



Growth characteristics of wheats varying in winterhardiness and dwarf bunt reaction  
by Janet Eileen Goodell

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in  
Agronomy  
Montana State University  
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Abstract:

In 1974, the People's Republic of China placed an embargo on all wheat shipped from Pacific Northwest ports due to the presence of dwarf bunt spores. The embargo eliminated Montana wheat from this market. Prior to the embargo, dwarf bunt, caused by *Tilletia controversa* Kuhn, was only a minor problem in Montana. Consequently, most resistant cultivars have been developed in states with milder winters and have only low to moderate winterhardiness. If host resistance is to be used to control dwarf bunt, cultivars with adaptive characteristics must be developed. The objective of this research was to examine relationships among growth characteristics, winterhardiness, and dwarf bunt reaction.

Ten winter wheats varying in winterhardiness and dwarf bunt reaction were planted in the falls of 1982 to 1984. Samples were taken at various growth stages, and growth rates were calculated as dry weight per heat unit. The heat units accumulated in reaching particular stages were noted.

The less winterhardy cultivars had more fall growth than the more hardy cultivars, but high fall growth rates were not always associated with dwarf bunt resistance. High growth rates through early spring were associated with dwarf bunt resistance, but not with winterhardiness. Growth rates prior to anthesis were related to neither characteristic.

It appears that vegetative growth rates per se of winterhardy wheats are not incompatible with dwarf bunt resistance.

The heat unit requirement for reproductive initiation was associated with both winterhardiness and dwarf bunt reaction. Resistant cultivars reached this stage earlier in the spring than did the most winterhardy cultivars, perhaps allowing them to escape infection but making them more vulnerable to late winter or early spring freezing stress. It is unlikely that a highly winterhardy wheat with dwarf bunt resistance could be developed.

While grain-filling duration was not related to winterhardiness or the time at which anthesis begins, grain growth rate was. The early group of cultivars had a higher grain growth rate than did the late group. Late cultivars must fill grains during a more stressful period and may not grow to their full potential. The heat unit requirement for anthesis was greatest for the most winterhardy cultivars, but the heat units accumulated from reproductive initiation to anthesis was not related to winterhardiness. It may be possible to select for both late reproductive initiation and early anthesis.

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in

Agronomy

MONTANA STATE UNIVERSITY  
Bozeman, Montana

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of a thesis submitted by

Janet Eileen Goodell

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

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## ABSTRACT

In 1974, the People's Republic of China placed an embargo on all wheat shipped from Pacific Northwest ports due to the presence of dwarf bunt spores. The embargo eliminated Montana wheat from this market. Prior to the embargo, dwarf bunt, caused by Tilletia controversa Kuhn, was only a minor problem in Montana. Consequently, most resistant cultivars have been developed in states with milder winters and have only low to moderate winterhardiness. If host resistance is to be used to control dwarf bunt, cultivars with adaptive characteristics must be developed. The objective of this research was to examine relationships among growth characteristics, winterhardiness, and dwarf bunt reaction.

Ten winter wheats varying in winterhardiness and dwarf bunt reaction were planted in the falls of 1982 to 1984. Samples were taken at various growth stages, and growth rates were calculated as dry weight per heat unit. The heat units accumulated in reaching particular stages were noted.

The less winterhardy cultivars had more fall growth than the more hardy cultivars, but high fall growth rates were not always associated with dwarf bunt resistance. High growth rates through early spring were associated with dwarf bunt resistance, but not with winterhardiness. Growth rates prior to anthesis were related to neither characteristic. It appears that vegetative growth rates per se of winterhardy wheats are not incompatible with dwarf bunt resistance.

The heat unit requirement for reproductive initiation was associated with both winterhardiness and dwarf bunt reaction. Resistant cultivars reached this stage earlier in the spring than did the most winterhardy cultivars, perhaps allowing them to escape infection but making them more vulnerable to late winter or early spring freezing stress. It is unlikely that a highly winterhardy wheat with dwarf bunt resistance could be developed.

While grain-filling duration was not related to winterhardiness or the time at which anthesis begins, grain growth rate was. The early group of cultivars had a higher grain growth rate than did the late group. Late cultivars must fill grains during a more stressful period and may not grow to their full potential. The heat unit requirement for anthesis was greatest for the most winterhardy cultivars, but the heat units accumulated from reproductive initiation to anthesis was not related to winterhardiness. It may be possible to select for both late reproductive initiation and early anthesis.

## INTRODUCTION

Dwarf bunt of winter wheat, caused by Tilletia controversa Kuhn, has drawn much attention during recent years, despite the fact that it is limited in distribution and sporadic in occurrence. In 1974, the People's Republic of China placed an embargo on all wheat shipped from Pacific Northwest ports because of the existence of dwarf bunt spores on wheat shipped from those ports. The pathogen has not been reported in that country, and the quarantine was implemented to prevent its introduction. Montana exports a substantial portion of its wheat that is shipped west. Thus, the embargo eliminated Montana wheat from one of the world's largest markets (Cramer et al., 1978; Mathre and Johnston, 1976; Trione, 1982).

Prior to the embargo, dwarf bunt was only a minor production problem in several localized areas of Montana, and little effort to eliminate the disease had been made. In other northwestern states, dwarf bunt presents a greater problem. Consequently, most dwarf bunt resistant cultivars available to Montana farmers have been those developed in other states with milder winters. One exception to this is Winridge, a wheat with moderate winterhardiness, released by the Montana Agricultural Experiment Station in 1983 (Taylor et al., 1983). No cultivars with both a high level of winterhardiness and resistance to dwarf bunt are known.

Disease resistant cultivars generally provide the simplest, most effective, and most economical means of controlling plant disease (Sill, 1982). Although systemic seed treatments for control of dwarf bunt have been registered, use has not been great because of the high cost of chemicals, variable results, and the availability of dwarf bunt

resistant cultivars (Hoffman, 1982). To eradicate dwarf bunt by the use of resistant cultivars, it is apparent that cultivars which are not only resistant to dwarf bunt, but also have necessary adaptive characteristics, must be produced. In Montana, winterhardiness is of prime importance.

The objective of this research was to examine relationships among growth rates, winterhardiness, and dwarf bunt reaction in wheat.

PART 1  
PRE-ANTHESIS ACTIVITY

## LITERATURE REVIEW

### The Dwarf Bunt Fungus

Dwarf bunt, a soilborne disease, is endemic in areas where its development is favored by significant snow cover (Fernandez et al. 1978). Germination of teliospores is slow (1-3 months) and has an obligate temperature requirement of 1-10 degrees C (Trione, 1982). Persistent snow cover throughout the winter months provides an environment favorable for attack and protects the inoculum from weather extremes (Tyler and Jensen, 1958). Infection originates from teliospores germinating at or near the soil surface. The site of penetration of the host plant is presumed to be the tiller initials (Hoffman, 1982).

Most disease resistance has a physiological or biochemical basis (Sill, 1982). Infection by dwarf bunt is closely associated with the stage of plant development (Hoffman and Purdy, 1967). Plants entering the infection period with only a few tillers generally have the highest incidence, while plants with many tillers have a low incidence or escape infection entirely. In older plants with larger and more differentiated crowns, some tillers are beyond the point of susceptibility or are out of reach of invading mycelium; in younger plants, the entire crown area may be invaded by mycelium before many tillers are differentiated. Dewey (1956) suggested that the pathogen may enter older plants through young, late-formed tillers.

Studies involving artificial inoculation of the coleoptile with dwarf bunt fungi indicate that both susceptible and resistant genotypes can be penetrated by hyphae. Hansen (1958) discovered that the fungal hyphae in resistant genotypes were retarded compared to those in susceptible genotypes. Fernandez et al. (1978) reported that, after penetration of the coleoptile in a highly susceptible genotype, hyphae spread throughout the primordial leaf and nodal tissue, reaching the growing point before internodal elongation. In two of the resistant genotypes examined, hyphae followed a similar route but almost always failed to invade the growing point and thus ultimately failed to sporulate. In the highly resistant P.l. 178383, the few hyphae detected were usually confined to the first and second leaves, well away from the growing point. They concluded that two types of resistance can be described: one that is influenced by temperature changes, in which mycelia are established in host tissue but are arrested before reaching the growing point, and another that is intrinsic, in which fungal development is minimal after infection. They speculated that the first type of resistance is expressed when infected plants resume growth during rising temperatures in the spring, and that prolonged incubation at cold temperatures might negate such resistance by allowing additional time for the fungus to reach the growing point.

To summarize, the early development of the pathogen is its most crucial stage. The hyphae must reach the tiller initials before internodal elongation, or the pathogen will not sporulate in the mature head (Fernandez et al, 1978; Hansen, 1958; Trione, 1982).

The Influence of Growth and Development  
on Winterhardiness

A species' ability to tolerate low temperatures is a primary factor determining its area of adaptation and distribution (Gusta et al., 1982). Winterhardiness is determined by two major factors: (1) genetic ability of the plant to develop a certain degree of resistance to negative temperatures and (2) external conditions under which this ability is developed (Trunova, 1982). Wheats vary in their ability to harden, to acquire the hardened condition earlier in the fall, and to retain it later in the spring (Fowler and Gusta, 1977b; Olien, 1967; Worzella and Cutler, 1941).

Levitt (1972) reported close relationships between cold tolerance and growth, development, and dry matter accumulation. Fowler and Gusta (1977a) obtained significant negative correlations between  $LT_{50}$  and plant height and leaf number, all measured in the fall.  $LT_{50}$  is the temperature down to which 50 percent of the crowns survive (Fowler and Gusta, 1977a). Significant negative correlations have also been found between a field survival index (FSI) and dry leaf weight and  $LT_{50}$  (Fowler et al., 1981).

Once cold acclimation of winter wheat has taken place, a high level of hardiness can be maintained for several months (Gusta and Fowler, 1976; Olien, 1967). However, alternate freezing and thawing or exposure to temperatures slightly above freezing for several days will reduce the hardiness level (Fowler and Gusta, 1977b; Gusta and Fowler, 1977; Olien, 1967). Temperature requirements for resumption of growth

vary considerably among genotypes (Olien, 1967). The extent and timing of this dehardening process are critical to plant survival.

In winter wheat, differentiation of the spike is not evident in the fall (Kiesselbach and Sprague, 1926). Apex elongation, accompanied by the appearance of double ridges, marks the beginning of the reproductive stage and generally occurs in March or April (Bonnett, 1966). The time of initiation of the reproductive phase of wheat is an important factor in predisposing the plant to spring frost injury (Single, 1961). In late winter or early spring, depending on the genotype, and in response to suitable temperatures, the apical meristem is thrust upward away from the crown by elongation of the lowest internodes of the culm. If this elongation positions the young head above the soil surface prior to sharp spring freezes, the head may be killed (George, 1972, 1982).

Genotype differences have been reported for the time of resumption of apex development. The negative correlation between the degree of development of the apical meristem and the level of winterhardiness is important (Bendarenke and Mitropolenko, 1979; Chaudhry and Taylor, 1984; Mitropolenko, 1978).

Bonnett (1966) reported that the time of reproductive initiation differs among maturity groups and within the same maturity group, and that a genotype initiates spike development in accord with its time of heading. This implies that there is also a negative correlation between time of heading and winterhardiness rating. Fowler et al. (1981) did not find a significant correlation between the field survival index and heading date, although it was nearly so. Bonnett (1966) concedes that if a larger number of genotypes had been used, it is likely that some

might, at heading, shift out of the maturity class in which they were placed on the basis of spike initiation. Halloran and Penell (1982) found large differences among genotypes for the duration of the spikelet formation-to-heading phase. They suggested that rates of reproductive initiation and stem elongation appear to be largely independent.

#### Temperature, Growth, and Development

Among environmental factors, temperature is considered the primary determinant of plant development rate (Bauer et al., 1984). Regardless of how favorable light and moisture conditions are, a certain minimum temperature is required before any growth can take place (Kinger, 1922). A linear relationship between winter wheat leaf extension and temperature has been reported (Gallagher et al., 1979; Hay and Wilson, 1982). This relationship stops below 0 degrees C, however (Gallagher et al., 1979). The base photoperiod for leaf initiation has been shown to be zero hours, reflected in the fact that more than half the leaves have been initiated before plant emergence. Leaf initiation also showed a rather weak response to increasing photoperiods (Baker and Gallagher, 1983).

A correlation between temperature and reproductive development rates in wheat has also been found (Aitken, 1966; Ford et al., 1981; Frank and Bauer, 1982; Friend et al., 1963; Halloran, 1977; Halloran and Penell, 1982; Halse and Weir, 1970; Lang, 1952; Marcellos and Single, 1971; Nuttonson, 1966; Pirasteh and Welsh, 1980; Rahman and Wilson, 1978). Lang (1952) reported a temperature dependent, but light independent, process considered to be involved in the actual induction of

floral primordia. Aitken (1966) discovered that, in winter wheat, temperature had a striking effect on the rapidity of reproductive initiation while photoperiod was of small importance. Baker and Gallagher (1983) found a threshold photoperiod of only four hours for spikelet initiation in winter wheat. Chaudhry and Taylor (1984) reported a difference in number of days and heat units to reproductive initiation between locations with different temperature regimes but nearly identical photoperiods. Thus, temperature was shown to be a dominant factor in this process.

Halloran (1977) stated that it is possible that temperature may influence the rate of both pre- and post-initiation development, and that differing temperature optima may exist among genotypes for processes determining the rate of development in wheat. Studies on the influence of high temperature on development rate in wheat as time from germination to anthesis indicated significant differences in genotype response (Halse and Weir, 1970).

#### The Heat Unit Concept

Heat units or growing degree days is a simple means of relating plant growth, development, and maturation to air or soil temperature. Different species of plants have different base temperatures below which they do not grow. At temperatures above this base, the amount of plant growth is approximately proportional to the amount of heat accumulated (heat units) (Dethier and Vittum, 1963). Ideally, for each species of plant, and for different genotypes within a species, maturity is reached when the heat units have accumulated to a certain sum. That sum

required for a particular crop has been assumed to be a constant value and is termed the varietal constant (Wang, 1960).

The use of heat units to estimate growth rate and stage has been criticized because it has no theoretical basis. Yet, equations derived from heat units have been compared with other energy summation indices and theoretically-based equations and were found to be equal in precision (Kiniry and Keener, 1982; Sastry and Chakravarty, 1982). Bauer et al. (1984) compared the use of heat units to photothermal units (PTU) and days from emergence in developing crop calendars. The precision of estimating growth rates and stages for spring wheat with heat units was the same as with PTU and superior to days. Gilmore and Rogers (1958) and Tsotsis (1958) found accumulated heat units to be an improvement over calendar days for predicting flowering dates in maize.

The disadvantages of using calendar-day maturity ratings become obvious when genotypes are compared under several environmental conditions. The dates of heading and ripening of any given wheat genotype often varied considerably not only in different localities, but also from year to year within any given locality in a study done by Nuttonson (1966). Likewise, the temperature data showed considerable variation. The temperature variations appeared to be a major factor in determining the rate of seasonal growth and development of wheat.

The heat unit system is accurate enough to be a useful tool, but considerable error may be involved in it, too. This error is revealed as a variation in the number of heat units required for a genotype to complete a particular stage of development. This variation is not completely random, but shows a definite relationship to trends in the

climatic conditions (Arnold, 1959). The heat unit requirement was found to be less under cool conditions than under warm ones. Lana and Haber (1952) found that with hot weather and drought conditions, the heat unit requirement for sweet corn was greatest. In an evaluation of the effect of temperature on the number of days to heading of ten wheats, Pirasteh and Welsh (1980) noted all genotypes headed more rapidly at the higher temperatures. More heat units were used at the warmer temperatures, however, leading them to conclude that only part of the increased heat was translated to accelerated heading.

Tsotsis (1958) also found significant differences between the accumulated heat units for a specific variety grown in different seasons. He suggested that a system considering heat units separately for each of the various stages of growth might increase accuracy of predictions. Wang (1959) divided the life cycle of several crops into the underground, vegetative, flowering, and fruiting stages. The standard set of observations on spring wheat used by the Canadian Department of Agriculture includes date of planting, emergence, jointing, heading, flowering, soft dough, and harvest ripe (Anonymous, 1959).

## MATERIALS AND METHODS

### Genotypes

Ten winter wheat cultivars known to differ in dwarf bunt reaction and in winterhardiness were studied. The cultivars with at least some resistance to dwarf bunt vary for winterhardiness as do those that are susceptible. The winterhardiness ratings correspond to average winter survival at Montana locations (Taylor, 1984). The dwarf bunt reaction ratings are based on reactions to dwarf bunt races prevalent at Kalispell, Montana (Hoffman and Waldher, 1982 and 1984). These isolates have been found to be avirulent on BT genes 5, 8, 10, and 11 and possibly on BT genes 4 and 6 (Grey, 1985). Winridge was planted the second and third years only, due to a seed packaging error. Cultivar descriptions are given in Table 1.

### Environments

Year One (1982-1983). Experiments were planted at two locations on the Arthur H. Post Field Research Laboratory near Bozeman, Montana, on October 1, 1982 (Environment 1) and October 13, 1982 (Environment 2) in Amsterdam silt loam soil. The sites were about 0.8 km apart, and Environment 2 was slightly elevated compared to Environment 1.

Year Two (1983-1984). Experiments were planted at two sites (Environments 3 and 4) at Montana State University on September 24,

1983. Soil tests indicated that Environment 3 had higher levels of nitrogen and phosphorus than did Environment 4.

Year Three (1984-1985). Seeds were planted in adjacent sites at the Post Farm on September 24, 1984, for use in Experiment 1 only. Environment 5 was fertilized with ammonium sulfate (110 kgs/ha), while Environment 6 was unfertilized.

#### Experimental Design

With the exception of the rows used in reproductive initiation determination, a randomized complete block design was used. Six replications were planted for each experiment. Plots were hills with 28 seeds per hill. The hill plots were planted by hand at 30-centimeter spacings. For reproductive initiation determination, plots were not replicated. Chaudhry and Taylor (1984) found no significant differences for time of reproductive initiation among blocks in any of the nine locations they studied, including Bozeman.

#### Experiments

In order to discover if relationships exist between growth rates and winterhardiness or dwarf bunt reaction, dry weight was measured several times during the growing season. This information was also used to determine if there are growth characteristics of highly winterhardy wheats which prohibit dwarf bunt resistance and vice versa.

Growth was measured as follows:

1. Experiment 1--late fall and early spring. Plants were allowed to harden in the fall before above-ground dry

matter accumulation was measured. This was done to determine if the amount of growth taking place before the onset of winter is associated with winterhardness level or dwarf bunt reaction. The plots in several environments could not be sampled in the fall, and were taken in the spring as soon as conditions allowed. Hill plots were cut at ground level, dried at 60 degrees C until they reached a constant weight, and weighed.

2. Experiment 2--reproductive initiation. Double ridges on the apical meristem mark the beginning of reproductive development. Cultivars which reach this stage early in the spring become vulnerable to spring freezing. Dwarf bunt hyphae must reach the meristem before this time in order to complete the fungus's life cycle. Plants were removed from single-row plots adjacent to the hill plots at about twice-weekly intervals beginning in late March. The shoots were dissected in the manner described by Bonnett (1966) to note the appearance of double ridges. When three out of four main tillers of a particular cultivar had reached double ridge stage, the corresponding hill plots were cut and handled as in Experiment 1.
3. Experiment 3--anthesis. By this stage, vegetative growth has ceased and grain development begins. If anthesis occurs too late, the grains must grow during a time of increasing drought stress. This experiment was planted in a nine-hill design to avoid border affects from other cultivars. Each

plot was cut when about two-thirds of the heads in that plot had reached anthesis. Plants were then sun-dried for about five days and weighed.

The date that each plot was cut was noted for use in heat unit and growth rate calculations.

#### Heat Unit and Growth Rate Calculation

Accumulated heat units (HU) for a growth or development period were calculated by summing, over time, heat units accumulated during the 24-hour interval from midnight to midnight where:

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

and where  $T_{max}$  and  $T_{min}$  are the daily maximum and minimum air temperatures (Bauer et al., 1984) and  $T_b$ , the base temperature, is 0 degrees C (Baker and Gallagher, 1983; Davidson and Campbell, 1983). When  $T_{min}$  or  $T_{max}$  for the day was less than 0 degrees C, it was considered to be 0 degrees C (Bauer et al., 1984). Temperatures were measured at 1.5 meters above the soil surface. Growth rates were defined as milligrams dry weight per hill per accumulated heat unit.

#### Statistical Analyses

Analyses of variance were performed to determine if differences existed among cultivars and to establish cultivar rankings for growth rates. Combined analyses over environments and years were performed using the methods given by McIntosh (1983). Cultivars and environments were considered to be fixed and random, respectively. Analysis of

variance was not used on the reproductive initiation data which had no replications.

Simple linear regressions were done using averages over all environments as the dependent variables and either the winterhardness or the dwarf bunt reaction ratings as the independent variable. Contrasts were utilized to compare the group means. Groupings are given in Table 1.

Table 1. Cultivars, their descriptions, and dwarf bunt reaction and winterhardness groups.

Cultivar	ID number	Class	Height*	WH**	BT genes@	Dwarf bunt rxn.#
Crest (CST)	CI 15075	HRW	105	3	3,10	4
Centurk (CTK)	CI 13880	HRW	100	4	--	1
Norstar (NRS)	CI 17735	HRW	153	8	--	1
Norwin (NRW)	PI 491533	HRW	85	8	--	1
Nugaines (NGN)	CI 13968	SWW	93	2	1,4	3
Redwin (RWN)	CI 17844	HRW	107	5	--	1
TAM 105 (TAM)	CI 17826	HRW	97	3	--	2
Weston (WTN)	CI 17727	HRW	119	4	4,10	5
Winalta (WN)	CI 13670	HRW	140	7	--	2
Winridge (WNR)	CI 17902	HRW	117	6	4,10,?	5

<u>Winterhardness groups+</u>			<u>Dwarf bunt reaction groups++</u>	
1	2	3	R	S
CST	CTK	NRS	CST	CTK
NGN	RWN	NRW	NGN	NRS
TAM	WTN	WN	WTN	NRW
	WNR		WNR	RWN
				TAM
				WN

\* Ten-year average at Bozeman, MT, in centimeters (Montana Agricultural Experiment Station, 1982).

\*\* Winterhardness: 10=very winterhardy; 1=not winterhardy.

@ Genes for dwarf bunt resistance (Hoffman, 1974; Hoffman and Waldher, 1975).

# Dwarf bunt reaction: 5=highly resistant; 1=completely susceptible.

+ 3=most winterhardy; 1=least winterhardy.

++ R=cultivars containing Bt genes (<50% infection); S=cultivars with no Bt genes (>50% infection).

## RESULTS AND DISCUSSION

### Experiment 1

Three sites were sampled in the fall and, due to early persistent snow cover, three sites were sampled in the spring as soon as conditions allowed. The analyses of the resultant data were separated on that basis.

#### Fall Growth Rates

Of the three sites sampled in the fall, only two were used in combined analyses. According to Roberts and Grant (1968), the interaction of age of plant and cold hardiness is sufficiently great to change the ranking of cultivars. In their studies at Lethbridge, Alberta, a definite maximum hardiness was associated with wheat seeded seven to nine weeks before freeze-up. Environment 2, planted October 13, 1982, was five weeks old on November 19, when it was cut. Waiting an additional two to four weeks would probably not have changed the results, as most growth had likely subsided due to prolonged cool temperatures and the resultant hardening process. The cultivar rankings in this environment differed markedly from those in the two other environments, and therefore data from Environment 2 was not used in the combined analysis (Table 17, Appendix).

The results of the combined analysis over two environments are given in Table 2. There was a highly significant environment by

cultivar interaction, but the rankings within the contrast groups are the same in both environments.

Table 2. Mean squares for fall growth rate and for growth rate through early spring of nine and ten cultivars and two and three environments, respectively.

Source	Fall		Early Spring	
	df	Mean squares	df	Mean squares
Blocks/Env.	10	.0385	14	10.0700
Environments	1	2.5400 **	2	14.1000 ns
Cultivars	8	.2432 ns	9	.4048 ns
Env. x Cultivar	8	.1448 **	18	.4626 **
Error	80	.0398	120	.2004

\*\* Significant at the .01 level of probability.  
ns Not significant at .05 level of probability.

Winterhardness and fall growth rates. The mean growth rate of the mid-winterhardy group (2) was significantly greater than that of the most winterhardy group, but the mean growth rate of the least winterhardy group was not (Table 3). The regression of growth rate on winterhardness rating was also not significant. This suggests that no meaningful relationship exists between winterhardness and fall growth rates. However, if the growth rate of Crest is disregarded, a trend can be discerned. Ashraf and Taylor (1974) noted that Crest has atypical fall growth characteristics and suggested that it may possess a genetic system for emergence and plant height factors unique from the other winter wheat cultivars they studied. Crest's rank in Table 4 suggests that this uniqueness might also be important here. The regression of growth rate on winterhardness rating with Crest excluded is negative.

and significant at the 6 percent level (Figure 1). It is probable that a negative relationship exists between fall growth rate and winter-hardiness.

Table 3. Group means for fall growth rate averaged over two environments (mgs/HILL x HU).

Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(2) .877 a	(R) .824 a	(R) .824 a
(1) .793 ab	(S) .755 a	(3) .664 a
(3) .664 b		

Means followed by different letters are significantly different at the .05 level of probability by LSD.

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes for dwarf bunt resistance; (S)=contain no Bt genes.

Table 4. Cultivar means for fall growth rate averaged over two environments.

Cultivar	Growth rate (mgs/HILL x HU)
Weston	1.023
TAM 105	.929
Centurk	.831
Nugaines	.780
Redwin	.778
Winalta	.777
Crest	.668
Norwin	.660
Norstar	.554

5% LSD = .379.

Dwarf bunt reaction and fall growth rates. The regression of growth rate on the dwarf bunt reaction rating was not significant. The group mean of susceptible cultivars did not differ from that of the cultivars with at least some resistance (Table 3). The regression with Crest excluded is positive and significant (Figure 2). Fall growth rate, and thus the size of the plants during the winter, is associated with dwarf bunt reaction in these cultivars. Hoffman and Purdy (1967) showed that the number of infected plants decreases as stage of plant development advances in susceptible cultivars, inoculated at various stages. Tyler's results (1958) showed that as wheat plants age, they become less susceptible to dwarf bunt infection. Dwarf bunt resistance is due in part to an advanced stage of development in the fall which could be reflected in a high fall growth rate. This does not imply that high fall growth rates are a necessity for dwarf bunt resistance in Montana, borne out by the fact that Crest, with a high level of resistance, had a comparatively low mean fall growth rate. Winridge, with a high level of resistance, had only a moderate fall growth rate in Year Two (Table 19, Appendix).

Winterhardiness versus dwarf bunt reaction in relation to fall growth rates. The mean fall growth rate for the cultivars with resistance did not differ from that of the most winterhardy cultivars (Table 3). Yet when Crest is excluded from the analysis, the contrast becomes significant at the .05 level (Table 18, Appendix). The regressions illustrated in Figures 1 and 2 show winterhardiness to be negatively associated with and dwarf bunt resistance to be positively associated with fall growth rates. While dwarf bunt resistance may be favored by

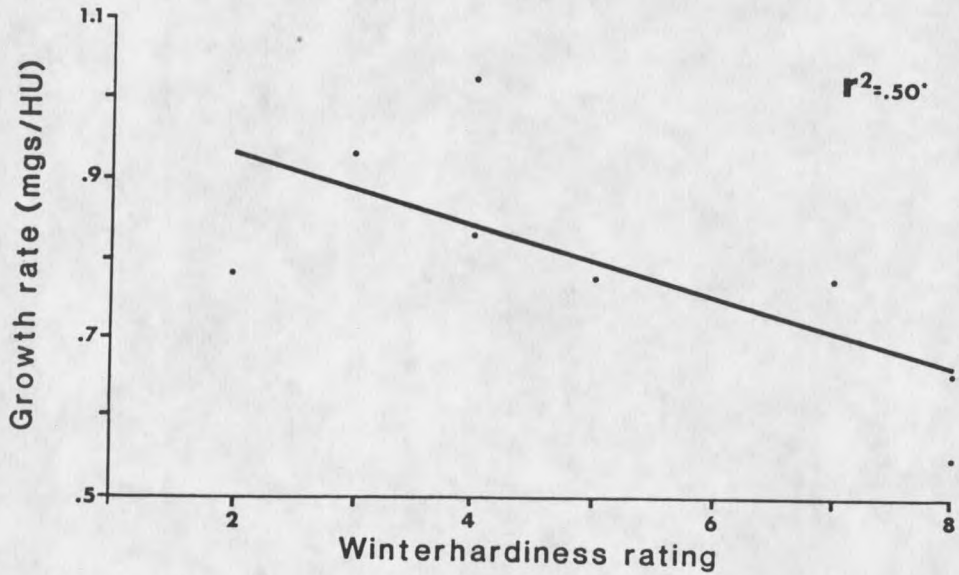


Figure 1. Regression of fall growth rate on winterhardness rating with Crest excluded.

\* Significant at the .06 level of probability.

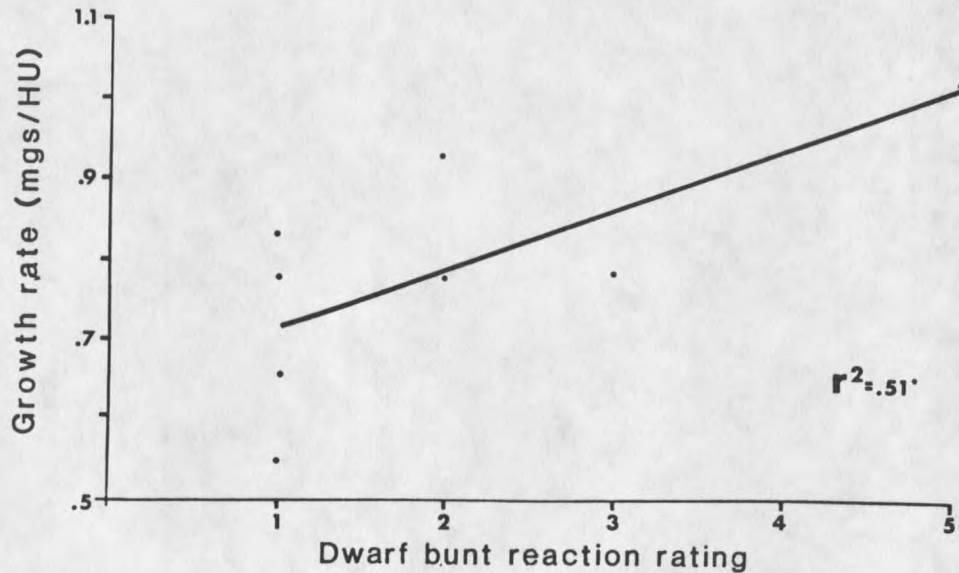


Figure 2. Regression of fall growth rate on dwarf bunt reaction rating with Crest excluded.

\* Significant at the .05 level of probability.

high fall growth rates, the comparatively low fall growth rates usually associated with high winterhardiness do not preclude resistance in Montana. Crest's low fall growth rates demonstrate this.

#### Growth Rates through Early Spring

The results of the analysis of the three sites cut in early spring are given in Table 2. Winridge was included in this analysis.

Winterhardiness and growth rates through early spring. The regression of growth rate on winterhardiness rating is not significant. Neither are any of the contrasts between winterhardiness groups (Table 21, Appendix), indicating no relationship between the average growth rates of these wheats up to this time and their winterhardiness ratings.

Dwarf bunt reaction and growth rates through early spring. The regression of growth rate on dwarf bunt reaction rating was positive and significant (Figure 3). This agrees with the regression of fall growth rate on reaction rating with Crest excluded. Crest showed comparatively aggressive growth by early spring (Table 5). Early vegetative growth rates appear to be important for dwarf bunt resistance.

Winterhardiness versus dwarf bunt reaction in relation to growth rates through early spring. The contrast between the most winterhardy and the resistant groups was not significant. The ranking of cultivars in Table 5 shows that Norwin, a very winterhardy cultivar, has a high growth rate. Winridge, which combines a high level of dwarf bunt resistance with moderate winterhardiness, has the highest growth rate. There seems to be no conflict between high winterhardiness and dwarf

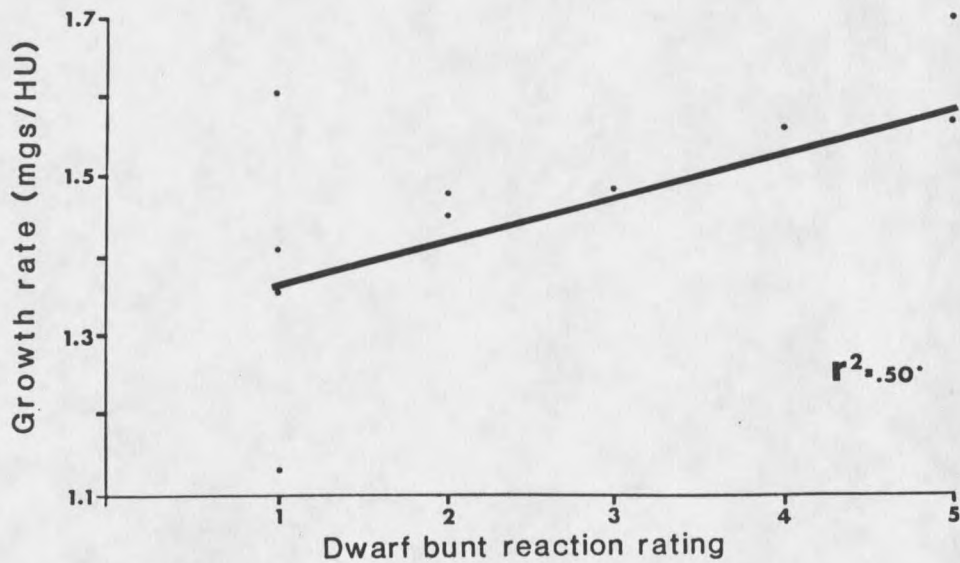


Figure 3. Regression of growth rate through early spring on dwarf bunt reaction rating.

\* Significant at the .05 level of probability.

Table 5. Cultivar means for growth rate through early spring averaged over three environments.

Cultivar	Growth rate (mgs/HILL x HU)
Winridge	1.704
Norwin	1.601
Crest	1.551
Nugaines	1.486
TAM 105	1.484
Winalta	1.455
Norstar	1.410
Centurk	1.362
Redwin	1.143

5% LSD = .490

bunt resistance in terms of vegetative growth rates which would prevent the traits from being combined in one genotype.

### Experiment 2

#### Heat Units Accumulated Prior to Reproductive Initiation

Cultivar means are listed in Table 6. Although there were some differences in the cultivar rankings for heat units accumulated prior to anthesis among the four environments, Spearman-rank correlations indicate that the rankings are highly correlated. This agrees with Chaudhry and Taylor (1984) who reported that the rankings of the wheats they studied did not differ among locations.

Table 6. Cultivar means for heat units accumulated prior to reproductive initiation averaged over four environments.

Cultivar	Heat Units
Norstar	874
Norwin	859
Winalta	859
Redwin	853
Centurk	821
TAM 105	801
Nugaines	790
Weston	777
Crest	754

Differences among environments were evident. These differences were largely due to dissimilarities between the years (Table 7). Nearly twice as many heat units were accumulated in the fall of the second year

than in the fall of the first year (Table 8). This had little effect on reproductive development; as nearly the same amount was accumulated in the spring of both years. Within the first year, plants in Environment 2 accumulated less heat units in the fall, but more in the spring than did those in Environment 1. The plants in this site were so immature in the fall that they probably required additional heat units in the spring to reach a stage where reproductive development was possible.

Table 7. Environment means for heat unit accumulation prior to reproductive initiation averaged over nine cultivars.

Environment	Year	Heat units
1	1	716
2	1	738
3	2	933
4	2	934

Table 8. Mean heat unit accumulations prior to January 1 and from January 1 to reproductive initiation averaged over nine cultivars.

Environment	Year	Heat Units	
		Prior to Jan. 1	After Jan. 1
1	1	258	459
2	1	224	514
3	2	445	488
4	2	445	489

Winterhardiness and reproductive initiation. The regression of accumulated heat units on winterhardiness rankings was positive and highly significant (Figure 4). The winterhardy cultivars require more

heat units to begin the reproductive stage of development than do less hardy cultivars. This agrees with Chaudhry and Taylor's (1984) conclusion that high winterhardiness is associated with late reproductive initiation.

In less winterhardy wheats, the meristem changes from the vegetative to the reproductive phase early in the spring. These morphological changes, probably accompanied by biochemical change, make the plant vulnerable to late winter and early spring cold stress that often occurs in Montana.

Dwarf bunt reaction and reproductive initiation. The regression of accumulated heat units on dwarf bunt reaction ratings is negative and highly significant (Figure 5). The resistant cultivars require fewer heat units to reach reproductive initiation than do the susceptible cultivars. The double ridge stage is followed by the upward movement of the apical meristem through the soil surface (Bonnet, 1966). Fernandez et al. (1978) found that one type of dwarf bunt resistance is demonstrated by the ability of the growing point to escape infection by outgrowing the dwarf bunt mycelia. For the cultivars studied in this experiment, the rapid spring development of the apical meristem or, in other words, the comparatively low heat unit requirement for such development, may be a main avenue of resistance to dwarf bunt in Montana.

Winterhardiness versus dwarf bunt reaction in relation to reproductive initiation. The ranking of cultivars in Table 6, along with the previous findings regarding reproductive initiation, lead to the conclusion that dwarf bunt resistance does conflict with high winterhardiness. The first three cultivars to reach reproductive

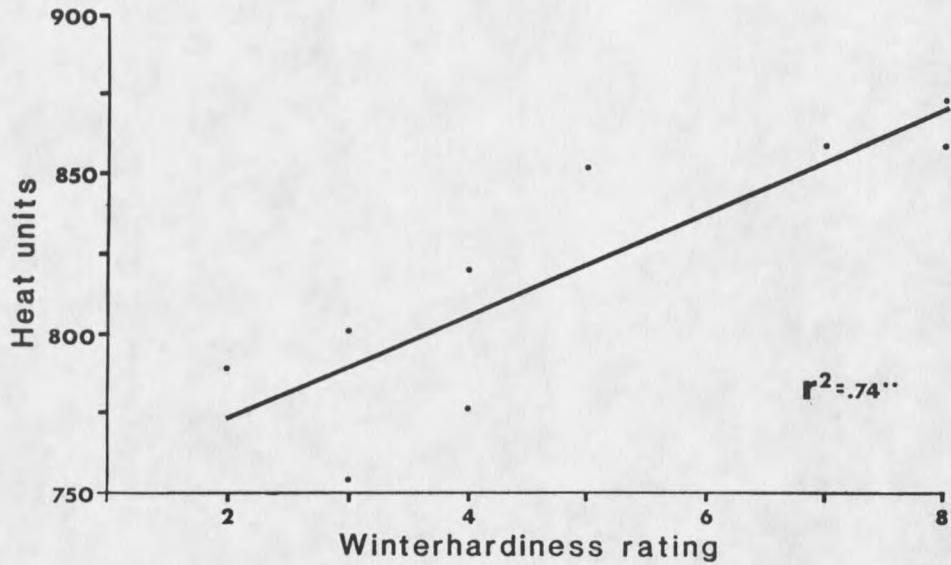


Figure 4. Regression of mean heat units accumulated between planting and reproductive initiation on the winterhardness ratings of nine cultivars (four environments).

\*\* Significant at the .01 level.

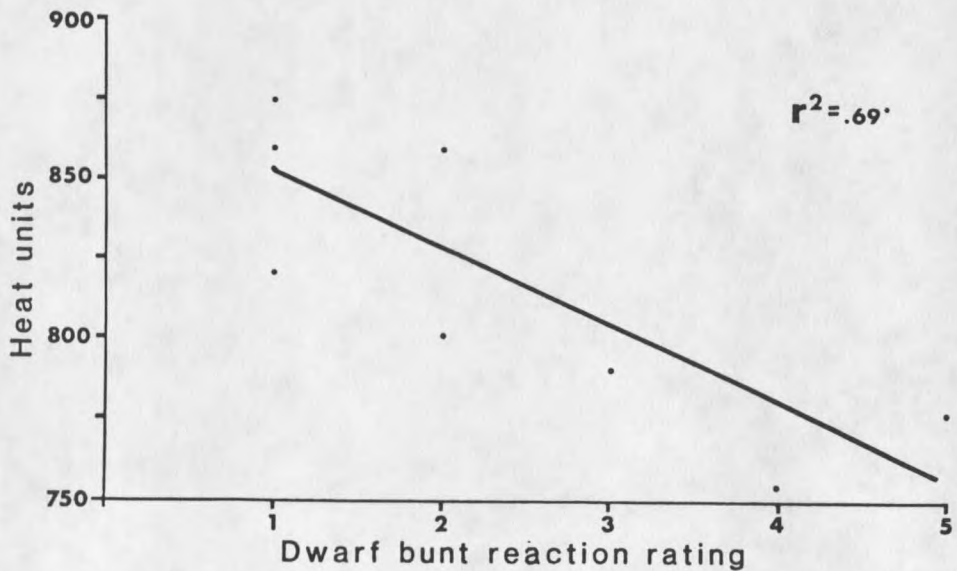


Figure 5. Regression of mean heat units accumulated between planting and reproductive initiation on the dwarf bunt reaction ratings of nine cultivars (four environments).

\* Significant at the .05 level.

initiation are those with Bt genes for resistance, while the last three are the most winterhardy cultivars studied. TAM 105 contains no Bt genes but does show some resistance at the Kalispell, Montana location. Its resistance may be due to its earliness in reaching the reproductive stage.

If dwarf bunt resistance requires early initiation and upward growth of the meristem, while a high level of winterhardiness depends on late initiation, then it may be difficult to combine the two traits. Winridge, the cultivar nearest this goal, is only moderately winterhardy. In Year Two, it was the last of the resistant wheats to reach reproductive initiation. However, it reached this stage before the wheats with high winterhardiness (Table 21, Appendix).

#### Growth Rates through Reproductive Initiation

Due to the positive linear relationship between temperature and growth rates, it is likely that the cultivars sampled later in the spring would exhibit higher growth rates because they are allowed to grow during a period of rapidly rising temperatures (Figure 6). This supposition is verified by the analysis of growth rates through reproductive initiation. Table 23 of the appendix gives the contrast results from the group mean growth rates.

Due to the effect of temperature and the different sampling dates, it is difficult to establish whether one group has a higher growth rate than another throughout this part of the season. It can be concluded that cultivars which reach reproductive initiation later in the season generally have a higher growth rate at that time than do earlier

cultivars at the time they reached that stage. The mean squares and cultivar means are given in Table 22 of the appendix.

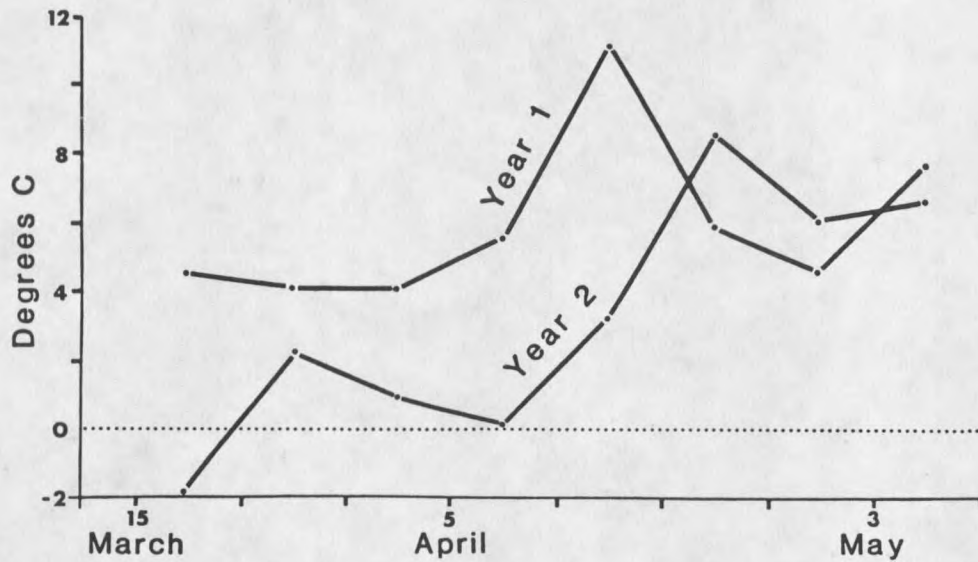


Figure 6. Mean weekly air temperatures during springs of Years One and Two (1983 and 1984), respectively.

### Experiment 3

#### Heat Units Accumulated Prior to Anthesis

The mean squares from the analysis of heat units accumulated from planting to anthesis are given in Table 9. The highly significant differences among environments is largely due to the difference between the two years (Table 10). As was pointed out in the discussion of experiment two, the environments in the second year accumulated about 200 more heat units in the fall than did those in the first year.

In addition, there were very high temperatures immediately preceding anthesis in the second year. Pirasteh and Welsh (1980) found that, when subjected to high temperatures, wheat accumulates more heat

units before flowering than when subjected to longer cool periods. They speculate that the plant cannot utilize all the heat units that accumulate on hot days.

The environment X cultivar interaction is also highly significant. However, when considering group means for the contrasts, the rankings of the group means are similar for all four environments.

Table 9. Mean squares for heat units accumulated prior to anthesis of nine cultivars and four environments.

Source	df	Mean Squares	
		From planting	From reproductive initiation
Blocks/Env.	20	1345 x 10	122.4
Environments	3	2054 x 10 **	3460 x 10 **
Cultivars	8	8916 x 10 **	4424 x 10 **
Env. x Cultivar	24	4665 **	7557 **
Error	160	111.9	118.9

\*\* Significant at the .01 level of probability.

Table 10. Environment means for heat units accumulated from planting to anthesis averaged over nine cultivars.

Environment	Year	Mean
1	1	1470
2	1	1423
3	2	1781
4	2	1784

Winterhardness and anthesis. The regression of accumulated heat units on winterhardness rating is not significant. The contrast

between winterhardness groups does reveal a difference between the most winterhardy group and the other two less hardy groups (Table 11). This is not surprising since the winterhardy wheats reach reproductive initiation later in the spring than do the others.

Table 11. Group means for heat units accumulated prior to anthesis averaged over four environments.

From Planting to Anthesis		
Winterhardness	Dwarf bunt reaction	High winterhardness vs. dwarf bunt resistance
(3) 1665 a	(S) 1626 a	(3) 1665 a
(2) 1597 b	(R) 1594 b	(R) 1594 b
(1) 1581 b		

From Reproductive Initiation to Anthesis		
Winterhardness	Dwarf bunt reaction	High winterhardness vs. dwarf bunt resistance
(3) 791 a	(R) 811 a	(R) 811 a
(1) 790 a	(S) 771 b	(3) 791 a
(2) 771 a		

Means followed by different letters are different at the .01 level of probability by LSD.

Means followed by the same letter are not different at the .05 level of probability.

(1)=least winterhardy; (3)=most winterhardy.

(R)=Contain Bt genes for dwarf bunt resistance; (S)=contain no Bt genes.

Winterhardness was not associated with heat units accumulated from double ridge stage to anthesis. This is borne out in an analysis of heat units accumulated between reproductive initiation and anthesis. There are differences among the cultivars (Tables 9 and 12), but the

regression of heat units on winterhardness rating is not significant with an extremely low  $r^2$  ( $0.6170 \times 10^{-4}$ ). The contrasts among the three winterhardness groups also were not significant (Table 11). Apparently the winterhardness level of these wheats is not related to the number of heat units required for heads to develop once they have been initiated.

Table 12. Cultivar means for heat units accumulated from reproductive initiation to anthesis averaged over four environments.

Cultivar	Heat units
Nugaines	863
Norstar	824
Crest	796
Redwin	790
Norwin	783
Weston	775
Winalta	765
Centurk	748
TAM 105	713

5% LSD = 52

Dwarf bunt reaction and anthesis. The regression of heat units accumulated from planting to anthesis on dwarf bunt reaction rating was not significant, and neither was that of heat units accumulated from reproductive initiation on dwarf bunt reaction. However, the contrasts between the resistant and susceptible groups were highly significant for both heat units accumulated from planting to anthesis and from reproductive initiation to anthesis (Table 11). While the resistant cultivars

require less heat units over the entire growing season to flower than do the susceptible ones, they require more heat units to reach anthesis after the head has been initiated.

Winterhardiness versus dwarf bunt reaction in relation to anthesis. The contrast of the most winterhardy group against the dwarf bunt resistant group for heat units from planting to anthesis is highly significant, with the winterhardy wheats requiring more heat units to flower (Table 11). This is again a consequence of the winterhardy wheats reaching reproductive initiation later in the spring than the resistant cultivars do. The heat units accumulated between reproductive initiation and anthesis are not significantly different for the two groups (Table 11). There is no difference between the wheats with high levels of hardiness and those with dwarf bunt resistance for heat units required to develop the head once initiated; but, because the resistant cultivars are more precocious in the spring, they tend to flower earlier. This difference between wheats with high winterhardiness and those with resistance is probably not a barrier to combining the traits. For example, Nugaines reaches reproductive initiation rather early in the spring, but requires a relatively large number of heat units to come to flower, and thus flowers about the same time as the most winterhardy wheats.

#### Growth Rates Prior to Anthesis

The results of the analyses for growth rates prior to anthesis are given in Table 24 of the appendix. The differences among cultivars are amplified when only the growth from reproductive initiation is

considered. This is due to the majority of growth taking place while only half the total heat units were accumulated.

Although it appears that the average growth rates throughout the growing season until flowering are related to both winterhardiness and dwarf bunt reaction (Table 25, Appendix), further analyses reveal a significant association between growth rates and plant height (Figures 7 and 8). Tillering does not necessarily overcome differences in plant height where plant weight before grain filling is of interest. Average cultivar heights are given in Table 1.

It is clear that low growth rates up to this time are associated with the shorter cultivars. This explains the significant contrasts where the least winterhardy group had the lowest growth rates. The three cultivars in this group are relatively short wheats (<101 cm) (Table 1 and Table 26, Appendix).

The resistant cultivars were also found to have lower growth rates. Again, two of the shorter wheats are in this group. In contrast, the most winterhardy group contains the two tallest wheats studied.

Because of the effect of plant height, it is difficult to determine whether winterhardiness or dwarf bunt reaction are related to growth rate during this period of growth. Mature plant height was not related to growth rates during seedling growth.

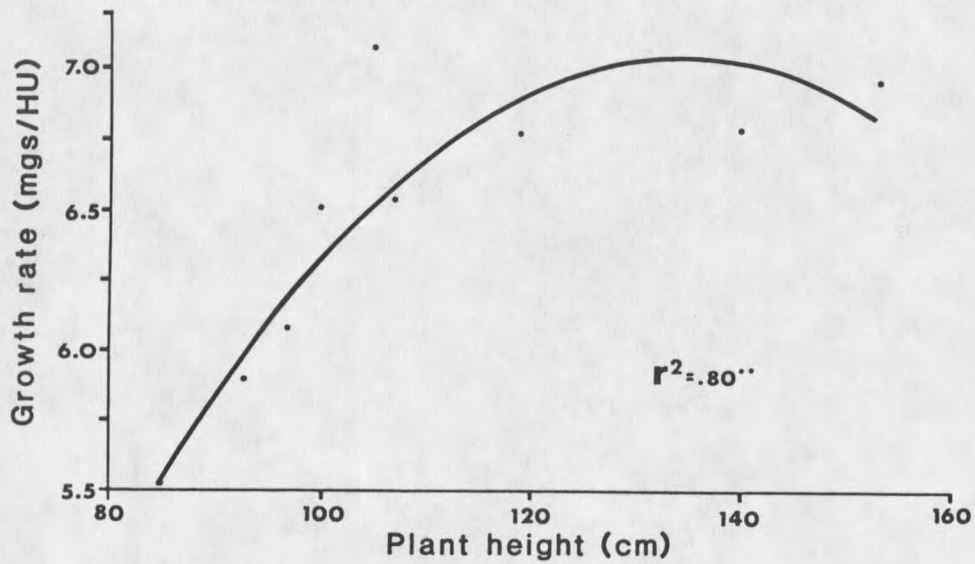


Figure 7. Regression of growth rate from planting to anthesis on the plant height of nine cultivars (mean of four environments).

\*\* Significant at the .01 level of probability.

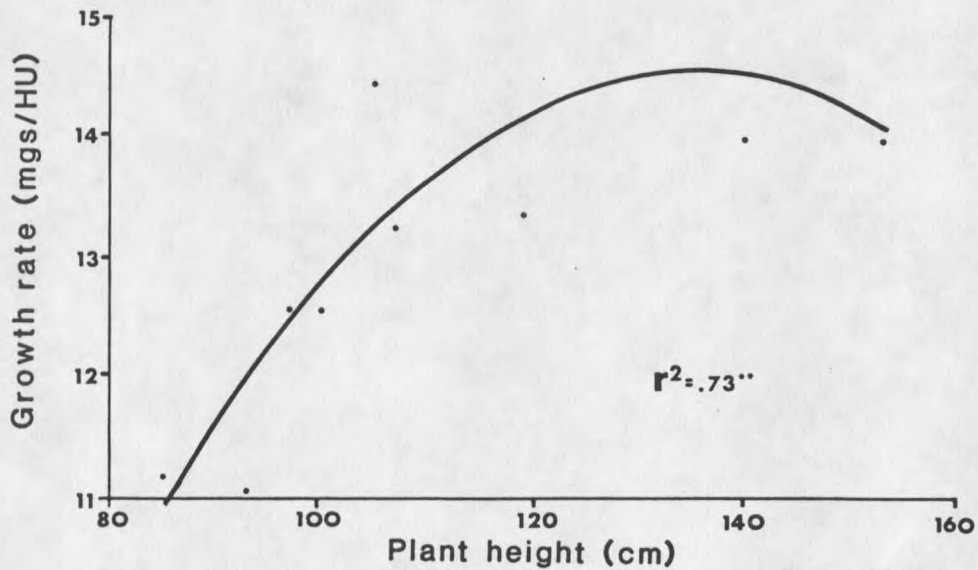


Figure 8. Regression of growth rate from reproductive initiation to anthesis on the plant height of nine cultivars (mean of four environments).

\*\* Significant at the .01 level of probability.

## SUMMARY

There was a trend for the more winterhardy cultivars to have less fall growth than less winterhardy cultivars. While high fall growth rates were generally associated with dwarf bunt resistance, they do not appear to be a necessity for resistance. Winterhardiness level was not related to the growth rate through early spring. Dwarf bunt resistance was associated with a high growth rate through early spring. Growth rates prior to anthesis were not related to winterhardiness or dwarf bunt reaction, but were related to plant height. It does not appear that vegetative growth rates of resistant wheats must preclude winterhardiness or vice versa. Resistant wheats may have low fall growth rates (as Crest does) characteristic of winterhardy wheats and winterhardy wheats may have high early spring growth rates (as Norwin does).

The time at which growth stops in the fall and begins in the spring was not studied here and may have an effect on both traits.

Of the characteristics studied, the heat unit requirement for reproductive initiation was the one most highly associated with winterhardiness and dwarf bunt reaction. The cultivars with resistance to dwarf bunt and the less winterhardy cultivars reach this point earlier in the spring than do winterhardy cultivars, making them more vulnerable to early spring freezing stress. Resistant cultivars may begin apical growth and development early in the spring, thereby outgrowing dwarf bunt mycelia and escaping infection. Because of these relationships, it

may be difficult to develop a dwarf bunt resistant wheat with a high level of winterhardiness.

Dwarf bunt susceptible cultivars required more heat units to reach anthesis than did the resistant cultivars, but less to bring the head to flowering once it had been initiated. The heat unit requirement for anthesis was found to be greater for the most winterhardy cultivars than for less winterhardy cultivars. The difference was due entirely to the greater heat unit requirement for reproductive initiation in more winterhardy cultivars. The heat units accumulated between reproductive initiation and anthesis were similar for all three winterhardiness groups. It should be possible to select for both late reproductive initiation and early anthesis.

**PART 2**  
**GRAIN-FILLING ACTIVITY**

## LITERATURE REVIEW

Most wheat-producing areas in Montana require a rather high level of winterhardiness in the cultivars grown. Late reproductive initiation is associated with winterhardiness (Chaudhry and Taylor, 1984); and relatively late anthesis has been shown, in Part I, to result from this adaptative characteristic. Thus winterhardy wheats generally tend to begin grain-filling later in the season than do nonwinterhardy wheats. The standard criterion for "earliness" of wheat cultivars is the days to heading. While this measure is rapid, some cultivars may be misclassified if the time to reach physiological maturity is ignored.

Grain growth and development, from fertilization to maturity, falls into several phases. Initially, free endosperm nuclei are formed in a temperature-dependent process (Hoshikawa, 1961). After cell walls have formed and starch deposition begins, a period of linear growth ensues for several weeks (Evans et al., 1975; Pinthus and Sar-Shalom, 1978; Scott et al., 1957; Sofield et al., 1974), followed by an asymptotic approach to the mature grain weight (Gebeyehou et al., 1982a; Hanft and Wych, 1982; Sofield et al., 1974). The termination of dry weight increase is succeeded by a rapid water loss (Scott et al., 1957).

The influence of temperature on grain-filling is well established. An increase in temperature is associated with an increase in the rate and a decrease in the duration of dry matter accumulation (Campbell and Davidson, 1979; Ford et al., 1976; Johnson and Kanemasu, 1983; Marcellos

and Single, 1972; Spiertz, 1974; Wiegand and Cuellar, 1981). In addition, temperature has been shown to be more important than photoperiod or moisture stress in influencing grain growth and maturation (Campbell and Davidson, 1979; Marcellos and Single, 1972; Thorne, 1974). Thorne (1974) suggested that temperature acts directly on the growth of grains via their capacity to accumulate carbohydrates.

Total grain dry weight is the result of the rate at which the grain accumulates dry matter and the duration of this process. Marcellos and Single (1972) found that the differences in the duration of grain-filling among eight spring wheat cultivars were not statistically significant, but acknowledged that additional studies would be required to establish the generality of this finding. Similar grain filling durations were found, too, by Housley et al. (1982) among nine soft red winter wheats.

Yet, it has also been shown that wheat cultivars may differ for duration of grain-filling. Hanft and Wych (1982) reported that the mean number of days from anthesis to maximum kernel weight for eight hard red spring wheats depended on planting date and genotype. Gebeyehou et al. (1982a, 1982b) observed differences among eleven durum wheat cultivars for the length of the grain-filling period.

Contrary results have been reported for genotype influence on the rate of grain-filling as well. Sofield et al. (1974) and Meredith and Jenkins (1976) found the grain growth rates to be similar among the wheats they studied. Meredith and Jenkins limit this conclusion to the main growth period; thus possibilities for differences in the early and latter part of the grain-filling period were not ruled out.

Pinthus and Sar-Shalom (1978) found differences in rate of grain dry matter accumulation among five spring wheat cultivars. The wheats studied by Gebeyehou et al. (1982a) also exhibited differences for filling rate, as did those observed by Asana and Williams (1965). Although Housley et al. (1982) found no significant differences for duration of the grain-filling period, the genotypes did differ for rate of dry matter accumulation.

There appears to be no published literature regarding the relationship of winterhardness level or dwarf bunt reaction with these two grain-filling characteristics.

## MATERIALS AND METHODS

The grain-filling period is considered to be the time between anthesis and physiological maturity (PM), the point at which maximum grain dry weight is achieved.

Cultivars and environments were the same as those for Part 1. Statistical analyses of grain-filling durations and grain growth rates were performed as outlined in Part 1.

### Data Collection

Heads were tagged when anthers first emerged from the middle section of the head. Thirty-six to forty-five heads of each cultivar were tagged daily for four to six days. The number of heads tagged daily and number of tagging days varied among both cultivar and environment depending on the speed at which the anthesis period progressed.

Heads tagged at anthesis were sampled first at the early or soft dough stage, next, at the mid-dough stage, and thereafter, about every four days.

Sampling consisted of harvesting heads at the appropriate stage, six heads per replication, and removing two basal kernels from four central spikelets. The forty-eight kernels thus obtained were combined, weighed, oven dried to a constant weight at 60 degrees C, and reweighed. In order to prevent excessive moisture loss, the stems were cut at least one foot below the head and taken indoors for immediate processing.

### Experimental Design

Three sets of four 3-meter rows were planted for each cultivar the first year. The sets were laid out in a randomized complete block design. In the second year, the number of sets was increased to four with six rows in each set. Replications consisted of the heads within a cultivar which were tagged on a specific day. The number of replications for each cultivar varied depending on the number of days tagging was possible.

### Physiological Maturity Determination

The data from each cultivar within each environment were analyzed separately for determination of physiological maturity. The sampling at which physiological maturity was considered to have been reached was determined by use of a least significant difference procedure with a lack of dry weight increase significant at  $p < .05$  defining physiological maturity (Afuakwa and Crookston, 1984; Lee et al., 1979).

### Heat Unit and Growth Rate Calculation

Daily heat units were computed as in Part I. Heat unit summations for each replication were made from anthesis (the date on which that replication was tagged) to the stage at which physiological maturity for that cultivar/environment had been determined to have been reached. This summation was considered to be the grain-filling duration.

Growth rates were defined as milligrams grain dry weight at physiological maturity per heat unit accumulated during grain-filling.

## RESULTS AND DISCUSSION

Grain-filling Duration

The combined analysis over all four environments showed no significant differences among the cultivars for duration of grain-filling (Table 13). However, individual analyses of each environment indicate there were highly significant differences (Table 27, Appendix). Cultivar means for duration averaged over all four environments are given in Table 14.

Table 13. Mean squares for grain-filling duration and grain growth rate of nine cultivars and four environments.

Source	df	Mean Squares	
		Duration	Growth rate
Block/Env.	19	5,173	.40500
Environments	3	270,500 **	.88640 ns
Cultivars	8	19,480 ns	1.80500 **
Env. x Cultivar	24	12,570 **	.33630 **
Error	122	1,535	.05098

\*\* Significant at the .01 level of probability.

ns Not significant at the .05 level of probability.

Cultivar rankings for grain-filling duration were different between all locations (Table 29, Appendix). Redwin was the only cultivar that was fairly consistent in its ranking from environment to environment (relatively long durations). There are large shifts in ranking among the other cultivars with no discernable pattern, indicating complex environment X cultivar interactions.

Table 14. Cultivar means for grain-filling duration and grain growth rate averaged over four environments.

Cultivar	Duration (HU's)	Cultivar	Growth rate (mgs/HILL x HU)
Redwin	702	TAM 105	3.076
Weston	685	Weston	2.851
Nugaines	670	Winalta	2.581
Centurk	654	Centurk	2.551
Norwin	651	Norwin	2.343
Winalta	634	Crest	2.301
Crest	632	Norstar	2.287
Norstar	617	Nugaines	2.269
TAM 105	608	Redwin	2.265
5% LSD = 73		5% LSD = .379	

Rankings of the winterhardiness group means and the dwarf bunt reaction group means vary among environments as well (Table 30, Appendix). Thus the highly significant interactions are also important in interpreting the group contrasts.

In the second year (Environments 3 and 4), anthesis began later, with the days during and immediately following having quite high temperatures. Droughty conditions, along with high temperatures, hastened grain-filling. In Environment 3, where accumulated heat units are comparatively few, grains were often shriveled and smaller in size. Physiological maturity may not have been reached by some cultivars in this environment as growth was simply halted by lack of water.

Winterhardiness and grain-filling duration. The contrast of group means averaged over all four environments reveals a comparatively longer duration for mid-winterhardy wheats and equal durations for the other

two winterhardiness groups (Table 15). The mid-winterhardy group had a longer duration than the other two groups in all three environments that had significant differences for group means (Table 30, Appendix).

Table 15. Group means for grain-filling duration and grain growth rate averaged over four environments.

Grain-filling Duration (HU's)		
Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(2) 680.3 a	(R) 662.0 a	(R) 662.0 a
(1) 636.4 b	(S) 644.4 a	(3) 634.2 a
(3) 634.2 b		
Grain Growth Rate (mgs/48 SEEDS x HU)		
Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(2) 2.556 a	(S) 2.517 a	(R) 2.474 a
(1) 2.549 a	(R) 2.474 a	(3) 2.404 a
(3) 2.404 a		

Means followed by different letters are significantly different at the .05 level of probability by LSD.

Means followed by the same letter are not significantly different at the .05 level.

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes for dwarf bunt resistance; (S)=contain no Bt genes.

Cultivars were grouped according to when they reached anthesis to determine if early anthesis is related to longer grain-filling durations. Table 16 gives the mean anthesis date, number of heat units accumulated by anthesis, and the respective group for each cultivar. The result of the contrast between the early and late groups for

grain-filling duration is not significant (Table 29, Appendix). Long grain-filling durations do not appear to be related to time of anthesis.

Table 16. Anthesis date, accumulated heat units at anthesis, and anthesis group of nine cultivars averaged over four environments.

Cultivar	Anthesis date	Accumulated heat units	Anthesis group
TAM 105	June 26	1525	early
Crest	29	1558	early
Weston	29	1563	early
Centurk	30	1576	early
Winalta	July 03	1635	late
Redwin	04	1653	late
Norwin	04	1653	late
Nugaines	05	1661	late
Norstar	08	1708	late

While there were significant differences between the two anthesis groups within individual environments, the same group did not always have the longest mean duration. It is apparent that some characteristic other than winterhardiness or anthesis date is involved in determining the length of grain-filling.

Dwarf bunt reaction and grain-filling duration. The results of the contrast between the mean durations of resistant and susceptible cultivars are given in Table 15 and Table 30 of the appendix. The contrasts of means from individual environments give inconsistent results, with the resistant group having longer durations in Environments 1 and 4 and a shorter and equal duration in Environments 2 and 3, respectively. No environmental factors unique to Environments 1 and 4

have been discovered. The two sites were separated by about 10 Km and were planted at different dates. The contrast involving all four environments reveals no difference between the two group means, indicating no relationship between dwarf bunt reaction and grain-filling duration.

Winterhardiness versus dwarf bunt reaction in relation to grain-filling duration. In the first year (Environments 1 and 2), the dwarf bunt resistant group had longer grain-filling durations than did the most winterhardy group (Table 30, Appendix). In the second year, there was no difference between the two groups. Crest, in particular, had comparatively short durations in the second year when compared to the other cultivars. This cultivar appears to be largely responsible for the lack of difference between the two groups in Environments 3 and 4. The comparison of group means from all environments indicates no difference between the two groups for grain-filling duration (Table 15).

#### Grain Growth Rate

The stress conditions in the second year did not significantly alter the mean growth rate. Significant Spearman rank correlations within years indicate that the major source of the interaction is the difference between the years. Cultivar means are given in Table 13 and Table 31 of the appendix.

The analyses of variance revealed differences among cultivars for rate of grain-filling (Table 13 and Table 27, Appendix).

Winterhardiness and grain growth rate. The contrasts between the winterhardiness groups in the individual environments, when significant, show that the least winterhardy group has a higher mean growth rate than

the most winterhardy group (Table 31, Appendix). The group means averaged over all environments are given in Table 15 and indicate that the most winterhardy group has the lowest mean growth rate, although it is not significantly lower than the other means.

It is probable that level of winterhardiness is related to grain growth rate for the cultivars studied. Since the most winterhardy wheats generally reach anthesis later than do the less hardy wheats (Part 1), their grains are growing during a period in which they are more likely to be stressed by low moisture. Conversely, less hardy cultivars are often able to complete grain development before this stress arises. (Nugaines is an exception, as it is not winterhardy but reaches anthesis relatively late.) This is borne out by the significant negative relationship between grain growth rate and heat units accumulated prior to anthesis (Figure 9). The contrast between anthesis groups is shown in Table 29 of the appendix. The "early" anthesis group had a significantly higher grain growth rate than did the "late" group.

Dwarf bunt reaction and grain growth rate. The difference in environment between the two years had a pronounced effect on the contrasts of the two reaction groups (Tables 31 and 32, Appendix). In the first year (Environments 1 and 2), the resistant group means exceed those of the susceptible group; but the susceptible group means are greater in the second year. The group means averaged over the four environments are not different from one another (Table 15).

The differences within environments are again most likely due to the time at which the cultivars reach anthesis (Figure 9). Because the resistant cultivars are generally earlier (Part 1), they are not as

affected by water stress. In the second year, however, Nugaines was greatly influenced by the stress encountered. Nugaines is atypical of the resistant wheats studied in that it reached anthesis later. Although Winridge was studied the second year only, it appears that it, too, was adversely affected by moisture stress (Table 32, Appendix).

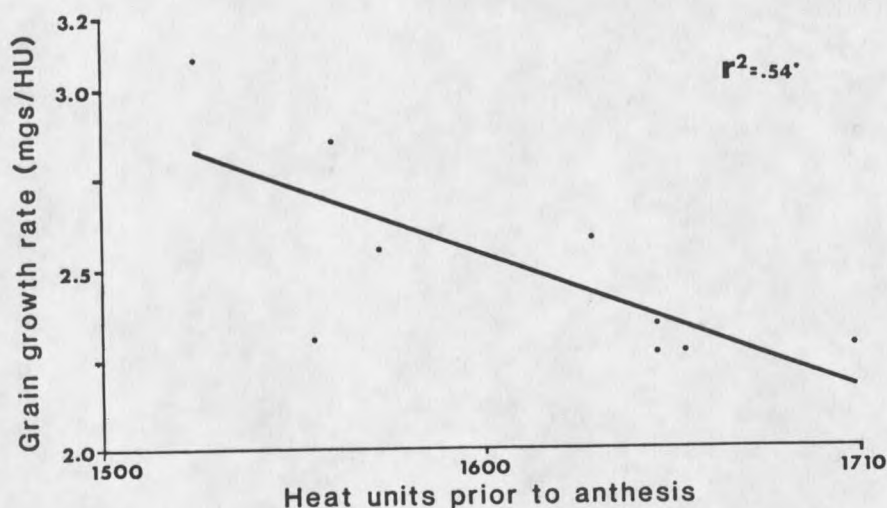


Figure 9. Regression of the grain growth rate of nine cultivars on heat units accumulated prior to anthesis (mean of four environments).

\* Significant at the .05 level.

Winterhardiness versus dwarf bunt reaction in relation to grain growth rate. While the mean growth rate of the resistant group was greater than that of the most winterhardy group in the first year's environments, the ranking between the two groups was the opposite in Environment 3. It appears that in environments with earlier anthesis and adequate moisture, resistant cultivars have higher growth rates. Yet, in environments where severe stress is present, the differences are minimized, most likely due to its effect on later resistant cultivars such as Nugaines and Winridge.

## SUMMARY

Differences in duration of grain-filling were found within environments, but the environment by cultivar interactions masked those differences when environments were combined. The mid-winterhardy group had a longer grain-filling duration than the least winterhardy and most winterhardy groups. Dwarf bunt reaction was not related to duration.

Grain-filling duration was not related to the time at which it begins (anthesis). When the mean duration of the four earliest cultivars was compared to that of the five later cultivars, the difference was not significant. The duration of grain-filling may be determined by grain-filling rate. Two of the wheats with relatively long durations, Redwin and Nugaines, have the lowest mean grain growth rates. When adequate soil moisture is present, the grains of these cultivars may continue developing longer, thus reaching their maximum attainable size. Duration may also be associated with other traits not studied here such as water-use efficiency.

Differences in grain growth rate were apparent within all environments and across environments. There was a trend for the most hardy group to have a lower growth rate than the less hardy groups. This is because the hardy wheats generally reach anthesis later and produce their grains during a more stressful period. Grain growth rate was associated with the time anthesis occurs, with the early group having a greater mean growth rate. Dwarf bunt reaction was not related to grain

growth rate when all environments were considered, and the differences between reaction groups in the individual environments can be attributed to the timing of anthesis.

**OVERALL SUMMARY**

The less winterhardy cultivars studied tend to have more fall growth than the more winterhardy cultivars. High fall growth rates are associated with dwarf bunt resistance but do not appear to be a requirement for resistance. High growth rates through early spring were associated with dwarf bunt resistance but not with level of winterhardiness. Growth rates prior to anthesis are related to neither characteristic in the cultivars studied. It appears that the vegetative growth rates of winterhardy wheats are not incompatible with dwarf bunt resistance.

The heat unit requirement for reproductive initiation was associated with both winterhardiness and dwarf bunt reaction. The dwarf bunt resistant cultivars reached this stage earlier in the spring than did the most winterhardy cultivars. This may allow them to escape infection but makes them more vulnerable to late winter and early spring freezing stress. For this reason, it is unlikely that a highly winterhardy wheat with dwarf bunt resistance could be developed.

Although the heat unit requirement for anthesis was greater for the most winterhardy cultivars than for less winterhardy cultivars, the difference was due to their greater heat unit requirement for reproductive initiation. Because heat units accumulated from reproductive initiation to anthesis was not related to winterhardiness, it may be possible to select for both late reproductive initiation and early anthesis.

It is desirable that a winterhardy wheat be developed which begins the grain-filling stage relatively early in the season. While grain-filling duration was not found to be related to either winterhardiness

or the time at which anthesis begins, grain growth rate was. The group of cultivars which reach anthesis earliest had a higher mean grain growth rate than did the group which flowers later. Late cultivars must produce their grains during a period of greater water stress and may not grow to their full potential.

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**APPENDIX**

Table 17. Cultivar means for fall growth rate in Environment 2.

Cultivar	Growth rate (mgs/HILL x HU)
Winalta	.407
Weston	.403
Centurk	.393
TAM 105	.307
Nugaines	.307
Redwin	.268
Norwin	.255
Crest	.164
Norstar	.152

5% LSD = .130

Table 18. Group means for fall growth rates averaged over two environments with Crest excluded (mgs/HILL x HU).

Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(2) .877 a	(R) .902 a	(R) .902 a
(1) .855 ab	(S) .755 a	(3) .664 b
(3) .664 b		

Means followed by different letters are different at the .05 level of probability by LSD.

Means followed by the same letter are not different at the .05 level of probability.

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes; (S)=contain no Bt genes.

Table 19. Cultivar means for fall growth rate in Environment 6 (including Winridge).

Cultivar	Growth rate (mgs/HILL x HU)
Weston	.757
Redwin	.751
Winalta	.714
TAM 105	.683
Crest	.623
Winridge	.611
Nugaines	.607
Norwin	.521
Centurk	.495
Norstar	.470

5% LSD = .271

Table 20. Group means for growth rate through early spring averaged over three environments (mgs/HILL x HU).

Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(1) .151 a	(R) .160 a	(R) .160 a
(3) .149 a	(S) .141 a	(3) .149 a
(2) .146 a		

Means followed by the same letter are not different at the .05 level of probability by LSD.

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes; (S)=contain no Bt genes.

Table 21. Cultivar means for heat units accumulated prior to reproductive initiation averaged over two environments.

Cultivar	Heat Units
Norstar	988
Norwin	988
Winalta	988
Redwin	974
Winridge	929
TAM 105	929
Centurk	903
Nugaines	903
Weston	903
Crest	826

5% LSD = 5.3

Table 22. Mean squares and cultivar means for growth rate through reproductive initiation.

Source	df	Mean square
Blocks/Env.	18	2.36
Environments	3	22.00 **
Cultivars	8	15.43 **
Env. x Cultivar	24	2.93 **
Error	144	.87

Cultivar	Growth rate (mgs/HILL x HU)
Winalta	4.850
Norwin	4.663
Centurk	4.201
Redwin	4.132
Norstar	3.764
TAM 105	3.749
Weston	3.437
Nugaines	3.289
Crest	2.005

5% LSD = 1.146

\*\* Significant at the .01 level of probability.

Table 23. Group means for growth rate through reproductive initiation averaged over four environments (mgs/HILL x HU).

Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(3) .443 a	(S) .473 a	(3) .443 a
(2) .392 b	(R) .291 b	(R) .291 b
(1) .301 c		

Means followed by different letters are significantly different at the .01 level of probability by LSD.

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes; (S)=contain no Bt genes.

Table 24. Mean squares for growth rates prior to anthesis of nine cultivars and four environments.

Source	df	Mean Squares	
		From planting	From reproductive initiation
Blocks/Env.	20	1.24	5.360
Environments	3	32.94 **	184.500 **
Cultivars	8	6.71 **	34.710 **
Env. x Cultivar	24	1.15 ns	3.860 **
Error	160	1.94	1.571

\*\* Significant at the .01 level of probability.

ns Not significant at the .05 level of probability.

Table 25. Group means for growth rate prior to anthesis averaged over four environments (mgs/HILL x HU).

From Planting to Anthesis		
Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(2) 6.799 a **	(S) 6.493 a ns	(3) 6.436 a
(3) 6.436 ab	(R) 6.394 a	(R) 6.394 a
(1) 6.162 b		

From Reproductive Initiation to Anthesis		
Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(2) 13.68 a **	(R) 13.32 a **	(3) 13.04 a *
(3) 13.04 a	(S) 13.23 b	(R) 12.32 b
(1) 12.06 b		

\*, \*\* Means followed by different letters are significantly different at the .05 and .01 levels of probability, respectively.

ns Means followed by the same letter are not significantly different at the .05 level of probability.

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes; (S)=contain no Bt genes.

Table 26. Group means for plant height (centimeters).

Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
(1) 96	(R) 104	(3) 126
(2) 110	(S) 114	(R) 104
(3) 126		

(1)=least winterhardy; (3)=most winterhardy.

(R)=contain Bt genes; (S)=contain no Bt genes.

Table 27. Mean squares for grain-filling duration and grain growth rate in individual environments.

Source	df	Mean Squares	
		Duration	Growth rate (x 10)
<u>Environment 1</u>			
Block	5	5,376	.5324
Cultivar	8	10,900 **	3.5710 **
Error	29	830.7	.1503
<u>Environment 2</u>			
Block	4	7,644	.7309
Cultivar	8	7,719 **	3.7510 **
Error	24	77.92	.0893
<u>Environment 3</u>			
Block	5	4,738	7.8880
Cultivar	9	6,495 **	12.2300 **
Error	24	1,367	.7397
<u>Environment 4</u>			
Block	5	3,667	6.6360
Cultivar	9	27,790 **	11.3300 **
Error	24	2,894	.8005

\*\* Significant at the .01 level of probability.

Table 28. Cultivar means for grain-filling duration in individual environments.

Cultivar duration (HU's)		Cultivar duration (HU's)	
Environment 1		Environment 2	
Crest	775	Redwin	762
Weston	772	Centurk	760
Nugaines	764	TAM 105	755
Redwin	761	Crest	721
Winalta	738	Weston	695
Centurk	735	Nugaines	695
Norwin	734	Winalta	670
TAM 105	654	Norwin	659
Norstar	651	Norstar	657
5% LSD = 34		5% LSD = 64	

Cultivar duration (HU's)		Cultivar duration (HU's)	
Environment 3		Environment 4	
Nugaines	620	Weston	739
Redwin	618	Redwin	692
Norwin	575	Nugaines	640
Winridge	564	Norstar	625
TAM 105	561	Norwin	624
Norstar	561	Winridge	611
Weston	551	Winalta	601
Winalta	537	Centurk	600
Centurk	521	Crest	557
Crest	512	TAM 105	485
5% LSD = 43		5% LSD = 63	

Table 29. Group means for grain-filling duration and rate averaged over four environments. (Groups are based on order of anthesis.)

Anthesis	Duration (HU's)	Growth rate (mgs/48 SEEDS x HU)
Early	644.6 a	.270 a
Late	654.9 a	.235 b

Means followed by the same letter are not significantly different at the .05 level by LSD.

Means followed by different letters are significantly different at .05 level of probability.

Table 30. Group means for grain-filling duration in individual environments (HU's).

Envir.	Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
1	(2) 756.2 a *	(R) 770.3 a **	(R) 770.3 a **
	(1) 730.9 b	(S) 709.4 b	(3) 707.3 b
	(3) 707.3 c		
2	(2) 739.0 a **	(S) 712.3 a *	(R) 703.7 a **
	(1) 723.8 b	(R) 703.7 b	(3) 661.7 b
	(3) 661.7 c		
3	(1) 564.3 a ns	(S) 564.5 a	(R) 561.5 a
	(2) 563.4 a	(R) 561.5 a	(3) 557.2 a
	(3) 557.2 a		
4	(2) 660.2 a **	(R) 636.5 a *	(R) 636.5 a
	(3) 616.5 b	(S) 603.0 b	(3) 616.5 a
	(1) 560.4 c		

\*, \*\* Means followed by different letters are significantly different at the .05 and .01 levels of probability, respectively.

ns Means followed by the same letter are not significantly different at the .05 level.

Table 31. Group means for grain growth rate (mgs/48 SEEDS x HU).

Envir.	Winterhardiness	Dwarf bunt reaction	High winterhardiness vs. dwarf bunt resistance
1	(1) .266 a *	(R) .268 a	(R) .268 a **
	(2) .265 a	(S) .261 a	(3) .253 b
	(3) .253 b		
2	(1) .270 a	(R) .288 a **	(R) .289 a **
	(2) .268 a	(S) .257 b	(3) .265 a
	(3) .265 a		
3	(1) .241 a	(S) .248 a **	(3) .229 a *
	(3) .229 ab	(R) .206 b	(R) .206 b
	(2) .222 b		
4	(1) .254 a **	(S) .251 a *	(3) .221 a
	(2) .236 ab	(R) .218 b	(R) .218 a
	(3) .221 b		

\*, \*\* Means followed by different letters are significantly different at the .05 and .01 levels of probability, respectively.

Table 32. Cultivar means for grain growth rate in individual environments (mgs/48 SEEDS x HU).

<u>Cultivar</u>	<u>Growth Rate</u>	<u>Cultivar</u>	<u>Growth Rate</u>
<u>Environment 1</u>		<u>Environment 2</u>	
Weston	.308	Weston	.328
TAM 105	.302	Nugaines	.300
Nugaines	.264	Winalta	.274
Winalta	.254	TAM 105	.271
Norstar	.254	Norwin	.269
Norwin	.251	Norstar	.253
Redwin	.249	Centurk	.240
Centurk	.238	Crest	.239
Crest	.232	Redwin	.237
5% LSD = .014		5% LSD = .012	
<u>Cultivar</u>	<u>Growth Rate</u>	<u>Cultivar</u>	<u>Growth Rate</u>
<u>Environment 3</u>		<u>Environment 4</u>	
TAM 105	.315	TAM 105	.336
Centurk	.270	Centurk	.273
Winalta	.263	Weston	.264
Weston	.259	Winalta	.245
Crest	.229	Crest	.224
Norstar	.213	Redwin	.223
Norwin	.212	Norstar	.212
Redwin	.201	Norwin	.208
Nugaines	.179	Nugaines	.201
Winridge	.159	Winridge	.183
5% LSD = .032		5% LSD = .033	

