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

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 Tiiletia 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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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.I. 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 that 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 aviralent 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 winterhardiness 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:

$$HU = \frac{Tmax + Tmin}{2} - Tb$$

and where Tmax and Tmin are the daily maximum and minimum air temperatures (Bauer et al., 1984) and Tb, the base temperature, is 0 degrees C (Baker and Gallagher, 1983; Davidson and Campbell, 1983). When Tmin or Tmax 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 winterhardiness 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 winterhardiness 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

Winterhardiness groups+			Dwarf bunt reaction groups++	
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).

** Winterhardiness: 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.

Winterhardiness 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 winterhardiness rating was also not significant. This suggests that no meaningful relationship exists between winterhardiness 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 winterhardiness 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 winterhardiness.

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.

<u>Dwarf bunt reaction and fall growth rates</u>. 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).

<u>Winterhardiness versus dwarf bunt reaction in relation to fall growth rates</u>. 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

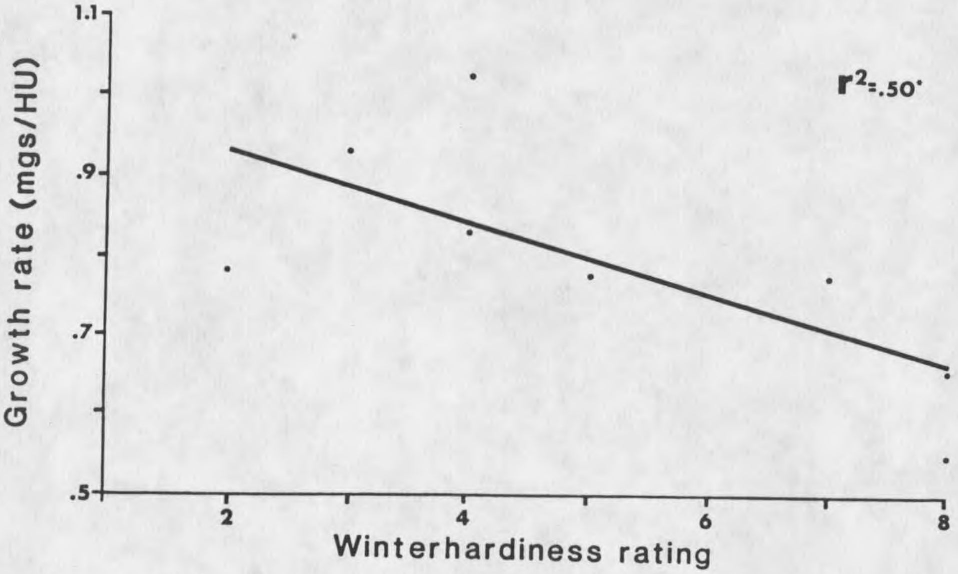

Figure 1. Regression of fall growth rate on winterhardiness rating with Crest excluded.

* Significant at the .06 level of probability.

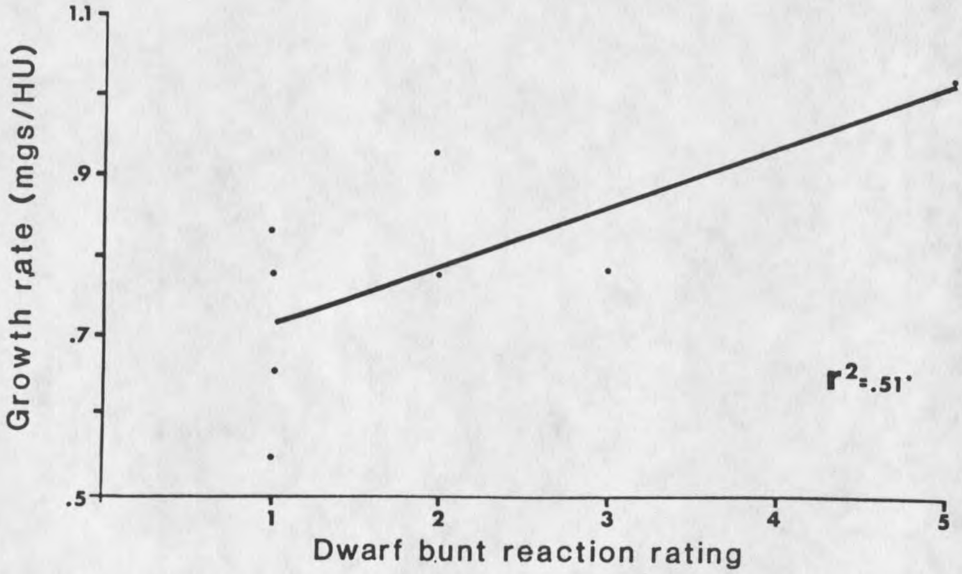

Figure 2. Regression of fall growth rate on dwarf bunt reaction rating with Crest excluded.

* 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

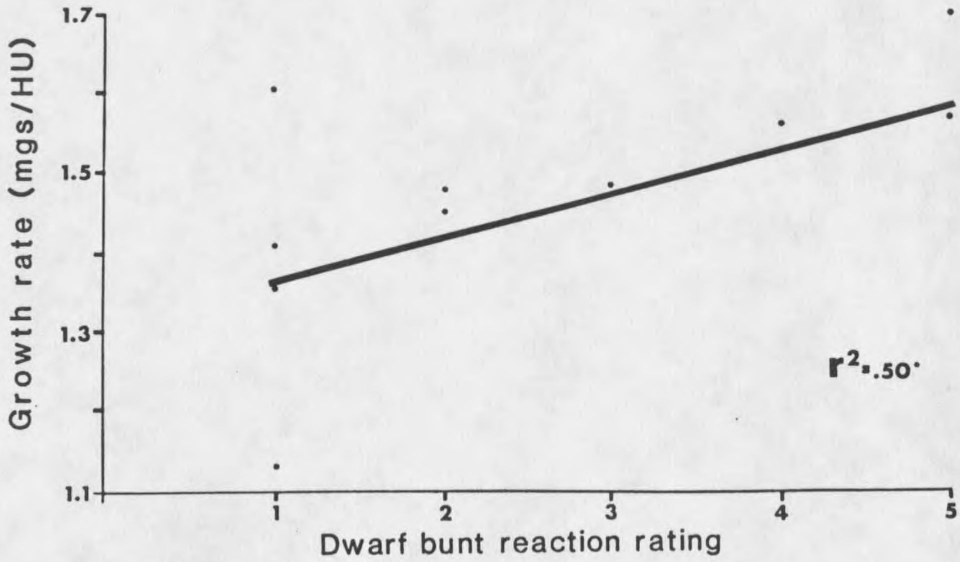

Figure 3. Regression of growth rate through early spring on dwarf bunt reaction rating.

* 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.

		Heat Units	
Environment	Year	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 comparatibely 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

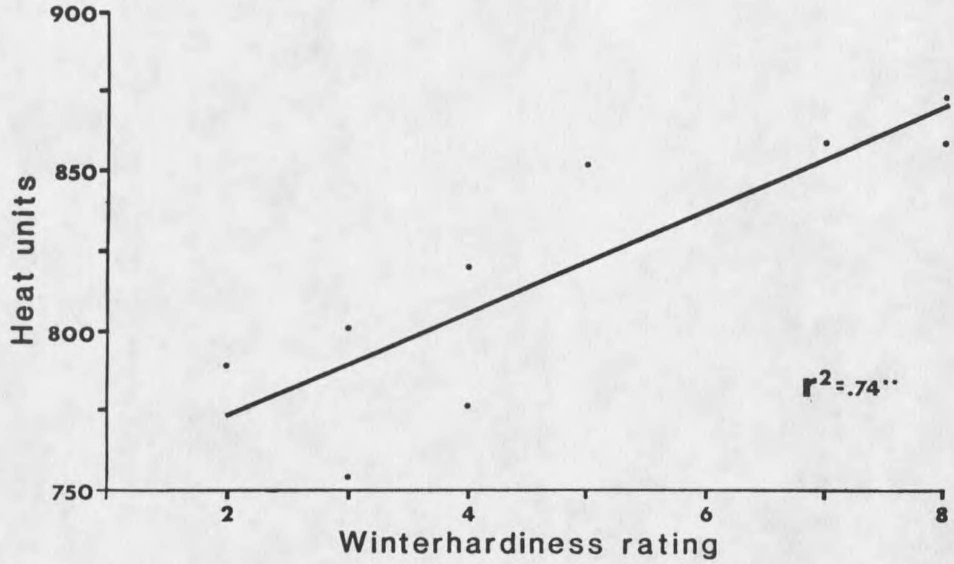

Figure 4. Regression of mean heat units accumulated between planting and reproductive initiation on the winterhardiness ratings of nine cultivars (four environments).

** Significant at the .01 level.

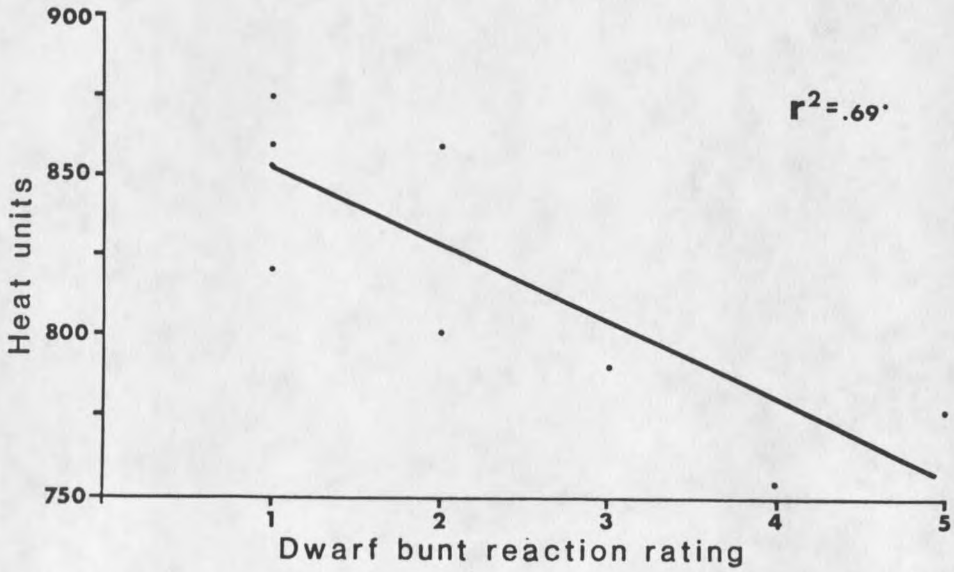

Figure 5. Regression of mean heat units accumulated between planting and reproductive initiation on the dwarf bunt reaction ratings of nine cultivars (four environments).

* 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