



The relationship of morphological factors to field spring survival in winter wheat
by Muhammad Ashraf

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY in Crop and Soil Science

Montana State University

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Abstract:

The developmental morphology of five winter wheat genotypes was studied in controlled environments and field conditions. The objective was to determine the relationship of external leaf development and the apical meristem. It was found that: (a) winter wheat was vegetative from germination to appearance of the fifth leaf, (b) the transitional stage was short-lived, occurring during the expansion of the fifth leaf, (c) the reproductive stage began with the appearance of the sixth leaf, (d) genotypes developmental growth was similar in the vegetative and transitional stages and varied in the reproductive stage, (e) all field-grown genotypes entered the winter at the same stage of growth, (f) visual observation was a good measure to determine the plant developmental stages, (g) plants similar in development stage to field-grown material could be produced in the controlled environment chamber.

The relationships of various morphological factors of six diverse winter wheat genotypes, planted at five depths, to the mature plant height and the field spring survival was studied in controlled environments with and without light. It was concluded that: (a) the genotypes differed in coleoptile length, emergence rate index, seedling height, crown node depth, secondary root length and number, number of tillers and foliar dry weight, (b) Froid, Yogo and Crest had long coleoptiles, high E.R.I.s and tall seedlings, but MT 6928, Cheyenne and Itana had short coleoptiles, low E.R.I.s and short seedlings, (c) Froid and Yogo developed the shallowest crown nodes followed by Cheyenne, MT 6928, Itana and Crest in light, in dark Cheyenne and Itana switched their positions, (d) in the dark, the crowns tended to form farther away from the seed, (e) in the lighted environments, Froid and Yogo were generally in the top rank regarding secondary root length, number of secondary roots and tillers and seedling dry weight, (f) the ranking of the genotypes for crown node depth and secondary root length measured under field situation was similar to that obtained for the lighted growth chamber.

The planting depths varied significantly for all the characteristics.

The shallow plantings showed the highest E.R.I., the tallest seedlings, the shallowest crowns, the longest secondary roots, the most secondary roots and tillers and the highest seedling dry weights. The depth X genotype interactions varied significantly for the last five characteristics in the foregoing sentence in the light and for the E.R.I. in the dark.

The results further showed that (a) all the characteristics except E.R.I. and subcrown internode length in dark, significantly correlated with one another, (b) the mature plant height had positive correlation with seedling height and subcrown internode length in dark and with no other factor both in dark and light, (c) the nonsignificant association of the mature plant height with the coleoptile length indicated a possibility of developing short plants with long coleoptiles, (d) the field spring survival had no significant association with the coleoptile length, E.R.I., and the seedling height (in dark) and was positively associated with the secondary root length, and number (in light), (e) the correlation of foliar dry weight and E.R.I. with spring survival was positive and significant when Crest was excluded, (f) in both dark and light, the crown node depth was negatively associated with the field spring survival.

The association of crown node depth, secondary root length and E.R.I. with field spring survival suggested screening for these characteristics in winter wheat breeding programs.

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TO FIELD SPRING SURVIVAL
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MUHAMMAD ASHRAF

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Approved:

K.C. Feltner
Head, Major Department

H. Allan Taylor
Chairman, Examining Committee

Henry L. Parsons
Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

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ABSTRACT

The developmental morphology of five winter wheat genotypes was studied in controlled environments and field conditions. The objective was to determine the relationship of external leaf development and the apical meristem. It was found that: (a) winter wheat was vegetative from germination to appearance of the fifth leaf, (b) the transitional stage was short-lived, occurring during the expansion of the fifth leaf, (c) the reproductive stage began with the appearance of the sixth leaf, (d) genotypes developmental growth was similar in the vegetative and transitional stages and varied in the reproductive stage, (e) all field-grown genotypes entered the winter at the same stage of growth, (f) visual observation was a good measure to determine the plant developmental stages, (g) plants similar in development stage to field-grown material could be produced in the controlled environment chamber.

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INTRODUCTION

Winter killing is an important problem limiting winter wheat production in northern latitudes of the United States. Although much has been published about winterkill and notable progress in breeding winterhardy varieties has been made, the exact causes of injury to plants and the mechanisms for the differential survival of genotypes remain to be determined.

Winter wheat presently is screened for winterhardiness primarily under field conditions. Winterkilling of wheat plants in field environments is unpredictable with complete killing or survival frequently occurring.

Most attempts to develop adequate laboratory methods of testing for winterhardiness, to supplement or replace the field tests, are related to physiological factors which influence cold hardening of the plants. Such research has encountered difficulties in finding a suitable assay for determining the level of cold hardiness. Contradictory views exist in the literature about the importance of the accumulation of various synthates to the cold hardening of the plants.

The success of winter wheat is initially dependent on the establishment of good and vigorous fall stands. Further elaboration of the effect of morphological factors influencing fall stand

establishment seems justified. The need is also felt for information regarding the relationship between the fall stand establishment factors and field spring survival. Such information should contribute to the selection and differentiation of a genotype on the basis of winterhardiness.

In brief, the purpose of these studies was to attempt, under controlled conditions, to identify growth or morphological characteristics related to winterhardiness of winter wheat.

In considering various aspects of winterhardiness and research approaches that might yield information useful to winter wheat researches, it became apparent that little information was available concerning developmental morphology.

The objectives of the first study reported were:

1. To examine the developmental growth stages in diverse winter wheat genotypes to determine the relationship of external leaf development and the apical meristem.

2. To determine if controlled environment chambers produce plants similar in developmental stages to those field-grown.

The objectives of the second study discussed were:

1. To examine coleoptile lengths of winter wheat genotypes in controlled environments and to relate the results with other

morphological characters such as seedling height, subcrown internode length and emergence.

2. To study the association of these characteristics with field spring survival.

The aim of the third study was to determine the relationship of the crown node location with other seedling characteristics and field spring survival of diverse winter wheat genotypes.

REVIEW OF LITERATURE

General

Winterhardiness of winter wheat is considered to be the result of fall stand establishment, tolerance of cold winter temperatures and the ability to resume spring growth at the proper time.

Andrews (1960) reported that cold hardening of winter wheat is influenced by temperature, duration of hardening, light, moisture and stage of development of plants. He indicated that optimum conditions for hardening vary with species and with genotypes within a species.

The cold tolerance of most plants is enhanced by the environmental factors that depress growth such as low temperature, insufficient moisture, short photoperiods in the plants that accumulate starch and low nitrogen levels (Alden and Hermann, 1971).

Voblikova (1963) found that both the intensity and the spectrum of light under which winter wheat is grown influence frost hardiness. High intensities of light induced more hardiness than low intensities in winter wheat at low temperature (Andrews, 1960). Trunova (1965) found that no cold resistance developed regardless of light intensities and photoperiod when the temperature was above 10C. He concluded that at a low hardening temperature and high light intensity high frost resistance of winter wheat plants could

be developed both on short and on continuous days. His results also indicated that photoperiod could influence the development of cold resistance. Frost resistance was achieved on an eight-hour day during one week of hardening. Kneen and Blish (1941) also reported reduced cold hardening at decreased light intensities in winter wheat. The average survival of six winter wheat varieties after low-temperature hardening for 43 days and then freezing for 24 hours at -15°C was 84, 64 and 11 percent, respectively, for "full light", "intermediate light" and "low light".

According to Suneson and Peltier (1938) maximum hardening of winter wheat during November results from a radiation-temperature balance reacting with day-length and drought influence to give maximum accumulation of organic reserve.

Hardiness was found to be associated with low respiratory activity which appears to be related to maintenance of higher sugar reserves (Bula and Smith, 1954; Levitt, 1956; Zech and Pauli, 1960; Barta and Hodges, 1970). Other reports, however, indicate a less significant role for simple sugars in the cold-hardening mechanism. Kolosha (1965) failed to establish a relation between the reducing sugars and frost resistance in winter wheat. Similar results were supported by those of Kaplya (1964). A decrease in sugar content during hardening was reported in winter wheat by Newton (1922).

Mel'nikova (1964) observed that an increase in soluble sugars in the presence of increased protein nitrogen did not improve the cold resistance of winter wheat. He suggested that the ratio of soluble sugars to protein nitrogen should be considered in determining the contribution of sugars to the development of cold hardiness.

Many early workers attempted to relate changes in various forms of nitrogen such as soluble nitrogen, protein nitrogen, amino nitrogen, non-protein nitrogen and total nitrogen to frost hardiness. Because of the crude methods employed in these studies, results were often inconsistent and most investigations were of little value (Levitt, 1956).

Pauli and Mitchell (1960) found that soluble protein nitrogen and soluble non-protein nitrogen were higher, water content was lower, and free amino acids and amides were higher in hardened plants than in unhardened wheat plants on a fresh weight basis. Zech and Pauli (1962) reported an increase in the concentration of water soluble protein during hardening. Vasil'yev, Lebedeva, and Rafikova (1964) observed that an increase in water soluble protein content in winter wheat during hardening was accompanied by a decrease in salt-, alcohol- and alkali-soluble proteins, upon cooling to -10°C in 24 hours. Zech and Pauli (1960) found that water soluble protein nitrogen and total sugars in leaves and crown of winter wheat were

associated with cold resistance. However, Toman and Mitchell (1968) failed to show any relationship between water soluble protein and cold hardness.

Dexter (1934) reported an inverse correlation between hardness and soluble salts in winter wheat. In general, hardness was associated with a high percentage of dry matter and with low concentration of soluble salts. Dexter, Tottingham and Graber (1932) proposed the measurement of electrical conductivity to find the degree of cold hardness. This technique was modified by Stuart (1939) and Wilner (1959). The measurement of resistance was suggested by Filinger and Cardwell (1941) and ninhydrin determination method was proposed by Moore and Stein (1954). Cordukes, Wilner and Rothwell (1966) compared the conductance, resistance and ninhydrin methods of measuring cold injury on the same turfgrass plant and found that these methods had no agreement with one another. They and Siminovich, Therrien, Gfeller and Rheaume (1964) criticized the Dexter method of conductivity measurement and considered it unreliable.

There has been considerable interest in testing for cold resistant varieties in the coleoptile or sprouting seed stage. Grahl (1956) described a method of testing for cold resistance in the coleoptile stage. Seeds were germinated at room temperature until the coleoptiles were 5 mm long, hardened for 3 days at 0C

with 16-hr day length, then frozen at -5.7°C . After thawing for one day at 0°C , these were transplanted to the greenhouse, where cold resistance was assessed by regrowth after 14 days. Dantuma (1958) could not obtain consistent results by using the method described by Grahl. Investigations concerned with winterhardiness have shown that it is difficult to find a suitable assay for determining the level of cold resistance (Hodges, Svec and Barta, 1970).

In winter oat crosses, Finker (1966) found transgressive segregation for increased hardiness. It was expressed both as greater resistance to leaf kill resulting from fall freezes and higher percent of winter survival. Similar results were reported by Suneson and Marshall (1967) in wild oat studies. Wilner (1965) studying progeny of reciprocal crosses between hardy and tender apple varieties observed that cold resistance was more influenced by the maternal than the paternal parent. He suggested that factors for cold resistance may be cytoplasmic in origin.

To determine the winterhardiness in winter wheat, Vasil'yev (1961) used a spring survival scale which he defined as the difference in the number of plants on a test plot from the time of entering winter to the time of leaving winter.

Developmental Morphology

Early studies on the development of wheat plant were of a general descriptive nature, with more emphasis on development of the kernel than of the whole seedling.

Jensen (1918) cited a number of publications dealing with the morpho-developmental history of wheat grain. He described and illustrated the development of the spike and flower and showed that primordia of the spikes are present 21 days after seeding when leaves above ground measure 10 to 15 cm in length.

Percival (1921) reported that in the resting wheat embryo, the terminal primary bud is visible with its axis and two or three rudimentary leaves. Similar views were reported by Bonnett (1966).

Kiesselbach and Sprague (1926) reported that in winter wheat differentiation of the spike was not evident in the fall season and the plant remained essentially dormant during December, January and February due to low temperatures. The importance of temperature and photoperiod in determining time in each growth phase of wheat plants was stressed by McKinney and Sando (1933). Purvis (1934) found that the initiation of the reproductive phase of winter cereals is presumably the result of the plants' response to either low temperature during early growth stages or to photoperiodic variations. The interaction of temperature and daylength during germination determine

both the minimal number of leaves formed before differentiation of flower primordia begins and the rate of growth of meristematic tissue. Purvis suggested that in assigning a plant to its photoperiodic category, the time of formation of flower primordia should be considered rather than the time of emergence of the inflorescence.

A great acceleration in the development of spikes due to long photoperiod was reported by Ahrens and Loomis (1963). On long days at 24C, non-vernalized plants headed in 140 to 170 days compared with 100 days for well-vernalized plants. With 11-hour days, heading dates did not differ. The non-vernalized plants grown with 11-hour days headed in 200 days.

Aitken (1961) found the time to flower initiation in Australian oats depended greatly on the varietal response to photoperiod and temperature. Aitken (1966) also studied the difference between spring and winter flowering characters in wheat, rye, barley and oats in several field environments with mean temperatures ranging from 10-22C and mean photoperiod from 10 1/2-16 hrs. He found that spring cereal varieties all flowered at a low leaf number, showing insensitivity to temperature and photoperiod. However, flower initiation was at a higher leaf number in the winter cereal varieties and within winter types it was at a higher leaf number at a higher temperature than at a lower temperature.

McCall (1934) studied the crown and upper portion of wheat plants and found a definite positional and vascular relationship between nodal vascular plate, leaf, root and axillary bud origin.

Nilson, Johnson and Gardner (1957) reported that the culm of the wheat plant is generally composed of six internodes, five of which extend above the soil surface. Although the varieties of wheat they examined differed widely in plant height, all showed a common internode pattern. Characteristically, the basal internode of the culm was the shortest, and each successively higher internode was longer than the one below it. In tall growing varieties the increment of length of successively higher internodes was greater than in short statured types.

Cooper (1956), working on developmental analysis in the cereals, reported the rate of leaf appearance on any shoot as linear and unaffected by initiation of the spikelet bud on that shoot. The elongation of the shoot apex was reported as exponential, being gradual during vegetative growth but increasing at spikelet initiation.

Bonnett (1936) described, with illustrations, the main stages in the development of the shoot, the spike and the spikelet of wheat. He gave the sequence of initiation of the developmental phases and grouped them into vegetative, transitional, and reproductive stages.

In the vegetative stage, leaf initials are produced and tillers develop actively. The inception of the reproductive stage is indicated by the appearance of double ridges on the apex, the upper member of which develops into the spikelet initial. He reported that by the time the wheat plant has two leaves, the 6th leaf primordium can be seen. Later, Bonnett (1961) studied the oat plant and grouped its life cycle into stages similar to wheat. Recently Bonnett (1966) more thoroughly summarized the information in this area for maize, wheat, barley, rye and oats. The stages of development and their initiation and the shape and growth of apices were generally found to be similar in these crops.

Similar studies by Barnard (1955) on the histogenesis of the inflorescence and flower origin of wheat, indicated that the apical meristem of the spike and spikelet was similar to that of the vegetative axis. The histogenesis of glumes, lemmas, palea, lodicules and carpels was essentially the same as that of a foliage leaf, whereas the stamens arise as cauline structures like the spikelet and flower primordia. The ovule was derived directly from the apex of the flower primordia.

In inbred lines of corn, Leng (1951) found certain patterns of development which were inherited in the F_1 . Within a line, the

number of leaves externally visible gave a fairly good indication of the rate of internal development.

Aitken (1967) studied the leaf primordia formation in winter wheat and found a positive correlation between leaf stage and total nodes. A comparison of wheat and rye at leaf stage seven showed that the flower initiation at that stage could occur in many more nodes in rye than in wheat. In later work on non-destructive methods for estimation of flower initiation in clover and cereals, Aitken (1971) determined the number of immature leaf nodes between the top open leaf of the shoot at the time of flower initiation and the first reproductive node to be genetically controlled. He indicated that five immature vegetative leaf nodes must develop in wheat after flower initiation before heading occurs, whether the plant is early flowering (leaf stage four at flower initiation) or late flowering (leaf stage ten at flower initiation).

Arnold (1969), working with corn, found the number of leaves on the main stalk to be a most useful physical characteristic for evaluating the time required between planting and tassel initiation, between planting and pollen shed and between planting and silking.

Most of the work in this area has been concerned with either histological origin of tissues or external morphology, however,

Taylor and Frey (1972) showed the close relationship between external leaf morphology and apical meristem developmental stage for diverse oat genotypes.

Coleoptile Length

During the past decade attention has been focused on the relationship between coleoptile length, seedling emergence and stand establishment in wheat. The observations that poor seedling emergence can be a major shortcoming of winter wheat establishment led to research concerning coleoptile length and emergence rate.

Livers (1958) and Sunderman (1964) viewed the coleoptile as a structure of considerable importance, directly correlated to winter wheat emergence. According to McCallum and Hehn (1962) plant mortality in winter wheat can result from the failure to emerge above the soil surface. Coleoptiles of slow emerging varieties generally rupture below the soil surface (Craddock and Vogel, 1955).

Chaudhry and Allan (1963) reported that winter wheat selections with long coleoptiles emerged faster and generally resulted in a better stand, whereas those with short coleoptiles emerged more slowly and produced poor stands. Earlier, Allan et al. (1961) and Bohnenblust, Kolp and Richardson (1962) also reported high correlations between coleoptile length and emergence percentage. The

selections with long coleoptiles emerged more readily than selections with short ones. Livers (1958), in field and laboratory studies, ascribed the superior seedling vigour of variety Blackhull over the variety Westar to coleoptile length. He reported that varieties with good emergence had longer coleoptiles.

Kaufmann (1968) concluded that for four winter wheat varieties, seed size had no effect on the coleoptile length or emergence. Contrary to this, Parodi, Patterson and Nyquist (1970) showed a significant influence of seed size upon coleoptile elongation and seedling fresh weight.

Taylor and McCall (1936) reported that temperatures of 24C and 20C increased the length of coleoptile of 'Hard Federation' and 'Turkey' wheats as compared with temperatures of 16C and 12C, respectively.

Emergence percentage and coleoptile length for nine winter wheat varieties, grown under two temperatures and four depths, were determined by Sunderman (1964). He found that high temperatures reduced coleoptile length and decreased the ability of seedlings to emerge properly. Contrary to this, Favereau et al. (1968) reported that coleoptile lengths are increased by elevated temperatures.

Burleigh (1962) showed that 60F was near optimum for maximum coleoptile elongation in winter wheats, whereas a temperature of

80F reduced coleoptile length notably. His growth chamber results showed coleoptile reduction was closely associated with emergence ability. Allan, Vogel and Burleigh (1962) reported a positive correlation between emergence rate index and coleoptile length measured in wheat grown at 50F or 90F. They also reported that the coleoptile lengths of winter wheat selections grown at 90F were from 26 to 19 percent below the selections grown at 60F.

The importance of seeding depth on the coleoptile length of wheat was determined by Percival (1921). He noted that coleoptile length increased with planting depth. Similarly, Bohnenblust, Kolp and Richardson (1962) found that coleoptile length seemed to be an important character in determining percent emergence at a five-inch planting depth. Sunderman (1964), in his experiment on nine winter wheat varieties planted at two-, three-, four- and five-inch depths, reported that percent emergence and coleoptile length were positively correlated. The correlation was highest for varieties sown four inches deep. A significant depth X variety interaction was obtained and as the depth of seeding was increased, coleoptile lengths increased. Kaufmann (1968) obtained significant differences between varieties for coleoptile lengths of wheat and barley at 8C and with oats at 21C. With seeding depths of 2.5, 5.0, and 7.5 cm,

there were significant barley varietal differences for both coleoptile length and emergence. Tests indicated that coleoptile length in barley varied with variety, seeding depth, size of seed and soil type.

Favereau et al. (1968) and Feather, Qualset and Vogt (1968) reported a positive association between coleoptile length and culm height for both semidwarf and non-semidwarf spring wheat.

Chaudhry and Allan (1963) found a significant positive correlation between coleoptile length and seedling height of four winter wheat crosses and a low degree of association of these characteristics with plant height. Later, Chaudhry and Allan (1966) positively correlated coleoptile length and culm length of winter wheat genotypes. A direct and positive relationship occurred between subcrown internode length and coleoptile length. Coleoptile length, emergence rate index, subcrown internode length and culm length were all inter-related, with minor exceptions.

Favereau et al. (1968), in comparing a group of spring wheats of different plant heights, determined that the tall genotypes (122-128 cm) had the longest coleoptiles (61.4-61.5 mm), while the semidwarfs (70-80 cm) developed significantly shorter coleoptiles (46.0-47.1 mm). Feather, Qualset and Vogt (1968) noted that

coleoptiles of short strawed spring wheat varieties were only 50 to 75 percent as long as those of taller varieties. Earlier, Allan, Vogel and Peterson (1962) showed that the coleoptile growth rate of the semidwarf selections was in most cases much lower than that of the standard height varieties.

Kolp et al. (1967), working with six winter wheat genotypes, maintained that as soil compaction increased, coleoptile length of wheats was reduced and total plant emergence and the rate of emergence also decreased. Differences in coleoptiles existed among the varieties grown in compacted and non-compacted soil. The varieties that produced long coleoptile without compaction produced the longest coleoptile under compaction. As soil pressures were increased, coleoptile length and emergence rate were reduced.

The nature of the genetic mechanism controlling coleoptile elongation is not well understood. Most reports (Allan et al., 1961; Allan and Vogel, 1964; Chaudhry and Allan, 1963; Allan, Pritchett and Patterson, 1968) indicated the presence of a complex mechanism, where both major and minor modifying genes are involved.

Emergence

A good rapid seedling emergence is one of the basic requirements for successful stand establishment of cereal crops (Chaudhry and Allan, 1963; Kolp et al., 1967).

The studies of Allan, Vogel and Peterson (1962) showed a positive correlation of emergence rate index with coleoptile length and mature plant height for plants grown at 50 or 90F. Similar results were reported by Chaudhry and Allan (1963). Field observations of 12 winter wheat varieties by Helmerick and Pfeifer (1954) revealed that the varieties differed in ability to grow and establish stands. The variety Yogo produced significantly better fall emergence than Cheyenne. Significant varietal differences in emergence rate were also reported by Allan, Vogel and Peterson (1962).

The rate of emergence of 20 winter wheats in the greenhouse was determined by Bohnenblust, Kolp and Richardson (1962). Percentage emergence from a three-inch planting depth did not differ significantly among varieties. As the planting depth was increased, the differences among varieties became significant. Their studies showed a significant correlation between rate of emergence and percentage of emergence at three-, four- and five-inch planting depths. Burleigh, Allan and Vogel (1965), working with 8 winter wheat varieties of diverse height found the highest emergence rate for all genotypes at the two-inch planting depth, whereas the four-inch depth produced the lowest emergence rate indexes.

The effect of soil compaction on emergence was noticed by Kolp et al. (1967) who found that the total plants emerged and the rate of emergence decreased with an increase in soil compaction.

Crown Node

Martin (1927) reported that crown and meristematic tissue are the most hardy parts of winter wheat plant. Vasil'yev (1961) and Nelson and Olein (1966) described the crown as an important key region for winterhardiness and winter survival.

Salmon (1933), working with winter wheat and rye, noted that crown discoloration after exposure to severe cold was associated with plant survival. According to Young and Feltner (1966), the survival of barley is highly dependent upon the amount of crown tissue damaged. A certain amount of crown development in the fall was considered essential by Stewart and Whitfield (1965) for good winter survival of winter wheat and for normal resumption of plant growth the following spring. Olein, Marchetti and Chomyn (1968) reported that freezing damage to the crown tissue of winter barley was critical because new roots arise from this tissue during the spring season.

Pauli (1962) attributed the reduction in survival and recovery of winter wheat subjected to successive freezing to the decrease

in vascular connections in the crown tissue. Marshall (1965) showed that in fully cold-hardened winter oats the recovery from freezing was more closely associated with the characteristics of the crown than those of the leaves. The crown of a plant maintains living cells throughout the winter and produces new shoots when temperatures rise in the spring (Dobrenz, 1967).

Location of crown node

Taylor and McCall (1936) showed that the location of the crown in relation to the soil surface could influence tillering and crown root development in both spring and winter wheat.

Tavcar (1930) found that winterhardy varieties of wheat, barley and oats have their crowns deeper in the soil. Similar results were reported by Webb and Stephens (1936) for winter wheat. They compared the crown node depth of winter varieties sown on October 28, 1931 in suboptimum moisture conditions in the field, using a grain drill. They observed a considerable variation of depth of crown in the plants of the same variety, such as 38 mm to 90 mm, 25 to 76 and 18 to 78 mm.

Taylor and McCall (1936) compared 'Hard Federation', a spring wheat and 'Turkey', a winter wheat variety, in a greenhouse trial using cork mulch to reduce soil surface evaporation. They observed

that the crown was formed soon after germination of seed and winter hardy varieties had crowns deeper in the soil.

Factors affecting location of the crown node

Kassovitch (1894) and Kuleshov and Marchenko (1963) found that plants grown in insufficient illumination and higher temperature form crowns at shallower depths than those grown in full sunlight and lower temperature. Dickson (1923) and McKinney (1923) found that the depth of crown varied with environmental factors, depths of seeding, amount of light and temperature. Similarly, Taylor and McCall (1936) determined that the depth of the crown in wheat is influenced by variety, environment and depth of seeding. An increase in temperature from 12C to 24C caused the crown to form 83% nearer the soil surface for Turkey winter wheat and 61% closer to the soil surface for Hard Federation spring wheat. Webb and Stephens (1936) reported the formation of the crown in winter wheat nearer the soil surface when the temperature was higher and vice versa. Ferguson and Boatwright (1968) concluded that both light and temperature influence the location of the crown node in winter wheat. As light intensity decreased or temperature increased, the crown node formed farther from the seed or nearer to the soil surface. Node location was strongly affected by variety X temperature X light interaction. Their study revealed that for winterhardy and nonhardy varieties

the depth of crown varied with temperature. At 10C nonhardy varieties had shallower crowns than the hardy varieties, but at 20 and 25C there seemed to be no significant difference. They further showed that crown node location in the winter wheat varieties utilized were influenced by surface straw litter. As the rate of surface straw was increased, the crown formed farther from the seed. They attributed this effect to reduced light caused by surface straw.

Taylor and McCall (1936), Webb and Stephen (1936) and Ferguson and Boatwright (1968) all maintained that deep seeded wheat forms crown nodes deeper than shallow seeded wheat, but not in proportion to the difference in seeding depth. A common opinion among earlier investigators (Robbins (1931) and Locke and Clark (1924)) was that the crown is formed at a rather constant depth below the soil surface irrespective of depth seeded. According to Robbins (1931), the crowns are formed at a depth of one inch below the soil surface, whereas Locke and Clark (1924) contended they develop just below the soil surface.

In selection programs under controlled conditions, Metcalf et al. (1970) viewed the exact temperature and percent moisture of the crowns as important factors in ranking plants for winter hardiness. Studies of barley by Follet and Reichman (1972) revealed top weight and root weight were positively correlated with the crown weight.

Sallans (1961) reported that depth of crown is a heritable character as shown by the lines from a cross having deep crowns and shallow crowns. McKenzie (1971) was of the view that the inheritance of this character is simple and not complex.

Secondary Roots

A reduction of secondary root development in wheat can result in lowering the yields (Webb and Stephens, 1936). The studies of Filinger and Cardwell (1941) indicated that well-rooted plants are injured less by freezing temperature than plants not well-rooted. Janssen (1929) stated that in winter wheat all new roots in the spring develop from the crown of the plant and not from the old roots. Weaver (1926) found that wheat crown nodes develop when tillers appear.

In studying soil water and soil temperature influence on dry-land winter wheat, Black (1970) observed high positive correlations of number of heads, number of tillers and grain yields with number of secondary roots. The number of root primordia was highly correlated ($r = .72$) with the number of tiller buds for all treatments.

Cohen and Tadmor (1969) reported that in all grass species the rate of root elongation increased 2 to 3 fold over a 10-20°C temperature range. Over this range the rate increased faster in the upper soil layer than in the deeper layer.

STUDY I

DEVELOPMENTAL MORPHOLOGY OF THE APICAL MERISTEM

OF WINTER WHEAT GENOTYPES IN CONTROLLED

AND FIELD ENVIRONMENTS

I. Developmental Morphology of the Apical Meristem of Winter Wheat Genotypes in Controlled and Field Environments

This study examined developmental growth stages and determined the relationship of external leaf morphology and the apical meristem utilizing diverse winter wheat genotypes in controlled and field environments.

MATERIALS AND METHODS

Genotypes

Five diverse winter wheat genotypes were used to examine the apical meristem development in relation to external leaf morphological stages: (a) Crest (CI 13880) has early to medium maturity, medium height, poor winterhardiness, is resistant to stripe rust and dwarf bunt and recommended for western Montana; (b) Froid (CI 13872) has late maturity, excellent winterhardiness, is tall, resistant to stem rust and recommended for northeastern Montana; (c) MT 6928 has early to medium maturity, poor winterhardiness and is a semidwarf; (d) Winoka (CI 14000) is late maturing, tall, resistant to stem rust, has good winterhardiness, and is recommended in Montana's major winter wheat growing areas; (e) Nugaines (CI 13968) is a late maturing, semidwarf, soft white winter wheat with poor winterhardiness.

Controlled Environments

To make the data from the growth chamber meaningful, long-time averages of field climatological data were used to establish day length and a diurnal temperature curve for the September to July winter wheat growth period. The maximum and minimum daily temperatures, photoperiod and corresponding field growing season are shown in Table 1. Light intensity in the growth chamber was about 1500 foot candles.

General Methods

The material for the study was grown in five-inch sterilized clay pots containing screened silt loam soil mixed 50 percent with peat. Six seeds of each genotype for the first two sampling stages and three seeds per pot for the remaining stages were planted three inches deep. The pots were placed in the controlled environment chamber immediately after seeding.

There were five genotypes, thirteen stages of plant sampling and three replications in a randomized block design. Specimens preserved in FAA (Sass, 1964) were dissected and the development stage of the main shoot apex was recorded. The same sampling procedure was followed for field grown materials as for those in the growth chambers except that six plants were examined rather than three. The

Table 1. Air temperatures and photoperiods applied during each week of wheat growth in the growth chamber with corresponding period in the field.

Weeks in chamber	Corresponding to field period	Temperature (°F) ^{1/}		Photoperiod (hrs)
		Maximum	Minimum	
First	Sept. 18-Oct. 3	67	44	13
2nd	Oct. 4-Oct. 17	61	31	12
3rd	Oct. 18-Nov. 3	57	31	11
4th	Nov. 4-Nov. 17	47	27	10
5th	Nov. 18-Nov. 30	47	27	10
6th & 7th	Dec-Jan-Feb ^{2/}	36	28	10
8th & 9th	Mar. 4-Apr. 3	40	22	12
10th	Apr. 4-Apr. 17	48	28	13
11th	Apr. 18-May 3	48	28	14
12th	May 4-May 17	61	39	15
13th	May 18-June 3	61	39	15
14th	June 4-June 17	66	45	16
15th	June 18-July 3	66	45	16

^{1/} From long-time averages of local field climatological data.

^{2/} Average at ground surface under snow cover.

dissected or exposed apex was transferred to Farmer's solution for future study or photographing.

Sampling Stages

Samples of growth chamber seedlings were taken at various visual stages of development. The plants were carefully removed, cleaned of soil and immediately killed and preserved in FAA (Sass, 1964).

The sampling stages designated from S00 to S11 were:

- S00 - Coleoptile emergence from the soil.
- S0 - Appearance of first leaf or full coleoptile length.
- S1 - Appearance of tip of second leaf or full expansion of first leaf.
- S2 - Appearance of tip of third leaf.
- S3 - Full expansion of second leaf.
- S4 - Appearance of tip of fourth leaf.
- S5 - Full expansion of third leaf.
- S6 - Appearance of tip of fifth leaf.
- S7 - Full expansion of fourth leaf.
- S8 - Appearance of tip of sixth leaf.
- S9 - Full expansion of fifth leaf.
- S10 - Appearance of seventh leaf.
- S11 - Full expansion of sixth leaf.

Six plants per genotype were taken at the S4, S6, S8 and S10 stages from the field grown materials. After sampling, the materials were killed and preserved in the same manner as those from the growth chamber.

Characteristics Studied

The characteristics studied and the observations made in this experiment were:

1. Leaf appearance and expansion - The appearance of a leaf was marked when a tip of the leaf first showed up from the fold of the previous leaf. Full expansion of the leaf was considered to be when its ligule had emerged from the sheath of the preceding leaf or when the leaf could be visually divided into leaf blade and leaf sheath.
2. Total number of leaves removed at dissection.
3. Leaf primordia - During vegetative stages all ridges or bumps on the shoot apex were taken as leaf primordia. Double primordial ridges, so called "double ring", were recorded as spikelet initials (Purvis, 1934; Bonnett, 1935, 1936, 1966; Aitken, 1961).
4. Tiller primordia - Tiller buds and primordia were counted before and after dissection of the apex.
5. The shape and size of shoot apex and the number and shape of ridges on the apex of various genotypes were noted.

RESULTS AND DISCUSSION

Vegetative Stage

The vegetative stage is the early stage of growth where leaves, tillers and adventitious roots are initiated and develop (Bonnett, 1966).

Emergence of coleoptile and appearance of first leaf

Seedlings were removed and examined eight days after seeding for emergence of the coleoptile stage and nine days after seeding or one day after emergence (Table 2) for appearance of the first leaf stage. For both stages, the apical meristem was very small and round, partly enclosed in the fold of the third leaf. The size and shape of the apex were similar in all five genotypes.

Appearance of second leaf or full expansion of first leaf

This stage coincided with 12 days after seeding or four days after emergence (Table 2). Two leaves were removed for apex examination in all genotypes except Crest where three leaves were taken off. Comparative size and folds of these leaves were similar to that described above. One tiller primordium was also visible in all genotypes except Nugaines which had none.

Table 2. Growth stage and time of plant samplings of five winter wheat genotypes grown in controlled environments.

Growth stage symbol	Growth stage	Days after seeding	Days after emergence
S00	Emergence of coleoptile	8	--
S0	Full coleoptile or appearance of 1st leaf	9	1
S1	Appearance of 2nd leaf or full expansion of 1st leaf	12	4
S2	Appearance of 3rd leaf	31	23
S3	Full expansion of 2nd leaf	32	24
S4	Appearance of 4th leaf	68	60
S5	Full expansion of 3rd leaf	70	62
S6	Appearance of 5th leaf	85	77
S7	Full expansion of 4th leaf	91	83
S8	Appearance of 6th leaf	96	88
S9	Full expansion of 5th leaf	99	91
S10	Appearance of 7th leaf	102	94
S11	Full expansion of 6th leaf	102	94

The shoot apex looked like a small, shiny, hemispherical button (Figure 1). Little variation in size among the genotypes was noted. The shoot apex was larger in Froid and MT 6928 than in Crest, Nugaines and Winoka. Two leaf primordia were visible on the apices of all genotypes.

Appearance of third leaf or full
expansion of second leaf

This stage occurred 31 days after seeding or 23 days after emergence (Table 2). The sixth leaf primordium could be seen on the shoot apex. Two to three tiller primordia were also visible in all genotypes. The apex, surrounded one side by the fifth leaf, was long in MT 6928 and Crest, shorter and broader in Froid, and was smaller in Nugaines and Winoka. Two to three leaf primordia were visible from the unsurrounded side of the apex. Full expansion of second leaf was noticed one day after the appearance of third leaf. No important differences in leaf and tiller number and apex size were observed among the samples (Figure 2).

Appearance of fourth leaf or full
expansion of third leaf

The tip of the fourth leaf appeared 60 days after emergence, whereas the third leaf was fully expanded two days after the appearance of the fourth leaf (Table 2). Three fully expanded and one just

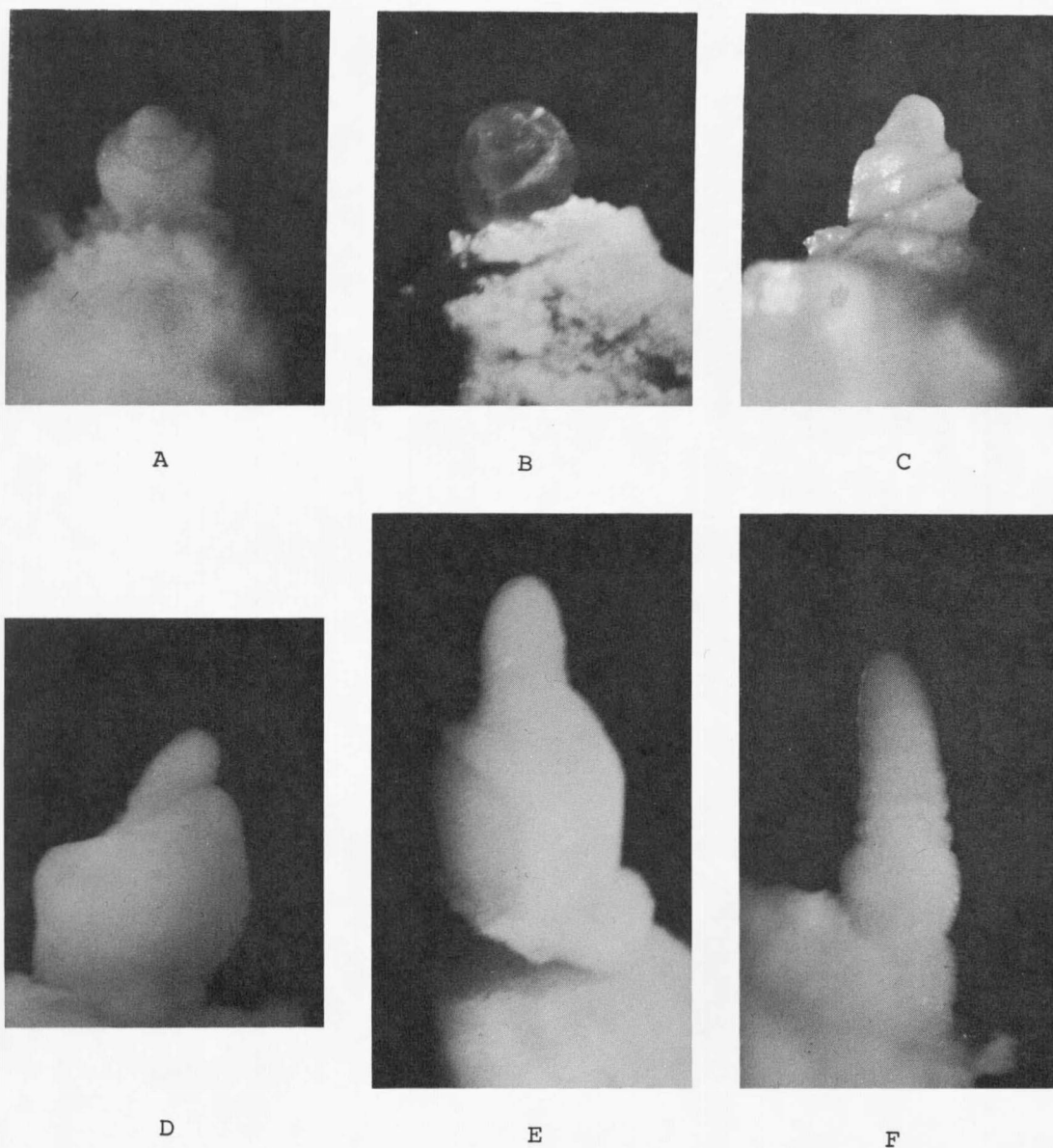
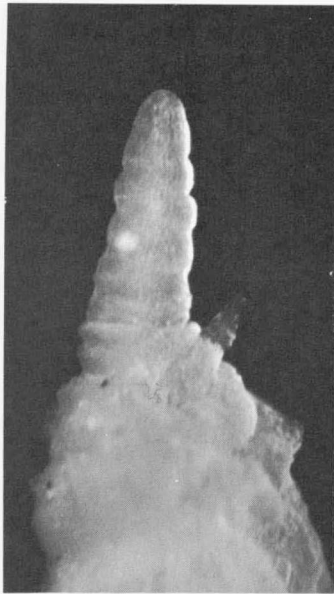
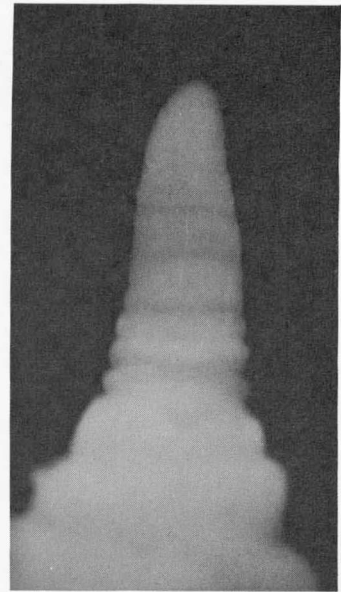


Figure 1. Stages of development of apical meristem in winter wheat (X70). A. Shoot apex and leaf primordia at appearance of third leaf; B. Shoot apex and leaf primordia at appearance of fourth leaf; C. Shoot apex and leaf primordia at full expansion of third leaf; D. Shoot apex beginning to elongate (beginning of transitional stage) at appearance of fifth leaf; E. Elongated shoot apex (transitional stage) appearance of sixth leaf; F. Elongated shoot apex with many primordial ridges (end of transitional stage or just before spikelet initiation) at full expansion of fifth leaf;

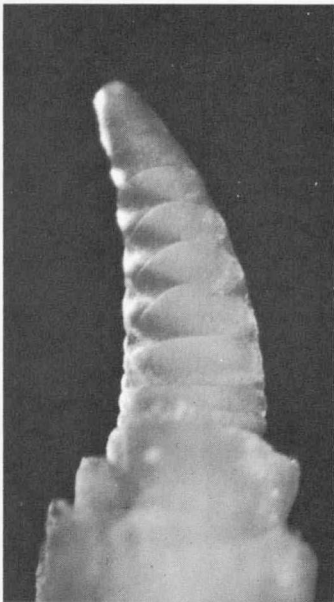
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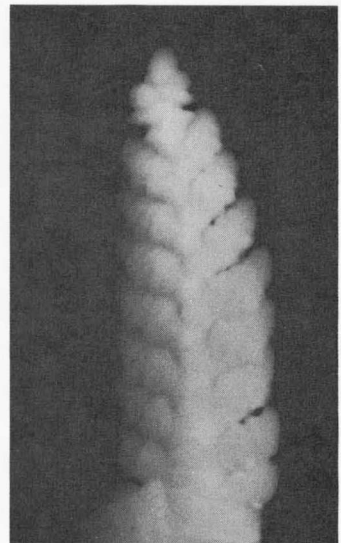
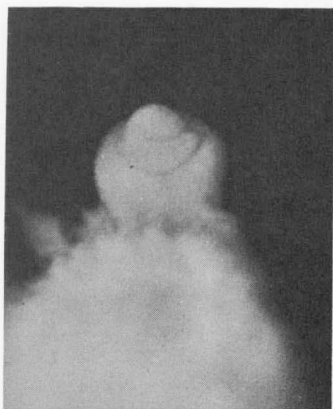


Figure 1. (continued)

G. Shoot apex showing 'double rings' beginning of spikelet formation at appearance of seventh leaf; H. Double rings advanced; I. Lower part of double ring growing to form spikelets at full expansion of sixth leaf; J. Spike with spikelets showing florets initiation at appearance of eighth leaf.



A



B



C



D

Figure 2. Vegetative stage in apices of two winter wheat genotypes of different maturity. Shoot apex and leaf primordia at appearance of third leaf (X70); A. in Winoka (late maturing); B. in Crest (early maturing). Elongating tip of shoot apex with leaf primordia at appearance of tip of fifth leaf; C. in Winoka and D. in Crest.

appearing leaves were removed. Besides these, two small needle shaped leaves were also taken off before the apex was exposed. Three small primordial tillers were visible in all genotypes except Nugaines, which showed four. The apical meristem was a small round tip in Crest, better developed in Froid, and medium sized in other genotypes. In the samples taken at full expansion of the third leaf, the apices of Crest and MT 6928 were longer and more advanced, the apex of Froid was shorter and broader and the apices of Winoka and Nugaines were smaller.

The field samples, taken on April 2, matched well with those taken April 4, the corresponding time in the growth chamber materials (Table 3). On dissection of the samples, generally five leaves were removed before the apex was exposed. The apex was found enclosed in the sixth leaf whereas the primordia of 7th and 8th leaves could be seen on the uncovered side of the apex. The apices of Crest and MT 6928 had elongated tips and were more developed than those of the Froid, Nugaines and Winoka. The visible tillers were two to three in Froid and Nugaines, but were three in all samples of Crest, MT 6928 and Winoka.

In both growth chamber and field materials the apices generally showed a trend towards elongation which indicated the entering to the transitional stage.

Table 3. Comparison of dates of morphological development in the field with those in the growth chamber.

Morphological development	Field date	Growth chamber	
		Growth chamber date	Corresponding field date
Seeding	Sept. 25	July 27	Sept. 18
Emergence	--	Aug. 4	Oct. 3
Appearance of 1st leaf	--	Aug. 5	Oct. 4
Appearance of 2nd leaf	--	Aug. 8	Oct. 7
Appearance of 3rd leaf	Feb. 19	Aug. 27	Dec-Feb 28
Appearance of 4th leaf	Apr. 2	Oct. 3	Apr. 4
Appearance of 5th leaf	Apr. 14	Oct. 20	Apr. 18
Appearance of 6th leaf	Apr. 30-May 3	Oct. 31	May 4-10
Appearance of 7th leaf	May 15-May 20	Nov. 6	June 2

Transitional Stage

The transitional stage occurs between the vegetative and the reproductive stages and is marked by elongation of the shoot apex (Bonnett, 1966).

Appearance of fifth leaf

The sampling for this stage was done 77 days after emergence (Table 2). Seven to eight leaves were removed to expose the well elongated shoot apex. Crest and MT 6928 showed similar elongation, greater than Froid. The leaf primordia on the apices were more conspicuous and visible like ridges or bumps with alternate arrangements. Such ridges of primordia were better developed in the case of Crest and MT 6928 as compared to Froid, Winoka and Nugaines.

In the field samples elongation and tapering of the apices were similar to those from the growth chamber. The apex of MT 6928 was more developed than that of Froid and was like that of Crest. The Nugaines apex was also large like Crest, but those of Froid and Winoka were smaller (Figure 2) in all cases, three to five tillers could be seen both in advanced or primordial form.

In both growth chamber and field studies all the genotypes manifested variation in length of shoot apices, but were in a similar stage of transition. There was a close coincidence of sampling dates

in the field with that corresponding to the field simulated conditions in growth chamber studies (Table 3).

Full expansion of fourth leaf

The stage was sampled 83 days after emergence (Table 2). Seven leaves were removed to expose the shoot apex. The 11th leaf primordium was visible and very conspicuous under the dissecting scope. The genotypes had four tillers except MT 6928 with six. The apices were in the transitional stage except for Crest and MT 6928, which were more advanced in length and also depicted 'double rings'. The transition stage, generally, was of much shorter duration in all genotypes as compared to vegetative stage (Table 4). This is in agreement with Bonnett (1935). No sampling was made from the field at this growth stage.

Reproductive Stage

The beginning of the reproductive stage is indicated by the appearance of double ridges. During this stage certain internodes of the stem elongate and the spikelet parts differentiate and increase in size (Bonnett, 1966).

Table 4. Relationship of visual leaf development stage and developmental stage of shoot apex for five winter wheat genotypes.

Genotype	Visual leaf developmental stage	Approximate date of occurrence in field	No. of $\frac{1}{2}$	
			Leaves	Tillers
<u>Vegetative stage</u>				
Crest	Emergence to appear- ance of 5th leaf	Sep. 25-Apr. 12	8	3
Froid	"	"	8	2
MT 6928	"	"	8	3
Winoka	"	"	7	3
Nugaines	"	"	8	3
<u>Beginning of transitional stage</u>				
Crest	Appearance of 5th leaf	Apr. 14	9	5
Froid	"	"	9	4
MT 6928	"	"	8	4
Winoka	"	"	7	3
Nugaines	"	"	8	5
<u>Beginning of reproductive stage</u>				
Crest	Full expansion of 4th leaf	Apr. 24	11	5
Froid	Appearance of 6th leaf	May 3	11	10
MT 6928	Full expansion of 4th leaf	Apr. 24	11	7
Winoka	Appearance of 6th leaf	May 3	10	5
Nugaines	Appearance of 6th leaf	Apr. 30	10	5

^{1/} Visual and primordial.

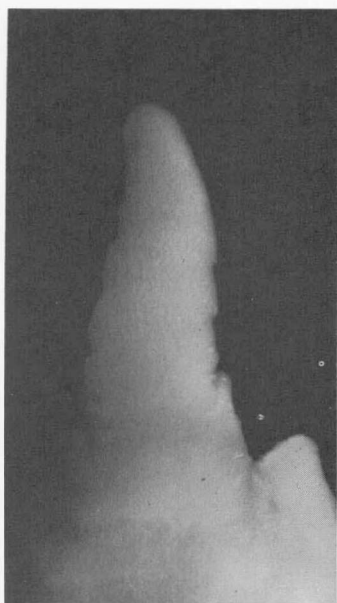
Appearance of sixth leaf or full
expansion of fifth leaf

The sampling of plants at the appearance of the sixth leaf and full expansion of the fifth leaf was done 88 days and 91 days from emergence, respectively. In all genotypes eight leaves, five fully expanded and three still expanding, were removed to expose the apices. The apices of all genotypes showed paired ridges called 'double rings', which indicated that all genotypes had entered the reproductive stage as discussed by Purvis (1934), Evans and Grover (1940), Gott, Gregory and Purvis (1955) and Bonnett (1966). Crest and MT 6928 showed broader and more double rings than the others. The lower ridge of the double ring represented a leaf primordium and the second or upper ridge of the ring was the spikelet initial. Tillers numbered five in Crest, Winoka and Nugaines, seven in MT 6928 and ten in Froid.

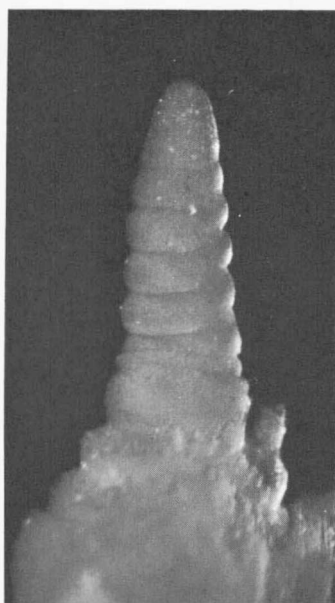
The apices of the samples taken at full expansion of fifth leaf had the double ring well advanced, showing the upper edge of the ring more developed than the lower one. The small variation that existed due to the ridge sizes ranked Crest at the top, followed by Nugaines and MT 6928. Froid had the medium sized rings, whereas Winoka showed the smallest rings of all (Figure 3).

The field samples, taken at the appearance of the tip of sixth leaf, showed 'double rings' on their apices. The size of the

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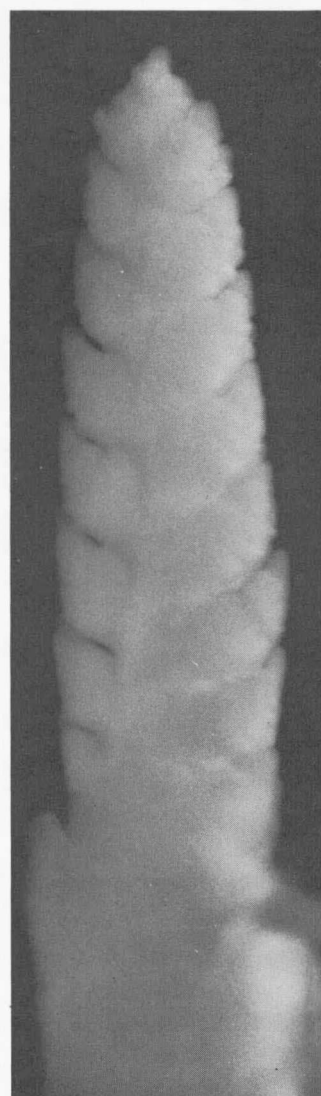


A



B

D



C

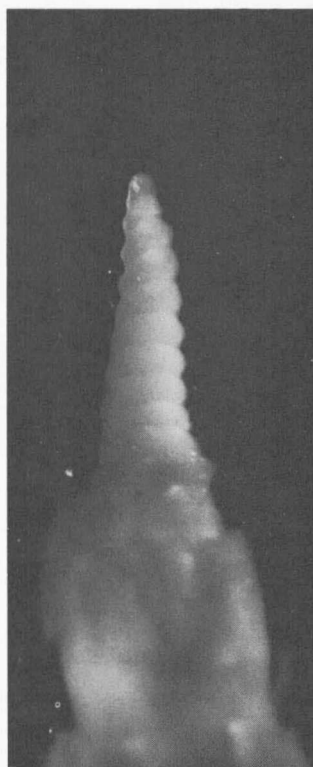


Figure 3.

rings was almost the same in all genotypes except Winoka which had the smallest ridges and apex. At the time of spikelet initiation, the leaf primordia present at the base of apex were still developing and expanding into leaves.

Appearance of seventh leaf or full
expansion of sixth leaf

The samples at these stages were taken 94 to 98 days after emergence (Table 2). Ten large and small leaves were removed to expose the apical meristem of the main shoot. The genotypes showed variation for tiller numbers and the shape and size of apical meristem of the main shoot. The apices of Crest and MT 6928 depicted a well advanced reproductive stage. In these genotypes the initiation of florets could be seen while in others the 'double rings' were well advanced in development and only the spikelet's initials were visible. Even at this stage Winoka had the smallest apex and indicated least development of the upper part of the 'double ring' or the spikelet initiation.

In the field materials the apices at the appearance of the seventh leaf stage showed an advanced reproductive stage. Floret initiation and differentiation were more visible in Crest, followed by MT 6928 with respect to the size and the development of the spike. Froid, Nugaines and Winoka all had similar apices depicting spikelet

differentiation. The initiation and development of spikelet and floret were generally noticed first in the middle of the apex. Similar observations were recorded by Purvis (1934), Gott et al. (1955) and Barnard (1955).

The stem from crown node to the apex was only about 3.5 cm long at this stage, which occurred at the end of May in the field. The apex length was only 2.5 mm at this stage. After this stage, winter wheat internodes elongate very rapidly.

SUMMARY

Developmental morphology of five winter wheat genotypes, grown in controlled environment and field situations, was studied by examining the apical meristem at various leaf stages.

The growth stages of the five genotypes were divided into three main stages; vegetative, transitional and reproductive. Each of these stages was distinguished from the other by the development, size and shape of apical meristem (Figure 1). The vegetative stage extended from germination to the appearance of the tip of the fifth leaf. At this point the plants entered into the transitional stage. The transitional stage was short-lived and continued only during the expansion period of the fifth leaf. Before full expansion of the fifth leaf or at appearance of the sixth leaf, the reproductive stage was initiated.

From fall to mid-spring (September 25 to April 12), the winter wheat plants remained in the vegetative stage in which the apical meristem of the main shoot produced tiller and leaf primordia. The apex of the main shoot remained short and round at the tip. The beginning of the transitional stage was marked by the exponential elongation of apices. This occurred for about 10 days during the month of April (Table 4). Then the 'double rings' were visible on the apex, which indicated the initiation of the reproductive stage (Bonnett, 1966) in the last week of April in Crest and Mt. 6928, and

the first week of May for Froid, Winoka and Nugaines (Table 4). During this stage the growing point differentiated into spikelets and then florets, and the terminal spikelet was differentiated at the apex tip. These developments continued from the full expansion of the fifth leaf to the appearance of spike from the boot.

The initiation and duration of the three stages were similar for all genotypes except Crest and MT 6928 which entered the reproductive stage one week earlier (Table 4). Crest and MT 6928, the genotypes possessing early to medium maturity, differed from all other later maturing genotypes with respect to size of apices. Their apices were longer than others and showed the initiation and differentiation of the reproductive stage earlier than other genotypes. This may be the reason for early maturity in these two genotypes. Bonnett (1966) advanced similar views.

The studies revealed that the developments in the shoot apex were gradual and continuous and did not happen as a group (Figure 1). The stage classification suggested by Bonnett (1935) and used by Evans and Grover (1940) seemed more understandable in view of the changes in the apex. It was also evidenced that all winter wheat genotypes were at the same morphological growth stage when they entered winter period.

Among the five genotypes there was a good relationship between the external leaf morphology and the apical meristem developmental stage. However, there was a difference in the size of the apices of the main shoot of the genotypes, especially in the reproductive stage (Figure 3).

The general pattern of inflorescence development was similar in all genotypes, but differences occurred among genotypes for the time the spikelet initiates and the rate of subsequent development.

The rate of elongation of the apical meristem was gradual during vegetative growth but increased during spikelet initiation. Differences occurred in the rate of elongation of apex.

The leaves appeared in a similar gradual manner during the vegetative stage in all the genotypes. There seemed to be no relationship between the rapidity of leaf primordia appearance and earliness or lateness of heading. Leaf primordia were visible as alternate ridges around the shoot apex.

The relationship of the internal development stage to external morphology of the plant is helpful when there are only a few plants of a particular genotype or when rapid estimation of development stage is needed. The apical stage of the plant can be known without dissection or destruction of the plant by the use of leaf appearance scale. The knowledge of flower initiation occurring at

leaf stage five in winter wheat can partition the period from sowing to heading thus affording analysis of plant response to environmental factors as in winterhardiness studies. Differences in the rate of differentiation and development may suggest reasons for variation in maturity.

The use of controlled environment chamber, field climatological data and diverse winter wheat genotypes enabled me to not only duplicate field conditions, but more importantly to produce plants comparable to field grown materials in both external and apex developmental stages.

STUDY II

THE RELATIONSHIP OF COLEOPTILE LENGTH AND OTHER
MORPHOLOGICAL CHARACTERISTICS OF WINTER
WHEAT TO FIELD SPRING SURVIVAL

II. The Relationship of Coleoptile Length and other Morphological Characteristics of Winter Wheat to Field Spring Survival

This study examined coleoptile lengths of winter wheat genotypes under a darkened controlled environment and related this character with other morphological factors such as seedling height, subcrown internode length and emergence rate. The association of all these characters with the mature plant height and the field spring survival was examined.

MATERIALS AND METHODS

Genotypes

Six diverse hard red winter wheat genotypes of known field spring survival were used in this study. These genotypes with their general description, plant height and spring survival are listed in Table 5.

General Methods

Seeds of six winter wheat genotypes were planted in sterilized 4-inch clay pots, using greenhouse soil composed of silt loam soil and peat in a 1:1 ratio. The soil moisture was kept at or near field capacity. Ten seeds in each pot were planted at equal distance from the center and sides of the pot and from seed to seed to prevent the possible placement and potside effect. At planting, the soil of each pot was removed to reach the required depth of seeding.

Table 5. General description of six winter wheat genotypes studied.

Genotype		Description	Plant height (in)	Spring survival (%)
Froid	(CI 13872)	Tall, late maturing, excellent winterhardiness	40	72 ^{1/}
Yogo	(CI 8033)	Tall, late maturing, excellent winterhardiness	39	64
Cheyenne	(CI 8885)	Tall, late maturing, fair winterhardiness	36	50
MT 6928		Semidwarf, early maturing, poor winterhardiness	31	21
Itana	(CI 12933)	Tall, mid to late season maturity, poor winterhardiness	36	27
Crest	(CI 13880)	Medium height, early maturing, poor winterhardiness	32	12

^{1/} Field average eight station years except MT 6928 with two station years.

The seeds were placed in the pots with their embryos upward. The removed soil of each pot was replaced on the seeds with equal pressure of packing. The pots were placed in the darkened growth chamber immediately after seeding. Seed lots were uniformly viable and treated with fungicide. Seeds of equal size were used to eliminate a possible bias due to differences in seed size.

The temperature regime applied in the growth chamber represented the average field air temperature at the Bozeman Research Station during the germination and seedling stages of winter wheat. For this purpose the day and night average temperature curves were constructed from the hourly mean temperatures. (Table 1, Page 28).

Observation, Statistical Designs and Analysis

Seedling emergence counts were begun 5 to 6 days after seeding and were recorded daily until emergence ceased. An emergence rate index was calculated for the first four days of emergence by multiplying the first day's emergence by 4, second day's by 3, third day's by 2, and fourth day's emergence by 1. The total of these weighted values was called Emergence Rate Index (E.R.I.) of a genotype.

Two weeks after sowing the seedlings were removed carefully from the pots and their coleoptile lengths, seedling height, and sub-crown internode length were recorded.

The trial included 6 genotypes and 5 planting depths (one inch increments) and was conducted with 4 replications in a randomized block design. All the blocks were rerandomized every third day to eliminate possible position effects inside the growth chamber.

Averages determined for all pots (each pot was a plot) were used for the analysis of variance of all the characteristics. Correlations among all characteristics were calculated.

RESULTS AND DISCUSSION

Coleoptile Length

The six winter wheat genotypes differed significantly for the coleoptile lengths (Table 6). Crest, Yogo and Froid had the coleoptile lengths of 8.1, 8.1 and 7.9 cm, respectively, and differed significantly from Itana, MT 6928 and Cheyenne with 7.4, 7.0 and 6.6 cm, respectively (Table 7). The significant varietal difference at various seeding depths was in agreement with the findings of Kaufmann (1968).

The coleoptile length of the winter wheat genotypes varied significantly with the planting depths (Table 6). Froid, Yogo and Crest had the longest coleoptiles at all depths with significantly longer coleoptiles than Itana, MT 6928 and Cheyenne at the two-, three-, four- and five-inch planting depths (Table 7). At all depths the longest coleoptiles were found in Crest and Froid and the shortest in MT 6928 and Cheyenne. Yogo, which showed significantly shorter coleoptiles than Froid and Crest at the one-inch depth, was similar to these genotypes at deeper plantings. The three-inch depth seemed to be optimum for Itana because this was the only depth where it was in the first rank of coleoptile lengths. Crest had the longest coleoptiles of all genotypes at the four- and five-inch depths.

The comparison between the planting depths indicated that the coleoptile lengths for each depth significantly differed from the

Table 6. Mean squares from analysis of variance for various characteristics measured on six winter wheat genotypes planted at five depths in a darkened controlled environment.

Source of variation	Degrees of freedom	Mean squares for:			
		Coleoptile length	Emergence rate index	Seedling height	Subcrown internode length
Genotypes	5	7.837**	31.791**	180.416**	34.868**
Depths	4	18.021**	216.129**	24.577**	51.322**
Genotype X depth	20	0.255	5.862**	4.126	2.423
Error	87	0.297	1.471	4.086	1.609

** Significant at .01 level.

Table 7. Coleoptile lengths (cm) of six winter wheat genotypes grown at five planting depths in a darkened controlled environment.

Genotype	Coleoptile length (cm) and rank, respectively, for planting depths of:					
	One in.	Two in.	Three in.	Four in.	Five in.	Average
Froid	7.3 a ^{1/} 1	7.3 ab 3	8.1 ab 3	8.3 ab 3	8.5 ab 3	7.9 ab 3
Yogo	6.4 bc 3	7.8 a 1	8.6 a 1	8.6 ab 2	9.0 a 2	8.1 ab 2
Cheyenne	5.6 c 5	5.8 c 6	6.9 c 6	7.3 d 6	7.5 c 6	6.6 e 6
MT 6928	5.6 c 6	6.4 c 5	7.4 bc 5	7.5 cd 5	8.0 bc 5	7.0 d 5
Itana	6.1 b 4	7.0 b 4	7.9 ab 4	8.0 bc 4	8.2 bc 4	7.4 c 4
Crest	6.8 ab 2	7.4 ab 2	8.3 ab 2	8.8 a 1	9.3 a 1	8.1 a 1

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

others except for the three- and four-inch depths (Table 8). This may be due to equal adaptation of all the genotypes to these two depths, at which the genotypes are generally seeded. The results showed that at the deepest planting the longest coleoptiles occurred. Mean coleoptile lengths of 6.3, 7.0, 7.9, 8.1 and 8.4 cm were observed for the one, two, three, four- and five-inch depths, respectively. As the depth of planting increased, the coleoptile lengths increased. The greatest increase in the coleoptile length at the five-inch depth over the one-inch was 2.6 cm for Yogo, followed by Crest, MT 6928, Itana, Cheyenne and Froid with 2.5, 2.4, 2.1, 1.9 and 1.2 cm, respectively (Table 7).

Cheyenne had the shortest coleoptile at the one-inch depth and did not exhibit comparable increases at the deeper plantings. MT 6928, on the other hand, did show increases in the coleoptile length at greater depths. This is further evidenced by percentage increase in the coleoptile length at the five-inch depth over that of one-inch planting depth; 42.6, 41.4, 36.2, 33.6, 31.1 and 16.6 percent for MT 6928, Yogo, Crest, Itana, Cheyenne and Froid, respectively. The coleoptile tends to grow longer if the seed is planted deeper in the soil. Similar findings were reported early by Sunderman (1964).

Table 8. Coleoptile lengths (cm), emergence rate index, seedling height (cm) and subcrown internode length of winter wheat genotypes at various planting depths in a darkened controlled environment.

Planting depths:	Coleoptile length (cm)		Emergence rate index (E.R.I.)		Seedling height (cm)		Subcrown internode length (cm)	
1-inch	6.3	d ^{1/} 5 ^{2/}	28.2	a 2	22.4	bc 4	3.6	d 5
2-inch	7.0	c 4	29.6	a 1	23.3	ab 2	5.0	c 4
3-inch	7.9	b 3	19.8	b 4	24.3	a 1	6.7	ab 2
4-inch	8.1	b 2	20.6	b 3	22.7	bc 3	7.3	a 1
5-inch	8.4	a 1	7.0	c 5	21.6	c 5	6.2	b 3

^{1/} Values within each characteristic followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

^{2/} Rank.

The winter seedlings developed longer coleoptiles and shallower crown nodes under the stress of deep planting. This could be related to greater cell length or cell number, as has been suggested by Allan et al. (1962). Burleigh et al. (1965) pointed out the lack of light at greater depths as a possible cause of excessive coleoptile elongation. At very shallow depths growth of coleoptiles may be suppressed by light.

The relationship of coleoptile length with mature plant height of the winter wheat genotypes was measured. The correlation coefficient including Froid, Yogo, Itana and MT 6928 was .95^{**} (Table 9). An exception to this association was noticed in Cheyenne which is a tall variety but gave a short coleoptile. On the other hand, a medium tall genotype, Crest, exhibited the long coleoptile. Cheyenne and Crest seemed to have different genetic mechanism for coleoptile length as compared to other genotypes. The significant positive correlation of mature plant height with the coleoptile length found in this study corroborated those of Allan et al. (1962), Feather et al. (1968) and Favereau et al. (1968). This differs from the findings of Parodi et al. (1970) who found a nonsignificant correlation coefficient between coleoptile length and mature plant height. The contradiction can be attributed to the genotypes used in the study, as already pointed out by Allan et al. (1968).

Table 9. Correlations between mature plant height and other characteristics of winter wheat genotypes planted at five depths in a darkened controlled environment.

Mature plant height of:	Correlation coefficient (r)			
	Coleoptile length	E.R.I.	Seedling height	Subcrown internode length
Cheyenne, Crest, Froid, Itana, MT 6928, Yogo	.35	.37	.83*	.83*
Cheyenne, Froid, Itana, MT 6928, Yogo (excluding Crest)	.73	.96**	.98**	.78
Crest, Froid, Itana, MT 6928, Yogo (excluding Cheyenne)	.50	.40	.87*	.33
Froid, Itana, MT 6928, Yogo (excluding Crest & Cheyenne)	.95**	.997**	.99**	.90

*, ** Significant at .05 and .01 levels, respectively.

A correlation coefficient of .93 of coleoptile length with field spring survival (Table 10) showed that except for Cheyenne and Crest, those genotypes possessing good spring survival also had longer coleoptiles. The lack of a higher correlation was probably influenced by the fact that means across all planting depths were used in the calculation.

Emergence

Genotypes differed significantly for E.R.I. (Table 6). Among the six genotypes, Crest had the highest E.R.I. of 29.7 which differed significantly from MT 6928 and Cheyenne with E.R.I.s of 13.0 and 16.7, respectively (Table 11). Froid (25.2) and Yogo (24.6) were second in the rank followed by Itana (20.7). Generally Crest, Froid and Yogo were outstanding in rate of emergence, Itana was intermediate, and Cheyenne and MT 6928 were low in E.R.I.

The multiple range test on the emergence rate of genotypes planted one-inch deep showed no statistically significant difference between Froid, Crest, Yogo, Cheyenne and Itana (Table 11). Only Froid and Crest had significantly higher E.R.I.s than MT 6928.

The E.R.I.s of Crest and MT 6928 ranked high and low, respectively, at all depths of planting. The response of MT 6928, a semi-dwarf, is in agreement with Allan et al. (1962). Rankings of emergence rate indexes among the five depths of plantings varied

Table 10. Correlations between field spring survival and other characteristics of winter wheat genotypes planted at five depths in a darkened controlled environment.

Field spring survival of:	Correlation coefficient (r)			
	Coleoptile length	E.R.I.	Seedling length	Subcrown internode length
Cheyenne, Crest, Froid, Itana, MT 6928, Yogo	.16	.12	.66	.83*
Cheyenne, Froid, Itana, MT 6928, Yogo ... (excluding Crest)	.58	.79	.84	.74
Crest, Froid, Itana, MT 6928, Yogo (excluding Cheyenne)	.42	.21	.75	.97**
Froid, Itana, MT 6928, Yogo (excluding Crest & Cheyenne)	.93	.88	.89	.98*

*, ** Significant at .05 and .01 levels, respectively.

Table 11. Emergence rate index (E.R.I.) of six winter wheat genotypes grown at five planting depths in a darkened controlled environment.

<u>Emergence rate index (E.R.I.) and rank, respectively, for planting depths of:</u>													
<u>Genotype</u>	<u>One in.</u>		<u>Two in.</u>		<u>Three in.</u>		<u>Four in.</u>		<u>Five in.</u>		<u>Average</u>		
Froid	35.3	a ^{1/} 1	31.8	ab 3	23.5	a 3	26.0	b 3	9.5	bc 3	25.2	b	2
Yogo	27.3	ab 3	37.0	a 1	24.8	a 1	31.3	ab 2	2.8	c 5	24.6	b	3
Cheyenne	27.0	ab 4	25.8	c 5	14.0	b 5	8.3	cd 5	8.5	bc 4	16.7	d	5
MT 6928	21.8	b 6	19.5	d 6	14.0	b 6	7.3	d 6	2.3	c 6	13.0	e	6
Itana	26.0	ab 5	28.8	bc 4	17.8	ab 4	15.5	c 4	15.3	ab 2	20.7	c	4
Crest	31.8	a 2	35.0	a 2	24.8	a 2	35.3	a 1	21.5	a 1	29.7	a	1

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

considerably for Yogo, Froid and Itana. Yogo ranked in the highest group at the two- and three-inch deep plantings but dropped to second and fifth at the four- and five-inch depths, respectively. Froid was in the top group of E.R.I.s at one- and three-inch depths, and dropped to third at four- and five-inch deep plantings. Itana showed a medium E.R.I. in one- to four-inch depths, but rose to second at five-inch depth. Burleigh et al. (1962) reported Itana demonstrated a unique ability to emerge fairly well under deep planting.

The winter wheat genotypes showed significant differences in emergence rate at all depths, which is contrary to the results reported by Bohnenblust et al. (1962). However, the genotypes showed the maximum variation in their emergence rate at four-inch deep planting. It can be deduced that the laboratory emergence tests, sown at a depth of four inches, should be very effective in determining differences in the ability of varieties to emerge.

Seedlings from one-inch depth began to emerge five days after planting, whereas from two-, three-, four- and five-inch depths, seedlings appeared after 7, 8, 9 and 10 days after planting, respectively. The comparison between the depths, in terms of number of days taken to obtain 50% emergence, showed that planting depths of one-, two-, three-, four- and five-inches took 6.5, 7.5, 9.0, 11.5 and 13.9 days, respectively. The difference among these values was

statistically significant. Fifty percent emergence was achieved in 8-9 days by Crest and Froid, in 9 days by Itana, 10 days by Yogo and Cheyenne, and in 12 days by MT 6928.

The variation in emergence due to depths of planting was highly significant (Table 6). The highest emergence rate indexes were 29.6 and 28.2 for the two- and one-inch planting depths, respectively (Table 8, Page 58). The three- and four-inch depths had E.R.I.s of 19.8 and 20.6, while the five-inch depth had a low E.R.I. of 10.0. These results indicate that the deeper the winter wheat is planted, the longer it takes to achieve total emergence.

The highly significant genotype X depth interaction indicated that the genotypes responded differentially to the depths of planting for E.R.I. (Figure 4 and Table 11). Froid showed highest E.R.I. at one-inch and dropped to third at the four- and five-inch depths. Itana was fifth at the one-inch and second at the five-inch depth. Yogo was third at the one-inch, first in rank at the two- and three-inch depths, second at the four-inch and fifth at the five-inch planting depth.

The correlation between E.R.I. and mature plant height for all genotypes, excluding Crest, was highly significant ($r = .96$, Table 9). Crest, a medium tall variety, showed the highest overall emergence rate. The positive correlation between the emergence rate

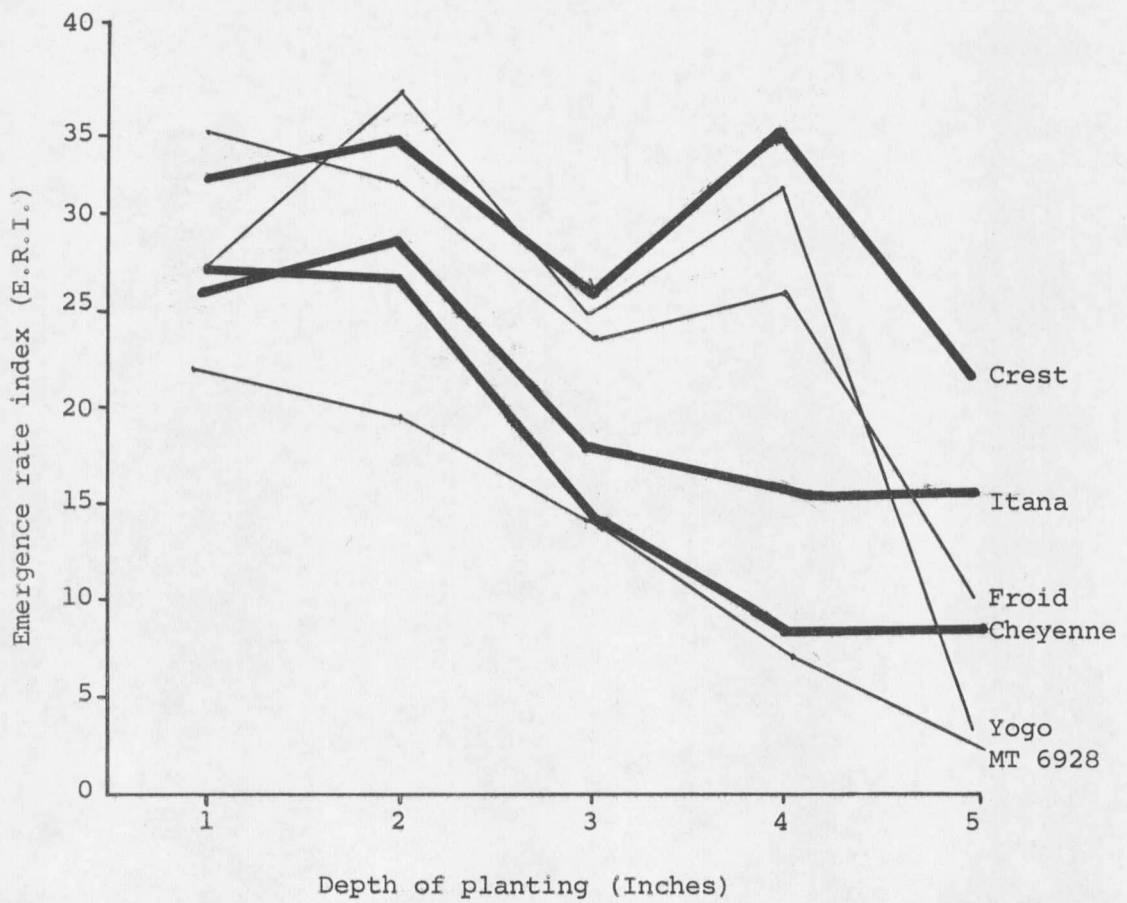


Figure 4. Emergence rate index (E.R.I.) of six winter wheat genotypes planted at five depths.

index and mature plant height as reported by Allan et al. (1962) and Chaudhry and Allan (1963) was confirmed in my study. The association of better and faster emergence with taller genotypes was further evidenced when only Froid, Yogo, Itana and MT 6928 were considered in the correlation ($r = .997$, Table 9, Page 60). Crest and Cheyenne showed a different response. Cheyenne is a tall variety, but gave emergence rate next lowest to MT 6928. Crest has a medium height, but gave the highest emergence rate index. The different response of Cheyenne and Crest, compared to other genotypes, may be attributed to different genetic systems controlling height and emergence factors.

Seedling Height

Seedling heights, measured after 12 days of growth in complete darkness, differed significantly among the genotypes (Table 6). Averaged over all depths, Froid, Yogo, Crest, Itana, Cheyenne and MT 6928 had the seedling heights of 27.1, 24.6, 23.3, 22.8, 21.4 and 18.2 cm, respectively (Table 12).

The seedling height within each depth varied significantly among the genotypes (Table 12). Froid was among the tallest and MT 6928 the shortest at all depths. Ranking for Itana seedling length varied from second to fifth at various planting depths. Seedlings of Cheyenne were longer than MT 6928 at all depths.

Table 12. Seedling height (cm) of six winter wheat genotypes planted at five depths in a darkened controlled environment.

<u>Seedling height (cm) and rank, respectively, at plantings depths of:</u>																		
<u>Genotype</u>	<u>One in.</u>			<u>Two in.</u>			<u>Three in.</u>			<u>Four in.</u>			<u>Five in.</u>			<u>Average</u>		
Froid	27.4	a	^{1/} 1	27.3	a	1	26.9	ab	2	27.4	a	1	26.3	a	1	27.1	a	1
Yogo	24.0	b	2	24.4	b	2	27.5	a	1	24.0	b	2	22.9	ab	3	24.6	b	2
Cheyenne	21.2	c	5	23.2	b	4	23.4	c	5	20.5	cd	5	18.6	bc	5	21.4	d	5
MT 6928	17.1	d	6	19.1	c	6	20.2	d	6	18.6	d	6	15.8	c	6	18.2	e	6
Itana	22.5	bc	3	22.5	b	5	23.5	c	4	22.1	bc	4	23.4	a	2	22.8	c	4
Crest	22.3	bc	4	23.3	b	3	24.6	bc	3	23.8	b	3	22.8	a	4	23.3	bc	3

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

The variation in the seedling height due to the depths of seeding was highly significant (Table 6). Generally, the seedling heights increased with every successive depth of planting up to the three-inch depth which gave the maximum average height of 24.3 cm (Table 8, Page 58). Further planting depths of four- and five-inches decreased seedling heights.

The relationship of seedling height with the mature plant height of the genotypes was studied. The correlation was significant ($r = .83$) for all genotypes, but was highly significant ($r = .98$) when Crest was excluded (Table 9). Crest, though a medium tall variety, emerged early, had long coleoptiles, and tall seedlings. The response of Crest, as previously indicated, may be attributed to the fact that the characteristics of emergence, coleoptile length, and seedling height being under the control of different genetic mechanisms. The significant positive correlation between seedling height and mature plant height found in my study verifies the results of Chaudhry and Allan (1963). The correlation between seedling height and spring survival was not significant in my study (Table 10).

Subcrown Internode Length

The subcrown internode length was measured on the seedlings grown in complete darkness (same as coleoptile length studies). The data should be considered with this in mind. The analysis of

variance (Table 6) showed highly significant difference among the genotypes and planting depths for subcrown internode length. The three- and four-inch planting depths gave the longest subcrown internodes (Table 8).

Froid, Yogo, Itana, MT 6928, Cheyenne and Crest showed subcrown internode lengths of 7.7, 6.9, 5.8, 5.3, 4.8 and 4.2 cm, respectively (Table 13).

At all depths Froid was first and Yogo was generally second for subcrown internode length, except for the three-inch planting depth where their positions were switched (Table 13). Crest, in all cases, was at the bottom with the shortest internode. Itana and MT 6928 showed medium internode lengths at one- to four-inch depths with Itana jumping to second at the five-inch depth. The position of Cheyenne consistently preceded Crest. The multiple range test showed the maximum diversity in genotypes for this characteristic at four-inch deep planting. As with other characteristics, Itana demonstrated a unique change in its rank and response to the four-inch seeding.

Since a long subcrown internode means a shallow crown node, it can be said that for both the average and individual planting depths, Froid and Yogo had the shallowest crown nodes. The deepest crown nodes were found in Crest, Cheyenne, MT 6928 and Itana.

The shallower seedlings showed the tendency of long subcrown internode genotypes, e.g. Froid and Yogo, to form their crowns

Table 13. Subcrown internode length (cm) of six winter wheat genotypes planted at five depths in a darkened controlled environment.

Subcrown internode length (cm) and rank, respectively, at planting depths of:													
Genotype	One in.		Two in.		Three in.		Four in.		Five in.		Average		
Froid	4.9	a ^{1/} 1	7.1	a 1	7.7	ab 2	10.7	a 1	8.3	a 1	7.7	a 1	
Yogo	4.1	ab 2	5.8	b 2	8.8	a 1	9.2	b 2	6.5	ab 3	6.9	b 2	
Cheyenne	3.2	bc 5	4.2	c 5	6.0	cd 5	5.3	de 5	5.4	abc 4	4.8	cd 5	
MT 6928	3.3	bc 4	4.8	bc 3	6.5	bc 3	6.7	cd 4	5.0	ab 5	5.3	c 4	
Itana	3.6	bc 3	4.2	c 4	6.5	bc 4	7.3	c 3	7.3	ab 2	5.8	c 3	
Crest	2.7	c 6	4.0	c 6	4.9	d 6	4.7	e 6	4.7	bc 6	4.2	d 6	

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

farther away from the seed. In the case of the one-, two- and three-inch depths, the crown node formed above the soil surface for Froid and Yogo. This is attributed to lack of light during germination, emergence and growth, and leads to the conclusion that in darkness crown nodes tend to form farther away from the seed. Light probably has an important role in the suppression of crown formation near the soil surface. This agrees with the findings of Kassowitsch (1894), Kuleshov and Marchenko (1963) and Ferguson and Boatwright (1968).

Subcrown internode length was associated with mature plant height and field spring stand survival with correlations of .83 and .83, respectively (Tables 9 and 10, Pages 60 and 62). The positive correlation of subcrown internode and spring survival suggests that winter wheat genotypes with long subcrown internodes, or shallow crown depths, have higher field spring survival values. Froid, Yogo, Itana, MT 6928 and Crest clearly manifest this correlation.

Cheyenne was an exception, because although it has good field spring survival, it did not exhibit shallow crowns. This is not surprising since field spring survival is the result of many acting and interacting morpho-developmental, physiological and environmental factors. Additionally, Cheyenne may possess genetic mechanisms which result in a differential interaction of these factors. A winter wheat genotype may have poor fall stand establishment, but

may withstand low temperatures better or may have a strong spring recovery potential and vice versa.

These results show that the tall winter wheat genotypes, e.g. Froid and Yogo, which have good spring survival, have long coleoptiles, early and better emergence, and shallow crown nodes. The semidwarf genotype, MT 6928, had poor spring survival, short coleoptiles, poor and delayed emergence and deep crown nodes. Such consistency in characteristics was not noticed in Cheyenne and Crest. Cheyenne, a tall winter wheat with good spring survival, had short coleoptiles, poor emergence, and deep crown nodes. Crest, however, is shorter and has poor spring survival, long coleoptiles and excellent emergence, but had the deepest crown nodes of all other genotypes. Poor spring survival may be due to deep crown nodes and a lack of cold tolerance.

With Cheyenne, which possesses poor fall stand establishment characteristics, the good spring survival may be due to its favourable physiological response during winter or a properly timed and vigorous spring recovery capability.

Association of Characteristics

Highly significant positive correlations were found between coleoptile length and seedling height, coleoptile length and subcrown internode length, emergence rate index and seedling height, and seedling height and subcrown internode length (Table 14). These

Table 14. Correlations (r) between various characteristics of six winter wheat genotypes planted at five depths in a dark controlled environment.

	Coleoptile length	Emergence (E.R.I.)	Seedling height	Subcrown internode
Coleoptile length	1.000			
Emergence (E.R.I.)	-.096	1.000		
Seedling height	0.341**	.504**	1.000	
Subcrown internode length	0.487**	-.076	.542**	1.000

** Significant at .01 level.

correlations, although confounded by the effects of depths of planting and of genotypes, showed that the genotypes with long coleoptiles produce crown nodes near the soil surface and have taller seedlings; early emerging genotypes produce tall seedlings and tall seedling genotypes have shallow crown nodes. The correlations between coleoptile length and emergence rate index, and emergence rate index and subcrown internode were nonsignificant.

In order to eliminate any possible variation due to different depths of planting, the correlations within individual depths were calculated (Table 15). The correlation between coleoptile length and seedling height was significant at all depths. Significant correlations were obtained between E.R.I. and seedling height, except at the five-inch depth, and between seedling height and subcrown internode length at all depths.

The association between coleoptile length and E.R.I. was nonsignificant over all depths, but was significant at each individual depth of planting (Table 15). The correlation calculated over all data was confounded by depth effects.

The correlation of coleoptile and subcrown internode lengths, which was highly significant when overall means were used, was reduced to the level of nonsignificance when each depth was individually examined (Table 15). This resulted from an exaggeration of correlations when overall data was used. The E.R.I. and subcrown

Table 15. Correlations (r) among various characteristics measured on six winter wheat genotypes planted at five depths in a darkened controlled environment.

Characteristics	Correlation coefficient
Coleoptile length vs. emergence rate index-Average	0.096
1-inch depth	0.464*
2-inch depth	0.468*
3-inch depth	0.654**
4-inch depth	0.604**
5-inch depth	0.382*
Coleoptile length vs. seedling height-Average	0.341**
1-inch depth	0.691**
2-inch depth	0.480*
3-inch depth	0.549**
4-inch depth	0.512*
5-inch depth	0.380*
Coleoptile length vs. subcrown internode length-Average	.487**
1-inch depth	0.354
2-inch depth	0.295
3-inch depth	0.256
4-inch depth	0.061
5-inch depth	0.060
Emergence rate index vs. seedling height-Average	.504**
1-inch depth	.659**
2-inch depth	.570**
3-inch depth	.590**
4-inch depth	.730**
5-inch depth	.193

Table 15 (continued)

Characteristics	Correlation coefficient
Emergence rate index vs. subcrown internode length-Average	-.076
1-inch depth	.440*
2-inch depth	.283
3-inch depth	.175
4-inch depth	.247
5-inch depth	.296
Seedling height vs. subcrown internode length-Average	.542**
1-inch depth	.614**
2-inch depth	.580**
3-inch depth	.628**
4-inch depth	.653**
5-inch depth	.780**

*, ** Significant at .05 and .01 levels, respectively.

internode were not significantly correlated either for overall or individual depth means except at one-inch depth.

Allan et al. (1962) reported that coleoptile lengths of winter wheat varieties were positively correlated with their emergence rate index. My study also indicated that coleoptile length, recorded at all planting depths, significantly correlated with the emergence rate index. The highest correlation was obtained with data from the four-inch depth. This is in agreement with Sunderman (1964), Livers (1958), Allan et al. (1961) and Chaudhry and Allan (1963).

A positive correlation between coleoptile length and seedling height reported by Chaudhry and Allan (1963) was verified by this study. The relationship between coleoptile length and subcrown internode length found by Chaudhry and Allan (1966) was corroborated in my study where overall means were used, but not for individual planting depths. However, the subcrown internode length was correlated with seedling height in both cases.

The correlations between mature plant height and other characters studied are given in Table 9 (Page 60). A significant positive correlation between plant height and seedling length, and between plant height and subcrown internode was obtained, when all six winter wheat genotypes were included. Plant height was not significantly correlated with coleoptile length and E.R.I. The correlation between plant height and E.R.I. was highly significant when Crest

was excluded from the calculations. The association of plant height with coleoptile length, E.R.I., and seedling length were highly significant, when both Crest and Cheyenne were excluded. I previously noted that Crest and Cheyenne did not behave as other genotypes with respect to the characteristics under study. The apparent departure of Cheyenne and Crest from what seems to be a general pattern for other genotypes is indicative of the presence of different genetic factors controlling the expression of some characteristics.

The fact that plant height did not significantly correlate with coleoptile lengths of all genotypes indicate that shorter plants with longer coleoptiles can be produced. Crest, considered to be of short stature but having a long coleoptile, is an example.

The association of spring survival with other characters in all genotypes was not significant except with subcrown internode length (Table 10, Page 62). Although this positive correlation shows that longer subcrown internodes, or shallow crowns, are associated with better spring survival, a conclusive statement cannot be made since this experiment was conducted in darkness and crown node establishment is affected by light (Kassowitsch, 1894; Ferguson & Boatwright, 1968). Another study in light is required to make a definite decision regarding the trend of crown node effect, pointed out by these observations.

SUMMARY

The relationship of coleoptile length, emergence rate index (E.R.I.) seedling height and subcrown internode length with field spring survival and mature plant height of six diverse winter wheat genotypes was studied in a dark controlled environment chamber. Average Bozeman, Montana field temperatures for the mid-September to November growth period were applied. The six winter wheat genotypes Cheyenne, Crest, Froid, Itana, MT 6928 and Yogo were planted at one-, two-, three-, four- and five-inch depths and the foregoing characteristics measured and evaluated.

A significant genotype difference was found for planting depths, in general, and for each individual depth when coleoptile length, emergence rate index, seedling height and subcrown internode length were examined.

When averaged across depths, long coleoptiles, high E.R.I.s and tall seedlings were measured in Froid, Yogo and Crest. Short coleoptiles, low E.R.I.s and short seedlings were found in MT 6928, Cheyenne and Itana. Long subcrown internodes were found in Froid and Yogo, while the short subcrown internodes occurred in Itana, MT 6928, Cheyenne and Crest.

In general, when individual planting depths were examined, the longest coleoptile lengths, highest E.R.I.s and seedling heights

were found in Froid, Yogo and Crest with lower values for MT 6928 and Cheyenne.

Coleoptile lengths for each depth differed significantly. The deepest planting (five-inch) had the longest coleoptiles. The percentage increase in the coleoptile length at five-inch depth over that of one-inch planting depth was 42.6%, 41.4%, 36.2%, 33.6%, 31.1% and 16.6% for MT 6928, Yogo, Crest, Itana, Cheyenne and Froid, respectively.

Tall genotypes such as Froid, Yogo and Itana generally had the longest coleoptiles while the semidwarf, MT 6928, had the shortest coleoptiles.

The correlations of coleoptile length, emergence rate index (E.R.I.), seedling height and subcrown internode with the mature plant height were significant when Cheyenne and Crest were excluded in the case of coleoptile length and only Crest excluded for E.R.I. The apparent departure of Cheyenne and Crest from what seemed to be a general pattern for other genotypes was indicative of the presence of different genetic factors controlling the same characters in these genotypes.

The variation in E.R.I. due to genotype X depth interaction was highly significant. The maximum variation of genotypes in emergence rate occurred at the four-inch planting depth, which also generally gave the longest subcrown internode. Under deep plantings,

Itana demonstrated a unique ability to emerge fairly well and to change to a higher rank for seedling height and subcrown internode length.

Seedling height increased with an increase in planting depth up to three inches, and then decreased for four- and five-inch depths.

An examination of the average length of subcrown internode resulted in a descending ranking of Froid, Yogo, Itana, MT 6928, Cheyenne and Crest. When grown in the dark Froid and Yogo exhibited the shallowest crown nodes while Crest, Cheyenne, MT 6928 and Itana had deeper crown nodes. The shallower the seeding, the greater the tendency of long subcrown internode genotypes, such as Froid and Yogo, to form their crowns farther away from the seed. In the case of the one-, two- and three-inch depths, the crown nodes formed above the soil surface, particularly in the case of Froid and Yogo. In the absence of light, the crown node tends to form farther away from the seed.

Generally, tall genotypes, such as Froid and Yogo, had excellent spring survival, long coleoptiles, early and better emergence, and developed shallow crown nodes. Whereas, MT 6928, a shorter genotype, had poor spring survival, short coleoptiles, poor and delayed emergence and deep crown nodes. Itana, a medium tall genotype with

poor spring survival, exhibited medium long coleoptile and E.R.I., but had deep crown nodes.

There were highly significant positive correlations between coleoptile length and seedling height, coleoptile length and subcrown internode length, emergence rate index and seedling height, and between seedling height and subcrown internode length.

A highly significant correlation was noted between coleoptile length and emergence rate index at the three- and four-inch planting depths. The nonsignificant correlation of plant height and coleoptile length indicated the possibility of developing short plants with long coleoptiles.

The positive association of spring survival with subcrown internode length indicated that shallow crown winter wheat genotypes, measured in the dark, exhibit better spring survival. In this regard, a conclusive statement was premature since the crown node establishment could have been affected by the absence of light. A future study of this characteristic in the light was suggested.

STUDY III

THE RELATIONSHIP OF CROWN NODE LOCATION, SECONDARY

ROOT LENGTH AND FOLIAR DRY WEIGHT TO FIELD

SPRING SURVIVAL IN WINTER WHEAT

III. The Relationship of the Crown Node Location, Secondary Root Length and Foliar Dry Weight to Field Spring Survival in Winter Wheat.

This study was conducted to determine the relationship of crown node location, number and length of secondary roots, emergence rate index, seedling height, number of tillers and seedling dry weight to the known level of field spring survival in winter wheat.

MATERIALS AND METHODS

General Methods

The same six winter wheat genotypes as discussed in Materials and Methods of Study II on page 50 were used; Froid, Yogo, Cheyenne, MT 6928, Itana and Crest (Table 5, Page 51). Seeds were planted in four-inch pots, one-, two-, three-, four- and five-inches deep. General methods for this experiment were the same as for Study II.

Diurnal temperatures and day lengths applied in the growth chamber during the germination and seedling stages of winter wheat represented long-time averages at the Bozeman, Montana Field Research Station (Table 1, Page 28).

Observations, Statistical Designs and Analysis

The emergence rate index (E.R.I.) was calculated from the daily seedling emergence counts of the first four days. For the method used to calculate E.R.I., refer to MATERIALS and METHODS of Study II.

The seedlings were carefully removed from the pots 40 days after seeding. The crown node depth, seedling height (from the soil surface to the tip), number and length of secondary roots and the number of visible tillers were recorded. The dry weights of the oven-dried seedlings were taken.

The trial included six genotypes and five planting depths and was conducted with four replications in a randomized complete block design. The pots within each block were rerandomized every third day to eliminate possible position effect inside the growth chamber.

Averages were determined for all pots, each pot was a plot, and these values were used for the analysis of variance for each characteristic. To determine the associations, all possible correlations among the characteristics and among the planting depths, using variates in one depth, were calculated.

RESULTS AND DISCUSSION

Emergence

The emergence rate index (E.R.I.) differed significantly among planting depths and genotypes (Table 16). Crest showed the highest average emergence rate index of 16.6 over all depths (Table 17). Next in order were Yogo, Froid, Itana, MT 6928 and Cheyenne with 15.0, 14.8, 11.8, 11.4 and 11.2 E.R.I.s, respectively.

The highest E.R.I. of 20.2 was calculated for one-inch planting depth, followed by the three-, two-, four- and five-inch planting depths with 15.3, 14.8, 10.8 and 6.2, respectively (Table 18). These results indicated that the shallowest planting gave the highest rate of emergence. With an increase in the planting depth, the rate of emergence decreased significantly.

No significant differences were noted among the genotypes for emergence rate at the one- and five-inch depths (Table 17). At two-, three- and four-inch depths, Crest, Froid and Yogo had the higher rate of emergence, whereas Itana, MT 6928 and Cheyenne had the lower E.R.I.s.

Emergence began five days after planting for the one-inch depth, six, eight, nine and eleven days after for the two-, three-, four- and five-inch planting depths, respectively. The genotype X depth interaction for E.R.I. was nonsignificant which indicates a similar genotype response for planting depths.

Table 16. Mean squares from analysis of variance for various characteristics measured on six winter wheat genotypes planted at five depths in a lighted controlled environment.

Mean squares for:								
Source of	Degrees	E.R.I.	Seedling	Crown	Secondary	Number of	Number	Seedling
			height	node	root	secondary	of	dry
				depth	depth	roots	tillers	weight
Depths	4	665.47**	972.79**	3929.51**	41801.50**	20.43**	24.99**	1.88**
Genotypes	5	104.60**	105.69**	706.30**	4869.20**	2.38**	3.69**	0.12**
Depths X genotypes	20	36.99	10.02	71.53**	1130.42**	0.63**	0.45*	0.03**
Error	87	24.28	8.37	26.25	151.63	0.30	0.24	0.01

*, ** Significant at .05 and .01 levels, respectively.

Table 17. Emergence rate index (E.R.I.) of six winter wheat genotypes planted at five depths in a lighted controlled environment.

<u>Emergence rate index (E.R.I.) and rank, respectively, for plantings depths:</u>															
<u>Genotype</u>	<u>One in.</u>		<u>Two in.</u>		<u>Three in.</u>		<u>Four in.</u>		<u>Five in.</u>		<u>Average</u>				
Froid	23.0	a ^{1/} 1	18.0	a 1	17.3	a 2	11.5	abc 3	4.3	a 5	14.8	ab 3			
Yogo	19.0	a 4	15.8	ab 3	21.0	a 1	14.3	ab 2	4.8	a 4	15.0	ab 2			
Cheyenne	21.5	a 3	15.3	ab 4	13.5	b 4	3.8	c 6	2.0	a 6	11.2	c 6			
MT 6928	17.5	a 6	10.0	b 6	12.8	b 6	10.0	bc 4	6.8	a 3	11.4	c 5			
Itana	18.3	a 5	12.3	ab 5	13.3	b 5	6.5	bc 5	8.5	a 2	11.8	bc 4			
Crest	21.8	a 2	17.8	a 2	14.3	ab 3	18.5	a 1	10.8	a 1	16.6	a 1			

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

Table 18. Average emergence rate index (E.R.I.), seedling height (cm), crown node depth (mm), secondary root length (mm plant) and number, tiller number and foliar dry weight (g) of winter wheat genotypes at various planting depths in a lighted controlled environment.

Planting depths	E.R.I.	Seedling height (cm)	Crown node depth (mm)	Secondary root length (mm)	Secondary root number	Tiller number	Foliar dry weight (g/seedling)
1-inch	20.2 a ^{1/}	31.8 a	17.1 c	106.0 a	2.8 a	3.1 a	0.76 a
2-inch	14.8 b	29.1 b	16.8 c	51.6 b	1.7 b	2.1 b	0.56 b
3-inch	15.3 b	26.4 c	18.2 c	30.6 c	1.4 b	1.8 c	0.39 c
4-inch	10.8 c	21.9 d	29.9 b	10.8 d	0.9 c	0.9 d	0.17 d
5-inch	6.2 d	15.6 e	46.4 a	0.8 e	0.3 d	0.5 e	0.08 e

^{1/} Values within each characteristic followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

The correlation between the emergence rate index and field spring survival was nonsignificant. However, the value rose to significant level ($r = .82$) when Crest was excluded (Table 19). Crest, with low field spring survival, produced highest E.R.I.

The correlation coefficient between emergence rate index and mature plant height was .05 and nonsignificant when all genotypes were included. It rose to .64 when Crest was excluded. Crest behaved differently than others and although it is a medium tall variety, it showed the highest E.R.I. The positive correlation between the E.R.I. and mature plant height corroborated my findings reported in the previous section and those reported by Allan et al. (1962), and Chaudhry and Allan (1963).

Seedling Height

A highly significant variation was found among the genotypes for the seedling height (Table 16). Crest, Yogo and Froid had the tallest seedlings with 27.1, 26.9 and 26.5 cm, respectively (Table 20). Cheyenne, Itana and MT 6928 followed with 24.8, 22.2 and 22.1 cm, respectively.

The seedling height of genotypes within each of the five planting depth varied significantly (Table 20). Generally Crest, Froid and Yogo had the longest seedlings and Itana and MT 6928 the shortest at all depths. The least variation in the seedling height

Table 19. Correlations (r) of various characteristics of winter wheat genotypes with field spring survival in a lighted controlled environment.

Characteristics in growth chamber	Field vs. growth chamber	Field spring survival ^{1/}	
		All genotypes	Genotypes excluding Crest
Emergence rate index (E.R.I.)		.11	.82*
Seedling height		.44	.98**
Crown node depth	.90*		
Crown node depth (3-inch)	.93**		
Crown node depth (Field) ^{2/}		-.97**	
Crown node depth		-.93**	
Crown node depth (3-inch)		-.95**	
Secondary root length	.90*		
Secondary root length (Field) ^{2/}		.99**	
Secondary root length		.67	.96**
Number of roots		.91**	
Number of tillers		.74	
Foliar dry weight		.71	.95**

^{1/} Field spring survival given in Table 5, Page 51.

^{2/} From field data.

*, ** Significant at .05 and .01 levels, respectively.

Table 20. Seedling height (cm) of six winter wheat genotypes planted at five depths in a lighted controlled environment.

Seedling height (cm) and rank, respectively, for planting depths of:													
Genotype	One in.		Two in.		Three in.		Four in.		Five in.		Average		
Froid	32.8	a ^{1/} 3	29.7	ab 3	26.1	abc 3	25.4	a 1	18.6	a 1	26.5	ab 3	
Yogo	33.4	a 2	29.8	ab 2	29.7	ab 2	24.9	a 2	16.8	ab 2	26.9	a 2	
Cheyenne	31.9	ab 4	29.0	ab 4	25.4	abc 4	21.6	a 4	16.3	ab 4	24.8	b 4	
MT 6928	28.8	bc 6	26.9	b 6	23.1	c 6	21.3	a 5	10.7	b 6	22.1	c 6	
Itana	29.6	b 5	27.0	b 5	23.8	c 5	15.8	b 6	14.7	ab 5	22.2	c 5	
Crest	34.1	a 1	32.2	a 1	30.1	a 1	22.4	a 3	16.6	ab 3	27.1	a 1	

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

among the genotypes was observed at four-inch deep planting. The genotype X depth of planting interaction was nonsignificant. Itana, which ranked low at one- to four-inch depths, showed a unique response to deep planting. It rose to the top rank at five-inches depth.

The variation in the seedling height due to depths of planting was highly significant (Table 16). The seedling heights, ranging from 31.8 to 15.6 cm for the one- and five-inch depths, decreased with each increase in planting depth (Table 18, Page 90). This trend held for all genotypes (Table 20).

The correlation between the seedling height and field spring survival was nonsignificant. However, the value rose to highly significant level ($r = .98$) when Crest was excluded (Table 19). Crest, with low field spring survival, produced tall seedlings and behaved differently than other genotypes.

Crown Node Depth

The analysis of variance for crown node depth showed highly significant differences among the genotypes, depths of planting, and the depth X genotype interaction (Table 16, Page 88).

The crown node depths of the six winter wheat genotypes for five planting depths are given in Table 21. Froid and Yogo had the shallowest crown node depths of 16.3 and 21.4 mm while Crest had the

Table 21. Crown node depth of six winter wheat genotypes planted at five depths in a lighted controlled environment.

	<u>Crown node depth (mm) and rank, respectively, for planting depths of:</u>													
<u>Genotype</u>	<u>One in.</u>		<u>Two in.</u>		<u>Three in.</u>		<u>Four in.</u>		<u>Five in.</u>		<u>Average</u>			
Froid	14.9	b ^{1/} 6	12.3	b 6	7.8	d 6	19.3	c 6	27.5	c 6	16.3	d 6		
Yogo	15.4	b 5	13.4	b 5	15.5	c 5	21.0	c 5	41.6	bc 5	21.4	c 5		
Cheyenne	19.5	a 1	18.8	a 3	16.5	c 4	31.6	b 4	46.0	ab 4	26.5	b 4		
MT 6928	17.0	ab 4	16.2	ab 4	21.9	b 2	32.7	b 3	48.8	ab 3	27.3	b 3		
Itana	17.9	ab 2	18.9	a 2	21.9	b 3	34.4	b 2	54.7	ab 2	29.6	b 2		
Crest	17.7	ab 3	21.0	a 1	25.8	a 1	40.4	a 1	59.6	a 1	32.9	a 1		

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

deepest at 32.9 mm. Cheyenne, MT 6928 and Itana had crown depths of 26.5, 27.3 and 29.6 mm, respectively.

Comparing on the depths of planting, the deepest crown development, 46.4 mm, was observed for five-inch deep planting (Table 18).

The next in rank were four-, three-, one- and two-inch depths with average crown node depths of 29.9, 18.2, 17.1 and 16.8 mm, respectively.

The increase in the depth of crown node with increased planting depths was not in the same proportion. With an increase of one-inch from second to third-inch planting depth, the crown node formed only 1.4 mm deep, which was nonsignificant. The increase for the four- over the three-inch planting was 11.7 mm and for the five- over the four-inch planting was 16.5 mm.

The response of genotypes varied with planting depths as shown by highly significant depth X genotype interaction (Table 16). Cheyenne had the shallowest crown node at the one-inch and changed to fourth in rank at the three-, four- and five-inch depths. Crest was third at the one-inch and first with the deepest crowns at all other depths. MT 6928 changed from fourth rank at the one- and two-inch to second at the three-inch and third at the four- and five-inch depths (Figure 5).

The variation for crown node depth among the genotypes within each depth was found significant for all planting depths (Table 21).

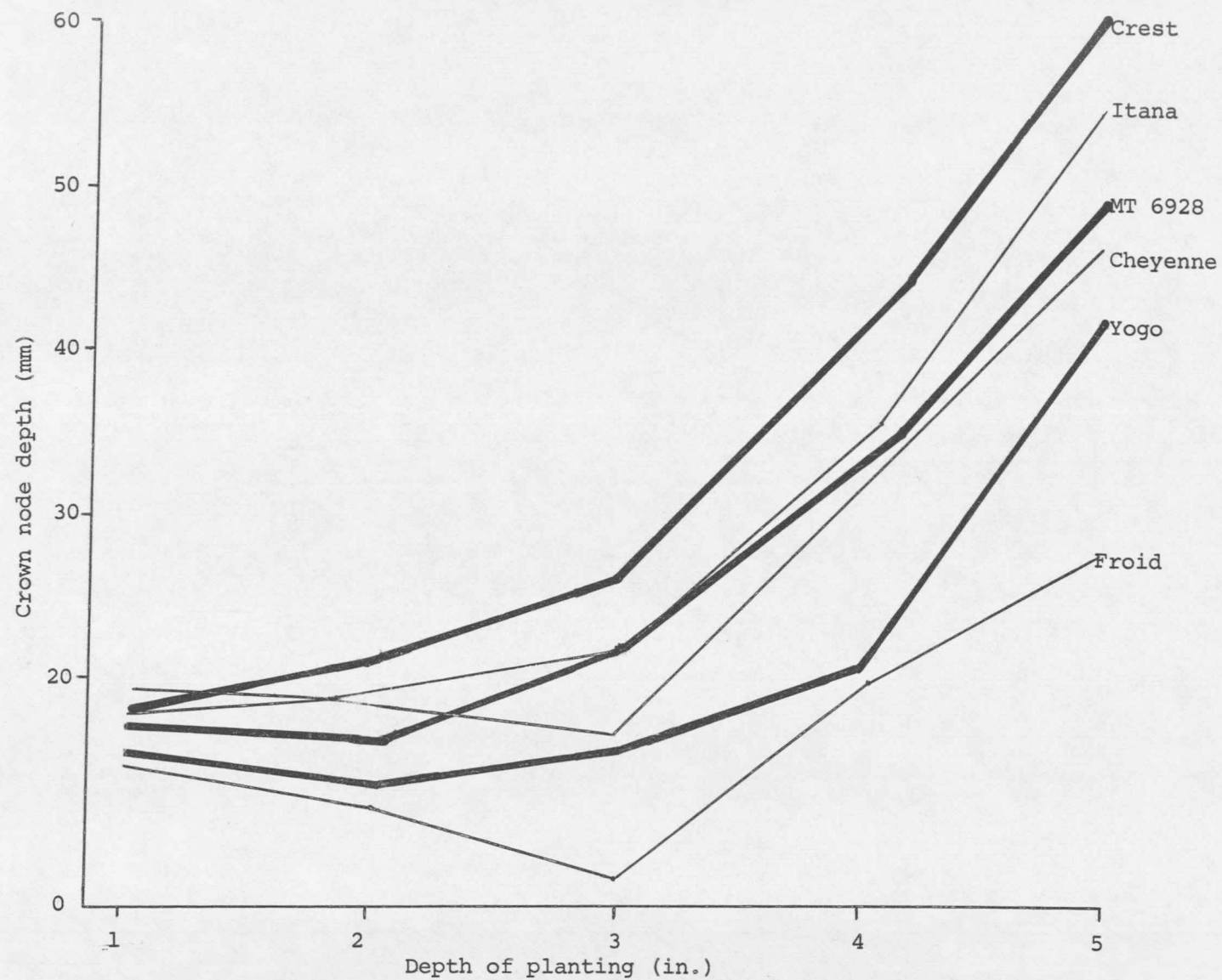


Figure 5. Crown node depth of six winter wheat genotypes planted at five depths.

Crest formed the deepest crowns at two-, three-, four- and five-inch plantings. Froid and Yogo developed shallow crowns at all depths. Itana and MT 6928 showed no significant difference from Crest in crown node depth at one-, two-, four- and five-inch depths. Cheyenne, which showed the deepest crown at one- and two-inches, ranked in the middle at increased depths. The maximum diversity among genotypes for this characteristic was observed at three-inch planting.

The data given in Table 21 showed that crown node depths either decreased or remained at the same level for Froid, Yogo and Cheyenne for the one-, two- and three-inch depths and then increased at further depths. Crest, Itana and MT 6928 exhibited deeper crowns with increasing depths.

Crown node depths of the six winter wheat genotypes, planted about three inches deep, were also measured under field conditions. The average crown depths of 10 seedlings each from six replications were 47.5, 48.9, 52.4, 62.9, 65.4 and 65.4 mm from the soil surface for Froid, Yogo, Cheyenne, MT 6928, Itana and Crest, respectively. In the field, as in the growth chamber, Froid and Yogo showed shallow crowns, Cheyenne was medium and MT 6928, Itana and Crest formed deeper crowns. The correlation between the crown node depths measured in the field and those of the growth chamber (average) was significant ($r = .90$, Table 19, Page 92). It was highly significant when the

values at three-inch depth in the growth chamber was compared with those in the field ($r = .93$).

The correlations of average field spring survival with the average crown node depths in the field and the growth chamber were negative and significant (Table 19). Similar significant associations between the crown node depth in both situations and the field spring survival was found when the survival values of only the year 1971 were used. The significant negative correlations showed that high spring survival was associated with the shallow crown node development. In other words, the findings indicated that as field spring survival increased, the crown tended to form nearer the soil surface. Froid, with the highest average field spring survival of 72 percent, showed the shallowest crown node depth of 16.3 mm in the growth chamber. Crest, however, with the lowest survival of 12 percent developed crowns 32.9 mm from the soil surface.

As indicated in my previous study reported in Section II, those winter wheat genotypes which possess greater field spring survival developed shallow crown nodes and vice versa. My findings are not in agreement with the conclusions of Taylor and McCall (1936) and Webb and Stephens (1936) who reported that winterhardy varieties formed their crowns deeper as compared to nonhardy varieties. Taylor and McCall compared only one winter wheat variety with one spring

wheat variety and used cork mulch. Webb and Stephens drilled the seeds in a field having varied and sub-optimum moisture. Factors, such as light, temperature, soil and soil moisture, and depth of seeding probably influenced the location of crown nodes in their studies.

Secondary Root Length

The analysis of variance in Table 16 (Page 88) indicated highly significant differences among the depths of planting, genotypes and the depth X genotype interaction for secondary root length.

Yogo and Froid had the longest secondary root with 60.6 and 53.8 mm, respectively (Table 22). Cheyenne and Crest was medium with 43.3 and 35.8 mm, while MT 6928 and Itana and the least secondary root lengths with 23.4 and 22.8 mm, respectively.

The one-inch planting depth resulted in the highest total secondary root length of 106.0 mm (Table 18, Page 90). Further increased planting depth consistently reduced root lengths.

The higher total length of secondary roots which developed at the shallower planting depths are in agreement with the findings of Cohen and Tadmor (1969). These results may be attributed to higher temperature prevailing around the region of crown node at shallow planting depths. The increase in root formation with an elevated temperature has been reported by Burns (1972) and Cohen and Tadmor (1969).

Table 22. Secondary root length (mm/plant) of six winter wheat genotypes planted at five depths in a lighted controlled environment.

Secondary root length (mm) and rank, respectively, at planting depths of:													
Genotype	One in.		Two in.		Three in.		Four in.		Five in.		Average		
Froid	131.9	b ^{1/} 2	58.1	ab 2	44.6	a 2	33.3	a 1	1.4	a 2	53.8	a 2	
Yogo	159.6	a 1	62.6	a 1	52.2	a 1	25.8	b 2	3.0	a 1	60.6	a 1	
Cheyenne	130.8	b 3	57.4	ab 3	28.5	b 3	0.0	c 6	0.0	a 6	43.3	b 3	
MT 6928	57.8	d 5	36.0	b 6	20.7	b 5	2.7	c 3	0.0	a 4	23.4	c 5	
Itana	56.4	d 6	40.0	ab 5	14.6	b 6	2.3	c 4	0.5	a 3	22.8	c 6	
Crest	99.5	c 4	55.7	ab 4	23.1	b 4	0.8	c 5	0.0	a 5	35.8	b 4	

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

The comparative response of six winter wheat genotypes under different planting depths showed significant variations (Table 22). The genotypes ranked in four classes for the one-inch depth, three for the two-inch, two for the three-inch, three for the four-inch, and one for the five-inch planting depth. The secondary root length of the genotypes varied with planting depths resulting in a highly significant depth X genotype interaction (Figure 6 and Table 16). Cheyenne ranked third at one-, two- and three-inch depths developed no secondary roots at four- and five-inches. Itana was sixth at one- and three-inch, fourth at four-inch and third in rank at five-inch depth. MT 6928 fifth at one- and three-inches was third and fourth at four- and five-inch depths, respectively.

Secondary root lengths of the six genotypes were also measured under field conditions where the planting depth was about three inches. The average root lengths measured were 52.1, 49.3, 35.7, 21.0, 24.3 and 19.2 mm for Froid, Yogo, Cheyenne, MT 6928, Itana and Crest, respectively. The ranking of the genotypes was similar to that obtained for this character measured in the growth chamber. The field and growth chamber data were significantly correlated ($r = .90$, Table 19, Page 92).

The correlation of secondary root lengths of genotypes obtained under field conditions and the average field spring survival was positive and significant (Table 19). The secondary root length

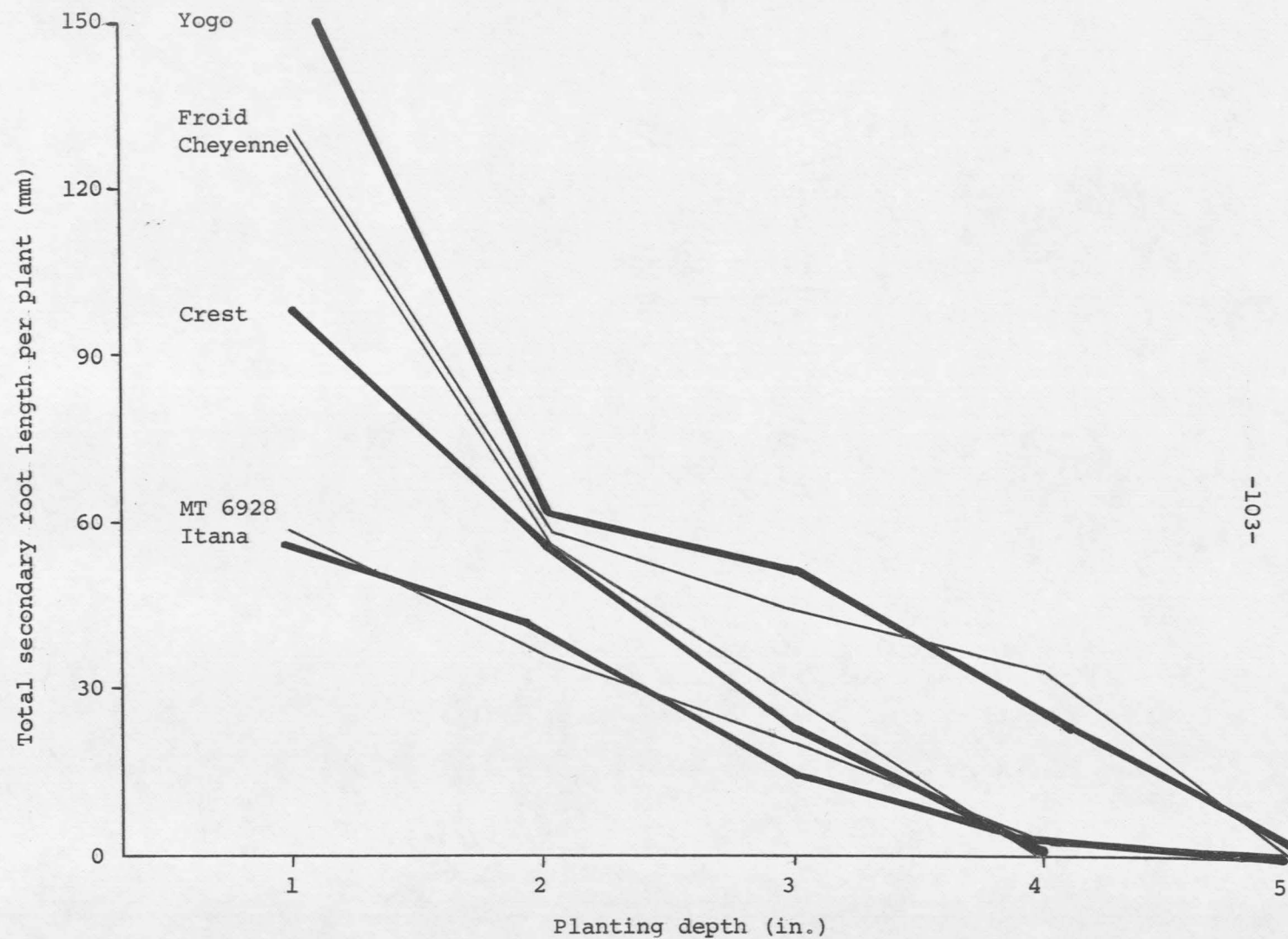


Figure 6. Secondary root length of six winter wheat genotypes planted at five depths.

from the growth chamber also correlated with the average field spring survival. The correlation coefficient was high ($r = .67$), but non-significant. It became highly significant ($r = .96$) when Crest was excluded from the calculation. Crest behaved differently than other genotypes. It has low spring survival, but gave comparatively greater secondary root length. The high positive correlations between the field spring survival and secondary root length indicates that higher spring survival is associated with increased total secondary root length.

The winter wheat genotypes, which possess high spring survival, also had shallow crown formation and increased lengths of secondary roots (Tables 5, 21 and 22). This relationship may be attributed to the influence of a more favourable temperature regime on root growth associated with shallow crowns. As previously discussed, increased secondary roots is a growth characteristic strongly related to spring survival. The importance of secondary root development shown by these studies corroborates the results of Filinger and Cardwell (1941).

Number of Secondary Roots

A highly significant difference was found among the planting depths, genotypes and the depth X genotype interaction for the number of secondary roots (Table 16, Page 88).

Froid and Yogo and the highest number of secondary roots, 1.9 and 1.8 per seedling, respectively. This was significantly greater than Cheyenne, Crest, Itana and MT 6928 with 1.3, 1.2, 1.2 and 1.1, respectively (Table 23).

The number of secondary roots decreased with increased planting depth from 2.8 for the one-inch to 0.3 for the five-inch depth (Table 18, Page 90).

The significant depth X genotype interaction for numbers of secondary roots indicated that genotypes responded differentially to the planting depths. At the one-inch depth Yogo averaged 3.7 secondary roots per plant, while Froid and Cheyenne had 3.2 and 3.18, respectively. Froid had more than Yogo at four-inch depth, while Cheyenne showed lower root number at two- and three-inch and none at four- and five-inch depths (Figure 7).

The correlation of the number of secondary roots and the average field spring survival was positive and significant ($r = .91$, Table 19, Page 92). This indicated that in the six winter wheat genotypes studied, high spring survival was associated with the formation of higher numbers of secondary roots.

Number of Tillers

The analysis of variance of number of tillers per plant showed significant variations among planting depths, genotypes and the depth X genotype interaction (Table 16, Page 88).

Table 23. Number of secondary roots and tillers per seedling of six winter wheat genotypes averaged over five planting depths in a lighted controlled environment.

Genotype	Number of secondary roots			Number of tillers		
	No.		Rank	No.		Rank
Froid	1.9	a ^{1/}	1	2.2	a	1
Yogo	1.8	a	2	2.1	a	2
Cheyenne	1.3	b	3	1.3	c	4
MT 6928	1.1	b	6	1.7	b	3
Itana	1.2	b	5	1.2	c	6
Crest	1.2	b	4	1.3	c	5

^{1/} Values within each characteristic followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

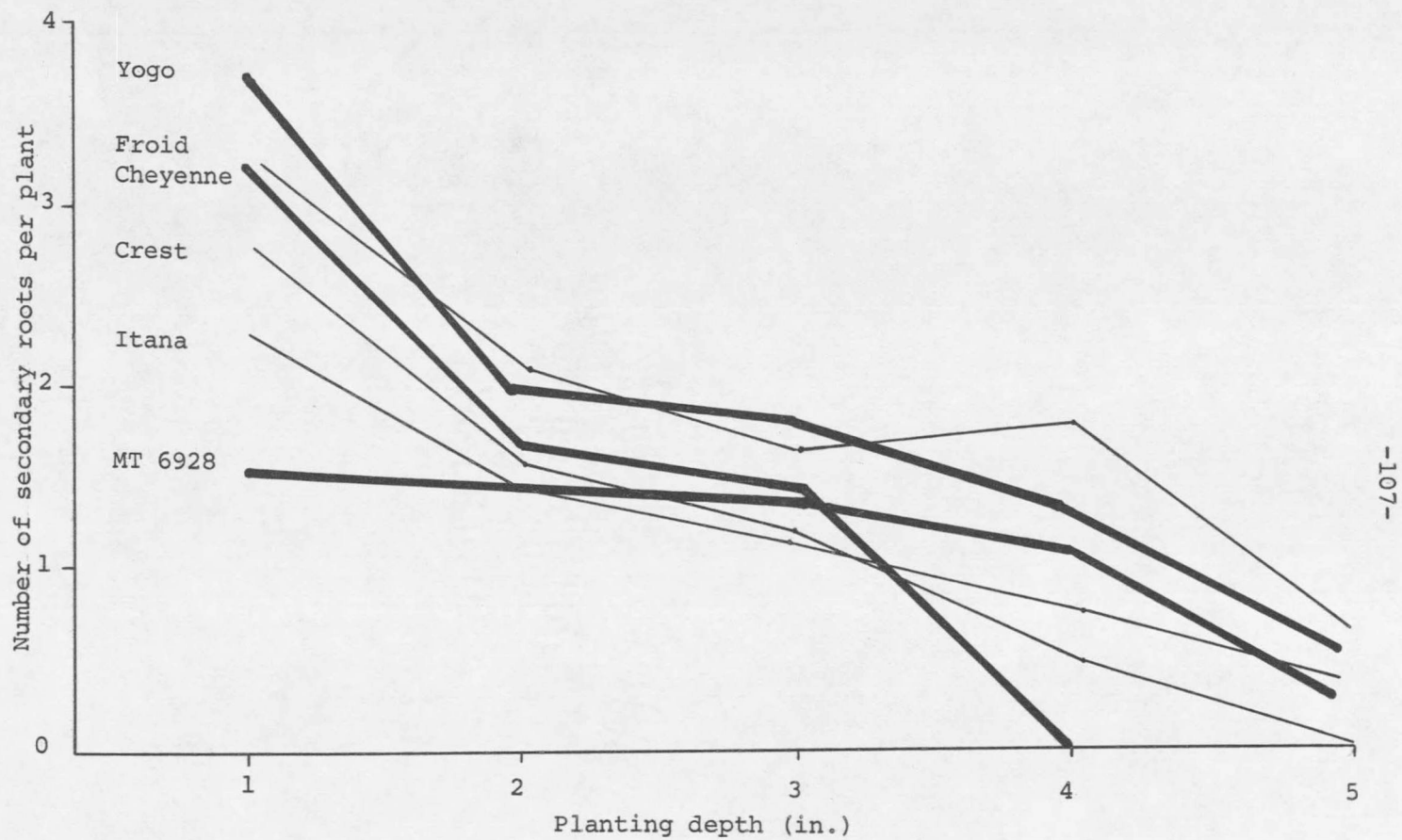


Figure 7. Number of secondary roots of six winter wheat genotypes planted at five depths.

Froid and Yogo had the highest number of tillers per plant, 2.2 and 2.1, respectively. MT 6928 was intermediate with 1.7 and Cheyenne, Crest and Itana had 1.3, 1.3 and 1.2, respectively. MT 6928 showed significantly more tillering than the latter three genotypes (Table 23).

The one-inch planting depth gave the highest number of tillers (3.1) followed by the two-, three-, four- and five-inch depths with 2.1, 1.8, 0.9 and 0.5, respectively (Table 18, Page 90). The results indicated that shallower planting depths were associated with increased tillering. The differential genotype behavior for tiller number at various planting depths is shown in Figure 8. Froid at one-inch depth gave 3.6 tillers per plant, the highest of all other genotypes. It decreased to 1.2 at three-inch depth, the lowest value for all five winter wheat genotypes. Itana was the lowest at one- to three-inch depths, the fourth at four-inch and third at the five-inch planting depth.

The number of tillers per seedling of the genotypes and their field spring survival were positively correlated ($r = .74$, Table 19, Page 92). The genotypes with high spring survival were found to produce greater number of tillers. The nonsignificant r -value may be due to the response of MT 6928 which has poor spring survival but gave high number of tillers.

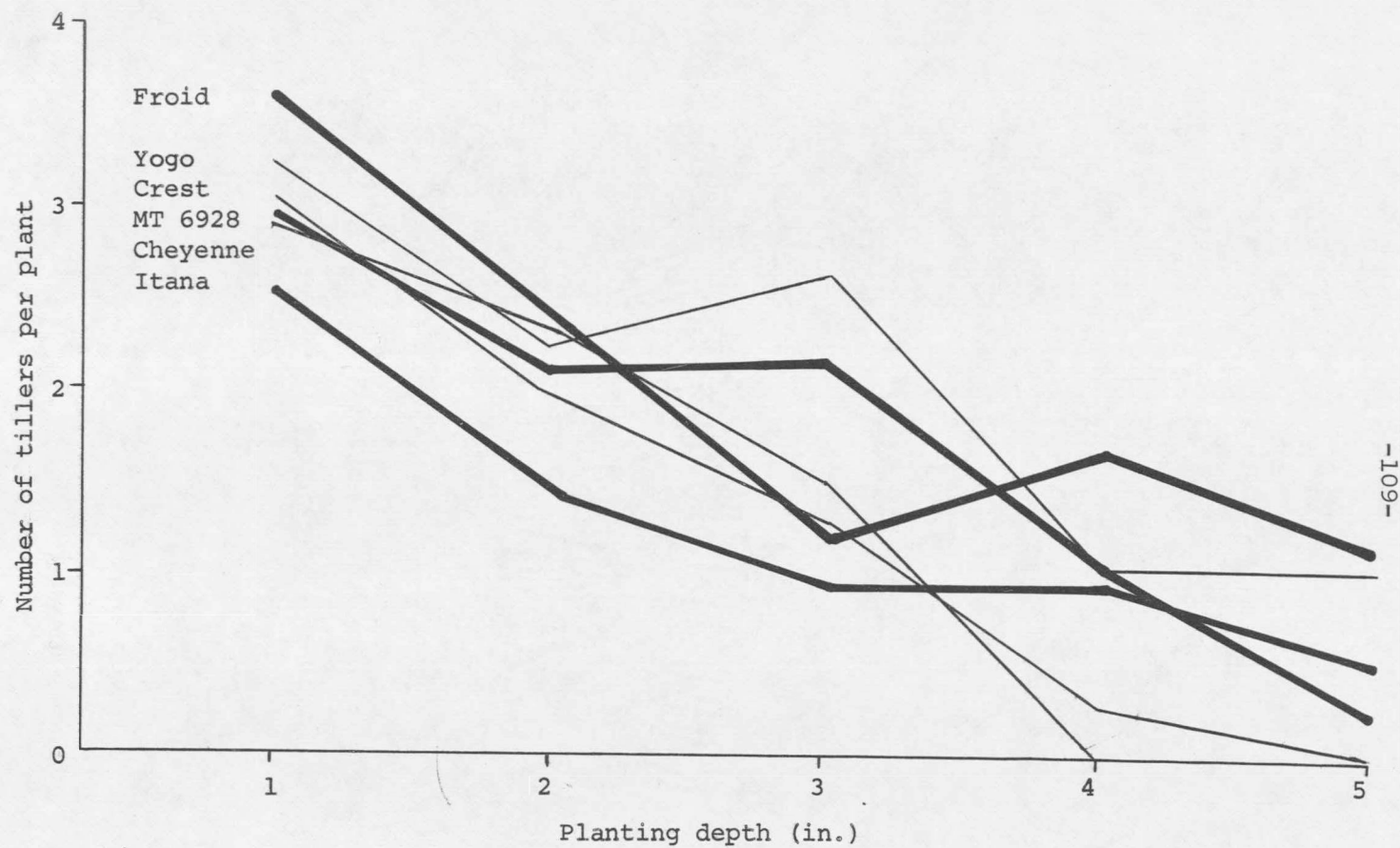


Figure 8. Number of tillers per plant of six winter wheat genotypes planted at five depths.

Dry Weight of Seedlings

Highly significant differences were found among planting depths, genotypes and the depth X genotypes interaction for the foliar dry weight per seedling (Table 16, Page 88).

Froid had the highest dry weight of .50g, significantly higher than Yogo (.44g), Cheyenne and Crest (.40g each). Itana and MT 6928 gave the lowest seedling dry weight of .30g each (Table 24).

Dry weight decreased with increased planting depths from .76g for one-inch to .08g for the five-inch level (Table 18, Page 90).

The seedling dry weight of the six winter wheat genotypes are compared in Table 24. Froid was the highest at all planting depths except five-inches. The rankings for seedling dry weight varied for Itana and MT 6928 (Figure 9). Both ranked at or near the bottom at the one-, two- and three-inch depths. MT 6928 was intermediate at four- and five-inches and Itana rose to first rank at the five-inch depth. Cheyenne, second at one-inch depth, was first at two inches, intermediate at three-inches, and ranked at bottom for the four- and five-inch depths. In this experiment, as in the experiment II, grown in darkness, Itana showed a unique behaviour of better performance at deep planting depths.

The correlation of seedling dry weight with the average field spring survival was nonsignificant ($r = .71$). This correlation was highly significant ($r = .95$) when Crest was excluded from the

Table 24. Foliar dry weight per seedling (g) of six winter wheat genotypes planted at five depths in a lighted controlled environment.

Foliar dry weight (g/seedling) and rank, respectively, for planting depths of:																		
Genotype	One in.			Two in.			Three in.			Four in.			Five in.			Average		
Froid	.99	a	<u>1</u> / 1	.66	a	1	.55	a	1	.23	a	2	.07	abc	4	.50	a	1
Yogo	.74	bc	2	.65	a	2	.52	ab	2	.24	a	1	.06	bc	5	.44	b	2
Cheyenne	.87	ab	4	.59	a	4	.40	bc	3	.08	b	6	.04	c	6	.40	b	3
MT 6928	.54	d	6	.40	b	6	.32	c	4	.16	ab	4	.10	ab	2	.30	c	5
Itana	.59	cd	5	.44	b	5	.25	c	6	.10	b	5	.11	a	1	.30	c	6
Crest	.84	ab	3	.62	a	3	.29	c	5	.19	ab	3	.08	abc	3	.40	b	4

^{1/} Values within each depth followed by the same letter do not differ significantly at the .05 level of significance according to Duncan's Multiple Range test.

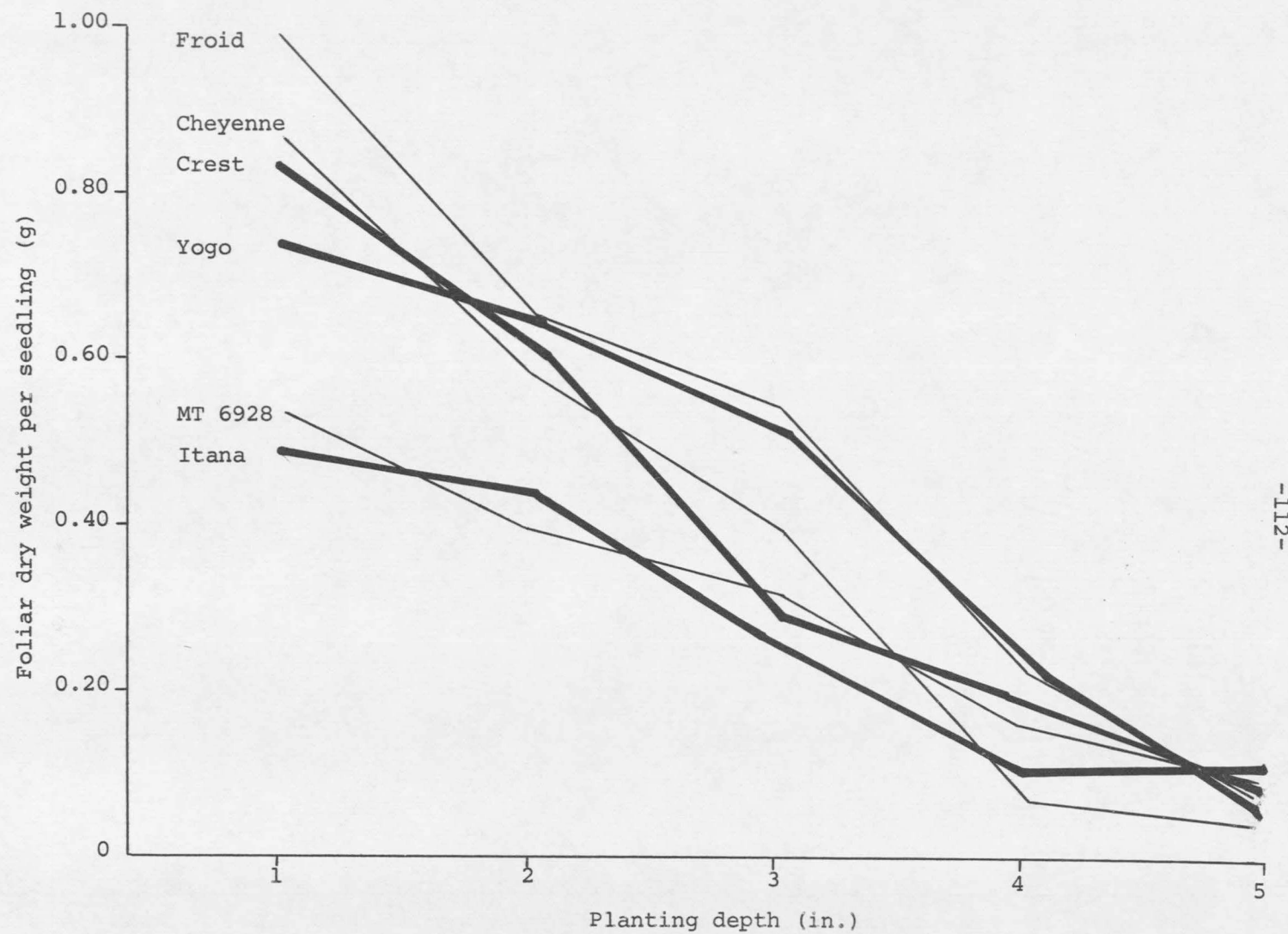


Figure 9. Dry weight of seedlings of six winter wheat genotypes planted at five depths.

calculation (Table 19, Page 92). The response of Crest, a variety with poor winterhardiness showing a medium seedling dry weight, was different than other genotypes and seemed to be controlled by a different genetic mechanism.

Association of Characteristics

Seedling height, crown node depth, secondary root length and root number, number of tillers, emergence rate and seedling dry weight of six winter wheat genotypes were correlated (Table 25).

Seedling height was found to be positively correlated with secondary root length and number, emergence rate index, number of tillers, and dry weight of seedling (Table 25). A highly significant negative correlation ($r = -.74$) was obtained between seedling height and crown node depth. The correlation, although confounded by the planting depths and genotypes, revealed that the genotypes with greater seedling heights tend to develop crown nodes nearer the soil surface.

Crown node depth was significantly and negatively correlated (Table 25) with secondary root length ($r = -.58$) and number ($r = -.67$), with emergence rate index ($r = -.43$), number of tillers ($r = -.71$) and with foliar dry weight ($r = -.68$).

Secondary root length had highly significant positive correlations with number of roots and tillers, emergence rate index and

Table 25. Correlations among various characteristics of six winter wheat genotypes planted at five depths in a lighted controlled environment.

Characteristics	Seedling height	Crown node depth	Secondary root length	Secondary root number	Number of tillers	E.R.I. ^{1/}	Seedling dry weight
Seedling height	1.000						
Crown node depth	-.738**	1.000					
Secondary root length	.736**	-.575**	1.000				
Secondary root number	.747**	-.665**	.866**	1.000			
Number of tillers	.782**	-.710**	.786**	.838**	1.000		
E.R.I. ^{1/}	.691**	-.431**	.604**	.603**	.626**	1.000	
Seedling dry weight	.837**	-.675**	.879**	.825**	.842**	.738*	1.000

*, ** Significant at .05 and .01 levels, respectively.

^{1/} E.R.I. is emergence rate index; see MATERIALS AND METHODS.

seedling dry weight (Table 25). Similarly, the correlations of the number of secondary roots with the tiller number, emergence rate index and seedling dry weight were significant and positive.

A high positive correlation was observed between tillering and emergence, tillering and dry weight of seedlings and emergence rate index and dry weight. These associations showed that high tillering genotypes may emerge fast and produce high dry weights.

Generally, the correlations in Table 25 show that rapid emergence of the six winter wheat genotypes studied is associated with tall seedlings, development of shallow crown nodes, more and longer secondary roots, increased tillers, and higher seedling dry weight.

The negative correlation between crown node depth and length of secondary roots indicated that shallow crowns are associated with increased development of secondary roots. It was observed that quantity of roots for all genotypes generally decreased as the planting depth increased. As previously indicated, the development of secondary roots may be the result of more suitable temperature at upper levels of soil. Better root formation may be an important factor in winter-hardiness of winter wheat.

SUMMARY

The relationships of emergence rate index (E.R.I.) seedling height, crown node depth, secondary root length and number, number of tillers and seedling foliar dry weight of plants grown in a controlled environment with field spring survival of six diverse winter wheat genotypes were studied. Average field temperatures and photoperiods for the mid-September to November field growth period were applied. The six winter wheat genotypes, Froid, Yogo, Cheyenne, MT 6928, Itana and Crest were planted at one-, two-, three-, four- and five-inch depths and the above characteristics measured.

Significant differences among the planting depths and genotypes were found for all the characteristics studied. The depth X genotype interactions were significant for crown node depth, secondary root length, number of secondary roots and tillers, and seedling dry weight.

Crest, Yogo and Froid had the highest emergence rate indices and seedling heights, whereas MT 6928 had the lowest.

Froid and Yogo were generally in the top rank regarding secondary root length, number of secondary roots and tillers. Cheyenne was medium and Itana was at the bottom. MT 6928 had the lowest secondary root length and number, but was second in rank for the number of tillers. Froid and Yogo had the shallowest crown nodes with Cheyenne, Itana, and MT 6928 intermediate, and Crest the deepest.

Dry weight of seedling was highest for Froid, intermediate for Yogo, Cheyenne and Crest, and was lowest for MT 6928 and Itana.

The shallowest planting showed the highest E.R.I., the tallest seedlings, the shallowest crowns, the longest secondary roots, the most secondary roots and tillers and the highest seedling dry weight. These characteristics decreased as the planting depth increased.

In general, when individual planting depths were examined, the highest E.R.I.s and seedling lengths were found in Crest, Yogo and Froid. Shallowest crowns, greatest root length and number, and the highest dry weight were observed in Froid. Crest formed the deepest crowns.

Emergence began five days after planting for one-inch depth, six, eight, nine and eleven days after for the two-, three-, four- and five-inch planting depths, respectively. The depth of crown increased with increasing planting depth but not in the same proportion.

The correlation of E.R.I. and seedling height with the mature plant height was nonsignificant for all genotypes, but was positive and high ($r = .64$) when Crest was excluded.

The significant and negative correlation of the crown node depth with field spring survival indicated that hardy winter wheat genotypes tend to develop shallower crowns than nonhardy genotypes.

The ranking of the genotypes for crown node depth and secondary root length measured under field situation was similar to that obtained for the growth chamber. The results of both situations significantly correlated with each other both for crown node depth and secondary root length.

The positive correlation of tiller number and root number with the field spring survival showed that high spring survival was associated with the formation of higher number of secondary roots and the production of more tillers,

The association of seedling dry weight and the field spring survival was positive and significant for the genotypes Froid, Yogo, Cheyenne, MT 6928 and Itana.

The correlations of E.R.I., seedling height, secondary root length and foliar dry weight of winter wheat genotypes studied with the field spring survival were nonsignificant. The correlations were significant when Crest was excluded. The response of Crest, as previously indicated, was due to its high rank regarding these characteristics, but possessing the low spring survival. Crest showed the deepest crown node of all genotypes. This may be a major contributory factor towards poor spring survival in Crest.

All the characteristics under study were found to be significantly correlated with one another. Crown node depth showed negative correlations while all others were positively correlated. The values

indicated that shallow crown nodes were associated with fast emergence, tall seedlings, long and more secondary roots, high tillering and increased seedling dry weights.

GENERAL SUMMARY OF STUDIES
I, II AND III.

The developmental morphology of five diverse winter wheat genotypes was studied by examining the apical meristem at various leaf stages of plants grown in controlled environments and field situations. This allowed the determination of the relationship of external leaf morphology and the apical meristem.

Winter wheat remained in the vegetative stage from germination to the appearance of the fifth leaf. The transitional stage was short-lived occurring during the expansion of the fifth leaf. The reproductive stage began with the appearance of the sixth leaf. Genotype developmental growth was similar in the vegetative and transitional stages and varied in the reproductive stage. The developmental stages were similar in greenhouse and field-grown plants. All field-grown genotypes entered and left the winter period at the same stage of growth ruling out the possibility of varied developmental stages being a cause for differential spring survival. Visual observation was a good measure to determine the plant development stages.

The relationship of various morphological characteristics of six diverse winter wheat genotypes to the mature plant height and field spring survival was studied in controlled environments with and without light. Froid, Yogo, Cheyenne, Itana, MT 6928 and Crest having 72, 64, 50, 27, 21 and 12 percent field spring survival, respectively, were planted at one-, two-, three-, four- and five-inch

depths. These genotypes differed in coleoptile length, E.R.I., seedling height, crown node depth, secondary root length, number of secondary roots, number of tillers and foliar dry weight, in both light and dark environments. Froid, Yogo and Crest had long coleoptiles, high E.R.I.s and tall seedlings but MT 6928, Cheyenne and Itana had short coleoptiles, low E.R.I.s and short seedlings.

In both dark and light, Froid and Yogo developed the shallowest crown nodes, followed by Cheyenne, MT 6928, Itana and Crest in light. In the dark Cheyenne and Itana switched their positions.

In the lighted environments, the highest seedling dry weight was measured for Froid, intermediate for Yogo, Cheyenne and Crest and was the lowest for MT 6928 and Itana. Froid and Yogo generally were in the top rank regarding secondary root length, number of secondary roots and tillers, Cheyenne was intermediate, followed by Itana. MT 6928 had the lowest secondary root length and number, but was second in rank for the number of tillers.

The planting depths varied significantly for all the characters both in the light and dark except at the three- and four-inch depths for coleoptile length. In the light the shallow plantings showed the highest E.R.I., the tallest seedlings, the shallowest crowns, the longest secondary roots, the most secondary roots and tillers and the highest seedling dry weight. These characteristics decreased as the planting depth increased. In general, individual

planting depths exhibited greater coleoptile lengths in the dark, higher E.R.I.s and seedling heights both in the dark and in the light for Froid, Yogo and Crest.

The depth X genotype interactions were significant for E.R.I. in the dark and for crown node depth, secondary root length, number of secondary roots and tillers and foliar dry weight in the light.

In the dark, the crown nodes tended to form farther away from the seed. In the case of one-, two- and three-inch depths, the crown nodes, particularly of Froid and Yogo, formed above the soil surface.

The ranking of the genotypes for the crown node depth and secondary root length measured under field situation was similar to that obtained for the lighted growth chamber.

All the characteristics studied except E.R.I. and subcrown internode length in the dark were significantly correlated with one another. Shallow crowns were associated with fast emergence, tall seedlings, long and more secondary roots, high tillering and increased seedling dry weight.

In the dark, the mature plant height was significantly associated with seedling height and subcrown internode length and non-significantly correlated with coleoptile length and E.R.I., whereas in light the correlation was not significant with any characteristic. The nonsignificant correlation of plant height and coleoptile length

indicated the possibility of developing short plants with long coleoptiles.

In both dark and light the crown node depth was significantly and negatively associated with the field spring survival of the winter wheat genotypes.

In the dark, the coleoptile length, E.R.I. and seedling length had no significant association with the field spring survival.

In the light, the secondary root length and number were positively and significantly associated with the field spring survival. The correlations of foliar dry weight, E.R.I., and seedling height with the spring survival were positive and nonsignificant. This association was significant when Crest was excluded. This is because of the unique response of Crest, which possesses the lowest field spring survival but ranked high in these characteristics.

The association of crown node depth, secondary root length and E.R.I. with field spring survival suggested screening for these characteristics in winter wheat breeding programs.

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