04	.66	.72**	.19	.71**	.54	-.69**	1.00	
% PROTEIN	-.22	.05	.00	-.36	.20	-.35	.55	.52	-.15	.50	1.00

*, **Significant at P = .05, P = .01 level, respectively. (Degrees of Freedom Varies)

relatively small degree of interaction (Figure 22) is probably due to the strongly compensating components causing nonsignificant yield differences. Thus, the number of spikes per unit area were similar among the isotypes, and the distribution of available nitrogen would not have been different. In the space planted environments, there were large and significant yield differences caused by the number of kernel components causing strong correlations with percent protein. Thus, it seems that the number of kernels/unit area is the principal factor affecting the protein content of the kernels.

Environmentally induced correlations (Table 17) suggest that environments producing taller plants will produce plumper and heavier kernels. It is also implied that a late planted environment will produce more thin kernels and lighter kernels. It seems that an environmentally induced change in heading date within an isotype will approximate a genetically induced heading date change among the isotypes in the percent thin response, the kernel weight response, and possibly in the percent plump response, supporting similar observations with the yield component responses.

The rationale explaining these similarities in environmentally versus genetically induced responses is again based on both the reduced soil moisture and the reduction in period from planting to heading associated with later planting dates. An early planted environment will maintain the vegetative stage longer due to reduced

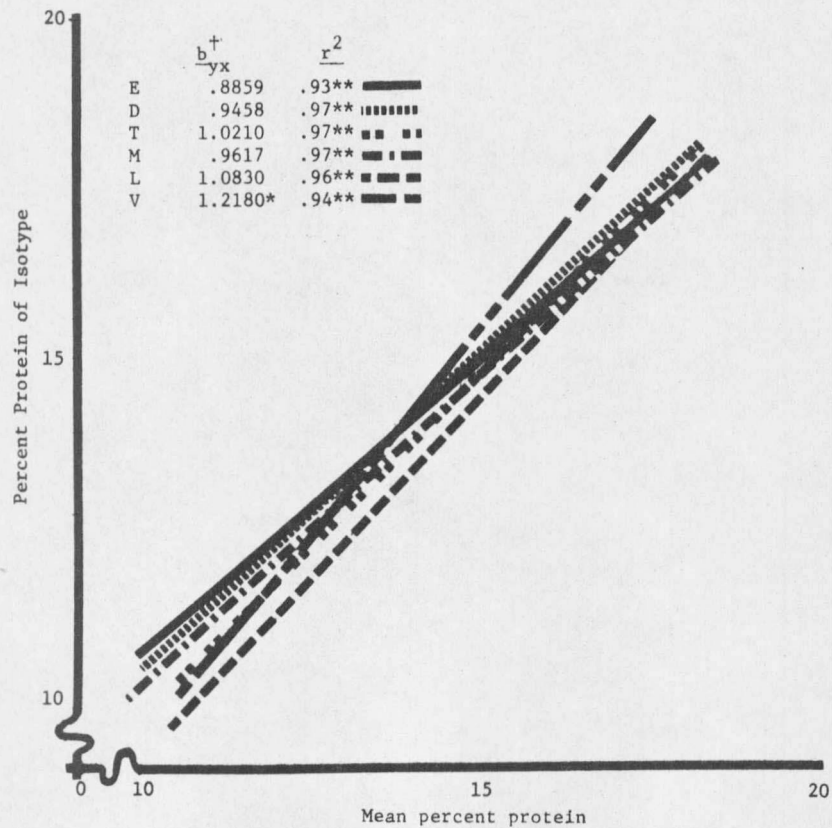


Figure 22. Regression analysis showing responses of percent protein in the kernels of six Titan heading date isotypes over 14 environments. *,** Significant at $p = .05$, $p = .01$, respectively. $\dagger$ t-test shows probability ($p = .05$) that $H_0: b \neq 1.00$.

daylength and temperatures than a late planted environment, allowing a plant to grow taller and still head earlier in the growing season. The resultant greater available soil moisture allows plumper and heavier kernels to be developed.

Moisture stresses at the flowering and soft dough stages have been reported to reduce kernel weights and plumpness (Day and Thompson, 1975; and Wells and Dubetz, 1966), which is consistent with the observation that the organ developing most rapidly at the period of stress will show stress the most (Aspinall et al., 1964). Thus, it is logical that the trait best used for drought resistance selections would be kernel weight and size as suggested by Wells and Dubetz (1966), and not heading date pleiotropic characters such as plant heights, leaf areas or kernels per spike, since kernel development occurs during the period of greatest water deficiency near the end of the growing season.

Two studies on the inheritance of kernel weights, kernel size, plant heights, and test weights have reported both positive and or negative genotypic correlations between these traits in F_1 , F_2 , and F_3 generations (Morsi and Abo-Elenein, 1975; and Nasr et al., 1974). The results are consistent with those reported here. However, no efforts were made in either study to measure heading date differences of heritabilities. It is a strong possibility that the genetic correlations are due to pleiotropic effects caused by heading date differences alone, since their responses follow very closely the responses observed

in the isotypic series studied here. Caution should be taken in heritability studies to not assume linkages, but to look for a common genetically controlled trait that may control the other morphological responses by adjustments of the developmental allometry of the plant. If a controlling genetic trait does exist, then selection for any of the correlated traits will be consistent and dependent upon the expression of the controlling gene, implying linkage which is in fact pleiotropy.

SOIL WATER EXTRACTION EXPERIMENT

Analysis of variance comparing varietal effects on soil moistures at each depth in the Fort Ellis, 1977, experiment revealed no significant differences between isotypes at any soil depth. The reason for this is quite possibly due to the extremely dry conditions at that location causing a uniformly dry soil moisture regime down to the third foot level. Beyond this level there was an inconsistent sandstone hard-pan preventing sampling at some of the lower soil depths (Figure 23). The lack of significant responses, probably due to either the extreme soil variability or the consistent dryness of the soil, may account for the lack of any significant correlations with moisture content at the soil depth studied.

The Bozeman, 1977 experiment was irrigated once, but did show significant differences at the first three foot levels, and the

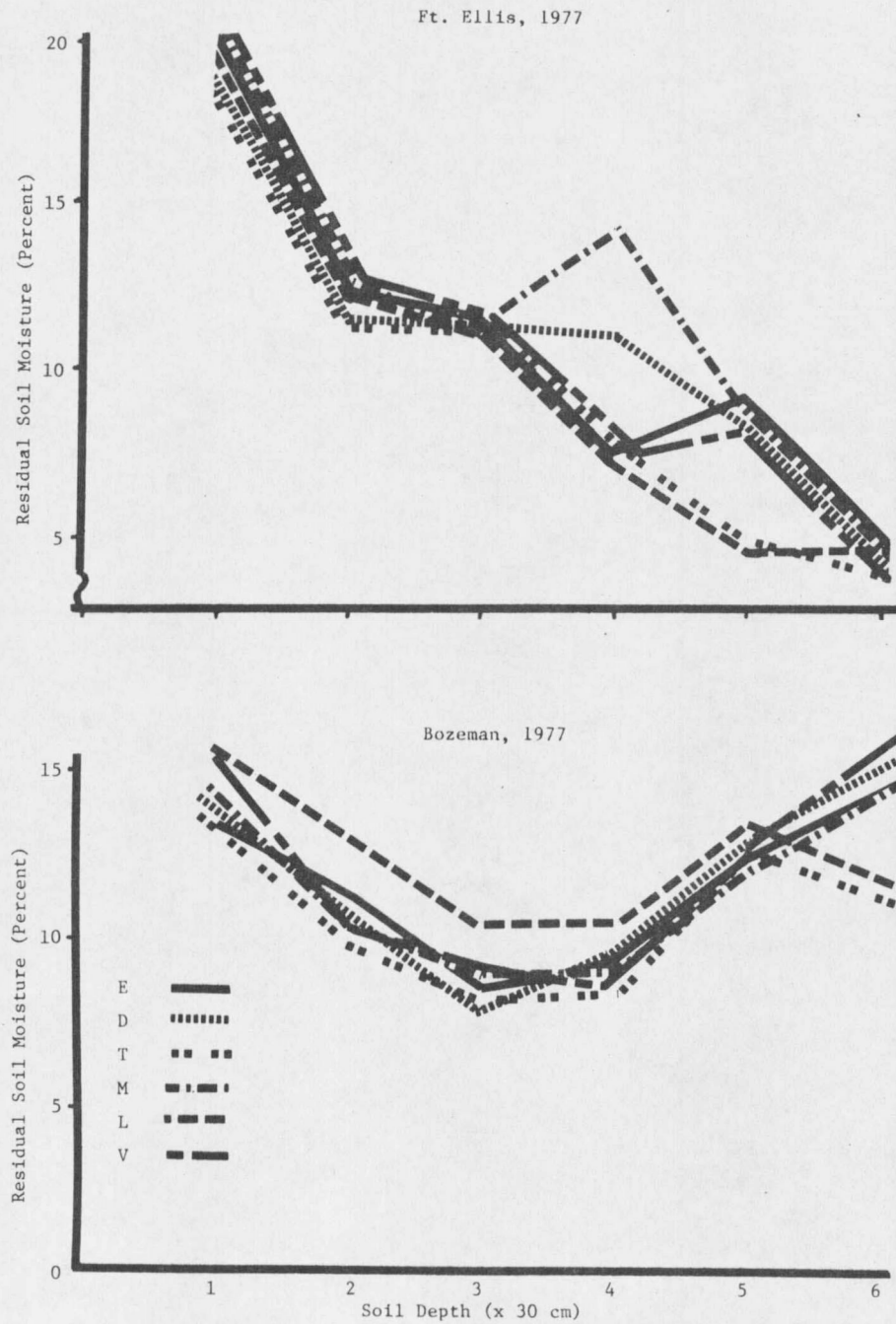


Figure 23. Residual soil moisture remaining at each soil depth (x 30 cm) following harvest at a dryland (Ft. Ellis) and an irrigated (Bozeman) environment.

responses were more uniform among the soil depths. The soil is an Amsterdam silt loam which has a characteristic mollic epipedon to about 30 cm, a B₂ argillic horizon, and a CCa horizon starting at approximately 120 cm and continuing to about 240 cm. The highest yielding isotype (early composite) removed the most soil moisture from the first 30 cm level. The late isotype withdrew the least water from the first two 30 cm levels (Figure 23), resulting in significant correlations between heading date and percent residual soil moisture at the first and third 30 cm levels ($r=.92^{**}$ and $.85^{*}$, respectively, Figure 24). Although at only one location, these correlations seem to refute the hypothesis that later heading isotypes will utilize more soil moisture. However, yield must be considered in this implied statement. Yield, spikes/30 cm² and kernel weights are all negatively correlated to heading date at this environment ($r=-.87^{*}$, $-.88^{*}$ and $-.99^{**}$ respectively). Thus, the heading date to moisture correlations are probably due to increased demands due to higher yields caused by increased tillers and kernel weights in the early isotypes as shown by the negative correlation between kernel weights and the first 30 cm soil moisture and the similar pattern of these traits to residual soil moisture at each depth (Figure 24). Kernels per spike were positively correlated to heading date and consequently to the percent moisture at the third level ($r=.92^{**}$ and $.84^{*}$, respectively). Thus, it appears that if different maturities create yield and yield component response differences, these

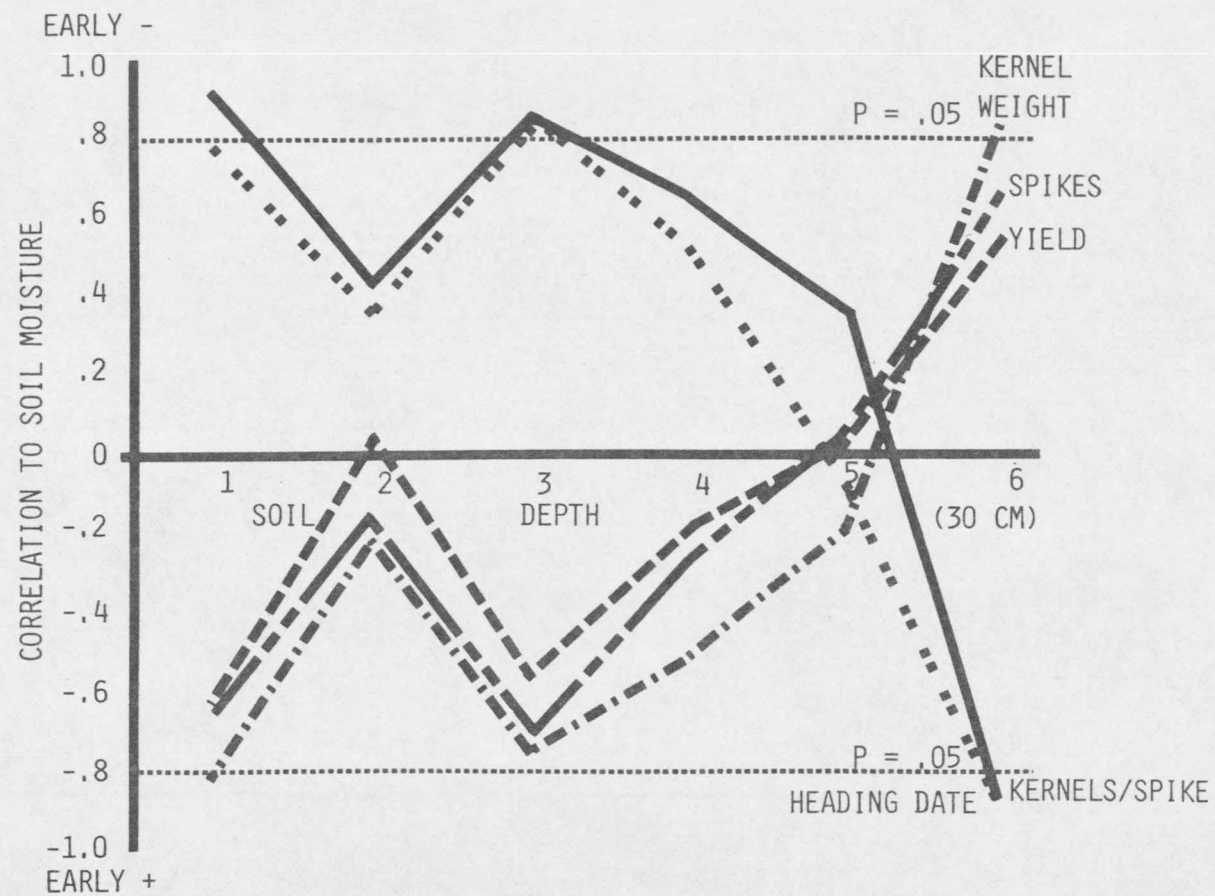


Figure 24: Correlations of heading dates, spikes/30 cm², kernels/spike, kernel weights and yield to residual soil moisture at each soil depth in Bozeman, 1977.

responses may be due to differences in utilization of the soil moisture associated with growth differences, supporting our previous hypothesis of hormonal component control being dependent upon moisture availability.

The correlation pattern present in the 6th 30 cm level is also illustrative of maturation rate induced pleiotropic responses. The development of root systems is a highly coordinated, hormonally regulated process with strong, stress related compensatory growth patterns (Grosset et al., 1975). Thus, a positive correlation between heading dates in the first 30 cm levels, implies a reduced utilization of soil moisture for the late heading isotypes, possibly caused by the ability of the later types to develop roots into the lower foot levels due to the increased growth duration. This explains the plant height to soil moisture correlation at level six ($r = -.82^*$), and correlations of percent moisture to kernels per spike and kernel weights ($r = -.86^*$ and $.83^*$, respectively) and probably the associated correlations to heading dates.

PERCENT SHATTERING

Percent shattering was measured while determining spikes/30 cm² and seeds/spike. In the material studied, it could be considered as a product of differing heading dates, since each environment was harvested at the same time and the earlier heading isotypes were drier and more apt to shatter. The shatter percentages are, however, very small

and the degree of shattering is dependent upon handling of the collected heads, as well as the heading date and the dryness at harvest as shown by the correlation to heading dates (Table 15). The small percentages combined with the variable nature of expression reduced the probability of obtaining any regular pattern of response between isotypes at different environments as shown by the statewide regression analysis (Figure 25). There were only two of the total twelve environments studied which produced significant isotypic effects in the percent shattering response and thus, this trait is not summarized in the parallelipiped analysis, nor by the Duncans Multiple Range test. The late heading isotype did have a significant isotype x environment interaction (Figure 25). The genetic heading date differences between the isotypes produced a strong pattern of genetic correlations between percent shattering and the other variables (Table 15) correlated to heading date.

Chlorophyll response differences were also minimal and non-significant. Consequently, the analysis of this trait was not included in this report.

SOURCE SEED ANALYSIS

The possibility exists that due to the observed difference in kernel weights, percent plump and percent thin kernels between the early heading and late heading isotypes, a difference in number of kernels

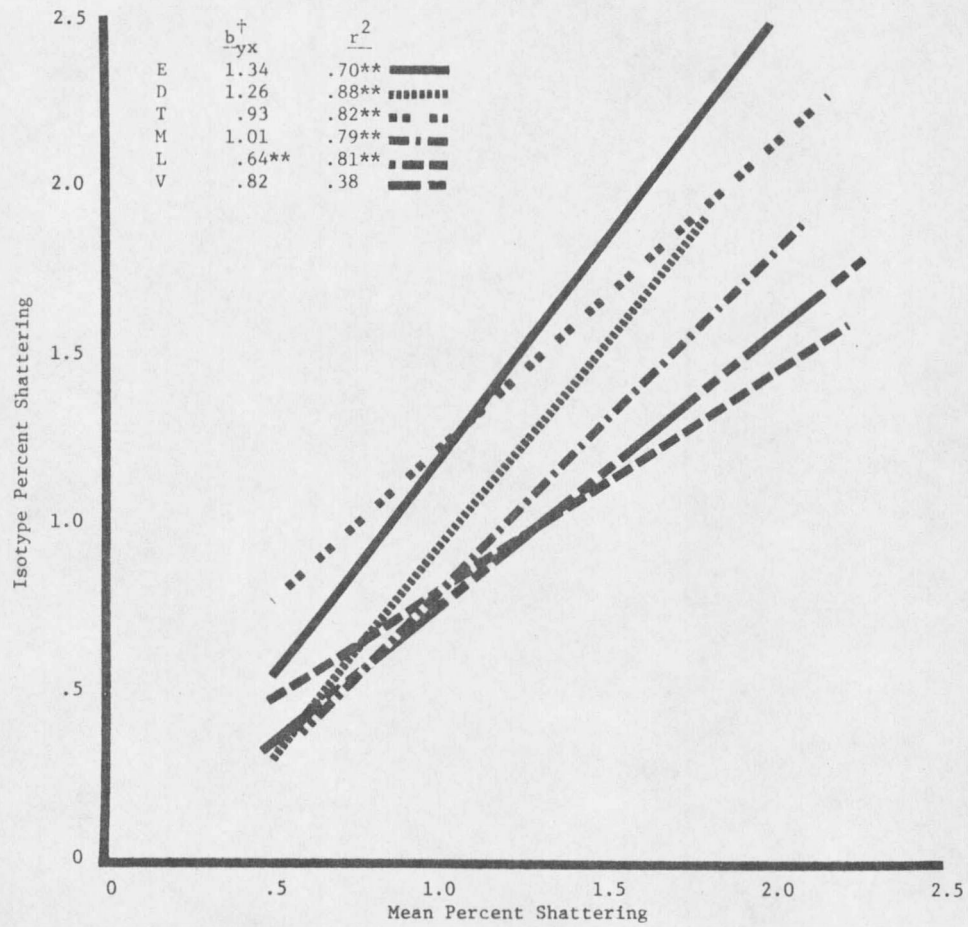


Figure 25. Regression analysis showing percent shattering of six Titan heading date isotypes over 14 environments. *, **Significant at $p = .05$, $p = .01$, respectively; $\dagger$ - t-test showing $H_0: b = 1.00$.

planted could have occurred with the method used for measuring seeds. The source seed was increased in 1975 at Bozeman to assure similar environmental background. If the source seed used to plant these nurseries was significantly plumper for the earlier isotypes than for the later isotypes, then the number of kernels planted per 30 cm² could have been significantly fewer for the earlier than the later heading isotypes. If this occurred, then the early isotypes would have been able to produce more tillers due to more available space and the plumper and more vigorous seedlings. To avoid this, the source seed was tested for kernel weight, number of kernels in the container used to measure kernels, and the weight of the kernels in this volume. Ten replications were used for each analysis of variation and a Duncan's Multiple Range were performed on each test.

The results of this analysis are presented as a parallelepiped in Figure 26. There were significant differences between the isotypes for each variable studied. However, the range of responses were very small and consisted of a minimal percentage of the total mean response in each trait. It is concluded that a variation of 300 to 350 kernels per 30 cm is not going to cause the range and magnitude of yield component responses observed in this study.

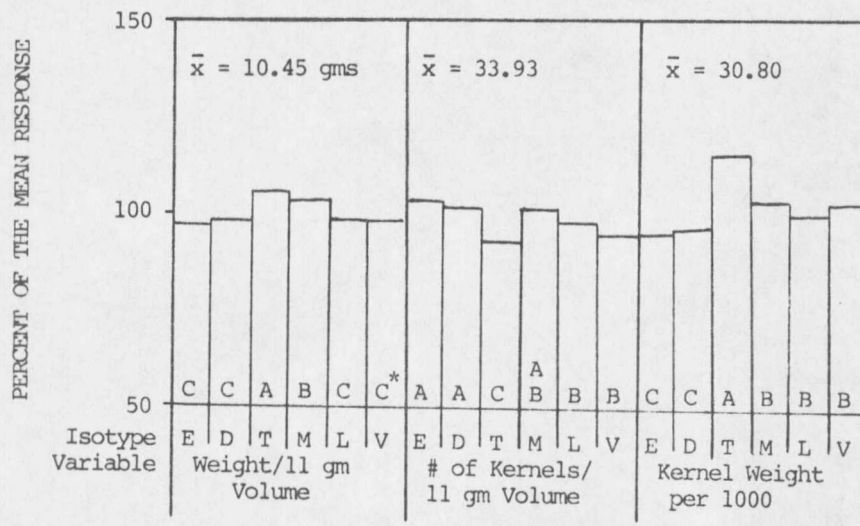


Figure 26: Mean Percentage analysis histogram and Duncan's Multiple Range Test* comparing the mean kernel weights, and number of kernels and weight of 11 gram planting volume for the source kernels of the environmental yield trials.

*Separate letters denote significantly different means ($p = .05$).

CONCLUSIONS

The genetic heading date of a plant is going to pervade all aspects of a plant's growth and adaptation to an environment. The typical complexities of studying heading dates have been alleviated by using isogenics with genetically different heading dates, but similar degrees of photoperiod and thermal sensitivities, due to the common Titan genotypes. The similar degrees of sensitivity have eliminated most isotype x environment interactions for heading date expression which have previously confounded this type of study (Bell, 1939; Takahashi and Yasuda, 1971).

Analysis of the traits by correlation, path analysis, regression, analysis of variance, Duncan's Multiple Range and percentage of the mean analysis have shown that the responses are mediated by the heading date of the isotype in two ways. The simple genetic elongation of the growing period will affect those traits which are dependent upon growth rates, and which are under the strongest genetic control and were shown to have minimal degrees of genotype x environment interactions as shown by a statewide regression analysis.

Water availability was the second factor affected by genetic heading date. In Montana environments, the majority of available water has been shown to arise mainly from spring precipitation. Thus, as the growing period progresses, the amount of residual soil moisture is

depleted. Early heading isotypes will consequently have more available water at any one developmental stage than the late heading isotypes.

The yield and yield component responses were controlled by genetic heading dates over the fourteen yield trial environments and one space planted nursery in the same two manners. However, due to the developmental allometry of the yield components, path analysis could be used to clarify their relative effects on yield and on each other, as well as the other described methods of analysis.

Parallelipiped analysis revealed that tillers/30 cm² and kernels per spike typically had larger differences in response between the isotypes than did kernel weight. However, correlation analysis at each environment revealed that tillers/30 cm² and kernel weights were not consistently significantly or negatively correlated to heading dates. Kernels/spike were highly correlated to the genetically determined heading date in all but one environment, including the space planted nursery. Statewide regression analysis also revealed that tillers/30 cm² and kernel weights produce more mean associated genotype x environment interactions than the environmentally consistent kernels per spike response. It was postulated that instead of tillers/30 cm² being under strong genetic control as postulated by previous authors, that kernels per spike is genetically and hormonally controlled and expresses a strong feedback effect on tillers/30 cm². Kernel weight responses seem to be mediated by the compensating pattern of the first two

components and their demand on nutrients. The genetic maximum kernel weights may be controlled by palea and lemma, however, the size of the palea and lemma does not seem to be controlled by the size of the leaf meristem as postulated by Grafius (1978).

The environmentally induced response of each isotype revealed that of the yield components tillers/30 cm² and kernel weights expressed the strongest direct effect on yield responses. This supports the conclusions found with genetic heading dates that these two traits are the most variable among environments. The unaccounted for portion was large, preventing definite conclusions.

When each environment was analyzed separately, it was found that those environments which were planted early, headed early. In these early heading environments, the primary component controlling yield was kernels per spike, perhaps due to the larger amount of residual soil moisture remaining after the late heading isotypes spike development was complete. This may allow late tillers to be developed, reducing the tiller differences between the early and the late isotypes. Any yield differences between the isotypes would thus be due to the consistent kernels/spike advantage of the late isotype.

In the later planted environments where residual soil moisture becomes more limiting, and stresses become greater, the early isotypes consistently produced more tillers/30 cm² and fewer kernels per spike, but heavier and plumper kernels than the late heading isotypes. In

these late planted environments, tillers/30 cm² expressed the strongest direct effect on yield, due to the large tiller differences between isotypes. The larger number of tillers found on the early heading isotypes was theoretically due to more residual soil moisture remaining after spike development than is found with the late isotypes. This greater residual soil moisture allowed a second crop of tillers to occur in the early isotypes, thus affecting yield. In support of this theory, soil moisture determinations revealed more residual soil moisture at the fifth and sixth foot level for the early types than the later isotypes after harvest, in one environment measured, even though less moisture was available at the first foot level.

These findings imply that under field conditions selection between plants for actual tiller numbers will not be effective. Kernel weight selection will be more effective, especially for drought, but will still be largely influenced by environmental factors. Kernels per spike will be the most heritable and stable component to select for in populations with varying yield components. Possibly the best combination of traits for Montana environments will be an early cultivar that produces a better than average number of kernels per spike with a moderate but stable ability to tiller. This is especially true in Montana, since in most commercial fields plants produce only one or two tillers.

The morphological responses support the conclusions based upon the yield and yield component responses. Plant heights revealed a consistent pattern of response between the environments, and an overall positive correlation to heading dates. Also leaf width, length and area were positively correlated to heading dates in a space planted nursery, as were main culm internode lengths. These positive correlations to heading date, and the consistent environmental response of plant heights all imply pleiotropic responses similar to kernels per spike. Plant heights also had a weak correlation to environmentally induced heading dates, as did kernels per spike, and there were no isotype x environment interactions found.

Kernel traits such as percent plump, percent hin, were shown to be correlated to heading dates. But, unlike the previously mentioned traits, the responses of these traits are highly affected by environmental variation. This was shown by large degrees of genotype x environment interactions in the regression analysis and the range of response patterns in the parallelipiped analysis.

Also these traits were not correlated to heading dates in the space planted nursery as they were in the average drilled nursery, implying stress induced correlations as were found for kernel weights.

The environmentally and genetically induced variations both produced significant correlations between heading dates and kernel weights

and percent thin kernels. This implies that genetic and environmental delays in heading dates affect kernel development similarly.

Further research is needed to verify this hypothesis of yield component control. One method would be to analyze isogenics for two and six row barleys to determine whether the genetically increased kernels per spike consistently reduces the number of tillers. Also, early and late heading isotypes in combination with the two and six row isotypes could reveal any interactions of these genetic traits on the yield component responses. Soil moisture studies incorporating yield component responses should also be made in greater detail.

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