



Inheritance of subcrown internode length in five winter wheat crosses  
by Willard Galen Thompson

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree Of  
MASTER OF SCIENCE in Agronomy  
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Abstract:

Eight winter wheat cultivars and the F<sub>i</sub> and F<sub>2</sub>- generations of five crosses among the cultivars were used in studying the inheritance of subcrown internode length (internode between coleoptilar node and the third node above). Crosses included 'Yogo' X 'Nugaines'; MT 6928 X 'Froid'; MT 6928 X Crest-34; 'Yogo' X Yogo SS; and 'Winoka' X 'Cheyenne'. Standard errors were calculated by pooling sums of squares over parents and nesting them across blocks. The standard errors were used to delineate statistically different phenotypic groups in the F<sub>2</sub> frequency distribution, providing estimates of gene numbers.

Gene action was determined by using Student's t-test to show whether the F<sub>1</sub> was equal to one of the parents (dominance), the midparent (additivity), or, greater or less than either parent (heterosis).

Three of the crosses indicated heterotic gene action, one gave no estimate, and one indicated dominance for long subcrown internodes. The latter cross was the only one which gave an estimate of gene numbers. At least two genes were determined to influence subcrown internode length.

Correlations were calculated for several anatomical characteristics in the F<sub>2</sub> generation. The number of plants emerged was positively correlated with individual seed weight. Emergence date was negatively correlated with subcrown internode length in three of five crosses, indicating that in some crosses early emergence may be used as a selection criterion for long subcrown internodes. Emergence date was negatively correlated with seedling length in all five F<sub>2</sub>'s. Selection of early emerging types should therefore result in tall seedlings. Seedling length was positively correlated with subcrown internode length in three of the five F<sub>2</sub>'s and negatively with another. This sign reversal of the correlations could be due to linked genes in the coupling stage for the positive correlations and in repulsion for the negative correlation.

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Date October 19, 1973

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IN FIVE WINTER WHEAT CROSSES

by

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A thesis submitted to the Graduate Faculty in partial  
fulfillment of the requirements for the degree

of

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in

Agronomy

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## ABSTRACT

Eight winter wheat cultivars and the  $F_1$  and  $F_2$  generations of five crosses among the cultivars were used in studying the inheritance of subcrown internode length (internode between coleoptilar node and the third node above). Crosses included 'Yogo' X 'Nugaines'; MT 6928 X 'Froid'; MT 6928 X Crest-34; 'Yogo' X Yogo SS; and 'Winoka' X 'Cheyenne'. Standard errors were calculated by pooling sums of squares over parents and nesting them across blocks. The standard errors were used to delineate statistically different phenotypic groups in the  $F_2$  frequency distribution, providing estimates of gene numbers.

Gene action was determined by using Student's t-test to show whether the  $F_1$  was equal to one of the parents (dominance), the midparent (additivity), or, greater or less than either parent (heterosis).

Three of the crosses indicated heterotic gene action, one gave no estimate, and one indicated dominance for long subcrown internodes. The latter cross was the only one which gave an estimate of gene numbers. At least two genes were determined to influence subcrown internode length.

Correlations were calculated for several anatomical characteristics in the  $F_2$  generation. The number of plants emerged was positively correlated with individual seed weight. Emergence date was negatively correlated with subcrown internode length in three of five crosses, indicating that in some crosses early emergence may be used as a selection criterion for long subcrown internodes. Emergence date was negatively correlated with seedling length in all five  $F_2$ 's. Selection of early emerging types should therefore result in tall seedlings. Seedling length was positively correlated with subcrown internode length in three of the five  $F_2$ 's and negatively with another. This sign reversal of the correlations could be due to linked genes in the coupling stage for the positive correlations and in repulsion for the negative correlation.

## INTRODUCTION

Crown node placement is a suggested anatomical adaptive characteristic related to winter survival in winter wheat (Triticum aestivum L. em Thell) and frost tolerance in spring wheat. Both environmental and genetical factors play roles in plant growth and development, but from a plant breeding viewpoint, only characters which are passed from generation to generation in a clear cut manner (highly heritable) lend themselves to genetic manipulation.

Although crown node placement, which is equated with sub-crown internode length or crown depth, is influenced by environmental factors, knowledge of genetic systems influencing this characteristic may be of practical importance. Breeding for specific, adapted subcrown internode lengths may be a major concern in developing new wheat cultivars. In addition, the possible correlation of subcrown internode length with other plant characteristics might yield valuable genetic information for use in plant breeding programs.

The purpose of this study was to examine the mode of inheritance of subcrown internode length utilizing five crosses involving eight winter wheat cultivars. Additionally, the relationship of subcrown internode length to

other morpho-developmental characteristics of winter wheat was investigated.

## LITERATURE REVIEW

Variation in subcrown internode length may be attributed to either genetical effects or environmental factors, or to the interaction between genetical and environmental effects. The impact of various environmental factors has been studied in reasonable detail. When the soil temperature was lowered from 24 to 12 C by Taylor and McCall (1936), the subcrown internode lengths of 'Hard Federation' spring wheat and 'Turkey' winter wheat were reduced from  $31.7 \text{ mm} \pm 0.51$  to  $12.3 \text{ mm} \pm 0.32$ , and from  $22.3 \text{ mm} \pm 0.42$  to  $3.9 \text{ mm} \pm 0.21$ , respectively. The effects of planting depth and soil temperature were interrelated. Differences between cultivars were greatest when seeding depth was 18 mm as opposed to 45 mm, and the soil temperature was 12 C as compared to 15, 20, and 24 C. Genetic variation is suggested by the fact that the winter cultivar consistently had a shorter subcrown internode than the spring cultivar. They also reported the formation of single coleoptile tillers from coleoptile axillary buds, which formed a deeper crown than the primary culms. They concluded that if the main crown was injured by low temperature, soil heaving, winds, or grazing livestock, the coleoptile tiller might remain to produce a plant.

Webb and Stevens (1936) reported that higher temperatures and shallow seeding produced shallow crowns. In addition, they reported a developmental abnormality associated with planting depth and temperature. Among cultivars they found that from 6 to 79% of the plants observed had two elongated internodes below the soil surface and from 0 to 13% had three. This phenomenon was observed more frequently under conditions of deep seeding and/or high temperature. These field data were difficult to interpret due to uncontrollable temperature, brevity in recording temperature, and variability in depth of seeding.

Significant genotypic and planting depth differences for subcrown internode length were found among six winter wheat cultivars by Ashraf (1973). Maximum diversity among cultivars was found at the 7.5 cm planting depth compared to 2.5, 10.0, and 12.5 cm depths. High negative correlations (significant at  $P = .01$ ) were reported between crown depth and average winter survival for both growth chamber ( $r = -.93$ ) and field ( $r = -.97$ ) experiments. Additionally, crown depth was significantly ( $P = .01$ ) associated with seedling height ( $r = -.74$ ) and emergence rate index

( $r = -.43$ ). The growth chamber studies were significantly ( $P = .01$ ) correlated ( $r = .93$ ) with field studies.

The adaptive significance of deep crowns may involve more than winter survival. Sallans (1961) reported that deep spring wheat crowns may confer an escape type of resistance against pathogenic fungi, such as Helminthosporium sativum P.K. and B. (Bipolaris sorokiniana [Sacc. in Sorok. (Shoemaker)]), and Fusarium spp. which penetrate roots. Furthermore, in field observations with spring wheat, he reported that wheat cultivars with shallow crowns were differentially killed by spring frost and restricted in crown (adventitious) root development under conditions of dry top soil.

Genetic studies suggest subcrown internode length is conditioned by relatively few loci, but there is variation in the nature of gene action. McKenzie (1971) studied the inheritance of subcrown internode length in six crosses involving four spring wheat cultivars. He concluded that two genes, showing no dominance, influenced subcrown internode length. Single gene  $F_1$  heterosis, based on midparent values, was found in all crosses involving one of the cultivars.

Sallans (1961) reported standard errors for depth to crown of 2.57, 1.66, and 2.47 mm in single plant lines of three selected spring wheat cultivars. He studied sub-crown internode length in 49  $F_9$  and  $F_{10}$  lines, developed from the cross 'Thatcher' X 'Reward', which have short (27 mm) and long (45 mm) subcrown internodes, respectively. The lines had mean subcrown internode lengths ranging from the short parent to the long parent. The 49 lines were grouped into three distinct groups based on internode length. One group was not significantly different from the mean of the short parent, another from the mean of the long parent and the third was between, but significantly different, from both parental means.

The fundamental concepts of quantitative genetic variation have been developed by Mather (1949). In the simplest cases, at least three parameters must be defined. The midparent,  $m$ , is defined as the average of two parents. In a single locus, diploid case, this would be the average effect of two alleles. Additive gene effect or gene action is described in terms of the departure ( $d$ ) of either homozygote (i.e., parent) from  $m$ . In theory,  $m = 0$ , and homozygous parents deviate symmetrically from  $m$ . Thus, the

additive effect,  $d$ , is assigned either a positive or negative value. Dominance is defined as the departure of the  $F_1$  from  $m$  and is designated  $h$ .

According to Mather and Jinks (1971), complete dominance places  $h$  equal to either  $+$  or  $-d$ . They expanded this point by stating that crossing two strains, which breed true for a given character, will produce a heterozygous  $F_1$  which, if gene action is completely additive, will have a mean equal to  $m$ . The  $F_1$  mean would equal  $\pm d$  if gene action were completely dominant. An  $F_1$  mean between  $h$  and  $+d$  or between  $h$  and  $-d$  would indicate partial dominance.

## MATERIALS AND METHODS

### Genetic Materials

Eight winter wheat cultivars and the F<sub>1</sub> and F<sub>2</sub> generations of five crosses among the cultivars were used in an attempt to determine the inheritance of subcrown internode length.

The parents were chosen for reported differences in subcrown internode length (Ashraf, 1973). They included: (a) 'Nugaines' (C.I. 13968), a semidwarf soft white winter wheat with poor winterhardiness, late maturity and short subcrown internodes; (b) MT 6928 (TX 55-391-56-D8/WMT, 2-11-4-3), an early maturing, semidwarf Montana line with poor winterhardiness and short subcrown internodes; (c) 'Yogo' (C.I. 8033), a tall, late maturing cultivar with excellent winterhardiness and long subcrown internodes; (d) Yogo SS (Norin 10/Brevor//3\*YG, 1-2-3-1), a semidwarf backcross derived selection with short to intermediate subcrown internodes; (e) 'Froid' (C.I. 13872), a tall cultivar with excellent winterhardiness, late maturity, and long subcrown internodes; (f) 'Cheyenne' (C.I. 8885), a tall, late maturing cultivar with fair winterhardiness and intermediate to long subcrown internodes; (g) Crest-34, a line row component of 'Crest', with short subcrown internodes; and

(h) 'Winoka' (C.I. 14000), a tall, late maturing cultivar with good winterhardiness and intermediate length subcrown internodes.

The above cultivars were crossed in the following combinations:

Yogo (L*)	X	Nugaines (S)
MT 6928 (S)	X	Froid (L)
MT 6928 (S)	X	Crest-34 (S)
Yogo (L)	X	Yogo SS (S)
Winoka (I)	X	Cheyenne (I-L)

(\*L = long (70-75 mm), I = intermediate (55-60 mm), and S = short (45-50 mm) subcrown internodes, respectively)

The F<sub>1</sub> seed was a "bulk" of a number of hand crosses with the F<sub>2</sub> seed produced from the bulked F<sub>1</sub>. Parental seed used was not from the plants originally used in the crosses.

#### Experimental Design

Parents, F<sub>1</sub>'s and F<sub>2</sub>'s were planted 75 mm deep on a one and one-half inch grid, in a walk-in growth chamber. A 1:1 sifted, sterilized mixture of Amsterdam silt loam soil and peat was used in the six inch deep bench. A light gradient of 1,000 foot candles at the center of the growth

chamber to 700 foot candles at the perimeter was measured during the course of the experiment. The center of the growth chamber was about 2 C warmer than the perimeter.

Two blocks were used to maximize ability to account for the light and temperature effects. The five crosses were randomized within each block. There were 17, 17, 11, and 166 seeds of the P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, and F<sub>2</sub> generations, respectively, planted at random within each cross. Thus, 422 seeds per cross with a total of 2,110 seeds were planted for all generations, all crosses, and both blocks.

#### General Methods

A diurnal temperature of 18/7 C (day/night) was used to approximate fall field conditions from September 18 to October 3 (Ashraf, 1973). The photoperiod was 13 hours for the first 12 days after planting, then 16 hours until the plants were harvested.

Plants were harvested approximately 8 weeks (53 days) after seeding. This period of growth is adequate for permanent crown placement (Taylor, 1973; McKenzie, 1971; Taylor and McCall, 1936). Seedlings were marked at the soil surface with a felt tipped pen. Next, a cube of soil containing 8 to 10 seedlings was removed and seedlings

separated from the soil by shaking. Seedling length, defined as distance in mm from the caryopsis to the seedling tip was scored on all plants. Similarly, subcrown internode length, measured as the distance in mm from the seed to the subsurface node, and crown depth, measured as the distance from the subsurface node to the soil surface (indicated by the mark noted above) were recorded. Emergence was recorded as days after appearance of the first coleoptile. The identity of each seedling was retained by its original row-column designation.

Examination of plants at harvest revealed the presence of both one and two nodes between the seed and soil surface. Calculations involving subcrown internode length were based solely on single node plants. Other calculations used both single and double noded individual plant data.

Means and variances of subcrown internode length were calculated for each generation in each block from single plant observations. Significant differences among parents,  $F_1$ 's, and  $F_2$ 's were determined using Student's t-test with nested error terms. The nested error permitted error estimates from more than one block by pooling

sums of squares within blocks and nesting them between blocks.

Correlations ( $r$ ) for seed weight versus number of emerged plants, subcrown internode length, seedling length, and emergence date were calculated with means of  $P_1$ ,  $P_2$ ,  $F_1$ , and  $F_2$ . Correlations for emergence date versus subcrown internode length and seedling length, as well as seedling length and subcrown internode length were estimated with data from individual plants for each generation within each cross.

Contingency chi-square methods were used to test the independence of emergence and parentage among the  $F_2$  populations. Similar methods were used to test the independence of number of double noded plants and  $F_2$  populations.

#### Gene Number Estimates

Estimates of gene number were made by subdividing phenotypic frequency distributions of the  $F_2$ 's. A standard error, estimating environmental effects, was calculated for each cross by pooling sums of squares over the parents and  $F_1$  of that cross if two-tailed F-tests for variances proved non-significant. If the F-tests were significant, the standard error was based on the least variable parent.

The subdivision of the  $F_2$  phenotypic distributions, for estimating minimum numbers of segregating loci, is based on starting from an assumed, known phenotypic class which represents a single genotype. Two cases must be recognized to establish an appropriate base from which the subdivision is made. In case I, gene action is apparently additive and recognized by  $\bar{F}_1 = \bar{F}_2 = m$  (Figure 1). In this case, the starting point is the estimated  $F_2$  mean. This is equivalent to the multiple heterozygote, regardless of the number of segregating loci. The model assumes that all individuals within  $\pm 2$  S.E. of this mean are of the same genotype. Thus, the first step is to subdivide the  $F_2$  phenotypic distribution in the range  $\pm 2$  S.E. from the mean. If this area is referred to as A, the next step is to plot an area 4 S.E. from both the positive (+B) and negative (-B) limits of A. All individuals within each of these two areas are assumed to have the same phenotype and differ from individuals in any other area. The procedure is repeated in units of 4 S.E. until the limits of the  $F_2$  distribution are reached. Due to error effects, it is possible, if not likely, that each phenotypic class (or area) represents more than one genotype. In this case, the estimated number is low. An over estimate is highly unlikely.

$$\bar{P}_1 = 2$$

$$\bar{P}_2 = 6$$

$$\bar{F}_1 = 4$$

$$\bar{F}_2 = 4$$

$$1 \text{ S.E.} = 0.25$$

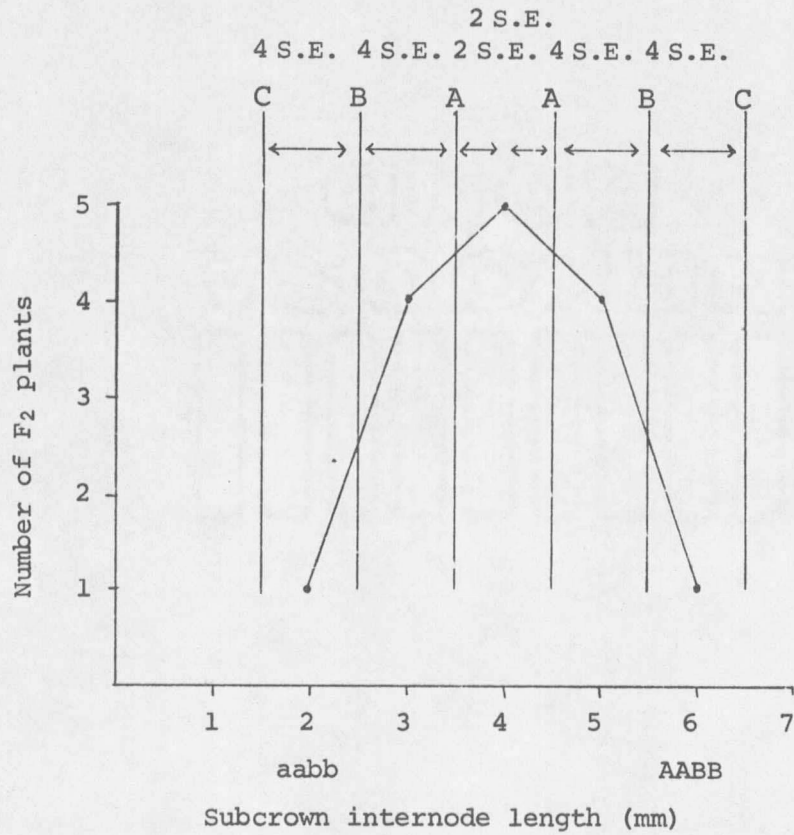


Figure 1. Example of case I gene action.

In the case II,  $\bar{F}_1 = \bar{F}_2 \neq m$  or  $F_1 \neq F_2 \neq m$ , either of which may include a transgressive  $\bar{F}_1$  (Figure 2). In this situation, the gene action is obviously not additive in nature, and the  $F_2$  mean does not represent a specific genotype. Thus, subdivision of the  $F_2$  phenotypic distribution from the  $F_2$  mean is invalid in estimating number of segregating loci. To deal with a known genotype, the simplest procedure is to take the mean of the presumed homozygous recessive parent, the parent with a mean value farther removed from the  $F_1$  mean. With a starting point identified, the subdivision of the phenotypic distribution follows the procedure outlined for case I. The parent mean replaces the  $F_2$  mean with the first separation being 2 S.E. followed by groupings of 4 S.E. until the limits of the other (high) parent are reached.

Estimation of number of loci may be made when the number of phenotypic classes is known and the gene action has been determined. Dominant gene action would result in a maximum of  $2N$  phenotypic classes and additive gene action would result in a maximum of  $3N$  phenotypic classes where  $N$  is the number of loci. This model will give estimates of gene number only with purely additive or dominant

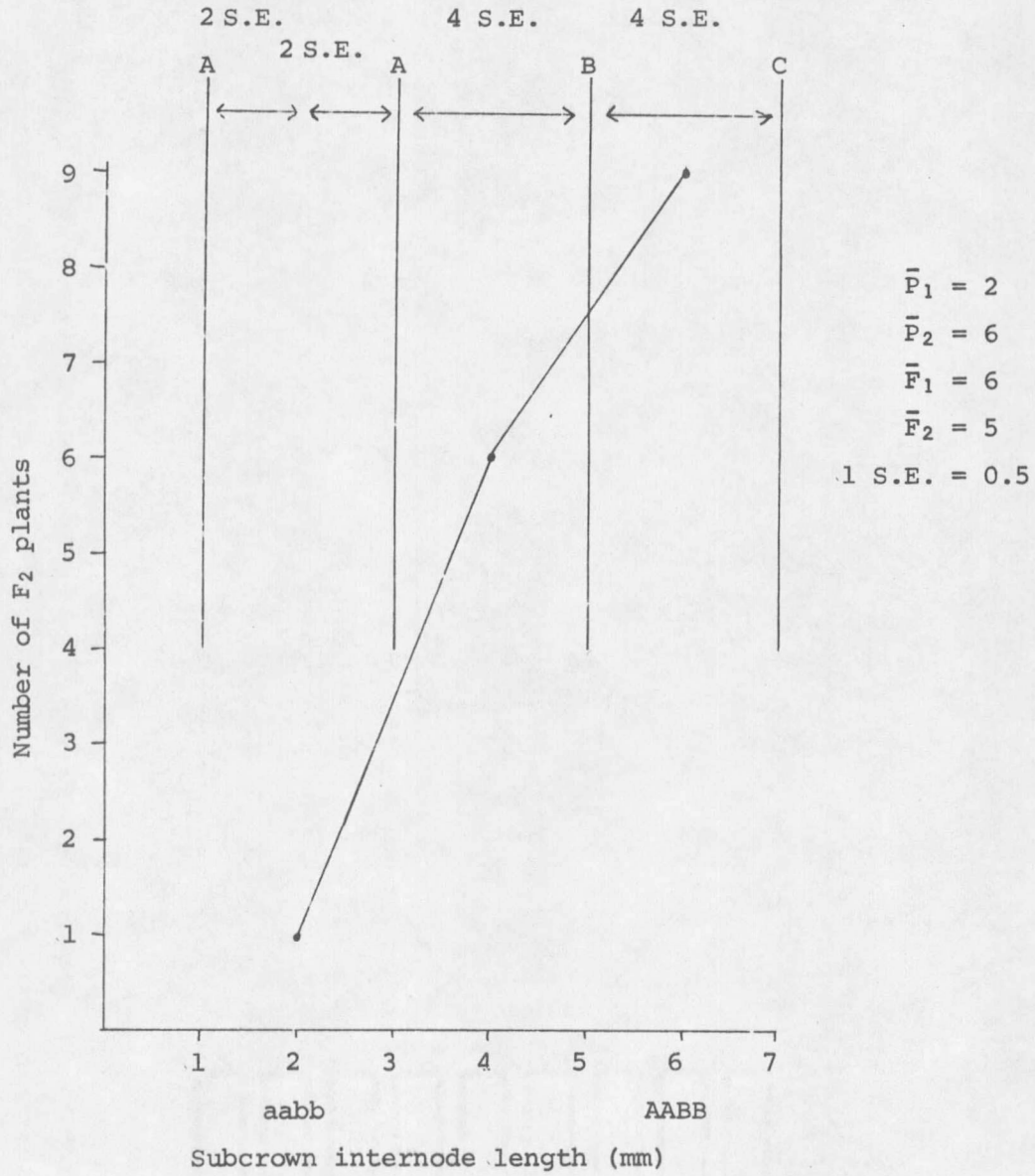


Figure 2. Example of case II gene action

gene action because of the unknown number of phenotypic classes associated with epistotic types of gene action.

## RESULTS AND DISCUSSION

### Gene Action

Initial analysis to determine which of the two general cases is appropriate revealed that for all crosses only case II (dominance) is acceptable to estimate number of segregating loci. In no cross were the conditions for case I (additivity) met. It therefore appears that additive gene action is relatively unimportant in conditioning subcrown internode length (Table 1). The crosses Yogo X Nugaines, MT 6928 X Crest-34, and Yogo X Yogo SS had  $F_1$  means greater than either parent or the  $F_2$  mean. The  $F_1$  exhibited a heterotic response. These three crosses involved long X short subcrown internode cultivars. This heterotic  $F_1$  response is in agreement with McKenzie's (1971) results.

In the MT 6928 X Froid cross, the  $F_1$  was not significantly different from Froid, the long internode parent, indicating dominance for long subcrown internodes (Table 1). The  $F_2$  differed significantly from either parent, although parental plant numbers were low.

In the fifth cross, Winoka X Cheyenne, no significant differences were noted except for Cheyenne vs. the  $F_2$ . The cross involved intermediate X intermediate subcrown

Table 1. Student's t-test comparing P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, and midparent mean values for subcrown internode length in five winter wheat crosses.

Cross	P <sub>1</sub> vs P <sub>2</sub>	P <sub>1</sub> vs F <sub>1</sub>	P <sub>1</sub> vs F <sub>2</sub>	P <sub>2</sub> vs F <sub>1</sub>	P <sub>1</sub> vs F <sub>1</sub>	F <sub>1</sub> vs F <sub>2</sub>	P <sub>1</sub> vs MP	P <sub>2</sub> vs MP	F <sub>1</sub> vs MP	F <sub>2</sub> vs MP
Yogo X Nugaines	3.70**	- 3.75**	-1.74	-10.19**	-6.80**	3.57**	0.94	-2.14	4.27**	6.93**
MT 6928 X Froid	-8.71**	-12.95**	-6.21**	- 2.00	2.17*	4.19**	-3.43**	2.60*	6.03**	3.29**
MT 6928 X Crest-34	2.69*	- 2.58*	0.97	- 4.44**	-3.52**	3.83**	1.19	-0.77	2.51*	0.94
Yogo X Yogo SS	1.39	- 3.34**	-0.43	- 4.86	-2.17*	3.91**	0.54	-0.50	3.42**	2.63**
Winoka X Cheyenne	-2.21	- 1.44	-0.62	1.19	2.18*	0.90	-0.90	0.68	0.03	-1.38

\*, \*\* - Significant at 5 and 1% levels, respectively.

internode parents. The absence of significance suggests that both parents had similar genetic complements controlling subcrown internode length.

#### Gene Numbers

The use of standard errors and  $F_2$  means and distributions to determine phenotypic classes (see Materials and Methods) revealed two distinct phenotypic classes in all crosses except MT 6928 X Crest-34 and Winoka X Cheyenne which had three (Figures 3 and 4). The cross MT 6928 X Froid (Figure 4) was the only cross which did not show a heterotic type of gene action but did show dominance which could be associated with gene numbers. Therefore, an estimate of gene number may be made only for this cross. Two phenotypic classes and dominant gene action indicated one gene contributed major effects to subcrown internode length. The heterogeneous nature of the parents in this cross (Figure 4) resulted in an  $F_1$  population somewhat variable for subcrown internode length. In addition to one major, dominant gene, other genes with "minor" effects could have influenced the phenotypic expression. The high variances of parents and  $F_1$  could have inflated the standard errors used for separating phenotypic classes resulting in an

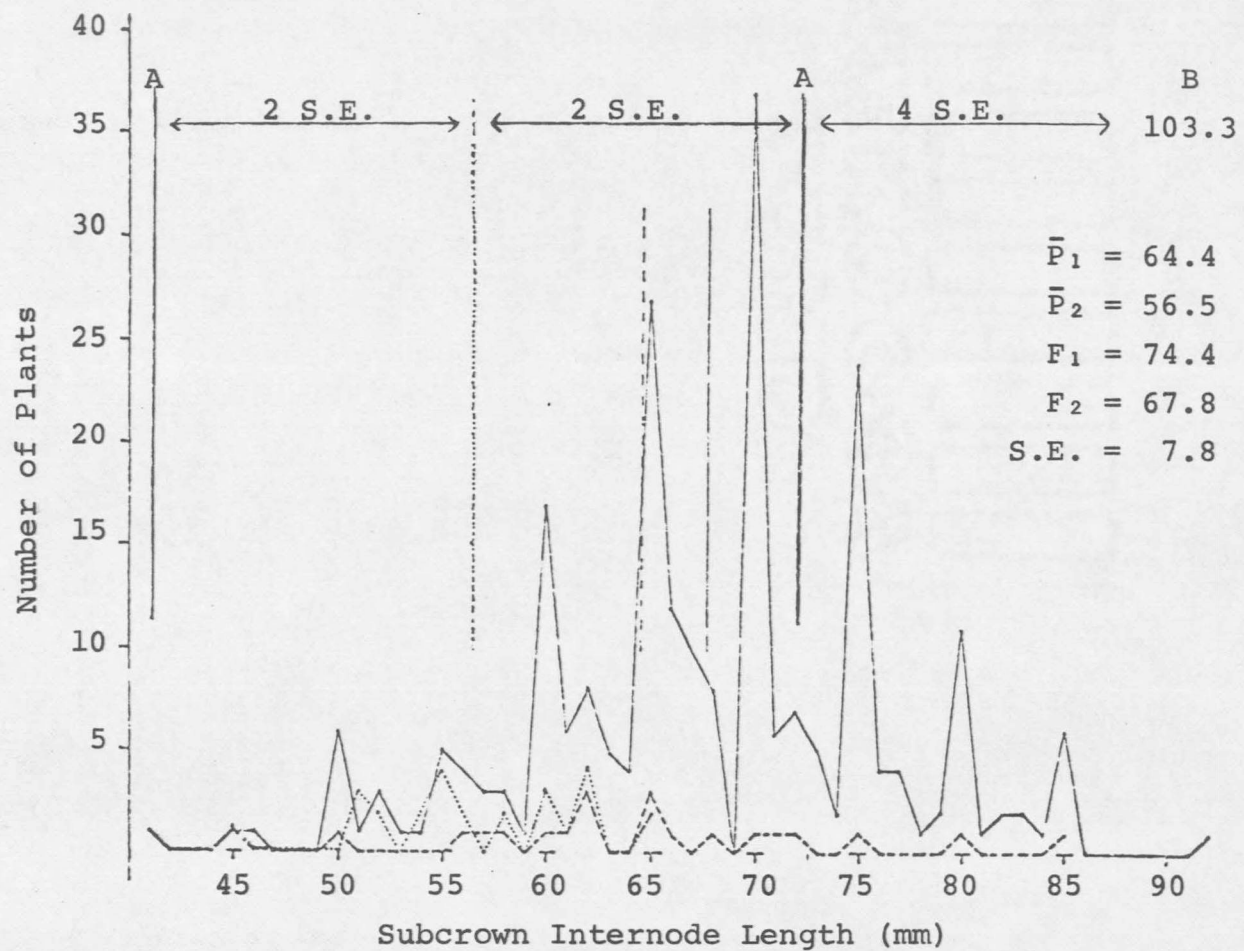


Figure 3.  $F_2$  frequency distribution of subcrown internode length for the cross Yogo X Nugaines

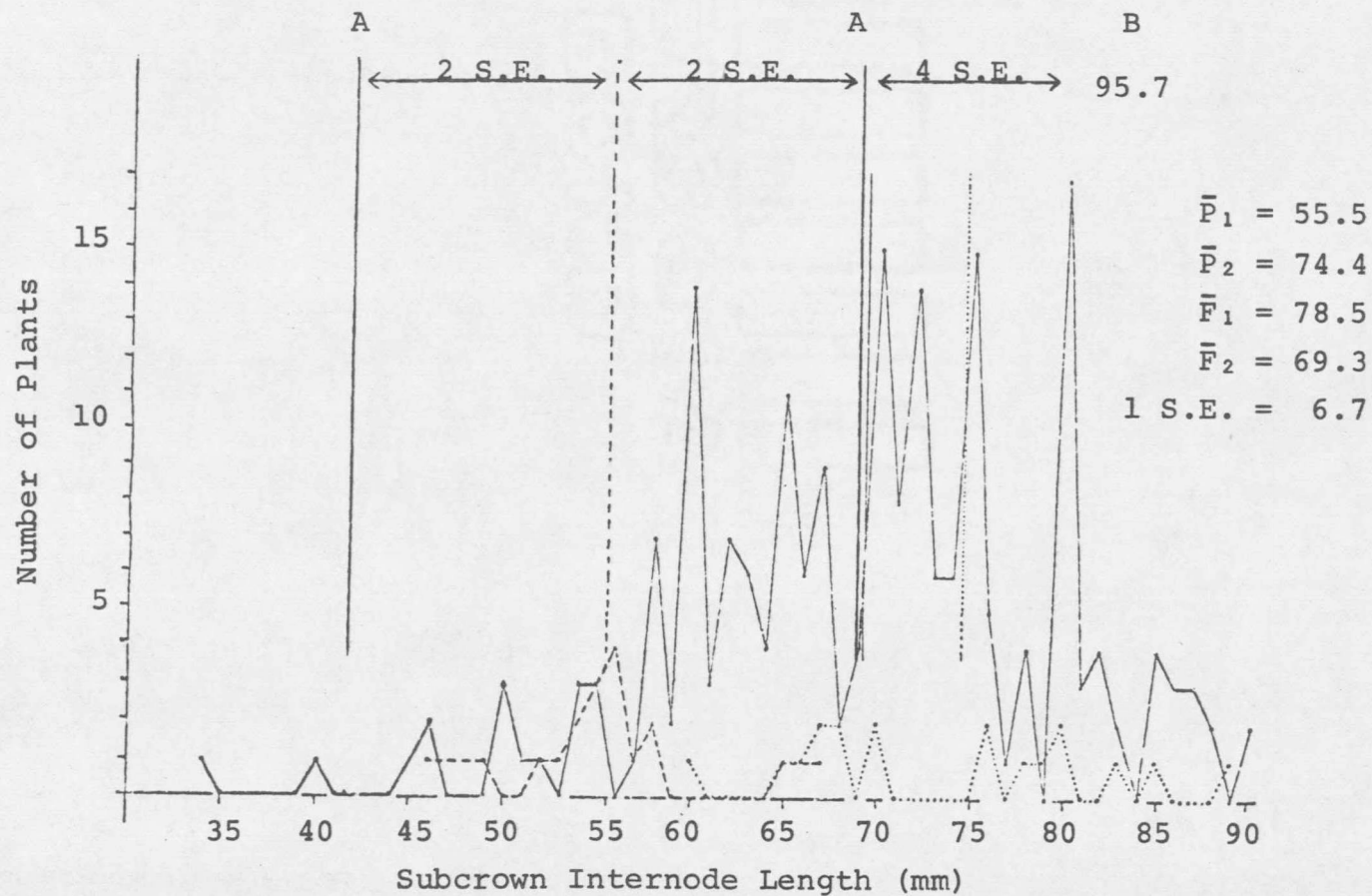


Figure 4.  $F_2$  frequency distribution of subcrown internode length for the cross MT 6928 X Froid

underestimation of true gene numbers. The generation means, gene action, number of F<sub>2</sub> phenotypic classes, and estimated number of genes for all five crosses are presented in Table 2. As previously stated, Sallans (1961), reporting on three randomly selected single plant lines of cultivars, found standard errors for crown node depth of 1.66, 2.47, and 2.57 mm. McKenzie (1971) reported two genes controlled subcrown internode length in six spring wheat crosses. His frequency distributions depicting percent versus subcrown internode length showed considerable overlap of parents. Possibly, his estimates of gene number were low due to heterogeneous parents.

#### Correlations

Parental, F<sub>1</sub> and F<sub>2</sub> seed weight means were correlated with mean number of plants emerged, mean subcrown internode length, mean seedling length and mean emergence date (Table 3). Only the correlation between number of plants emerged and seed weight was significant. Average seed weights ranged from 0.0195 to 0.0407 g. There was no significant association of seed weight with subcrown internode length.

Table 2. Mean subcrown internode length of eight parents, F<sub>1</sub>, and F<sub>2</sub> generations of five crosses and proposed mode of gene action, number of F<sub>2</sub> phenotypic classes, and estimated number of loci.

Cross	Mean subcrown internode length (mm)	Mode of gene action	F <sub>2</sub> phenotypic classes	Estimated number of loci
Yogo X Nugaines				
P <sub>1</sub>	64.44			
P <sub>2</sub>	56.52			
F <sub>1</sub>	74.45			
F <sub>2</sub>	67.79	epistosis	2	†
MT 6928 X Froid				
P <sub>1</sub>	55.48			
P <sub>2</sub>	74.45			
F <sub>1</sub>	78.46			
F <sub>2</sub>	69.34	dominance	2	1#
MT 6928 X Crest-34				
P <sub>1</sub>	53.86			
P <sub>2</sub>	45.89			
F <sub>1</sub>	61.10			
F <sub>2</sub>	51.49	epistosis	3	†

Table 2 (continued)

Cross	Mean subcrown internode length (mm)	Mode of gene action	F <sub>2</sub> phenotypic classes	Estimated number of loci
Yogo X Yogo SS				
P <sub>1</sub>	61.49			
P <sub>2</sub>	56.84			
F <sub>1</sub>	70.40			
F <sub>2</sub>	62.40	epistosis	2	†
Winoka X Cheyenne				
P <sub>1</sub>	58.93			
P <sub>2</sub>	66.97			
F <sub>1</sub>	63.05			
F <sub>2</sub>	60.62	no estimate	3	†

† - Due to deviation from simple main affects gene action, estimates can not be made.

# - Heterogeneous nature of the parents and wide F<sub>2</sub> phenotypic frequency distribution indicate two or more genes.

Table 3. Correlation (r) of mean seed weight with four plant character means.

	No. pairs	r
Individual seed weight vs. number plants emerged	20	0.5586*
Subcrown internode length	18	-0.2871
Seedling length	18	0.1764
Emergence date	18	0.1879

\* - Significant at 5% level

Individual plant correlations were calculated for emergence date vs. subcrown internode length, emergence date vs. seedling length, and seedling length vs. subcrown internode length. Correlations were calculated for each generation within each cross, but only those for the  $F_2$  are presented (Table 4) because of low numbers of plants (12-26 pairs) in the parents and  $F_1$ 's.

Correlations of  $F_2$  emergence date and subcrown internode length were significant and negative for Yogo X Nugaines, MT 6928 X Froid, and MT 6928 X Crest-34. Thus, in some genotypes there is a negative association between rapid emergence and long subcrown internodes. Correlations comparing emergence and seedling length were significant and negative for all  $F_2$  populations showing that rapid emergence and tall seedlings were, in this study, always associated.

Correlations for seedling length vs. subcrown internode length were significant and positive for Yogo X Nugaines, MT 6928 X Froid, and Yogo X Yogo SS indicating that tall seedlings and long subcrown internodes are associated. The Winoka X Cheyenne cross was negative and significant indicating the reverse of the other three  $F_2$ 's. Possibly

Table 4. Correlations (r) of anatomical plant characteristics based on individual plant values in the F<sub>2</sub> generation.

	No. pairs	r
Emergence date vs. subcrown internode length		
Yogo X Nugaines	245	-0.2185 **
MT 6928 X Froid	207	-0.2176 **
MT 6928 X Crest-34	162	-0.1621 *
Yogo X Yogo SS	208	-0.0946
Winoka X Cheyenne	210	-0.0501
Emergence date vs. seedling length		
Yogo X Nugaines	304	-0.4285 **
MT 6928 X Froid	275	-0.4280 **
MT 6928 X Crest-34	291	-0.4412 **
Yogo X Yogo SS	254	-0.4427 **
Winoka X Cheyenne	301	-0.4223 **
Seedling length vs. subcrown internode length		
Yogo X Nugaines	245	0.2701 **
MT 6928 X Froid	207	0.3545 **
MT 6928 X Crest-34	162	0.0285
Yogo X Yogo SS	208	0.3149 **
Winoka X Cheyenne	210	-0.3375 **

\*, \*\* - Significant at the 5 and 1% levels, respectively.

the other three crosses had linked genes for these characters and the fourth cross had linkage of an opposite phase. If this is the case, one would have to establish what phase the linkage is in to effectively use seedling length as a selection criterion for internode length.

#### Contingency $X^2$

Contingency  $X^2$  was used to determine if the presence of double crown nodes (see Materials and Methods) was a function of generation. The contingency  $X^2$  was not significant ( $X^2 = 13.73$ , 7 d.f.,  $p = 0.1-0.05$ ) for the parents. Thus, there was no significant association of parents and double nodes. The  $F_2$   $X^2$  was significant ( $X^2 = 64.25$ , 4 d.f.,  $p < 0.005$ ) but became non-significant when MT 6928 X Crest-34 and Winoka X Cheyenne were deleted ( $X^2 = 2.0$ , 2 d.f.,  $p = 0.25-0.10$ ). This indicated the number of double nodes in these  $F_2$ 's is influenced by the parents in the cross.

Dependency of the number of plants emerged on generation and cross was also analyzed by contingency  $X^2$ . The parents were independent ( $X^2 = 7.92$ , 7 d.f.,  $p = 0.5-0.25$ ), but the  $F_2$  was dependent in the Yogo X Yogo SS cross ( $X^2 = 42.48$ , 4 d.f.,  $p < 0.005$ ). When this  $F_2$  was deleted,

the contingency  $X^2$  was no longer significant ( $X^2 = 0.9418$ , 3 d.f.,  $p = 0.90-0.75$ ). The number of plants emerged in this  $F_2$  was lower than the other  $F_2$ 's, possibly due to genetic anomalies.

## SUMMARY

A minimum of two genes was found to control sub-crown internode length. However, due to high standard errors of the parents, I conclude the parents were composed of homozygous lines heterogeneous for this trait. The gene action was heterotic in the  $F_1$ 's of three of the five crosses. This was possibly due to the specific combining ability of Yogo and Crest-34 in their respective crosses. Only the cross MT 6928 X Froid indicated dominant gene action and Winoka X Cheyenne gave no estimate.

In crosses such as the ones in this study, which resulted in heterotic  $F_1$ 's, fixation for subcrown internodes of maximum length will be difficult. Crosses exhibiting dominant gene action with two genes for subcrown internode length would provide the opportunity for fixing long internodes.

The correlations indicated one might select for tall seedlings with some degree of success by selecting for individual plants which emerge rapidly. In certain crosses one could select for increased subcrown internode length by selecting for either rapid emergence or tall seedlings. The nonuniformity of correlations could be due to closely linked genes governing the characters under study.

The next step for further refinement in estimates of gene action and gene number is the development of lines within varieties which are more homozygous for genes controlling subcrown internode length. This would resolve whether parental variation is nearly equal to  $F_2$  variation (as noted in this study) because of the environmental effect which could be the sole reason for variation, or whether the parents used truly were genetically variable for loci controlling subcrown internode length with a resulting underestimate of true gene numbers.

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#### LITERATURE CITED

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APPENDIX

Appendix Table 1. Number of single and double noded plants in P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, and F<sub>2</sub> generations.

	Yogo X Nugaines	MT 6928 X Froid	MT 6928 X Crest-34	Yogo X Yogo SS	Winoka X Cheyenne
Single crown nodes					
P <sub>1</sub>	21	19	22	19	22
P <sub>2</sub>	26	18	18	13	20
F <sub>1</sub>	21	20	21	20	22
F <sub>2</sub>	245	206	162	208	210
Double crown nodes					
P <sub>1</sub>	9	11	10	9	5
P <sub>2</sub>	7	12	13	17	12
F <sub>1</sub>	0	1	0	2	0
F <sub>2</sub>	59	69	129	46	91

