Inheritance of factors associated with drought tolerance
by Hamdollah Kazemi

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Abstract:
Common wheat (Tritioum aestivum L.) is not generally considered drought tolerant, but several morphological and agronomic traits, including leaf, total root, and stomatal number, root mass, root/shoot ratio, rate of root elongation, and speed of germination have been reported to be associated with drought tolerance.

The objective was to study the mode of gene action and inheritance of these traits as they relate to drought tolerance in spring wheat cultivars under growth chamber, greenhouse, and field conditions.

Type of gene action was determined from the performance of parental lines and and progenies of crosses of 9 female and 3 male parents. Narrow sense heritabilities were estimated by the ratio of additive genetic variance to phenotypic variance following a model proposed by J. E. Grafius. Variation among progenies of male and/or female parents is interpreted as due to additive gene effects.

The results of the studies indicated that leaf number and root mass with relatively high narrow sense heritabilities of 55 and 80%, respectively, for F2 generations could be selected for in early generations through a straight selection program. Total root number, root/ shoot ratio, and rate of root elongation, with relatively low narrow sense heritabilities of 33, 32, and 26% (both for F1 and F2 generations), respectively, may not be easily fixed through a direct early generation straight mass selection program, but they can be used as criteria for selection of genotypes for drought tolerance. Narrow sense heritabilities for speed of germination, under simulated drought, for F1 and F2 crosses, were not markedly high; 34 and 24% without osmotic stress and 39% with "12" atmosphere osmotic potential (both for F1 and F2 generations), respectively. Therefore, this trait cannot be selected for through a straight selection program, but it may be used as a guide to screen faster germinating genotypes from slower germinating ones. Significant among cultivar means variation for stomatal number, for both adaxial and abaxial surfaces, under both field and greenhouse conditions, was detected. Significant genotype by environmental interaction precluded the isolation of components of genetic variations. It could thus be concluded that a straight selection program for stomatal number in spring wheat may" not be effective.

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TABLE OF CONTENTS

LIST OF TABLES

ABSTRACT

Common wheat (*Triticum aestivum* L.) is not generally considered drought tolerant, but several morphological and agronomic traits, including leaf, total root, and stomatal number, root mass, root/shoot ratio, rate of root elongation, and speed of germination have been reported to be associated with drought tolerance.

The objective was to study the mode of gene action and inheritance of these traits as they relate to drought tolerance in spring wheat cultivars under growth chamber, greenhouse, and field conditions.

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The results of the studies indicated that leaf number and root mass with relatively high narrow sense heritabilities of 55 and 80%, respectively, for F_2 generations could be selected for in early generations through a straight selection program. Total root number, root/shoot ratio, and rate of root elongation, with relatively low narrow sense heritabilities of 33, 32, and 26% (both for F_1 and F_2 generations), respectively, may not be easily fixed through a direct early generation straight mass selection program, but they can be used as criteria for selection of genotypes for drought tolerance. Narrow sense heritabilities for speed of germination, under simulated drought, for F_1 and F_2 crosses, were not markedly high; 34 and 24% without osmotic stress and 39% with "12" atmosphere osmotic potential (both for F_1 and F_2 generations), respectively. Therefore, this trait cannot be selected for through a straight selection program, but it may be used as a guide to screen faster germinating genotypes from slower germinating ones. Significant among cultivar means variation for stomatal number, for both adaxial and abaxial surfaces, under both field and greenhouse conditions, was detected. Significant genotype by environmental interaction precluded the isolation of components of genetic variations. It could thus be concluded that a straight selection program for stomatal number in spring wheat may not be effective.

INTRODUCTION

The world food supply depends heavily on wheat. Wheat accounts for a major portion of the total human caloric intake. Continued research to stabilize and expand the yield ceiling of this crop, so it can provide a subsistence level of food for the world's ever increasing population, must be given top priority.

Moisture stress, or drought conditions, appears to be a major factor limiting wheat production in semi-arid regions of the world. There is evidence, however, that certain wheat cultivars can tolerate drought and survive under moisture stress conditions.

Many anatomical and morphological plant characteristics, such as higher root mass, root/shoot ratio, total number of roots, speed of germination, and rate of root elongation, lower stomatal frequencies, leaf area, and leaf numbers, are reported to increase drought tolerance. Thus, selection of genotypes possessing these traits could possibly increase yield levels of spring wheat cultivars in areas of low precipitation. The value of these traits in developing drought tolerant cultivars is also a function of their heritabilities.

Although plant geneticists have made great progress in adapting crops to semi-arid environments, drought tolerance, because of its complex nature of inheritance, has received little attention, and progress in developing drought tolerant cultivars has been slow.

However, it is possible to increase drought tolerance in spring wheat through various plant breeding methods.

Thus, I sought to determine the comparative genetic variance and estimate heritabilities of several traits that are reported to be associated with drought tolerance so that plant breeders can use these traits in breeding programs.

LITERATURE REVIEW

Overview

Common wheat (*Triticum aestivum* L.), a hexaploid, is one of the oldest cultivated crops; it was domesticated at least 5,000 years ago (Briggle, 1967; Evans et al., 1975). It is grown between 30° and 55° latitude in the north temperate zone and 25° and 40° in the south temperate zone in areas of annual precipitation between 30 and 110 cm. This species is not considered drought resistant (Whiteside, 1941), and it cannot tolerate long periods of water scarcity. However, it can adjust to stress conditions so that it may withstand periods of drought.

Drought and Drought Tolerance

Drought is a term which is variously defined. Conditions which may severely damage one crop may have little effect on others. Drought is seldom solely a matter of inadequate moisture. The condition is frequently associated closely with, and aggravated by, high temperature (Heyne and Laude, 1940; Heyne and Brunson, 1940), low humidity, rapid air movement, and bright sunshine (Julander, 1945; Kramer, 1959). Viets (1971) defines it as "any period when water deficiency, either acute or chronic, affects plant growth and the decision on what to plant and how to grow it. Drought may mean short periods without rain in humid regions or be the prevailing condition in the desert." While Kramer (1959) describes it as "deficiency of available soil

moisture which produces internal water deficits in plants severe enough to reduce plant growth."

The drought tolerance of a plant is also a complex of many characteristics which are difficult to analyze (Heyne and Brunson, 1940). The analysis of such a complex problem and the mode of reaction of drought tolerance in crops require an ever increasing collection of information which plant breeders can use and incorporate into breeding programs. Bayles et al. (1937) in an extensive evaluation of drought resistance of several spring wheat cultivars stated that the ability of a plant to have a low transpiration rate without detrimental reduction in the process of photosynthesis and the ability of root systems to take in moisture as fast, or faster than the plant transpires constitute the nature of drought resistance of that plant. Burton (1964) defined drought resistance, as it applies to humid conditions, as the ability of a plant to remain green and grow under periods of moisture stress, while under arid conditions it may mean the ability of a plant to survive an extended drought. Wright (1964) defined it a little differently and stated that a plant can be considered drought resistant when it is capable of establishing, developing and maintaining itself during periods of water scarcity and producing economically acceptable yield under moisture stress. Moisture stress is the most important limiting factor which can affect wheat production in

semi-arid regions of the world, and it prevails when transpiration exceeds water absorption to cause a negative water balance. Drought tolerant plants, through several moisture related mechanisms, such as absorption of water by root system and stomatal closure, are able to avoid such a deficit (Chang, 1968).

Importance of Water for Plant Growth

Water is a universal solvent which has an important role in plant growth. Practically all aspects of plant growth are affected by its scarcity (Laude, 1971). Kramer (1963), in a review of water stress and plant growth, indicated that a) water is an essential chemical compound which is responsible for the turgidity and enlargement of plant cells; b) it is considered the major tissue component of the biologically active organism; c) it has an important role in photosynthetic activity of green plants; and finally d) it is a solvent in which salts and sugars dissolve and thus facilitates their movement from cell to cell, tissue to tissue and organ to organ. It is, therefore, reasonable to state that water stress reduces the yield, changes the pattern of root and shoot growth (Weaver, 1926), affects the quality of crops, flower formation, and seed production, reduces photosynthetic rate and in general increases respiration rate (Chang, 1968).

According to Kramer (1963) "plant growth is controlled directly by plant water stress and only indirectly by soil water stress." He believes that soil water content alone is not adequate to evaluate the effect of water supply on crop yield. Kramer (1963) and Viets (1971) are of the opinion that it is the internal plant water balance that affects growth directly, because during water deficit, absorption falls behind water loss, mainly through transpiration which is dependent upon leaf area and structure and on environmental factors such as temperature, relative humidity, wind and stomatal number and aperture length. On the other hand, absorption of water is controlled by the extent and efficiency of the root system (Todd et al., 1962; Kramer, 1963). Thus, during periods of high temperature and low humidity even those plants growing in the soil near field capacity may be subjected to severe water stress (Hurd, 1971; Kramer, 1963). While during cool and humid weather when transpiration is low, plants growing in dry soil may not be subjected to severe water stress; thus, it is not safe to assume that a certain level of soil water potential (tension) will be accompanied by an equivalent degree of plant water stress.

Water stress in general decreases photosynthetic rates (Wardlaw, 1967), influences cell elongation through lower turgor pressure and eventually reduces plant size (Laude, 1971), and decreases stomatal opening. Drought condition also reduces the rate of CO_2 assimilation (Hsiao and Acevedo, 1974; Laude, 1971), transpiration, nutrient uptake

(Laude, 1971; Wardlaw, 1967), and protein synthesis (Hsiao and Acevedo, 1974).

Plant growth and development are the results of internal processes which are controlled by environmental factors such as moisture, temperature, radiation, nutrients and gases. Any stress from an abnormal amount of any of these factors can either accelerate or reduce these internal processes (Levitt, 1969). Moisture stress, too much or too little, can be equally harmful and eventually kill the plants. The former is called flooding injury and the latter drought injury (Levitt, 1969).

Classification of Plants With Regard to Drought

Plant species differ in their ability to withstand drought. According to Kramer (1959), plants can fall into four categories with regard to their reaction to moisture: a) plants that cannot endure drought. They are very quickly dehydrated and are injured as soon as soil moisture becomes deficient; b) plants that have low resistance to dehydration such as cacti. These are the plants that typically have thick cutin, small numbers of stomata as well as low rates of water loss; c) drought enduring plants, the protoplasm of which can tolerate dehydration. Mosses, lichens, seed plants and ferns are included in this class; and d) plants that have moderate ability to tolerate dehydration. These are the plants that have the capacity to improve

water absorption and reduce water loss whenever needed. They are the so-called drought resistant crop plants. In order for these crop plants to resist the injuries of moisture stress, they have to either a) avoid (exclude) the stress from their tissue or b) tolerate (endure) the effect of drought (Levitt, 1969). According to this classification there can be three types of survival mechanism which give the plants the ability to resist drought: (1) tolerant avoiders, (2) intolerant avoiders, and (3) tolerant non-avoiders.

Water Use Efficiency

Burton (1964) indicated that drought resistance in plants is a favorable characteristic, but in general it is not correlated with water use efficiency and yield. Water use efficiency and drought tolerance of five selections of boer love grass (*Eragrostis curvula* Nees) at seedling stage, in both greenhouse and growth chambers, were observed by Wright and Dobrenz (1970) and a negative correlation coefficient, $r = -0.80$, between these two traits was obtained; water use efficiency was lowest for drought tolerant seedlings. Hurd (1974), working with several semidwarf wheat cultivars, found no close association between water consumption and yield of the grain produced. Hsiao and Acevedo (1974) and Sullivan and Eastin (1974), in their studies of the basis for differences in water use efficiency and drought resistance, concluded that these two plant characteristics are

frequently unrelated and that they should not be considered as synonymous. However, plant modifications for drought resistance may increase the water use efficiency under drought conditions. Burton (1964) also indicated that water use efficiency of small grains can be increased by breeding cultivars for early maturity, awnedness, higher rate of growth and deeper and wider root distribution.

Adaptive Characteristics of Plants Related to Drought

The adaptation of plants to drought conditions has been attributed to numerous anatomical and morphological plant characteristics. Volkens, a great plant geographer (cited by Openheimer, 1960), established the adaptive principles that contribute to the plant's resistance to drought. He claimed that traits such as smaller leaf size and number, thickened epidermis as a result of impregnation of cell walls with cutin, presence of trichomes on the leaf surfaces to reduce the velocity of air movement, smaller intercellular spaces, extensive root system as compared to shoot, reduced total area of the stomata per unit of surface and higher vacuolar sap concentration, would contribute to the adaptive habit of the plants with respect to drought. Ferguson et al. (1972), May and Milthorpe (1962), Moss et al. (1974), and Kramer (1959), through their extensive work and literature reviews, enumerated traits that have been found to be related to higher yield under drought conditions. They believe that leaf traits

(orientation, hair, reflectance, color, leaf area index), stomata characters (frequency, size and behavior), root factors (distribution, ability to absorb water, root hairs, water transport, ability to grow in dry soil, penetration, diameter and length and branching pattern), and awns and maturation are adaptive characteristics of cereal plants to dry regions.

The extent of root growth, its effective length per unit volume of soil, and depth of root zone are important in plant resistance to drought, according to Meirion et al. (1973).

Leaf color is another adaptive characteristic for semi-arid regions. Ferguson et al. (1972) studied photosynthetic rates of several greenhouse grown isogenic barley lines for leaf color and reported that pale colored lines had lower photosynthetic rates than their normal counterparts, but at times pale colored lines may outyield normal colored plants under drought conditions. Ferguson et al. (1973) and Ferguson (1974), using isogenic barley lines, found that the canopy temperature in light colored lines was significantly lower than normal colored lines. Thus, they concluded that the difference was probably associated with increased reflection from the light colored canopies.

Awned barley types were reported to be better adapted to semi-arid regions than awnless types. Ferguson et al. (1973) and Ferguson (1974) indicated that an awned canopy was significantly cooler than an

awnless canopy; awned cultivars may function to dissipate heat thus reduce water loss more than awnless ones.

Rates of water loss from cut plants of many species have been studied and results obtained indicate that drought tolerant plants lose water less readily than drought susceptible species (Dedio, 1975; Levitt, 1972; Teoh et al., 1967). Bayles et al. (1937) demonstrated that dessication resistance of wheat is a varietal characteristic in spring wheat and slower water losses from excised plants in spring wheat was associated with drought resistance. They also reported that drought resistant cultivars have lower dry-down rates than susceptible cultivars. 'Hope,' a drought susceptible spring wheat cultivar, lost its water more easily, under two temperatures (60° and 75°F) and soil moisture conditions (deficient and optimum) than 'Kubanka,' a drought resistant cultivar. Sandhu and Laude (1958) and Dedio (1975) indicated that water retention ability of wheat cultivars was associated with drought and heat tolerance. Water retention ability of wheat leaves was also studied by Salim et al. (1969); they reported that higher water retention represents avoidance of water loss by cereal crops and thus it makes an important contribution to the overall performance during drought.

Whenever there are moisture shortages, smaller cell size protects the plants against excessive dehydration (Kramer, 1959; Levitt, 1972; Whiteside, 1941). Kolkunov (cited by Aamodt and Johnston, 1936)

selected four pure lines of 'Beloturka' wheat differing in cell size and grew them under different moisture conditions. He found that under drought conditions, pure lines with smaller cells were superior to lines with larger cell size while under moist conditions the reverse was true. Investigations during the last decade indicate that presence of water in the cell wall (apparent free space) has received special attention. The water retained in this space could enable the plant to withstand periods of water stress (May and Milthorpe, 1962, Teoh et al., 1967). Thus, the cell wall may play an important role in moisture regimes of all arid and semi-arid vegetation with regard to drought resistance, irrespective of whether other adaptive features are developed or not (Teoh et al., 1967).

In many parts of the world where moisture is a limiting factor, early maturity is one of the most important adaptive traits that contributes to drought tolerance. Early maturing plants develop fewer tillers, have less leaf area which maintains less transpiring surface than late maturing cultivars throughout the growing season and have higher water use efficiency (Derera et al., 1968). However, early maturing cultivars generally are not able to obtain their full yield potential. Therefore, it seems necessary to combine earliness with high yielding ability to produce cultivars with maximum yields.

Tests to Measure Drought Tolerance

The traits noted above are of little value to the plant breeder, unless specific indices are devised to screen the drought resistant plants (Sandhu and Laude, 1958), and traits ranked according to their importance on the basis of their heritabilities and contributions to the final yield (Moss et al., 1974).

Although many traits have been reported to be associated with drought tolerance, no specific characters have been identified with which drought tolerance can be measured directly (Wright, 1971). Various tests and techniques have been proposed to evaluate plant response to soil and atmospheric drought. Some of the empirical tests, to separate lines of differing levels of tolerance, are root/shoot ratio, extent of root growth, rate of root elongation, root distribution, high temperature chamber tests, chlorophyll stability index test, water retention ability of plants, proline test and isogenic analysis.

Root systems can be studied directly, by excavation, by growing plants in nutrient solution, by growing plants in containers easily taken apart or by the use of radioactive tracers and dyes (Hall et al., 1953).

The radioactive tracer technique is a method to study the distribution and activity of roots, and it is based on the location of readily detectable substances such as P^{32} at a given distance from and

below the plant and observing how the radioactive material is taken up by the plant (Bassett et al., 1970; Hall et al., 1953). The uptake of the tracer element provides an indication of the presence and activity of the root at the location of tracer placement. Burton et al. (1954) used uptake of P^{32} as a criterion to appraise the relative drought resistance of several grass species. They reported that the uptake of P^{32} was well correlated with drought resistance and thus suggested that P^{32} uptake could be indicative of water uptake.

Rate of root elongation was studied by Muzik and Whitworth (1962) who devised a glass faced box technique. This technique has been used to examine root distribution and pattern of root growth in wheat, corn, several other grass species, and beans (Muzik and Whitworth, 1962).

Germination of seeds under concentrated solutions to provide media with high osmotic potential has been proposed as a rapid method for measuring drought resistance of different genotypes (Helmerick and Pfeifer, 1954). This technique was used to detect significant differences in germination percentage between inbreds and hybrids of sweet and field corn (Williams et al., 1967).

Wheat is subject to damage by adverse climatic conditions, such as heat and drought, but loss may be minimized in strains possessing genes for resistance to these conditions. The high temperature-chamber technique has been proposed to be a valuable test for measur-

measuring drought tolerance in plant species. This is a technique through which different species and cultivars at the seedling stage can be exposed to low relative humidity and high temperature for a specified period of time, and then rewatered. Then, their percentage recovery, or severity of heat damage after a period of time, can be used as an index for drought tolerance. Plants with lower injury ratings after exposure to high temperature are classified as drought resistant genotypes (Kilen and Andrew, 1969; Williams et al., 1967). Sandhu and Laude (1958) exposed wheat cultivars to temperatures of 55.5 to 56.5°C for 24-26 hours and found that cultivars were significantly different. They concluded that the yield per acre of cultivars grown under severe drought in the field and laboratory was associated with drought tolerance. Heat or high temperature tests are believed to be of greatest value in screening for drought resistance because of their speed, cost, and the large amount of materials that can be screened (Kilen and Andrew, 1969).

Subjecting the seedlings to permanent wilting point for certain periods of time and rating the severity of wilting injury after rewatering has also been reported by Williams et al. (1967) to be a rapid and simple technique to screen drought tolerant genotypes from non-drought tolerant genotypes.

Chlorophyll stability has been found to be correlated well with drought resistance. In this test, samples of seedling leaves are

are heated in distilled water and the difference between light transmission of heated and unheated leaf filterates will indicate drought resistance. Genotypes with higher relative drought resistance exhibit a greater chlorophyll stability (Kilen and Andrew, 1969; Kaloyereas, 1958). Drought tolerant genotypes thus would have higher photosynthetic ability during drought as compared with susceptible ones (Dedio, 1975).

The ability of plants to recover their normal photosynthesizing power, when at or below normal turgor, has been reported to contribute to the knowledge of drought resistance. Todd and Webster (1965) studied the effect of repeated drought on the photosynthetic rate of winter wheat and oat (*Avena sativa* L.) cultivars. They found no meaningful correlation between photosynthetic rate and drought tolerance, but they claimed that drought hardy cultivars had relatively higher photosynthetic rate, when they recovered their turgidity. The non-drought tolerant cultivar of wheat, 'Ponca,' and oat cultivars, 'Cimarron' and 'Arkwin' in general showed slower photosynthetic rate, both under drought and after rewatering. They concluded that all cultivars investigated carried a higher photosynthesizing ability at a lower turgor after the plants had been subjected to a single drought period.

The onset of permanent wilting point is less easily detected in monocots than in dicots (Bailey, 1940). Thus, a technique, water balance measurement, was proposed to facilitate tests for drought

resistance of grass species. Water balance is a term, as it is used here, to indicate the amount of water that a plant has lost on the incidence of permanent wilting. It is expressed as percentage of its water content when turgid (Bailey, 1940). The higher the water balance, the better is the tolerance of plants to drought. Bailey (1940) studied water relation of *Agropyron smithii, Bromus marginalus*, and *Agroyron ciliare*, and found that their water balances were approximately 42, 49, and 50, respectively. *Agropyron ciliare* tolerated more dehydration without injury than did the other two species.

The so-called "proline test" is a new technique which is used to determine water deficiency in plants. According to Hsiao and Acevedo (1974) and Pálfi and Juhász (1971), drought resistant plants under moisture stress synthesize more proline than drought susceptible plants but the role of this amino acid is unclear.

Eslick and Hockett (1974) claimed that there may be genetically controlled characteristics that will contribute to water use efficiency, thus a simple and rapid test for this purpose should be devised to select for the traits and identify genes that contribute to greater water use efficiency. They proposed that isogenic analysis could be a satisfactory method to detect genes associated with water use efficiency and could be a great help to the plant breeder. Thus, isogenic analysis may speed up the evaluation of specific morphological

characteristics that contribute to yield which is correlated with drought resistance (Hurd, 1968).

Critical Stages of Wheat to Drought

Plants vary in their response to drought at different growth stages. One stage, from the standpoint of drought injury, may be more critical than others. Aamodt and Johnson (1936) reported that plants exhibit different capacities for resisting moisture stress at various growth stages. Seeds may not be harmed when they undergo almost complete dehydration; this may also be true for the seeds the first few days following germination. Thereafter, when leaves develop, they become susceptible to desiccation (Aamodt and Johnston, 1936). Meirion et al. (1973) and Milthorpe (1950) reported that three day old seedlings of wheat with coleoptile about 3 to 4 mm in length, due to the prevalence of a high proportion of meristematic to elongated cells, could survive a loss of 98 to 99% of their total water content. They claimed that after 17 days of germination, when the cells elongate, roots become drought susceptible and are injured when 80% of the water is lost, while shoots survived even at a water loss of 90%.

The length of drought period affects resumption of growth. The roots of 3-5 day old wheat seedlings were subjected to drought for a period of 3 hours and found to grow at a slower rate than non-stressed

plants. Those that were dried for 9 hours grew even more slowly (Milthorpe, 1950). Milthorpe (1950) studied changes in the drought resistance of wheat seedlings during germination and pointed out that "as long as some root primordia remained in the meristematic condition, the plant could recover when rewatered." He indicated that the persistance of roots in the primordial condition may be a factor in drought resistance of grasses.

In wheat there are three distinct age periods associated with different degrees of drought resistance (Meirion et al., 1973): a) coleoptylar stage when coleotyle length is 3 to 4 mm, b) the period until the first leaf stage, and c) the period between the emergence of first leaf and 17 days after soaking. The first stage is completely drought resistant and the second and third stages lose their resistance when 98 and 92% of their water content, respectively, is lost (Meirion et al., 1973). Aamodt and Johnston (1936) exposed plants of several drought resistant and susceptible spring wheat cultivars to drought at four growth stages (stooling, shooting, soft dough, and hard dough) and found that greater reduction in kernel yield occurred in the soft dough stage; they concluded that at this stage cultivars were extremely susceptible to drought. They also reported that greater leaf loss resulted when plants were exposed to drought in the shooting stage than stooling stage. Bayles et al. (1937) claimed that

the occurrence of drought during the period from shooting to the end of flowering was most serious to cereal plants.

Different organs of the same plant have been reported to differ in their ability to draw moisture from other organs. Tumanov (cited by Aamodt and Johnston, 1936) found that leaves of sorghum withdrew water from the stem under soil moisture stress while those of buckwheat lacked this ability. According to Krasnosselsky-Maximov (cited by Aamodt and Johnston, 1936), the leaves of cereals, when exposed to dry wind, can draw water from the inflorescences. May and Milthorpe (1962) indicated the two most drought susceptible stages of wheat are a) during stem elongation and spikelet differentiation, and b) anthesis. Slight drought conditions during anthesis would have a marked effect on the number of florets which set seed. Floral organs are most sensitive to drought (May and Milthorpe, 1962). Dawney (1971) indicated that water stress during the period of tasseling, silking, pollination, and grain filling reduced yield by 50% in corn.

Genotypic Differences Among Plants Related to Drought

May and Milthorpe (1962) and Levitt (1956) indicated that certain plant species can tolerate drought and survive under moisture stress conditions. These plants are probably able to carry out their metabolic activities under low water potential or are able to absorb more water from the soil to compensate the loss. Sullivan and Eastin

(1974) working with sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) reported that genotypic differences did exist between these species both at species and varietal levels. They suggested that factors contributing to drought resistance can be selected and used in breeding programs. Hunt (1962) studied water requirements of Russian wildrye (*Elymus junceus* Fisch.) and intermediate wheatgrass (*Agropyron intermedium* (Host) Beauv.) and found that differences in water requirements between species and genotypes within species were real and significant; thus, he concluded that water requirements in these range grasses were highly heritable. According to Ray et al. (1974) there is a potential for breeding more efficient cotton cultivars with respect to water requirements. Keller (1953) examined 16 selected genotypes of orchard grass (*Dactylis glamorata*) and indicated a significant difference among them in their water requirements. He pointed out that these differences reflect genetic differences among genotypes for water requirements. Williams et al. (1967) exposed 20 day old corn seedlings for six hours to 52°C temperature and separated drought resistant genotypes from the susceptible genotypes. Williams et al. (1969) reported that the inheritance of drought tolerance for sweetcorn followed a pattern of partial to complete dominance rather than over dominance. Relative drought tolerance of seedlings of 15 dominant species of prairie grasses was studied by Mueller and Weaver (1942) and the results of the experiment showed that blue grama

(*Bouteloua gracilis*), a short stature grass, was the most drought tolerant species. It was also noticed that leaves of the short grass seedlings were rarely injured by temperatures as high as 63°C.

Hurd (1974) reported the results of crossing and backcrossing of 'Pelissier,' a densely rooting durum wheat to 'Lakota,' a sparsely rooting cultivar under moisture stress; the breeding program resulted in the release of two high yielding drought tolerant cultivars which had the dense root systems typical of Pelissier. He concluded that root patterns are heritable characteristics and that an extensive pattern of root growth favors higher crop yields under drought conditions, and, therefore, selection for higher yields under dryland conditions will result in lines that would have extensive root systems. Heyne and Brunson (1940) studied mode of inheritance of drought resistance in crosses made between inbred lines of corn of known reaction to drought under controlled conditions and found that tolerance to drought was definitely heritable and gene action was intermediate to dominant. Hurd (1971), in an extensive literature review in relation to breeding for drought resistance in wheat, indicated that the principle for breeding for yield, as an indicator of drought condition, is the same regardless of climatic conditions. He suggested that in breeding for drought resistance, plant breeders should accumulate plus genes that are plus in a semi-arid condition. Thus, in breeding programs for

drought, careful selection of parents for "plus" characteristics should be given prime importance.

Root and Shoot Studies

The root system must be considered the most important part of the plant. It plays an important role in plant anchorage, water and nutrient uptake, food translocation, and storage. Understanding root morphology, pattern of growth, physiology and anatomy, and factors, especially moisture, that influence root growth is of utmost importance. Patterns of root growth and development are difficult to study. As a result, comparatively few studies have been reported, while on the other hand, the above ground parts of the plant have been studied to a greater extent. Reitz (1974) stated that ". . . it is a shame that so little is known about what constitutes an effective root system and how roots modify their own microclimate."

Spring wheat has a sympodial or fibrous root system which penetrates deeply into the subsoil. Perhaps because of a shorter growing season and low temperature, it has a less extensive root system than winter wheat (Evans et al., 1975; Locke and Clark, 1924; Troughton, 1962; Weaver, 1926). Its root system consists of the original embryonic or seminal roots and the crown or adventitious roots (McCall, 1934; Pinthus and Eshel, 1962; Troughton, 1962; Wellington, 1966).

The term seminal root system is used to include those roots that are formed at the seed (McCall, 1934; Webb, 1936). Its growth and penetration into the soil are affected by the degree of embryo development, and by external environmental factors (McCall, 1934; Webb, 1936). The apparent function of seminal roots is to supply the plant with water and minerals until such time as adventitious roots develop. Several investigators (Ferguson and Boatwright, 1968; Locke and Clark, 1924; McCall, 1934; Troughton, 1962; Webb, 1936) have indicated that these roots may remain active and functional through the growth period of the plant. Boatwright and Ferguson (1967) found that amputation of either seminal or adventitious roots in spring wheat in the seedling stage of growth reduces the yield and delays tillering, but reduction in yield with only primary roots was more pronounced than when the plants had only adventitious roots. They concluded that the adventitious roots were physiologically more active than primary roots. In some regions where extremely dry soil prevails, spring wheat often does not form adventitious roots, but grows to maturity, with reduced yield, from seminal roots alone (Boatwright and Ferguson, 1967; Locke and Clark, 1924; Webb, 1936). Passioura (1972) reported that grain yield can be increased by forcing the plants to rely solely on one seminal root because single rooted plants use less water before anthesis than normally rooted plants. He also indicated that by forcing

the plants to rely only on one seminal root, the ease with which the plant extracts water from the soil is increased.

Wheat cultivars have been reported to exhibit obvious differences in tolerance or resistance to drought (Hurd, 1974). According to Pinthus and Eshel (1962) and Troughton (1962), there are heritable differences in the extent of differentiation and distribution of embryonic roots. Salim et al. (1969) found that 'Cheyenne,' a drought hardy cultivar, produces more and longer seminal roots than drought susceptible Ponca under moisture stress. McCall (1934) stated that within a cultivar the larger and broader caryopses have the capacities to produce a greater number of seminal roots than smaller and lighter ones. Wellington (1966) stated that elongation of the radicle is more rapid in mature embryo than in immature embryo. Differences in the number of primary roots in two drought resistant cultivars, 'Milturum,' and 'Caesium,' and two drought susceptible cultivars, 'Marquis' and 'Reward' spring wheat were observed by Aamodt and Johnston (1936). The results of their experiment revealed that roots of drought resistant cultivars were profusely branched. They found that for drought resistant cultivars, the average number of primary roots was lower than for drought susceptible ones. According to Modestov (cited by Brenchly and Jackson, 1921), different races of wheat and oats grown under identical environmental conditions reflected essential differences in length and weight of their root. Pinthus and Eshel (1962)

indicated that rooting patterns of wheat vary with cultivar. In their studies of wheat root development, they found marked varietal differences in distribution of the root system.

Drought resistance in spring wheat has been reported to be positively associated with an extensive root system. Reitz (1974) reported that 'Hope,' a spring wheat cultivar, due to its poor root system, was always the first to show signs of stress under dry conditions.

The crown in spring wheat is the series of nodes with short internodes that forms usually close to the soil surface. The location of the crown is important for at least two reasons: a) it is the site of adventitious root development, and b) perhaps it plays an important role in drought resistance and winter survival (Ashraf, 1973; Boatwright and Ferguson, 1967; Hurd, 1971; Sallans, 1961). Although depth of crown is influenced mainly by environmental conditions (Ferguson and Boatwright, 1968), the point at which adventitious roots develop is a varietal characteristic in wheat (Ashraf, 1973; Webb, 1936). Sallans (1961) observed that Thatcher, a drought tolerant spring wheat cultivar, had a shorter subcrown internode and thus plants were not killed by late spring frost, while Rescue in a nearby field, possibly due to the longer sub-crown internodes, showed a higher percentage of frost killing. Sallans (1961) studied the heritability of crown depth in wheat and barley and stated that there is strong evidence to

suggest that the varietal differences in depth of crown formation is genetically controlled. Therefore, it seems reasonable to believe that this trait would be a reliable criterion for selection to develop drought tolerant cultivars.

Adventitious roots are formed below the crown nodes and arise usually 3 to 4 weeks after planting (Weaver, 1926). Time of initiation of these roots and factors influencing their formation and growth are of interest because of their roles on growth, yield, nutrient uptake, and over winter survival of small grains (Boatwright and Ferguson, 1967; Ferguson and Boatwright, 1968; Hurd, 1969). They are harder, thicker, stronger, and whiter in color than seminal roots and grow horizontally first before they turn downward (Kmoch et al., 1957; Peterson, 1965).

Wilson et al. (1976) observed the role of individual root systems of short coleoptile blue grama under drought conditions and reported that seedlings must survive on the seminal roots until conditions become favorable for the development of adventitious roots. However, they emphasized that plant survival in the field depends on extension of adventitious roots. They indicated that wheat can survive with only seminal roots because its xylem vessels have a higher rate of water uptake than blue grama.

The number of adventitious roots is not constant and depends on the number of tillers (Black, 1970; Pinthus and Eshel, 1962; Troughton,

1962; Weaver, 1926). Kilen and Andrew (1969), working with corn, concluded that drought susceptible lines had more tillers than drought resistant lines. Hurd (1969) found wheat plants that tiller profusely are not suitable for drought conditions. He believes that tillers or extra florets produced would bear no seed while they would waste available moisture. Troughton (1962) reported that a rather close relationship between number of nodal roots and tillers exists. But, according to Zijlstra (cited by Brouwer, 1966), such a relationship has not been confirmed. This disagreement in the literature on the relationship of tiller and adventitious root number indicates that factors other than tiller number affect the initiation and development of the adventitious roots. Root development of winter wheat was studied by Kmoch et al. (1957); they reported that 40 days after planting, the number of adventitious roots was small, while a dense network of roots at this time was due to the seminal roots. But at later stages of growth, under normal growing conditions, the number of adventitious roots may surpass that of seedling roots (Locke and Clark, 1924). Adventitious roots cannot elongate under extreme drought conditions (Webb, 1936; Boatwright and Ferguson, 1967; Ferguson and Boatwright, 1968). Therefore, efforts should be made to that adventitious roots are formed and elongated before the onset of drought. The number of adventitious roots, a component of the total root weight, reportedly have a high

heritability and are positively correlated with drought tolerance and grain yield (Derera et al., 1968).

The root system has been considered important for the maintenance of water balance in the plant as a characteristic of drought tolerant plants (Weaver, 1926). Therefore, plants that have an extensive root system are in a better position to exploit a larger soil volume for moisture and absorb the required volume of water and also to tolerate moisture stress in relatively dry environments (Pearson, 1974; Teoh et al., 1967). The significance of root development in relation to drought tolerance in spring wheat has been emphasized by Aamodt and Johnston (1936). Improvement of the root system could offer considerable promise for raising the yield ceiling in areas of low precipitation. The rooting pattern of cereal crops has been investigated both under irrigation and moisture stress conditions. Several plant root characteristics have been found to have close association with drought tolerance. According to Aamodt and Johnston (1936) plants with higher moisture absorbing power are in the most favorable position to resist drought. High number and branching pattern, deeper crown, and length per unit weight of root are a few of the many factors that may contribute to drought resistance (Salim et al., 1965; Kmoch et al., 1957).

Root development of spring wheat was investigated by Maximov and Kruzilin (1936). They reported that total weight of the root,

number and weight of the nodal roots, under irrigation, was higher than under moisture stress, but they indicated that the amount of roots developed in drought conditions was higher in lower soil horizons.

According to Hurd (1964) cultivars with higher numbers of primary and secondary roots were more drought tolerant than those with a lower number of total roots. Thatcher and Pelissier, two drought resistant cultivars, were reported to have higher total root numbers than 'Cypress,' the less drought tolerant cultivar. Weaver (1926) studied the number and branching pattern of spring wheat roots under irrigated and non-irrigated conditions and reported that the number of roots and branches, six weeks after planting, may be the same in both conditions, but average branch length was considerably longer in drought conditions.

Hurd (1971) correlated root system with drought tolerance in Pelissier, a durum wheat, and found that extensive root system and drought tolerance were positively associated. Weaver (1926), in a study dealing with corn roots, observed marked differences in the ratio of branch roots to main roots in four inbred lines of corn. He suggested that these differences among the lines were inherited. Mitchell (1970) said that corn cultivars selected for drought tolerance tended to have increased root mass. Hurd (1974) believed that the selection for higher yields under moisture stress would result in

larger root systems. Ray et al. (1974) and Passioura (1972) disagreed with Hurd's (1974) conclusion and suggested that a small rooted plant may use limited water more efficiently. Disagreement such as this indicates that there is much to be learned about factors contributing to drought tolerance. According to Kmoch et al. (1957) weight of root alone is not necessarily a measure of absorbing area of the root system. Therefore, other parameters of root systems, the abundance and density of root and depth of root, should be taken into consideration. Hurd (1968) observed root development of several spring wheat cultivars and stated that ". . . one can not expect yields to be directly correlated with total root length nor with total dry weight of root . . .," but it can be understood that an extensive root system will help the plants to avoid yield reduction caused by moisture stress. Working with 'Pitic,' a drought tolerant spring wheat with an extensive root system, Hurd (1974) pointed out that, although no specific correlations have been made, there appear to be a close positive association between weight of root washed out of the soil from this cultivar and yield of grain per plant.

Sorghum has a root system which contributes to its drought tolerance. Mitchell (1970) indicated that drought tolerance in sorghum is increased by higher root numbers which provides more water extraction from the root medium. According to Plummer (1943) root development prior to summer drought was related to the initial success or

failure of seedling root growth. May and Milthorpe (1962) and Carceller and Soriano (1972) found that the roots of desiccation-pre-treated wheat seedlings had significantly greater root growth than non-treated ones. May and Milthorpe (1962) reported that the increased drought resistance in pre-treated plots was only a result of increased absorption of water by a larger root system.

Root diameter affects water uptake. Winter wheat plants with finer branched roots have been reported to withstand moisture stress better than those with thicker roots (Hurd, 1971).

Hurd (1971) claimed that plants with extensive root systems may have more surface area to absorb water. Higher root mass, on a dry weight basis, could contribute to water use efficiency. Teare et al. (1973) found that sorghum, because of higher root mass, was more efficient in water use than soybeans.

A high root/shoot ratio is an adaptive characteristic of plants under drought conditions (Levitt, 1972). Drought and heat hardy wheat cultivars have been reported to have a higher root/shoot ratio than non-hardy cultivars (Sandhu and Laude, 1958). Salim et al. (1965) studied the root development of two winter wheat cultivars, Cheyenne, drought resistant, and Ponca, drought susceptible cultivars have excessive top growth compared to root growth which in turn increases transpiration over absorption. They also indicated that barley plants produce a larger total root system and less leaf than oats. These two

traits have been advantageous to barley plants growing in water deficient regions of the world.

Openheimer (1960) indicated that high root/shoot ratio, evaluated as the ratio of length, fresh or dry weight, is the characteristic of the plant under dry regions. He also reported that numerous xerophytes, already in the germination stage, have the greater capacity of root growth. He believed that this preponderant root growth in a plant species was a hereditary character. The root/shoot ratio is controlled by both genetics and environmental factors, such as nutrient, moisture, light and temperature. Pearson (1974) suggested that in discussions of a normal or optimal root/shoot ratio for a given genotype, certain elements of environment should be included. The shoot is dependent upon the root for its need for nutrient and water. In case of deficiency of these substances, the shoot is liable to be more affected than the root (Brouwer, 1966). Root/shoot ratio increases when nitrogen supply diminishes (Evans et al., 1975). This means that the shoot is more affected by nitrogen deficiency than the roots. Moisture stress also reduces shoot growth more than root growth, and as a result root/shoot ratio increases under drought conditions (Brouwer, 1966; Evans et al., 1975; Harris, 1914; Hsiao and Acevedo, 1974; Kmoch et al., 1957; Mitchell, 1970). Kmoch et al. (1957) and Weaver (1926) indicated that moisture stress affects thicknesses of the root. Roots from dry condition were found to be more

branched and finer than those from under adequate moisture. Higher light intensities reduce shoot growth, while under low light intensities not only is shoot growth favored (Evans et al., 1975; Mitchell, 1970), but also root growth is restricted (Pearson, 1974). Temperature is another important factor which controls shoot and root growth. Evans et al. (1975) and Brouwer (1966) indicated that lower temperatures decrease shoot growth while its growth increases with increasing temperatures.

Rate of Root Elongation

The amount of available soil moisture that a plant can absorb depends upon the extent and depth that roots penetrate the soil. Although the number and volume of the roots in deeper zones may be small, they may allow the plants to utilize subsoil moisture. The elongation of wheat roots is confined to a region behind the root tips and the rate of growth of a single root and its extension vary from 0.5 to 3 cm per day for both seminal and adventitious roots (Evans et al., 1975). In areas where there is little rainfall during the growing season, continuous growth and penetration of roots throughout the plant's development would be beneficial in maintaining water balance in the plant (Salim et al., 1965; Hurd, 1968). Thus, selection and breeding plants for rapid rate of growth and extent of branching of roots may result in increased drought resistance and successful seedling establishment (May and Milthorpe, 1962). Hurd (1964,1968,1971)

stated that a rapidly penetrating root system is essential for cultivars grown under semi-arid conditions. He indicated that Thatcher and Pelissier, which are considered drought tolerant cultivars, have the ability to penetrate the soil more rapidly than other cultivars investigated. Talanov (cited by Aamodt and Johnston, 1936) indicated that one of the important traits that allows Milturum and Caesium to survive well under drought conditions is their ability to penetrate into the soil faster during early stages of growth.

Significant differences among plant species with respect to root extension have been reported (Black, 1968; Burton et al., 1954). Such differences may be heritable and could have beneficial consequences in drought tolerance. Black (1968) stated that "plants themselves play an important part in influencing availability of soil water through their capability to extend roots downward into the moist soil." Varietal differences for root penetration of wheat were detected by Hurd (1969) and he indicated that root penetration into the soil can be a factor for plant survival under impending drought. Burton et al. (1954) using radioactive phosphorus (P^{32}) to trace root penetration of several southern grasses found significant variation between species; Coastal Bermuda (*Cynodon dactylon*) was the most and Pensacola Bahia (*Paspalum notatum*) the least rapidly penetrating species. They concluded that species having higher rates of root penetration, other things being equal, are able to withstand drought after transplanting.

Genetic variability in root development in relation to drought tolerance to several spring wheat cultivars was studied by Derera et al. (1968), and they reported that there were significant varietal differences for the rate of root penetration. They also indicated that varieties with higher rates of penetration possessed finer and more branched root systems.

Derwyn et al. (1966) tested the effect of seed weight on growth rate of several grass species and found that heavier seeds had higher growth rates than smaller seeds. They also observed that there was substantial variation from seedling to seedling.

Concentration of ribonucleic acid (RNA) in the cell has been reported to influence the rate of root growth in beans and corn seedlings (Ingle and Hageman, 1964). The relationship of RNA content and rate of growth for corn inbred lines and their hybrids was studied by Woodstock and Skoog (cited by Ingle and Hageman, 1964), and they found that the rate of growth of the inbred lines was directly proportional to the amount of RNA in the root tip, while this was not true for the hybrids. Wright (1971) reported that the relationship between RNA activity and root elongation is similar to the relationship between the net metabolic activity and seedling vigor.

Rate of root growth seems to be of importance in drought resistance. Selection of parents and isolation of genotypes with a higher

rate of root growth would be an initial and potentially fruitful breeding objective.

Speed of Germination Under a Simulated Drought Stress

Higher speed of germination and percentage emergence in the spring prior to the summer drought appear to determine the initial success or failure of spring wheat seedlings. Thus, selection of cultivars or lines to germinate faster and produce vigorous seedlings under drought conditions should be a definite contribution to the successful production of spring wheat in semi-arid areas of the world.

A seed is an embryonic plant which is in an inactive stage. Its germination is the resumption of growth. A wheat caryopsis is composed of three principle interacting parts a) embryo, b) endosperm, and c) seed coat which bring about the process of germination (Evenari, 1956). According to Toole et al. (1956) three distinct stages can be recognized during the process of germination 1) water uptake or imbibition which makes the seed turgid, 2) cellular elongation that occurs first in the coleorhiza, and 3) cell division which takes place first in the root tip. Thus, the imbibed seed swells, and the embryo pushes the radicle and plumule out, the former at a somewhat more rapid rate than the latter (Brouwer, 1966; Locke and Clark, 1924; McCall, 1934; Peterson, 1965; Wellington, 1966). Swelling is due mainly to the absorption of water by the protein molecules present in the embryo, aleurone layer, and endosperm.

Growth period of the grass seedling has been divided into three distinct stages (Whalley et al., 1966): 1) the heterotrophic stage, the period between imbibition and emergence of first leaf; 2) the transition stage, the phase between emergence and commencement of the photosynthetic activity of seedling, but before endosperm exhaustion, and 3) the autotrophic stage, the period after reserve food depletion, when the seedling is self-sustaining through photosynthesis. Imbibition and germination of seeds require favorable internal and external conditions (Toole et al., 1956). Thus, the heterotrophic or early stage of development, in addition to water, temperature and oxygen, can be affected by a number of other factors such as seed size, light, dormancy, and area of seed coat in contact with moisture.

Derwyn et al. (1966) stated that there is a close relationship between seedling vigor and seed size in grasses; vigorous seeds germinate rapidly. They indicated that seeds of larger size contain larger amounts of reserve material which can be used up for greater growth of embryo, and thus, they concluded that larger seeds give rise to earlier radicle emergence under adverse conditions. According to Evans et al. (1975) the larger the seed the greater the reserve and faster it can be established. McDaniel (1969) demonstrated that heavier seeds in barley had a greater growth potential than seeds of the same line with lighter weight. Fransen and Cooper (1976) studied the effect of seed size on emergence of sainfoin (*Onobrychis* spp.)

seedlings and reported that seedlings from larger seed emerged more rapidly than those from smaller seeds. They also found that an increase in seed size was associated with an increase in all parts of the embryo. Thus, they concluded that an increase in size of embryonic organs may be of importance to rapid germination. The relationship of seed size and germination of a wheat cultivar, 'Elmar,' was studied by Kittock and Law (1968). They found that germination was increased with seed weight. Wright (1971), discussing the importance of seed energy reserve in relation to germination and emergence, concluded that seed weight has shown a positive association with percentage of germination.

Dormancy in cereal grains is relatively transient. When the grains are used as seeds, dormancy is seldom a problem, but conditions of the embryo and endosperm of the caryopsis can influence development during germination (Wellington, 1966). The area of contact of seed with moisture affects germination. Wellington (1966) reported that for complete germination not over 3/4 of the seed surface should be submerged.

Wheat seed can germinate at a temperature ranging from 4 to 37°C but the optimal temperature is about 20-25°C (Evans et al., 1975).

The first step in germination of seed is the imbibition of water, and the amount of water imbibed influences the speed of

germination of the wheat caryopsis is 35 to 45% of grain dry weight; a higher percentage of water in the seed increases the rate of germination.

Seedling stage drought tolerance has been regarded as the most critical period for drought tolerance in perennial grasses (Mueller and Weaver, 1942), and it has been defined as the period from initial embryo germination until the stored food reserve of the seed is exhausted. Because speed of germination and initial embryo development could contribute to drought tolerance, screening the seedling for a higher rate of germination has been a successful technique for applied genetical investigations (Wright, 1971). Bolsunov, Snoep, and Poulov (cited by Aamodt and Johnston, 1936) reported that "an index for drought resistance may be obtained by studying the osmotic pressure of germinating seed as determined by salt or sugar solutions." They indicated that cereal seeds selected for tolerance to higher osmotic potentials yielded higher under drought conditions than unselected material. Derwyn et al. (1966) stated that speed of germination of *Schismus arabicus* and its success and ease of establishment under adverse conditions were highly correlated. Hurd (1971) reported that the ability of sorghum cultivars to germinate in sugar and salt solutions have been correlated with their drought resistance. Hurd (1974) later stated that germination percentage of spring wheat cultivars under osmotic stress was correlated well with results of field trials

for drought hardiness. In Kaul's test (cited by Hurd, 1974), Pitic, at 20 atm. mannitol solution, germinated 49%; 'Manitou,' a backcross of Thatcher, 27%; 'Giza,' 5%; and 'Carazinho, 3%. Openheimer (1960) indicated that quick germination and penetration of the primary root into the soil has been proven to be of utmost importance under desert conditions if seedlings are to survive in the subsequent dry period. Plummer (1943) found that slow growth of the primary root of *Agropyron smithii* and species of Festuca and Elymus caused them to fail in seedling establishment. Manohar (cited by Levitt, 1972) and McGinnies (1960) stated that although germinability of seed under higher concentration of solutes has been used as an index for drought tolerance, the results are conflicting. Aamodt and Johnston (1936) studied the speed of germination of several drought resistant and susceptible spring wheat cultivars. They concluded that the drought resistant properties of Caesium and Milturum cannot be attributed necessarily to the superior germinability of their kernels. Kneebone (1957), McGinnies (1960), Helmerick and Pfeifer (1954), Herbel and Sosebee (1969), Tadmore and Harpaz (1969), and Hunter and Erickson (1952) reported that increased moisture stress induced by mannitol delayed germination and initial growth, reduced rate of germination, and decreased the total germination percentage of several range grasses.

According to several investigators, rate of germination is a species and varietal characteristic (Wright, 1971; Evans et al., 1975;

Sharma, 1973; Helmerick and Pfeifer, 1954). Sharma's (1973) work on comparative drought tolerance of several pasture species under drought simulated by mannitol revealed that species were significantly different in their response to drought at germination. He found that the rate and total germination of all species declined with increasing moisture stress; however, the extent of such reduction varied considerably. Evans et al. (1975) indicated that emergence rate in wheat is genetically controlled and has a high positive correlation with coleoptile length and plant height. Helmerick and Pfeifer (1954) germinated seeds of both 'Yogo' and Cheyenne under mannitol induced moisture stress conditions and found that the former had a significantly higher percentage of germination and faster growth than the latter. They concluded that the difference between these two cultivars was genetic rather than due to environment.

Study of drought effect on seed germination has been mainly restricted to field conditions. But because of the difficulties involved in maintaining satisfactory control over moisture and other environmental factors in the field, program controlled investigations, in the laboratory, of drought effects on germination seem to be valuable (Wright, 1971). For this purpose, different osmotic agents have been used in the study of effect of moisture stress on germination. Parmar and Moore (1966,1968) reported that NaCl, as an osmotic agent, had toxic effects in solutions at concentrations above 7 atm. on

germination of alfalfa seed. Lagerwerff and Eagle (1961) and Kaul (1966) reported that sucrose molecules were either actively taken up by the seedling root or like mannitol, are subject to quick microbial degradation; sucrose may also cause a marked reduction in the rate of root hair growth (Parmar and Moore, 1968). Tadmore and Harpaz (1969) compared the effect of mannitol, glucose, and sucrose on germination of seeds of range species and found that mannitol affected germination less adversely than glucose and sucrose.

Polyethylene glycols (PEG) or carbowaxes are also used as osmotic agents. They are available in different molecular weights, ranging from approximately 300 to 20,000. Carbowaxes of lower molecular weight have been used in various osmotic studies, but no observations have been reported of its physiological toxicity to plants (Helmerick and Pfeifer, 1954; Jackson, 1962). At higher molecular weights, they contain considerable amounts of aluminum and magnesium which may cause physiological toxicity to most plants (Lagerwerff and Eagle, 1961). Kaul (1966) reported that polyethylene glycol of 20,000 molecular weight exerted only osmotic stress while that of 6,000 exerted osmotic plus toxic effects. Jackson (1962) stated that carbowaxes were exerting some direct effect upon the process of elgonation of root hairs quite apart from an osmotic effect.

Stomatal Studies

Epidermal cells of plant taxa are closely attached and continuous in a compact manner without intercellular spaces. This continuity is interrupted by minute openings which are limited to specialized cells called guard cells (Fahn, 1974). The guard cells and opening constitute the stoma, which is the pathway for gaseous exchange. Stomata develop from the protoderm, the meristem of epidermis. The protodermal cells divide unequally and give rise to a large and a small cell rich in protoplasm that constitute the two guard cells (Fahn, 1974; Kramer, 1969). The middle lamellae of the two guard cells disintegrate. As a result, they separate and a minute pore develops (Meidner and Mansfield, 1968). In wheat, stomata are found on the sheath, glumes, lemmas, paleas, awns, and leaves (Teare et al., 1972). They are found in single or double parallel rows on the adaxial leaf surface, and usually in single rows, fewer in number, on the abaxial surface (Briggle, 1967; Hayward, 1948; Fahn, 1974; Shearman and Beard, 1972). Below the stomata, toward the mesophyll cells, a larger intercellular space, the stomatal chamber, can be found. The guard cells of the Graminae are bone shaped and elongated. The middle portion of these cells is thick walled while the ends are thin walled. As a result of higher turgor pressure, the ends swell and push the middle portion apart and thus the stoma opens.

Stomata have been shown to be of importance in photosynthesis, transpiration, water use efficiency, drought tolerance, and winter hardiness (Miskin et al., 1972; Sapra et al., 1975; Teare et al., 1972; Teare et al., 1971). Stomatal pores are the main pathway of gaseous exchange between leaves and environment. Sapra et al. (1975) reported that transpiration, water use efficiency, dry matter production and CO_2 diffusion are influenced by the size of the pore and density and distribution of stomata on the leaf epidermis. Dobrenz et al. (1969) studied stomatal density (number per unit of leaf area) in relation to water use efficiency and found that drought tolerant clones of blue panic grass (*Panicum antidotale*) had fewer stomata per unit area than drought susceptible clones, while they noticed that clones selected for high forage production under irrigation had significantly higher stomatal numbers than others. Thus, a significant negative correlation ($r = -0.84$) between drought tolerant clones and mean stomatal density was obtained while correlation between water use efficiency and stomatal density was negative and non-significant ($r = -0.47$). They concluded that clones with higher stomatal frequencies were not drought tolerant (Dovrenz et al., 1969). Inverson and Hockett (1968) in their study of transpiration as related to stomatal frequency found a low positive relationship between high stomatal number and high transpiration rate. According to Reitz (1974) drought tolerant plants may influence evapotranspiration by rapidity of their

growth, water uptake and retarding the loss of water through epidermis and stomata. Reitz believes that it would be an error to associate drought resistance and water use efficiency too closely.

Miskin et al. (1972) studied transpiration rate of barley (*H. vulgare*) lines that differed in stomatal density. They concluded that stomatal density had a prominent effect upon transpiration rate. They claimed that a 25% decrease in stomatal frequency decreased the rate of transpiration by 24%, while they noticed that these lines maintained a similar photosynthetic rate as lines with high stomatal frequencies. Heichel (1971) reported that a *Zea maize* L. cultivar with lower stomatal frequency had higher net photosynthesis than cultivars with higher stomatal densities.

Tan and Dunn (1973,1975) reported that there were significant differences in stomatal frequency, length of the guard cells and pollen grain diameter in different ploidy levels and leaf positions. They used these traits as an indirect method for the identification of ploidy level in smooth bromegrass (*Bromus inermis*). They found that stomatal frequency decreases with an increase in ploidy level while pollen grain diameter and guard cell length are positively associated. Thus, it was concluded that stomatal frequency was negatively correlated with pollen grain diameter and guard cell length. These results were confirmed by Sapra et al. (1975) who indicated that leaves of hexaploid triticales had higher numbers of stomata and smaller guard

cell length than octaploid triticales. Number of stomata per unit area is influenced by environmental factors. Cole and Dobrenz (1970) reported that stomatal density can be altered by such factors as light intensity, temperature and soil moisture levels under which plants grow. Teare et al. (1971) stated that plants under optimal environmental conditions had lower stomatal frequencies than when under stress. In alfalfa, according to Cooper and Qualls (1967), there were 20% more stomata under sunlight than in shade. Ormrad and Renney (1968) in a survey of weed leaf stomata claimed that stomatal frequency was higher on the leaves of plants grown in partial shade than on those grown in the full sun. Miskin and Rasmussen (1970) found that intensity of light affected the frequency of stomata significantly and, in general, frequency increased as the intensity of light was increased. On the other hand, temperature had little effect on the stomatal frequencies and differences between treatments were not statistically significant.

Kolkunov (cited by Aamodt and Johnston, 1936) studied stomatal size in a number of wheat cultivars known to differ in degrees of drought tolerance and found that the more resistant cultivars were characterized by small stomata. Cain and Potzger (cited by Cole and Dobrenz, 1970) found that black huckleberry grown under drought conditions had greater stomatal density while plants grown under optimum moisture conditions had fewer stomata per unit area. Ciha and Brun

(1975) reported that stomatal frequency on the abaxial surface in soybean (*Glycine max*) decreased with temperature while temperature had no effect on the adaxial surface. They also indicated that leaf area increased with temperature and decreased with light intensity. Because of these two situations, they concluded that in soybean the total number of stomata per leaflet may vary significantly with light or temperature.

According to Wood (1934), stomatal frequency is controlled more closely by gene action than by environment. Teare et al. (1971) stated that by crossing plants having high and low stomatal frequency, it could be possible to change stomatal density of progenies and thus alter associated physiological processes.

In corn, Heichel (1971) found a consistent difference in stomatal frequencies between cultivars in different generations. He claimed that there was a simple genetic system which controls stomatal and epidermal cell frequencies. He pointed out that the system was a dominant gene action for low epidermal cell frequencies and partial dominance for low stomatal frequencies. This suggests that stomata and epidermal cell frequencies are under the control of the same genetic system. Miskin et al. (1972) found that there is little dominance for stomatal frequency in barley and broad-sense heritability was estimated by the parent-progeny regression method to be 22 to 74% in F_2 and F_3 generations, respectively. The relatively high F_3

heritability estimate may encourage early generation selection for stomatal frequency.

Stomate number and size vary within and between leaves and leaf surfaces on single plants, clones, cultivars and species (Cole and Dobrenz, 1970; Hunt, 1962; Shearman and Beard, 1972; Miskin and Rasmussen, 1970; Sapra et al., 1975; Ormrad and Renney, 1968; Teare et al., 1971). In this study they obtained a negative correlation between stomatal size and frequency. Frequency, size, and distribution of stomata in triticale, rye, and wheat leaves were studied by Sapra et al. (1975). The results of the study indicated that rye had higher stomatal frequencies but stomata smaller in size than wheat and triticale.

Miskin and Rasmussen (1970) detected significant differences in density of stomata among barley cultivars. Dobrenz et al. (1969) reported that stomatal density was significantly different among clones of blue panic grass. Eckerson (1908) found that the largest size of stomata occur in wheat (*Triticum aestivum* L.). She also claimed that in general there was more variation in frequency than in size among the plant species she studied.

Ormrad and Renney (1968) stated that most of the weedy plant species which they investigated had higher stomata on the abaxial than adaxial surface while in blue panic grass, corn, barley, creeping bent

grass (*Agrostis palustris*) and alfalfa (*Medicago sativa*) the opposite is true.

Teare et al. (1971) found that tips of the leaves of wheat (*Triticum aestivum* L.) had lower stomatal frequencies than did the leaf base. They also indicated that tips and leaf bases were more variable than the mid portion of leaves, and the adaxial surface was less variable than the abaxial surface. In contrast with the results obtained by Miskin and Rasmussen (1970), Teare et al. (1971) found no significant relationship between guard cell length and stomatal frequency in wheat. In corn, as in wheat, stomatal frequency lf leaves decreases from apex downward and decreases from the leaf tip to base.

Tan and Dunn (1975) reported a high positive correlation between abaxial and adaxial stomatal frequency in *Bromus inermis*. They stated that in general there were lower stomatal frequencies on leaf tips, but stomata were larger in size; cultivars of *Bromus inermis* were found to be more variable in stomatal frequency than in length of the guard cells at three positions of the same leaf. According to Sapra et al. (1975), wheat stomatal frequencies decrease with descending leaf position, but this is not necessarily true for rye and triticale. Blue panic grass leaves adjacent to the inflorescence had significantly lower stomata density than leaves at the middle and base of the culm, while no significant differences among stomatal frequencies of different positions on the leaf were detected (Dobrenz et al., 1969). On

the other hand, terminal leaves in wheat (Teare et al., 1971) and barley (Miskin et al., 1972) have higher stomatal frequencies compared to lower leaves. Sapra et al. (1975) found that frequency of stomata on the base, middle, and tip of the adaxial surface for wheat did not change appreciably while in the case of rye and triticale it increased.

Length of guard cells in wheat, for base, middle, and tip did not change while stomatal size (length of guard cells) increased with descending leaf position in rye and triticale (Sapra et al., 1975).

Quantitative Genetics

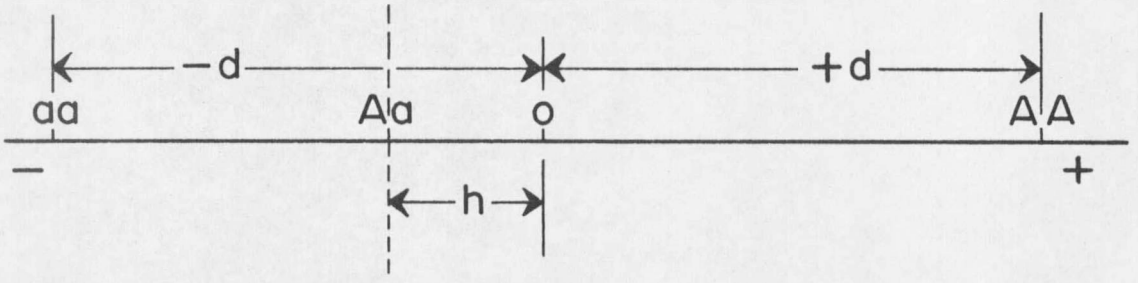
Many agronomically important traits, including several associated with drought tolerance, do not follow patterns of simple Mendelian inheritance; rather, they vary continuously such that individuals cannot be discretely placed into clear-cut classes. In the immediate post-Mendelian period, extensive arguments were raised over the heritability of continuously varying traits. Basically, three studies, all reported in the first two decades of the 20th century, resolved the issue. In 1909, Johannsen developed the "pure line theory" through which the impacts of environment vs genetic effects were separated through studying the variation in seed size in beans. From his studies fundamental concepts of genotype and phenotype evolved. In the same period (1910), Nilsson-Ehle studied continuous variation in kernel color of wheat and East (1916) suggested that variation in corolla

tube length in tobacco (*Nicotiana longiflora*) could be attributed to two causes--environmental effects and heritable components. Thus, by about 1920 the major controversies over the inheritance of varying (quantitative) traits had been resolved.

Rather complex statistical models are used to analyze quantitative genetic traits. According to Allard (1956) and Cockerham (1956), Fisher was the first to partition genotypic variance into components. Fisher's work established three basic components of genetic variation: additive, dominance, and epistatic. Additive variation is most easily fixed through selection and is of most interest to plant breeders, whereas, both dominance (intra-allelic interaction) and epistatic variation (inter-allelic interaction) are of lesser importance (see Grafius et al., 1952b).

Mather (1949) simplified many concepts proposed by Fisher. He stated that the total, or phenotypic variability, which is expressed and measured by variance, can be divided into three components: a) additive and heritable (d), the portion of total variance that can be easily fixed and estimated from the observations made on a population (Falconer, 1961); b) non-additive and heritable (h), that portion which is unfixable and unavailable for use in the selection of true breeding strains; and c) environmental and non-heritable variation (E). The magnitude of additive and dominance (non-additive) variation as measured by 'd' and 'h' determine the genetic properties of the

population. These two components of the total variability explain the joint action of all genes controlling a character. The action of all these effects at a locus is defined and explained by Mather (1949) according to the following scheme



where '0' is the mid parent, or average of homozygous parents, from which deviations are measured.

'h' is the dominant gene effect and its value can be either positive or negative. It is measured as the deviation from '0'

When there is no dominant gene action, 'h' becomes zero, the F_1 equals the mid parent, and the gene action is exclusively additive. As the value of 'h' increases, positively or negatively (i.e. the absolute value of 'h' increases), the additive component of variance decreases.

The effects -d and +d represent the average effect of AA and aa, the homozygous parents. Overdominance would be the case where the value of Aa would be smaller than -d or greater than +d.

The distinction between heritable and non-heritable characters which are continuous cannot be accomplished by mere inspection. Their study and distinction require a special type of statistical analysis

while the results are interpeted in Mendelian fashion. This is a complementary technique to the Mendelian analysis which deals with individual gene effects rather than multiple gene action.

Gene action affecting a quantitative trait in self-pollinated crops can be studied in biparental and polyparental crosses. A biparental cross is the case where the test material originates from only two, genetically different, parents. The analysis of data coming from the polyparental experimental material have been concentrated (Allard, 1956) on 1) the diallel analysis, 2) factorial method, and 3) variance component method of genetic analysis.

Diallel analysis is a procedure in which a set of 'N' homozygous lines are chosen (randomly or fixed) and crosses among those lines are made. The maximum number of generations would be N^2, consisting of a) 'N' inbred lines, b) $N(N-1)/2$ F_1's, and c) $N(N-1)/2$ reciprocal F_1's. This is a technique that becomes laborious and expensive when a considerable number of lines are evaluated.

The factorial method, according to Allard (1956), is a technique that characterizes gene action through the frequency distribution associated with each genotype by a mean and standard deviation. The plant breeder who makes many crosses, with continuously varying traits, does not have a definite way of predicting the comparative values of these crosses in advance.

Early generation testing by variance component analysis has also been proposed to be a safe and rapid method of predicting the value of a given cross (Atkins and Murphy, 1949; Grafius, 1952a; Harrington, 1940; Immer, 1941; Suneson and Riddle, 1944). It is thought that early generation selection could result in high yielding progenies in later generations. However, not all the workers have found this system useful in selecting high yielding crosses on the basis of parental performance before any crosses were made. According to Harrington (1940), testing of a replicated bulk F_2 population could determine the yielding potentialities of wheat crosses. Immer (1941) suggested that yielding ability of parental lines can be determined by means of replicated yield trials of F_2 or F_3 generations. Suneson and Riddle (1949) found that testing F_1 hybrids for yield in barley could be a workable method of evaluating the parents. Atkins and Murphy (1949) initiated an experiment to determine the yielding abilities of oat crosses in early generations of bulk oat populations and reported that "the bulk population which gave the highest yield in replicated tests in early segregating generations did not produce the greatest proportion of high-yielding segregates in subsequent generations, according to the results of a one-year test." Thus, they see no merit in the bulk population method of breeding. They stated that high-yielding germ plasm may be lost during early generation selection of the crosses. But they

indicated that bushel weight of early generations was significantly correlated with the yield obtained in later generations.

Grafius et al. (1952b) studied the performance of F_2 progenies and their respective parents. They were able to separate the total genetic variance into 1) additive genetic variance, and 2) non-additive (dominance and epistasis) genetic variance. They concluded that the additive component of the total genetic variance was a measure of parental prepotency in progeny; failure to produce a given effect was due to the non-additive, allelic and non-allelic, gene interaction. Grafius observed that the confusing effects of dominance and epistasis decrease and the magnitude of additive genetic variance, because of increased homozygosity, increases in later generations.

Analysis of components of variance, which is based on the principle of Mendelian genetics, can be done best by partitioning the variation into two categories, additive and non-additive variances.

Additive genetic variance can be estimated from mean squares for among progeny of different females and for among progeny of different males. This portion of genetic variance is a measure of the ability of parents to produce a given effect in the progeny, or parental prepotency. Its effects are cumulative and its magnitude influences the heritability of the trait that is under investigation.

After the analysis of variance components is completed, the next step is to estimate the heritability of the trait. This may suggest how the quantitative trait could be altered by selection.

Heritability is the ratio of genetic to phenotypic variability. This ratio is also referred to as broad sense heritability.

$$h^2_{(B)} = \frac{\sigma^2_G}{\sigma^2_p}$$

Because of the dominance and epistatic effects, the true value of heritability cannot be measured; it is rather over estimated. While narrow sense heritability which measures the true value of heritability is estimated by the ratio of the additive genetic variance (σ^2_d) to the phenotypic variance (σ^2_p)

$$h^2_{(N)} = \frac{\sigma^2_d}{\sigma^2_p}$$

where $\sigma^2_p = \sigma^2_G + \sigma^2_E$ (environmental variance)

$\sigma^2_G = \sigma^2_d + \sigma^2_h$ (variance due to dominance effect)

$+ \sigma^2_I$ (variance due to epistasis)

Thus $$h^2_{(N)} = \frac{\sigma^2_d}{\sigma^2_d + \sigma^2_h + \sigma^2_I + \sigma^2_E}$$

Note that the main factor of heritability in this case is only the additive genetic variance. Thus, whenever there is high narrow sense heritability, early generation selection would be worthwhile. Expected genetic gain is the ultimate goal of the plant breeder. Its magnitude depends upon heritability of the trait and extent of the variability within the base population. Genetic gain is estimated by the following formula

$$G = h^2 \times R = h^2(\bar{X}_s - X_o)$$

where G stands for the genetic gain

h^2 represents heritability in percent

$(\bar{X}_s - \bar{X}_o)$ represents the reach (R)

$\bar{X}_s$ is the mean of the selected population

$\bar{X}_o$ is the mean of the original population

A statistical model for estimating the components of genetic variance to calculate the heritability of a trait, as measured by early generation bulk method progeny test, was proposed by Grafius (1952a) and Comstock and Robinson (1948). In this model which is based on additivity, a "j" number of homozygous lines used as female (f) parents are crossed in all possible ways with a "k" number of male (m) parents. The offspring: jk (F_1), jk (F_2), etc., are produced in bulk and used as the experimental material in replicated (r) trials (Cockerham, 1956; Grafius, 1952a). As the result of this crossing,

components of variance, M_1, M_2, M_3, and M_4 (Table 1) between self-pollinated bulk progenies from the crosses of homozygous lines were estimated according to the following model proposed by Grafius (1952a) (Table 1). Expectation of mean squares in this table are given in terms of variance components and the values of specific variances are calculated as follows:

$$\sigma^2_m = (M_1 - M_3)/rj = [(\sigma^2_e + r\sigma^2_{m.f} + rj\sigma^2_m) - (\sigma^2_e + r\sigma^2_{m.f})]/rj$$

$$\sigma^2_f = (M_2 - M_3)/rk = [(\sigma^2_e + r\sigma^2_{m.f} + rk\sigma^2_f) - (\sigma^2_e + r\sigma^2_{m.f})]/rk$$

$$\sigma^2_{m.f} = (M_3 - M_4)/r = [(\sigma^2_e + r\sigma^2_{m.f}) - \sigma^2_e]/r$$

$$\sigma^2_e = M_4$$

In this model, total variance = $\sigma^2_e + \sigma^2_m + \sigma^2_f + \sigma^2_{m.f}$ and additive variance = $\sigma^2_m + \sigma^2_f$.

The estimate of narrow sense heritability ($h^2_{(N)}$) of a trait for any generation would be:

$$h^2_{(N)} = \frac{\text{additive variance}}{\text{total variance}} = \frac{\sigma^2_m + \sigma^2_f}{\sigma^2_e + \sigma^2_m + \sigma^2_f + \sigma^2_{m.f}}$$

The magnitude of $h^2_{(N)}$ would indicate whether or not the trait under consideration would respond to early generation selection.

Table 1. Analysis of variance model showing components of genetic variation for self-pollinated bulk progenies from crosses of homozygous lines[1/]

Source of variation	df	MS	Expectation of Mean Squares*
Total	jkr-1		
Replication	r-1		
Crosses	JK-1		
- Between progenies of different males	K-1	M_1	$\sigma^2_e + r\sigma^2_{m.f} + rj\sigma^2_m$
- Between progenies of different females	j-1	M_2	$\sigma^2_e + r\sigma^2_{m.f} + rk\sigma^2_f$
- Interaction	(K-1)(j-1)	M_3	$\sigma^2_e + r\sigma^2_{m.f}$
Error	(r-1)(JK-1)	M_4	σ^2_e

* σ^2_e: environmental variance

$\sigma^2_{m.f}$: variance due to interaction of male and female effect

σ^2_m: variance due to male effect

σ^2_f: variance due to female effect

[1/] from Grafius 1952a

Application of this model for the analysis of quantitative gene action assumes the following conditions:

1 - Homozygosity of parents

2 - Normal diploid segregation

3 - Only environmental difference between reciprocal crosses exist (no maternal effect)

4 - No linkage

5 - Independence of non-allelic genes (no epistasis) and genes 1 to n have equal effects

6 - No multiple allele

7 - Treatment and environmental effects are additive

8 - Experimental errors are randomly, independently and normally distributed about zero mean and with common variance, σ^2

9 - No dominance

The validity of the 5th and 9th assumptions, no epistasis and no dominance are tested with the model, but variation due to these effects is not separated. Several traits have been reported to correlate with drought tolerance. It is my objective to study mode of inheritance and heritability of some of these factors, as they relate to drought tolerance, by isolating the components of genetic variance for each trait according to the Grafius's model (1952a) discussed above.

MATERIALS AND METHODS

Genetic Stock

Four greenhouse and growth chamber pilot studies were undertaken to detect genetic variability among spring wheat cultivars for certain traits that are reported to be associated with drought tolerance. These cultivars, their C.I. or selection No., maturity class (early, medium, and late), plant height class, and 100 kernel weight are listed in Table 2.

The pilot experiments were designed to study

1. Root and shoot growth
2. Rate of root elongation
3. Speed of germination
4. Stomatal number

The first two experiments involved all 20 cultivars; the third, speed of germination, involved 'Short Rescue,' 'Fortuna,' and 'Thatcher'; while the fourth study, a study of stomatal number, was conducted with the 12 cultivars footnoted (Table 2).

Extended studies of the above-mentioned traits were initiated to find fundamental information about the mode of inheritance of the traits related to drought tolerance. Experiment No. 1, the root and shoot studies, utilized 12 parental lines (Table 2), selected from the pilot study, representing 9 female and 3 male parents, in addition to their F_2 progenies. Experiments Nos. 2 and 3, rate of root

Table 2. Cultivar name, CI or selection number and agronomic characteristics of spring wheat cultivars (obtained from Montana spring wheat improvement program) used in pilot studies

Cultivar Name	CI or selection No.	Maturity class	Plant height class	100 kernel weight (grams)
Fronteira 1/	12019	Late	Tall	3.858
Frondoso 1/	12078	Late	Tall	3.436
Oleson Dwarf 1/	MT 37	Early	Short	3.580
Short Centana	MT 6728	Late	Short	2.879
Shortana	15233	Medium	Medium	2.754
Centana	12974	Late	Tall	2.875
Norana	15927	Late	Medium	3.409
Norana sib	MT 7156	Medium	Medium	2.949
Twin 2/	14588	Late	Medium	2.487
Fielder	17268	Medium	Medium	3.410
Era 2/	13986	Late	Medium	3.008
Borah	17267	Early	Medium	3.317
Olaf	15930	Early	Medium	3.718
Short Rescue 2/	'73 Row 1953	Late	Short	2.351
Medium Rescue 2/	'73 Row 1816	Medium	Medium	2.751
Rescue 2/	12435	Medium	Tall	2.907
Fortuna 2/	13596	Early	Tall	4.186
Tioga 2/	17286	Early	Tall	3.761
Ellar 2/	17289	Early	Tall	3.612
Thatcher 2/	10003	Early	Tall	2.353

1. Cultivars used as male parents in extended inheritance studies
2. Cultivars used as female parents in extended inheritance studies

elongation and speed of germination, respectively, consisted of parental lines, plus F_1 and F_2 progenies. The stomatal study, Experiment No. 4, involved only parental lines as did the pilot study of stomata.

F_1 seeds were produced in summer 1974 and 1975, by crossing each of the female parents with each of the male parents in all possible combinations at the Agricultural Experiment Station situated about 9 kilometers west of the Montana State University campus. The F_2 seeds were produced by self-pollination of F_1 plants in the greenhouse during the winter 1974-1975.

All preliminary studies were analyzed following standard analysis of variance methods. Since these studies included only cultivars that were assumed to be homozygous, variation among treatments was assumed to reflect genetic variation, but this could not be partitioned into components. The analysis of extended studies, subdivision of components of genetic variation, and ultimate estimates of heritabilities followed an analysis of variance model proposed by Grafius (1952a) and discussed in detail above.

Root and Shoot Studies

Two experiments were conducted in the greenhouse at Montana State University in the summers of 1974 and 1975.

The first experiment was conducted in June, 1974 with 20 cultivars of diverse agronomic traits and adaptation (Table 2) in a split

plot design with 3 replications and 3 growth durations (3, 6, and 9 weeks) to evaluate the growth patterns of root and shoot, as well as related traits. Growth durations were assigned to main plots and cultivars to sub-plots. Six seeds of each cultivar were planted in plastic pots filled with 3 parts soil and 1 part river washed sand. The soil and sand mixture were steamed and thoroughly mixed prior to the experiment. The volume of mixed soil and sand was judged visually so that all pots had equal volumes of sand and soil. Pots were 15 cm in diameter and 15 cm in depth. Seeds were planted in each pot at a depth of 2.5 cm in a circular pattern at a distance of 5 cm from the center of the pot. The pots were irrigated with tap water when needed; thus, moisture was not a limiting factor. Temperature range of both ends of benches, where ports were located, were recorded twice daily, morning and evening; the overall mean soil temperatures were 17.4°C morning and 20.9°C evening. In order to reduce the error resulting from the temperature gradient, the pots, located in each block were rerandomized periodically. For each harvest, that is at 3, 6, and 9 weeks of age, plants were harvested by dumping the pots and washing the roots. Removal and cleaning of roots were facilitated by flooding the pots several hours prior to the process of washing soil from the roots. The pots were then immersed into a barrel filled with clean water. While holding the plant shoots, pots were tipped over and kept submerged until the soil and sand were washed free from

the roots. Roots and shoots were then cleaned carefully, with a moderately gentle stream of water using a spray nozzle. The cleaned roots and shoots were then transfereed into a large pan filled with clean water and any adhering organic matter was removed.

At the end of each growth period, the following traits were measured:

1. Leaf number
2. Total root number (seminal and adventitious)
3. Root mass
4. Root/shoot ratio

Dry weights of the root and shoot were determined by drying plant material in an oven at 100°C for 94 hours, and were then expressed as grams per plant. Root to shoot ratio was determined on a dry weight basis. Data for all traits were analyzed following standard analysis of variance methods.

The second greenhouse experiment was initiated in June 1975, in a randomized complete block design with three replications, to evaluate the same traits as in the pilot study. Parents and F_2 progenies were separately randomized in each block and re-randomized periodically to minimize the effect of a bias due to temperature. Temperature of the pots was measured by soil thermometer located at both ends of the benches and recorded twice daily, morning and evening. The

overall mean temperature during the experimental period was 17.7°C for the morning and 24.4°C for the evening.

In order to wash and clean the roots free of soil efficiently and completely, sets of 93 pots (having the same dimension, seedling depth and spacing, and soil-sand mixture as in the first experiments) were planted at two day intervals. Eighteen seeds of each of the parental lines (in three replications) and 54 seeds of each of the F_2 progenies (3 pots per replication and 9 pots in the whole experiment, each containing six seeds) were used. After 42 days, the plants were harvested, roots were washed free of the soil and the same traits were estimated as in the pilot study.

The data were analyzed and interpreted following the Grafius (1942a) model.

Rate of Root Elongation

Genetic variation for rate of root elongation was evaluated in a controlled environmental chamber pilot study in the summer of 1974. The experiment was conducted in a completely random design and replicated twice in time.

Based on significant differences among the cultivar means and root and shoot studies, an extensive study was initiated to verify the genetic variability of the rate of root elongation under controlled environment in the summer of 1975.

The physical design of the experiment consisted of: 1) a pan, 90x63 cm, 2.54 cm deep, filled with water; 2) a wooden frame, 92x65 cm, 15 cm deep, placed around the pan; 3) fourteen 62x30 cm masonite boards, 4 mm thick, overlaid by white blotter paper which could be inserted into the grooves cut at a 45° angle on the longer side panels of the frame (the blotters absorbed water from the pan underneath the frame); and 4) the seeds, which were grown on these slanted boards over a period of 8 days.

Blotters were divided into two equal units, each containing a lot of 10 seeds. Genetic stocks were arranged in groups. A group consisted of 10 seeds each of one male and one female parent, 10 of their F_1 seeds, and 40 of their F_2 seeds. Seeds were grouped in units of 10; thus, there were four sets of 10 seeds for the F_2 and a single set for each of the parents and F_1. Seeds were held in position on the blotter paper by tissue paper stretched over them. Blotters, seeds and tissue papers then were covered by "Saran" wrap which was taped on the backside of the board, for physical support, to protect seedlings while measurements were made, and also to prevent excessive evaporation of water from the blotter surface. Pan, boards, and frame were carefully sterilized by 10% Chlorox solution and washed, before adding seeds, to control fungal growth. The experiment was conducted in a growth chamber at 20°C, photoperiod of 16 hours and light

intensity of approximately 1000 foot candles at canopy level. Tap water was added to the pan daily to compensate for the volume evaporated.

The first replication of the experimental material was conducted in the summer of 1975. Each replication consisted of 27 groups and it was completed in 7 runs. Each run, except the last one, constituted 4 groups. The second replication was initiated in winter of 1975 and completed in early spring of 1976.

In general, no measurable germination was detected up to 24 hours after imbibition and thereafter the length of the longest root of each seedling was measured by compass daily and the daily mean length and growth rate were calculated by the method proposed by Maguire (1962). The data were analyzed and interpreted following the Grafius (1942a) model.

Speed of Germination Under Simulated Drought Stress

In the spring of 1975, rate and cumulative germination percentage of three spring wheat cultivars, Short Rescue, Fortuna, and Thatcher, were studied under artificial drought induced by dissolving mannitol ($HOCH_2(CHOH)_4CH_2OH$)[1/] in distilled water to provide solutions of specific osmatic potential. These solutions are easy to prepare, and,

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[1/] J. T. Baker Chemical Company, Phillipsburg, New Jersey.

according to Powell and Pfeifer (1957), the solute does not affect the metabolic activities of the seedlings.

The aqueous solution consisted of distilled water, as control or zero osmatic potential, and solutions of D-mannitol to provide 12 and 24 atmospheres osmatic potential. The amounts of mannitol to be dissolved in distilled water, for desired osmatic potentials, were calculated from the following approximate formulae:

$$\text{Osmotic potential} = p = \frac{gRT}{mv}$$

$$\text{Grams of mannitol} = g = \frac{pvm}{RT}$$

where v = volume of solvent (distilled water) in liter

m = molecular weight of mannitol (182.2)

R = 0.08205 liter atmosphere per degree per mole (constant)

T = absolute temperature

Thus, an amount of 182.2 and 364.4 grams of mannitol, at 20°C, were dissolved independently in two liters of distilled water and solutions of approximately 12 and 24 atmospheres osmotic potential were obtained.

Based on significant varietal difference for both rate and cumulative germination percentage, a more extensive study was initiated in the summer of 1976, under controlled simulated drought conditions.

Germination tests were conducted in sterilized disposable plastic petri-dishes of about 90 mm inner diameter and 12 mm depth covered

with a tight lid to prevent excessive evaporation. Solutions representing the same osmotic potentials as those used in the pilot study were used. Each petri-dish contained a) four plies of Whatman No. 2 filter paper to hold adequate moisture for imbibition and germination process, b) eight cc of aqueous solution, and c) seeds during the period of study.

Seeds were chosen randomly, treated with Arasan, laid on the pre-moistened filter papers inside the petri-dishes and arranged in such a pattern that embryo ends of the caryopsis were in one direction.

The experimental design was a randomized complete block consisting of 171 treatments[1/] and replicated twice in time. Seeds were germinated in a darkened germination chamber for a period of 14 days. To reduce the effect of a temperature gradient inside the germinator, only the middle 9 shelves of 16 were used in this experiment. Temperature was recorded daily for both the top (1st) and bottom (9th) shelf during the course of the experiment; mean temperature for the upper

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Parents and progenies	No. of seeds used	No. of parents or progenies	Osmotic concentrations (atm)	No. of treatment
male parents	50	3	0,12 & 24	9
female parents	50	0	0,12 & 24	27
F_2 progenies	50	27	0,12 & 24	81
F_1 progenies	50	27	0 & 12	54
Total Treatments				171

shelf was 19.7±1.5 and for the bottom 21.7±1.5. Relative humidity was not controlled; therefore, both the trays and petri-dishes were randomly rearranged daily. This was done to diminish both the effect of condensation which occurred differently in different trays and the effect of the temperature gradient.

Petri-dishes were exposed to light for about 10 minutes daily, only when seeds were examined and scored for germination. Filter papers inside the petri-dishes were examined daily and when necessary distilled water was added by eye dropper to compensate for the amount of water evaporated or condensed. When adding water, care was taken so that water was not poured directly on the seeds. Visual observation indicated that evaporation from the petri-dishes was quite small and thus minute amounts of water added to or evaporated from the petri-dishes are assumed not to affect conclusions or interpretations of results.

The seeds were considered germinated when the imbibed seeds met the following criteria: a) presence of both plumule and radicle; and b) plumule at least the length of the caryopsis. Those seeds with either plumule or radicle but not both, were considered abnormal or non-germinated.

The number of seeds germinated was recorded daily and germinated seeds were removed from the petri-dishes daily. Effects of osmotic concentrations on the speed of germination were expressed by the

method described by Maguire (1962) and data were analyzed by the standard methods for randomized complete block design. Narrow sense heritability was calculated as previously described.

Stomatal Study

In the winter of 1975, a greenhouse pilot study involving 12 cultivars (Table 2) was conducted using pots 15 cm in diameter and 15 cm in depth, each filled with soil and containing six seeds. The pots were arranged in a completely random design on a greenhouse bench. At anthesis, when the leaves were fully expanded, stomatal impressions of the central portion of both adaxial and abaxial surfaces of the leaf immediately below the flag leaf were made in the laboratory by the method proposed by Saravella et al. (1961) with some modification. This is a technique that facilitates rapid stomatal counts and measurements of their closed apertures. Sampling for stomatal impression was repeated twice. Twenty randomly chosen microscopic fields (1.17 mm^2) were scored for stomatal number on both leaf surfaces for two plants within each cultivar.

In spring 1975, a more extensive study in both the greenhouse and field, using the same cultivars, was initiated. In the greenhouse 15 seeds of each cultivar were planted in pots 26 cm in diameter and 20 cm in height, and in the field, 50 seeds per cultivar were seeded in rows 50 cm apart and 5 meters long. The experiment, both in the

greenhouse and field was set up in a completely random design. Plants in the greenhouse were watered, as needed, with complete nutrient solution, while in the field, due to timely precipitation, they were not irrigated. From both the greenhouse and field, 10 plants were sampled from each of the 12 cultivars (a total of 240 plant samples). Leaf impressions of both the adaxial and abaxial surfaces were made from the central portion of the leaf immediately below the flag leaf at the anthesis stage of development. Thus, a total of 480 impressions was made.

Leaves were collected in the field and the greenhouse and stored immediately in pre-moistened plastic bags. In preparing the stomatal impressions, undamaged disease-free leaves were pinned to a flat, clean cardboard surface and sprayed with a commercial fixative, Tuffilm,[1/] and allowed to harden for approximately 10 minutes. Transparent scotch tape was then pressed to the treated leaf surface and peeled off immediately. The Tuffilm coating bearing the stomatal impression was removed with the tape. The tape-film complex was transferred to a clean glass slide and merely pressed to it. For better stomatal impressions care was taken to apply the tape on the leaf surface with uniform and gentle pressure in order to avoid fingerprints on the surface of the tape and prevent deformation of the

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[1/] M. Grambacher, Inc., New York, Cat. No. 643.

structure of the stomatal complex. Six random fields from each slide were scored for stomatal number using a standard compound microscope with a total magnification of 125X.

Data for both studies were analyzed following standard analysis of variance methods to test for variation within and among cultivars. In addition, rank correlation among cultivars was estimated to determine the stability of cultivars grown in different environments.

RESULTS AND DISCUSSION

Root and Shoot Studies

The data for all traits measured (leaf number, total root number, root mass, and root/shoot ratio) in the pilot greenhouse study for different growth durations are shown in Table 3.

The data for these traits were analyzed by the standard least squares method and results are summarized in Tables 4, 5, 6, and 7. Variance ratio for growth duration for the traits studied were statistically highly significant. The block differences were not significant. This implies that the experimental area was generally uniform. Leaf number and total root (seminal and adventitious) number, among cultivars studied, were significant at the 5% probability level (Tables 4 and 5), while for root mass (Table 6) and root/shoot ratio (Table 7) the differences were real at the 1% probability level. This may reflect genetic differences among cultivars for leaf number, total root number, root mass, and root/shoot ratio.

No significant cultivar by growth duration interaction (Tables 4, 5, 6, and 7) was detected for any of the traits. This indicates that all cultivars studied reacted the same for the three growth durations for all traits. Based on the results of this pilot study in terms of differences among cultivars, 12 diverse cultivars representing 9 female and 3 male parents (Table 2) were selected for further studies. The two cultivars, Thatcher and Rescue, were included in the

Table 3. Data for four agronomic traits from 20 spring wheat cultivars for each of three growth durations

Cultivars	Leaf No. Growth duration weeks			Total Root No. Growth duration weeks			Root Mass (g/plant) Growth duration weeks			Root/Shoot Ratio Growth duration weeks		
	3	6	9	3	6	9	3	6	9	3	6	9
Fronteira	3.83	9.72	9.68	6.50	14.44	18.02	0.068	0.198	0.225	0.708	0.400	0.230
Frondoso	4.78	7.04	11.15	6.61	10.75	17.87	0.061	0.139	0.265	0.521	0.348	0.154
Oleson	5.28	5.89	6.98	9.50	12.53	15.14	0.064	0.100	0.140	0.520	0.266	0.164
Dwarf												
Short	5.63	6.09	11.88	7.80	12.70	15.15	0.058	0.133	0.173	0.630	0.401	0.205
Centana												
Shortana	5.08	6.89	7.67	7.68	12.72	12.50	0.055	0.119	0.091	0.560	0.312	0.169
Centana	3.83	7.22	6.78	8.72	12.00	11.45	0.057	0.110	0.088	0.671	0.264	0.145
Norana	4.00	6.55	7.22	6.78	10.05	10.61	0.050	0.079	0.088	0.694	0.263	0.164
Norana Sib	3.91	6.28	6.61	7.04	8.91	8.84	0.041	0.066	0.070	0.641	0.293	0.164
Twin	4.12	6.83	8.07	6.43	11.67	12.53	0.038	0.126	0.126	0.422	0.362	0.201
Fielder	3.93	7.05	9.79	6.67	10.89	16.90	0.047	0.135	0.203	0.528	0.511	0.220
Era	3.77	7.07	7.94	6.95	12.55	13.89	0.051	0.114	0.113	0.654	0.291	0.162
Borah	4.94	8.61	6.72	6.39	13.89	12.28	0.047	0.142	0.108	0.388	0.230	0.140
Olaf	4.22	6.93	9.63	7.58	13.10	17.44	0.061	0.132	0.182	0.642	0.330	0.175
Short	6.03	9.52	19.53	5.83	13.36	22.07	0.037	0.134	0.241	0.544	0.464	0.185
Rescue												
Medium	4.84	13.92	7.33	7.13	12.50	12.18	0.043	0.137	0.107	0.384	0.184	0.181
Rescue												
Rescue	4.33	7.19	11.89	6.11	10.17	19.96	0.055	0.081	0.217	0.647	0.304	0.138
Fortuna	3.94	6.11	6.16	6.61	11.39	9.78	0.059	0.099	0.076	0.578	0.243	0.142
Tioga	4.11	5.94	6.11	7.33	10.44	11.66	0.057	0.097	0.106	0.564	0.266	0.144
Ellar	4.00	6.12	6.11	7.18	10.27	12.34	0.071	0.102	0.104	0.634	0.265	0.144
Thatcher	3.89	6.48	7.11	6.93	10.14	13.50	0.046	0.096	0.122	0.582	0.285	0.159
LSD P.05		5.26			5.25			.095			.154	

Table 4. Analysis of variance for leaf number measured on 20 spring wheat cultivars in each of three growth durations (3, 6, and 9 weeks) in a greenhouse pilot study

Source of variation	df	SS	MS	F
Total (plot)	8	785.28		
Blocks	2	68.74	34.37	NS
Growth duration		604.34	302.17	**
Error (A)	4	112.20	28.05	
Total (sub-plot)	179	2746.28		
Variety	19	381.26	20.07	*
Variety x growth duration	38	419.11	11.03	NS
Error (B)	114	1160.63	10.18	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Table 5. Analysis of variance for total root number measured on 20 spring wheat cultivars in each of three root growth durations (3, 6, and 9 weeks) in a greenhouse pilot study

Source of variation	df	SS	MS	F
Total (plot)	8	1783.56		
Blocks	2	58.32	29.16	NS
Growth duration	2	1564.56	782.28	**
Error (A)	4	160.68	40.17	
Total (sub-plot)	179	3815.33		
Variety	19	332.99	17.53	*
Variety x growth duration	38	542.49	14.27	NS
Error (B)	114	1156.29	10.14	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Table 6. Analysis of variance for root mass measured on 20 spring wheat cultivars in each of three growth durations (3, 6, and 9 weeks) in a greenhouse pilot study

Source of variation	df	SS	MS	F
Total (plot)	8	.2900		
Blocks	2	.0198	.0099	NS
Growth duration	2	.2516	.1258	**
Error (A)	4	.0185	.0046	
Total (sub-plot)	179			
Variety	19	.1230	.0065	**
Variety x growth duration	38	.1271	.0033	NS
Error (B)	114	.0023		

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Table 7. Analysis of variance for root/shoot ratio measurement on 20 spring wheat cultivars in each of three growth durations (3, 6, and 9 weeks) in a greenhouse pilot study

Source of variation	df	SS	MS	F
Total (plot)	8	5.4250		
Blocks	2	.0551	.0275	NS
Growth duration	2	5.1860	2.5930	**
Error (A)	4	0.1839		
Total (sub-plot)	179	7.2610		
Variety	19	.3807	0.0200	**
Variety x growth duration	38	.4602	0.0121	NS
Error (B)	114	.9951	0.0087	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

study because of their apparent drought tolerance and susceptibility, respectively. The mean performance of parental lines and their respective F_2 progenies, for the traits studied, are presented in Table 8 where the first three listed parents were used as males. These data were analyzed for each trait following standard analysis of variance methods for a randomized complete block design, and analysis of variance for leaf number, total root number, root mass and root/shoot ratio are presented in Tables 9, 10, 11, and 12, respectively. These tables indicate that blocking for all traits was effective, and the block differences for all traits, except leaf number, significant at 5% level, were highly meaningful.

Female parents showed highly significant differences for leaf number (Table 9), while no meaningful variation for the other traits, total root number, root mass and root/shoot ratio was detected (Tables 10, 11, and 12).

Male parents exhibited highly significant variation for all traits (Tables 9, 11, and 12), except total root number (Table 10). Note that there was no significant variation among parents for total root number (Table 10), while high ly significant variation among both the progenies of female and of male parents was detected. This might be explained in terms of a simple genetic model in which the same phenotype is caused by different genotypes that yield segregation in the F_2; such a model is presented as follows:

Table 8. Mean values for four agronomic traits scored on 12 parental lines and their 27 F_2 progenies in a greenhouse study

Parents and F_2 progenies	Leaf number	Total root number	Root mass (g/plant)	Root/shoot ratio
Fronteira	7.89	8.89	0.098	0.344
Frondoso	9.95	8.33	0.094	0.243
Oleson Dwarf	5.98	9.02	0.040	0.224
Twin	9.28	6.94	0.050	0.237
Era	7.91	7.94	0.047	0.250
Short Rescue	10.30	7.75	0.038	0.241
Medium Rescue	7.96	6.83	0.033	0.196
Rescue	8.56	7.13	0.044	0.173
Fortuna	6.45	6.89	0.036	0.154
Tioga	5.33	6.44	0.026	0.163
Ellar	7.19	8.51	0.035	0.180
Thatcher	8.09	7.24	0.036	0.212
Twin x Fronteira	8.90	8.85	0.075	0.256
Twin x Frondoso	7.70	8.40	0.068	0.257
Twin x Oleson Dwarf	5.89	8.75	0.048	0.233
Era x Fronteira	8.57	7.71	0.080	0.302
Era x Frondoso	7.88	7.84	0.075	0.287
Era x Oleson Dwarf	6.81	7.17	0.034	0.189
Short Rescue x Fronteira	9.38	7.93	0.066	0.318
Short Rescue x Frondoso	9.31	8.33	0.068	0.263
Short Rescue x Oleson Dwarf	6.49	6.05	0.028	0.228
Medium Rescue x Fronteira	8.90	8.47	0.085	0.346
Medium Rescue x Frondoso	9.78	7.70	0.083	0.364

Table 8 (continued)

Parents and F_2 progenies	Leaf number	Total root number	Root mass (g/plant)	Root/shoot ratio
Medium Rescue x Oleson Dwarf	6.60	6.59	0.038	0.200
Rescue x Fronteira	9.89	8.09	0.089	0.319
Rescue x Frondoso	8.38	6.97	0.064	0.296
Rescue x Oleson Dwarf	6.23	6.56	0.034	0.184
Fortuna x Fronteira	7.19	6.76	0.059	0.219
Fortuna x Frondoso	7.28	7.00	0.048	0.176
Fortuna x Oleson Dwarf	6.02	6.60	0.030	0.182
Tioga x Fronteira	8.76	6.91	0.071	0.228
Tioga x Frondoso	7.76	6.77	0.062	0.215
Tioga x Oleson Dwarf	6.27	6.68	0.039	0.192
Ellar x Fronteira	9.05	6.90	0.073	0.298
Ellar x Frondoso	9.17	7.00	0.060	0.207
Ellar x Oleson Dwarf	5.87	6.16	0.033	0.207
Thatcher x Fronteira	8.99	7.01	0.066	0.242
Thatcher x Frondoso	9.74	7.09	0.062	0.199
Thatcher x Oleson Dwarf	6.33	6.02	0.030	0.261
LSD P .05	2.07	1.80	0.026	0.082

Table 9. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for leaf number based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	116	360.25			
Blocks	2	14.35	7.17		*
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	52.02	6.50		**
Male parents	2	23.69	11.84		**
F_2 progenies	(26)	143.95	--		
Progenies of females	8	20.12	2.51	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	NS
Progenies of males	2	106.74	53.37	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	17.09	1.06	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	76	126.24	1.66	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$):

$\sigma^2_f = (2.51 - 1.66)/9 = .094$

$\sigma^2_m = (53.37 - 1.66)/27 = 1.915$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{2.009}{3.669} = 55\%$

Table 10. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for total root number based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	116	187.25			
Blocks	2	30.96	15.49		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	8.12	1.01		NS
Male parents	2	0.79	0.40		NS
F_2 progenies	(26)	52.47	--		
Progenies of females	8	29.68	3.71	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	**
Progenies of males	2	12.18	6.09	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	10.61	0.66	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	76	74.96	0.88	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$)

$\sigma^2_f = (3.71 - 0.99)/9 = 0.302$

$\sigma^2_m = (6.09 - 1.99)/27 = 0.189$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{0.491}{1.481} = 33\%$

Table 11. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for root mass (g/plant) based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	116	0.05965			
Blocks	2	0.00279	.00140		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	0.00137	.00017		NS
Male parents	2	0.00694	.00347		**
F_2 progenies	(26)	0.02822	--		
Progenies of females	8	0.00354	0.00044	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	*
Progenies of males	2	0.02274	0.01137	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	0.00194	0.00012	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	76	0.00810	0.00011	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$)

$\sigma^2_f = (.00044 - .00011)/9 = .000036$

$\sigma^2_m = (.01137 - .00011)/27 = .00042$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{.000456}{.000566} = 80\%$

Table 12. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for root/shoot ratio based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	116	.60032			
Blocks	2	.14876	.07438		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	.02315	.00289		NS
Male parents	2	.03413	.01706		**
F_2 progenies	(26)	.19832	--		
Progenies of females	8	.06472	.00809	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	**
Progenies of males	2	.07409	.03705	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Females × Male progenies	16	.05950	.00372	$\sigma^2_e + r\sigma^2_{m\times f}$	*
Error	76	.14577	.00192	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** = F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$)

$\sigma^2_f = (.00809 - .00372)/9 = .000485$

$\sigma^2_m = (.03705 - .00372)/27 = .001234$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{.00172}{.00544} = 32\%$

AAbb x aaBB

↓

Aa Bb

↓

1 AABB	2 AaBB	1 aaBB
2 AABb	4 AaBb	2 aaBb
1 AAbb	2 Aabb	1 aabb

where A = B

a = b

The interaction among progenies of female and progenies of male parents for all traits except for root/shoot ratio was non-significant (Tables 9, 10, 11, and 12). This may indicate that each female parent or male parent behaved the same when taken over all male or female parents. The progeny of female by the progeny of male parent interaction is a measure or estimate of variation due to non-additive genetic effects (Table 12). Since it is non-significant for leaf number, total root number, and root mass, the conclusion is that additive gene effects condition the traits.

Variance component analysis proposed by J. E. Grafius (1952a) was applied to estimate the additive components of the genetic variance for the traits studied. Narrow sense heritability for these traits was determined using mean squares from each analysis if variance as follows:

$$h^2_{(N)} = \frac{\text{Additive genetic variance}}{\text{Total or phenotypic variance}} = \frac{\sigma^2_m + \sigma^2_f}{\sigma^2_m + \sigma^2_f + \sigma^2_{m\times f} + \sigma^2_e}$$

(See the statistical model discussed on page 58).

Heritability percentages are summarized in Table 13. These show that there is relatively high fixable additive genetic variation for leaf number and root mass, and root/shoot ratio but not for total root number and root/shoot ratio. Total root number and root/shoot ratio had the lowest heritabilities, 33 and 32% respectively, while root mass had the highest narrow sense heritability (80%). Characters with high narrow sense heritability can be most readily altered through selection. This stems from the relationship $G = h^2 R$ which has been described on page 57.

Means for parents, mid-parents, and F_2 progenies, for leaf number, total root number, root mass, and root/shoot ratio, are presented in Tables 14, 15, 16, and 17, respectively. Examination of these tables indicates that not all the crosses reacted in the same way, but in general they reflect relatively higher additive than non-additive gene action; gene action and relationships between parents and mid-parents have been discussed on page 52. Non-additive gene action is apparent from heritability estimates summarized in Table 13, because, if all the genetic variance was due to the additive variance, the heritability would be 100%. Since this is not the case there must be some non-additive gene action which was not detected using the variance component model (Tables 14, 15, 16, and 17).

Mean leaf number for parents, mid-parents, and F_2 progenies is summarized in Table 14. This table shows that 15 of the 27 F_2 crosses

Table 13. Components of genetic variance and narrow sense heritability for four traits derived from 9 female and 3 male parents and their 27 F_2 progenies

Traits	Additive genetic variance σ^2_d	Phenotypic variance σ^2_p	Narrow sense heritability $h^2_{(N)}$ %
Leaf number	2.009	3.669	55
Total root number	0.491	1.481	33
Root mass (g/plant)	0.000456	0.000566	80
Root/shoot ratio	0.00172	0.00544	32

Table 14. Mean values for leaf number for each parent, the F_2 population and mid-parent (MP) values for 27 crosses derived from 9 female and 3 male parents

Crosses	$\bar{P}_1$ [1/]	$\bar{P}_2$ [1/]	$\bar{F}_2$	MP
Twin x Fronteira	9.28	7.89	8.90	8.59
Twin x Frondoso	9.28	9.95	7.70	9.62
Twin x Oleson Dwarf	9.28	5.98	5.89	7.63
Era x Fronteira	7.91	7.89	8.57	7.90
Era x Frondoso	7.91	9.95	7.88	8.93
Era x Oleson Dwarf	7.91	5.98	6.81	6.95
Short Rescue x Fronteira	10.30	7.89	9.38	9.10
Short Rescue x Frondoso	10.30	9.95	9.31	10.13
Short Rescue x Oleson Dwarf	10.30	5.98	6.49	8.14
Medium Rescue x Fronteira	7.96	7.89	8.90	7.93
Medium Rescue x Frondoso	7.96	9.95	9.78	8.96
Medium Rescue x Oleson Dwarf	7.96	5.98	6.60	6.97
Rescue x Fronteira	8.56	7.89	9.89	8.23
Rescue x Frondoso	8.56	9.95	8.38	9.26
Rescue x Oleson Dwarf	8.56	5.98	6.23	7.27
Fortuna x Fronteira	6.45	7.89	7.19	7.17
Fortuna x Frondoso	6.45	9.95	7.28	8.20
Fortuna x Oleson Dwarf	6.45	5.98	6.02	6.22
Tioga x Fronteira	5.33	7.89	8.76	6.61
Tioga x Frondoso	5.33	9.95	7.76	7.64
Tioga x Oleson Dwarf	5.33	5.98	6.27	5.66
Ellar x Fronteira	7.19	7.89	9.05	7.54
Ellar x Frondoso	7.19	9.95	9.17	8.57
Ellar x Oleson Dwarf	7.19	5.98	5.87	6.59
Thatcher x Fronteira	8.09	7.89	8.99	7.99
Thatcher x Frondoso	8.09	9.95	9.74	9.02
Thatcher x Oleson Dwarf	8.09	5.98	6.33	7.04

[1/] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

Table 15. Mean values for total root number for each parent, the F_2 population and mid-parent (MP) values for 27 crosses derived from 9 female and 3 male parents

Crosses	$\bar{P}_1$ [1/]	$\bar{P}_2$ [1/]	$\bar{F}_2$	MP
Twin x Fronteira	6.94	8.89	8.85	7.92
Twin x Frondoso	6.94	8.33	8.40	7.64
Twin x Oleson Dwarf	6.94	9.02	8.75	7.98
Era x Fronteira	7.94	8.89	7.71	8.42
Era x Frondoso	7.94	8.33	7.84	8.14
Era x Oleson Dwarf	7.94	9.02	7.17	8.48
Short Rescue x Fronteira	7.75	8.89	7.93	8.32
Short Rescue x Frondoso	7.75	8.33	8.33	8.04
Short Rescue x Oleson Dwarf	7.75	9.02	6.05	8.39
Medium Rescue x Fronteira	6.83	8.89	8.47	7.86
Medium Rescue x Frondoso	6.83	8.33	7.70	7.58
Medium Rescue x Oleson Dwarf	6.83	9.02	6.59	7.93
Rescue x Fronteira	7.13	8.89	8.09	8.01
Rescue x Frondoso	7.13	8.33	6.97	7.73
Rescue x Oleson Dwarf	7.13	9.02	6.56	8.08
Fortuna x Fronteira	6.89	8.89	6.76	7.89
Fortuna x Frondoso	6.89	8.33	7.00	7.61
Fortuna x Oleson Dwarf	6.89	9.02	6.60	7.96
Tioga x Fronteira	6.44	8.89	6.91	7.67
Tioga x Frondoso	6.44	8.33	6.77	7.39
Tioga x Oleson Dwarf	6.44	9.02	6.68	7.73
Ellar x Fronteira	8.51	8.89	6.90	8.70
Ellar x Frondoso	8.51	8.33	7.00	8.42
Ellar x Oleson Dwarf	8.51	9.02	6.16	8.77
Thatcher x Fronteira	7.24	8.89	7.01	8.07
Thatcher x Frondoso	7.24	8.33	7.09	7.79
Thatcher x Oleson Dwarf	7.24	9.02	6.02	8.13

[1/] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

Table 16. Mean values for root mass (g/plant) for each parent, the F_2 population and mid-parent (MP) values for 27 crosses derived from 9 female and 3 male parents

Crosses	$\bar{P}_1$ [1/]	$\bar{P}_2$ [1/]	$\bar{F}_2$	MP
Twin x Fronteira	0.0500	0.0978	0.0750	0.0739
Twin x Frondoso	0.0500	0.0945	0.0685	0.0723
Twin x Oleson Dwarf	0.0500	0.0399	0.0478	0.0450
Era x Fronteira	0.0470	0.0978	0.0802	0.0724
Era x Frondoso	0.0470	0.0945	0.0755	0.0708
Era x Oleson Dwarf	0.0470	0.0399	0.0343	0.0435
Short Rescue x Fronteira	0.0376	0.0978	0.0657	0.0677
Short Rescue x Frondoso	0.0376	0.0945	0.0680	0.0661
Short Rescue x Oleson Dwarf	0.0376	0.0399	0.0277	0.0388
Medium Rescue x Fronteira	0.0335	0.0978	0.0851	0.0657
Medium Rescue x Frondoso	0.0335	0.0945	0.0831	0.0640
Medium Rescue x Oleson Dwarf	0.0335	0.0399	0.0377	0.0367
Rescue x Fronteira	0.0443	0.0978	0.0893	0.0711
Rescue x Frondoso	0.0443	0.0945	0.0644	0.0694
Rescue x Oleson Dwarf	0.0443	0.0399	0.0341	0.0421
Fortuna x Fronteira	0.0356	0.0978	0.0595	0.0667
Fortuna x Frondoso	0.0356	0.0945	0.0481	0.0651
Fortuna x Oleson Dwarf	0.0356	0.0399	0.0298	0.0378
Tioga x Fronteira	0.0259	0.0978	0.0707	0.0619
Tioga x Frondoso	0.0259	0.0945	0.0622	0.0602
Tioga x Oleson Dwarf	0.0259	0.0399	0.0394	0.0329
Ellar x Fronteira	0.0350	0.0978	0.0731	0.0664
Ellar x Frondoso	0.0350	0.0945	0.0605	0.0648
Ellar x Oleson Dwarf	0.0350	0.0399	0.0329	0.0375
Thatcher x Fronteira	0.0358	0.0978	0.0660	0.0668
Thatcher x Frondoso	0.0358	0.0945	0.0618	0.0652
Thatcher x Oleson Dwarf	0.0358	0.0399	0.0315	0.0379

[1/] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

Table 17. Mean values for root/shoot ratio for each parent, the F_2 population and mid-parent (MP) values for 27 crosses derived from 9 female and 3 male parents

Crosses	$\bar{P}_1$ [1]	$\bar{P}_2$ [1]	$\bar{F}_2$	MP
Twin x Fronteira	.237	.344	.256	.290
Twin x Frondoso	.237	.243	.257	.240
Twin x Oleson Dwarf	.237	.224	.233	.230
Era x Fronteira	.250	.344	.302	.297
Era x Frondoso	.250	.243	.287	.246
Era x Oleson Dwarf	.250	.224	.189	.237
Short Rescue x Fronteira	.241	.344	.318	.292
Short Rescue x Frondoso	.241	.243	.263	.242
Short Rescue x Oleson Dwarf	.241	.224	.228	.232
Medium Rescue x Fronteira	.196	.344	.346	.270
Medium Rescue x Frondoso	.196	.243	.295	.219
Medium Rescue x Oleson Dwarf	.196	.224	.200	.210
Rescue x Fronteira	.173	.344	.319	.258
Rescue x Frondoso	.173	.243	.296	.208
Rescue x Oleson Dwarf	.173	.224	.184	.198
Fortuna x Fronteira	.154	.344	.219	.249
Frotuna x Frondoso	.154	.243	.176	.198
Fortuna x Oleson Dwarf	.154	.224	.182	.189
Tioga x Fronteira	.163	.344	.228	.253
Tioga x Frondoso	.163	.243	.215	.203
Tioga x Oleson Dwarf	.163	.224	.192	.193
Ellar x Fronteira	.180	.344	.298	.262
Ellar x Frondoso	.180	.243	.207	.211
Ellar x Oleson Dwarf	.180	.224	.207	.202
Thatcher x Fronteira	.212	.344	.242	.278
Thatcher x Frondoso	.212	.243	.199	.227
Thatcher x Oleson Dwarf	.212	.224	.261	.218

[1] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

exhibited predominantly additive gene action. Ten of these 15 crosses, because their F_2 means are near the values for the mid-parent, indicate high additive gene action, and the remaining 5 crosses, though within the parental ranges, are distributed near low or high parents. These crosses may contribute less to the heritability of the trait. Data summarized in Table 14 indicate that 12 of F_2 means show transgressive patterns of segregation. In spite of the non-significant progeny of female x progeny of male parent interaction (Table 9), comparison of parents, mid-parent and F_2 means for individual crosses suggests a complex form of gene action. All parents except Fortuna were involved in transgressive F_2 populations, Fronteira and Frondoso were most frequently involved (4 cases each). This suggests that these two parents may account for much of the non-additive variation in leaf number. In a breeding program, populations derived from crosses involving these or related parents might not respond rapidly to selection. However, based on considerable additive gene action among crosses and because there is no significant interaction between the progenies of female and male parents, it could be concluded that this trait could be selected for in early generations.

Higher root numbers have been reported to contribute to drought resistance. Hurd (1974) indicated that Thatcher and Pelissier, two drought resistant spring wheat cultivars, had higher root number than 'Cyprus,' the less drought resistant cultivar. Resistance of sorghum

to drought has also been thought to be due to higher root number (Mitchell, 1970). Table 15 shows the prepotency of parents in their respective F_2 progenies. Most of the crosses in this table show an apparent transgressive pattern of segregation. Only a few crosses, such as Medium Rescue x Frondoso and Rescue x Fronteira exhibited additive gene action (Table 15).

Since not many F_2 means fall at or near mid-parent, this trait shows a relatively low narrow sense heritability (33%) which is a measure of the extent of additive gene action (Table 13). However, this low heritability could not be necessarily attributed to non-additive gene action. Firstly, because of non-significant interaction between the progeny of female parents and progeny of male parents; secondly, no significant difference between parents and their respective F_2 progenies could be detected. This suggests minimal genetic variation. Another logical explanation is high error effects in scoring root number. This might mask genetic differences. Regardless, selection might be of limited effectiveness due to low narrow sense heritability. Because this trait is conditioned by low additive gene action, it can be concluded that a straight mass selection program for this trait may not be an effective method to alter root number in offspring; some other breeding program, such as a hybrid program, should be employed.

High heritability of root mass is shown in Table 13. This table indicates that over 80% of the phenotypic variability, for root mass among cultivars, is attributable to additive gene effects.

The quantitative values of root mass for high parent, low parent, mid-parent and F_2 populations are shown in Table 16. Note that, based on the relationships between parents, F_2 means and mid-parent values for each cross, 19 of 27 crosses exhibited additive gene action; this reflects the high $h^2_{(N)}$ value for this trait. This result is in agreement with Openheimer (1960) that the greater root growth in plant species is a heritable character, with Hurd (1974) who indicated that dense root systems were highly heritable, and with Keller (1953), Ray et al. (1974) and Sullivan and Eastin (1974) that genetic differences for root mass between plants at species and cultivar levels existed. Table 16 also shows that in only 5 crosses were the F_2 values slightly larger than mid-parents. This suggests dominant gene action which is also a component of total genetic variance.

In three crosses, involving 'Era,' 'Short Rescue,' and Fortuna as female parents and 'Oleson Dwarf' as the male parent, the progenies produced slightly less than the low parents. However, the root mass of the parents in these crosses were so much alike that the apparent transgressive segregation of F_2 progenies could have resulted from experimental error rather than negative over dominance. Because the pattern was uniquely associated with crosses involving Oleson Dwarf, the

possibility of a specific gene effect, non-additive, presumptively epistatic, cannot be discounted. The high heritability suggests great potential for gain from selection for root mass.

Narrow sense heritability of the root/shoot ratio was estimated to be approximately 32% (Table 13). Although this is not a relatively high heritability, it may be used as a criterion for selection for drought resistance. According to Sandu and Laude (1958) drought and heat hardy plants have higher root/shoot ratios than susceptible ones, but this is a selective criterion which could be affected by environmental factors such as light, nutrient, and temperature (Pearson, 1974). Comparison of parents, F_2 means and mid-parents indicate that over 65% of the means of F_2 progenies show additive gene action (Table 17). In only one-third (9 crosses) of the crosses did the mean of the F_2, possibly due to non-additive gene action (Table 12), exceed those of parental lines (Table 17).

Traits such as leaf number, total root number, root mass and root/shoot ratio which are reported to be associated with drought tolerance in wheat plants are complex. Each of these characters could be the end product of the effects of many genes. In such a case, it is a common practice to evaluate heritability in order to breed effectively for these traits. If a trait has high heritability, it should be select for in early generations.

Evaluation of these traits in diverse parental lines and their 27 possible crosses, on the basis of performance of the bulked F_2 progenies, were made to estimate heritabilities. Modes of gene action, additive and non-additive, that were speculated to indicate the parental prepotency, were confirmed fairly well by their respective narrow sense heritabilities that are summarized in Table 13, and by parent, mid-parent, and F_2 relationships (Tables 14, 15, 16, and 17).

High heritability indicates higher additive genetic variance while lower heritability could reflect higher non-additive, dominance and epistatic, components of genetic variance or sensitivity to environmental effects. The non-additive portion of total genetic variance, from the plant breeder's point of view, is of lesser value, because the effects of intra- and inter-allelic gene action reduce the effectiveness of direct selection in early generations. In later generations, non-additive effects may be fixed and of lesser concern so long as large populations are carried throughout the breeding program. On the other hand, traits with relatively high additive genetic variance, such as root mass, and leaf number (Table 13) are fixable and could be altered through a straight selection program. Traits with lower additive genetic variance such as total root number and root/shoot ratio (Table 13) could not be easily fixed with such a simple early generation selection program. Therefore, some more sophisticated breeding methods should be formulated, because the proportion of

crosses, in a randomly mating population, for example, with higher root mass would be higher than those crosses with low root mass.

Thus, it could be concluded that traits with higher additive components of genetic variance will be highly heritable and may be less sensitive to the environmental fluctuations; as Sallan (1961) claimed, factors contributing to drought resistance could be selected for and used in breeding programs.

One additional point must be stressed. Traits such as leaf number and root mass are themselves complex. Heritability estimates reflect the total gene effects for components and component interaction. A trait such as root/shoot ratio is even more complex. Although the ratio is expressed as a single value, the inheritance of this trait is a complex function of the inheritance of roots and of shoots, both of which are complex. The heritability is more than an average of the values for the components, but methods available do not permit analysis of genes for only the ratio. The heritability estimate, thus, is a tool of potential value to the plant breeder, but it does not afford a meaningful level of fundamental genetic resolution.

Experiments along this line need to be continued with the inclusion of parents, F_1, F_2, and F_3 generations to substantiate the results that were obtained. As was the case for root mass, once again,

it would appear that Oleson Dwarf might represent a unique genotype in terms of specific combining ability. This also merits further study.

Rate of Root Elongation

The rates of root elongation of 20 spring wheat cultivars were evaluated by the method proposed by Maguire (1962) and cultivar means are presented in Table 18. Fortuna, Centana, Tioga, and Olaf with rates of elongation indices, 6.52, 6.38, 6.27, and 6.08, respectively, were fast growing. Cultivars in the Rescue group (Short Rescue, Medium Rescue, and Rescue) with indices 3.17, 4.60, and 4.52, respectively, were slower growing.

Analysis of rate of root elongation data of the cultivars is shown in Table 19. Highly significant differences among cultivars were detected. Cultivar differences in rate of root penetration into the soil have been reported to be due to genetic variability (Derera et al., 1968; Black, 1968; Burton, 1954). Therefore, the highly significant variance ratio may reflect the genetic differences among the 20 spring wheat cultivars studied.

Analysis of variance among 27 major groups, each consisting of a male parent, a female parent, and their F_1 and F_2 progenies, is shown in Table 20. There are highly significant differences between the replications (runs). Blocking was effective in reducing error.

Table 18. Rate of root elongation in 20 spring wheat cultivars in a growth chamber pilot study (indices according to Maguire 1962)

No.	Cultivar	Rate of root elongation	No.	Cultivar	Rate of root elongation
1	Fronteira	5.98	11	Era	5.90
2	Frondoso	5.12	12	Borah	5.47
3	Oleson Dwarf	5.95	13	Olaf	6.08
4	Short Centana	5.55	14	Short Rescue	3.17
5	Shortana	5.77	15	Medium Rescue	4.60
6	Centana	6.38	16	Rescue	4.52
7	Norana	4.12	17	Fortuna	6.52
8	Norana sib	5.16	18	Tioga	6.27
9	Twin	5.44	19	Ellar	4.67
10	Fielder	5.40	20	Thatcher	5.58

LSD .05 = 1.35

Table 19. Analysis of variance of rate of root elongation indices of 20 spring spring wheat cultivars

Source of variation	df	SS	MS	F
Total	39	34.72		
Cultivar	19	26.28	1.383	**
Error	20	8.48	.422	

Table 20. Analysis of variance for rate of root elongation indices among 27 major groups, each group consisted of a male and a female parent and their respective F_1 and F_2 progenies

Source of variation	df	SS	MS	F
Total	215	198.453		
Replication (run)	1	61.304	61.304	**
Treatment (group)	26	124.847	4.803	**
Error	188	12.302	.065	

Apparently this trait is highly sensitive to small environmental fluctuations.

The F ratio among the groups was statistically highly significant, and thus it could explain genetic differences that exist among the groups. These differences have a potential for scientists interested in breeding for drought resistance. Thus, selection of crosses for higher rate of root penetration may result in increased drought resistance and successful seedling establishment, because, according to Hurd (1964,1968,1971), rapid rate of root penetration is indispensible for drought resistance.

The mean rate of root elongation indices for the parental lines, F_1 and F_2 populations, in the extended study, are shown in Table 21. Note that F_1 progenies rated relatively low compared with parents and F_2 progenies. The order of parental lines and their F_1 and F_2 populations for root elongation indices were as follows: female parents (3.99) > male parents (3.80) > F_2 progenies (3.68) > F_1 progenies (3.58)(Table 21).

Oleson Dwarf, from the male parents, and Twin, from the female parents, have the highest rate of root elongation indices with 4.79 and 5.03, respectively (Table 21). Frondoso, from the male parents, and Rescue and Short Rescue, from the female parents with 3.17, 3.05, and 3.10 were slow grading cultivars (Table 21).

Table 21. Rate of root elongation indices and 100 kernel weight of 12 spring wheat cultivars (9 female and 3 male parents) and 27 F_1 and F_2 progenies

Parents + F_1 and F_2 progenies	Rate of root elongation	100 kernel wt. (g)
Male parents		
Frontiera	3.46	3.86
Frondoso	3.17	3.22
Oleson Dwarf	4.79	3.59
Mean	3.80	
Female parents		
Twin	5.03	2.95
Era	4.10	3.13
Short Rescue	3.10	2.53
Medium Rescue	4.16	3.06
Rescue	3.05	3.35
Fortuna	4.14	4.45
Tioga	4.22	4.10
Ellar	4.15	3.87
Thatcher	3.93	2.87
Mean	3.99	
F_1 progenies		
Twin x Fronteira	2.54	1.65
Twin x Frondoso	4.05	1.64
Twin x Oleson Dwarf	4.50	1.98
Era x Fronteira	3.26	2.10
Era x Frondoso	2.59	2.13
Era x Oleson Dwarf	3.60	2.51
Short Rescue x Fronteira	3.07	2.04
Short Rescue x Frondoso	1.93	2.19
Short Rescue x Oleson Dwarf	4.87	2.32
Medium Rescue x Fronteira	2.89	3.06
Medium Rescue x Frondoso	3.40	2.08
Medium Rescue x Oleson Dwarf	4.70	3.24
Rescue x Fronteira	3.20	2.03
Rescue x Frondoso	2.63	1.99

Table 21 (continued)

Parents + F_1 and F_2 progenies	Rate of root elongation	100 kernel wt. (g)
Rescue x Oleson Dwarf	4.80	2.13
Fortuna x Fronteira	2.88	1.87
Fortuna x Frondoso	3.77	2.70
Fortuna x Oleson Dwarf	4.49	2.96
Tioga x Fronteira	3.63	2.34
Tioga x Frondoso	4.11	2.20
Tioga x Oleson Dwarf	4.13	2.45
Ellar x Fronteira	3.54	2.47
Ellar x Frondoso	3.91	2.75
Ellar x Oleson Dwarf	3.81	2.12
Thatcher x Fronteira	2.79	2.14
Thatcher x Frondoso	3.55	2.05
Thatcher x Oleson Dwarf	3.89	2.43
Mean	3.58	
F_2 progenies		
Twin x Fronteira	2.78	4.02
Twin x Frondoso	3.06	3.84
Twin x Oleson Dwarf	4.50	3.82
Era x Fronteira	3.58	4.03
Era x Frondoso	3.05	3.69
Era x Oleson Dwarf	3.55	3.55
Short Rescue x Fronteira	3.18	3.15
Short Rescue x Frondoso	2.44	3.38
Short Rescue x Oleson Dwarf	3.81	1.95
Medium Rescue x Fronteira	2.80	3.56
Medium Rescue x Frondoso	3.66	3.59
Medium Rescue x Oleson Dwarf	3.93	2.37
Rescue x Fronteira	2.87	3.58
Rescue x Frondoso	3.15	3.74
Rescue x Oleson Dwarf	4.50	3.44
Fortuna x Fronteira	3.90	3.90
Fortuna x Frondoso	4.03	3.91
Fortuna x Oleson Dwarf	4.20	3.45
Tioga x Fronteira	3.62	3.73
Tioga x Frondoso	4.20	3.74
Tioga x Oleson Dwarf	4.32	3.76
Ellar x Fronteira	4.05	3.76

Table 21 (continued)

Parents + F_1 and F_2 progenies	Rate of root elongation	100 kernel wt. (g)
Ellar x Frondoso	3.94	3.62
Ellar x Oleson Dwarf	4.20	3.17
Thatcher x Fronteira	3.68	3.74
Thatcher x Frondoso	3.82	3.53
Thatcher x Oleson Dwarf	4.45	3.68
Mean	3.68	

In general, all the crosses, F_1 and F_2, involving Oleson Dwarf as the male parent, rated higher for rate of root elongation than the crosses where Fronteira and Frondoso were used as the male parents (Table 21). The more slowly growing crosses, both in F_1 and F_2, were Twin x Frondoso and Short Rescue x Frondoso. This may mean that a unique pattern of gene action is controlling the rate of root elongation. The correlation coefficient ($r = .19$) between seed weight and rate of root elongation was non-significant, perhaps due to all seeds being in the optimum seed size range. This may indicate that there is little or no association between these two plant characteristics for seed sizes in the range of this study. Derwyn et al. (1966), on the other hand, reported that growth rate of several grass species was higher when heavier seeds were used.

Analysis of variance for rate of root elongation indices of parental lines, F_1 and F_2 progenies, are presented in Tables 22 and 23. There are highly significant block (run) differences; blockings increased the precision of the experiment. More variation among male parents than among female parents was detected (Tables 22 and 23); however, in the F_1 study, variation among both male and female parents was non-significant (Table 22). On the other hand, male parents in F_2 crosses were statistically different at the 5% level of significance (Table 23).

Table 22. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for rate of root elongation indices based on 9 female and 3 male parents and their 27 F_1 progenies

Source of variation	df	SS	MS		F
Total	77	92.13			
Blocks (runs)	1	19.53	19.53		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	5.89	0.74		NS
Male parents	2	3.00	1.50		NS
F_1 progenies	(26)	29.97	--		
Progenies of females	8	3.03	0.38	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	NS
Progenies of males	2	15.07	7.53	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	11.87	0.74	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	38	31.33	0.82	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$):

$\sigma^2_f = (0.38 - .82)/6 = -.073$

$\sigma^2_m = (7.53 - .82)/18 = .373$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{.300}{1.12} = 26\%$

Table 23. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for rate of root elongation indices based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	77	83.59			
Blocks (runs)	1	35.67	35.67		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	5.89	0.74		NS
Male parents	2	3.00	1.50		*
F_2 progenies	(26)	17.51	--		
Progenies of females	8	6.03	0.75	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	NS
Progenies of males	2	6.45	3.23	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	5.03	0.31	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	38	20.27	0.53	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$):

$\sigma^2_f = (.75 - .53)/6 = .0367$

$\sigma^2_m = (3.23 - .53)/18 = .1500$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} + \frac{.1867}{.7167} = 26\%$

F ratios for among the progenies of female parents, in both F_1 and F_2 crosses, are non-significant (Tables 22 and 23), while for among the progeny of male parents they are statistically significant at the 1% level of probability (Tables 22 and 23). This is indicative of genetic variability among the progenies of male parents.

No significant interaction between progenies of female and male parents was detected (Tables 22 and 23). This indicates that either males respond in the same manner to all females, or the reverse. Thus, no significant non-additive genetic variation was detected. The nature of inheritance did not change between F_1 and F_2. That is, the inclusion of the segregating (F_2) generation did not expose any form of gene action not apparent in the F_1. From this it appears that F_1 analysis is not more, or less, effective than F_2 analysis. Since developing large numbers of F_2 seeds is far easier than developing F_1 seeds, in the future genetic analysis for this and similar traits could be done more efficiently using F_2's.

Heritabilities based on both F_1 and F_2 crosses were obtained by determining the proportion of additive to the phenotypic variance, and found to be approximately 26% in both generations. These estimates indicate how much progress could be made through direct selection and also how they can be used as a guide to determine the best type of selection program.

Narrow sense ($h^2_{(N)}$) heritabilities for this trait are relatively low. This may indicate that rapid progress through a simple straight mass selection program, in early generation for this trait, could not be effective due to low heritabilities. With dominance, selection should be based on progeny tests; with other non-additive, epistatic types of inheritance, generally, early generation selection is not markedly effective. Thus, progress from selection for rate of root elongation because of its low heritability, will be slow.

Mean performance of parental lines, mid-parent values, F_1 and F_2 progenies are presented in Table 24. Eleven of the 27 F_1 crosses and 13 of the 27 F_2 crosses which fall within the parental ranges reflected predominantly the additive component of genetic variability (Table 24). Note that not many of these 27 crosses fall at or near mid-parent. They are either closer to or exceed low or high parents. This is reflected in the low heritability estimates (Tables 22 and 23). Table 24 indicates that the means of 16 F_1's and 14 F_2's are transgressive, the mean rates of root elongation of progenies exceed those of parents. Because there is no progeny of female by progeny of male parent interaction, and because there are no significant differences between these crosses and their respective low or high parents (Table 24), the transgressive segregation of these crosses is not explained nor identified by the variance component analysis.

Table 24. Mean values for rate of root elongation indices for each parent, the F_1 and F_2 populations and mid-parent (MP) values for 27 crosses derived from 9 females and 3 male parents

Crosses	$\bar{P}_1$ [1/]	$\bar{P}_2$ [1/]	$\bar{F}_1$	$\bar{F}_2$	MP
Twin x Fronteira	5.26	3.03	2.54	2.78	4.15
Twin x Frondoso	4.89	3.58	4.06	3.07	4.24
Twin x Oleson Dwarf	4.94	5.55	4.51	5.00	5.25
Era x Fronteira	4.54	3.84	3.26	3.59	4.19
Era x Frondos	3.77	2.40	2.59	3.05	3.09
Era x Oleson Dwarf	4.00	4.71	3.60	3.55	4.36
Short Rescue x Fronteira	3.61	3.28	3.08	3.18	3.45
Short Rescue x Frondoso	2.11	2.72	1.93	2.44	2.42
Short Rescue x Oleson Dwarf	3.59	4.74	4.87	3.82	4.17
Medium Rescue x Fronteira	4.36	3.34	2.89	2.80	3.85
Medium Rescue x Frondoso	3.78	3.60	3.40	3.66	3.69
Medium Rescue x Oleson Dwarf	4.33	5.21	4.70	3.93	4.77
Rescue x Fronteira	2.78	2.71	3.20	2.87	2.75
Rescue x Frondoso	2.51	2.55	2.63	3.15	2.53
Rescue x Oleson Dwarf	3.87	5.23	5.30	4.51	4.55
Fortuna x Fronteira	4.00	3.82	2.88	3.90	3.91
Fortuna x Frondoso	4.10	2.98	3.77	4.03	3.54
Fortuna x Oleson Dwarf	4.32	4.57	4.99	4.20	4.45
Tioga x Fronteira	4.18	4.22	3.63	3.62	4.20
Tioga x Frondoso	4.87	4.00	4.11	4.20	4.44
Tioga x Oleson Dwarf	3.63	4.63	4.13	4.33	4.13
Ellar x Fronteira	4.30	2.92	3.54	4.05	3.61
Ellar x Frondoso	4.62	2.84	3.91	3.94	3.73
Ellar x Oleson Dwarf	3.55	4.36	3.81	4.20	3.96
Thatcher x Fronteira	4.21	4.05	2.79	3.69	4.13
Thatcher x Frondoso	3.80	3.89	3.55	3.83	3.85
Thatcher x Oleson Dwarf	3.80	4.06	3.89	4.45	3.93

[1/] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

Speed of Germination Under a Simulated Drought Stress

Rate and percentage of germination of three spring wheat cultivars evaluated in the preliminary study under simulated drought stress are shown in Table 25. Because of the extreme range of percent levels, probability levels based on the analysis of variance may be biased. No adjustments or transformations were made to account for this possibility.

Analysis of variance of the rate of germination of three cultivars under drought conditions (Table 26) indicates significant variation among means of the cultivars studied. It is also apparent that interaction of cultivar by osmotic potential is non-significant. This means that cultivars, under different osmotic potentials, behave in a consistent manner with respect to osmotic potential.

The cumulative percentage of germination of these cultivars (Table 27) indicates that they differ in their ability to germinate in solutions representing different osmotic potential. Thatcher germinated more rapidly under all conditions and had a germination of 55% the third day, compared to 32 and 19% for Short Rescue and Fortuna, respectively.

Thatcher, which is drought tolerant, had the highest total germination at the end of 14 days, under 12 and 24 atmosphere osmotic potentials (Table 27); although the germination of Thatcher was

Table 25. Mean rate and percentage germination of 3 spring wheat cultivars germinated in solutions representing three osmotic potentials (O.P.)

Cultivar	Rate of Germination (indices)			Percent Germination		
	Zero O.P.	12 O.P.	24 O.P.	0 atm O.P.	12 atm O.P.	24 atm O.P.
Short Rescue	28.9	3.4	.02	89.3	52.7	0.7
Fortuna	26.6	3.6	.03	99.3	60.7	0.7
Thatcher	37.9	8.5	.76	98.0	93.3	16.7

Table 26. Analysis of variance of rate of germination (indices) of three spring wheat cultivars in solutions representing three osmotic potentials

Source of variation	df	SS	MS	F
Total	26	5665.47	--	--
Blocks	2	128.21	64.11	NS
Treatments	(8)	(5216.45)	652.06	**
Variety	2	170.14	85.07	*
O.P.	2	4953.94	2476.96	**
Cultivar x O.P.	4	92.37	23.09	NS
Error	16	320.81	20.05	--

NS - non-significant
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Table 27. Cumulative germination percentage for three cultivars of spring wheat, each grown in three solutions of different osmotic potential for a 14 day period

Day of Study	Cultivars								
	Thatcher	Fortuna	Short Rescue	Thatcher	Fortuna	Short Rescue	Thatcher	Fortuna	Short Rescue
	0 atm.			12 atm.			24 atm.		
1									
2									
3	55.3	19.3	32.7						
4	92.6	69.3	73.9						
5	97.3	88.0	82.6	3.3		0.7			
6	98.0	96.7	89.3	23.3		2.7			
7		99.3		43.3	3.3	4.0			
8				59.3	10.0	6.0			
9				74.6	15.3	21.3	0.7		
10				83.3	25.3	29.3	1.3		
11				88.7	32.7	34.0	1.3		
12				92.0	43.3	42.0	3.3		
13				92.6	54.6	43.0	8.7	.7	
14				93.3	60.7	52.7	16.7	.7	.7

affected seriously when osmotic potential was increased from 12 to 24 atmospheres (Table 27).

All cultivars germinated in a similar pattern at "0" osmotic potential. Germination started at the third day and was completed by the sixth, except for Fortuna which changed from 97 to 99% from the sixth to seventh day. At the highest osmotic level, only Thatcher showed significant germination, and germination was not evident until the ninth day; only 17% of the seeds germination within 14 days. For both Short Rescue and Fortuna, less than 1% of the seeds germinated; germination was evident on the fourteenth and thirteenth day, respectively. Cultivar differences with respect to osmotic potential were more evident at 12 atmosphere osmotic potential. Visible germination was evident for Thatcher and Short Rescue on the fifth day, but Thatcher germinated more rapidly, by the eighth day, germination for Thatcher was 59% and for Short Rescue only 10%. At the end of 14 days, the values were 93 and 53%, respectively. Fortuna started later (seventh day) and was slower, but total germination of Fortuna was greater than for Short Rescue, 61 and 53%, respectively.

Rate of germination of all cultivars decreased as the osmotic potential of the solutions increased (Table 25); however, Thatcher had the highest germination rate under conditions of both 12 and 24 atmosphere osmotic potentials.

Although laboratory results cannot be compared directly with field conditions, cultivars reacted differently under induced stress conditions that simulated drought, and percentage and rate of germination were greatly retarded. These results are in agreement with Kaul (1966) and McGinnies (1960). It can be concluded that Thatcher germinates better than Short Rescue and Fortuna under simulated drought conditions; thus, Thatcher logically could be expected to be more drought tolerant than either Short Rescue or Fortuna.

Data indicate that rate of germination was reduced as the concentration of the germination medium increased from zero to 12 atm. osmotic potential; rate of germination was highest in the control, followed by the 12 atm. osmotic potential (Table 28). But, when osmotic potential increased to 24 atmospheres, none of the treatments, parents, F_1 and F_2 populations, could meet the criteria set for germination. Thus, no measurement was taken under 24 atmospheres osmotic potential. Reduced rate of germination under higher osmotic concentration is in full agreement with Tadmore et al. (1969), Helmerick and Pfeiffer (1954), Herbel and Sosebee (1969) and McGinnies (1960) that increased moisture stress induced by D-mannitol delayed germination and reduced rate of germination in several range grasses. A significant positive correlation coefficient, $r = .55$ ($r^2 \simeq .30$), between the rate of germination at zero and 12 atmospheres osmotic potential was obtained; thus, there is a similar pattern of response of the parents,

Table 28. Rate of germination (indices) of 12 spring wheat cultivars (9 female and 3 male parents) and 27 F_1 and F_2 progenies under zero, and twelve atm osmotic potentials and 100 kernel weight

Parents + F_1 and F_2 progenies	Average rate of germination 0 O.P.	12 O.P.	100 kernel wt. (g)
male parents			
Fronteira	18.22	1.82	3.86
Frondoso	12.96	2.05	3.44
Oleson Dwarf	18.55	2.99	3.58
female parents			
Twin	22.45	4.96	2.49
Era	20.40	3.34	3.01
Short Rescue	18.45	3.74	2.35
Medium Rescue	17.85	3.09	2.75
Rescue	17.80	2.54	2.91
Fortuna	14.85	2.22	4.19
Tioga	13.73	2.81	3.76
Ellar	15.74	4.73	3.61
Thatcher	20.99	3.86	2.35
F_1 progenies			
Twin x Fronteira	22.67	3.99	1.65
Twin x Frondoso	20.87	2.37	1.64
Twin x Oleson Dwarf	24.70	5.62	1.98
Era x Fronteira	19.73	3.11	2.100
Era x Frondoso	21.67	2.48	2.130
Era x Oleson Dwarf	29.17	4.03	2.51
Short Rescue x Fronteira	15.84	2.33	2.04
Short Rescue x Frondoso	21.44	2.12	2.19
Short Rescue x Oleson Dwarf	21.71	4.32	2.32
Medium Rescue x Fronteira	19.88	4.40	3.051
Medium Rescue x Frondoso	17.81	3.17	2.081
Medium Rescue x Oleson Dwarf	21.95	3.57	3.240
Rescue x Fronteira	22.37	4.03	2.031
Rescue x Frondoso	21.67	3.92	1.99

Table 28 (continued)

Parents + F_1 and F_2 progenies	Average rate of germination 0 O.P.	Average rate of germination 12 O.P.	100 kernel wt. (g)
Rescue x Oleson Dwarf	18.97	4.29	2.13
Fortuna x Fronteira	11.57	0.0	1.87
Fortuna x Frondoso	32.02	0.70	2.70
Fortuna x Oleson Dwarf	19.12	3.50	2.96
Tioga x Fronteira	8.00	0.91	2.34
Tioga x Frondoso	17.85	1.61	2.20
Tioga x Oleson Dwarf	20.31	2.47	2.45
Ellar x Fronteira	20.80	5.05	2.47
Ellar x Frondoso	21.56	4.20	2.75
Ellar x Oleson Dwarf	21.05	4.68	2.12
Thatcher x Fronteira	20.25	4.49	2.14
Thatcher x Frondoso	19.76	3.81	2.05
Thatcher x Oleson Dwarf	19.15	4.68	2.43
F_2 progenies			
Twin x Fronteira	19.46	.80	4.02
Twin x Frondoso	19.50	1.44	3.84
Twin x Oleson Dwarf	23.13	6.01	3.82
Era x Fronteira	17.29	2.70	4.03
Era x Frondoso	19.18	3.13	3.69
Era x Oleson Dwarf	18.38	4.98	3.55
Short Rescue x Fronteira	21.87	2.67	8.15
Short Rescue x Frondoso	21.10	3.33	3.38
Short Rescue x Oleson Dwarf	24.63	8.49	1.95
Medium Rescue x Fronteira	17.40	2.44	3.56
Medium Rescue x Frondoso	16.82	2.66	3.59
Medium Rescue x Oleson Dwarf	20.08	5.02	2.37
Rescue x Fronteira	19.70	3.77	3.58
Rescue x Frondoso	19.92	3.43	3.74
Rescue x Oleson Dwarf	20.96	4.56	3.44
Fortuna x Fronteira	18.40	1.76	3.90
Fortuna x Frondoso	16.81	2.56	3.91
Fortuna x Oleson Dwarf	19.58	1.25	3.45
Tioga x Fronteira	19.81	3.34	3.74
Tioga x Frondoso	18.98	3.34	3.74

Table 28 (continued)

Parents + F_1 and F_2 progenies	Average rate of germination 0 O.P.	12 O.P.	100 kernel wt. (g)
Tioga x Oleson Dwarf	21.17	3.68	3.76
Ellar x Frontiera	19.95	2.54	3.76
Ellar x Frondoso	20.12	3.43	3.62
Ellar x Oleson Dwarf	24.07	7.11	3.17
Thatcher x Fronteira	18.89	2.89	3.74
Thatcher x Frondoso	20.66	3.86	3.53
Thatcher x Oleson Dwarf	20.55	3.44	3.68

F_1 and F_2 populations to zero and 12 atmosphere osmotic potential, although means differed in response to osmotic conditions.

Rate of germination of F_1 and F_2 populations, involving Oleson Dwarf as the male parent, were higher both at zero and at 12 atmospheres, compared with the other male parent. Oleson Dwarf and Frontiera from the male group and Twin, Era, Short Rescue, and Thatcher from the female group (Table 28) germinated faster than the rest. This is also true under 12 atmospheres where Oleson Dwarf had a higher rate of germination than Fronteira and Frondoso; Twin, Era, Short Rescue, and Thatcher scored higher in rate of germination than the rest of the female parents (Table 28). The rate of germination of Ellar, a faster germinating cultivar under 12 atmospheres, due to fungal infection under zero atmospheres, scored low.

F_1 crosses of Fortuna x Fronteira, under zero and 12 atmospheres, and Fortuna x Frondoso, under 12 atmospheres, and F_1 and F_2 populations of Tioga x Fronteira and Tioga x Frondoso under both concentrations rated poorly (Table 28). This was probably due to the fungal infection. It seems that when seeds lie in the medium without adequate moisture for germination, they may be subject to fungal damage. Hunter and Erickson (1952) reported that when corn, rice, soybean, and sugar beet seeds were in a soil at or near wilting point that is not moist enough for the seeds to germinate, seeds will be covered by the mycelia of fungi. They believe that the imbibed seeds that are not

able to germinate, remain moist, tender and fleshy and thus are apt to be attacked by fungi which cause decay. Kernel weight of the parents, F_1 and F_2 crosses and their respective rates of germination, both at zero and 12 osmotic potential, were correlated. Correlation coefficients and coefficients of determination of seed weight and rate of germination under zero osmotic pressure were 0.20 and 0.04 and under 12 osmotic pressure were -0.20 and 0.04, respectively. Although correlation coefficients were statistically significant, only 4% of the total variation in the rate of germination of parents, F_1 and F_2 progenies is attributable to seed size, 96% of the variation is not linearly related to seed size. This result is not in full agreement with Derwyn et al. (1966) that larger seeds in grass give rise to earlier radicle emergence under adverse conditions and with Fransen and Cooper (1976) that larger seeds in sainfoin (*Onobrychis* spp.) emerged more rapidly than smaller seeds, and with Kittock and Law (1968) that germination was positively associated with seed weight in wheat. Low correlation coefficient values could have resulted from the optimum range, rather than extreme range, of seed sizes used in the experiment. In such a condition, a low correlation coefficient value is to be expected.

The analysis of variance of rate of germination for F_1 and parental lines under distilled water are shown in Table 29. There were no significant differences between blocks and among female and male

Table 29. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for speed of germination indices at "0" atmosphere osmotic potential based on 9 female and 3 male parents and their 27 F_1 progenies

Source of variation	df	SS	MS	EMS	F
Total	77	1588.11			
Blocks	1	0.38	.38		NS
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_1 progenies	1	--	--		
Female parents	8	136.20	17.02		NS
Male parents	2	39.40	19.70		NS
F_1 progenies	(26)	783.64	--		
Progenies of females	8	291.50	36.44	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	*
Progenies of males	2	143.72	71.86	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	350.44	21.90	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	38	521.15	13.71	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$):

$\sigma^2_f = (36.44 - 13.71)/6 = 3.788$

$\sigma^2_m = (71.86 - 13.71)/18 = 3.231$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{7.019}{20.729} = 34\%$

parents. But the variance ratios for both the progenies of female and of male parents were significant at 5 and 1% level, respectively. The non-significant interaction between the progenies of female and male parents indicates an absence of intra- and inter-allelic interactions.

The analysis of variance for parental lines and F_2 populations, germinated in distilled water reveals a highly significant block difference and a statistically non-significant difference among female and male parents and between the progenies of the female parents (Table 30), while a highly significant variation between the progenies of male parents was detected (Table 30).

Heritabilities based on F_1 and F_2 populations under distilled water were estimated and found to be 34 and 24%, respectively. These results confirm those of Wright (1971), Helmerick and Pfeiffer (1952), Evans (1975), and Sharma (1973) that rate of germination is genetically controlled and is a species and varietal characteristic; however, the heritability for rate of germination is relatively low and thus this trait cannot be easily fixed through a straight selection program. Table 31, which presents the mean performances of F_1 and F_2 progenies, parents and mid-parents values under zero osmotic potential, indicates that over 70% of the F_1's and F_2's exhibit a phenotype more extreme than that of one parent. Because there is no significant difference between F_1 and/or F_2 means and their respective high or low parents, and no interaction between progenies of female by male parents was

Table 30. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for speed of germination indices at "0" atmosphere osmotic potential based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	77	989.60			
Blocks	1	244.51	244.51		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	136.20	17.02		NS
Male parents	2	39.40	19.70		NS
F_2 progenies	(26)	197.90	--		
Progenies of females	8	110.61	13.83	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	NS
Progenies of males	2	57.11	28.56	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	30.17	1.89	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	38	276.03	7.26	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$):

$\sigma^2_f = (13.83 - 7.26)/6 = 1.095$

$\sigma^2_m = (28.56 - 7.26)/18 = 1.183$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m / \sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{2.278}{9.538} = 24\%$

Table 31. Mean values for speed of germination (indices) under "0" atmosphere osmotic potential for each parent, the F_1 and F_2 populations and mid-parent (MP) values for 27 crosses derived from 9 female and 3 male parents

Crosses	$\bar{P}_1$ [1/]	$\bar{P}_2$	$\bar{F}_1$	$\bar{F}_2$	MP
Twin x Fronteira	22.45	18.22	22.67	19.46	20.33
Twin x Frondoso	22.45	12.96	20.87	19.50	17.70
Twin x Oleson Dwarf	22.45	18.55	24.70	23.13	20.50
Era x Fronteira	20.40	18.22	19.73	17.29	19.31
Era x Frondoso	20.40	12.96	21.67	19.18	16.68
Era x Oleson Dwarf	20.40	18.55	29.17	18.38	19.47
Short Rescue x Fronteira	18.45	18.22	15.84	21.87	18.34
Short Rescue x Frondoso	18.45	12.96	21.44	21.10	15.71
Short Rescue x Oleson Dwarf	18.45	18.55	21.71	24.63	18.50
Medium Rescue x Fronteira	17.85	18.22	19.88	17.40	18.04
Medium Rescue x Frondoso	17.85	12.96	17.91	16.82	15.41
Medium Rescue x Oleson Dwarf	17.85	18.55	21.95	20.08	18.20
Rescue x Fronteira	17.80	18.22	22.37	19.70	18.01
Rescue x Frondoso	17.80	12.96	21.67	19.92	15.38
Rescue x Oleson Dwarf	17.80	18.55	18.97	20.96	18.17
Fortuna x Fronteira	14.85	18.22	11.57	18.40	16.54
Fortuna x Frondoso	14.85	12.96	23.02	16.81	13.90
Fortuna x Oleson Dwarf	14.85	18.55	19.12	19.58	16.70
Tioga x Fronteira	13.73	18.22	8.00	19.81	15.98
Tioga x Frondoso	13.73	12.96	17.85	18.98	13.34
Tioga x Oleson Dwarf	13.73	18.55	20.31	21.17	16.14
Ellar x Fronteira	15.74	18.22	20.80	19.95	16.98
Ellar x Frondoso	15.74	12.96	21.56	20.12	14.35
Ellar x Oleson Dwarf	15.74	18.55	21.05	24.07	17.14
Thatcher x Fronteira	20.99	18.22	20.25	18.89	19.61
Thatcher x Frondoso	20.99	12.96	19.76	20.66	16.98
Thatcher x Oleson Dwarf	20.99	18.55	19.15	20.55	19.77

[1/] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

detected, the apparent transgressiveness of progeny means could be due to error and environmental fluctuations rather than non-additive gene action. Rate of germination for F_1's in general scored higher than parental lines (Table 31). This high rate may be the result of heterosis, or minimal genetic differences among parents. This agrees with McDaniel's (1969) work that seeds of barley hybrids germinated faster than their respective parents.

The analysis of variance for the rate of germination of the F_1 crosses and parents and for the F_2 progenies and parents, germinated under 12 atmospheres osmotic potential, are shown in Tables 32 and 33, respectively. Blocking was quite effective and differences among blocks under both cases are highly significant.

Variation in germination at 12 atm. osmotic potential among male and among female parents was not significant (Tables 32 and 33), but there is significant variation among the progenies of female and among the progenies of male parents.

No significant interaction between progeny of female parents by progeny of male parents, in F_1 crosses, was detected (Tables 32); thus, neither intra- nor inter-allelic interactions appear to contribute significantly to genetic variation for this trait. F_2 populations, on the other hand, reacted differently (Table 33) and exhibit a significant interaction between the progenies of female and the progenies of

Table 32. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for speed of germination indices at 12 atmosphere osmotic potential based on 9 female and 3 male parents and their 27 F_1 progenies

Source of variation	df	SS	MS	EMS	F
Total	77	295.75			
Blocks	1	90.95	90.95		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_1 progenies	1	--	--		
Female parents	8	14.15	1.77		NS
Male parents	2	1.52	0.76		NS
F_1 progenies	(26)	101.57	--		
Progenies of females	8	63.29	7.91	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	**
Progenies of males	2	19.04	9.52	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	19.24	1.20	$\sigma^2_e + r\sigma^2_{m\times f}$	NS
Error	38	80.83	2.13	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritability ($h^2_{(N)}$):

$\sigma^2_f = (7.91 - 2.13)/6 = 0.963$

$\sigma^2_m = (9.52 - 2.13)/18 = 0.410$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{1.373}{3.503} = 39\%$

Table 33. Analysis of variance and expected mean square (EMS) following a factorial model to estimate genetic components of variance, and estimates of components of genetic variation and narrow sense heritabilities ($h^2_{(N)}$) for speed of germination indices at 12 atmosphere osmotic potential based on 9 female and 3 male parents and their 27 F_2 progenies

Source of variation	df	SS	MS	EMS	F
Total	77	423.30			
Blocks	1	187.86	187.86		**
Generations	(38)	--	--		
Males vs Females	1	--	--		
Parents vs F_2 progenies	1	--	--		
Female parents	8	14.15	1.77		NS
Male parents	2	1.52	0.76		NS
F_2 progenies	(26)	151.33	--		
Progenies of females	8	36.15	4.52	$\sigma^2_e + r\sigma^2_{m\times f} + rm\sigma^2_f$	*
Progenies of males	2	60.23	30.11	$\sigma^2_e + r\sigma^2_{m\times f} + rf\sigma^2_m$	**
Female × Male progenies	16	54.95	3.43	$\sigma^2_e + r\sigma^2_{m\times f}$	*
Error	38	60.43	1.59	σ^2_e	

NS - non-significance
* - F exceeds the 5% level of significance
** - F exceeds the 1% level of significance

Estimation of narrow sense heritabilities ($h^2_{(N)}$):

$\sigma^2_f = (4.52 - 3.43)/6 = .1805$

$\sigma^2_m = (30.11 - 3.43)/18 = 1.4822$

$h^2_{(N)} = \sigma^2_f + \sigma^2_m/\sigma^2_f + \sigma^2_m + \sigma^2_e + \sigma^2_{m\times f} = \frac{1.6627}{4.2354} = 39\%$

male parents at the 5% level of probability, under 12 atmospheres osmotic pressure.

Heritability of the trait for both F_1 and F_2 crosses were estimated by the ratio of additive to phenotypic variance and found to be approximately 39 and 39%, respectively. Although these values are not high, for a complex trait such as the rate of germination, it could be used as a tool to screen for faster germinating genotypes from slow germinating ones. Mean performance of parental lines, mid-parents, and their respective F_1 and F_2 populations under 12 atmospheres osmotic potential are presented in Table 34. Low heritability of this trait can also be depicted from this table. Table 34 indicates that approximately two-thirds of the F_1 and F_2 means were transgressive. Once again, it should be pointed out that transgressiveness of F_1 means should not, or is assumed not to be due to over dominant gene action, because interaction between the progeny of female by the progeny of male parents is statistically non-significant (Table 32). But, because the progeny of female by male parents interaction in F_2 is significant at the 5% probability level (Table 33), the transgressiveness of the F_2 means and relatively low additive genetic variance based on F_2 crosses could be attributed to the non-additive, dominance or epistatic, components of genetic variability.

Table 34. Mean values for speed of germination indices under 12 atmospheres osmotic potential for each parent, the F_1 and F_2 populations and mid-parent (MP) values for 27 crosses derived from 9 female and 3 male parents

Crosses	$\bar{P}_1$ [1/]	$\bar{P}_2$	$\bar{F}_1$	$\bar{F}_2$	MP
Twin x Fronteira	4.96	1.82	3.99	0.80	3.39
Twin x Frondoso	4.96	2.05	2.37	1.44	3.51
Twin x Oleson Dwarf	4.96	2.99	5.62	6.01	3.98
Era x Fronteira	3.34	1.82	3.11	2.70	2.58
Era x Frondoso	3.34	2.05	2.48	3.13	2.69
Era x Oleson Dwarf	3.34	2.99	4.03	4.98	3.16
Short Rescue x Fronteira	3.73	1.82	2.33	2.67	2.78
Short Rescue x Frondoso	3.74	2.05	2.12	3.33	2.90
Short Rescue x Oleson Dwarf	3.74	2.99	4.32	8.49	3.36
Medium Rescue x Fronteira	3.09	1.82	4.40	2.44	2.46
Medium Rescue x Frondoso	3.09	2.05	3.17	2.66	2.57
Medium Rescue x Oleson Dwarf	3.09	2.99	3.57	5.02	3.04
Rescue x Fronteira	2.54	1.82	4.03	3.77	2.18
Rescue x Frondoso	2.54	2.05	3.92	3.43	2.30
Rescue x Oleson Dwarf	2.54	2.99	4.29	4.56	2.77
Fortuna x Fronteira	2.22	1.82	0.00	1.76	2.02
Fortuna x Frondoso	2.22	2.05	0.70	2.56	2.13
Fortuna x Oleson Dwarf	2.22	2.99	3.50	1.25	2.60
Tioga x Fronteira	2.81	1.82	0.91	2.86	2.32
Tioga x Frondoso	2.81	2.05	1.61	3.34	2.43
Tioga x Oleson Dwarf	2.81	2.99	2.47	3.68	2.90
Ellar x Fronteira	4.73	1.82	5.05	2.54	3.28
Ellar x Frondoso	4.73	2.05	4.20	3.43	3.39
Ellar x Oleson Dwarf	4.73	2.99	4.68	7.11	3.86
Thatcher x Fronteira	3.86	1.82	4.49	2.89	2.84
Thatcher x Frondoso	3.86	2.05	3.81	3.86	2.96
Thatcher x Oleson Dwarf	3.86	2.99	4.68	3.44	3.43

[1/] P_1 is the first (female) and P_2 is the second (male) parent for all crosses

Stomatal Studies

Significant variation due to differences among plants within cultivars, and adaxial (Ad) and abaxial (Ab) surface, under two environments, greenhouse vs. field conditions, was detected for number of stomata per microscopic field (Table 35). In general, considering overall cultivars (Table 36), the mean number of stomata per microscopic field was greater for field grown plants (62.3) than greenhouse plants (54.3), and in both environments the adaxial surface had significantly more stomata (65.3) than the abaxial surface (51.3). Thus, field grown plants, probably due to higher light intensity and other adverse environmental stresses, showed approximately 10 and 15% increases in abaxial and adaxial stomatal number, respectively. Given an appropriate design, significant variation among cultivar means is interpreted as reflecting genetic differences between cultivars just as it would in a varietal yield trial. The experimental design provided tests for variation among plants within a cultivar with pooled estimates of error of microscopic fields within plants, and to test variation among cultivar means with variation among plants within cultivars. The analysis of variance for the adaxial and abaxial surfaces under both environments are summarized in Tables 37, 38, 39, and 40. Because plant breeders potentially are interested in breeding for stomatal number, it is important to determine if there is a significant genotype (cultivar) by environment interaction, which would

Table 35. F values reflecting variation among plants within cultivars for stomatal number in a greenhouse and field study for 12 spring wheat cultivars

Cultivars	Greenhouse			Field		
	Ad + Ab	Ad	Ab	Ad + Ab	Ad	Ab
Fronteira	11.55	7.72	6.05	11.20	6.70	2.40
Frondoso	14.26	11.59	8.82	5.16	3.46	5.30
Oleson Dwarf	11.49	8.07	8.43	8.99	5.75	7.48
Twin	23.32	14.32	10.80	16.31	5.06	15.40
Era	16.57	6.68	19.09	35.99	21.41	20.10
Short Rescue	13.86	9.73	9.51	13.19	6.90	9.10
Medium Rescue	7.69	6.68	9.63	8.94	4.08	6.75
Rescue	63.42	95.36	17.35	8.01	4.01	5.66
Fortuna	2.90	10.91	7.51	29.81	16.05	16.78
Tioga	19.79	14.63	5.71	20.17	21.04	7.95
Ellar	11.66	7.81	4.55	16.71	19.48	9.56
Thatcher	15.25	15.45	5.49	15.08	7.85	7.33

Table 36. Comparison of mean stomatal number (per 1.17 mm^2 microscopic field) in 12 spring wheat cultivars grown under greenhouse and field conditions. Upper and lower leaf surfaces

Leaf surface	Ad	Ad	Mean
Field	68.6	56.0	62.3
Greenhouse	62.0	46.6	54.3
Mean	65.3	51.3	

Table 37. Analysis of variance for the adaxial (middle position of second leaf) stomatal number (per 1.117 mm^2 microscopic field) of 12 spring wheat cultivars. 1975 - field studies

Source of variation	df	SS	MS	F
Total	719	73543.30		
Between cultivars	11	19010.10	1728.20	**
Within cultivars	108	34590.80	320.30	**
Error	600	19942.30	33.20	

Table 38. Analysis of variance for the abaxial (middle position of the second leaf) stomatal number (per 1.17 mm^2 microscopic field) of 12 spring wheat cultivars. Field studies

Source of variation	df	SS		F
Total	719	59544.00		
Between cultivars	11	16344.11	1485.80	**
Within cultivars	108	27438.58	253.96	**
Error	600	15771.29	26.28	

Table 39. Analysis of variance for adaxial (middle position of second leaf) stomatal number (per 1.17 mm^2 microscopic field) of 12 spring wheat cultivars. Greenhouse study

Source of variation	df	SS		F
Total	719	78526.0		
Between cultivars	11	28067.0	2551.54	**
Within cultivars	108	36973.54	342.34	**
Error	600	13485.47	22.47	

Table 40. Analysis of variance for abaxial (middle position of second leaf) stomatal number (per 1.17 mm^2 microscopic field) of 12 spring wheat cultivars. Greenhouse study

Source of variation	df	SS	MS	F
Total	719	53052.44		
Between cultivars	11	19285.22	1753.70	**
Within cultivars	108	21197.74	196.27	**
Error	600	12569.48	20.94	

Table 41. Stomatal number (per 1.17 mm^2 microscopic field) of the middle position of the second leaf (flag leaf = leaf no. 1) of 12 spring wheat cultivars under greenhouse and field conditions

Cultivars	Greenhouse	Field
	Ad + Ab	Ad + Ab
Fronteira	106.88	121.43
Frondoso	109.65	119.76
Oleson Dwarf	107.83	143.46
Twin	113.67	132.83
Era	92.95	104.71
Short Rescue	120.10	129.68
Medium Rescue	125.80	126.36
Rescue	114.31	126.36
Fortuna	122.45	126.17
Tioga	105.23	126.43
Ellar	93.53	126.15
Thatcher	90.75	112.05

suggest that cultivars do not behave the same way under different environmental conditions. A significant interaction could hinder progress through selection. The 'within cultivar' component unfortunately may reflect genetic differences, environmental effects, or combinations of these two which cannot be separated. The impact of environment seen (Table 41) suggests that genetic differences are equally manifest in either the greenhouse or field; the maximum difference between cultivar means, or range for greenhouse grown plants, was 35 and for field grown plants nearly 39. From this, it might be concluded that plant breeders could work in either or both the greenhouse and field. However, the consistency of cultivars over environment can be estimated readily with a rank correlation of cultivar means of field grown versus greenhouse grown plants. A high rank correlation indicates consistent performance, and a low correlation would reflect the inconsistent performance of the cultivar under two conditions or would reflect the genotype by environment interaction (Table 42). Note that although all values except the rank correlation between the differences (the bottom line) are statistically significant, on the whole coefficients of determination (r^2) are low, 26, 43, and 26% for Ad, Ab and total stomata, respectively. This suggests that there is a marked inconsistency among cultivars between the two environments. The cultivar means reflect this directly. For example, in the field, Oleson Dwarf ranked highest in stomata number, for the adaxial surface, but

Table 42. Rank correlation of 12 spring wheat cultivars for stomatal number. Greenhouse vs. field conditions

Surfaces	Rank correlation coefficient
Ad vs. Ad	0.51
Ab vs. Ab	0.66
(Ad + Ab) vs. (Ad + Ab)	0.52
(Ad - Ab) vs. (Ad - Ab)	0.17

Table 43. Ranking based on cultivar mean stomata per 1.17 mm^2 microscopic field

Cultivars	Adaxial		Abaxial	
	Field	Greenhouse	Field	Greenhouse
Fronteira	9	8	9	8
Frondoso	10	6	6	6
Oleson Dwarf	1	7	1	6
Twin	5	5	2	4
Era	12	12	12	12
Tioga	4	9	8	7
Fortuna	8	3	3	2
Ellar	7	10	5	11
Thatcher	11	11	11	11
Rescue	2	2	10	9
Short Rescue	3	4	4	3
Medium Rescue	6	1	7	1

in the greenhouse it ranked seventh. In the greenhouse, Medium Rescue ranked highest, while in the field it ranked sixth. Only Era and Thatcher had identical ranks of twelfth and eleventh, respectively, the lowest two in the field and greenhouse (Table 43). For the abaxial surface, where the rank correlation is higher, the same pattern still persists; Era and Thatcher are consistent and, for example, Oleson Dwarf is highest in the field but ranks sixth in the greenhouse (Table 43).

From these studies I conclude that the differences between cultivar means reflect in part genetic differences in the number of stomata; thus, this trait could be changed by selection. The within cultivar variation could be either genetic or environmental, or a combination of the two, which could be further tested using more highly inbred, experimental lines; and finally, this trait would be difficult to breed for because of the impact of environment and the apparent genotype by environment interaction reflected in the relatively low rank correlation coefficients.

SUMMARY AND CONCLUSIONS

Common wheat (*Triticum aestivum* L.) is not generally considered to be drought tolerant; however, variation for relative drought tolerance has been attributed to several traits, including leaf and stomatal density, root number, root mass, root to shoot ratio, rate of root elongation, and speed of germination. All of these traits are genetically complex and have received little attention from plant breeders; thus, the development of drought tolerant cultivars has been comparatively slow.

Because drought conditions limit crop production in many areas of the world, the development of drought tolerant cultivars is a reasonable plant breeding goal. To attain this goal, understanding the inheritance of traits associated with drought tolerance is essential. Plant breeding strategies may be dictated in part by the heritability and number of loci conditioning any given trait; high narrow sense heritabilities, which reflect a preponderance of genetic variation due to additive gene action, suggest great potential for rapid progress through direct selection in early generations and few loci suggest potential rapid fixation in self-pollinating species.

It was my objective to study mode of inheritance and heritability of these traits, as they relate to drought tolerance, by isolating the components of genetic variance, into additive and non-additive effects for each trait following an analysis of variance model

proposed in 1952 by J. E. Grafius. Additive genetic variance is estimated from the mean squares for "among the progeny of different female parents" and for "among the progeny of different male parents." Non-additive genetic variances are estimated from the mean squares for the progeny of female by progeny of male interaction.

Growth chamber, greenhouse, and field pilot studies were carried out to estimate the magnitude of genetic variation among 20 spring wheat cultivars for leaf and root number, root mass, root to shoot ratio, rate of root elongation, speed of germination, and stomatal density which are reported to be associated with drought tolerance. Genetic variation for speed of germination in response to an osmotic stress was studied with three cultivars of spring wheat, and genetic variation for stomatal number was studied using 12 cultivars. All pilot studies were analyzed following standard analysis of variance methods; variation among cultivar means was interpreted as reflecting, in part, genetic differences.

Although significant "among cultivar mean variation for stomatal number" was detected, both "within cultivar" and "environmental" sources of variation precludes further analysis.

As a result of the pilot studies for root and shoot growth patterns, from the original 20 cultivars, 12 were selected as parents for experiments to estimate components of variation: 3 served as male parents and 9 as female. Following a factorial type of analysis

proposed by Grafius, variation among progenies of male and/or female parents is interpreted as due to additive gene effects. Narrow sense heritability were estimated from experiments with either parents and F_1's or parents and F_2's or both, and with the following results:

1. Narrow sense heritability for leaf number was estimated to be 55%. This may mean that selection for leaf number could be done in early generations.

2. Total root number (seminal and adventitious) is conditioned by low additive gene action. Only 33% of the phenotypic variability is accounted for by fixable components of genetic variance. Thus, a straight mass selection program may not be an effective method to alter the number of roots in the offspring.

3. Over 80% of the total phenotypic variability for root mass among progenies is attributable to additive gene action. Root mass with relatively high additive variance components may be less subject to environmental fluctuations and selection could thus be made in early generations.

4. Narrow sense heritability for root/shoot ratio was estimated to be 32%. Although additive genetic variance for this trait is not especially high, it may be used as a criterion for the selection of genotypes for drought tolerance.

5. Narrow sense heritability for rate of root elongation is about 26% based on the analysis of both F_1's and F_2's. Thus, an early

generation straight mass selection for this trait because of its low heritability likely would not be markedly effective.

6. Narrow sense heritability for speed of germination, under simulated drought conditions, for both F_1 and F_2 crosses, were not markedly high, 34 and 24% under "0 atm" osmotic potential and 39 and 39% under "12 atm" osmotic potential, respectively. Therefore, this trait cannot be fixed easily through a straight selection program, but it may be used as a guide to screen faster germinating genotypes from slower germinating ones.

7. Significant variation among cultivar means and among plant within a cultivar, for both adaxial and abaxial stomatal number and both greenhouse and field, was detected. The difference among cultivar means reflected, in part, genetic differences in the number of stomata; thus, stomatal number could be changed by selection. The variation within cultivars could be due to gene action or environmental effects, or a combination of the two which could be further tested using more highly selected inbred experimental lines. A marked inconsistency among cultivars between the two environments suggests that there is a significant genotype by environment interaction; therefore, a straight mass selection program would not be expected to be effective.

In all traits mentioned above, narrow sense heritabilities, estimated by the Grafius model, were confirmed fairly well by parents, mid-parents, and F_1 and/or F_2 mean relationships.

LIST OF REFERENCES

LIST OF REFERENCES

Aamodt, O.S. and W.H. Johnston. 1936. Studies on drought resistance in spring wheat. Can. J. Res. 14:122-152.

Allard, R.W. 1956. Biometrical approach to plant breeding. Brookhaven symposia in biology. No. 9 Genetics in plant breeding, pp. 69-88.

Ashraf, Muhammad. 1973. The relationship of morphological factors to field spring survival in winter wheat. Ph.D. thesis, Montana State University, Bozeman, Montana.

Atkins, R.E. and H.C. Murphy. 1949. Evaluation of yield potentialities of oat crosses from bulk hybrid tests. Agron. J. 41:41-45.

Bailey, L.F. 1940. Some water relations of three western grasses. I. The transpiration ratio. Amer. J. Bot. 27:122-128.

Bassett, D.M., J.R. Stockton and W.L. Dickens. 1970. Root growth of cotton as measured by P uptake. Agron. J. 62:200-203.

Bayles, B.B., J.W. Taylor and A.T. Bartel. 1937. Rate of water loss in wheat varieties and resistance in artificial drought. J. Amer. Soc. Agron. 29:40-52.

Black, A.L. 1970. Adventititous roots, tillers, and grain yields of spring wheat as influenced by N-P fertilization. Agron. J. 62:32-36.

Black, C.A. 1968. Soil-plant relationship, 2nd Ed., John Wiley & Sons, NY, pp. 111-116.

Boatwright, G.O. and H. Ferguson. 1967. Influence of primary and/or adventitious root systems on wheat production and nutrient uptake. 59:299-302.

Brenchly, W.E. and V.A. Jackson. 1921. Root development in barley and wheat under different conditions of growth. Ann. Bot. 35:533-56.

Briggle, L.W. 1967. Morphology of wheat plant. In Wheat and wheat improvement. Edit. by K.S. Quisenberry and L.P. Reitz. Amer. Soc. of Agron. Publ. No. 13. Madison, Wisconsin, pp. 89-116.

Brouwer, R. 1966. Root growth of grasses and cereals. in The Growth of cereals and grasses. Edit. by F.L. Milthorpe and J.D. Ivins. London, pp. 153-166.

Burton, G.W. 1964. The geneticist's role in improving water-use efficiency by crops. in Research on water, A.S.A. Spec. Pub. No. 4. Soil Sci. Soc. Amer., Madison, Wisconsin, pp. 95-103.

_____, E.H. DeVane and R.L. Carter. 1954. Root penetration, distribution and activity in southern grasses measured by yields, drought symptoms and P^{32} uptake. Agron. J. 46:229-233.

Carceller, M.S. and A. Soriano. 1972. Effect of treatments given to the grain, on the growth of wheat roots under drought conditions. Can. J. Bot. 50:105-108.

Chang, J.H. 1968. Climate and agriculture, an ecological survey. Chicago, Aldine Publ. Co., pp. 118-128.

Ciha, A.J. and W.A. Brun. 1975. Stomatal size and frequency in soybeans. Crop Sci. 15:309-313.

Cockerham, C.C. 1956. Analysis of quantitative gene action. Brookhaven symposia in biology. No. 9. Genetics in plant breeding. Upton, New York, pp. 53-68.

Cole, D.F. and A.K. Dobrenz. 1970. Stomate density of alfalfa (*Medicago sativa* L.). Crop Sci. 10:61-63.

Comstock, R.E. and H.F. Robinson. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4:254-266.

Cooper, C.S. and M. Qualls. 1967. Morphology and chlorophyll content of shade and sun leaves of two legumes. Crop. Sci. 7:672-73.

Dedio, W. 1975. Water relations in wheat leaves as screening tests for drought resistance. Can. J. Plant Sci. 55:369-378.

Derera, N.F., D.R. Marshall and L.N. Balaam. 1968. Genetic variability in root development in relation to drought tolerance in spring wheat. Expl. Agr. 5:327-337.

Derwyn, R., B. Whalley, C.M. McKell and L.R. Green. 1966. Seedling vigor and the early nonphotosynthetic stage of seedling growth in grasses. Crop Sci. 6:147-150.

Dobrenz, A.K., L.A. Wright, A.B. Humphrey, M.A. Massengale and W.R. Kneebone. 1969. Stomate density and its relationship to water-use efficiency of blue panic grass (*Panicum antidotale* Retz.). Crop Sci. 9:354-357.

Downey, L.A. 1971. Effect of gypsum and drought stress on maize (*Zea mays* L.). I. Growth, light absorption and yield. Agron. J. 63:569-572.

Eckerson, S.H. 1908. The number and size of the stomata. Bot. Gazette 46:221-224.

Eslick, R.F. and E.A. Hockett. 1974. Genetic engineering as a key to water-use efficiency. Agric. Meterol. 14:13-23.

Evans, L.T., I.F. Wardlaw and R.A. Fischer. 1975. Crop physiology. Some case histories. Edit. by L.T. Evans. Cambridge University Press, London, pp. 101-149.

Evenari, M. 1956. Seed germination. in Radiation biology, vol. III. Edit. by A. Hollaender. McGraw-Hill Book Co., Inc., pp. 519-549.

Fahn, A. 1974. Plant anatomy, Second Ed., Pergamon Press, Oxford, New York, Toronto, Sydney, Braunschweig, pp. 165-198 and 235-282.

Falconer, D.S. 1961. Introduction to quantitative genetics. The Ronald Press Co., New York, p. 365.

Ferguson, H. 1974. Use of variety isogens in plant water-use efficiency studies. Agric. Meteorol. 14:25-29.

_____, R.F. Eslick and J.K. Aase. 1973. Canopy temperature of barley as influenced by morphological characteristics. Agron. J. 65:425-428.

_____, C.S. Cooper, J.H. Brown and R.F. Eslick. 1972. Effect of leaf color, chlorophyll concentration, and temperature on photosynthetic rates of isogenic barley lines. Agron. J. 64:671-673.

_____ and G.O. Boatwright. 1968. Effects of environmental factors on the development of the crown node and adventitious roots of winter wheat (*Triticum aestivum*). Agron. J. 60:258-260.

Fransen, S.C. and C.S. Cooper. 1976. Seed weight effects upon emergence, leaf development, and growth of the sainfoin (*Onobruchis* spp.) seedling. Crop Sci. 16:434-437.

Grafius, J.E. 1952a. A statistical model for estimating the components of genetic variance in bulk yield tests of self-pollinated small grains. S. Dak. State Col. Tech. Bul. 9.

_____, W.E. Nelson and V.A. Dirks. 1952b. The heritability of yield in barley as measured by early generation bulked progenies. Agron. J. 44:253-257.

Hall, N.S., W.F. Chandler, C.H.M. vanBavel, P.H. Reid and J.H. e Anderson. 1953. A tracer technique to measure growth and activity of plant root systems. North Carolina Agr. Exp. Sta. Tech. Bull. 101. 40 p.

Harrington, J.B. 1940. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Can. J. Res., C, 18:578-584.

Harris, F.S. 1914. The effect of soil moisture, plant food and age on the ratio of tops to roots in plants. J. Amer. Soc. Agron. 6:65-75.

Hayward, H.E. 1948. The structure of economic plants. The Macmillan Co., N.Y., pp. 141-177.

Heichel, G.H. 1971. Genetic control of epidermal cell and stomatal frequency in maize. Crop Sci. 11:830-832.

Helmerick, R.H. and R.P. Pfeifer. 1954. Differential varietal response of winter wheat germination and early growth to controlled limited moisture condition. Agron. J. 46:560-562.

Herbel, C.H. and R.E. Sosebee. 1969. Moisture and temperature effects on emergence and initial growth of two range grasses. Agron. J. 61:628-631.

Heyne, E.G. and A.M. Brunson. 1940. Genetic studies of heat and drought tolerance in maize. J. Am. Soc. Agron. 32:803-14.

_____ and H.H. Laude. 1940. Drought resistance of corn seedlings to high temperatures in laboratory tests. J. Am. Soc. Agron. 32:116-126.

Hsiao, T.C. and E. Acevedo. 1974. Plant response to water deficits, water-use efficiency, and drought resistance. Agric. Meteorol. 14:59-84.

Hunt, O.J. 1962. Water requirement of selected genotypes of *Elymus junceus* Fisch. and *Agropyron intermedium* (Host) Beauv. and their parent-progeny relationships. Crop Sci. 2:97-99.

Hunter, J.R. and A.E. Erickson. 1952. Relation of seed germination to soil moisture tension. Agron. J. 44:107-109.

Hurd, E.A. 1974. Phenotype and drought tolerance in wheat. Agric. Meteorol. 14:39-55.

_____. 1971. Can we breed for drought resistance? in Drought Injury and Resistance in Crops. Crop Sci. Soc. Amer. Publ. 2:77-88.

_____. 1969. A method of breeding for yield of wheat in semi-arid climates. Euphytica 18:217-226.

_____. 1968. Growth of roots of seven varieties of spring wheat at high and low moisture levels. Agron. J. 60:201-205.

_____. 1964. Root study of three wheat varieties and their resistance to drought and damage by soil cracking. Can. J. Plant Sci. 44:240-248.

Immer, F.R. 1941. Relation between yielding ability and Homozygosis in barley crosses. J. Amer. Soc. Agron. 33:200-206.

Ingle, J. and R.H. Hageman. 1964. Studies on the relationship between ribonucleic acid content and rate of growth of corn root. Plant Physiol. 39:730-734.

Iverson, G.W. and E.A. Hocket. 1968. Transpiration rate and stomatal frequency in barley. Montana Academy of Sciences 28:13-19.

Jackson, W.T. 1962. Use of carbowaxes (polyethylene glycol) as osmotic agents. Plant Physiol. 37:513-519.

Julander, O. 1945. Drought resistance in range and pasture grasses. Plant Physiol. 20:573-599.

Kaloyereas, S.A. 1958. A new method of determining drought resistance. Plant Physiol. 20:232-233.

Kaul, R. 1966. Relative growth rates of spring wheat, oats, and barley under polyethylene glycol-induced water stress. Can. J. Plant Sci. 46:611-617.

Keller, W. 1953. Water requirement of selected genotypes of orchardgrass; *Dactylis glomerata* L. Agron. J. 45:622-625.

Kilen, T.C. and R.H. Andrew. 1969. Measurement of drought resistance in corn. Agron. J. 61:669-671.

Kittock, D.L. and A.G. Law. 1968. Relationship of seedling vigor to respiration and tetrazolium chloride reduction by germinating wheat seeds. Agron. J. 60:286-288.

Kmoch, H.G., R.E. Ramig, R.L. Fox, and F.E. Koehler. 1957. Root development of winter wheat as influenced by soil moisture and nitrogen fertilization. Agron. J. 49:20-25.

Kneebone, W.R. 1957. Selection for seedling vigor in native grasses under artificial moisture stress. Amer. Soc. Agron., Agron. Abstr., p. 55.

Kramer, P.J. 1969. Plant and soil water relationships: A modern synthesis. McGraw-Hill, N.Y., pp. 314-321.

_____. 1963. Water stress and plant growth. Agron. J. 55:31-35.

_____. 1959. Plant Physiology, vol. II. Edit. by F.C. Steward. Academic Press, New York and London, pp. 705-709.

Lagerwerff, J.V. and H.E. Eagle. 1961. Osmotic and specific effects of excess salts on beans. Plant Physiol. 36:572-477.

Laude, H.M. 1971. Drought influence on physiological processes and subsequent growth. in Drought Injury and Resistance in Crops. Crop Sci. Soc. Amer. Publ. 2:45-56.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York and London, pp. 229-271.

_____. 1969. Introduction to plant physiology. Saint Louis, The C.V. Mosby Company, pp. 280-286.

_____. 1956. The hardiness of plants. Academic Press, Inc., Publishers, New York, N.Y., pp. 199-229.

Locke, L.F. and J.A. Clark. 1924. Development of wheat plants from seminal roots. J. Amer. Soc. of Agron. 16:261-268.

Maguire, J.D. 1962. Speed of germination - Aid in selection and evaluation for seedling emergence and vigor. Crop Sci. 2:176.

Mather, K. 1949. Biometrical Genetics. Dover Publication, Inc., p. 158.

Maximov, N.A. and A.S. Kruzilin. 1936. Influence of irrigation on the development of the root system of spring wheat plants. Plant Physiol. 11:457-60.

May, L.H. and F.L. Milthorpe. 1962. Presowing hardening of plants to drought. An appraisal of the contribution of P.A. Henckel. Field Crop Abstr. 15:93-98.

McCall, M.A. 1934. Developmental anatomy and homologies in wheat. J. Agric. Res. 48:283-321.

McDaniel, R.G. 1969. Relationship of seed weight, seedling vigor and mitochondrial metabolism in barley. Crop Sci. 9:823-827.

McGinnies, W.J. 1960. Effect of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-162.

Meidner, H. and T.A. Mansfield. 1968. Physiology of stomata. McGraw-Hill, N.Y., pp. 1-25.

Meirion, T., S.L. Ranson and J.A. Richardson. 1973. Plant Physiol. Fifth Ed., London.

Milthorpe, F.L. 1950. Changes in the drought resistance of wheat seedlings during germination. Ann. Bot. Lond. N.S. 14:79-89.

Miskin, K.E., D.C. Rasmusson and D.N. Moss. 1972. Inheritance and physiological effects of stomatal frequency in barley. Crop Sci. 12:780-783.

_____ and D.C. Rasmusson. 1970. Frequency and distribution of stomata in barley. Crop Sci. 10:575-578.

Mitchell, R.L. 1970. Crop growth and culture. The Iowa State University Press, Ames, Iowa, pp. 173-194.

Moss, D.N., J.T. Woolley and J.F. Stone. 1974. Plant modification for more efficient water use: The challenge. Agric. Meteorol. 14:311-320.

Mueller, I.M. and J.E. Weaver. 1942. Relative drought resistance of seedlings of dominant prairie grasses. Ecology 23:387-398.

Muzik, J.J. and J.W. Whitworth. 1962. A technique for the periodic observation of root system in situ. Agron. J. 54:56.

Oppenheimer, H.R. 1960. Adaptation to drought: xerophytism. in Arid Zone Research - XV. Plant water relations in arid and semi-arid conditions. pp. 105-138.

Ormrod, D.J. and A.J. Renney. 1968. A survey of weed leaf stomata and trichomes. Can. J. Plant Sci. 48:197-209.

Pálfi, G. and J. Juhász. 1971. The theoretical basis and practical application of a new method of selection for determining water deficiency in plants. Plant and Soil 34:503-507.

Parmar, M.T. and R.P. Moore. 1968. Carbowax 6000, mannitol, and sodium chloride for simulating drought conditions in germination studies of corn (*Zea mays* L.) of strong and weak vigor. Agron. J. 60:192-195.

_____ and _____. 1966. Effects of simulated drought by polyethylene glycol solutions on corn (*Zea mays* L.) germination and seedling development. Agron. J. 58:391-392.

Passioura, J.B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Pearson, R.W. 1974. Significance of rooting pattern to crop production and some problems of root research. in The plant root and its environment. Edit. by E.W. Carson. University Press of Virginia, Charlottesville, Virginia.

Peterson, R.F. 1965. The wheat plant and its morphological development. in Wheat. Interscience Publ., Inc., New York, pp. 17-33.

Pinthus, M.J. and Y. Eshel. 1962. Observations and the development of the root system of some wheat varieties. Israel J. Agric. Res. 12:1, pp. 13-20.

Plummer, A.P. 1943. The germination and early development of twelve range grasses. J. Amer. Soc. Agron. 35:19-34.

Powell, L.M. and R.P. Pfeifer. 1957. The effect of controlled limited moisture on seedling growth of Cheyenne winter wheat selections. Agron. J. 48:555-557.

Ray, L.L., C.W. Wendt, and J.E. Quisenberry. 1974. Genetic modification of cotton plants for more effective water use. Agric. Meteorol. 14:31-38.

Reitz, L.P. 1974. Breeding for more efficient water use--is it real or a mirage. Agric. Meteorol. 14:3-11.

Salim, M.H., G.W. Todd and C.A. Stutte. 1969. Evaluation of techniques for measuring drought avoidance in cereal seedlings. Agron. J. 61:182-185.

_____, _____ and M.A. Schlehuber. 1965. Root development of wheat, oats, and barley under conditions of soil moisture stress. Agron. J. 57:603-607.

Sallans, B.J. 1961. Inherent differences in depth of crown in wheat and barley. Can. J. Plant Sci. 41:493-8.

Sandhu, A.S. and H.H. Laude. 1958. Tests of drouth and heat hardiness of winter wheat. Agron. J. 50:79-81.

Sapra, V.T., J.L. Hughes and G.C. Sharma. 1975. Frequency, size, and distribution of stomata in Triticale leaves. Crop Sci. 15:356-358.

Sarvella, P., J.R. Meyer and A. Owings. 1961. A Scotch tape method for counting or measuring stomata. Crop Sci. 1:81-82.

Sharma, M.L. 1973. Simulation of drought and its effect on germination of five pasture species. Agron. J. 65:982-987.

Shearman, R.C. and J.B. Beard. 1972. Stomatal density and distribution in agrostis as influenced by species, cultivar, and leaf blade surface and position. Crop Sci. 12:822-823.

Sullivan, C.Y. and J.D. Eastin. 1974. Plant physiological responses to water stress. Agric. Meteorol. 14:113-127.

Suneson, C.A. and O.C. Riddle. 1944. Hybrid vigor in barley. J. Amer. Soc. Agron. 36:57-61.

Tadmore, N.H., Y. Cohen and Y. Harpaz. 1969. Interactive effects of temperature and osmotic potential on the germination of range plants. Crop Sci. 9:711-774.

Tan, Geok-Yong and G.M. Dunn. 1975. Stomatal length, frequency, and distribution in *Bromus inermis* Leyss. Crop Sci. 15:283-286.

_____ and _____. 1973. Relationship of stomatal length and frequency and pollen grain diameter to ploidy level in *Bromus inermis* Leyss. Crop Sci. 13:332-334.

Teare, I.D., E.T. Kanemasu, W.L. Powers and H.S. Jacobs. 1973. Water-use efficiency and its relation to crop canopy area, stomatal regulation, and root distribution. Agron. J. 65:207-211.

_____, A.G. Law and G.F. Simmons. 1972. Stomatal frequency and distribution on the inflorescence of *Triticum aestivum*. Can. J. Plant Sci. 52:89-94.

_____, C.J. Peterson and A.G. Law. 1971. Size and frequency of leaf stomata in cultivars of *Triticum aestivum* and other Triticum species. Crop Sci. 11:496-498.

Teoh, T.S., L.A.G. Aylmore and J.P. Quirk. 1967. Retention of water by plant cell walls and implications for drought resistance. Aust. J. Biol. Sci. 20:41-50.

Todd, G.W. and D.L. Webster. 1965. Effects of repeated drought periods on photosynthesis and survival of cereal seedlings. Agron. J. 45:399-404.

_____, F.W. Ingram and C.A. Stutte. 1962. Relative turgidity as an indication of drought stress in cereal plants. Proc. Oklahoma Acad. Sci. 42:56-60.

Toole, E.H., S.B. Hendricks, H.A. Borthwick and V.K. Toole. 1956. Physiology of seed germination. Ann. Rev. of Plant Physiol. 1:299-319.

Troughton, A. 1962. The roots of temperate cereals (wheat, barley, oats, and rye). Commonwealth Agricultural Bureaux, Hurley Berkshire.

Viets, F.G. Jr. 1971. Effective drought control for successful dry-land agriculture. in Drought injury and resistance in crops. CSSA Spec. Publ. No. 2, Crop Sci. Soc. Amer., Madison, Wis., pp. 57-76.

Wardlaw, I.F. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. Aust. J. Biol. Sci. 20:25-39.

Weaver, J.E. 1926. Root habit of wheat. Root development of yield crops. McGraw-Hill Book Company, Inc.

Webb, R.B. and D.E. Stephens. 1936. Crown and Root development in wheat varieties. J. Agric. Res. 52:569-83.

Wellington, P.S. 1966. Germination and seedling emergence. Edit. by F.L. Milthorpe and J.D. Ivins. in The growth of cereals and grasses. Butterworths, London.

Whalley, D.B., C.M. McKell and L.R. Green. 1966. Seedling vigor and the early non-photosynthetic stage of seedling growth in grasses. Crop Sci. 6:147-150.

Whiteside, A.G.O. 1941. Effect of soil drought on wheat plants. Sci. Agric. 19:320-334.

Williams, T.V., R.S. Snell and C.E. Cress. 1969. Inheritance of drought tolerance in sweet corn. Crop Sci. 9:19-22.

_____, _____ and J.F. Ellis. 1967. Methods of measuring drought tolerance in corn. Crop Sci. 7:179-182.

Wilson, A.M., D.N. Hyder and D.D. Briske. 1976. Drought resistance characteristics of blue grama seedlings. Agron. J. 68:479-484.

Wood, J.G. 1934. The physiology of xerophytism in Australian plants, the stomatal frequencies, transpiration and osmotic pressures of scherophyll and tomentose succulent leaved plants. J. Ecol. 22:69-87.

Wright, L.N. 1971. Drought influence on germination and seedling emergence. in Drought injury and resistance in crops. Crop Sci. Soc. Amer. Publ. 2:19-41.

_____ and A.K. Dobrenz. 1970. Efficiency of water use and seedling drouth tolerance of boer lovegrass, *Eragrostis curvula* Nees. Crop Sci. 10:1-2.

_____. 1964. Drouth tolerance - Program-controlled environmental evaluation among range grasses genera and species. Crop. Sci. 4:472-474.

Kazemi, Hamdollah
Inheritance of factors associated with drought tolerance