



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
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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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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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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.

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 -15C 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 hardiness.

Dexter (1934) reported an inverse correlation between hardiness and soluble salts in winter wheat. In general, hardiness 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 hardiness. 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.

