



Inheritance of factors associated with drought tolerance
by Hamdollah Kazemi

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Crop and Soil Science
Montana State University
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Abstract:

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.

Type of gene action was determined from the performance of parental lines 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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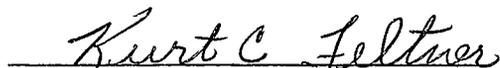
DOCTOR OF PHILOSOPHY

in

Crop and Soil Science

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MONTANA STATE UNIVERSITY
Bozeman, Montana

February, 1977

ACKNOWLEDGMENTS

I would like to express my sincere appreciation to the following:

Drs. S. R. Chapman and F. H. McNeal, who served as my major professors, for their professional guidance, friendship, encouragement, and personal support during the course of this study and preparation of this thesis.

Drs. J. H. Brown, A. L. Scharen, and R. E. Lund for their professionalism, contributions, and criticisms to this thesis.

Dr. F. P. McCandless for serving on my graduate committee, as the graduate representative.

Dr. K. C. Feltner, head of the Plant and Soil Science Department, for making the Montana Agricultural Experiment Station field and laboratory facilities available throughout this study.

The University of Azarabadegan, Tabriz, Iran, and Ministry of Science and Higher Education, Iran, for granting me the leave of absence and monetary contributions. Without their financial support, attending graduate school would have been impossible.

My wife, Akhtar Kazemi, for her encouragement, assistance with the laboratory research, for her sacrifice, and endless patience throughout my graduate work.

My sons, Babak and Bahram, and my daughter, Zohreh, for their love, sacrifice, and trust.

TABLE OF CONTENTS

	<u>Page</u>
VITA	ii
ACKNOWLEDGMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
ABSTRACT	xii
INTRODUCTION	1
LITERATURE REVIEW	3
Overview	3
Drought and Drought Tolerance	3
Importance of Water for Plant Growth	5
Classification of Plants with Regard to Drought	7
Water Use Efficiency	8
Adaptive Characteristics of Plants Related to Drought	9
Tests to Measure Drought Tolerance	13
Critical Stages of Wheat to Drought	18
Genotypic Differences Among Plants Related to Drought	20
Root and Shoot Studies	23
Rate of Root Elongation	34
Speed of Germination Under a Simulated Drought Stress	37
Stomatal Studies	44
Quantitative Genetics	51
MATERIALS AND METHODS	62
Genetic Stock	62
Root and Shoot Studies	64

	<u>Page</u>
Rate of Root Elongation	67
Speed of Germination Under a Simulated Drought Stress	69
Stomatal Study	73
RESULTS AND DISCUSSION	76
Root and Shoot Studies	76
Rate of Root Elongation	100
Speed of Germination Under a Simulated Drought Stress	113
Stomatal Studies	132
SUMMARY AND CONCLUSIONS	140
REFERENCES	145

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Analysis of variance model showing components of genetic variation for self-pollinated bulk progenies from crosses of homozygous lines	60
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	63
3. Data for four agronomic traits from 20 spring wheat cultivars for each of three growth durations	77
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	78
5. Analysis of variance for total root number measured on 20 spring wheat cultivars in each of three root growth durations in a greenhouse pilot study	78
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	79
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	79
8. Mean values for four agronomic traits scored on 12 parental lines and their 27 F ₂ progenies in a greenhouse study	81

<u>Table</u>	<u>Page</u>
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	83
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	84
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 variance and narrow sense heritabilities ($h^2_{(N)}$) for root mass based on 9 female and 3 male parents and their 27 F_2 progenies	85
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	86
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	89
14. Mean values for leaf number for each parent, the F_2 population and mid-parent values for 27 crosses derived from 9 female and 3 male parents	90
15. Mean values for total root number for each parent, the F_2 population and mid-parent values for 27 crosses derived from 9 female and 3 male parents	91

<u>Table</u>	<u>Page</u>
16. Mean values for root mass (g/plant) for each parent, the F_2 population and mid-parent values for 27 crosses derived from 9 female and 3 male parents	92
17. Mean values for root/shoot ratio for each parent, the F_2 population and mid-parent values for 27 crosses derived from 9 female and 3 male parents	93
18. Rate of root elongation in 20 spring wheat cultivars in a growth chamber pilot study (indices according to Maguire 1962)	101
19. Analysis of variance of rate of root elongation indices of 20 spring wheat cultivars	101
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	102
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	104
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	108
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	109

<u>Table</u>	<u>Page</u>
24. Mean values for rate of root elongation indices for each parent, the F_1 and F_2 populations and mid-parent values for 27 crosses derived from 9 females and 3 male parents	112
25. Mean rate and percentage germination of 3 spring wheat cultivars germinated in solutions representing three osmotic potentials (O.P.)	114
26. Analysis of variance of rate of germination indices of three spring wheat cultivars in solutions representing three osmotic potentials (O.P.)	114
27. Cumulative germination percentage for three cultivars of spring wheat, each grown in three solutions of different osmotic potential for a 14 day period	115
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	118
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	123
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	125
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 values for 27 crosses derived from 9 female and 3 male parents .	126

<u>Table</u>	<u>Page</u>
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 at germination indices at 12 atmosphere osmotic potential based on 9 female and 3 male parents and their 27 F_1 progenies	128
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	129
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 values for 27 crosses derived from 9 female and 3 male parents	131
35. F values reflecting variation among plants within cultivars for stomatal number in a greenhouse and field study for 12 spring wheat cultivars	133
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	134
37. Analysis of variance for the adaxial (middle position of second leaf) stomatal number (per 1.17 mm^2 microscopic field) of 12 spring wheat cultivars. Field studies	134
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	135

<u>Table</u>	<u>Page</u>
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	135
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	136
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	136
42. Rank correlation of 12 spring wheat cultivars for stomatal number. Greenhouse vs. field conditions	138
43. Ranking based on cultivar mean stomata per 1.17 mm ² microscopic field	138

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 CO₂ 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 out-yield 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 desiccation 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 persistence 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 glomerata*) 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 (Knoch 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 Knoch 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; Knoch 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; Knoch et al., 1957; Mitchell, 1970). Knoch 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.

