

AN ABSTRACT OF THE THESIS OF

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Title: TEMPERATURE AND MOISTURE EFFECTS ON STAND  
ESTABLISHMENT OF SEVEN WINTER WHEAT CULTIVARS  
AND SELECTED PROGENY (TRITICUM AESTIVUM, L EM  
HELL)

Abstract approved: \_\_\_\_\_

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Laboratory studies were conducted under different temperature and moisture regimes to evaluate the effects of temperature and moisture on stand establishment and seedling characteristics associated with stand establishment. Percent stand and days to 25% emergence were used as indexes of stand establishment. Seedling characteristics analyzed were: shoot length, coleoptile length, seedling dry weight, and Adenosine Triphosphate (ATP) content. Each of these characteristics were tested with regards to predicting stand establishment over a wide range of temperature and moisture conditions. Experiments on stand establishment were also conducted under field conditions at the Sherman Experiment Station in north-central Oregon. The degree of association between stand establishment estimates obtained in the field and estimates of stand establishments obtained in the laboratory

was determined. Attempts were also made to determine the mode of inheritance of coleoptile length and Adenosine Triphosphate and the association of these characteristics with stand establishment in early generations.

Seven soft white winter wheat cultivars (Yamhill, Moro, Stephens, McDermid, Hyslop, Luke, and Daws) were used in the laboratory and field experiments. Parents,  $F_1$ s, and  $F_2$ s from crosses among four of the cultivars (Yamhill, Moro, McDermid, and Daws) were utilized in the inheritance studies of coleoptile length and ATP. Broad sense heritability estimates for coleoptile length were computed using the parental and  $F_2$  variances. Frequency distribution of coleoptile length were tested for their fit to normality by use of the chi square test. Narrow sense heritability estimates for coleoptile length and Adenosine Triphosphate were computed using the standard unit (correlation) and regression methods.

Three temperatures levels (8, 15, and 22°C) and three soil moisture levels (-2, -4, and -6 bars) were used to study the effects of temperature and moisture on stand establishment and stand establishment characteristics of the seven cultivars in the laboratory. Different temperature and moisture levels exhibited significant effects on percent stand, days to 25% emergence, shoot length, coleoptile length, seedling dry weight, and ATP. Increasing temperature from 8 to 22°C resulted in decreases in percent stand, days to 25% emergence, and coleoptile

length. Shoot length, seedling dry weight, and ATP increased as temperature was increased from 8 to 22<sup>o</sup>C. Increasing moisture stress from -2 to -6 bars had a significant negative effect on percent stand, emergence rate, and each of the seedling characteristics studied.

Coleoptile length was found to be the best predictor of percent stand over the entire range of temperature and moisture combinations utilized in the laboratory. Percent stand was observed to decrease whenever coleoptile length was less than the depth of planting. Shoot length was found to be the best predictor of days to 25% emergence over the entire range of temperature and moisture levels.

Semi-dwarf cultivars produced poorer stands than tall cultivars due to their coleoptile length. This difference in stand establishment capability was most pronounced under the warmest temperature (22<sup>o</sup>C) and the greatest moisture stress (-6 bars).

Estimates of minimum gene number together with data obtained from frequency distribution indicated that the inheritance of coleoptile length was controlled by one to three major genes and possibly some modifier genes. The close agreement between broad and narrow sense heritability estimates indicated that the expression of coleoptile length is controlled primarily by additive gene action. This suggests that selection for coleoptile length in early generations should give reliable estimates of coleoptile length expression in later generations.

The heritability of Adenosine Triphosphate (ATP) was found to be subject to cytoplasmic influence. Maternal effects in the  $F_1$  generation, the occurrence of considerable inbreeding depression in the  $F_2$  generation, and relatively low narrow sense heritability estimates suggest that ATP can not be used as a selection character for seedling vigor in early generations of wheat in a conventional breeding program.

Several characteristics (coleoptile length, ATP, plant height, and seed weight) were tested for their association with percent stand in the  $F_1$  and  $F_2$  populations. None of these characteristics were significantly correlated with percent stand. Of these characteristics, coleoptile length produced the highest correlations with percent stand in the  $F_1$  and  $F_2$  generations. The use of coleoptile length as a selection character for percent stand in early generations appears promising.

Temperature and Moisture Effects on Stand Establishment  
of Seven Winter Wheat Cultivars and Selected Progeny  
(*Triticum Aestivum*, L em thell)

by

Michael Patrick Conway

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Date thesis is presented November 4, 1977

Typed by Opal Grossnicklaus for Michael Patrick Conway

IN DEDICATION TO

My wife, Sylvia, my son, Jeff, and my daughter, Terese.

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TEMPERATURE AND MOISTURE EFFECTS ON STAND  
ESTABLISHMENT OF SEVEN WINTER WHEAT  
CULTIVARS AND SELECTED PROGENY  
(TRITICUM AESTIVUM, L EM THELL)

INTRODUCTION

Obtaining adequate stands of fall planted wheat in dryland areas of the Pacific Northwest became a serious problem with the introduction of semi-dwarf wheat to the area in the 1950's. Failure of semi-dwarfs to establish good stands has been attributed primarily to a failure of the coleoptile to reach the soil surface under conditions of deep seeding. Deep seeding into residual moisture is required if successful stands are to be obtained when using the current summer fallow practices.

A common practice in dryland areas is to plant in late August or early September into residual moisture stored from the previous fallow period. At this time soil temperature is high and soil moisture is typically limited. Stand establishment problems are intensified under these conditions. For this reason, emphasis has been placed on differentiating among cultivars on the basis of stand establishment under conditions of high temperature and low soil moisture.

Stands established from early seedings often exhibit excessive vegetative growth and disease susceptibility. Because of this, maximum yields are often obtained from mid to late planting dates

(Sept. 15-Oct. 15). Temperature and moisture conditions present at these later seeding dates differ considerably from those prevalent at earlier seeding dates. A minimal amount of attention has been focused on differentiating among cultivars for stand establishment at these later planting dates.

Because of the variability in planting date, it would be desirable to utilize a screening technique that is capable of identifying wheat lines with good emergence over a wide range of temperature and moisture conditions. This is difficult to do in the field due to a lack of environmental control. It would, therefore, be preferable to develop a laboratory procedure to test for emergence properties.

Selection for good stand establishment has been based on the identification of morphological seed and seedling characteristics associated with stand establishment. Several useful characteristics have been identified: coleoptile length, shoot length, seedling dry weight, and seed weight. However, the relative importance of these characteristics as indicators of stand establishment has not been sufficiently investigated.

Selection for good emergence on the basis of morphological traits alone may not give accurate estimates of emergence ability. For instance, it has been demonstrated that cultivars with coleoptiles of comparable lengths vary in their emergence capacities. To distinguish among such cultivars, it may be useful to use biochemical

components of seeds as indexes of seedling vigor. One such compound, Adenosine Triphosphate, has been shown to be a good index of seedling vigor. However, the association of this compound with emergence of seedlings under various temperature and moisture combinations has not been investigated.

To determine if selection for stand establishment can be effective in early generations, it is essential to gain an understanding of the amount and nature of genetic variation associated with stand establishment characteristics. The importance of these various characteristics in relation to stand establishment of early generations must also be determined if effective selection is to be practiced.

The objectives of this study were to determine:

1. The effect of temperature and moisture on stand establishment and characteristics associated with stand establishment.
2. Cultivar differences in stand establishment under various temperature and moisture combinations, particularly in relation to plant height.
3. Seedling characteristics that are consistently good predictors of stand establishment over a wide range of temperature and moisture combinations.
4. The agreement between stand establishment estimates obtained in the laboratory with estimates obtained in the field.
5. The heritability and gene action controlling coleoptile length and

Adenosine Triphosphate and the association of these and other characteristics with stand establishment in early generations.

## LITERATURE REVIEW

Seed and Seedling Characteristics Associated  
with Stand EstablishmentColeoptile length

Under the summer fallow system currently practiced in the dryland areas of the Pacific Northwest, planting depth is determined by the availability of stored moisture in the soil profile. Deep seeding often results in poor stand establishment. This is attributed to a rupturing of the coleoptile beneath the soil surface which subsequently results in a failure of the seedling to emerge. Early investigations showed that cultivars with long coleoptiles emerged better from deep seedings than did cultivars with short coleoptiles (Craddock and Vogel, 1955; Livers, 1958; Allan, Vogel, and Craddock, 1961; and Burleigh, Allan, and Vogel, 1965). Gul and Allan (1976) measured the coleoptile lengths of 93 wheat lines in the laboratory, and observed significant correlations with emergence rate in the field.

Since the introduction of semi-dwarf wheats to the Pacific Northwest, stand establishment problems have intensified. It has been suggested that a close association exists between plant height and coleoptile length. Allan, Vogel, and Peterson (1962) found, without exception, that the coleoptile lengths of 100 semi-dwarf wheat selections were one-half to three-fourths the length of the standard height

cultivars tested. In another study, phenotypic and genotypic correlations between plant height and coleoptile length were found to be high. This suggested that the coleoptile length of  $F_3$  lines could be predicted accurately from the culm lengths of  $F_2$  plants (Allan et al., 1961). In a study involving crosses among two tall and two short wheat cultivars, Chowdhry and Allan (1963) observed an inconsistent relationship between plant height and coleoptile length in the  $F_2$  generation. In one cross a significant positive correlation was observed. In the remaining three crosses, the correlations were low or non-significant. This suggested to the authors that the association between plant height and coleoptile length is not absolute and that it may be possible to select short plants with long coleoptiles. In a recent study, Allan and Pritchett (1973) observed a highly significant correlation coefficient between coleoptile length and culm length in  $F_3$ 's and  $F_4$ 's from a cross between tall and short lines.

Differences in the mode of inheritance of coleoptile length and culm length have been shown by various researchers (Allan et al., 1961; Chowdhry and Allan, 1963). Most researchers agree that although a close association exists between coleoptile length and plant height, it is doubtful that this relationship is a result of pleiotropism.

#### Shoot length and seedling weight

Shoot length has been shown to be a good indicator of seedling

vigor. Ching and Kronstad (1972), in comparing two wheat cultivars, found that the shoot length of germinated 'Yamhill' seedlings was at least 30% longer than that of 'Hyslop' seedlings. Results also showed that the cultivar 'Yamhill' had a higher overall energy level and energy charge than that of the 'Hyslop' seedlings. This indicated to the authors that a strong association existed between shoot length and seedling vigor for the two cultivars studied.

Shoot length has been associated with stand establishment by several researchers. First leaf growth at 32°C (measured at three and seven days) and first leaf growth at 10°C (measured at 15 days) was found by Allan et al. (1965) to be correlated significantly with emergence rate of 33 semi-dwarf wheat selections in the field. Similarly, Gul and Allan (1976) found that seedling height in 93 wheat lines was inconsistently related to emergence in laboratory tests but was generally related to emergence rate in the field. In a study involving barley cultivars, Ching et al. (1976) found a highly significant correlation between three day seedling shoot length and field emergence rate.

Seven day seedling dry weight has been used as an index of vigor for predicting field emergence of barley (Ching et al., 1977; McDaniel, 1969). Kittock and Law (1968) found a positive correlation among emergence rate and seedling dry weight in wheat. In a study of high and low protein seeds of soft white wheat cultivars, Garay

(1975) showed that a positive association existed between protein content, emergence rate, and dry weight of seedlings. Other studies have also shown a relationship between seedling vigor and seedling dry weight (Ching and Kronstad, 1972 and Ries and Everson, 1973).

### Seed size

The effect of seed size within a given cultivar on the germination and seedling growth of wheat has been thoroughly investigated. Small seeds are known to germinate faster than large seeds. Seedlings from small seeds produce longer roots and shoots during early stages of growth but their growth rate, in comparison to seedlings from larger seeds, is reduced at later stages (Garay, 1975). Gubanov and Bertii (1971) found that ten day old wheat seedlings obtained from large seeds had 1.7 times more dry matter than those from small seeds. In barley, McDaniel (1969) found that fresh weight, seedling mitochondrial protein, and mitochondrial biochemical activity were positively correlated with seed weight.

The relative importance of using seed weight to predict emergence capacity between cultivars is questionable. Allan et al. (1965) concluded in a study of 33 wheat lines that seed weight did not correlate well with emergence rate. In barley, seed weight was found to be a good predictor of field emergence (Ching et al., 1976). Vahabian (1977) stated that the effect of seed size of wheat on stand establishment

is very much dependent on locations and cultivars. Gul and Allan (1976) reported that kernel weight of 93 wheat lines inconsistently correlated with emergence rate in the laboratory, but exhibited a consistent positive relationship with emergence in the field. They attributed this to the greater moisture stress in the laboratory (-2.0 to -14.4 bars) as opposed to the low moisture stress present in the field (3.0 bars). In a study of several species of grass, Whalley et al. (1966) found that seed weight not only affected growth rate, but large seeds kept growing longer than did small seeds. Work by Ries and Everson (1973) showed that seedling vigor was related to seed size in 25 spring wheat cultivars. Large seeds produced larger seedlings because they contained more protein.

Seed weight differences between cultivars may be useful in distinguishing among cultivars for stand establishment. However, the differential reaction of cultivars to seed size as it affects stand establishment may diminish its effectiveness.

### Adenosine Triphosphate

Selection for good emerging wheat lines on the basis of morphological traits alone may not give a sufficient estimate of emergence ability. For instance, wheat lines with comparable coleoptile lengths differ in their emergence rates (Allan, Vogel, and Peterson, 1962). This difference may be due to physiological mechanisms, which

regulate the growth of wheat seedlings. It would be helpful to the wheat breeder to be able to measure differences among segregating wheat lines on a physiological basis.

Adenosine Triphosphate (ATP) appears to be a good index of seedling vigor because of the importance of ATP in the biosynthesis and transport of metabolites during seed germination. It is needed for the biosynthesis of proteins, ribonucleic acid, deoxyribonucleic acid, and other cell components, and is the energy for transport of metabolites in and out of the cell (Ching, 1972). The ATP content of isolated wheat embryos increases 5-fold during the first 30 minutes and 10-fold during the first hour of germination (Obendorf and Marcus, 1974). The major pathway for ATP biosynthesis is through mitochondrial oxidative phosphorylation in non-green tissue and photosynthetic phosphorylation in green tissue. The efficiency of mitochondrial oxidative phosphorylation has been used as an index of seedling vigor in wheat (Sarkisian and Srivastava, 1969 and Zobl et al., 1972) and also in barley by McDaniel (1969).

Adenosine Triphosphate content has been related to seedling vigor and stand establishment by several researchers. Ching and Kronstad (1972) showed that the higher amount of ATP in cultivar 'Yamhill' over cultivar 'Hyslop' was due to higher synthesis and utilization of ATP by Yamhill. Similarly, Vahabian (1977) observed that the cultivars 'Moro' and 'Yamhill' which exhibit good stand

establishment, also have high levels of ATP. In barley, Ching et al. (1976) found a high correlation between ATP content of seedlings after three days of germination and emergence in the field.

### Environmental Effects on Stand Establishment and Emergence Characteristics

#### Soil moisture, germination, and seedling growth

Before germination commences, wheat seeds must imbibe a minimum of 40% water on a wet weight basis (Brown, 1965). The amount of water available to a seed is determined by the soil moisture content, soil matric potential, and the contact between the seed and soil water. Various researchers have reported decreased germination rates in wheat as soil moisture potential decreases (Pawloski and Shaykewich, 1972 and Tadmor, Cohen and Harps, 1969). The rate of seedling emergence of wheat is directly related to the moisture content of the soil (Hanks and Thorp, 1956). Gul and Allan (1976) found that the time required for emergence of wheat seedlings nearly doubled for each decrease of -4.0 bars in the water potential of the soil. Total stand, coleoptile length, seedling height, and root weight were similarly reduced. However, coleoptile length did not vary significantly from -2.0 to -6.0 bars. Lindstrom (1973) reported that the emergence rate of wheat planted at a 3 cm. depth was only slightly affected by water potentials greater than -4.0 bars. Satisfactory

emergence of the cultivars 'Nugaines' and 'McCall' was observed in the field down to a water potential of -7.7 bars. In addition, -7.7 bars was found to be the lower limit at which to expect stand establishment in the field under deep seedings.

#### Soil temperature, germination, and seedling growth

Temperature regulation of germination is a complex phenomenon that exerts its effect at multiple levels of seed metabolism. Sub and super optimum temperatures in the seedbed result in reduced growth, germination, and stand establishment. Tadmor et al. (1969) found that the rate of germination of wheat increases with temperature from 10 to 20°C. Cal and Obendorf (1972) studied the differential growth of corn hybrids seeded at cold root zone temperatures. They found that corn seedlings emerged after approximately 21, 15, and 5 days at germination temperatures of 12, 16, and 20°C., respectively. The reactivation of preexisting enzymes and organelles which occurs during early germination, is temperature dependent (Ching, 1972). Ching (1975) observed reduced specific activity of fumerase, ATPase, acid phosphatase, alpha amylase, protease, and glutamine synthetase in seeds germinated at 30°C. The activity of these enzymes, with the exception of protease, was also reduced at 10°C. Vahabian (1977) studied the effect of different temperatures on ATP content of seven wheat cultivars. Significant differences were found among the cultivars and temperature treatments for ATP. The cultivar X temperature interaction was also significant which indicates that cultivars

did not respond the same, relative to one another, for ATP at the different temperature levels. Further investigation of the response of ATP in wheat lines to both temperature and moisture should determine the usefulness of it as a predictor of emergence capacity.

Burleigh, Allan, and Vogel (1965) showed that high temperatures ( $32^{\circ}\text{C}$ ) caused reduced coleoptile elongation in wheat varieties which resulted in poor seedling emergence. Standard height varieties produced longer coleoptiles than the semi-dwarfs studied for all depths at  $10^{\circ}\text{C}$ , while at  $32^{\circ}\text{C}$  one semi-dwarf selection produced a coleoptile comparable in length to the standard height varieties. Sunderman (1964) found significant differences in coleoptile elongation between wheat varieties grown in vermiculite at 15 and  $27^{\circ}\text{C}$ . The average increase in coleoptile length of varieties grown at  $15^{\circ}\text{C}$  compared to those grown at  $27^{\circ}\text{C}$  was 47 mm.

#### Temperature x moisture interaction

Planting date in dryland areas of the Pacific Northwest is quite variable. Date of planting is determined by the availability of stored moisture in the soil profile. In years when moisture is adequate for stand establishment, most farmers prefer to plant in early to mid September. Optimum yields and control of soil erosion are obtained

by planting early. If stored moisture is inadequate for stand establishment, planting is delayed until the amount of available moisture in the soil profile is increased through precipitation. Because of the variability in planting date, temperature and moisture levels in the seedbed constantly change. It would be helpful to understand the interactive effect of temperature and moisture on stand establishment and seedling characteristics associated with stand establishment. Few researchers have addressed themselves to this problem.

Tadmor et al. (1969) studied the germination of wheat at 4, 10, 15, 20, and 25<sup>o</sup>C. and at various osmotic potentials. They found that the rate of germination of wheat was significantly affected by temperature at all osmotic potentials of 0 to -15 bars. At favorable temperatures, the greatest influence of osmotic potential on the rate of germination was observed. The more the temperature diverged from the optimum for germination, the more final germination became dependent on osmotic potential. In another study, the number of days required to obtain 50 and 80% germination of wheat in osmotic solutions and seedling emergence in soil was significantly increased by lowering either temperature or water potential. Lowering temperature delayed germination and emergence more than did lowering water potential, but even greater delays occurred when both factors were lowered (Halitligil, 1975).

Studies done to date on temperature x moisture interaction have

have focused on emergence per se and have not related the response of seedling characteristics associated with emergence (e. g. coleoptile length) to different levels of moisture and temperature. If selection for stand establishment is to be carried out on the basis of seedling characteristics rather than stand establishment per se, then the response of such characteristics to temperature and moisture must be determined.

### Depth of planting

In dryland areas, seed is planted in the fall with a deep furrow drill down to the moisture level. Under such a system, coverage over the seed in the furrow may vary considerably. At deeper seeding depths, failure of the coleoptile to reach the soil surface may result in a poor stand. With the introduction of semi-dwarf wheats, this became a considerable problem and research was begun in an effort to evaluate the effect of planting depth on stand establishment.

Burleigh, Allan, and Vogel (1965) analyzed varietal differences in coleoptile length and emergence of six wheat lines in response to temperature (10 and 32°C) and depth of planting (5, 7½, and 10 cm). A close correlation was found between emergence rate and coleoptile length for all three planting depths at both temperatures. The response of coleoptile length to planting depth was significant only at the cooler temperature (10°C). At the warmer temperature the longest

coleoptiles were attained at the shallowest depth (5 cm) for five of the eight cultivars. Differentiation between cultivars for emergence was possible at depths greater than five cm. Most of the cultivars were consistent in their ranking for emergence rate over the three depths. Allan, Vogel, and Peterson (1962) found a significant difference between the emergence rate of standard height and semi-dwarf wheat cultivars when planted in the field at depths of 9 cm. A significant correlation was found between plant height, coleoptile length, and field emergence. Gul and Allan (1976) observed a significant difference in emergence rate of 93 wheat lines in the field at planting depth of 8 and 10 cm. A significant reduction in emergence was observed at the deeper depth. They also observed that two lines that had high emergence rate values in the lab had significantly lower emergence rates in the field. They suggested that this occurred because the 3.5 cm depth of planting in the lab was not sufficiently deep to prevent emergence of wheat lines with short coleoptiles.

#### Inheritance of Coleoptile Length and Adenosine Triphosphate

##### Coleoptile length

Coleoptile length is of primary importance as a morphological trait in determining stand establishment. Many studies have shown that the poor emergence of semi-dwarf wheats from deep seedings is

due to their short coleoptile length. It would seem therefore, that selection for long coleoptile length among segregating lines should result in the simultaneous selection for good stand establishment. However, the effectiveness of early generation selection for coleoptile length depends on the heritability and the nature of the gene action controlling its expression. The expression of coleoptile length is known to vary with environment (Burleigh, Allan, and Vogel, 1965). Chowderry and Allan (1962) studied the heritability and gene action controlling coleoptile length in four winter wheat crosses planted at 15 °C. and a depth of 2.5 cm. Heritabilities in the narrow sense, obtained by the standard unit regression technique (Frey and Horner, 1957) were 47.4, 37.9, and 56.4% for three of the four crosses. In each cross, the broad sense heritability values were greater than the narrow sense heritability estimates. This indicated that the genotypic variability for coleoptile length consists of non-additive as well as additive genetic variance. Dominance was observed in the  $F_1$  population of three of the four crosses. This was further substantiated by the occurrence of a dominance component in the  $F_2$  variance. It was estimated that coleoptile length is controlled by one to four major genes and possibly several modifier genes. Vahabian (1977) analyzed the inheritance of coleoptile length by using a diallel cross among seven cultivars planted at two depths in the field (5 and 12 cm). He concluded that the inheritance of coleoptile length is polygenic with

most of the genes behaving additively. His conclusion was supported by the almost identical average length of midparents and  $F_1$ 's. Allan et al. (1961) reported that polygenic inheritance was found to control coleoptile length. In a diallel cross among soft red wheats, Parodi et al. (1970) showed a significant expression of heterosis and heterobelteosis in coleoptile elongation, with all  $F_1$  progenies surpassing the midparent and higher parent coleoptile lengths. It was suggested that the superiority of the  $F_1$  generation was due to the larger seed size of the hand-crossed seed. Regression of  $F_1$  on midparent and  $F_2$  on  $F_1$  were .957 and .783, respectively. The authors concluded that genetic variation in coleoptile elongation appeared to be controlled largely by additive gene action. This conclusion was supported by the closeness of the  $F_2$  and midparent values.

Coleoptile length and culm length inheritance were studied in  $F_1$  and  $F_2$  populations from spring wheat crosses involving 'Olsens Dwarf' and five tall cultivars by Hoff et al. (1973). In the  $F_2$  populations, both characters were quantitatively inherited. None of the  $F_2$  coleoptile length segregation patterns fit a normal distribution. Broad sense heritability estimates for coleoptile length ranged from 33 to 56%. Estimated minimum gene number controlling coleoptile length ranged from 1.0 to 2.8.

### Adenosine Triphosphate (ATP)

Adenosine Triphosphate has only recently been used as a measure of seedling vigor in wheat. In a six parent diallel study in wheat, Vahabian (1977) analyzed the inheritance of ATP. He found that the mode of inheritance of ATP can be explained based on mitochondrial complementation if negative, additive, and dominant complementation are assumed. The differences in ATP among  $F_1$ 's and reciprocals was explained by the difference in quantity or quality of the parental or maternal mitochondria. He suggested that selection for high ATP can be effective as early as the  $F_2$  generation.

Information is lacking on the relationship between stand establishment and ATP in segregating populations. The relative importance of ATP and the heritability of this character under a selection environment has not been determined.

## MATERIALS AND METHODS

Seven soft white winter wheat cultivars, Yamhill, Moro, Stephens, McDermid, Hyslop, Luke, and Daws were used in laboratory and field studies during 1976 and 1977. Two of these cultivars, Yamhill and Moro, are of standard height and the remaining five are semi-dwarfs. Cultivars were selected for their diversity in emergence ability, coleoptile length, and Adenosine Triphosphate content. All seven cultivars are currently being grown commercially in the Pacific Northwest.

The following crosses and their reciprocals were made at the Hyslop Agronomy Farm in the spring of 1976:

- 1) Yamhill x Daws
- 2) Yamhill x McDermid
- 3) Moro x Daws
- 4) Moro x McDermid

The  $F_1$  seed was harvested in August of 1976 and a portion of it was replanted at the same location to obtain  $F_2$  seed. Remnant  $F_1$  seed was retained for use in laboratory experiments.

The soil type at the Hyslop Agronomy Farm is a Woodburn silt loam. One hundred and twenty kg/ha ammonium nitrate (34% N) were applied prior to planting. In addition, plots were top dressed with 100 kg/ha urea (46% N) in early spring. Plots were hand weeded throughout the season.

Two field studies on stand establishment were conducted at the Sherman Experiment Station in north-central Oregon. The soil at this station is a deep, well drained medium textured soil. Fertilizer application was unnecessary at this site because the studies were terminated after emergence was complete. A summary of climatic data for both sites is presented in Appendix Table 2.

Laboratory experiments were conducted with the seven cultivars to evaluate the effect of temperature and moisture on stand establishment. The temperature and moisture levels used in these experiments were chosen to represent conditions in the seedbed over the range of planting dates used in the Pacific Northwest. The degree of correlation between stand establishment in the field and stand establishment in the laboratory was determined. Seedling characteristics were evaluated for their ability to consistently predict stand establishment in the laboratory over the wide range of temperature and moisture combinations utilized.

The mode of inheritance of coleoptile length and Adenosine Triphosphate was determined under laboratory conditions during the summer and fall of 1977. A specific combination of temperature and moisture which was determined to be the most useful for distinguishing among wheat lines on the basis of their coleoptile length and Adenosine Triphosphate content was used in these experiments. The degree of association between coleoptile length, Adenosine Triphosphate, and stand establishment was also determined for the parents and progeny of the crosses previously identified.

Study I. Effects of Temperature and Moisture on Stand Establishment and Seedling Characteristics Associated with Stand Establishment of Seven Wheat Cultivars

Part 1. Laboratory analysis of moisture and temperature effects on percent stand, emergence rate, coleoptile length, shoot length, and seedling dry weight

This experiment was conducted in the laboratory during the spring of 1977. Seeds of each of the seven cultivars were screened to a uniform size representative of the mean seed weight of the respective cultivar. This was done to remove within cultivar variation in emergence that might arise due to seed weight. Seed weight was determined on 100 air dry seeds of each cultivar. Germination determined before the start of the experiment ranged from 92 to 98% for the seven cultivars.

Moisture contents required to produce matric potentials of -2, -4, and -6 bars were obtained from a moisture retention curve on a Ritsville silt loam soil from the Moro Experiment Station in north central Oregon. Air dry soil was passed through a 3.0 mm sieve to remove clods. Enough soil sufficient for one replication was then prepared at moisture contents of -2, -4, and -6 bars by spraying the air dry soil with the appropriate amount of water determined from the moisture retention curve. Soil was mixed repeatedly during the spray treatment to insure equal distribution of moisture. Prepared soil was

stored in plastic bags and left to equilibrate for several days. At the end of the equilibration period, plastic germination boxes (32 x 28 x 12 cm) were utilized in the following manner. Moist soil at -2, -4, or -6 bars was placed in each box to a depth of 3.0 cm and compacted to a bulk density of  $1.0 \text{ g/cm}^3$ . Twelve seeds of each cultivar were treated with a fungicide and placed in rows on the soil surface. Distance between and within rows was 2.2 cm. Thin cardboard partitions were then placed between the rows to keep the emerging seedling of the cultivars separate. Additional moist soil at the appropriate moisture level was then placed over the seeds to a depth of 5.5 cm. Preliminary studies indicated that this depth was sufficient to distinguish among cultivars for emergence capacity. Bulk density of soil over the seeds was  $1.0 \text{ g/cm}^3$ . Plastic lids were then placed over each box and sealed with tape to prevent evaporative loss. Three boxes (one at each moisture level) were then placed in each of three growth chambers and held at constant temperatures of 22, 15, and  $8^\circ\text{C}$ . The growth chambers were kept completely dark to allow for maximum expression of coleoptile length.

The experiment was conducted as a randomized block split-split plot design. Experimental variables included: 1) temperature at three levels 2) soil matric potential at three levels 3) and the seven cultivars. Temperature was used as main plots, moisture as sub plots, and cultivar as sub-sub plots. Four replications were used.

Percent stand and emergence rate were used as indexes of stand establishment. The former is the classical estimate of stand establishment and was obtained by dividing the final number of emerged seedlings by the number of seeds planted per treatment, and multiplying the result by 100. Emergence was considered complete when no new seedlings emerged from the soil surface for a period of two days. The latter is an estimate of the rate at which a stand is established and can be considered an estimate of seedling vigor. Emergence rate was estimated as the number of days required for one-fourth of the seedlings of a given cultivar to emerge from the soil surface and is referred to as days to 25% emergence.

Several morphological seedling characteristics associated with percent stand and days to 25% emergence were measured. These characteristics were coleoptile length, shoot length, and seedling dry weight. Measurements of these characteristics were obtained as follows. At the completion of emergence, seedlings were tagged, removed from the soil, and washed thoroughly. Coleoptile length and shoot length were then recorded on seven seedlings of each cultivar per replication. Coleoptile length was measured from the point of attachment to the embryo axis. Shoot length was measured from the embryo axis to the tip of the primary leaf. The seven seedlings were then oven dried at 80°C to obtain an estimate of seedling dry weight.

Analyses of variance were used to obtain estimates of significance for main effects and interactions of temperature, moisture, and cultivar for percent stand, days to 25% emergence, shoot length, coleoptile length, and seedling dry weight. Multiple regression was used to determine which seedling characteristics were the best predictors of percent and days to 25% emergence over all levels of temperature and moisture. Simple correlation coefficients were calculated to determine the degree of association between percent stand, days to 25% emergence, shoot length, coleoptile length, seedling dry weight, and 100 seed weight. Regression techniques were used to determine the functional relationships of temperature and moisture with percent stand, days to 25% emergence, shoot length, coleoptile length, and seedling dry weight. The response of coleoptile length to temperature and moisture was analyzed to determine the temperature and moisture combination most useful for estimating the heritability of coleoptile length described in Study II, Part 1.

Part 2. Laboratory analysis of moisture and temperature effects on Adenosine Triphosphate

Seeds of each of the seven wheat cultivars were screened to a uniform size representative of the mean seed weight of each respective cultivar. Eight seeds per cultivar were then placed at random in separate plastic germination boxes (10 x 10 x 3 cm) between two

layers of filter paper. Solutions of mannitol at osmotic potentials of -2, -4, and -6 bars were prepared using the following formula presented by Helmerick and Pfeifer (1954):

$$\text{grams mannitol (g)} = \frac{PVm}{RT}$$

where: V = volume in liters

m = molecular weight of mannitol

R = .08205 liter atmospheres per degree  
per mole

T = absolute temperature

P = osmotic potential

Six milliliters of mannitol solution were placed in each box.

A lid was then placed over each box to prevent evaporation. Twenty-one germination boxes per replication (seven cultivars at three osmotic levels) were placed in each of three growth chambers held at constant temperatures of 8, 15, and 22<sup>o</sup>C. The chambers were kept completely dark throughout the duration of the experiment. After 72 hours, the boxes were removed from the chamber. Six seeds of each cultivar were selected at random from each tray and subjected to ATP analysis using the luciferine-luciferase technique described in Appendix Table 3.

The experiment was a randomized block, split-split plot design. Experimental variables included: 1) cultivar at seven levels 2) osmotic potential at three levels 3) temperature at three levels. Four replications were used.

Analysis of variance was used to obtain estimates of significance for main effects and interactions of temperature, moisture, and cultivar for ATP content. Simple correlation coefficients were obtained to determine the degree of association between ATP content, percent stand, days to 25% emergence, shoot length, coleoptile length, seedling dry weight, and 100 seed weight which were measured in part 1 of this study. Adenosine Triphosphate was included in the multiple regression analysis described in part 1 which was designed to determine which seedling characteristics were the best predictors of percent stand and days to 25% emergence over all levels of temperature and moisture. The functional relationship between temperature, moisture, and ATP was determined by regression techniques. The response of ATP to temperature and moisture was analyzed to determine the temperature and moisture combination most useful for the study of the heritability of ATP described in Study II, part 2.

Part 3. Field study on stand establishment  
of seven wheat cultivars

Two separate field studies on the stand establishment of seven wheat cultivars were conducted at the Sherman Experiment Station in April and September of 1977. These planting dates were chosen to obtain estimates of percent stand under diverse temperature and moisture conditions in the seedbed. The objective of these

experiments was to determine the degree of correlation between laboratory experiments on stand establishment and results on stand establishment from the field.

In both experiments, seeds representing the mean seed weight of each cultivar were hand planted in rows 1.2 meters long. Depth of coverage over the seeds was 7 cm. Distance between seeds within a row was 3 cm. On the first planting date (April 2) 30 seeds of each cultivar were planted per replication. The design consisted of a randomized block with five replications. On the second planting date (September 1) 25 seeds of each cultivar were planted per replication. The design was a randomized block with four replications. Percent stand was calculated for each cultivar by dividing the number of final seedlings emerged by the number of seeds planted and multiplying that figure by 100.

Moisture samples were taken at the seeding depth at the initiation of each experiment. A spring loaded thermograph recorder was used to measure temperature in the seed zone during the duration of each experiment.

Analyses of variance were computed on percent stand for both planting dates. Cultivar means were compared using Duncan's Multiple Range Test (DMRT). Simple correlation coefficients were computed between percent stand in the field at both planting dates and percent stand in the laboratory at three levels of temperature and three levels of moisture.

Study II. Inheritance of Coleoptile Length and Adenosine Triphosphate and Their Association with Stand Establishment of Four Wheat Crosses

When designing a laboratory screening technique to identify wheat lines with good stand establishment, it is helpful if seedling characteristics can be identified that give quick, accurate estimates of stand establishment potential. Such estimates can save the breeder time and can also enable him to screen large numbers of plants in segregating populations.

Early generation selection for stand establishment is desirable because undesirable genotypes can be eliminated. The success of early generation selection for stand establishment, based on morphological and/or biochemical seedling characteristics, depends on the heritability and nature of the genes controlling the expression of such characteristics. Therefore, to determine the usefulness of early generation selection for stand establishment, two seedling characteristics (coleoptile length and Adenosine Triphosphate were analyzed for their heritability in two laboratory studies. Parental,  $F_1$ , and  $F_2$  generations from the four crosses described earlier were used in these experiments.

Stand establishment of the three generations was estimated by calculating percent stand and days to 25% emergence for the parents,  $F_1$ s, and  $F_2$ s. Coleoptile length and Adenosine Triphosphate were

analyzed for their usefulness in predicting percent stand and days to 25% emergence. In addition, the degree of association of seed weight and plant height with percent stand, days to 25% emergence, coleoptile length, and Adenosine Triphosphate was also determined.

#### Part I. Inheritance of coleoptile length

Data from Study I, part 1, indicated that coleoptile length exerts its greatest effect on stand establishment under conditions of high temperature and low soil moisture. Under such conditions, a reduction in coleoptile length was observed. Indirect evidence was obtained which suggested that the negative effect of high temperature and low soil moisture increases with planting depth. Therefore, to analyze the heritability of coleoptile length a selection environment consisting of high temperature, low soil moisture, and relative deep planting depth was used.

The parental,  $F_1$ , and  $F_2$  seed were screened to obtain a uniform size representative of the mean seed weight of each respective parent,  $F_1$ , of  $F_2$  generation. This was done to remove the within line variation in coleoptile length, percent stand, and days to 25% emergence that might otherwise arise due to variations in seed size.

The laboratory analysis of the inheritance of coleoptile length was conducted as follows. Lots of air dry soil obtained from the Sherman Experiment Station were moistened to a moisture content

equivalent to -6 bars of matric tension by using the procedure outlined in Study I, part 1. After the soil was prepared and allowed to equilibrate, it was used in the following manner. Moist soil was placed in plastic trays (32 x 28 x 12 cm) to a depth of 3.0 cm and compacted to a bulk density of  $1.0 \text{ g/cm}^3$ . For each replication, 14 seeds of each  $F_1$ , 21 seeds of each parent, and 70 seeds of each  $F_2$  were then placed in rows on the soil surface. Distance between and within rows was 2.5 cm. Parents,  $F_1$ 's, and  $F_2$ 's were randomized within each tray. Separation between generations was achieved by the use of thin cardboard strips. Eleven trays were required for each replication. After planting, additional moist soil at -6 bars was placed over the seeds and compacted to a bulk density of  $1.0 \text{ g/cm}^3$ . Depth of coverage over the seeds was 7.0 cm. After each replication was prepared, it was placed in a growth chamber held at a constant temperature of  $22^\circ\text{C}$ . The chamber was kept completely dark throughout the duration of the experiment. The experimental design consisted of a randomized block with three replications. Reciprocal  $F_1$ 's and reciprocal  $F_2$ 's were included in the design. Coleoptile length was measured from the point of attachment to the embryo axis. Estimates of percent stand and days to 25% emergence were calculated as in Study I, part 1. These estimates were then used in part 3 of this study to determine their association with ATP, coleoptile length, seed weight, and plant height.

Analyses of variance were computed for coleoptile length of parents and both generations to determine the significance of differences between and within generations for coleoptile length. Reciprocal differences were tested for by the use of contrasts among means for the  $F_1$  and  $F_2$  generations.

Frequency distributions for coleoptile length of parents,  $F_1$ s, and  $F_2$ s were computed. To determine if the distributions of coleoptile length corresponded to a normal curve, the obtained and expected theoretical normal distributions were compared using the method reported by Leonard et al. (1957).

Broad sense heritability estimates were obtained from the variances of parent and  $F_2$  generations using the following formula:

$$H_{bs} = \frac{V_{F_2} - \frac{V_{P_1} + V_{P_2}}{2}}{V_{F_2}}$$

Narrow sense heritability estimates were determined by parent-progeny regressions and by the standard unit method reported by Frey and Horner (1957). The standard unit method is identical to correlation coefficients between parent and offspring. Such an estimate establishes a 100% ceiling on heritability.

Degree of dominance was calculated from the following formula reported by Griffing (1948):

$$h = \frac{F_1 - MP}{P_1 - MP}$$

where:  $F_1$  = mean of  $F_1$  population

MP = midparent value

$P_1$  = mean of parent with greatest  
expression of character

To estimate the minimum number of loci involved in coleoptile length expression, the Castle-Wright formula referred to by Frey (1949) was used:

$$n = \frac{(P_1 - P_2)^2}{8(V_{F_2} - V_{F_1})}$$

where:  $P_1$  = mean of parent 1

$P_2$  = mean of parent 2

$V_{F_2}$  = Variance of  $F_2$  population

$V_{F_1}$  = Variance of  $F_1$  population

## Part 2. Inheritance of Adenosine Triphosphate

Data from Study I, part 2, indicated that the greatest variation in ATP content between cultivars occurred under warm temperature and high moisture stress. Therefore, selection under these conditions for ATP content in germinated seedlings would be most

effective. With this in mind, a selection environment consisting of high temperature and relatively high moisture stress was used to study the heritability of ATP.

Parental,  $F_1$ , and  $F_2$  seed were obtained and screened as in part 1 of this study. In addition, the mean seed weight of each parent,  $F_1$ , and  $F_2$  was determined on 100 air-dried seeds. These weights were used to determine ATP/mg seed weight. The Moro x McDermid and the McDermid x Moro  $F_1$ s were not included in this study due to insufficient number of seed. All other  $F_1$ s and  $F_2$ s (including reciprocals) were included.

The laboratory analysis of Adenosine Triphosphate content was conducted as follows. Ten seeds of each parent and  $F_1$ , and 40 seeds of each  $F_2$  (per replication) were placed in separate plastic germination boxes (10 x 10 x 3 cm) between two layers of filter paper. A solution of mannitol at an osmotic potential of -6 bars was prepared using the method outlined in Study I, part 2. Eight milliliters of mannitol solution were placed in each box. A lid was then placed over each box to prevent evaporation. The germination boxes were then placed in a growth chamber held at a constant temperature of 22°C. The chamber was kept completely dark for the duration of the experiment. After 72 hours, the boxes were removed from the chamber. For each replication, eight seeds of each parent and  $F_1$  were subjected to ATP analysis using the luciferine-luciferase technique

described in the appendix. For each  $F_2$ , three sets of 12 seeds each were subjected to ATP analysis. The means of the three sets were combined to give one estimate of ATP content for each  $F_2$  in each replication. Therefore, ATP content per replication was estimated from eight seeds of each parent and  $F_1$  and from 36 seeds of each  $F_2$ .

Adenosine Triphosphate content was expressed as nmoles/seedling and as nmoles/mg seed weight. The latter estimate was used to correct for difference in seed weight between the three generations. The experimental design consisted of a randomized block with three replications.

Analyses of variance were calculated for ATP and ATP/mg to determine the significance of differences between and within generations. Reciprocal differences were tested for by the use of contrasts among means for the  $F_1$  and  $F_2$  generations.

Estimates of  $F_2$  variations were not possible due to the impracticality of testing individual seeds for Adenosine Triphosphate content. Therefore, broad sense heritability estimates were not calculated for ATP and ATP/mg.

Narrow sense heritability estimates and degree of dominance for ATP and ATP/mg were calculated using the formulas described in Study II, part 1.

Part 3. Association of coleoptile length, adenosine triphosphate, seed weight, plant height, and stand establishment in four wheat crosses

The relative importance of seed, seedling, or plant characteristics in predicting stand establishment in early generations must be determined if selection for stand establishment is to be effective. Therefore, several characteristics were measured to determine their relative importance in predicting percent stand and days to 25% emergence of parents,  $F_1$ s, and  $F_2$ s from the four crosses previously described. These characteristics were: coleoptile length, ATP, ATP/mg, seed weight, and plant height of parents and  $F_1$ s.

Percent stand, days to 25% emergence, and coleoptile length were measured in Study II, part 1. ATP, ATP/mg, and seed weight were measured in Study II, part 2. Plant height of parents and  $F_1$ s was measured at the Hyslop Agronomy Farm in July of 1977 on 30 mature plants of each parent and  $F_1$ . Plant height was measured from the base of the plant to the base of the tallest spike.

Functional analysis of variance were computed for percent stand and days to 25% emergence to determine the significance of differences between and within generations. Simple correlation coefficients were computed to determine the degree of association between percent stand, days to 25% emergence, coleoptile length, seed weight, ATP, ATP/mg, and plant height.

## RESULTS AND DISCUSSIONS

Study I. Effects of Temperature and Moisture on Stand Establishment and Seedling Characteristics Associated with Stand Establishment of Seven Wheat Cultivars

Results and discussions of Study I are presented in three parts.

Part 1 involves the presentation and discussion of results obtained from the analyses of variance for temperature and moisture effects on percent stand, days to 25% emergence, and four seedling characteristics. The seedling characteristics were shoot length, coleoptile length, seedling dry weight, and Adenosine Triphosphate (ATP). The correlations and regressions for percent stand, days to 25% emergence and the four seedling characteristics are presented in part 2. The results from field studies on stand establishment and the correlations between stand establishment in the field and stand establishment in the laboratory are presented in part 3.

Part 1. Analyses of variance

Analyses of variance were used to obtain estimates of significance for the main effects and interactions of temperature, moisture, and cultivar on percent stand, days to 25% emergence, and four seedling characteristics (Table 1). The mean values for percent stand, days to 25% emergence, and the four seedling characteristics at three

Table 1. Mean squares from the analysis of variance for percent stand, days to 25% emergence and four seedling characteristics measured on seven wheat cultivars evaluated in the laboratory.

Source of Variation	D. F.	Percent stand	Days to 25% emergence	Shoot length (mm)	Coleoptile length (mm)	Dry wt (mg)	ATP (nmoles/seedling)
Block	3	320.98	14.57	4660.40	519.43	30.70	32.091*
Temperature	2	7015.08**	4136.14**	97443.60**	2392.85**	267.11*	240.222**
Temp x Block (Error A)	6	544.30	11.07	3676.38	159.57	26.47	4.321
Moisture	2	3897.37**	873.06**	38819.50**	345.92**	43.89**	13.704**
Temp x Moisture	4	597.17**	23.80	7878.57**	40.88	9.15*	1.704**
Moist x Block + Temp x Moist x Block (Error B)	18	293.66	8.92	494.55	47.62	3.01	0.145
Cultivar	6	4560.36**	39.97**	29526.60**	4014.62**	187.47**	7.345**
Temp x Cult	12	448.27**	3.20**	1394.04**	61.29**	5.13	1.769**
Moist x Cult	12	119.15	2.03	880.65*	23.58	2.68	0.202
Temp x Moist x Cult	24	140.02	.98	395.71	15.38	3.96	0.174
Cultivar x Block + Temp x Cult x Block + Moist x Cult x Block + Temp x Moist x Cult x Block (Error C)	162	135.68	1.13	413.14	14.93	4.57	0.194
Total	251						
CV Error A		.37	.24	.37	.19	.20	.52
CV Error B		.27	.21	.14	.10	.08	.09
CV Error C		.19	.08	.12	.06	.10	.11

\*Significant at 5% level.

\*\*Significant at 1% level.

levels of temperature and moisture are presented in Table 2. The individual cultivar means averaged over all levels of temperature and moisture are presented in Table 3. Tables 2 and 3 are used to interpret the significance of the main effects and interactions from the analyses of variance.

Percent stand. Soil moisture had a significant effect on percent stand (Table 1). This effect was much greater at 15 and 22°C than at 8°C (Table 2). The relative difference in the effect of moisture as temperature is increased accounts for the significant temperature x moisture interaction observed for percent stand. Percent stand reaches a maximum at 8°C and a minimum at 22°C (Table 2).

The objective of testing the effect of temperature and moisture on percent stand was to determine at what temperature and moisture levels stand establishment problems were encountered. The results from Table 2 indicate that minimum stands were attained under high soil temperature (22°C) and high moisture stress (-6 bars).

The relationship between temperature, moisture, and percent stand is represented by the following equation:

$$\begin{aligned} \% \text{ stand} = & 58.34 - .099 \text{ temp} + 11.8 \text{ moist} \\ & - 1.30 \text{ moist}^2 - .293 \text{ temp} \times \text{moist} \end{aligned}$$

The  $R^2$  value obtained from this equation was .37. This indicates that 37% of the variation in percent stand was due to the effects of temperature and moisture.

Table 2. Means of percent stand, days to 25% emergence and four seedling characteristics measured at three levels of temperature and moisture on seven wheat cultivars.

Temp. (°C)	Soil moisture (bars)	Percent stand	Days to 25% emergence	Shoot length (mm)	Coleoptile length (mm)	Dry wt. (mg/seedling)	ATP (nmoles/seedling)
8	-2	69.7	19.6	125	75	19.9	2.5
	-4	73.1	20.7	124	72	18.7	2.3
	-6	67.9	24.9	119	70	18.7	2.1
15	-2	70.7	8.3	209	67	21.7	4.1
	-4	67.0	10.4	201	70	20.7	4.1
	-6	55.4	16.3	151	63	20.1	3.6
22	-2	59.1	6.3	205	60	23.7	6.3
	-4	57.3	7.6	176	62	22.1	5.8
	-6	40.9	11.4	142	58	21.1	4.8

Table 3. Cultivar means for percent stand, days to 25% emergence, seed weight, and four seedling characteristics evaluated in the laboratory.

Cultivar	% Stand	Days to 25% emergence	Shoot length (mm)	Coleoptile length (mm)	100 Seed wt (g)	Dry wt (mg)	ATP (nmoles/seedling)
Yamhill	79 a <sup>1</sup>	12.6 a	192.5 b	76.4 b	5.108	23.7 a	4.8 a
Moro	73 b	14.0 b	203.3 a	82.7 a	3.703	18.2 d	4.2 b
Luke	57 c	14.0 b	166.2 c	65.8 c	4.181	18.0 d	3.5 d
McDermid	57 c	14.6 c	146.1 e	59.8 d	4.466	20.2 c	3.6 d
Stephens	61 c	14.0 b	156.7 d	66.1 c	5.419	23.1 a	4.3 b
Hyslop	59 c	14.6 c	144.2 e	58.6 d	5.000	21.9 b	4.0 c
Daws	45 d	15.4 d	121.1 f	52.4 3	4.819	20.5 c	3.6 d

<sup>1</sup>DMRT; In each column, means followed by the same letter are not significantly different at the 5% level.

A large portion of the remaining variation can be accounted for by genetic differences between cultivars. Examination of the cultivar main effect in Table 2 verifies that this is the situation. The equation given above can be used to predict the mean percent stand for the seven cultivars at any level of temperature and moisture within the limits used in this experiment.

Stand establishment problems diminished when soil temperatures were lower and soil moisture stress was less. An explanation for this can be obtained by analyzing the differential reactions of the seven cultivars to temperature levels in terms of their stand establishment. The individual cultivar means for percent stand at each of the three temperature levels are presented in Table 4.

Table 4. Cultivar means for percent stand at three levels of temperature.

Cultivar	Temperature ( $^{\circ}$ C)		
	8	15	22
Yamhill	84	84	69
Moro	81	69	71
McDermid	64	64	44
Luke	57	63	54
Stephens	73	66	44
Hyslop	74	65	49
Daws	59	39	36

Analysis of Table 4 shows that the two tall cultivars, Yamhill and Moro, produced consistently good stands at all three temperature levels. The five semi-dwarf cultivars produced consistently poorer stands as temperature increased. The differences between the tall and semi-dwarf cultivars at each of the three temperature levels were explored by the use of contrasts among treatment sums (Table 5).

Table 5. Contrasts among tall and semi-dwarf groups for percent stand at three levels of temperature.

Contrast	L	D	S <sup>2</sup>	F
Tall vs. semi-dwarf (8°)	684	280	1670.9	23.3**
Tall vs. semi-dwarf (15°)	684	280	1670.9	23.3**
Tall vs. semi-dwarf (22°)	984	280	3458.0	25.4**

\*\*Significant at 1% level

$$L = \sum K_i T_j$$

where  $K_i$  = coefficient for  $j^{\text{th}}$  cultivar

$T_j$  = Treatment sum for the  $j^{\text{th}}$  cultivar

$$D = n \sum K_i^2$$

where  $n$  = number of replications

$$S^2 = L^2/D$$

$$F = S^2/\text{MSE}(c)$$

Significant differences were found between tall and semi-dwarf cultivars for percent stand at each of the temperature levels. This

difference was approximately twice as great at 22°C as it was at 15 and 8°C. It appears then, that a positive association exists between plant height and percent stand and that a negative association exists between temperature and percent stand. This association is discussed in the following section dealing with the effects of temperature and moisture on coleoptile length.

Coleoptile length. Soil moisture level had a significant effect on coleoptile length. Inconsistent results were obtained for differences in coleoptile length between -2 and -4 bars. However, comparison of -2 and -6 bars at each level of temperature reveals a consistent decrease in coleoptile length of seedlings grown under -6 bars (Table 2).

Temperature had a much greater effect on coleoptile length than did moisture as evidenced by the magnitude of the mean squares in Table 1. This effect was independent of the level of moisture as indicated by a lack of significance of the temperature x moisture interaction for coleoptile length. Coleoptile length reached a maximum at 8°C and a minimum at 22°C (Table 2). The greatest reduction in coleoptile length over the three levels of temperature and moisture occurred at a temperature of 22°C and a soil moisture content of -6 bars. The relationship between temperature, moisture, and coleoptile length is represented by the following equation:

$$\text{coleoptile length (mm)} = 79.23 - .753 \text{ temp} - .530 \text{ moist}$$

The  $R^2$  value for this equation was .157. Genetic differences between cultivars accounted for considerably more of the total variation in coleoptile length than did temperature and moisture combined as evidenced by the magnitude of the mean squares in Table 1.

Nevertheless, this equation can be used to estimate the mean coleoptile length for the seven cultivars for any combination of temperature or moisture levels within the limits used in this experiment.

Effects of temperature on coleoptile length are presented in Table 2. It can be observed that the greatest reduction in coleoptile length occurred under the warmest temperature at 22<sup>o</sup>C. The cultivar means for coleoptile length averaged over all levels of temperature and moisture can be observed in Table 3. Significant differences were noted between the two tall cultivars Yamhill and Moro, and the semi-dwarf cultivars. Daws had the shortest coleoptile length over all treatments.

A significant temperature x cultivar interaction was observed for coleoptile length (Table 1). To examine this interaction, the individual cultivar means are presented at each level of temperature in Table 6.

Table 6. Cultivar means for coleoptile length (mm) at three temperature levels.

Cultivar	Temperature ( $^{\circ}\text{C}$ )		
	8	15	22
Yamhill	80	78	71
Moro	85	83	80
McDermid	63	62	54
Luke	69	69	60
Stephens	74	66	58
Hyslop	65	59	52
Daws	59	52	46

Yamhill and Moro had the longest coleoptiles at each level of temperature. Daws consistently produced the shortest coleoptiles. Stephens exhibited a substantial increase in coleoptile length at the coolest temperature. McDermid and Hyslop showed moderate increases in coleoptile length as temperature decreased. The greatest differences between the tall and semi-dwarf groups appeared to be at  $22^{\circ}\text{C}$ .

The significance of the differences between the tall and semi-dwarf cultivars at each level of temperature were explored using contrasts among treatment sums (Table 7).

Table 7. Contrasts among tall and semi-dwarf cultivars at three levels of temperature for coleoptile length.

Contrast	L	D	S <sup>2</sup>	F
Tall vs. semi-dwarf (8 <sup>o</sup> )	660	280	1555.7	104.2**
Tall vs. semi-dwarf (15 <sup>o</sup> )	756	280	2041.2	136.7**
Tall vs. semi-dwarf (22 <sup>o</sup> )	860	280	2641.4	176.9**

\*\*Significant at 1% level.

The significance of the F tests in Table 7 indicates that differences between the tall and semi-dwarf groups for coleoptile length decreased as temperature was lowered from 22 to 8<sup>o</sup>C. This is explained by the observation that the semi-dwarfs (with the exceptions of Luke and McDermid) responded to lower temperatures by substantially increasing coleoptile length. The two tall cultivars exhibited negligible increases in coleoptile length as temperature was lowered from 22 to 8<sup>o</sup>C.

As was previously noted, there appears to be a close association between percent stand, temperature, and plant height. It was pointed out that minimum stands were observed under the warmest temperature level (22<sup>o</sup>C) and that the semi-dwarfs were more adversely affected by warmer temperatures than were the two tall cultivars. It seems more than coincidental that coleoptile length

was also found to be a minimum at 22°C and that the semi-dwarfs were more sensitive to increases in temperature than were the tall cultivars in terms of coleoptile length expression. It appears that a cause and effect relationship exists between plant height and percent stand. This is further substantiated by comparing the depth of planting (5.5 cm) with the cultivar means for coleoptile length at each of the temperature levels. At 22°C all of the semi-dwarf cultivars had mean coleoptile lengths either less than or slightly greater than the planting depth. The tall cultivars had mean coleoptile lengths much greater than 5.5 cm. At 8°C, all seven cultivars had coleoptile lengths substantially greater than the depth of planting. Furthermore, visual observations of seedlings grown under 22°C showed that the leaves of semi-dwarf cultivars became folded, distorted, and failed to emerge when the coleoptiles ruptured beneath the soil surface.

From the above discussion it is evident that a close association exists between temperature, coleoptile length, depth of planting, and percent stand. The relative importance of this association depends on the cultivar response to temperature in terms of coleoptile length expression. High temperature combined with deep planting can result in poor stand establishment of semi-dwarf cultivars. Soil moisture content has been shown to affect coleoptile length, but the magnitude of this effect is small in relation to the effects of temperature on

coleoptile length.

Days to 25% emergence. Days to 25% emergence was significantly affected by soil moisture (Table 1). Emergence was consistently delayed as moisture availability decreased, regardless of the level of temperature (Table 2). The effect of temperature on days to 25% emergence was much greater than the effect produced by moisture level (Table 1). The greatest delay in days to 25% emergence occurred at 8°C, -6 bars and the fastest emergence was observed at 22°C, -2 bars (Table 2).

Temperature and moisture are known to influence germination rate and seedling metabolism. The results of this study show that any deviation from optimum conditions of temperature and moisture had a negative effect on emergence rate. The relationship between temperature, moisture, and days to 25% emergence is represented by the following equation:

$$\text{Days to 25\% emergence} = 35.40 - 3.033 \text{ temp} + 1.536 \text{ moist} \\ + .0695 \text{ temp}^2$$

The  $R^2$  value for this equation was .934.

The effect of cultivar on days to 25% emergence was significant but comparatively small in relation to the main effects of temperature and moisture (Table 1). Cultivar Yamhill required the least number of days to reach 25% emergence and cultivar Daws required

the most. The other five cultivars differed little in their emergence rates (Table 3). The temperature x cultivar interaction was significant but relatively small in comparison with the main effects of temperature and cultivar. This indicates that the cultivars generally responded the same, relative to one another, in their emergence rate at the different temperature levels.

Days to 25% emergence is an estimate of seedling vigor. The generally small differences between cultivars for emergence rate indicates that the cultivars differ very little in seedling vigor. Therefore, days to 25% emergence may not be a useful index of stand establishment. Coleoptile length, as discussed in the previous section, appears to be a much more reliable index of stand establishment. The relative importance of coleoptile length and emergence rate in determining percent stand will be discussed in part 2.

Shoot length. Moisture level had a significant effect on shoot length (Table 1). Shoot length was relatively unaffected by moisture level at 8°C, but was markedly reduced when soil moisture was decreased from -2 to -6 bars at 15 and 22°C. The increasing difference between the effects of moisture levels as temperature is increased accounts for the significant temperature x moisture interaction observed in Table 1. Moisture stress appears to influence shoot length most when temperatures for growth are favorable (22°C).

The effect of temperature on shoot length was approximately three times as great as the effect of moisture. The greatest reduction in shoot length occurred at 8°C. Very little difference was observed between shoot length at 15 and 22°C. This indicates that shoot length was relatively insensitive to changes in temperature between these two levels. The effects of temperature and moisture can be predicted by the following equation:

$$\begin{aligned} \text{Shoot length} = & -62.83 + 31.09 \text{ temp} + 4.72 \text{ moist} - 777 \text{ temp}^2 \\ & - 1.01 \text{ temp} \times \text{moist} \end{aligned}$$

The  $R^2$  value for this equation was .562. Analysis of the comparative magnitude of the cultivar mean square in relation to the temperature and moisture mean squares (Table 1) indicates that a large portion of the remaining variation in shoot length can be accounted for by differences between cultivars.

A significant difference in shoot length was observed between the tall cultivars and the five semi-dwarfs (Table 3). This suggests that a close association exists between plant height and shoot length. However, the significance of this association was not studied.

Seedling dry weight. The effect of soil moisture level on seedling dry weight was significant but small in relation to the main effects of temperature and cultivar (Table 1). Consistent decreases in dry weight were observed as moisture stress increased at 15

and 22°C. At 8°C, increasing moisture stress from -4 to -6 bars had no effect on dry weight (Table 2).

Temperature significantly affected seedling dry weight. The effect of temperature on dry weight was approximately six times larger than the effect of moisture on dry weight (Table 1). Maximum dry weight was produced at the warmest temperature. Dry weight was consistently reduced as temperature decreased. The effect of temperature and moisture on seedling dry weight can be explained in terms of their effects on seedling metabolism. Unfavorable levels of either factor apparently cause a decrease in growth rate which is manifested in reduced seedling dry weight. The relationship between temperature, moisture, and dry weight is represented by the following equation:

$$\begin{aligned} \text{Seedling Dry Weight (mg)} &= 19.68 + .3188 \text{ temp} - 1.154 \text{ moist} \\ &= .003 \text{ temp}^2 - 1.01 \text{ temp} \times \text{moist} \end{aligned}$$

The  $R^2$  value for this equation was .29. The large effect of cultivar differences in dry weight which is not included in the above equation accounts for a large portion of the remaining variation.

Cultivars differed significantly in seedling dry weight. Yamhill and Stephens, which had the heaviest seed weight, produced the heaviest seedlings. Moro and Luke, which had the smallest seed

weight, produced the lightest seedlings. This suggests that a close association exists between seed weight and seedling dry weight.

The significance of this association is tested in part 2.

Adenosine Triphosphate. A decrease in ATP content was observed at all levels of temperature as moisture stress increased from -2 to -6 bars (Table 2). This decrease in ATP due to moisture stress was most pronounced at the warmest temperature (22°C). At 15 and 8°C, ATP appeared to be relatively insensitive to moisture stress. A slight interaction between moisture and temperature was observed but this interaction was comparatively small in relation to the main effects of temperature and moisture (Table 1).

The effect of temperature on ATP was considerably greater than the effect of moisture on ATP. Adenosine Triphosphate content increased substantially as temperature was increased from 8 to 22°C. Based on observations of dry weight, smaller ATP pools found in seedlings grown at low temperature is a result of low ATP synthesis. Larger ATP pools at high temperature enables greater synthetic activity which results in higher growth potential and seedling vigor. The following equation describes the relationship between temperature, moisture, and ATP:

$$n \text{ mole ATP/seedling} = 1.127 + .239 \text{ temp} - .192 \text{ moist}$$

The  $R^2$  value for this equation was .85.

Cultivars differed significantly in the amount of ATP produced per seedling (Table 3). Cultivars Moro, Yamhill, and Stephens contained the highest average levels of ATP. McDermid and Daws contained the least amounts of ATP. The cultivar x temperature interaction for ATP was relatively large compared to the main effect for cultivar. This indicates that the cultivars did not respond the same, relative to one another, at the different levels of temperature. To analyze this interaction, the individual cultivar means are presented for each level of temperature in Table 8.

Table 8. Cultivar means for ATP (nmoles/seedling) measured at three levels of temperature.

Cultivar	Temperature ( $^{\circ}$ C)		
	22	15	8
Yamhill	7.18 a <sup>1</sup>	4.43 a	2.71 a
Moro	6.34 b	4.03 bc	2.10 d
Luke	4.95 e	3.48 e	2.07 d
McDermid	5.05 e	3.73 de	2.24 cd
Stephens	5.96 c	4.38 a	2.56 ab
Hyslop	5.38 d	4.20 ab	2.40 bc
Daws	4.95 e	3.80 cd	* 2.16 cd

DMRT; In each column, means followed by the same letter are not significantly different at the 5% level.

At 22°C, Yamhill and Moro contained higher amounts of ATP than the other five cultivars. As temperature decreased, the differences between cultivars diminished. At 8°C, Moro exhibited a considerable drop in ATP content in relation to the other cultivars. Luke displayed a similar drop in ATP content at lower temperatures. The ATP content of Yamhill remained consistently high in relation to the other cultivars over the different temperature levels. At 22°C, Stephens and Hyslop ranked third and fourth in ATP content, respectively. At 15 and 8°C these two cultivars ranked second and third in ATP following Yamhill. McDermid and Daws contained relatively low amounts of ATP at each of the three temperature levels.

When ATP is analyzed in seedlings, the measurement is the difference between synthesized and utilized ATP at the time of analysis. Therefore, a low reading of ATP does not necessarily indicate that a given cultivar is producing low amounts of ATP. It could be that the cultivar is simply utilizing the ATP more rapidly than it can be synthesized. Conversely, a high reading of ATP does not necessarily mean that a cultivar is synthesizing high amounts of ATP. It could be that the cultivar is not utilizing what is produced. The considerable drop in ATP content of Moro at low temperature indicates that either a low amount of ATP is produced or that the ATP is utilized more rapidly than it is synthesized. Conversely,

the high amounts of ATP recorded in Stephens and Hyslop indicate that these cultivars either produce high amounts of ATP at low temperatures or that they do not use what is synthesized. With this in mind, the question arises as to the value of ATP content per se in terms of its use as an indicator of seedling vigor. The question can be resolved by comparing the ATP content of the seven cultivars with their emergence rate. This should give an indication of whether or not ATP content is a valid measurement of seedling vigor.

Results from Table 3 show that Yamhill had the highest ATP content and the fastest emergence rate. Daws, which had the slowest emergence rate, also had the lowest average ATP content. It appears then, that ATP content per se is a good index of seedling vigor.

Part 2. Correlation and regression between percent stand, days to 25% emergence, and four seedling characteristics measured in the laboratory

Correlation. Correlation coefficients among percent stand, days to 25% emergence, seed weight, and four seedling characteristics are presented in Table 9.

Percent stand was significantly correlated with coleoptile length and shoot length. Correlations of percent stand with days to 25% emergence and seedling dry weight produced small correlations of .089 and -.011, respectively. Non-significant, negative

Table 9. Correlation coefficients for percent stand, days to 25% emergence, seed weight, and four seedling characteristics measured on seven wheat cultivars.

	Percent stand	Days to 25% emergence	Coleoptile length (mm)	Shoot length (mm)	Seedling dry weight (mg)	ATP (nmoles/seedling)	100 seed weight
Percent Stand		.089	.805**	.413**	-.011	-.151	-.100
Days to 25% Emergence			.103	-.781**	-.501**	-.880**	-.108
Coleoptile Length				.443**	-.247*	-.151	-.391
Shoot Length					.272*	.647**	-.406
Seedling Dry Weight						.597**	.881**
ATP							.386

\*Significant at 5% level.

\*\*Significant at 1% level.

correlations were obtained for percent stand with ATP and 100 seed weight. Based on these simple correlation coefficients it appears that the best indicator of percent stand was coleoptile length. This verifies results discussed earlier pertaining to the association between temperature, coleoptile length, and percent stand. The fact that the correlation between days to 25% emergence and percent stand was low indicates that seedling vigor, as measured by days to 25% emergence, was not a good estimate of percent stand. The small, negative correlation between ATP and percent stand indicates that seedling vigor, as measured by ATP, was also a poor estimate of percent stand. It should be noted however, that the correlations mentioned above pertain only to percent stand observed when seeds were planted at a depth of 5.5 cm. Under this planting depth, coleoptile length was of primary importance in determining stand establishment. At planting depths less than 5.5 cm, coleoptile length may no longer be considered the primary factor in predicting stand establishment. It may well be that at shallow planting depths seedling vigor per se may be an important indicator of stand establishment.

Days to 25% emergence was significantly correlated with shoot length, seedling dry weight, and ATP. The highest correlation was obtained between days to 25% emergence and ATP ( $r = -.88$ ). This was expected because both of these characteristics are estimates

of seedling vigor and should therefore be closely associated. The relatively high correlations between days to 25% emergence and shoot length ( $r=.781$ ) and between days to 25% emergence and seedling dry weight ( $r=-.501$ ) indicates that seedlings that emerge quickly produce long shoots and more dry matter. The significant correlation between coleoptile length and shoot length ( $r=.443$ ) reveals that faster growing seedlings also have long coleoptiles. A negative correlation was observed between coleoptile length and seedling dry weight ( $r=-.247$ ). This occurred because the cultivar with the longest average coleoptile length, Moro, had the lightest seedlings and because two of the semi-dwarf cultivars, Hyslop and Stephens, had short coleoptiles but produced heavy seedlings. The same reasoning accounts for the negative relationship between coleoptile length and 100 seed weight ( $r=-.391$ ). The cultivars with heavy seed weights produced short coleoptiles (with the exception of Yamhill and Stephens) and the cultivars with the longest coleoptile, Moro, had the lightest seed weight.

Shoot length was significantly correlated with seedling dry weight ( $r=.272$ ) and with ATP ( $r=.647$ ). Correlations between seedling dry weight and ATP were also significant ( $r=.597$ ). This implies that seedlings with high energy potential, or high ATP, tend to have longer shoots and produce more dry matter. Furthermore, seedling dry weight was significantly correlated with 100 seed

weight. This indicates that heavy seeds produce heavier seedlings.

Multiple regression. In dryland areas of the Pacific Northwest, planting date changes from year to year depending on the moisture situation in the seedbed. If the amount of stored moisture is adequate for germination and emergence, farmers prefer to plant in September or early October. If the amount of stored moisture is inadequate for good stand establishment, planting is delayed.

Depending on the date of planting, temperature and moisture levels in the seedbed can vary considerably. Because of this, any seedling characteristic that is to be used in a laboratory screening procedure as a predictor of stand establishment should be able to predict stand establishment consistently irrespective of temperature and moisture fluctuations. For this reason, multiple regression analysis was used in this study to determine which seedling characteristics were consistently good predictors of percent stand and days to 25% emergence over the range of temperature and moisture combinations used in this study.

Several seedling characteristics were analyzed for their ability to predict stand establishment. These were: coleoptile length, shoot length, seedling dry weight, and ATP. The following equation containing three of these seedling characteristics (shoot length, coleoptile length, and ATP) was found to be the best predictor of days to 25% emergence. Seedling dry weight was not included in

this equation because it did not contribute substantially to the regression sum of squares.

$$\begin{aligned} \text{Days to 25\% emergence} = & 22.64 - .0973 \text{ shoot} + .2026 \text{ coleoptile} \\ & - 1.603 \text{ ATP} \end{aligned}$$

The  $R^2$  value for this equation was .91. Of the three characteristics, shoot length was found to be the best predictor of days to 25% emergence. It accounted for 61% of the observed variation in days to 25% emergence. Coleoptile length and ATP accounted for 25 and 5% of the remaining variation, respectively.

The following equation containing all four seedling characteristics, was found to be the best predictor of percent stand.

$$\begin{aligned} \text{Percent stand} = & -39.89 + .108 \text{ shoot} + .965 \text{ coleoptile} \\ & + 1.922 \text{ dry wt} - 4.689 \text{ ATP} \end{aligned}$$

The  $R^2$  value for this equation was .745. Of the four variables, coleoptile length was found to be the best predictor of percent stand. This verifies results discussed earlier. Coleoptile length accounted for 64.9% of the observed variation in percent stand. Of the remaining characteristics, shoot length accounted for 2.8%, ATP 3.1%, and dry weight 3.7% of the observed variation in percent stand.

These results show that shoot length gave the best estimate of days to 25% emergence over the entire range of environments

tested in this study. Coleoptile length was the next best estimate of days to 25% emergence, followed by ATP. The best predictor of percent stand was coleoptile length, followed by seedling dry weight, ATP and shoot length.

Part 3. Field study on percent stand of seven cultivars for two planting dates

The average temperature and soil moisture content at seeding depth for two planting dates are given in Table 10.

Table 10. Average temperature and soil moisture content at seeding depth for two planting dates in the field.

	Planting Date	
	April 2	Sept. 1
Temp ( $^{\circ}$ C)	10	17
Soil Moisture (bars)	-2	-4

Seedlings that emerged during April planting experienced cool temperatures and relatively low moisture stress. Seedlings that emerged during the September planting experienced warmer soil temperature and comparatively higher moisture stress.

Analyses of variances for percent stand at two planting dates are presented in Tables 11 and 12.

Table 11. Analysis of variance for percent stand measured on seven wheat cultivars in the field during April 1977.

Source of variation	D. F.	Mean square
Cultivar	6	334.65 N. S.
Block	4	66.90 N. S.
Error	24	141.02
Total	34	
<hr/>		
Coefficient of variation (%)	16.5	

Table 12. Analysis of variance for percent stand measured on seven wheat cultivars in the field during September 1977.

Source of variation	D. F.	Mean square
Cultivar	6	1273.67**
Block	3	1599.76**
Error	18	67.32
Total	27	
<hr/>		
Coefficient of variation (%)	19.3	

\*\*Significant at 1% level.

Differences between cultivars were not significant for the April planting. Differences between cultivars and between replications were highly significant for the September planting.

Cultivar means for percent stand at both planting dates are presented in Table 13. Although differences between cultivars were not significant for the April planting, the cultivar mean square was very close to being significant at the 5% level. This justifies the use of Duncan's Multiple Range Test for comparing cultivar means for percent stand at the two planting dates.

Table 13. Cultivar means for percent stand at two planting dates in the field.

Cultivar	Planting Date	
	April 2	Sept. 1
Yamhill	80.0 ab <sup>1</sup>	65 a
Moro	76.7 abc	47 bc
Luke	83.3 a	37 cd
Daws	61.3 c	22 e
Hyslop	65.3 bc	30 dc
McDermid	67.3 abc	67 a
Stephens	70.0 abc	30 de

<sup>1</sup>DMRT; Means followed by the same letter are not significantly different at the 5% level.

Analysis of Table 13 shows that the least variation in percent stand between cultivars occurred for the April planting. Estimates

of percent stand were relatively high for all cultivars at this planting date. Temperature in the seedbed during this time was relatively cool ( $10^{\circ}\text{C}$ ).

Comparatively poor stands were obtained for the September planting. Temperatures in the seedbed during this period averaged  $17^{\circ}\text{C}$  and moisture content was equivalent to -4 bars. The semi-dwarf cultivars, with the exception of McDermid, produced poorer stands than the tall cultivars.

In the previous discussion of temperature, moisture, and cultivar effects on stand establishment observed in the laboratory, it was pointed out that a close association existed between temperature, moisture, coleoptile length, and depth of planting. It was observed that percent stand and coleoptile length decreased as temperature was increased from 8 to  $22^{\circ}\text{C}$ . The coleoptile lengths of the semi-dwarf cultivars were observed to be less than or slightly greater than the planting depth of 5.5 cm. This was suggested as a plausible explanation for the decrease in percent stand of the semi-dwarf cultivars grown under  $22^{\circ}\text{C}$ . In the field experiment, the poor stands obtained from the September planting could be due to a number of causes. A greater planting depth (7 cm) was used in the field studies than was used in the laboratory studies on emergence. From the laboratory analysis of stand establishment, it was shown that the planting depth can restrict emergence of semi-dwarf cultivars if it is sufficiently

greater than their coleoptile length. Thus, planting depth was probably responsible for the poor emergence observed in September. The combination of relatively high temperature ( $17^{\circ}\text{C}$ ) and high moisture stress (-4 bars) present in the seedbed during the September emergence study may have acted to reduce coleoptile length of the semi-dwarf cultivars. Such a reduction in coleoptile length would also be expected to reduce emergence. However, this does not explain why McDermid, a semi-dwarf, had good emergence in the September field study. This would, however, explain why the other four semi-dwarf cultivars produced such poor stands.

Table 14 lists the correlation coefficients for percent stand measured at two dates in the field and in the laboratory at three temperatures and three soil moisture levels. In general, laboratory emergence under 15 and  $22^{\circ}\text{C}$  produced the highest correlation coefficients with field emergence at the two planting dates. Inconsistent correlations were obtained between emergence at different moisture levels in the laboratory and field emergence at either planting date.

The low correlations between percent stand at the coolest temperature in the laboratory ( $8^{\circ}\text{C}$ ) and percent stand measured in the field can be explained on the basis of planting depth. In the laboratory, planting depth was 5.5 cm. At  $8^{\circ}\text{C}$ , all of the cultivars had coleoptile lengths that exceeded 5.5 cm. Therefore, depth of planting was not a limiting factor to emergence at  $8^{\circ}\text{C}$  in the laboratory. In

Table 14. Correlation coefficients for percent stand measured at two dates in the field and in the laboratory at three temperatures and three soil moisture contents.

Laboratory		Field	
		April	Sept.
8°	-2	-.128	.210
	-4	.273	.477
	-6	.482	.279
15°	-2	.545	.475
	-4	.471	.669
	-6	.830*	.735
22°	-2	.779*	.503
	-4	.730	.524
	-6	.640	.410

\*Significant at 5% level.

the field, the depth of planting was 7 cm. This depth was sufficient to limit emergence in the field at both planting dates. As temperature was increased in the laboratory to 15 and 22°C, coleoptile length was shortened and planting depth became a factor in determining percent stand. The fact that planting depth was a limiting factor to emergence in the laboratory at 15 and 22°C but not at 8°C explains why the highest correlations were obtained between emergence in the laboratory at 15 and 22°C and field emergence.

Based on the results obtained from the laboratory and field experiments on stand establishment, it appears that selection for stand establishment in the laboratory should be performed on seedlings grown under relatively high temperature. The reason for this is that high temperature reduces coleoptile length. As previously noted, reductions in coleoptile length result in poor stand establishment when planting depth is the limiting factor.

Wheat lines that produce good stands under warm temperature can also be expected to produce good stands under cool temperature. This statement is based on the assumption that the coleoptile lengths of such lines will increase under cool temperature and therefore, stand establishment problems will diminish. If selection for stand establishment was to occur under cool temperature in the laboratory, the results may not apply to results obtained under warm temperature. This is illustrated by data presented in part 1 of this study.

Analysis of data in Table 4 reveals that Stephens and Hyslop produced good stands at 8°C but produced poor stands at 22°C. The coleoptile lengths of these two cultivars increased substantially as temperature was decreased (Table 6). Their increase in coleoptile length accounts for their relatively good stand establishment at the cooler temperature. If these two cultivars were selected for their stand establishment potential over a wide range of temperature levels, based only on their performance at 8°C, the results would be misleading because Hyslop and Stephens did not produce good stands under high temperature. Therefore, selection for stand establishment under warm temperature should give the best estimate of stand establishment over a wide range of temperature levels.

Based on the results presented in this study, the following conclusions can be drawn:

- 1) Temperature and moisture exert significant effects on percent stand, days to 25% emergence, shoot length, coleoptile length, seedling dry weight, and ATP.
- 2) The seven cultivars studied differed significantly in percent stand, days to 25% emergence, shoot length, coleoptile length, seedling dry weight, and ATP.
- 3) The most consistent predictor of percent stand under the laboratory conditions was coleoptile length.

- 4) Increasing temperature from 8 to 22<sup>o</sup>C and increasing moisture stress from -2 to -6 bars resulted in decreases in coleoptile length and percent stand.
- 5) Percent stand decreases when coleoptile length is less than the depth of planting.
- 6) Semi-dwarf cultivars have greater stand establishment problems than do tall cultivars because of their coleoptile length.
- 7) The most consistent predictor of days to 25% emergence was shoot length.
- 8) Seedling vigor criteria (days to 25% emergence, ATP) are not reliable predictors of percent stand when depth of planting exceeds coleoptile length.
- 9) Laboratory estimates of percent stand appear to be reliable estimates of percent stand in the field only when environmental conditions in the laboratory (temperature, moisture, depth of planting) simulate field conditions.
- 10) Selection for stand establishment under warm temperature should give the best estimate of stand establishment over the range of temperatures present in the seedbed during stand establishment in dryland areas of the Pacific Northwest.

Study II. Inheritance of Coleoptile Length and Adenosine Triphosphate and their Association with Stand Establishment of Four Wheat Crosses

Results and discussions are presented in three parts. Parts 1 and 2 involve the inheritance of coleoptile length and Adenosine Triphosphate (ATP), respectively. Part 3 concerns the association of several characteristics, including coleoptile length and ATP with stand establishment of the parents,  $F_1$ s, and  $F_2$ s from the four crosses previously identified.

Part 1. Inheritance of coleoptile length

The results of the analysis of variance for coleoptile length are presented in Table 15.

Differences between generations were not significant. This indicates close agreement between the phenotypic expression of coleoptile length for the three generations. The majority of the total variation due to generations was due to differences within the generations. Comparison of the parental  $F_1$ , and  $F_2$  mean squares shows that the greatest amount of variation occurred between the four parent lines. Significant differences were also observed between  $F_1$ s. The variation among  $F_2$  lines was not significant.

Table 15. Mean squares from the analysis of variance for coleoptile length involving parents and two generations.

Source of Variation	D. F.	Mean square
Replication	2	20.250
Generation	19	139.056**
Between Generations	2	13.263
Within Generations	17	153.855**
Within Parents	3	668.972**
Within F <sub>1</sub> s	7	73.238**
Within F <sub>2</sub> s	7	73.708
Generation x Replication	38	8.764
Total	59	
<hr/>		
Coefficient of Variability (%)	4.3	

\*\*Significant at the 1% level.

The mean coleoptile length, phenotypic variation, and the number of plants measured for parents and two generations are presented in Table 16.

Table 16. Number of plants, mean coleoptile length, and phenotypic variation of four crosses and two generations of wheat.

Cross	Popula- tion	No. of plants	Coleoptile length (mm)	Vari- ance
Yamhill x McDermid	Yam	30	79	86.05
	McD	30	58	56.03
	F <sub>1</sub>	60	71	59.64
	F <sub>2</sub>	288	71	160.78
Yamhill x Daws	Yam	30	79	86.05
	Daws	30	53	34.56
	F <sub>1</sub>	60	66	53.60
	F <sub>2</sub>	288	68	134.86
Moro x McDermid	Moro	30	82	35.08
	McD	30	58	56.03
	F <sub>1</sub>	60	76	46.55
	F <sub>2</sub>	288	71	124.82
Moro x Daws	Moro	30	82	35.08
	Daws	30	53	34.56
	F <sub>1</sub>	60	68	45.10
	F <sub>2</sub>	288	67	142.38

The mean values of the F<sub>1</sub> and F<sub>2</sub> generations show close agreement for each cross. This is indirect evidence for the assumption that

the expression of coleoptile length is largely controlled by additive gene action. If this were not the case, this close agreement would not be observed after selfing of the  $F_1$  generation.

The tall parents, Yamhill and Moro, produced mean coleoptile lengths of 79 and 82 mm, respectively. The two semi-dwarfs, Daws and McDermid, produced substantially shorter mean coleoptile lengths of 53 and 58 mm, respectively.

The presence of reciprocal effects in the  $F_1$  generations was tested for by the use of contrasts among  $F_1$  sums (Table 17).

Table 17. Contrast of coleoptile length involving  $F_1$  and reciprocal  $F_1$ .

	Semi-dwarf as ♀				Tall as ♀				L	D	S <sup>2</sup>	F
	Daws Yam	McD Yam	Daws Moro	McD Moro	Yam Daws	Yam McD	Moro Daws	Moro McD				
Treatment sums	191	198	204	226	204	225	199	229				
$F_1$ vs. recip.	+1	+1	+1	+1	-1	-1	-1	-1	-38	24	60.2	6.87*

\*Significant at 5% level.

In effect, the contrast in Table 17 amounts to a comparison of the coleoptile length of  $F_1$  seedlings produced from seeds in which the tall parents were used as females against seedlings from seeds in which the semi-dwarfs were used as females. The difference between the two groups was significant. When Yamhill was used as the female parent it produced seedlings with longer coleoptiles than when it was used as the pollen source. Moro did not produce any reciprocal effects. The maternal effect produced by Yamhill may have been

due to cytoplasmic differences between Yamhill and the two semi-dwarfs. This possibility will be discussed in the section dealing with the inheritance of ATP. Seed size differences between the  $F_1$ s does not explain the maternal effect produced by Yamhill. Large seeds would be expected to produce large seedlings and hence long coleoptiles, but observations showed that the  $F_1$  seed produced with Yamhill as the female parent was actually smaller than the  $F_1$  seed produced with Yamhill as the pollen source.

Generation means for coleoptile length as percent of midparent are given in Table 18. Close agreement between midparent,  $F_1$ , and  $F_2$  means is evident. Heterosis was observed in five of the eight  $F_1$  populations and in three of the four  $F_2$  populations. However the amount of heterosis was fairly small. The highest heterotic value was obtained by the Yamhill x McDermid  $F_1$ . This value was only 10% above the midparent. The Moro x McDermid  $F_1$ , and reciprocal  $F_1$  gave heterotic values of 109 and 107, respectively. No heterobeltosis was observed in any of the crosses. In general, the means of the three generations exhibited considerable agreement. The close agreement between the midparent,  $F_1$ , and  $F_2$  means is indicative of additive gene effects. The lack of inbreeding depression in the  $F_2$  generations also supports the contention that coleoptile length is primarily controlled by additive gene action.

The data on coleoptile length of the three generations are

Table 18. Generation means for coleoptile length expressed as % of midparent.

Cultivar and Generation	Mean coleoptile length (mm)	% Midparent
(Yamhill + McDermid)/2	68	100
Yamhill/McDermid F <sub>1</sub>	75	110
McDermid/Yamhill F <sub>1</sub>	66	98
Yamhill/McDermid F <sub>2</sub>	71	104
(Yamhill + Daws)/2	66	100
Yamhill/Daws F <sub>1</sub>	68	103
Daws/Yamhill F <sub>1</sub>	64	97
Yamhill/Daws F <sub>2</sub>	68	103
(Moro + McDermid)/2	70	100
Moro/McDermid F <sub>1</sub>	76	109
McDermid/Moro F <sub>1</sub>	75	107
Moro/McDermid F <sub>2</sub>	71	101
(Moro + Daws)/2	67	100
Moro/Daws/F <sub>1</sub>	66	98
Daws/Moro F <sub>1</sub>	68	101
Moro/Daws F <sub>2</sub>	66	98

presented graphically in the form of frequency polygons for the parents,  $F_1$ s, and  $F_2$ s in Figures 1-10.

The frequency polygons of the entire  $F_2$  and parent populations are presented in Tables 1 and 2, respectively. Comparison of the two figures reveals that the means of the  $F_2$  populations fall close to the midparent values. It is also evident that the parental genotypes were recovered in each of the  $F_2$  populations. This indicates that the sample size in each  $F_2$  population (288 plants) was large enough to allow all possible recombinations to occur. If three major genes are responsible for the control of coleoptile length expression then theoretically a population size of 64 plants of  $4^3$  would be required to recover the parental genotypes. Four and five genes increase the theoretical population size to 256 and 1024 plants, respectively. The fact that the parental genotypes were recovered in populations of 288 plants indicates that coleoptile length is controlled by four or less major factors. Furthermore, analysis of Figures 3, 5, 7, and 9 reveals that more than one of each parental type were recovered in each  $F_2$  population. Recovery of large numbers of parental types is improbable if four major genes are involved. For the reasons stated above it appears that coleoptile length is controlled by three or less major genes.

Analysis of Figures 1, 3, 5, 7, and 9 reveals that the apparent approach to normality of the  $F_2$  frequency distributions. Testing for

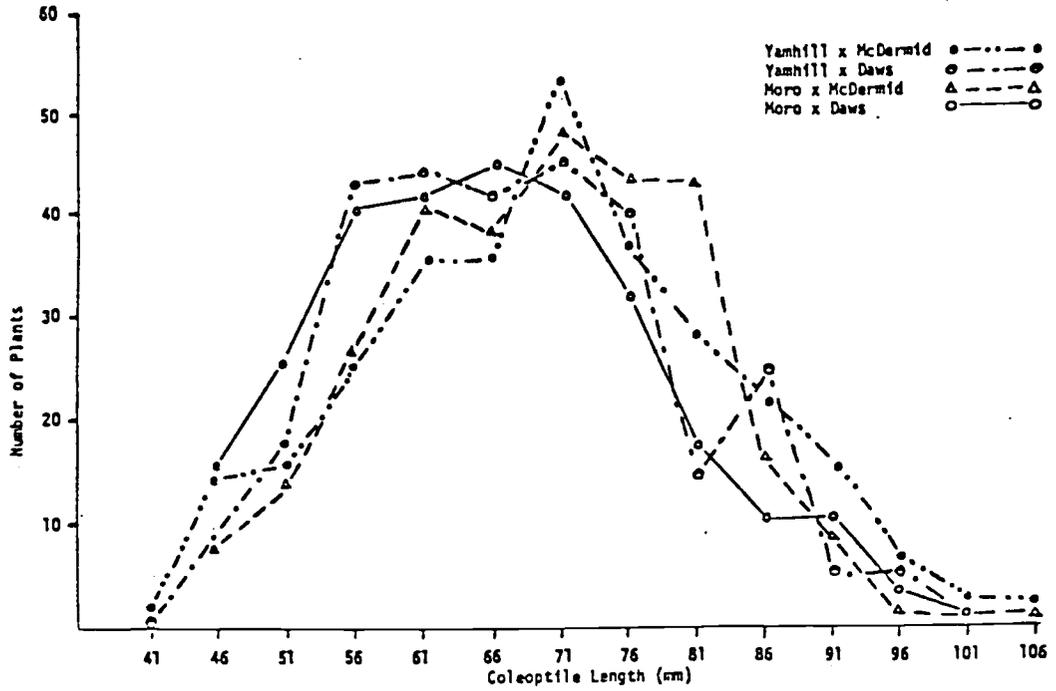


Figure 1. Frequency polygons for coleoptile length of  $F_2$  populations from four wheat crosses.

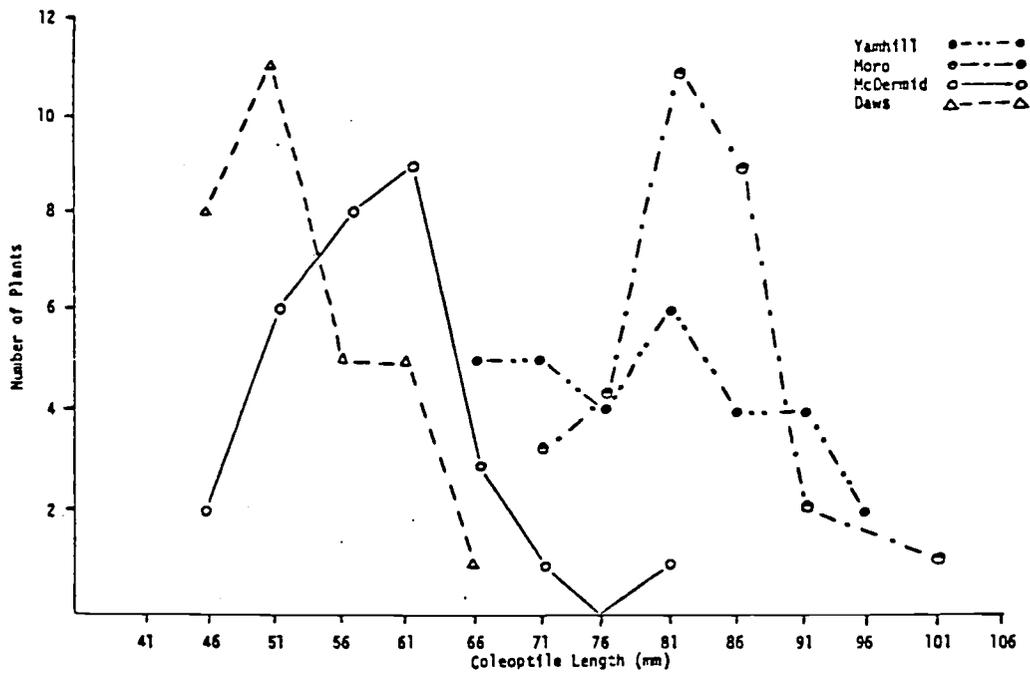


Figure 2. Frequency polygons for coleoptile length of parental lines involving four wheat crosses.

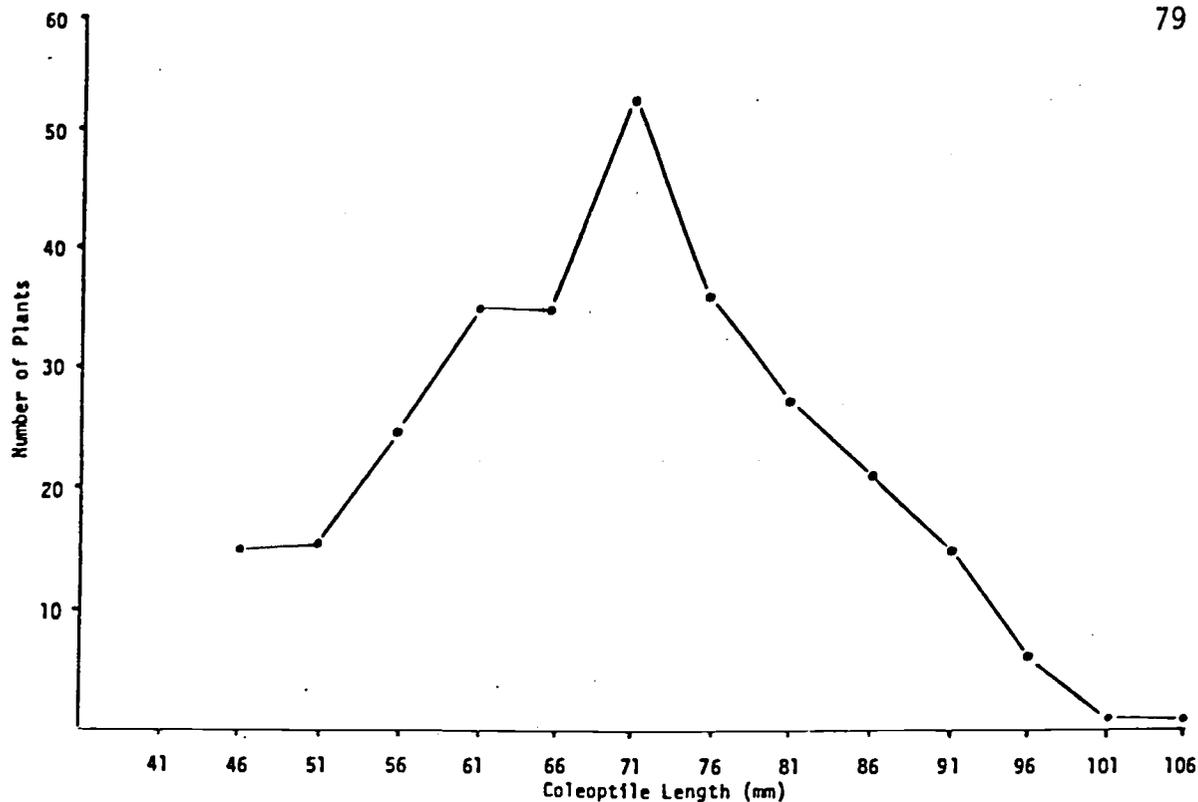


Figure 3. Frequency polygon of F<sub>2</sub> for coleoptile length in Yamhill x McDermid cross

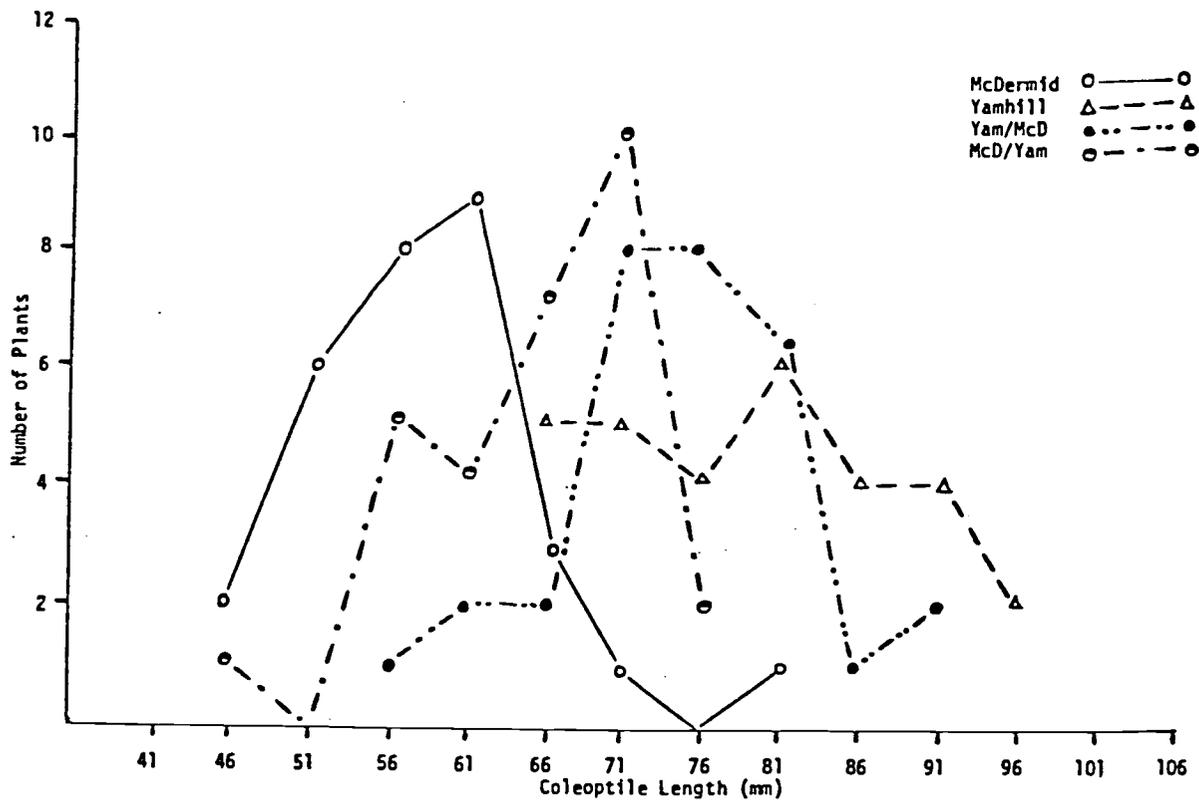


Figure 4. Frequency polygons of parents, F<sub>1</sub>, and F<sub>1</sub> reciprocal for coleoptile length in Yamhill x McDermid cross

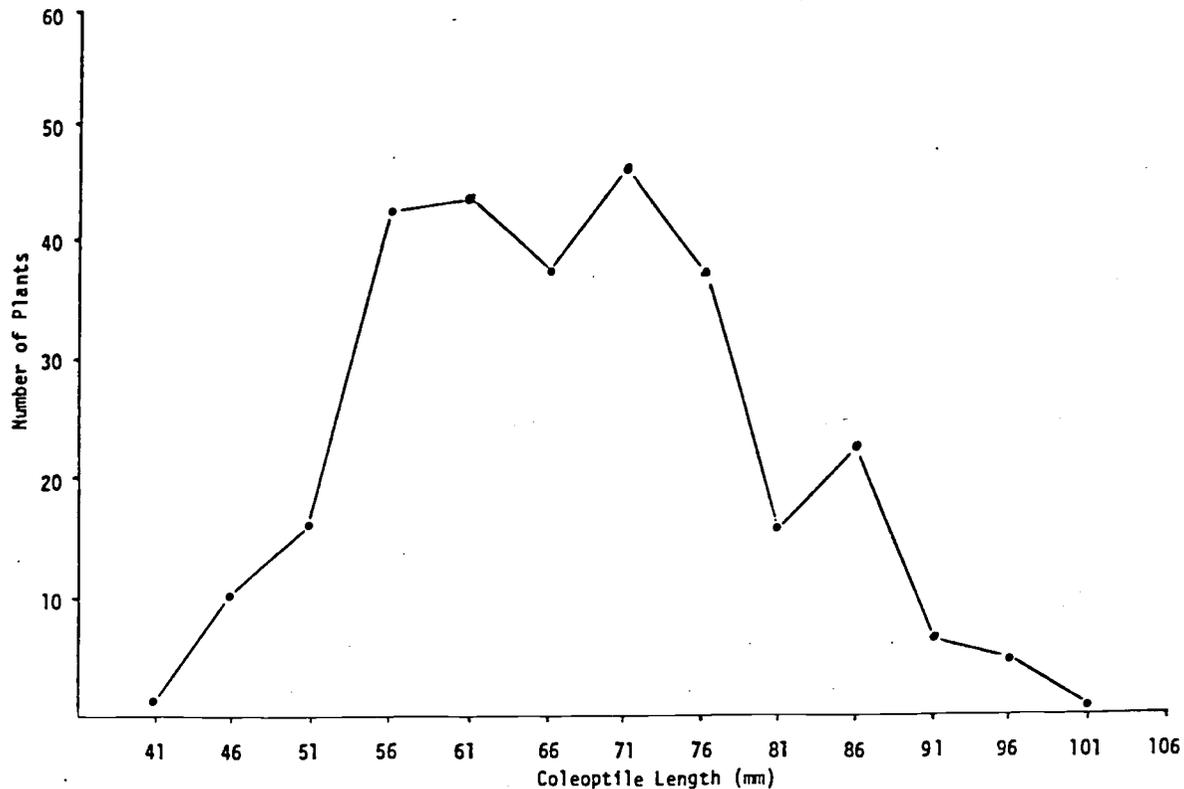


Figure 5. Frequency polygon of  $F_2$  for coleoptile length in Yamhill x Daws cross

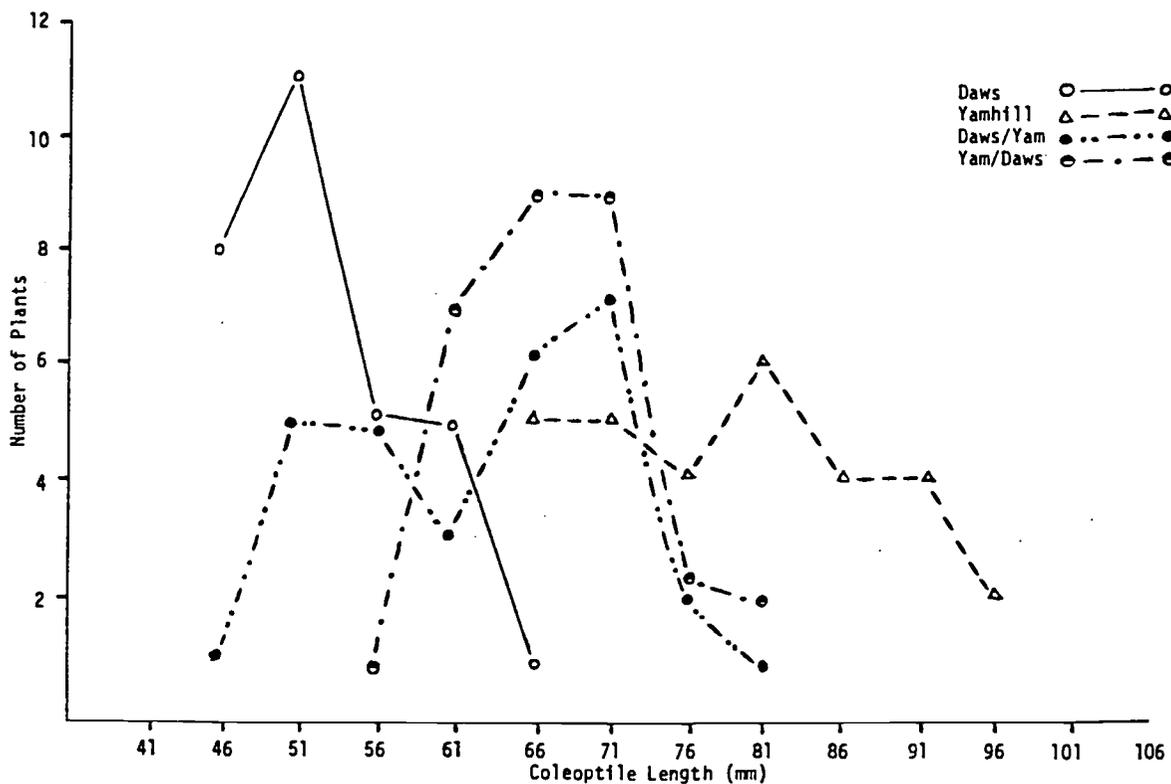


Figure 6. Frequency polygons of parents,  $F_1$ , and  $F_1$  reciprocal for coleoptile length in Yamhill x Daws cross

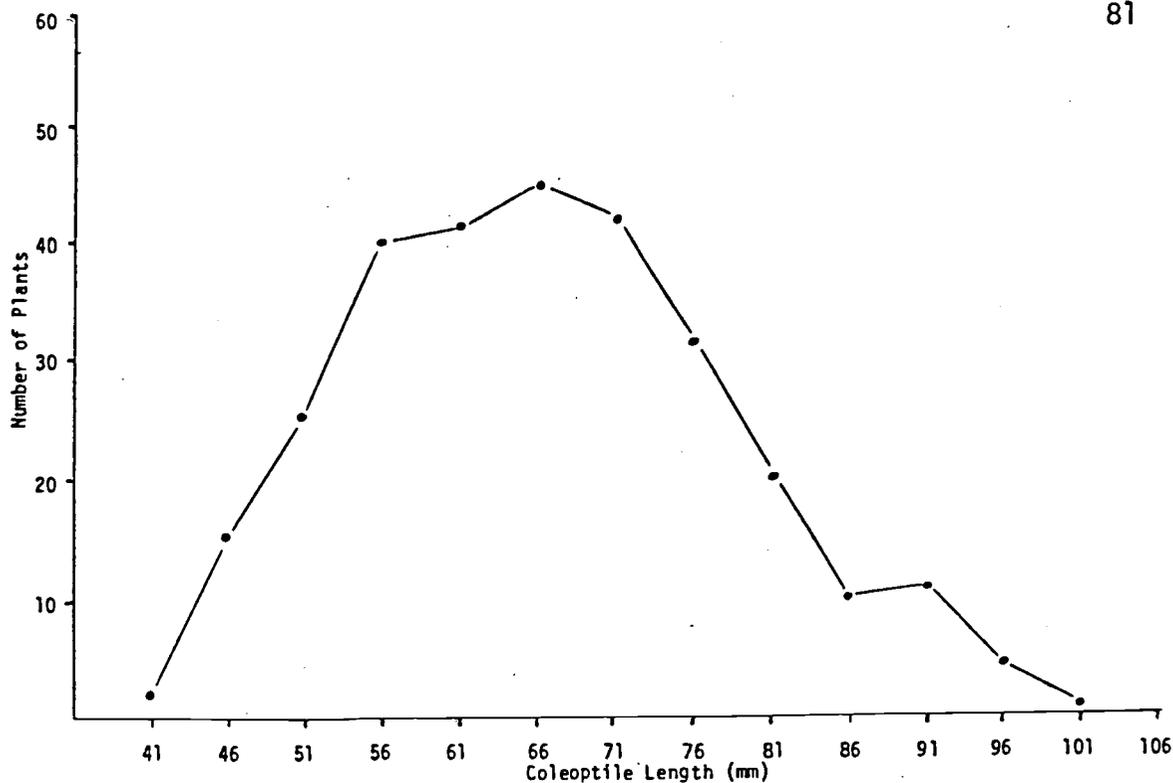


Figure 7. Frequency polygon of F<sub>2</sub> for coleoptile length in Moro x Daws cross

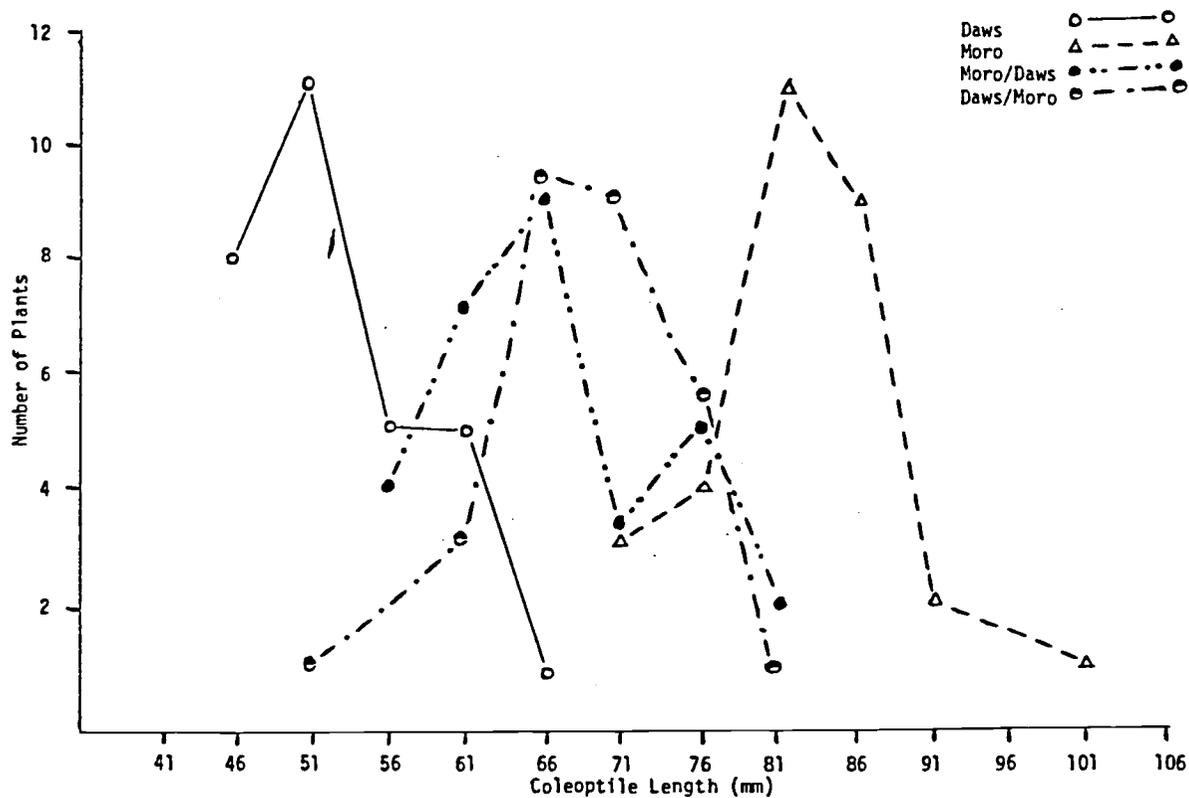


Figure 8. Frequency polygons of parents, F<sub>1</sub>, and F<sub>2</sub> reciprocal for coleoptile length in Moro x Daws cross

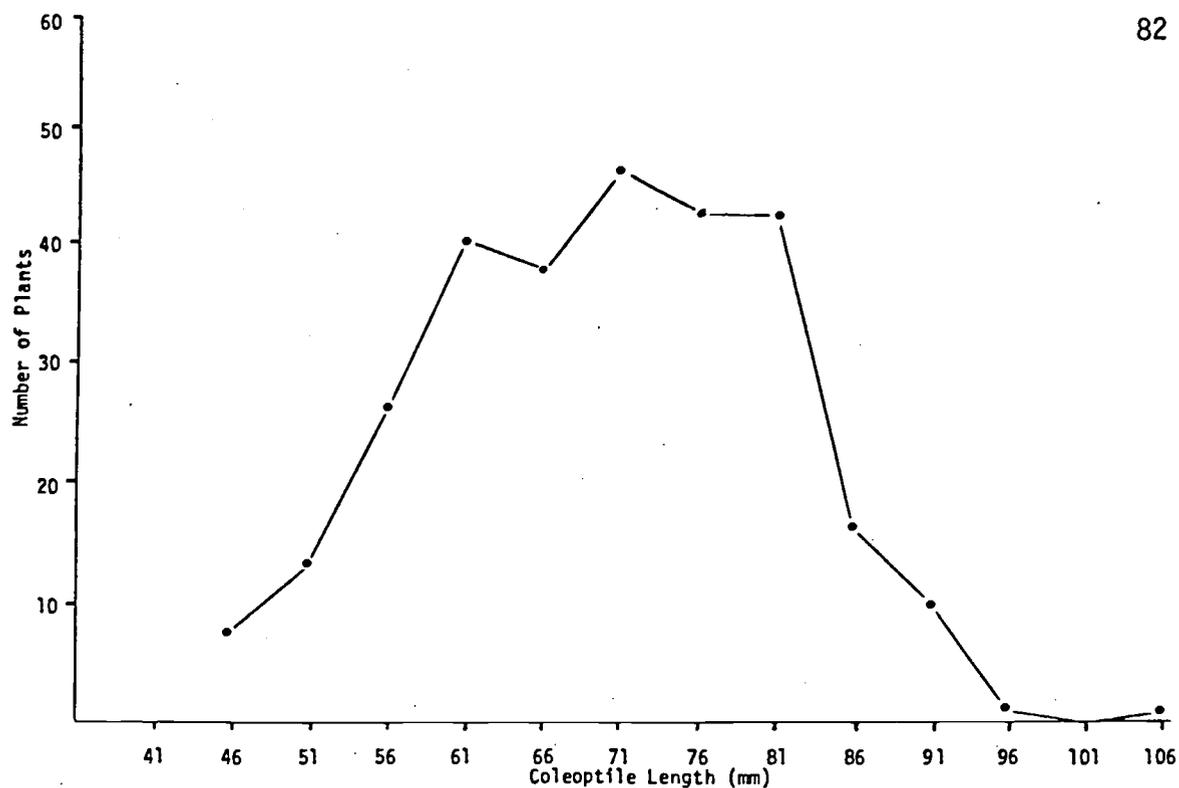


Figure 9. Frequency polygon of  $F_2$  for coleoptile length in Moro x McDermid cross

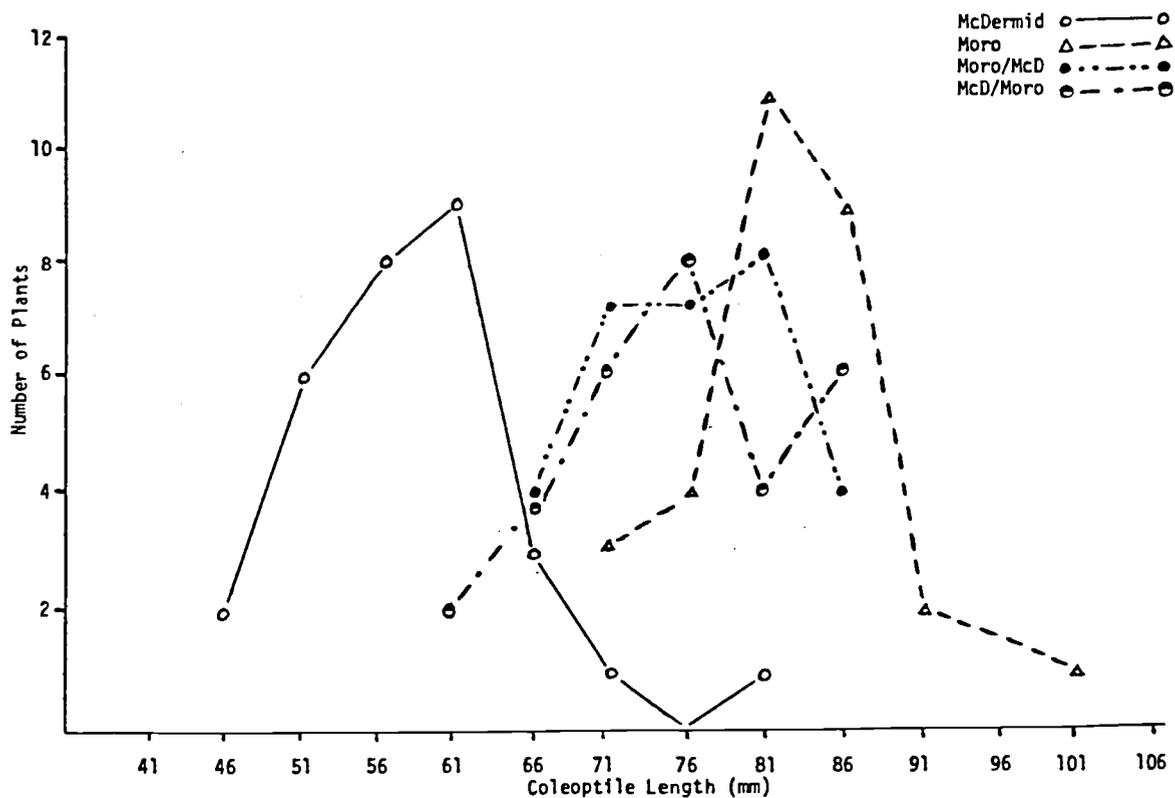


Figure 10. Frequency polygons of parents,  $F_1$ , and  $F_1$  reciprocal for coleoptile length in Moro x McDermid cross.

normality of population distribution can be used as a means of determining if coleoptile length is distributed as a discrete or continuous variable. Therefore, the parental  $F_1$  and  $F_2$  populations were tested for their approach to normality by means of chi square tests (Steel and Torrey, 1960; Leonard, Mann, and Powers, 1957). In such a test, results can be interpreted in several ways. If the parental and  $F_1$  frequency distributions approach normality, the environmental or non-heritable variance is normally distributed in those populations. If the data for an  $F_2$  population falls into discrete classes this indicates that coleoptile length is simply inherited which means that the population is composed of a relatively small number of genotypes. If the data from an  $F_2$  population appear normally distributed this generally indicates that the population is composed of a relatively large number of genotypes, each fluctuating about its own mean. Approach to normality could also occur in an  $F_2$  population if few genotypes are involved but the environmental effects on those genotypes is large. In such a case, the separations between the individual classes become less distinct and the population appears normally distributed.

Frequency tables for the parents,  $F_1$ s, and  $F_2$ s are presented in Tables 19-22. Some adjacent classes were combined in order to provide an expected frequency of at least four individuals per class. Chi squares obtained by comparing observed and expected ratios for

Table 19. Means, variances, standard deviations, and observed and expected frequency distributions for the parent, F<sub>1</sub>, and F<sub>2</sub> populations of the Yamhill x McDerimid cross.

Population	$\bar{X}$	$S^2$	S	Frequency Distribution in Number														N
				Upper Limit of Class														
				43.5	48.5	53.5	58.5	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	
Yamhill																		
Observed	79.0	86.1	9.3						5	5	4	6	4	4	2			30
Expected									4	4	7	6	5	3	1			30
McDerimid																		
Observed	58.0	56.0	7.5		2	6	8	9	3	1	0	1						30
Expected					3	5	8	7	4	2	1	0						30
F <sub>1</sub>																		
Observed	71.0	59.6	7.7		1	0	6	6	9	18	10	7	1	2				60
Expected					0	1	3	7	12	15	12	7	2	1				60
F <sub>2</sub>																		
Observed	71.0	160.8	12.7	0	15	16	24	35	35	53	37	28	21	15	7	1	1	288
Expected				4	7	13	23	33	41	45	43	33	24	12	6	2	1	288

Table 20. Means, variances, standard deviations, and observed and expected frequency distributions for the parent, F<sub>1</sub>, and F<sub>2</sub> populations of the Yamhill x Daws cross.

Population	$\bar{X}$	$S^2$	S	Frequency Distribution in Number														N
				43.5	48.5	53.5	58.5	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	
Yamhill																		
Observed	79.0	86.1	9.3						5	5	4	6	4	4	2			30
Expected									4	4	7	6	5	7	1			30
Daws																		
Observed	53.0	34.6	5.9		8	11	5	5	1									30
Expected					7	7	9	4	1									30
F <sub>1</sub>																		
Observed	66.0	53.6	7.3		1	5	6	10	15	16	4	3						60
Expected					1	2	7	13	16	13	7	1						60
F <sub>2</sub>																		
Observed	68.0	134.9	11.6	2	10	16	43	44	38	46	38	16	22	7	5	1	0	288
Expected				5	8	17	29	41	48	47	40	26	15	7	3	1	1	288

Table 21. Means, variances, standard deviations, and observed and expected frequency distributions for the parent, F<sub>1</sub>, and F<sub>2</sub> populations of the Moro x McDermid cross.

Population	$\bar{X}$	S <sup>2</sup>	S	Frequency Distribution in Number														N
				43.5	48.5	53.5	58.5	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	
Moro																		
Observed	82.0	35.1	5.9							3	4	11	9	2	0	1		30
Expected									2	6	10	8	3	1	0			30
McDermid																		
Observed	58.0	56.0	7.5		2	6	8	9	3	1	0	1						30
Expected					3	5	8	7	4	2	1	0						30
F <sub>1</sub>																		
Observed	76.0	46.5	6.8					2	8	13	15	12	10	0				60
Expected								2	7	13	16	13	6	2				60
F <sub>2</sub>																		
Observed	71.0	124.8	11.2	0	8	13	27	40	38	47	43	43	17	10	1	0	1	288
Expected				2	4	10	21	35	47	53	44	35	21	10	4	2	0	288

Table 22. Means, variances, standard deviations, and observed and expected frequency distributions for the parent, F<sub>1</sub>, and F<sub>2</sub> populations of the Moro x Daws cross.

Population	$\bar{X}$	S <sup>2</sup>	S	43.5	48.5	53.5	58.5	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	N
Moro																		
Observed	82.0	35.1	5.9							3	4	11	9	2	0	1		30
Expected										2	6	10	8	3	1	0		30
Daws																		
Observed	53.0	34.6	5.9		8	11	5	5	1									30
Expected					7	9	9	4	1									30
F <sub>1</sub>																		
Observed	68.0	45.1	6.7			1	6	10	18	12	10	3	0					60
Expected						1	4	10	17	16	9	2	1					60
F <sub>2</sub>																		
Observed	67.0	142.4	11.9	2	15	25	40	41	45	42	32	20	10	11	4	1		288
Expected				7	10	20	32	42	48	45	36	25	13	6	3	1		288

Table 23. Goodness of fit test for normality of observed data for coleoptile length of the parent,  $F_1$ , and  $F_2$  populations.

Population	Degree of Freedom	$\chi^2$	Probability
Yamhill	3	2.98	.50
Moro	1	0.60	.50
McDermid	1	1.14	.25
Daws	1	2.56	.10
$F_1$ Yamhill x McDermid	3	4.07	.25
$F_1$ Yamhill x Daws	3	4.70	.25
$F_1$ Moro x McDermid	2	0.93	.75-.50
$F_1$ Moro x Daws	3	3.42	.50-.25
$F_2$ Yamhill x McDermid	8	6.89	.75-.50
$F_2$ Yamhill x Daws	8	16.64	.05-.025
$F_2$ Moro x McDermid	8	11.67	.25-.10
$F_2$ Moro x Daws	8	9.73	.25

each cross are presented in Table 23. The probability column indicates the probability of getting a larger chi square value. Therefore, the higher the probability value, the better the fit to normality.

Of the parents, Yamhill and Moro had the most normally distributed populations ( $P=.5$ ). McDermid produced a comparatively poorer fit to normality ( $P=.25$ ). Daws did not fit a normal distribution ( $P=.10$ ).

Fits to normality were good for the Moro x McDermid ( $P=.75 - .50$ ) and the Moro x Daws ( $P=.50-.25$ )  $F_1$ s. Yamhill x McDermid and Yamhill x Daws exhibited comparatively poorer fits to normality ( $P=.25$ ). When Yamhill was used as one of the parents, poorer fits to normality occurred. This indicates that environmental variability is less normally distributed in the  $F_1$ s with Yamhill as a parent, than in the  $F_1$ s with Moro as a parent.

The Yamhill x McDermid  $F_2$  produced a good fit to normality ( $P=.75-.50$ ). The Moro x Daws  $F_2$  fit to a normal distribution at a probability of .25. The Yamhill x Daws and Moro x McDermid  $F_2$ s did not fit a normal distribution ( $P=.05-.025$  and  $.25-.10$ , respectively). However, these  $F_2$  populations also failed to show discrete classes. The discrepancy between the  $F_2$  populations in terms of their fits to normality makes it difficult to draw conclusions about the number of genes involved in the inheritance of coleoptile length in these populations. In the Yamhill x McDermid and Moro x Daws  $F_2$

populations the apparent fit to normality suggest that inheritance is quantitative in these populations. The comparatively poor fits to normality of the Yamhill x Daws and Moro x McDermid  $F_2$  populations suggest that few numbers of genotypes are present in those populations and that the environmental effects on the genotypes masks the distinctiveness of the individual classes.

Estimates of dominance in the  $F_1$  populations together with estimates of minimum gene numbers controlling the expression of coleoptile length are given in Table 24.

Table 24. Average coleoptile length of the high parent ( $\overline{HP}$ ), midparent ( $\overline{MP}$ ), and  $\overline{F_1}$ , difference between  $\overline{HP}$  and  $\overline{MP}$  (D), degree of dominance estimates, and minimum gene number for four wheat crosses.

Cross	$\overline{TP}$	$\overline{MP}$	$\overline{F_1}$	D	$d^{\frac{a}{d}}$	Minimum gene number
Yamhill x McDermid	79.0	68.5	71.0	10.5	0.238	0.545
Yamhill x Daws	79.0	66.0	66.0	13.0	0.000	1.040
Moro x McDermid	82.0	70.0	76.0	12.0	0.500	-920
Moro x Daws	82.0	67.5	68.0	14.5	0.035	1.080

$\frac{a}{d} = 1$  Complete dominance.  
 $= 0$  No dominance.

Estimates of dominance varied considerably among  $F_1$ s. The highest amounts of dominance were observed in the Yamhill x McDermid ( $d=.238$ ) and the Moro x McDermid ( $d=.5$ )  $F_1$ s. These two  $F_1$ s were also observed to have the greatest expressions of

heterosis (Table 18). Dominance was virtually non-existent in the Yamhill x Daws and Moro x Daws  $F_1$  s. This indicates that additive gene action is mainly responsible for the control of coleoptile length expression in these two populations, assuming that epistatic effects are negligible.

Minimum gene numbers controlling the expression of coleoptile length were found to be approximately equal to 1.0 for three of the four crosses. The Yamhill x McDermid cross gave an even lower estimate of .5. Analysis of Table 16 reveals that the total variance in this population was substantially greater than the variance within the other three  $F_2$  populations. The denominator in the formula for estimating minimum gene number represents the sum of the difference between the genetic and environmental variances with an  $F_2$  population. The environmental variance is estimated by the variance of the  $F_1$  population from which the  $F_2$  was derived. The genetic variance within the  $F_2$  is determined by the differences between genotypes. The greater the differences between genotypes, the larger the genetic variance. The variance due to genotypes is proportional to the number of genotypes in the population. When a large number of genotypes are present in an  $F_2$  population, the relative difference between them is small and therefore the genetic variance is also small. The converse is true when a small number of genotypes make up the population. The low estimates of minimum gene number

indicates that relatively few genotypes occur in the four  $F_2$  populations. If this is the case, the environmental effects on these genotypes must be substantial because discrete classes were not observed.

Heritability in the broad sense specifies the proportion of the total phenotypic variability that is due to genetic causes or the ratio of the genetic variance to the total variance. If the genetic variance accounts for the majority of the phenotypic variance then broad sense heritability estimate is high. Narrow sense heritability refers only to that part of the genotypic variance attributed to additive genetic factors. This is the component of variance that is of interest to the breeder of self-pollinated crops because it can be utilized.

Broad sense heritability estimates for coleoptile length of each of the four crosses are given in Table 25. Main cross and reciprocal  $F_2$ s were combined to provide estimates of the  $F_2$  variance for each cross. A pooled estimate of the midparent and  $F_2$  variances was used to obtain an estimate of broad sense heritability for the  $F_2$  population as a whole.

The Yamhill x McDermid and the Yamhill x Daws  $F_2$ s agreed closely in their broad sense heritability estimates (55.8 and 55.3%, respectively). The Moro x McDermid and Moro x Daws  $F_2$ s gave higher estimates of broad sense heritability (63.5 and 75.5%

respectively). The Moro x McDermid and Moro x Daws  $F_2$ s gave higher estimates of broad sense heritability (63.5 and 75.5% respectively). The pooled estimate of broad sense heritability indicates that approximately 62% of the phenotypic variance was due to genetic causes. The remaining 38% was produced by the environmental influence on the genotypes making up the population. Similar estimates of broad sense heritability for coleoptile length were obtained by Chowdry and Allan (1963) in a study involving four wheat crosses. They found broad sense estimates ranging from 46 to 78% for coleoptile length in four  $F_2$  populations.

Table 25. Broad sense heritability estimates for coleoptile length using the  $F_2$ /parental variance method.

Cross	MP variance	$F_2$ variance	$H_{bs}$ (%)
Yamhill x McDermid	71.040	160.785	55.8
Yamhill x Daws	60.305	134.865	55.3
Moro x McDermid	45.555	124.820	63.5
Moro x Daws	34.820	142.380	75.5
Pooled	52.930	140.713	62.4

The rather substantial amount of environmental variation (38%) observed in this study explains the apparent approach to normality of the  $F_2$  frequency distributions and the lack of discrete classes among genotypes in the  $F_2$  populations. The average variation due to environment is sufficiently large to produce distributions that appear

normally distributed when even as few as one major gene is involved (Allard, 1960). The sensitivity of coleoptile length to environmental influences under the controlled environment used in this study indicate that modifying genes may be involved in the expression of coleoptile length. Another plausible explanation for the large environmental variation within  $F_2$ s could be that some degree of dormancy was present in the  $F_2$  seeds at the time the experiment was conducted. This problem was anticipated and attempts were made to alleviate it by cold treatment of the  $F_2$  seed. However individual seeds may have varied in their rates of germination and this may have affected the expression of coleoptile length.

Narrow sense heritability estimates obtained by the regression and standard unit methods are presented in Table 26. Parent,  $F_1$ , and  $F_2$  replication means were used to obtain these estimates.

Table 26. Narrow sense heritability estimates for coleoptile length determined by regression and standard unit methods.

Comparison	Standard unit (%)	Regression (%)	$R^2$
$F_1$ on MP	56.6	27.9	32.0
$F_2$ on $F_1$	64.6	124.6	41.7

Estimates of narrow sense heritability obtained by the standard unit method are relatively close for the two comparisons. Estimates

obtained from the comparison of  $F_2$  with  $F_1$  gave the highest estimate (64.6%). Both estimates obtained by the standard unit method are very close to the pooled estimate of broad sense heritability of 62.4% (Table 25). This indicates that essentially all of the genotypic variance involved in the expression of coleoptile length is due to additive gene action. This observation agrees with results reported earlier concerning the closeness of the midparent,  $F_1$ , and  $F_2$  means in each of the four populations.

The discrepancy between the two estimates obtained by regression and the close agreement between the two estimates obtained by the standard unit method indicates that some type of environmental scaling factor was operating to increase the range of phenotypic variation in the  $F_1$  generation. This statement is based on the following observations. The regression coefficient indicates the amount of change in  $y$  for the unit change in  $x$ . Regression of  $F_1$  ( $X$ ) on midparent ( $y$ ) gave a low regression coefficient. This indicates that the amount of change in midparent was low in relation to a unit change in  $F_1$ . The reverse is true for regression of  $F_2$  ( $x$ ) on  $F_1$  ( $y$ ). In this instance the amount of change in  $F_1$  is large for a unit change in  $F_2$ . The environment scaling factor alluded to is most likely related to the fact that the  $F_1$  seed was one year older than the  $F_2$  seed. This difference in age could account for a larger range in the phenotypic variation among  $F_1$ s in comparison to that of parents and  $F_2$ s. In

addition the  $F_1$  seed was produced from artificial pollination which resulted in substantial differences in seed size between  $F_1$ s. This could have affected the range of phenotypic variance among  $F_1$ s. The standard unit method estimates are obtained by calculating the regressions on data coded in terms of standard deviation units. Such a regression is identical to correlation coefficients on the original data. Thus, the standard unit method corrects for any discrepancy that arises due to scaling factors.

The results and discussions dealing with the inheritance of coleoptile length lead to several conclusions: 1) The close agreement between midparent,  $F_1$ , and  $F_2$  means indicates that the expression of coleoptile length is controlled primarily by additive gene action. 2) The recovery of the parental types in each  $F_2$  population indicates three or fewer major genes are involved in the expression of coleoptile length. 3) The large environmental influence on the genotypes constituting the  $F_2$  populations is responsible for the apparent approach to normality and the lack of discrete classes of the  $F_2$  frequency distributions. 4) Coleoptile length exhibited a high narrow sense heritability as estimated by the standard unit method. 5) Selection for coleoptile length in early generations should give reliable estimates of coleoptile length expression in later generations.

Part 2. Inheritance of Adenosine Triphosphate

The parents,  $F_1$ s, and  $F_2$ s from the four crosses previously defined were tested for their Adenosine Triphosphate content in the seedling stage. The Moro x McDermid  $F_1$  and reciprocal  $F_1$  were not included in this study due to lack of sufficient seed.

The results of the analysis of variance for Adenosine Triphosphate (ATP) in the parents,  $F_1$ s, and  $F_2$ s are presented in Table 27. Adenosine Triphosphate was expressed as nmoles/seedling and as nmoles/mg seed weight. The latter was used to correct for differences in seed weight between the three generations.

Table 27. Mean squares from the analysis of variance for ATP and ATP/mg involving parents and two generations.

Source of variation	D. F.	ATP (nmole/seedling)	ATP/mg (nmole)
Replication	2	1.429**	.000850**
Generation	17	4.056**	.004422**
Between Generations	2	28.753**	.032497**
Within Generations	15	0.763**	.000679**
Within Parents	3	2.545**	.001624**
Within $F_1$ s	5	.712**	.000695**
Within $F_2$ s	7	.036	.000262**
Generation x Treatment	34	.115	.000072
Total	53		
Coefficient of variability (%)		7.2	7.4

\*\*Significant at the 1% level.

Differences between and within generations were highly significant for ATP and ATP/mg seed weight. The greatest contribution to the within generation mean square came from the differences among the parents for both ATP and ATP/mg. Differences among  $F_2$ s were highly significant for ATP/mg but nonsignificant for ATP.

The parental,  $F_1$ , and  $F_2$  means for ATP and ATP/mg are given in Table 28. Duncan's Multiple Range Test was used to test the significance of differences among parents,  $F_1$ s, and  $F_2$ s.

The  $F_1$  means for ATP were generally greater than the parental or  $F_2$  means. Exceptions were the McDermid x Yamhill, Daws x Moro, and Moro x Daws  $F_1$ s which did not differ significantly from the Yamhill parent. The two tall parents (Yamhill and Moro) had significantly higher ATP contents than did the two semi-dwarf parents (McDermid and Daws). This suggests that a positive association may exist between plant height and ATP. This possibility will be explored in Part 3 of this study. The semi-dwarf parents did not differ significantly from the  $F_2$ s in ATP content. The  $F_2$ s generally gave the lowest values for ATP. The low values for ATP of the  $F_2$  populations indicates that the ATP of the  $F_2$ s in this study may have been limited by the ATP content of the lower parent of the original cross. Similar results were found by Vahabian (1977). In a study of 15  $F_2$  populations he observed only one  $F_2$  population that had an ATP content significantly above the midparent.

Table 28. Mean value for ATP and ATP/mg at  $F_1$ 's,  $F_2$ 's, and reciprocals of four wheat crosses.

Parents and Crosses	ATP (nmole/seedling)	ATP/mg (nmole)
Yamhill	5.65 cd <sup>1</sup>	.119 e
Daws	3.96 f	.087 gh
McDermid	3.66 f	.082 h
Moro	4.56 e	.129 de
Yam x Daws $F_1$	6.47 ab	.172 ab
Daws x Yam $F_1$	6.74 a	.173 ab
Yam x McD $F_1$	6.30 ab	.161 bc
McD x Yam $F_1$	5.57 d	.135 cd
Daws x Moro $F_1$	5.53 d	.157 c
Moro x Daws $F_1$	6.11 bc	.175 a
Yam x McD $F_2$	3.96 f	.081 h
McD x Yam $F_2$	3.77 f	.073 h
Yam x Daws $F_2$	3.83 f	.076 h
Daws x Yam $F_2$	3.88 f	.078 h
Daws x Moro $F_2$	3.67 f	.083 h
Moro x Daws $F_2$	3.62 f	.085 gh
McD x Moro $F_2$	3.78 f	.101 f
Moro x McD $F_2$	3.74 f	.093 fg

<sup>1</sup>DMRT; Means followed by the same letter are not significantly different at the 5% level

Differences in ATP content due to seed size were eliminated by calculating ATP/mg seed weight. This had the effect of increasing the mean ATP content of the  $F_1$ s in relation to the ATP content of the parents and the  $F_2$ s. The  $F_1$  means, in general, were significantly greater than the parental or  $F_2$  means for ATP/mg. The only exception was the nonsignificant difference between the McDermid x Yamhill  $F_1$  and the Moro parent. In general, the  $F_2$ s did not differ significantly from the means of the two semi-dwarf cultivars for ATP/mg. Exceptions were the McDermid x Moro  $F_2$  which had a significantly greater ATP/mg than did McDermid.

Generation means for ATP and ATP/mg as percent of midparent and as percent of highest parent are given in Table 29. Heterosis was observed in each of the  $F_1$ s and heterobelteosis was observed in five of the six  $F_1$ s. Inbreeding depression was substantial in the  $F_2$  populations, ATP and ATP/mg were highest in the Moro x McDermid  $F_2$  but, the amount of inbreeding depression could not be determined for that population because the  $F_1$ s were not included in the study.

Comparison of the  $F_1$  means as percent of midparent and as percent of highest parent reveals that both heterosis and heterobelteosis estimates were highest when ATP was expressed in relation to seed weight. This occurred because the  $F_1$  seed weighed less than the seed of the parent lines.

Table 29. Generation means expressed as % of midparent and percent of high parent for ATP and ATP/mg seed weight.

Cultivar and Generation	ATP (nmole/seedling)	% midparent	% high parent	ATP (nmole)	% midparent	% high parent
Yamhill	5.65	--	--	.119	--	--
Moro	4.56	--	--	.129	--	--
McDermid	3.66	--	--	.082	--	--
Daws	3.76	--	--	.087	--	--
(Yamhill + McDermid)/2	4.65	100	82	.100	100	84
Yamhill/McDermid F <sub>1</sub>	6.30	135	111	.161	161	135
McDermid/Yamhill F <sub>1</sub>	5.57	120	99	.135	135	113
Yamhill/McDermid F <sub>2</sub>	3.87	83	68	.077	77	65
(Yamhill + Daws)/2	4.71	100	83	.103	100	86
Yamhill/Daws F <sub>1</sub>	6.47	137	114	.172	167	144
Daws/Yamhill F <sub>1</sub>	6.74	143	119	.173	168	145
Yamhill/Daws F <sub>2</sub>	3.85	82	68	.077	75	65
(Moro + Daws)/2	4.14	100	91	.108	100	84
Moro/Daws F <sub>1</sub>	6.11	148	134	.175	162	136
Daws/Moro F <sub>1</sub>	5.53	134	121	.157	145	122
Moro/Daws F <sub>2</sub>	3.65	88	80	.084	78	65
(Moro + McDermid)/2	4.11	100	90	.105	100	81
Moro/McDermid F <sub>2</sub>	3.76	91	82	.097	92	75

Estimates of dominance in the  $F_1$  populations for ATP and ATP/mg are presented in Tables 30 and 31, respectively. Main cross and reciprocal  $F_1$ s were combined to obtain these estimates. Estimates were greater than 1.0 for ATP and ATP/mg in each of the  $F_1$  populations. In fact, the average estimate of dominance for ATP and ATP/mg of the three populations were 2.48 and 3.57, respectively. This indicates a substantial amount of overdominance in these populations. Mitochondrial complementation, which is considered by some to contribute to heterosis, may also explain the high estimates of dominance. The mechanism of mitochondrial complementation is not understood. It is known that the reproduction of mitochondria is a cooperative effort between the nuclear genes and the genes in the mitochondrial DNA. Presumably, putting together the right combination of genotypes results in more efficient mitochondria. The estimates of dominance obtained in this study may indicate that favorable combinations of nuclear and cytoplasmic genes occurred for each of the  $F_1$  populations.

The inheritance of ATP has been shown to be subject to cytoplasmic influences (Vahabian, 1977). The major site of ATP synthesis in seedlings is the mitochondria located in the cytoplasm. In the  $F_1$  seeds most, if not all, of the mitochondrial DNA originate from the maternal parent. This being the case, it seems plausible that the efficiency of ATP synthesis or the pool size of ATP of an  $F_1$  or its

Table 30. Average ATP of the high parent ( $\overline{HP}$ ), midparent ( $\overline{MP}$ ), and  $\overline{F_1}$ , difference between  $\overline{HP}$  and  $\overline{MP}$  (D), and degree of dominance estimates for three wheat crosses.

Cross	$\overline{HP}$	$\overline{MP}$	$\overline{F_1}$	D	$d^a$
Yamhill x McDermid	5.65	4.65	5.93	1.00	1.28
Yamhill x Daws	5.65	4.71	6.60	.94	2.01
Moro x Daws	4.56	4.16	5.82	.40	4.15

$d^a$  = 1 Complete dominance  
 = 0 No dominance

Table 31. Average ATP/mg of the high parent ( $\overline{HP}$ ), midparent ( $\overline{MP}$ ), and  $\overline{F_1}$ , difference between  $\overline{HP}$  and  $\overline{MP}$  (D), and degree of dominance estimates for three wheat crosses.

Cross	$\overline{HP}$	$\overline{MP}$	$\overline{F_1}$	D	$d^a$
Yamhill x McDermid	.119	.100	.161	.019	3.21
Yamhill x Daws	.119	.103	.172	.016	4.31
Moro x Daws	.129	.108	.175	.021	3.19

$d^a$  = 1 Complete dominance  
 = 0 No dominance

reciprocal may be influenced more by the quantity or quality of the mitochondria of the maternal parent.

In Table 27, it was observed that the tall cultivars (Moro and Yamhill) conserved greater amounts of ATP and ATP/mg than did the two semi-dwarf cultivars (McDermid and Daws). If the superiority of Yamhill and Moro in ATP content is due to their mitochondria then this superiority should be transferred to their offspring when these two cultivars are used as females in crosses with McDermid and Daws. To determine if this cytoplasmic inheritance occurs, contrasts for ATP and ATP/mg were developed between the  $F_1$ s with Moro and Yamhill as females and their reciprocals. The results are presented in Tables 32 and 33.

Differences between main crosses and reciprocals were significant for both ATP and ATP/mg. In the Yamhill x Daws and Daws x Yamhill crosses it did not appear to make a difference if Yamhill was used as the male or female parent. However in the Yamhill x McDermid and Moro x Daws  $F_1$ s and reciprocals, higher ATP and ATP/mg contents were obtained when Yamhill and Moro were used as females in the cross. Based on this evidence, the assumption that ATP content of an  $F_1$  is determined by the ATP content of the maternal parent appears to be plausible. This indicates that cytoplasmic effects may influence the inheritance of ATP in the  $F_1$  generation. Analysis of Table 28 reveals that the reciprocal effects observed

Table 32. Contrast between  $F_1$ s and reciprocal  $F_1$ s for nmoles ATP/seedling.

	Semi-dwarf as ♀			Tall as ♀			L	D	S <sup>2</sup>	F
	Daws Yam	McD Yam	Daws Moro	Yam Daws	Yam McD	Moro Daws				
Contrast	20.22	16.71	16.59	19.41	18.9	18.33				
$F_1$ vs. rec	+1	+1	+1	-1	-1	-1	-3.12	18	.541	4.70*

\*Significant at 5% level.

Table 33. Contrast between  $F_1$ s and reciprocal  $F_1$ s for nmoles ATP/mg seed weight.

	Semi-dwarf as ♀			Tall as ♀			L	D	S <sup>2</sup>	F
	Daws Yam	McD Yam	Daws Moro	Yam Daws	Yam McD	Moro Daws				
Contrast	.519	.405	.471	.516	.483	.525				
$F_1$ vs. rec	+1	+1	+1	-1	-1	-1	-.129	18	.000924	12.83**

\*\*Significant at 1% level.

in the  $F_1$  generation did not appear in the  $F_2$  generation.

Narrow sense heritability estimates obtained by the regression and standard unit methods are presented in Table 34. Parental,  $F_1$ , and  $F_2$  means were used to obtain these estimates.

Table 34. Narrow sense heritability estimates for ATP and ATP/mg determined by regression and standard unit methods.

Comparison	Standard unit (%)		Regression (%)	
	ATP	ATP/mg	ATP	ATP/mg
$F_1$ on MP	71.4	57.5	68.4	42.9
$F_2$ on $F_1$	69.9	45.4	182.9	134.8

Estimates of narrow sense heritability for ATP/mg, calculated by both methods, were consistently lower than estimates obtained for ATP. Heritability estimates obtained from the comparison of  $F_1$  on midparent were generally the same, regardless of the method used to estimate the heritability. Heritability estimates obtained from the comparison of  $F_2$  and  $F_1$  means varied considerably depending on the method used. Regression of  $F_2$  on  $F_1$  means gave estimates of 182.9 and 134.8% for ATP and ATP/mg, respectively. The fact that these estimates are considerably greater than 100% indicates that the range of phenotypic variation in the  $F_1$  generation was greater than the range of phenotypic variation among  $F_2$ s.

Estimates of narrow sense heritability are useful only when a ceiling on heritability is established. Otherwise high estimates obtained through regression may be misleading. If broad sense estimates of heritability are available, a valid comparison can be made between the narrow sense estimates obtained through regression and broad sense estimates. In this study, broad sense heritability estimates could not be determined. Therefore, the most reliable estimate of narrow sense heritability was obtained by using the standard unit method. This method sets a maximum ceiling of 100% for the narrow sense heritability estimate. Furthermore, the most reliable estimates of narrow sense heritability, as determined by the standard unit method, would be expected to be the estimates obtained for ATP/mg because seed weight differences between the three generations were observed to affect ATP content.

The correlation coefficients (standard unit method) between  $F_1$ s and midparents and between  $F_1$ s and  $F_2$ s for ATP/mg were .575 and .454, respectively. These estimates indicate that additive gene effects account for approximately one-half of the phenotypic variance. The remaining one-half is attributed to environmental effects, non-additive gene action, and cytoplasmic influences.

Several conclusions can be drawn from the preceding results and discussions:

- 1) The presence of possible mitochondrial complementation and

maternal effects in the  $F_1$  generation, and the considerable inbreeding depression in the  $F_2$  generation indicates that the inheritance of ATP is subject to cytoplasmic influences.

- 2) Selection for higher ATP content should be limited to generations beyond the  $F_2$ .
- 3) The failure of the  $F_2$  populations to maintain high levels of ATP suggests that breeding for increased ATP content would require a large number of initial crosses in order to find favorable combinations that will produce high levels of ATP in later generations.

Part 3. Association of coleoptile length, Adenosine Triphosphate, seed weight, plant height, and stand establishment in four wheat crosses

Parents,  $F_1$ s, and  $F_2$ s from four crosses were tested for differences in emergence rate and percent stand. Correlation coefficients were determined for the association of percent stand and emergence rate with coleoptile length, ATP, seed weight, and plant height.

The results of the analysis of variance for days to 25% emergence and percent stand determined in the laboratory on parents,  $F_1$ s, and  $F_2$ s from four wheat crosses are presented in Table 35.

Differences between and within generations were significant for days to 25% emergence and percent stand. For days to 25%

emergence, significant differences were observed within parents but not within  $F_1$ s or within  $F_2$ s. For percent stand, significant differences were observed within parents and within  $F_1$ s, but not within  $F_2$ s

Table 35. Mean squares from the analysis of variance for days to 25% emergence and percent stand involving parents and two generations.

Source of variation	D F.	Days to 25% emergence	Percent stand
Replication	2	.254	150.617
Generation	19	1.315**	736.206**
Between generations	2	4.359**	4491.706**
Within generations	17	.958**	294.382*
Within Parents	3	4.694**	427.417*
Within $F_1$ s	7	.153	364.899*
Within $F_2$ s	7	.161	166.851
Replication x Generation	38	.162	124.880
Total	59		
Coefficient of variability (%)		4.7	16.4

\*Significant at 5% level.

\*\*Significant at 1% level.

The mean days of 25% emergence and percent stand for the parents,  $F_1$ s, and  $F_2$ s are given in Table 36. Duncan's Multiple Range Test was used to compare parental,  $F_1$ , and  $F_2$  means for days to 25% emergence and percent stand. The 100 seed weight of

the parents,  $F_1$ s, and  $F_2$ s, and the plant height of parents and  $F_1$ s are also given in Table 36.

From the analysis of variance (Table 35) it was observed that differences within  $F_1$ s and within  $F_2$ s were non-significant for days to 25% emergence. This is also evident from the close association of means within these two generations in Table 36. Analysis of Table 36 shows that the parents Yamhill and Moro generally required the same amount of time to emerge as did the  $F_1$ s and  $F_2$ s. McDermid and Daws required significantly more time to emerge than did Yamhill, Moro, or the  $F_1$ s and  $F_2$ s.

For percent stand, the Moro parent produced significantly better stands than did McDermid or Daws. Yamhill, McDermid, and Daws did not differ significantly in percent stand. In general, the  $F_1$ s produced better stands than either the parents or  $F_2$ s. This could be due to several causes. The  $F_1$ s were shown to have higher amounts of ATP than either the parents or  $F_2$ s. This is indicative of greater seedling vigor in the  $F_2$ s relative to the parents or  $F_2$ s. Another explanation of their high percent stand is the heterosis for coleoptile length was observed in the  $F_1$  population. In all probability it was a combination of these two factors that produced the high percent stands in the  $F_1$  generation. Of the  $F_1$ s, McDermid x Yamhill and Moro x Daws produced the poorest stands. These two  $F_1$ s and the Daws x Yamhill  $F_1$  did not differ significantly from Moro in

Table 36. Mean values for days to 25% emergence, percent stand, 100 seed weight, and plant height involving parents, F<sub>1</sub>s, and F<sub>2</sub>s from four wheat crosses.

Parents and Crosses		Days to 25% emergence	Percent stand	100 seed weight (g)	Plant height (cm)
	Yamhill	8.8 bc <sup>a/</sup>	52 fgh	4.747	73.9
	Moro	7.7 e	66 cdef	3.533	88.1
	McDermid	10.3 a	38 h	4.448	69.0
	Daws	10.2 a	46 gh	4.338	73.2
F <sub>1</sub>	Yamhill x McDermid	8.5 bcd	91 a	3.901	84.2
	McDermid x Yamhill	8.7 bc	69 bcdef	4.135	85.5
	Moro x McDermid	8.0 de	91 a	2.951	81.7
	McDermid x Moro	8.7 bc	83 abc	4.900	85.9
	Yamhill x Daws	8.7 bc	93a	3.764	87.7
	Daws x Yamhill	8.7 bc	76 abcde	3.895	87.6
	Moro x Daws	8.5 bcd	64 defg	3.488	93.5
	Daws x Moro	8.5 bcd	86 ab	3.507	93.4
F <sub>2</sub>	Yamhill x McDermid	8.2 cd	57 fg	4.876	
	McDermid x Yamhill	8.5 bcd	59 efg	5.148	
	Moro x McDermid	7.8 e	60 efg	4.032	
	McDermid x Moro	8.0 de	68 cdef	3.726	
	Yamhill x Daws	8.5 bcd	61 defg	4.997	
	Daws x Yamhill	8.3 bcde	78 abcd	4.991	
	Moro x Daws	8.2 cde	63 defg	4.289	
	Daws x Moro	8.2 cde	53 fgh	4.418	

<sup>a/</sup>DMRT: Means followed by the same letter are not significantly different at the 5% level.

percent stand. All other differences between parents and  $F_1$ s for percent stand were significant. The relatively small differences in coleoptile length among the  $F_2$  populations most likely accounts for the non-significant differences among the  $F_2$ s for percent stand.

Correlation coefficients between days to 25% emergence, percent stand, 100 seed weight, plant height, coleoptile length, ATP and ATP/mg for the three generations are given in Tables 37, 38, and 39.

For the parents (Table 37) percent stand was significantly correlated with days to 25% emergence and plant height. High correlations were also observed between percent stand and coleoptile length ( $r = .821$ ), percent stand and ATP/mg ( $r = .923$ ) and percent stand with seed weight ( $r = -.721$ ). Days to 25% emergence was significantly correlated with coleoptile length, ATP/mg, and plant height. Coleoptile length was significantly correlated with ATP/mg. A high but non-significant correlation also existed between coleoptile length and plant height ( $r = .892$ ). This confirmed results reported by several researchers about the association between these two characters.

In Study I, part 1, it was observed that measures of seedling vigor (ATP and days to 25% emergence) were not reliable estimates of percent stand for the range of temperature and moisture levels under which the seven cultivars were tested. The best predictor of percent stand was found to be coleoptile length. In Table 37 it can be observed that measures of seedling vigor (ATP and days to 25% emergence) in addition to coleoptile length, appear to be good estimates of percent stand. Although results of these two studies

appear to be contradictory it should be emphasized that the results in Table 37 apply only to the four cultivars tested and to the specific environment under which they were tested. The results obtained in Study I were obtained from a larger number of cultivars and over a wide range of temperature and moisture combinations. Therefore, the results obtained in Study I would be expected to give better estimates of the relative importance of days to 25% emergence and ATP in terms of their ability to predict stand establishment.

The correlation coefficients for characteristics measured in the  $F_1$  generation are presented in Table 38. None of the characteristics measured exhibited a significant correlation with percent stand. The highest correlation was observed between coleoptile length and percent stand ( $r=.638$ ). This appears to be the only reliable indicator of percent stand in the  $F_1$  generation. Days to 25% emergence was significantly correlated with seed weight in the  $F_1$  generation. This indicates that  $F_1$ s with the heaviest seeds were the slowest to emerge. Correlations among other characters were low and non-significant in the  $F_1$  generation.

In the  $F_2$  generation, percent stand did not exhibit a significant correlation with any of the measured characters. As was the case in the  $F_1$ s, the highest correlation was observed between percent stand and coleoptile length ( $r=.46$ ). Percent stand and ATP exhibited a relatively low correlation ( $r=.27$ ). Days to 25% emergence was

Table 37. Correlation coefficients for seven characteristics measured on four wheat cultivars.

	Days to 25% emergence	Coleoptile length	Seed weight	ATP	<u>ATP</u> mg	Plant height
Percent stand	-.958*	.821	-.721	.504	.923	.975*
Days to 25% emergence		-.950*	.612	-.641	-.980*	-.990**
Coleoptile length			-.347	.816	.970*	.892
Seed weight				.210	-.453	-.718
ATP					.776	.528
ATP/mg						.945*

\*Significant at 5% level.

\*\*Significant at 1% level.

Table 38. Correlation coefficients for seven characteristics measured on the F<sub>1</sub> generation from four wheat crosses.

	Days to 25% emergence	Coleoptile length	Seed weight	ATP	<u>ATP</u> mg	Plant height
Percent stand	-.318	.638	-.150	.300	.148	-.266
Days to 25% emergence		-.539	.759*	.314	-.157	-.073
Coleoptile length			.049	-.011	-.079	-.316
Seed weight				.091	-.582	-.298
ATP					.753	-.320
ATP/mg						.366

\*Significant at 5% level.

Table 39. Correlation coefficients for six characteristics measured on the F<sub>2</sub> generation from four wheat crosses.

	Days to 25% emergence	Coleoptile length	Seed weight	ATP	<u>ATP</u> mg
Percent stand	-.003	.460	.006	.269	.110
Days to 25% emergence		-.355	.850**	.209	-.868**
Coleoptile length			-.032	.501	.213
Seed weight				.491	-.965**
ATP					-.258

\*\*Significant at 1% level.

significantly correlated with seed weight ( $r=.850$ ) and ATP/mg ( $r=.868$ ). This indicates that  $F_2$ s with heavy seeds are slow to emerge and the highest ATP/mg is indicative of the fastest emerging  $F_2$ s.

Based on the preceding results and discussion, the following conclusions can be reached:

- 1)  $F_1$ s produced superior stands relative to parents and  $F_2$ s.

This can be attributed to the effects of heterosis in the  $F_1$  generation.

- 2) Of the characteristics measured, coleoptile length appears to be best predictor of percent stand in the early generations.

## SUMMARY AND CONCLUSIONS

The objectives of these studies were as follows: 1) to determine the effects of temperature and moisture on stand establishment and stand establishment characteristics; 2) to evaluate cultivar differences in stand establishment under various temperature and moisture regimes, with special emphasis on the relationship between plant height, coleoptile length, and stand establishment; 3) to identify seedling characteristics, both morphological and physiological, that are good indexes of stand establishment over a wide range of temperature and moisture combinations; 4) to determine the degree of association between stand establishment estimates obtained in the laboratory and estimates of stand establishment obtained in the field; 5) to analyze the mode of inheritance of coleoptile length and Adenosine Triphosphate and the association of these and other characteristics with stand establishment in early generations.

Seven winter wheat cultivars adapted to growing conditions in the Pacific Northwest were utilized in these studies. These were: Yamhill, Moro, McDermid, Luke, Hyslop, Daws, and Stephens Crosses, including reciprocals, were made among four of these cultivars (Yamhill, Moro, McDermid, and Daws).  $F_1$  and  $F_2$  seed was procured for study.

Laboratory experiments were conducted on the seven cultivars

to evaluate the effects of temperature and moisture on stand establishment. Temperatures of 8, 15, and 22 C and moisture levels equivalent to -2, -4, and -6 bars were used in these studies. These are typical of temperature and moisture levels present in the seedbed over the range of planting dates in the Pacific Northwest. Seedling characteristics (shoot length, coleoptile length, seedling dry weight, and ATP) were evaluated for their ability to consistently predict stand establishment over a wide range of temperature and moisture levels.

Field studies on stand establishment of the seven cultivars were conducted at the Sherman Experiment Station in north-central Oregon. Associations were determined between results obtained from these experiments and results obtained from the laboratory experiments on stand establishment.

The mode of inheritance of coleoptile length and Adenosine Triphosphate was determined under laboratory conditions. The parents,  $F_1$ s, and  $F_2$ s from the crosses among the four parents listed above were utilized in these experiments. The degree of association of coleoptile length, Adenosine Triphosphate, and several other plant characteristics with stand establishment of the parent,  $F_1$ , and  $F_2$  generations was also determined.

The following conclusions were drawn:

- 1) Temperature and moisture exert significant effects on percent stand, emergence rate, shoot length, coleoptile length,

- seedling dry weight, and Adenosine Triphosphate.
- 2) The most negative effect on stand establishment occurs when soil temperature is high, soil moisture content is low, and deep planting depth is used.
  - 3) Cultivars are affected to different degrees by temperature and moisture in their expression of stand establishment and seedling characteristics associated with stand establishment.
  - 4) Coleoptile length is the most consistent predictor of stand establishment under conditions when emergence is limited due to depth of planting.
  - 5) Semi-dwarf cultivars have greater stand establishment problems than do tall cultivars because of their coleoptile length. Stand establishment problems of semi-dwarf cultivars increase with depth of planting.
  - 6) Laboratory estimates of percent stand can be reliable estimates of percent stand obtained in the field provided that laboratory conditions sufficiently simulate field conditions.
  - 7) Selection for stand establishment under warm temperature should give the best estimate of stand establishment over the range of temperatures present in the seedbed during stand establishment in dryland areas of the Pacific Northwest.
  - 8) Narrow sense heritability estimates for coleoptile length were high relative to broad sense heritability estimates. This

indicates that coleoptile length expression is controlled primarily by additive gene action.

- 9) The inheritance of coleoptile length of the populations studied appeared to be controlled by one to three major genes. The sensitivity of coleoptile length to environmental variation suggested that modifying genes may also affect coleoptile length expression.
- 10) Heritability of Adenosine Triphosphate (ATP) is subject to cytoplasmic influence.
- 11) Maternal effects in the  $F_1$  generation, and the occurrence of considerable inbreeding depression in the  $F_2$  generation, suggests that ATP can not be used as a selection character for seedling vigor in early generations.
- 12) Coleoptile length is a good predictor of stand establishment in early generations of wheat.

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## APPENDICES

## APPENDIX I

## PEDIGREE AND DESCRIPTION OF CULTIVARS

- Yamhill: (Heines VII/Redmond (Alba)). A low tillering, mid tall, high yielding cultivar released by Oregon State University for areas having about 450 mm of rainfall.
- Moro: (P.I. 178383/Omar<sup>2</sup>). A tall, fast emerging club wheat cultivar developed by Oregon State University for dryland areas of the Pacific Northwest having about 300 mm of rainfall.
- Luke: (P.I. 278383/Burt)\* Sel. 101 - A semidwarf, high tillering cultivar released by Washington State University. This cultivar is recommended for dryland areas having 450 mm rainfall.
- Hyslop: (Nord Desprez/sel 101<sup>2</sup>). A semidwarf, high yielding cultivar released by Oregon State University for dryland areas with about 400 mm of rainfall.
- McDermid: (Nord Desprez/Sel 101<sup>2</sup>). A sister line of Hyslop. McDermid is a semidwarf, high yielding cultivar released by Oregon State University for dryland areas with about 400 mm of rainfall.
- Stephens: OR 65-116 Selection. Resulted from a cross between Nord Desprez and Pullman Selection 101. Released as foundation seed by Oregon State University in 1977. Has wide adaptation to most areas of the Pacific Northwest.
- Daws: (CI 14484/CI 13645/PI 178383). High tillering, high yielding, semidwarf winter wheat. Developed by Washington State University. Adapted to dryland areas of the Pacific Northwest. Noted for its poor emergence.

APPENDIX II  
 CLIMATIC DATA FOR CORVALLIS AND MORO, OREGON  
 DURING THE 1976-77 GROWING SEASON

Locations	Months	Temperature ( $^{\circ}$ C)			Precipitation (mm)
		Max.	Min.	Mean	
Corvallis	September	24.5	9.5	17.0	32.2
	October	19.0	5.0	12.0	31.7
	November	13.0	3.4	8.2	36.0
	December	6.3	- .39	3.0	37.3
	January	7.0	-2.3	2.4	24.3
	February	12.3	1.4	6.8	75.4
	March	11.2	1.4	6.3	129.2
	April	17.0	3.1	20.0	25.9
	May	16.4	5.3	11.0	87.1
	June	23.4	8.6	16.0	18.7
	July	25.7	9.4	17.5	3.0
	August	29.5	11.9	20.7	48.0
	September	21.3	8.7	25.0	90.9
	Total	--	--	---	649.7
Moro	September	24.1	3.8	13.9	1.0
	October	17.6	4.1	10.8	2.5
	November	9.6	8.3	5.2	10.9
	December	5.8	-2.9	1.4	5.0
	January	.22	-6.9	-3.4	4.5
	February	7.4	-1.9	2.8	16.0
	March	9.5	-0.6	4.4	12.7
	April	17.3	3.0	10.2	2.0
	May	15.0	3.9	9.5	68.6
	June	25.0	10.7	17.9	7.1
	July	25.6	11.3	18.5	9.3
	August	29.6	14.1	21.8	22.9
	September	19.8	6.3	13.0	22.4
	Total				184.9



to  $5 \times 10^{-5}$ ,  $5 \times 10^{-6}$ , and  $5 \times 10^{-7}$  M were prepared by adding additional HEPES buffer.

2. Seedling Extract:

- A. After 72 hours of germination, seedlings were removed from the growth chamber.
- B. The embryo axis of each seedling was separated from the endosperm and immersed in a test tube containing seven milliliters of boiling water.
- C. After ten minutes, the test tubes were removed from the boiling water and placed in an ice bath. One milliliter of seedling embryo extract was removed from each tube and diluted with one milliliter of Reagent B. This two milliliter sample was then used for the assay of light emission.

3. Assay of Light Emission:

- A. Light emission was assayed from the ATP standards of (0.2 ml) after adding 200  $\mu$ l enzyme preparation. Peak height of light emission at three seconds was recorded as percent intensity. The linearity of standards with respect to light emission was checked. The reading of the  $5 \times 10^{-6}$  standard was used in the calculation of ATP content.
- B. For each treatment, two replications of 0.2 ml seedling embryo extract were delivered into two small reaction

vessels. Light emission was recorded upon injection of the luciferin - luciferase preparation.

4. Calculation:

$$\text{nmoles ATP/seedling} = I(\text{sample}) \frac{5 \text{ nmoles}}{I(\text{standard})} \times \frac{7 \text{ ml}}{1 \text{ ml}} \times \frac{2 \text{ ml}}{1 \text{ ml}} \times \frac{1}{n}$$

where: I (sample) = average intensity for sample

I (standard) = average intensity for standard

n = number of seedlings