



The pleiotropic effects of maturity and row type isogenic lines on the yield stability and development of barley (*H. vulgare* L.)
by Virgil William Smail

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Crops and Soil Science
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Abstract:

An isogenic pair of 'Betzes' and an early heading backcross isogenic of Betzes, and 'Erbet', were grown in 214 environments. Consistent eight day reductions of heading dates between the pairs caused significant decreases in mean yields, plant heights, and percent thin kernels and increases in mean test weights, percent plump kernels, kernel weights, and percent protein. Regression analysis of the Erbet response on the Betzes response revealed that differences in plant heights and yields increased with increased means due to reduced stress levels. Differences in kernel characters increased with decreased mean responses due to increased stress levels. These genotype x environment interactions for plant heights and yields are hypothesized to be due to the pleiotropic effects of increased growth duration allowing more growth. The kernel character's genotypes x environment interactions are probably due to the drought avoiding nature of early heading cultivars.

Yield trials of the possible homozygous lines for the 2-row, 6-row (V,v), lateral spike fertility (I,i), and maturity (Ea,ea) genes in isogenic lines (BC7) in three varietal backgrounds were grown in six Montana environments. Yield, yield components, and morphological character data were collected on a replicated basis in each environment. Correlations between characters revealed a strong pattern of yield component compensation, but few significant correlations between the components and heading dates or yield. The 23 factorial analysis revealed strong main effects of the row type (v) gene and the maturity gene (ea) on yield and yield components over most of the environments studied. This and previous research have revealed a strong pleiotropic control of kernels/spike dependent upon genetic heading dates and row types (V,I) of barley. Tillering response is less strongly controlled and expresses a strong genotype x environment interaction, implying strong genetic control on the differences in kernels/spike between isolines and an environmentally induced control for kernel weight.

Kernel weights are probably affected by compensation of kernels/spike and tiller number interacting with the environment.

Twenty-six heading date isotypes in seven 2- and 6-row barley cultivars were planted in replicated yield trials in three Montana environments. Post-harvest soil moisture data were collected on a plot basis in 30 cm increments to a depth of 180 cm. These estimates of physiological root activity at a given soil depth were related to heading date, yield, yield components, and quality components. Significant negative correlations were obtained for isotypic heading date responses and mean soil moisture withdrawal for all but one of the varietal backgrounds. Kernels/spike and kernel weights were significantly correlated to heading dates. Kernels/spike were negatively correlated to kernel weight and spikes/meter in a compensating pattern in several stressed environments. Path analysis revealed that spikes/unit area expressed the strongest direct effect on yield of the three yield components. From these findings, a pattern of cause and effect on yield and yield component responses was postulated to be due to the differences in residual soil moistures, induced by genetically controlled differences in maturation rates.

Diethylsulfate mutagenesis and backcrossing were used to develop 14 heading date isotypes ranging over a 20 day period in 2-day increments. This isotypic series was grown in a replicated yield trial at Bozeman, MT in 1980. Analysis of variance revealed significant isotypic differences in heading dates, kernel weights, kernels/spike, yield, and spikes/30 cm². Correlation analysis of the earliest seven isolines revealed positive correlations of heading dates to spikes/ 30 cm² and yield, implying low early season stress. Correlations of heading dates to kernels/spike and kernel weights between the six latest isolines implies a pattern of late season stress avoidance due to the heading date differences. Strategies for improving the yield performance and stability of early lines utilizing this and previously reported data are presented.

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LINES ON THE YIELD STABILITY AND DEVELOPMENT
OF BARLEY (H. VULGARE L.)

by

VIRGIL WILLIAM SMAIL

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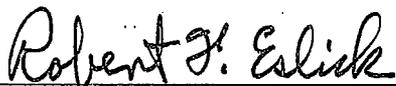
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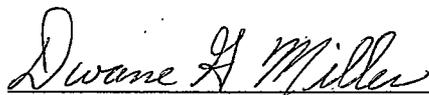
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ABSTRACT

An isogenic pair of 'Betzes' and an early heading backcross isogenic of Betzes, and 'Erbet', were grown in 214 environments. Consistent eight day reductions of heading dates between the pairs caused significant decreases in mean yields, plant heights, and percent thin kernels and increases in mean test weights, percent plump kernels, kernel weights, and percent protein. Regression analysis of the Erbet response on the Betzes response revealed that differences in plant heights and yields increased with increased means due to reduced stress levels. Differences in kernel characters increased with decreased mean responses due to increased stress levels. These genotype x environment interactions for plant heights and yields are hypothesized to be due to the pleiotropic effects of increased growth duration allowing more growth. The kernel character's genotypes x environment interactions are probably due to the drought avoiding nature of early heading cultivars.

Yield trials of the possible homozygous lines for the 2-row, 6-row (V,v), lateral spike fertility (I,i), and maturity (Ea,ea) genes in isogenic lines (BC7) in three varietal backgrounds were grown in six Montana environments. Yield, yield components, and morphological character data were collected on a replicated basis in each environment. Correlations between characters revealed a strong pattern of yield component compensation, but few significant correlations between the components and heading dates or yield. The 2^3 factorial analysis revealed strong main effects of the row type (v) gene and the maturity gene (ea) on yield and yield components over most of the environments studied. This and previous research have revealed a strong pleiotropic control of kernels/spike dependent upon genetic heading dates and row types (v,I) of barley. Tillering response is less strongly controlled and expresses a strong genotype x environment interaction, implying strong genetic control on the differences in kernels/spike between isolines and an environmentally induced control for kernel weight. Kernel weights are probably affected by compensation of kernels/spike and tiller number interacting with the environment.

Twenty-six heading date isotypes in seven 2- and 6-row barley cultivars were planted in replicated yield trials in three Montana environments. Post-harvest soil moisture data were collected on a plot basis in 30 cm increments to a depth of 180 cm. These estimates of physiological root activity at a given soil depth were related to heading date, yield, yield components, and quality components. Significant negative correlations were obtained for isotypic heading date

responses and mean soil moisture withdrawal for all but one of the varietal backgrounds. Kernels/spike and kernel weights were significantly correlated to heading dates. Kernels/spike were negatively correlated to kernel weight and spikes/meter in a compensating pattern in several stressed environments. Path analysis revealed that spikes/unit area expressed the strongest direct effect on yield of the three yield components. From these findings, a pattern of cause and effect on yield and yield component responses was postulated to be due to the differences in residual soil moistures, induced by genetically controlled differences in maturation rates.

Diethylsulfate mutagenesis and backcrossing were used to develop 14 heading date isotypes ranging over a 20 day period in 2-day increments. This isotypic series was grown in a replicated yield trial at Bozeman, MT in 1980. Analysis of variance revealed significant isotypic differences in heading dates, kernel weights, kernels/spike, yield, and spikes/30 cm². Correlation analysis of the earliest seven isolines revealed positive correlations of heading dates to spikes/30 cm² and yield, implying low early season stress. Correlations of heading dates to kernels/spike and kernel weights between the six latest isolines implies a pattern of late season stress avoidance due to the heading date differences. Strategies for improving the yield performance and stability of early lines utilizing this and previously reported data are presented.

INTRODUCTION

Barley (Hordeum vulgare L.) is a major food crop for semi-arid and marginal growth environments. Its high yield stability and high nutritive quality make it an ideal feed source in Montana, the United States, and the world. It is also used to produce beer in most parts of the world. With a projected trend toward drier climates, a clearer understanding of the factors governing barley's excellent yield stability is essential. Heading dates, photoperiod sensitivity, and row types are recognized as the major factors controlling adaptation to specific regions, but little specific research has been done on how these factors affect adaptation. The purpose of this thesis is to determine through isogenic analysis the effects of heading date and row type genes on barley yield stability, yield component development, and rooting patterns. The results will be applied to the specific problem of incorporating these hormonal characters into high yielding barley lines for adaptation in specific regions.

LITERATURE REVIEW

The Genetic Control of Barley Yield Levels and Stability

Yield and yield stability have traditionally been considered to be under complex genetic control. Numerous quantitative studies have shown redundant yield and yield components to be under strong additive control with minor inconsistent effects from dominant genetic components (Qualset, 1979; Tseng and Poehlman, 1974; Yap and Harvey, 1972). Very rarely has this type of information actually been utilized in breeding programs for yield selection (Qualset, 1979).

During the past decade reports have combined heritability estimates with genotypic and phenotypic correlations between morphological traits and yield. Positive genotypic correlations between yield and flag leaf areas, tiller number, kernel weights, plant heights, culm diameters, flag leaf area durations, and leaf angles have been reported (Dixit, 1973; Yap and Harvey, 1972; William and Hayes, 1979; Tseng and Poehlman, 1974; and Tewari, 1976). Positive correlations between heading dates and yield, plant height, kernels/ spike, and leaf areas have also been reported (Williams and Hayes, 1979; and Tewari, 1976). All of these characters except yield are under strong genetic control and each affects the adaptation of the plant to a particular environment.

Dixit (1973) has shown associations between heading dates and plant heights, implying that plant heights in this study are pleiotropically determined by the hormonally mediated heading date characters (Qualset, 1979). Smail (1979) revealed strong positive correlation between progressively later heading dates and plant heights consistent over 15 environments. Using a 'Titan' isogenic series he showed that early heading dates pleiotropically reduce plant heights by reducing the growth duration. Early heading dates, reduced leaf areas, number of rachis internodes, and kernels/spike. Kernel weights, tillers/30 cm, and percent plump kernels were increased by the stress avoidance character of the early heading dates depending upon the level of stress.

Quimby (1975) noted the strong pleiotropic importance to adaptation of heading date and plant height genes in sorghum cultivation. Qualset (1979) noted that plant height and maturity genes, both hormonally controlled factors, directly affect the adaptation of modern "green-revolution" wheats. These authors support Went's (1974) statement that

. . .quantitative characters under genetic control are expressed through hormones, transmissible from organ to organ. Qualitative characters are expressed through intercellular processes and are not hormonally controlled.

Qualset (1979) claims two levels of plant development control in wheat: (1) a small number of hormonal genes with major effects on

plant development and (2) a large number of minor genes involved in basic essential metabolic pathways, each having small effects.

Qualset (1979) describes three methods to determine which characters are controlled or affected by the major genes: (1) The environmental variable can be reduced by growth chamber studies to allow the expression of these genes without confounding genotype x environment interactions. Numerous studies on photoperiod sensitivity, heading date effects, stress responses, and photosynthetic efficiency have utilized this approach. (2) Simplifying genetic segregation ratios by reducing the number of segregating genes in crosses. This allows a clearer understanding of the phenotypic effects major genes have on morphological development by reducing the confounding effect of other major genes. The studies by Hockett and Standridge (1974) and Smail (1979) revealed numerous pleiotropic effects of two- and six-row genes and heading date isogenic lines, respectively, on yield component and morphological development. Simple culling of segregating populations for uniform plant heights, heading dates, and row types in barley will also eliminate major hormonal genes which may mask the effect of other major genes (Qualset, 1979; Eslick and Hockett, 1974). (3) Partitioning the character into more simply defined phenotypic divisions is accomplished by the development of specific assays for the separate components of a phenotypic expression. Ullrich and Eslick (1978) reported a high lysine bioassay

allowing them to effectively isolate the shrunken endosperm barley mutants into those with high lysine and those with other kernel mutational events. The development of accurate, rapid assays for biochemical events governing plant phenotypes is a major need for future breeding efforts and is the object of many breeding projects (Eslick and Hockett, 1974; Hall, et al., 1980).

Studies reporting simple genotypic and phenotypic correlations or genetic variances cannot isolate the direct effects of these major genes on the correlations between characters (Qualset, 1979) because they do not approach the problem in one of these three manners. Smail (1979), using a heading date isogenic series, hypothesized a control of yield component development that is crucial to an understanding of yield stability. This theory claims a stronger genetic control of kernels/spike mediated by a preferential hormonal allocation of nutrients to the developing spike, allowing the attainment of near genetic maximum expression of this character even under moderately stressed conditions. The competitive allocation of nutrient to the spike causes suppression of tiller development resulting in yield component compensation in stressed barley. The uniform yields between the Titan heading date isogenic lines in most environments implied that yield control was dependent upon the genotypic background rather than on the expression of the major genetic characters. Hockett and Standridge (1975) also reported similar uniform

yield levels between two- and six-rowed isogenic lines of barley. This contrasts with statements by Qualset (1979) and Quimby (1975). Major genes may control adaptation to a region, but minor genes, controlling basic metabolic and photosynthetic activity, seem to control the ultimate genetic yield ceilings. Barley lines with known high yield levels can be adapted to specific regions by incorporating essential major genes for adaptation into these lines. Grafius, et al. (1976) reported one such line which out yielded all previous lines by approximately 15 % even though it was adapted to Michigan environments.

The Genetic Control of Heading Dates in Spring Barleys

Photoperiodism was first defined as the elicitation of specific responses by the length of day and night periods (Garner and Allard, 1920). Physiological and morphological responses subject to photoperiodism are classed as photoperiod sensitive, while those characters not so controlled are classed as photoperiod insensitive (Aspinall, 1966). 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). Variations in sensitivity from very photoperiod sensitive to photoperiod insensitive have been reported (Aspinall, 1966). The ranking of heading dates among photoperiod

insensitive varieties are consistent regardless of the photoperiod, whereas rankings in heading dates among differentially photoperiod sensitive cultivars can vary drastically with the photoperiod (Bell, 1939; Takahashi and Yasuda, 1971).

Inheritance of heading dates in barley involves both dominant and recessive genes controlling early and late heading responses and can vary from simply to complexly inherited, depending upon the number of genes (Frey, 1954; Johnson and Ennis, 1964; Nilan, 1964; Smith, 1951). Recently, Fejer and Fedak (1979) reported the isolation of separate genetic controls of photoperiod sensitivity and earliness in a diallel of 'Olli' (insensitive), 'Mari' (insensitive), 'Conquest' (moderately sensitive) and three introductions. Smail (1979) reported similar findings by analyzing the heading date cultivar x environment interactions of isogenic lines of barley varying in relative heading date responses. Other researchers have presented evidence to support the concept of separate genetic controls for relative heading dates (earliness in a narrow sense) and photoperiodic responses in barley (Yasuda, 1978; Takahashi and Yasuda, 1971; Ha and Yasuda, 1977) and in wheat (Chinoy, 1950; and Keim, et al., 1973).

The pleiotropic effects of these two separate systems of genetic control on heading dates has created a great deal of confusion in the literature as to the character most strongly controlling spring

barley heading dates (Aspinall, 1963; Ha and Yasuda, 1977; and Ormrod 1963). Confounded with the photoperiod response is the effect of longer exposures to light, greater light intensity, and higher temperatures, all of which have been shown to increase the phasic development of barley (Faris, Krahn and Guitard, 1969; Aspinall and Paleg, 1964; Williams, 1974). There is little if any difference among cultivars in response to temperature increases of phasic development, due to a common enzymatic Q_{10} increased reaction rate (Takahashi and Yasuda, 1971). Williams (1974) has developed a maturity model for barley based on a biophothermal timescale which is adequately predictive for most Canadian grown barley. However, this depends upon the cultivars having moderate photoperiod sensitivity.

Barleys and other cereals originating from northern latitudes have greater photoperiod sensitivity than those found in the central latitudes (Carder, 1957; Francis, 1970). Photoperiod sensitivity allows spring planted barleys in the northern latitudes to compensate for differences in planting dates and still attain maximum yields (Smail, 1979). In contrast, the recent "green-revolution" cultivars of wheat have been notably day length insensitive since these new cultivars are recommended for central latitudes, and have been developed to most efficiently utilize high fertilization and irrigation

levels, making photoperiod compensation unimportant (Qualset, 1979). These homogeneous crop cultivars although highly suited to manipulated environmental parameters are not suited to nonmanipulated environments (Qualset, 1979).

The Effect of Maturity Differences on Barley Yield Responses

To reduce the environment x cultivar interactions which create confusing and inconsistent heading date responses among cultivars, most research on the effect of heading dates has been carried out in controlled growth chamber environments, effectively eliminating potential differences in varietal photoperiod and thermal responses (Paroda and Hayes, 1971). Reduced growth duration (Kirby and Eisenberg, 1966; Aspinall and Paleg, 1964; Guitard, 1970; and Downs, et al., 1959) in growth chambers produces correlated pleiotropic changes in plant heights, kernel weights, and kernels per unit area (Grafius, 1956; Mellish, et al., 1978; Riggs and Hayter, 1975; Tewari, 1976).

The environmental variable most strongly controlling yield and yield component interaction in the Northern Great Plains is plant available water (Ferguson, et al., 1970; Brown, 1971). Stored soil water on fallow ground from early spring rains supplies most of the plant available water for dryland crop development. There is a subsequent pattern of decreasing available water during the growing season. A similar pattern occurs following irrigation for the

duration of the growing season. These decreasing patterns of water availability approximate the convergent patterns of nutrient availability described by Grafius and Thomas (1971). The point at which the developing plants become stressed depends upon the genetic heading date and developmental rate of the plant. Early heading dates are therefore crucial to a plant's adaptation to dryland environments, due to stress avoidance (Smith, 1951).

Genetically controlled early heading has been shown to prevent the full expression of potential tillering capacity in nonstressed six-row barley (Grafius, 1956) by limiting vegetative development duration. Negative correlations between spike number and kernel weights, kernel number, and heading dates and positive correlations of heading dates with kernels/spike and plant heights have been reported in two separate diallel analyses of barley cultivars varying in heading dates (Riggs and Hayter, 1975). Specific pleiotropic responses due to genetic earliness were not reported in this study, possibly due to genotype x environment interactions.

A few studies have reported the effects of isogenic heading date differences on barley development (Mellish, et al., 1978; Yasuda, 1978). Yasuda (1978) found reduced culm length, spike length, kernels/spike, and grain yield and increased spikes/unit area with early isotypes compared to their recurrent parent in one environment. Similar findings were reported in a study utilizing 19 sib-lines

each with an early and a late pair (Eak,Eak) grown at three latitudes (Mellish, et al., 1978).

The Effect of Row Type Genes on Barley Yield Responses

Woodward (1949) described two loci which control spike types in commercial barley. Lateral fertility (I) and infertility (i) of the lateral florets and two-rowed (V) and six-rowed (v) barley characters interact to create four homozygous spike types: VVii, two-rowed with small flattened lemmas on infertile lateral florets (commercial two rows); VVII, two-rowed with large, rounded top lateral lemmas with approximately 3% of the laterals fertile; vvII, six-rowed with staminate fertile sessile laterals (commercial six rows); vvii, six-rowed with pedicellate fertile laterals (Hockett and Standridge, 1975).

Two- and six-rowed barleys comprise the two major classifications of spring barleys grown in the world. Traditionally two-rowed barleys are grown in the Intermountain West, Pacific Coast and Northern Great Plains regions while six-rowed barleys are grown in the California-Arizona regions, the Midwest Plains, and eastern states (Reid and Weibe, 1979). Though only two loci control this character, barley breeders traditionally have concentrated on only the row types common to their region and utilize the other types only for exotic germplasm. Eslick and Hockett (1974) reported that only 11 outside germplasms were added to the six-rowed North Dakota

pedigree breeding system since 1900. All of these were six-rowed cultivars. The reason for this hesitation to utilize different row types is probably due to a reported synergistic reduction in yield of lines selected from 2 x 6 row crosses (Harlan, et al., 1940).

Several authors have tried to determine whether the supposed superiority of six-rowed varieties is actually due to the gene controlling spike type or to broader genotypic differences. The more moist environments in which six-rowed genotypes are typically grown may have produced higher yielding phenotypes and developed different modes of adaptation than two-rowed genotypes (Hockett and Eslick, 1968; Hockett and Standridge, 1975; Wells, 1962; Wiebe, 1957; and Wiebe, et al., 1961).

Hockett and Standridge (1975) suggested that to truly understand the effect of the row type genes on plant adaptation, the four possible genetic combinations (VVII, VVii, vvII, and vvii) be established as isogenic lines in both six-rowed and two-rowed cultivars and analyzed for yield adaptation. This type of study should clarify the factors controlling the yield component responses of barley, and possibly those which should be improved for a given combination of genes and genotypes to enhance yields.

The Use of Residual Soil Moisture to Estimate
Physiological Root Activity

Much research has been reported on yield and yield component development of barley, little has been reported on the association of these characters to the rooting patterns of plants. Conrad (1937) related the amount of residual soil moisture in the soil following barley crops with the longevity of the growth cycle and the size of the crop yield. He revealed that the larger the crop yield, the deeper the dryland crop withdrew its soil moisture and dried out the soil profile. Brown's (1970) research in Montana environments revealed that most plant available water on dryland environments is deposited by the middle of June, implying that a cultivar's rooting patterns greatly determine the degree and type of stress imposed on a barley crop (Brown, 1981; Wells and Dubetz, 1966).

The type and fertility of the soil is a major concern in studies involving soil moisture stress, rooting patterns, and plant development. Higher fertility, limited soil water, warm temperatures, and lower soil bulk densities tend to enhance the rooting activity of barley crops (Brown, 1970; Conrad, 1937; Ferguson, et al., 1970; Hockett and Brown, 1981; Kirby, 1970; and Wells and Dubetz, 1966). Cultivar rooting differences and genotype x soil interactions have

been reported in response to differential stresses when three cultivars were tested on two soil types (Wells and Dubetz, 1966).

'Hannchen' and 'Betzes' were shown to have a higher resistance to soil moisture stress on a fertile loam versus a loamy-sand soil. Consequently, comparison of barley cultivar rooting patterns should be conducted on soils which allow the clear expression of genotypic rooting pattern differences.

Kirby (1970) and others (reviewed by Donald, 1963; and Pelton, 1969) have related increased evapotranspiration to increased plant densities due to increased rooting density. The increased rooting density increases the rate of soil moisture depletion at different periods of growth. The greater use of soil moisture early in the season was related to stresses at the grain filling stage, causing reduced kernel size.

Derera, et al. (1969), Hurd (1968 and 1974), and Cholick et al. (1977) have investigated differences in rooting patterns in wheat. Ries (1978) and Irvine, et al. (1980) have investigated the rooting and soil moisture withdrawal differences between plant height isogenics of semidwarf and tall genotypes of barley. Irvine, et al. (1980) used ^{32}P uptake and labelling as an indication of rooting capacity while Ries (1978) utilized residual soil moisture. No differences in soil moisture withdrawal due to the height difference were found over most of the rooting profile in either study.

The one exception was a very short isogenic barley line which withdrew less moisture in the 150 cm portion of the soil profile (Ries, 1978).

Brown (1981) has completed extensive research on patterns of soil moisture withdrawal with barley crops at Montana State University. neutron soil moisture probes and residual soil using moisture. In one 2-year study utilizing residual soil moisture, several isogenic lines varying in both plant height and maturity at different fertility levels (Hockett and Brown, 1970) had increased numbers of adventitious roots (AR) as fertility levels increased. The earliest isogenic line had poorer water use efficiency than the other isotypes at the highest yield and fertility levels. Six-rowed cultivars produced more roots than two-rowed cultivars and significant positive correlations between AR activity and yield, tiller number, total water use, and residual soil moisture were reported. This study utilized only two isotypic pairs varying in heading date (Betzes and Titan).

SECTION I: THE EFFECTS OF GENETICALLY INDUCED HEADING DATE
DIFFERENCES ON YIELD AND STABILITY OF MORPHOLOGICAL
DEVELOPMENT OF AN ISOGENIC BARLEY
(H. VULGARE) PAIR

Introduction

The genotype x environmental interaction of heading date responses due to different varietal photoperiod and thermal sensitivities is a universal hindrance in ascertaining the pleiotropic morphological effects of different heading dates on barley cultivars (Bell, 1939). This study was undertaken to determine the effect of an isogenic early heading date on the associated morphological and agronomic traits of barley, and to determine whether the effects were pleiotropic or stress induced.

Materials and Methods

An isogenic line of Betzes barley, Erbet, was developed by backcrossing the early gene from 'Prior', which is 8 days earlier than Betzes in flowering and heading date, into Betzes (Hockett and Eslick, 1972). The isoline was recommended for use in areas of short growing seasons, limited moisture, or late planting.

Since 1966, the isogenic pair of Erbet and Betzes has been grown simultaneously in 214 yield trial environments. The pair has been

included in Montana Intra-State Yield nurseries, the Western Regional, the Mississippi Valley and the Great Plains Regional Yield Nurseries. The plot arrangement in most nurseries is a randomized complete block design of all nursery entries including the Erbet-Betzes pair. Typically four replications of four row, 3.3 m long plots were used for each entry. Rows were spaced 30 cm apart. Mean responses of all replications of Erbet and Betzes at a specific environment were treated as a pair. The paired statistical comparisons include paired T-tests, regression, and correlation analysis of Erbet versus Betzes mean responses at each environment (Snedecor and Cochran, 1967).

Stepwise (step-up) regression analysis (Snedecor and Cochran, 1967) was performed on the overall analysis for Betzes and Erbet separately by two methods. The first analysis included the yield components, kernels/unit area, and kernel weights, as well as test weights, plant heights, percent plump and percent thin kernels, and heading dates. The second analysis did not include kernels/unit area or kernel weights. The analysis was performed by the SPSS stepwise regression analysis program (Nie, et al., 1975).

The methods of determining the separate traits studied on these two isogenic lines are described in detail by Hockett (1981). With few exceptions yields were determined by harvesting 480 cm of the central two rows of each plot and converting to a quintals/hectare (q/ha) basis. Heading dates are recorded as the Julian days at which

50% of the plants in a plot extrude the first floret from the collar. Plant heights (cm) are determined from ground level to the topmost floret, excluding the awn.

Results and Discussion

Compared to Betzes its early isotype, Erbet, was eight days earlier to head, three days earlier to mature, lower yielding (-5%), had fewer thin kernels and more plump kernels with a higher kernel weight, test weight, and protein content (+0.9%), and the plants were shorter. No significant differences in kernels per hectare or percent lodging were noted between the two isotypes (Table 1-1).

Typically, analysis of variance (ANOV) would be used to isolate the genotype x environment interaction. However, ANOV often falsely assumes similar variances among environments (Finlay and Wilkinson, 1963; Paroda and Hayes, 1971) and does not reveal actual patterns of interactions. Correlations, the coefficient of determination (r^2), and linear regression (byx) indicate both the pattern and degree of genotype x environment interaction.

The consistency of Erbet responses compared to Betzes over the environments, as indicated by the coefficient of determination (r^2), is shown in Table 1-1. If the erbet response closely approximates the Betzes response over the environments, the r^2 value is high

Table 1-1: Comparison of means, range, regression, and correlation analysis between Erbet and Betzes grown in a number of environments.

Trait	Environments (no.)	Betzes \bar{x}	Erbet \bar{y}	Difference [†] $\bar{x}-\bar{y}$	Regression Analysis [‡]		Total Range
					r^2	b_{yx}	
Yield (Q/ha)	214	31.5	29.6	1.9**	.83**	.89**	64.6
Test wt. (kg/hl)	201	65.5	67.6	-1.8**	.59**	.63**	28.3
% Plump (on 2.4 mm sieve)	155	56.0	68.5	-12.5**	.66**	.73**	99.4
% Thin (thru 2.2 mm sieve)	102	23.3	15.7	7.6**	.65**	.70**	98.6
Kernel wt. (mg)	27	34.5	36.6	-2.0**	.81**	.83**	40.3
Kernels/ha (x10 ⁶)	27	10.02	9.08	.94	.89**	.89**	10.7
Plant ht (cm)	173	73.2	66.7	6.5**	.84**	.82**	71.1
Heading date (Julian day)	150	182.0	174.0	8.0**	.93**	.98	104.0
Lodging (%)	67	48.3	42.3	6.0	.32*	.78*	99.0
Protein (%)	14	12.9	13.8	-0.9*	.84**	.99	7.8
Maturity date (Julian day)	16	213.6	210.5	3.1**	.84**	.94	38.0

†*,**Significant at $p = .05$, $p = .01$, respectively.

‡*,**Indicate significant correlations (r) and $b_{yx} \neq 1.00$ at $p = .05$, $p = .01$, respectively.

(Schmidt, et al., 1973). The greater the influence of small environmental fluctuations and error on either of the isotypes, the lower the coefficient of determination will be. Under certain conditions the low r^2 values and nonsignificant slopes can indicate that the isogene is modifying the response of a character from that observed with the normal genotype.

Significant r values were found for all paired comparisons made. The lowest coefficients of determination (r^2) were obtained for percent lodging, test weight, percent thin, and percent plump. The low lodging r^2 may be an artifact caused by the reduced plant heights associated with the early line preventing any lodging in environments where the Betzes maturity type may lodge slightly, resulting in a skewed distribution. The low r^2 for test weights, percent plump, or percent thin kernels may be due to differences in seed cleaning or cylinder speed threshing which drastically alter kernel determinations due to differential cleaning and cracking of kernels. High coefficients of determination reveal a similar response pattern between the two isotypes for the other characters analyzed.

The pattern of a genotype x environment (g x e) interaction is indicated by the slope (byx) and its position. A regression significantly different from a unit slope implies significantly different patterns of GxE interaction between the pairs induced by the single different gene. A unit slope would be obtained if the two cultivars

responded exactly the same in each environment. Instead of an environmental mean (Finlay and Wilkinson, 1963; Paroda and Hayes, 1971) or a gene-pool mean (Pederson, et al., 1978) used to classify the environments, the mean response of the parent isotype is the reference represented by the unit slope. The estimation of the associated effect of an isogene on a given trait's stability and degree of interaction in a given cultivar or isotype is possible by the use of the coefficient of determination (r^2), and deviation of the regression slope (byx) from the unit slope.

The regression analysis of heading date responses (Figure 1-1) reveals a very consistent 8-day mean difference in heading date between the isogenic pairs ($r^2 = .94^{**}$), regardless of the heading date at an environment (range = 104 days), Table 1-1. The high coefficient of variation (r^2) combined with the parallel slopes reveals that Erbet has a normal Betzes genotype x environment interaction. The large range in heading dates is induced by differences in planting dates, causing differences in photoperiods and temperatures, all of which are uncontrolled in this study. This pattern reveals the isolation of isotypic genetic earliness from genotypic photothermal sensitivity. The consistent 8-day difference is due to the single recessive earliness gene (Hockett, 1980) and its associated linkage block acquired from Prior (Hockett and Eslick, 1972). The confounding (g x e) interactions previously associated with

