Initiation of the reproductive stage in wheats varying in winterhardiness
by Sadiq Hussain Chaudhry

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Crop and Soil Science
Montana State University

Abstract:
The initiation and duration of the reproductive stage are important factors influencing the yielding ability of wheat. Lengthening the reproductive stage by delaying maturity increases yield potential if drought and high temperature stresses during anthesis and grain filling periods can be avoided. In this study the possibility of increasing yield potential by lengthening the reproductive period through earlier initiation of the reproductive stage was examined.

Field experiments were conducted over 3 years at western North American locations, differing in temperature and day length. Five cultivars of winter wheat (Triticum aestivum L.) were grown during 1980-81; during 1981-82 and 1982-83, 13 winter wheat and 1 winter rye (Secale cereale, L.) cultivars were grown.

Significant differences for days to initiation of the reproductive stage were found among cultivars, locations, years and environments. Location X cultivar, year X cultivar, and environment X cultivar interactions were also significant. However, similar rankings of cultivars for reproductive initiation at all locations suggested that cultivar X environment interactions were due to differential response of cultivars at several environments. Differences in double ridge formation on the shoot apex of wheat cultivars (initiation of the reproductive stage) were due mainly to temperature rather than daylength. Initiation of the reproductive stage in winter wheat cultivars responded linearly to the accumulated growing degree days.

A consistent negative correlation was found between winterhardiness and early initiation of the reproductive stage in winter wheat. Lengthening the reproductive period by selecting breeding lines which initiate this stage earlier in the spring may result in reduced winterhardiness. Seedling erect growth habit and light green color, which are related to low winterhardiness, were associated with earlier initiation. Conversely, prostrate growth and dark green color associated with high winterhardiness were correlated with late reproductive initiation. By selecting plants with the associated seedling characteristics the breeder can indirectly select for both occurrence of reproductive initiation and winterhardiness.

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APPROVAL

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Sadiq Hussain Chaudhry

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date May 16, 1985

Dedicated to my mother, grandmother and eldest sister whose wishes are fulfilled but who no longer live to share their happiness with me.

VITA

The author, Sadiq Hussain Chaudhry, is the son of Ch. Sher Mohammad and the late Nawab Begum. He was born on June 17, 1942, in Faisalabad (Lyallpur), Pakistan. He received his elementary and secondary education in his hometown and got a Bachelor of Science degree in Agriculture from West Pakistan Agricultural University, Faisalabad. In 1972, he obtained his Master of Science degree in Plant Breeding and Genetics from the University of Agriculture, Faisalabad. Mr. Chaudhry has been associated with the breeding program of Wheat Research Institute, A.A.R.I. Faisalabad since 1964.

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ABSTRACT

The initiation and duration of the reproductive stage are important factors influencing the yielding ability of wheat. Lengthening the reproductive stage by delaying maturity increases yield potential if drought and high temperature stresses during anthesis and grain filling periods can be avoided. In this study the possibility of increasing yield potential by lengthening the reproductive period through earlier initiation of the reproductive stage was examined.

Field experiments were conducted over 3 years at western North American locations, differing in temperature and daylength. Five cultivars of winter wheat (*Triticum aestivum* L.) were grown during 1980-81; during 1981-82 and 1982-83, 13 winter wheat and 1 winter rye (*Secale cereale* L.) cultivars were grown.

Significant differences for days to initiation of the reproductive stage were found among cultivars, locations, years and environments. Location X cultivar, year X cultivar, and environment X cultivar interactions were also significant. However, similar rankings of cultivars for reproductive initiation at all locations suggested that cultivar X environment interactions were due to differential response of cultivars at several environments. Differences in double ridge formation on the shoot apex of wheat cultivars (initiation of the reproductive stage) were due mainly to temperature rather than daylength. Initiation of the reproductive stage in winter wheat cultivars responded linearly to the accumulated growing degree days.

A consistent negative correlation was found between winterhardiness and early initiation of the reproductive stage in winter wheat. Lengthening the reproductive period by selecting breeding lines which initiate this stage earlier in the spring may result in reduced winterhardiness. Seedling erect growth habit and light green color, which are related to low winterhardiness, were associated with earlier initiation. Conversely, prostrate growth and dark green color associated with high winterhardiness were correlated with late reproductive initiation. By selecting plants with the associated seedling characteristics the breeder can indirectly select for both occurrence of reproductive initiation and winterhardiness.

INTRODUCTION

Winter wheat (*Triticum aestivum* L.) cultivars with high yield potential but low or moderate winterhardiness may produce a bumper crop under favorable conditions including no winter injury. Morrison and Vogel (1962) and Briggle and Vogel (1968) suggested that high production capability of cultivars is, in part, due to their ability to resume growth rather than maintain dormancy during winter or early spring periods of above freezing temperatures. However, at northern latitudes where temperatures of –30 C occur, only cultivars with adequate winterhardiness can survive.

Another factor influencing grain yield is the length of the reproductive stage. Grain yield potential could be increased by lengthening the duration of the reproductive phase (Jakolev, 1973). Lengthening the reproductive phase in cultivars by delaying maturity is associated with problems of high temperatures and water stress prevailing during anthesis and grain filling periods. Selection of genotypes with early initiation of the reproductive phase, however, could overcome these problems. The study of initiation of the reproductive stage included five winter wheats grown in 1980-81 at four locations, and 13 winter wheat and 1 winter rye cultivars grown in 1981-82 and 1982-83 at two and five locations, respectively. The objectives of this research were:

1. to examine cultivar variation, cultivar X location, and cultivar X year interactions for initiation of the reproductive stage, and
2. to investigate the relationship between reproductive initiation and adaptive characteristics, including winterhardiness and its related seedling characteristics.

LITERATURE REVIEW

Cultivar and Initiation of the Reproductive Stage

Shoot Apex Development

Methods of describing shoot apex development have evolved to the point where phenological events can be described quantitatively in terms of the onset of a particular stage. Using these methods, it should be possible to differentiate between shoot apex development and initiation of reproductive stage in different genotypes with respect to their adaptive behavior in a given environment.

Bonnett (1935) divided stem elongation in barley into two phases, i.e., phase of producing only leaf initials and phase of internode elongation and appearance of double ridges on the growing point. A year later, in 1936, he described and illustrated the developmental phases and grouped them into vegetative, transitional and reproductive stages. In explaining the double ridge formation as indication of initiation of the reproductive stage, he regarded the upper member of double ridge as spikelet initial. Furthermore, in 1966 he summarized the information in this area more thoroughly for maize, wheat, rye and oats. The stages of development, initiation and shape of apices were generally found similar in these crops. Other investigators, including Andersen (1954), Briggle (1967), Aitken (1967) and Lucas (1972), described the development stages of apical meristem in wheat and cereals.

Nerson et al. (1980) suggested a scale for assessment of the development of wheat spike consisting of 10 stages beginning with vegetative shoot apex and ending with differentiation of the terminal spikelet. Moncur (1981) described sequential development of shoot apices in a large number of field crops. In wheat, he regarded double ridge formation as the onset of floral initiation.

George (1982) devised and illustrated a refined scale of head development of winter wheats consisting of 12 stages. Using this scale, he identified cultivars vulnerable to winter-kill in fall and found his scale a useful measure to discard the lines which were likely to complete early developmental stages.

Another numerical staging scheme for measuring progression of inflorescence development in wheat was presented by Klepper et al. (1983). The system clearly measured two factors of importance in predicting yield: (1) the occurrence of the double ridge stage and (2) the termination of spikelet development.

Cultivar Variation for Initiation of Reproductive Stage

The amount of time required to begin floral initiation and the amount of time required to reach anthesis following initiation varies according to species and cultivar.

Sharman (1947) reported that the length of the shoot apex varied from species to species in Graminae, even within a single genus. For any particular species it was constant, provided shoots of the same maturity and of equivalent vigor were compared. In *Triticum* the length of the apex was short during vegetative phase, elongating rapidly only at inflorescence initiation.

Cooper (1956) found that the general pattern of inflorescence in cereals was similar but differences occurred among cultivars in the time at which spikelets were initiated.

Ashraf (1973) determined the relationship of development of external leaf morphological stages and apical meristem of shoot apex in five diverse winter wheats. According to his study the general pattern of inflorescence development was similar in all cultivars, but differences occurred among cultivars for the time of spikelet initiation.

Fisher (1973) reported a different pattern of development of apical meristem in Japanese short statured wheat, 'Norin 10' and its derivatives. The single ridges on the elongating shoot apex were considerably larger and double ridge formation was markedly delayed, resulting in a long apex with many single ridges which consequently gave rise to longer heads with more spikelets than in standard wheats.

Environment and Initiation of the Reproductive Stage

Effect of Environment on Initiation

Although genotype controls relative maturity, the control over the actual time of initiation of reproductive stage and subsequent development of inflorescence involves interaction of genotype with environmental components.

George (1972) examined the spike primordia of several winter wheat cultivars periodically after early sowing. In some cultivars the primordia remained near the crown and were protected from frost, while in others, early culm elongation exposed the primordia to winterkill. Cisar and Shands (1978), in a study of floral initiation and development in oats, concluded that late maturing cultivars had longer vegetative periods. They further concluded that a cultivar earlier in initiation combined with a longer time of panicle development is capable of utilizing longer season and gives higher grain yield per unit area provided the environmental factors are not adverse.

Increase in the rate of spikelet initiation and decrease in duration of spikelet initiation caused by late sowing in spring wheat varieties were reported by Stern and Kirby (1979). They found significant variety X time of sowing interaction for rate and duration of spikelet initiation. A significant effect due to planting date and variety on the number of days and accumulated growing degree days to reach different stages of development in nine oat cultivars was reported by Colville and Frey (1983). In general, the genotype X environmental interaction was not significant.

Water stress and seeding rates had no significant effect on the rate of development of apical meristem of winter wheat even though differences in morphological development were observed (Dunbar and Simka, 1981). Water stress during the late vegetative phase, just before spike initiation, adversely affected the number of fertile florets per spike in a semidwarf spring wheat (Oosterhuis and Cartwright, 1983).

Reproductive initiation differed greatly in six spring wheat cultivars of diverse climatic origin studied in growth chamber and field experiments (Halloran and Pennell, 1982). Rates of reproductive initiation and stem elongation for the cultivars within and between the two environments appeared to be largely independent. Development in hard red spring wheats was affected more by cultivar than by soil water content or fertilizer N level (Frank and Bauer, 1984).

Effect of Daylength and Temperatures on Initiation

Flowering in higher plants involves an initial differentiation reaction or floral induction, followed by initiation of reproductive stage and development. In winter wheat and other winter cereals, low temperatures are required for the initial reaction of floral induction. This low temperature induction is generally referred to as vernalization. Daylength and temperature have been reported by several investigators as the main regulating factors of reproductive initiation in winter and spring type cereals.

Adams (1924) was probably the first to point out the importance of temperature in relation to the daily photoperiod in wheat in influencing the time of sexual reproduction. He claimed that these two factors are interchangeable. Kiesselbach and Sprague (1926) reported that differentiation of the spike in winter wheat was not evident in the fall season, and the plants remained essentially dormant during December, January and February due to low temperatures. Brief data on temperature and photoperiod were presented by Mckinney and Sando (1930). Their results indicated that earliness in winter wheat was influenced both by low temperatures and by short days during early stages of development. In another study the importance of temperature and photoperiod in determining the duration of each growth phase of wheat plants was stressed by Mckinney and Sando (1933). They indicated the optimum requirement for earliness in winter wheats was low temperature and short days during the initial growth phase, whereas spring wheats had optima at the higher temperatures and the longer photoperiods. In 1935 they suggested that temperature and photoperiod length must increase with the development of plant in order to induce early sexual reproduction in winter and spring wheats.

Hamilton (1948) studied the development of apical meristem in four varieties of *Avena sativa* grown at two temperatures. He found that differentiation of tissues in the shoot occurred much earlier in plants grown at 28 C than at 16 C. At the lower temperature, growth followed the usual pattern but the higher temperature resulted in rapid maturation of tissues and inhibited panicle initiation. Time of flower initiation in Australian oats depended greatly on the varietal response to photoperiod and temperature (Aitken, 1961). Aitken (1966) also studied the differences between spring and winter flowering characteristics in wheat, rye, barley and oats in several field environments with mean temperatures ranging from 10–22 C and mean photoperiod from 10½ to 16 h. He found that flowering in spring cereal varieties showed insensitivity to temperature and photoperiod and occurred at a lower leaf number. However, in winter cereals, flower initiation was at a higher leaf number.

Floral initiation in Marquis wheat was earlier with each increase in light intensity from 200 to 2500 ft-C, and with each increase in temperature between 10 and 30 C (Friend et al., 1963). In a study on spring wheat Triple Dirk the time of appearance of double ridges was progressively delayed with an increase in number of short days (Lucas, 1972). Times of floral initiation, stem elongation and maturity varied by about one week among seven hard red winter wheat cultivars studied by Wiegand et al. (1978). When 1800 degree days had accumulated, from 12.7 to 16.2 fully expanded leaves were produced by the cultivars 'Improved Triumph' and 'TAM-W101', respectively. Fewer leaves were produced by early maturing cultivars. In another study in 1981, they reported that winter wheat cultivars remained vegetative during short days of winter and produced leaves linearly in response to cumulative heat units. Floral differentiation (double ridge stage), stem elongation (first node) and anthesis varied about a week among cultivars.

Studies by Ritchie (1980) in wheat and maize indicated more varietal variation for vegetative than for the reproductive phase, when duration of growth period was expressed as degree days. Generally, the number of leaves produced was directly proportional to degree days from emergence to floral initiation. Baker and Gallagher (1983), working with winter wheat, observed slower production of apical primordia in autumn and winter, then faster in spring as the weather became warmer. Spikelets were initiated three times as fast as leaves. Double ridges appeared when about 50% of the final number of spikelets were present. As a second part of the study, in 1983, they concluded that spikelet initiation responded in a linear fashion to photoperiod over the range experienced in the field, i.e., 11-16 h for winter wheat and 15.5-17.5 h for spring wheat. Leaf maturation in both types of wheats showed a rather weak response to photoperiod. The response of spikelet initiation rate to temperature was linear.

Midmore et al. (1982) reported faster development of most wheat cultivars at the hotter, lower locations compared with the cooler ones. High temperature delayed flowering in the vernalization-responsive cultivars up to initiation of the terminal spikelet and resulted in more leaves, spikelets and tillers than other cultivars at the hottest sites.

Colville and Frey (1983) examined nine oat cultivars and noticed a significant effect due to planting date and variety on the number of days and accumulated growing degree days to reach different stages of development. Mohapatra et al. (1983) observed delay in initiation of double ridges on the shoot apex, at high temperature (30 C) compared to low temperature (20 C) from germination onwards in an Australian spring wheat cultivar, 'Warimba'. The change in temperature did not affect the subsequent rate of spikelet development to stamen initiation. Frank and Bauer (1984) reported significant differences among cultivars of hard red spring wheat in growing degree days accumulated from planting to double ridge formation.

Initiation of the Reproductive Stage and Other Characteristics

Winterhardiness

Only a few studies have been reported about the relationship of initiation of reproductive stage with winterhardiness of wheat.

Avetisova (1972) reported slower apical meristem growth in winterhardy and frost resistant winter wheats compared to non-hardy and frost susceptible cultivars. The growth was virtually nil in most winterhardy and frost resistant types. The cessation of growth was accompanied by a restriction in the meiotic activity and a reduction in the nucleic acid contents in the apical meristems of hardy types. Bendarenke and Mitropolenko (1979) found a negative correlation between the degree of development of the growing point at development stage 3 (elongation of the stem apex) and winterhardiness of winter wheats; the less hardy the variety, the longer the growing point. Kuperman et al. (1979) from USSR examined the growing points of seven winter wheat cultivars after removal of snow-cover in winter. They reported that the hardiest varieties, Caesium 39, Ul Yanovka and Mironovka 808, had the shortest growing points; while the tender variety, Aurora, had the longest growing point. The moderately hardy types, such as Odessa 51, were intermediate in length of growing point. Kuperman and Turkova (1980) studied the growth of apical meristem in several winter wheat and winter rye varieties differing in winterhardiness. They reported that more rapid apical growth in autumn and winter was associated with reduced winterhardiness. Kenefic et al. (1981) reported that, under field conditions of South

Dakota, the less hardy winter wheat cultivars initiated inflorescence about 15 days earlier than hardy ones, but heading dates showed only about a 6-day difference.

Ashraf and Taylor (1974) concluded that long subcrown internode lengths (or shallow crowns) of winter wheat genotypes were associated with higher levels of winter survival under field conditions. George and Morrison (1975) reported early growth resumption tendency in winter wheat cultivars rendered them more vulnerable to winterkill or frost injury. Management practices like seeding directly into standing stubble or deep furrows which catch snow provide protection to winter wheat against winterkill (Aase and Siddoway, 1979). With these practices they were able to avoid winterkill even when air temperature occasionally approached -40 C, provided the wheat went through a proper hardening process. Fowler and Gusta (1979) developed a field survival index based on 43 winter wheat cultivars in 61 trials grown in Saskatchewan, Canada from 1972 to 1977. A wide range in field survival indices was observed for the cultivars considered. Their rating suggested that most successful winter wheat had only marginally greater winterhardiness than the minimum required for the area in which they were grown.

Seedling Characteristics

Little information is available in the literature about the relationship of initiation of the reproductive stage with seedling growth habit and seedling color in winter wheat. However, some investigators suggested the association of these seedling characteristics with winterhardiness.

Martin (1927) reported the association of seedling prostrate growth habit, dark color and narrow leaves with winterhardiness in wheat, but not in rye. Taylor and Olsen (1976) found relationship of fall and spring growth habit, spring vigor, and dark spring plant color with field percent winter survival and suggested the use of these seedling characteristics in screening of wheat lines for winterhardiness in breeding programs. Fowler et al. (1981)

reported that erect seedling plant growth habit was negatively related to winterhardiness. They further suggested use of this relationship for winterhardiness screening in wheat. Taylor et al. (1984) used several morphological seedling characteristics for winterhardiness evaluation in Montana wheat field trials. They used seedling growth habit, seedling color and leaf width to calculate winterhardiness index which they considered an effective field method of identifying winterhardy wheats.

MATERIALS AND METHODS

Cultivars

Five winter wheats were grown at four locations in 1980-81; 13 winter wheat and one winter rye cultivars were grown during 1981-82 and 1982-83 at 2 and 5 locations, respectively (Table 1). Included were hard red winter, soft red winter and soft white winter cultivars having a wide range of winterhardiness.

Locations

1980-81

Field experiments were planted (see Experimental Design) at the following four western North American locations representing a wide range of environments:

1. Bozeman, Montana (MT)
2. Pendleton, Oregon (OR)
3. Fort Collins, Colorado (CO)
4. Lethbridge, Alberta (AB)

For more information about locations, see Table 2.

In order to study the comparative influence of daylength and temperature on the reproductive initiation of winter wheat, two locations (Bozeman, MT and Pendleton, OR) were used. Both are at similar latitudes and, thus, have similar daylengths. These locations differ widely in growing degree days (Table 2).

Table 1. Cultivars (included in three years study), Their Parentage/Pedigree, Class, Origin and Winterhardiness Level.

Cultivar Name	CI Number	Parentage/Pedigree	Class†	Origin	Winterhardiness Score‡
Nugaines*	13968	CI 13253/CI 12692//Burt	SWW	WA, USA	2
Stephens	17596	Nord Desprez/Pullman Sel 101	SWW	OR, USA	2
Blueboy	14031	N10B/Anderson/Coker 55-9	SRW	NC, USA	2
TAM-W105	17826	Scout Sel	HRW	TX, USA	3
Crest*	13880	Westmont/2/PI 178383	HRW	MT, USA	3
Centurk	15075	KS8N/3/Hope/2 TK/4/CNN/Parker	HRW	NE, USA	4
Cheyenne	8885	Sel of Crimea	HRW	NE, USA	5
Redwin*	17844	YG/CNN//N10B14/3/3* YG	HRW	MT, USA	5
Froid	13872	MT 1904-7 Bulk-Winterhardiness	HRW	MT, USA	7
Winalta*	13670	Minter/Wichita	HRW	AB, Canada	7
Yogo	8033	Minturk 1/Belogiina//Buffum	HRW	MT, USA	7
Norstar*	17735	Winalta/Alabaskaja	HRW	AB, Canada	8
Alabaskaja	PI326301	—	HRW	USSR	8
Frontier (Rye)	CI182	—	WR	AB, Canada	9

Note: All cultivars were grown in 1981-82 and 1982-83.
*Grown in 1980-81.
†SWW = soft white winter, SRW = soft red winter, HRW = hard red winter, and WR = winter rye.
‡Based on scale 0–9 (derived from Taylor et al., 1984). See under Winterhardiness, p. 16.

Table 2. Experimental Locations for Three Years, Their Latitudes, Altitudes and Average Temperatures.

Year	Location	Latitude		Altitude (meters)	Average Temperature† (centigrade)
1980-81	Bozeman, MT	45	40	1455	2.24
	Pendleton, OR	45	43	453	5.91
	Fort Collins, CO	40	35	1525	5.16
	Lethbridge, AB	49	43	908	1.50
1981-82	Bozeman, MT	45	40	1455	-0.35
	Pendleton, OR	45	43	453	5.20
1982-83	Bozeman, MT	45	40	1455	0.79
	Pony, MT	45	40	1676	0.00
	Bridger, MT	45	18	1121	2.98
	Huntley, MT	45	55	911	1.62
	Moccasin, MT	47	3	1311	1.33

†Averaged over development period from October to April for respective years and locations.

1981-82

To confirm the results of previous year's study of comparative influence of daylength and temperature on the reproductive initiation, the number of cultivars was increased. Field experiments consisting of 13 winter wheats and one winter rye were planted at Bozeman, MT and Pendleton, OR (Table 1).

1982-83

The same set of 14 cultivars used in the previous year's study were grown at the following five Montana locations during 1982-83.

1. Bozeman
2. Pony
3. Bridger
4. Huntley
5. Moccasin

These locations differed greatly in temperatures (Table 2).

Experimental Design

Field experiments were planted with the help and cooperation of Experiment Station staff during the falls of 1980, 1981 and 1982; planting dates are given in Table 3. The experimental design was randomized complete block with three replications, consisting of 5 cultivars during 1980-81 and 14 cultivars during 1981-82 and 1982-83. Plots consisted of 4 rows, 30 cms apart and 3 m long. A planting rate of 8 grams of seed per 3 m row was used. Experimental design, plot dimensions and planting rates were the same for all locations and years.

Table 3. Planting Dates of Field Experiments Over Three Years.

Year	Location	Planting Date
1980-81	Bozeman, MT	25 September, 1980
	Pendleton, OR	24 October, 1980
	Fort Collins, CO	22 September, 1980
	Lethbridge, AB	29 September, 1980
1981-82	Bozeman, MT	18 September, 1981
	Pendleton, OR	22 October, 1981
1982-83	Bozeman, MT	23 September, 1982
	Pony, MT	24 September, 1982
	Bridger, MT	4 October, 1982
	Huntley, MT	22 September, 1982
	Moccasin, MT	20 September, 1982

Characteristics Studied

Initiation of Reproductive Stage

Initiation of the reproductive stage is marked by apical meristem development when there is visual indication of transition from vegetative to reproductive development. Morphologically it is a change from leaf primordia formation to spikelet primordia formation and is characterized by appearance of double ridges on the developing shoot apex. The upper ridge of a pair becomes prominent and differentiates into individual spikelet while the lower one develops into a leaf initial (Bonnett, 1936; Briggle, 1967; Clepper et al., 1983; George, 1982).

Plant Sampling. Plant samples were taken during the development of shoot apex at times and intervals shown below:

Year	Period of Sampling	Sampling Interval
1980-81	December to February March to April	twice a month once a week
1981-82 and 1982-83	Mid February to Mid May	once a week

At each sampling time 5-7 plants were dug from each plot. The plants were washed, roots and leaves cut off and specimens preserved in FAA (Sass, 1964).

Dissection and Data Collection. Three plant specimens per plot per sampling time were dissected using 40x magnification and the developmental stages of shoot apices were recorded. The Bonnett (1966) scale was used for rating the developmental stages of shoot apex for the 1980-81 study. The apices were later rated according to George (1982). This scale was more appropriate, having numerical values for each stage. George's scale was used for subsequent studies in 1981-82 and 1982-83. Developmental stages ranging from early vegetative to terminal spikelet formation were recorded on a scale of 1–12.

Estimation of Reproductive Initiation. Initiation of the reproductive stage in winter wheat and winter rye cultivars was indicated by formation of double ridges on the elongating shoot apex (Bonnett, 1936 and 1966; Briggle, 1967; George, 1982) and was regarded as stage 6 according to George's scale. Stage 6 was estimated for each replication by using regression equation from the linear regression of days to samplings from January 1 on the observed values of developmental stages of shoot apices at different sampling times.

High values of coefficient of determination (r^2) obtained for estimates of time of reproductive initiation support the reliability of these estimates. The range of r^2 values for estimates of days from January 1 to reproductive initiation in 5 cultivars (1980-81), and, in 14 cultivars (1981-82 and 1982-83) at different number of locations is given in Table 17 (see Appendix). The r^2 values are statistically significant except the lowest range values at Bridger, Montana and Pony, Montana during 1982-83.

The use of linear regression for estimating time of floral initiation was suggested by Andersen (1954) and Klepper et al. (1983). They reported linear development of apical meristem of shoot apex in winter wheat during reproductive initiation.

Winterhardiness

Cultivars were rated for winterhardiness on scale 0 to 9, with 0 being nonhardy (or very tender) and 9 very hardy. These ratings were extension of scale 0–5 used by Taylor et al. (1984), originally based on average percent winter survival data of cultivars from several locations throughout Montana over several years. The extended scale of 0–9 was used to account for small differences among cultivars. Winterhardiness scores of cultivars included in the study are listed in Table 1. Cultivars have a wide range of winterhardiness and those with a score of 3 or lower are poorly adapted to Montana locations. The winterhardiness scores given in Table 1 were used to examine relationship between winterhardiness and initiation of reproductive stage.

Seedling Characteristics

Two important seedling characteristics, seedling growth habit and seedling color are known to be highly associated with levels of winterhardiness of wheat cultivars (Fowler et al., 1981; Taylor and Olsen, 1976; Taylor et al., 1984). These seedling characteristics were further examined to establish their relationship with initiation of the reproductive stage in this study. Seedling growth habit and seedling color were rated on scale 1–5, with

1 upright to 5 prostrate growth habit, and 1 yellow green to 5 dark green seedling color. These scales were adopted by Taylor et al. (1984) based on several years of data at several Montana locations.

Growing Degree Days (GDD)

To study the response of cultivars for time of initiation of the reproductive stage to temperatures at various locations, the relationship of reproductive initiation and growing degree days (defined below) was examined during 1981-82 and 1982-83. Moreover, growing degree days were used to compare the influence of daylength and temperature on reproductive initiation at Bozeman, MT and Pendleton, OR during 1980-81 and 1981-82.

Soil temperature has an important influence on biological and biochemical processes of the developing young winter wheat plant (Smith, 1964). Due to the winter nature of this study, growing degree days were based on soil temperatures. In winter wheat during the initiation of the reproductive stage, the apical meristem of shoot apex remains below the soil surface. During this period, the plants may be covered by snow. Under these situations soil temperatures are more appropriate to use than air temperatures.

Estimation of Soil Temperatures. Soil temperatures were estimated from air temperatures using regression equations developed by Aase and Siddoway (1979) for 3 different snowcover depths:

1. For bare soil (no snowcover)

$$\hat{y} = 2.39 + .826x$$

2. For snowcover, trace – 5 inches

$$\hat{y} = 1.84 + .383x$$

3. For snowcover above 5 inches

$$\hat{y} = 1.17 + .279x$$

where $\hat{y}$ is the estimate of soil temperature (C)

x is the observed air temperature (C)

The r^2 values for the above three equations were significantly higher at $P = .01$, thus giving an indication of reliability of estimates.

Estimation of Growing Degree Days. Accumulated GDD were estimated from January 1 to the time of initiation of the reproductive phase for each cultivar at each location and for each year. Growing degree days were calculated from daily maximum and minimum soil temperatures (estimated by using regression equations as explained earlier) by the following formula

$$GDD = \frac{T_{max} + T_{min}}{2} - T_b$$

where GDD is growing degree days accumulated over a period of time

T_{max} is the maximum daily temperature (C)

T_{min} is the minimum daily temperature (C)

T_b is the base temperature

The base temperature (T_b) was 0 C (Baker and Gallagher, 1983; Bauer et al., 1984; Davidson and Campbell, 1983). When T_{min} for the day was less than 0 C, it was considered to be 0 C (Bauer et al., 1984).

Statistical Analysis

Time of initiation of the reproductive stage was estimated from the linear regression of days from January 1 to sampling dates on the observed values of development stages of apical meristems at differing sampling dates (Andersen, 1954; Klepper et al., 1983).

Analyses of variance of days to initiation of the reproductive stage were conducted separately for all three years over their respective cultivars and locations. Separation of cultivar means for days to initiation of the reproductive stage was accomplished using the least significance difference (LSD) method at 0.05 level (Lund, 1983).

The combined analysis of variance of days to reproductive initiation for 5 winter wheat cultivars was obtained by combining 11 locations in 3 years into 11 environments. A similar combined analysis of variance for days to reproductive initiation was obtained for 14 cultivars by combining 7 locations in 2 years into 7 environments. Environments were tested using the block/environment mean square. The pooled error mean square was used to test the significance for cultivar and environment X cultivar interaction mean squares.

Rankings of 14 cultivars for days to reproductive initiation at locations of 1981-82 and 1982-83 were tested by rank correlations calculated by using Spearman's Rank Correlation Method (Lund, 1983).

The relationship between days to reproductive initiation and winterhardiness, seedling growth habit and seedling color were examined using linear regression analysis. The days to reproductive initiation of 13 winter wheats were means at Bozeman location over two years in one analysis and means over two years at seven locations in the other. Linear regression analysis was also used to examine relationship of the reproductive initiation and accumulated growing degree days in 14 cultivars averaged over two locations in 1981-82 and over 4 locations in 1982-83. The same relationship was examined by regression analysis using 5 cultivars combined over 3 years and 14 cultivars combined over 2 years.

RESULTS AND DISCUSSION

Initiation of the Reproductive Stage, Genotypes and Environments

Environmental factors are known to affect the initiation of the reproductive stage and hence play an important role in altering the duration of vegetative and reproductive phases in wheat, and other cereals and grasses (Cisar and Shands, 1978; Evans, 1960; Halloran and Pennell, 1982).

Cultivars, Locations and Their Interactions for Initiation

In this study initiation of the reproductive stage was examined at several locations for 5 winter wheats during 1980-81; and 13 winter wheat and one winter rye cultivars during 1981-82 and 1982-83.

1980-81. The analysis of variance of days to reproductive initiation for 5 winter wheat cultivars grown at 4 western North American locations indicates significant differences among locations, cultivars and locations X cultivars at the .01 level (Table 4).

Table 4. Mean Square Values from the Analysis of Variance of Days from January 1 to Reproductive Initiation in 5 Cultivars at 4 Locations During 1980-81.

Source	d.f.	m.s.
Location	3	1397.67**
Block/Location	8	1.04
Cultivar	4	308.60**
Location X Cultivar	12	6.25**
Error	32	2.15

**Significant at .01 level.

Locations included in 1980-81 differ in their latitudes except Bozeman, MT and Pendleton, OR which are located at similar latitudes and hence have similar daylengths. Other locations differ in daylengths. The 4 locations differed in average temperature (Table 2). The different daylengths and temperatures at these locations provided different environments for studying the initiation of the reproductive stage in winter wheat.

Although location X cultivar interaction was significant, the cultivar rankings for initiation of the reproductive stage were similar at all locations (Table 5). Norstar, Winalta and Redwin were late in initiation and occupied top three ranks at all locations; while Crest and Nugaines were consistently early and ranked the same at all locations. The consistent rankings of cultivars for initiation time at different locations suggested that although the cultivar X location interaction was statistically significant, biologically the rankings were similar. The statistically significant interaction was due to differential response of cultivars at several locations (Table 5).

Table 5. Means and Rankings of 5 Cultivars for Days from January 1 to Reproductive Initiation at 4 Western North American Locations (1980-81).

	Pendleton OR		Fort Collins CO		Lethbridge AB		Bozeman MT		Average	
Norstar	85.9	5[‡]	95.9	4	105.0	5	105.2	4	98.0	5
Winalta	85.8	4	96.1	5	103.4	4	104.1	3	97.3	4
Redwin	84.0	3	90.6	3	102.0	3	106.5	5	95.8	3
Nugaines	77.8	2	86.0	2	98.2	2	98.9	2	90.2	2
Crest	72.7	1	83.6	1	93.9	1	95.0	1	86.3	1
LSD .05 =	2.5		2.1		3.4		1.7		1.1	

‡ Cultivar rankings in initiation, 1 = early, 5 = late.

Rank correlations among locations were not possible due to the small number of cultivars included in first year study. Fourteen cultivars were included the following year for a more reliable estimate.

1981-82. In 1981-82 significant differences were found among locations, cultivars and locations X cultivars (Table 6). The mean comparisons and rankings of reproductive initiation for 14 cultivars at two locations (Table 7) being very similar. The highly significant rank correlation of reproductive initiation of 14 cultivars at Bozeman and Pendleton (r = .94 in Table 9) suggests this trait may be evaluated in any of several environments.

Table 6. Mean Square Values from the Analysis of Variance of Days from January 1 to Reproductive Initiation in 14 Cultivars at 2 and 5 Locations During 1981-82 and 1982-83, Respectively.

Source	1981-82		1982-83	
	d.f.	m.s.	d.f.	m.s.
Location	1	10460.00**	4	2517.50**
Block/Location	4	0.53	10	4.30
Cultivar	13	539.15**	13	938.46**
Location X Cultivar	13	49.47	52	24.96**
Error	52	2.40	130	2.22

**Significant at .01 level.

Table 7. Means and Rankings of 14 Cultivars for Days from January 1 to Reproductive Initiation at 2 Locations (1981-82).

	Pendleton, OR		Bozeman, MT		Average	
Alabaskaja	109.8	14‡	124.2	13	117.0	14
Norstar	109.2	13	123.3	12	116.3	13
Yogo	105.1	11	126.1	14	115.6	12
Winalta	107.0	12	123.3	11	115.1	11
Froid	104.5	10	122.9	10	113.7	10
Redwin	102.2	9	120.4	8	111.3	9
Cheyenne	100.6	8	121.6	9	111.1	8
Nugaines	94.6	7	118.7	7	106.7	7
Blueboy	89.5	6	116.1	6	102.8	6
Stephens	88.8	5	114.4	4	101.6	5
TAM-W105	88.4	4	112.7	3	100.5	4
Centurk	85.0	2	115.3	5	100.1	3
Crest	86.2	3	111.4	2	98.8	2
Frontier (Rye)	66.8	1	99.9	1	83.3	1
LSD .05 =	2.8		2.1		1.7	

‡Cultivar ranking in initiation, 1 = early, 14 = late.

Another aspect of first and second year study, to examine the influence of daylength or temperature on initiation of the reproductive stage at Bozeman, MT and Pendleton, OR, will be discussed later in this chapter.

1982-83. In 1982-83 the same 14 cultivars used in previous year's study were examined for initiation of reproductive stage at 5 Montana locations. The differences among cultivars, locations, and locations X cultivars were significant (Table 6). However, the rankings for reproductive initiation were similar at all 5 locations (Table 8). Later initiating cultivars, Alabaskaja, Norstar, Yogo, Winalta and Froid, were generally top ranking at all locations; while Cheyenne and Redwin were intermediate, and the other cultivars were early in initiation at most locations.

In the combined analyses of variance including 5 cultivars over 3 years (Table 10) and 14 cultivars over 2 years (Table 11), highly significant differences among environments, cultivars, and environment X cultivar interaction were found. Moreover, significant differences among years for reproductive initiation were found at Bozeman with 5 cultivars over 3 years and 14 cultivars over 2 years (Table 12).

In similar studies, significant differences in initiation of reproductive stage were reported by Cooper (1956) between cultivars of cereals and by Ashraf (1973) between winter wheats. Stern and Kirby (1979) found a significant cultivar X environment interaction in spring wheat.

All sources of variation including cultivars, locations, years and their interactions were significantly different for initiation of the reproductive stage. However, similar rankings of cultivars for initiation of reproductive stage over locations and years were correlated (Table 9). The statistically significant interactions were due to differential response of several cultivars at several environments. These results suggest that winter wheat cultivars can be examined for initiation of the reproductive stage over a wide range of environments.

Table 8. Means and Rankings of 14 Cultivars for Days from January 1 to Reproductive Initiation at 5 Montana Locations (1982-83).

Cultivar	Huntley		Bridger		Bozeman		Moccasin		Pony		Average	
Alabaskaja	109.8	13‡	112.8	13	121.4	14	118.5	13	128.4	13	118.2	14
Norstar	107.9	11	111.6	11	119.7	13	119.7	14	128.5	14	117.3	13
Yogo	110.0	14	112.9	14	116.8	12	117.7	12	128.3	12	117.2	12
Winalta	108.0	12	109.4	7	114.9	10	116.0	9	124.5	10	114.6	11
Froid	106.3	10	112.2	12	112.2	8	116.8	11	122.4	7	114.0	10
Redwin	102.4	7	110.1	8	112.5	9	116.0	10	126.7	11	113.5	9
Cheyenne	102.8	8	110.6	10	115.8	11	114.7	8	123.4	8	113.5	8
Nugaines	104.8	9	110.2	9	112.1	7	114.6	7	123.6	9	113.1	7
Blueboy	99.2	6	109.1	6	110.6	6	114.2	6	120.9	6	110.8	6
Centurk	97.5	5	105.8	4	107.7	5	113.0	5	118.1	5	108.4	5
Stephens	94.7	3	108.2	5	107.5	4	112.7	4	116.8	4	108.0	4
Crest	94.5	2	104.4	3	105.9	2	108.6	3	114.8	3	105.6	3
TAM-W105	95.2	4	102.9	2	106.3	3	107.6	2	114.0	2	105.2	2
Frontier (Rye)	64.6	1	84.6	1	95.3	1	85.9	1	104.9	1	87.1	1
LSD .05 =	2.9		1.9		3.0		1.1		3.2		1.1	

‡ Cultivars ranking for initiation, 1 = early, 14 = late.

Table 9. Spearman Rank Correlation of 14 Cultivars for Days to Initiation of the Reproductive Stage from January 1 at 2 Locations (1981-82) and 5 Locations (1982-83).

		1981-82		1982-83				
		Bozeman	Pendleton	Bozeman	Pony	Bridger	Huntley	Moccasin
1981-82	Bozeman	1.00						
	Pendleton	.94**	1.00					
1982-83	Bozeman	.96**	.93**	1.00				
	Pony	.93**	.92**	.95**	1.00			
	Bridger	.90**	.86**	.87**	.84**	1.00		
	Huntley	.98**	.92**	.92**	.89**	.88**	1.00	
	Moccasin	.96**	.94**	.95**	.95**	.91**	.91**	1.00

**Significant at .01 level.

Table 10. Mean Square Values from the Analysis of Variance of Days from January 1 to Reproductive Initiation in 5 Cultivars Combined over 11 Locations in 3 Years (11 environments).

Source	d.f.	m.s.
Environment	10	2348.00**
Block/Environment	22	2.51
Cultivar	4	827.25**
Environment X Cultivar	40	15.68**
Error	88	2.29

**Significant at .01 level.

Table 11. Mean Square Values from the Analysis of Variance of Days from January 1 to Reproductive Initiation in 14 Cultivars Combined over 7 Locations in 2 Years (7 environments).

Source	d.f.	m.s.
Environment	6	3563.33**
Block/Environment	14	3.22
Cultivar	13	1439.23**
Environment X Cultivar	78	31.28**
Error	182	2.28

**Significant at .01 level.

Table 12. Mean Square Values from the Analysis of Variance of Days from January 1 to Reproductive Initiation at Bozeman, MT in 5 Cultivars over 3 Years and 14 Cultivars over 2 Years.

	Over 3 Years		Over 2 Years	
Source	d.f.	m.s.	d.f.	m.s.
Year	2	1174.00**	1	893.80**
Block/Year	6	1.40	4	2.12
Cultivar	4	197.18**	13	270.92**
Year X Cultivar	8	9.85**	13	7.10**
Error	24	2.63	52	1.43

**Significant at .01 level.

Comparative Influence of Daylength or Temperature on Initiation

The dates of initiation of the reproductive stage at two locations, Bozeman, MT and Pendleton, OR, were examined relative to temperatures and daylengths for two consecutive years, 1980-81 and 1981-82. These locations are similar in daylength due to similar latitudes but differ greatly in temperature (Tables 2 and 13). The average date of initiation of the reproductive stage at Pendleton was March 21 in 1980-81 and April 6 in 1981-82; whereas at Bozeman it was April 11 and April 28 for 1980-81 and 1981-82, respectively (Table 13). The number of growing degree days accumulated from January 1 to time of initiation were 461 and 537 in 1980-81 and 1981-82, respectively, at Pendleton; whereas growing degree days accumulated at Bozeman were 384 in 1980-81 and 313 in 1981-82 (Table 13). Earlier initiation was associated with higher number of growing degree days at Pendleton and, conversely, later initiation was related to a lower number of growing degree days at Bozeman for both years. This suggests that temperature was likely the main factor influencing initiation of the reproductive stage as opposed to daylength. If daylength had been the main controlling factor, initiation should have occurred at about the same time at Bozeman and Pendleton due to their similar daylengths.

Table 13. Initiation of Reproductive Stage at Two Locations Having Similar Daylengths and Different Growing Degree Days (GDD).

	Pendleton, OR	Bozeman, MT
Latitude	45 43	45 40
Elevation (meters)	453	1455
Time of Initiation		
1980-81	March 21 (day 81)	April 11 (day 102)
1981-82	April 6 (day 96)	April 28 (day 118)
GDD from January 1 to Initiation		
1980-81	461	384
1981-82	537	313

Initiation Response of Cultivars to Temperature

Response of cultivar reproductive initiation to temperature was examined relative to number of days required and accumulated growing degree days required for initiation. Correlations at 2 locations for year 1981-82 and at 4 locations for 1982-83 were higher than .96 and significant (Table 14). An overall correlation of number of days and growing degree days to reproductive initiation in 14 cultivars averaged over 6 locations (1981-82 and 1982-83) was highly significant (r = .988, Table 15). Another correlation between reproductive initiation and growing degree days in 14 cultivars averaged over two years at Bozeman, MT was also highly significant (r = .976, Fig. 1).

Table 14. Correlation of Days to Reproductive Initiation and Growing Degree Days to Reproductive Initiation from January 1, in 14 Cultivars at 2 Locations (1981-82) and 4 Locations (1982-83).

Year and Location	Correlation Coefficient (r)
1981-82	
Bozeman, MT	.979**
Pendleton, OR	.998**
1982-83	
Bozeman, MT	.965**
Bridger, MT	.963**
Huntley, MT	.992**
Moccasin, MT	.989**

**Significant at .01 level.

These correlations indicate that initiation of the reproductive stage in cultivars responded linearly to the accumulated growing degree days. These results corroborated those of Weigand et al. (1981), Colville and Frey (1983), Baker and Gallagher (1983), and Frank and Bauer (1984). The linear response of initiation to accumulated growing degree days confirms the earlier observation that the temperature was likely the main factor influencing initiation of the reproductive stage.

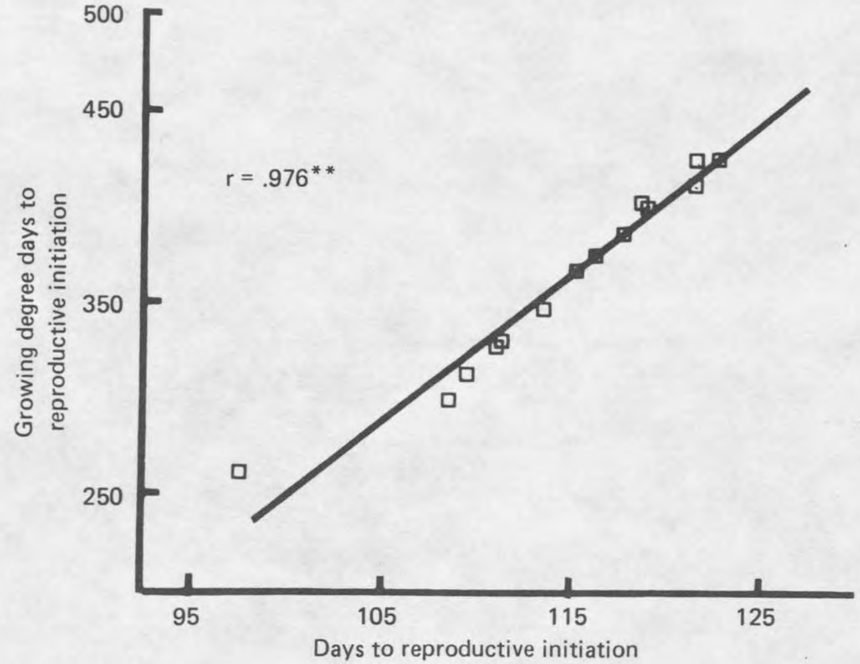

Figure 1. Correlation of days to reproductive initiation and growing degree days to reproductive initiation from January 1 in 14 cultivars at Bozeman, MT averaged over 2 years.

**Significant at .01 level.

Table 15. Days to Reproductive Initiation and Growing Degree Days to Reproductive Initiation from January 1, in 14 Cultivars Averaged over 6 Locations (1981-82 and 1982-83).

Cultivar	Days to Reproductive Initiation	Growing Degree Days to Reproductive Initiation
1. Alabaskaja	116.1	545.3
2. Norstar	115.1	533.8
3. Yogo	114.8	537.4
4. Winalta	113.1	519.5
5. Froid	112.5	516.3
6. Cheyenne	111.0	507.0
7. Redwin	110.6	500.0
8. Nugaines	109.2	488.2
9. Blueboy	106.4	465.7
10. Stephens	104.4	449.6
11. Centurk	104.0	445.1
12. TAM-W105	102.2	426.3
13. Crest	101.8	423.4
14. Frontier (Rye)	82.8	324.7
	r = .988**	

Relationship of Reproductive Initiation With Other Characteristics

Winterhardiness

Winterhardiness in wheat ensures good stands in wheat growing regions of the northern hemisphere where winter stress is likely during seedling stages. Cultivars used in this study of reproductive stage initiation ranged widely in their level of winterhardiness (Table 2). Lengthening the duration of the reproductive phase could result in increased yield potential of grain crops (Jakolev, 1973). Selecting for early initiation would lengthen the duration of the reproductive stage in wheat. The main objective of this study was to examine relationship of initiation of the reproductive stage with winterhardiness. It should be noted that increasing the length of reproductive stage by delaying maturity is often associated with drought and high temperature stresses.

The positive correlations of days to reproductive initiation and winterhardiness in 13 winter wheats at two 1981-82 locations and at five 1982-83 locations (Table 16) suggest that winterhardy cultivars are late initiating and less hardy ones are early initiating. This relationship is also illustrated in Figures 2 and 3. Early reproductive initiation is associated with reduced winterhardiness (r = –.82 in Fig. 2). Initiation dates and winterhardiness scores of 13 winter wheats are shown in Figure 3.

Table 16. Correlation of Days to Reproductive Initiation and Winterhardiness of 13 Winter Wheats, at 2 Locations in 1981-82 and 5 Locations in 1982-83.

Year and Location	Correlation Coefficient (r)
1982-82	
Bozeman, MT	.847**
Pendleton, OR	.894**
1982-83	
Bozeman, MT	.809**
Pony, MT	.617*
Bridger, MT	.650*
Huntley, MT	.823**
Moccasin, MT	.744**

*Significant at .05 level.
**Significant at .01 level.

This relationship suggests that lengthening the reproductive phase by earlier initiation would result in reduced winterhardiness. Earlier inflorescence initiation in less hardy winter wheats was also reported by George and Morrison (1975) and Kenefic et al. (1981). Moreover, studies of Bendarenke and Mitropolenko (1979), Kuperman et al. (1979), and Kuperman and Turkova (1980) indicated that rapid apical growth was associated with reduced winterhardiness and less hardy varieties had the longest growing points.

These results further suggest that breeders using early initiating winter wheat cultivars to increase yield potential should be satisfied with reduced winterhardiness. Further, in wheat growing regions requiring high level of winterhardiness, early initiating cultivars are not recommended.

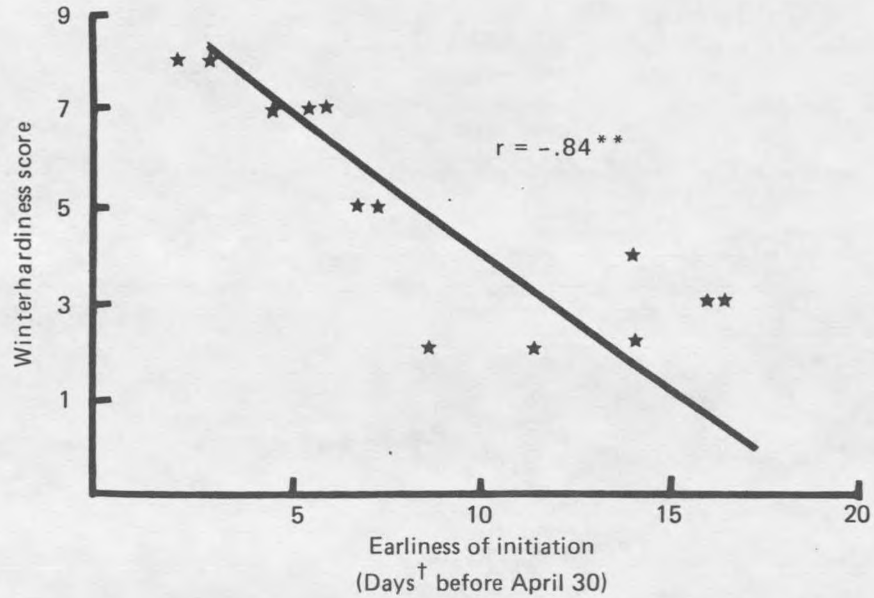

Figure 2. Correlation of early reproductive initiation and winterhardiness in 13 winter wheat cultivars.

†Averaged over 7 locations (1981-82 and 1982-83).

**Significant at .01 level.