DROUGHT RESISTANCE OF WHEAT SEEDLINGS

UNDER CONTROLLED MOISTURE

CONDITIONS

By

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CHAPTER I

INTRODUCTION

Water plays a very important role in crop production. The availability of water is a critical factor in arid and semi-arid regions. Kramer (15) reported that there are four general functions of water in plants: a) as the major constituent of physiological tissue, b) as a reagent in photosynthetic and hydrolytic processes, c) as the solvent in which solutes move from cell to cell and organ to organ, and d) as an important factor for the maintenance of turgidity necessary for cell enlargement and growth.

There are several environmental factors that can influence the growth and yield of crops. Water stress is one of the most widespread and serious environmental variables affecting plant growth (12). Growth retardation as a result of water deficiency is well known. Stocker (31) indicated that enzymatic activities are retarded by plant water deficits, and particularly the shortage of building material caused by the reduction of photosynthesis. Sullivan and Eastin (33) reported that specific enzymatic reactions or metabolic processes may have critical water potentials at which they are severely altered or cease to function.

Cereal production in the world is limited by a shortage of moisture nearly every year (10). Wheat is grown in the areas of the world where the average annual rainfall ranges from 25-177 cm (17). Decreased plant water potential causes reduction in photosynthesis, increased stomatal diffusion resistance and subsequently decreased yields (4).

Bayles et al. (2) reported that the ability of wheat plants to produce grain under drought conditions might be related to: a) the ability of the root systems to absorb water as fast as or faster than the amount of water lost by transpiration, and b) the ability of plants to limit transpiration and to continue the process of photosynthesis and assimilation under high evaporative demands. Sullivan and Eastin (33) state that it is necessary to have a complete understanding of the physiological responses to moisture stress including those factors related to drought resistance in order to accomplish plant modification for more efficient water use.

Limited success has been obtained in screening plants for drought tolerance by selection on the basis of morphological characters such as fewer stomata or more extensive root systems because of the genotype-environment interactions (39). Heyne and Laude (8) reported that the resistance to high temperature and moisture stress is an important factor to consider in the development of new cultivars of corn for semi-arid regions. Hurd (11) points out that in breeding for drought resistance in wheat, the breeder should select parents that a) have extensive root systems, b) maintain their photosynthetic process under stress, c) are productive under moisture stress, and d) grow fast at early growth stages.

The objectives of this study were to examine techniques for evaluating selected winter wheat cultivars for their drought resistance. The specific objective was to differentiate between the response of these cultivars at an early growth stage under moisture stress.

CHAPTER II

REVIEW OF LITERATURE

The effect of drought on cereal crops varies with the stage of growth at which the stress occurs. Henkel (7) reported that drought in cereals during spikelet formation, slightly decreased the yield of grain by decreasing the number of kernels in the head. Drought during the grain formation led to smaller kernels and incomplete filling of the head. Misra (21) conducted a greenhouse study in which wheat cultivars were subjected to varying periods of moisture stress at different growth stages to study their ability to withstand drought. This study revealed that exposure to drought at the boot stage was more injurious than at earlier stages of growth.

Classification and Definitions of Drought Resistance

Many definitions have been suggested for drought and drought resistance. Drought is used to describe the lack of soil moisture, and occurs when the available soil moisture is lowered to a point where the plant cannot absorb water rapidly enough to replace that lost to the air by transpiration (26). Singh et al. (28) suggest that drought resistance is the ability of the plant to obtain and retain water as well as carry out its metabolism during a period of low water potential in the tissue. Henkel (7) gives the following definition of drought re-

> Drought-resistant plants are those which in the process of ontogenesis are able to withstand the effect of drought and which can normally grow, develop and reproduce under drought conditions because of a number of properties acquired in the process of evolution under the influence of environmental conditions and natural selection (p. 363).

Shantz (27) classified plants which grow in regions subject to drought into four groups: 1) those which escape drought by a short, rapid growth period; 2) those which evade drought by conserving the limited moisture supply, by small size, restricted growth, wide spacing or low water requirement; 3) those which endure drought by passing into a drought dormant condition until water is again available to the roots; 4) those which resist drought by storing up a supply of water to be used when none can be obtained from the soil. Levitt (18) divided drought resistance into either drought avoidance or drought tolerance. He stated that the drought-avoiding plant maintains a high internal water potential in spite of the low environmental water potential to which it is exposed. Drought tolerance means a plant can survive a low tissue water content and/or water potential. Shantz (27) reported that drought evading is the most important group. Most of the cereals grown in semi-arid regions belong to this group.

Stomatal Movement and Stomatal Resistance

Stomata have a significant control over transpiration under normal conditions; therefore, the mechanism of stomatal movement appear to be very important (29). More than 80% of the water is lost through stomata (20).

Stomatal opening and closing are important mechanisms that should be understood because they are directly related to water loss. Waggoner and Zelitch (38) reported that stomatal opening is caused by turgor changes and the difference in turgor between guard cells and their adjacent cells. Salim (25) reported that stomata of hardened wheat plants when subjected to moisture stress remained open, while the stomata in non-hardened wheat plants closed. During moisture stress, stomata in sorghum close later than stomata in corn and wilt at a lower water potential than stomata in corn (32).

The amount of carbon dioxide which is fixed by leaves is directly related to the mechanism of stomatal opening and closing. Under moisture stress the stomata tend to close and the flow of carbon dioxide into the leaf through stomata is decreased. Brown and Rosenberg (3) indicated that most of the carbon dioxide fixed by leaves enters through the stomata of the leaf epidermis. Sullivan (34) reported that when the stomata close under moisture severe dessication may be avoided, but diffusive resistance to CO_2 exchange increases, photosynthesis decreases and yield is decreased.

Light intensity has a direct affect on the stomatal resistance. The size of stomatal aperture is regulated by photoactive and hydroactive processes (3). Quarrie and Jones (23) conducted experiments to compare the effects of abscisic acid (ABA) and moisture stress on leaf morphology and floral development in a spring wheat. Their results indicated that both ABA and moisture stress decreased the mean cell size, reduced the number of stomata per leaf, and increased the production of trichomes in all the leaves sampled. It was concluded that abscisic acid (ABA) could mediate many of the responses of wheat plants to prolonged moisture stress.

Transpiration and Transpiration Rate under Moisture Stress

The loss of water vapor from living plants is known as transpiration. Most of this water loss occurs through stomata. The amount of water loss by transpiration is affected by different factors such as plant species, intensity of solar radiation, soil condition, humidity of the atmosphere, leaf area, and some other factors.

The transpiration rate is more important than the transpiration per se because of difference in leaf area. The transpiration rate of plants as reported by Kramer (15) is determined by a) leaf structure and leaf area, b) the period in which stomata remain open, c) environmental factors such as temperature and atmosphere vapor pressure.

Under moisture stress the plant stomata tend to close and the amount of transpiration decreases as a result. Veihmeyer and Hendrickson (37) reported that the wilting of a plant does not indicate that water has ceased to move from the soil into the plant, but simply that transpiration has exceeded absorption and conduction.

The transpiration rate differs among species, and may be used an an indicator of drought resistance. Stefanouskii (30), using the drought chamber, found that *Triticum durum* transpired more rapidly than *T. vulgare* when subjected to drought; and Mediterranean wheats transpired more than similar cultivars from the Russian steppe region.

Growth and Growth Rate under Moisture Stress

Growth and growth rate are influenced by moisture stress. This influence is not the same for roots and shoots. Evans et al. (5) reported that with moderate moisture stress shoot growth may be reduced more than photosynthesis, but some root growth may reamin active, leading to a decrease in the shoot/root ratio. Sandhu and Laude (26) reported that the study of root/top ratios indicated that dry weight of roots was greater in proportion to top growth in drought hardy winter wheat cultivars than nonhardy cultivars from early tiller stage to the late stage of growth and development.

During a period of soil moisture stress, the growth of organs is influenced in this order of decreasing severity: leaves > stems > roots (22). Hagan et al. (6) found in Ladino clover that whereas green weight and shoot elongation were reduced significantly when soil moisture decreased into the lower half of the available range, photosynthesis, dry weight, and respiration rates were not appreciably affected until the moisture content in the entire root zone approached the permanent wilting percentage.

Germination Study

Moisture stress has an influence on germination. As moisture stress increases, germination is delayed, and the rate of germination is reduced. Helmercik and Pfeifer (9) used mannitol solutions to obtain moisture stress with winter wheat and reported that, as moisture stress increased, germination was delayed and the rate of seedling growth was reduced. Knipe and Herbel (14) reported that a moisture tension of three atmospheres did not greatly delay germination of several grass species tested. All the species which germinated at 11 atmospheres and higher had delayed germination at these higher levels of moisture stress. However, the total germination percentage and rates of initial seedling growth were reduced for several range grasses. Uhvits (36) tested the germination of alfalfa seeds, using sodium chloride and mannitol, at different concentrations ranging from 1 to 15 atmospheres. She found that sodium chloride was more inhibitory than mannitol. Therefore, she concluded that differences in response suggested a toxic effect of the sodium chloride.

Survival Study

Laude (16) defined survival as the ability of plants to avoid or postpone reaching levels of dryness which are injurious, and the ability to endure dehydration with a minimum of injury. Todd and Webster (35) conducted survival studies in which nine wheat cultivars were subjected to weekly cycles of drought followed by rewatering. Their results indicated that there was a continuing loss of plants with each successive cycle. Ridley and Todd (24) reported that when drought becomes severe, the older leaves are usually the first to die, followed by the younger leaves. They also point out that survival is dependent on maintenance of a viable shoot meristem. Otherwise, the plants do not recover from drought. Laude (16) indicated that young tissues, such as buds and meristems, often seem to have a higher degree of tolerance to lack of water than do older tissues.

Plant species differ in their ability to recover in terms of photosynthetic activity following a drought period (35). Stocker (31) discussed evidence suggesting that plants may go through a hardening process when they are exposed to drought which enables them to photosynthesize better while under moisture stress. The ability to photosynthesize while under moisture stress, or to recover more quickly after rewatering, might contribute to drought resistance.

Techniques of Testing for Drought Resistance

Many investigators reported that field drought tests are desirable, but the problem of testing for drought resistance in the field is hampered by the great fluctuations in moisture which can occur from year to year and from location to location. Therefore, it would seem to be very difficult to obtain the right conditions when needed. For these important reasons, several techniques have been used to facilitate the measurement of plant moisture stress. Salim (25) stated that many investigators reported the use of greenhouse and laboratory methods, employed artificial conditions, and used various physiological manifestations to test for drought resistance.

Stomatal resistance has been used as a technique for measuring drought resistance. Sullivan (34) pointed out that diffusive resistance or stomatal observations indicate that the internal water potential is kept high by retarded transpiration.

Germination of seeds under different levels of moisture has been used by several investigators. Uhvits (36) found that the higher the concentration of mannitol and sodium chloride, the lower the rate and percentage of germination of alfalfa seeds. She observed no germination of alfalfa seeds at 12 to 15 atmospheres.

A survival approach has been used in studies of drought injury and resistance. Levitt (19) reported that most investigators now determine drought resistance directly on the basis of drought survival. Misra (21) planted four cultivars of wheat and four strains of hybrid corn under dry periods of 11, 15 and 19 days at four stages. The percentage of plant recovery in these three different drought periods was 61, 34, and 26% respectively. This study with different cultivars of wheat revealed that exposure to drought at the boot stage was more injurious than exposure at earlier stages of growth. The percentage recovery decreased with increased age of the plants.

CHAPTER III

MATERIALS AND METHODS

Six cultivars of wheat were tested and evaluated for drought resistance. These cultivars were:

1. Rall - released in 1976 by Oklahoma Agriculture Experiment Station.

2. KanKing - developed by Earl G. Clark, Sedgwich, Kansas.

3. Triumph 64 - developed by Joseph E. Danne, El Reno, Oklahoma.

4. Payne (OK711092A) - released by Oklahoma Agriculture Experiment Station, 1977.

5. Sturdy - developed in 1966 by Texas Agricultural Experiment Station.

6. David - an introduction from Austria.

Three different studies were used: 1) a laboratory germination test using d-mannitol solutions ranging from 0 to 15 atmospheres; 2) a moisture stress study using two moisture levels; and 3) a survival study using two levels of moisture stress and different cycles. The last two studies were conducted in a controlled growth chamber.

Laboratory Germination and Drought Resistance

Germination tests were conducted in 1977, on the six wheat cultivars listed above.

First Experiment

Solutions of 0, 3, 6, 9, 12 and 15 atm of moisture tensions were prepared using d-mannitol and deionized distilled water.

The amount of mannitol and distilled water were calculated according to Van't Hoff formula: $-\Psi = m\ i\ R\ T$.

Where: Ψ = osmotic potential (atm)
m = molality of the solution
i = a constant for ionization (i=1.0)
R = gas constant (0.083 liter-atmospheres/mole-degree)
T = absolute temperature (C^o + 273)

The check treatment consisted of deionized distilled water, representing 0 atmospheres. Plastic germination containers with covers were used. The substratum for all containers was four thickness of absorbent germination tissue.

Fifty uniform seeds were placed in each container to which 8 ml of mannitol solution were added. A randomized complete block design was used with four replications. One replicate consisted of 36 containers of treatments randomly assigned to one tray as suggested by Ahring et al. (1). All containers were covered to prevent evaporation and placed in a germinator at 20^{o}C with a high humidity.

Second Experiment

The experimental design, wheat cultivars, and environmental conditions that were used in the second experiment were similar to the first experiment except that mannitol concentrations and the germinator were different. Solutions of 0, 9, 11, 13 and 14 atm of moisture tension were prepared as described in the first experiment.

Percentage germination counts were made after 7 days as the first count and after 14 days as the final count for both experiments. A seed was considered as germinated when the seedling met the following three criteria: a) the presence of a normal primary root, b) the presence of a normal primary shoot, and c) the absence of abnormal growth.

Moisture Stress Study

This study was conducted in the growth chamber to measure the differences among four different wheat cultivars. Four measurements: transpiration, diffusion resistance, total leaf area, and shoots-fresh and dry weight were taken under moisture stress conditions.

Cultivars of wheat, Rall, Payne, KanKing, and David, were selected from the germination study to be tested and evaluated for drought resistance under two levels of moisture stress. A randomized complete block design with six replications was used. Each replication consisted of ten pots representing treatments assigned at random. There were two check pots in each replication.

The check pots did not contain plants and were used to determine the loss of water from the soil by evaporation. Pots, 11.5 cm diameter and 9.5 cm deep, were filled with 625 grams of a mixture of two parts per volume of soil and one part of vermiculate. Nine seeds were planted in each pot; the seedlings were thinned to five per pot five days after emergence.

The plants were subjected to stress treatments at three weeks of age. Stress treatments 1 and 2 received a 150 and 100 cc of tap water, respectively. Then, water was withheld for the rest of the period during which the measurements were taken periodically through a five-day period.

A controlled growth chamber was used with 16-7^{o}C day-night temperatures, and 12-hour light period.

The pots were weighted each 24 hours for five consecutive days. The change in weight of pots with no plants represented the amount of evaporation. Rates of transpiration, for the given period, were measured by determining the rate of change in weight of pots, containing the experimental plants. Corrections for surface evaporation were made by subtracting the rate of change in weight of identically treated pots without plants. The rate of transpiration was expressed in terms of grams water per 24 hours per cm^2 of leaf area.

Stomatal resistance was measured with a Lambda LI-64S diffusive resistance meter made by Lambda Equipment Corporation, Lincoln, Nebraska, and a LI-20S sensor calibrated according to the methods of Kanemasu et al. (13). Resistance was measured on the upper surface of the third leaf approximately two cm away from the stem, each 24 hours for five consecutive days on a random basis of one plant a day.

At the end of the experiment, the plants were harvested to determine total leaf area and the fresh weight and dry weight of the shoots. The total leaf area was then measured by the use of a LI-COR Leaf Area Meter (Model LI-3000A, Lambda Instrument Corp., Lincoln, Nebraska).

Survival Study

This experiment was designed to test for seedling survival under various drought cycles. Four wheat cultivars of Rall, Payne, KanKing, and David were selected to be tested and evaluated under this study. Pots measuring 9 by 9 by 8 cm were filled with 420 grams of a mixture of two parts of soil and one part vermiculate. Thirty uniform seeds were planted per pot, and the seedlings were thinned to 20 per pot five days after emergence. The pots were placed in a controlled environment chamber with 20-12^{o}C day-night temperatures, and 12 hour light period.

After the plants reached two weeks of age, stress treatment 1 and stress treatment 2 pots were watered with 80 and 50 cc tap water, respectively. Then, the seedlings were held without watering seven days until they showed severe wilting, at which time the seedlings were rewatered. Three days later, the percentage recovery for the first cycle was recorded. The same procedure was repeated for three more cycles. Water was added at the beginning of each cycle.

CHAPTER IV

RESULTS AND DISCUSSION

Laboratory Germination and Drought Resistance

First Experiment

In this experiment, data on the seed germination of six wheat cultivars at different concentrations of d-mannitol are given in Tables I, II, and III. Germination decreased in response to increased mannitol concentration.

Duncan's multiple range test at the 0.05 level in Tables I, II, and III showed that there was no difference among cultivars under 0 atmospheres. At the lower mannitol concentrations (3 and 6 atm), the variation among cultivars was relatively small. However, under the higher concentrations (9 and 12 atm), the differences among cultivars were at a maximum. Therefore, greater opportunity exists to differentiate among cultivars under the higher levels of moisture stress (9 and 12 atm) than under lower levels of stress. The cultivars did not respond the same relative to one another under different moisture tensions as indicated by interaction between cultivars and mannitol levels.

Germination, after 7 days, was highly variable under 9 atmospheres. The cultivars David and Rall showed the lowest germination under this moisture level, while Sturdy showed the highest (Table I). After 14

TABLE I

THE PERCENTAGE GERMINATION FOR SIX WHEAT CULTIVARS AT SIX LEVELS OF MOISTURE TENSION AFTER 7 DAYS (FIRST COUNT)

Cultivar	Moisture Tension (Atm)						Average
	0	3	6	9	12	15	
Rall	88 a*	84 b	54 c	0 d	0 a	0 a	37 c
Triumph 64	95 a	92 a	54 c	5 cd	0 a	0 a	41 a
Payne	93 a	95 a	74 a	17 b	0 a	4 a	47 ab
Sturdy	95 a	85 b	71 ab	42 a	0 a	0 a	48 a
KanKing	90 a	84 b	67 b	8 c	3 a	0 a	42 b
David	90 a	89 ab	49 c	0 d	4 a	0 a	38 b

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

TABLE II

THE PERCENTAGE GERMINATION FOR SIX WHEAT CULTIVARS AT SIX LEVELS OF MOISTURE TENSION FROM DAY 7 TO DAY 14 (SECOND COUNT)

Cultivar	Moisture Tension (Atm)						Average
	0	3	6	9	12	15	
Rall	2 a*	3 a	35 a	72 a	50 a	2.0 ab	27 a
Triumph 64	0 a	1 a	39 a	80 a	21 c	0.5 ab	23 ab
Payne	0 a	2 a	20 b	63 b	16 cd	9.5 a	18 c
Sturdy	1 a	8 a	20 b	44 c	32 b	0.0 b	17 cd
KanKing	2 a	9 a	20 b	74 a	34 b	0.0 b	23 b
David	2 a	5 a	41 a	28 d	9 d	0.0 b	14 d

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

TABLE III

THE PERCENTAGE GERMINATION FOR SIX WHEAT CULTIVARS AT SIX LEVELS OF MOISTURE TENSION AFTER 14 DAYS (TOTAL COUNT)

Cultivar	Moisture Tension (Atm)						Average
	0	3	6	9	12	15	
Rall	90 a*	87 b	90 a	72 b	50 a	2 b	65 a
Triumph 64	95 a	93 ab	94 a	85 a	21 c	0	65 a
Payne	93 a	97 a	94 a	80 a	16 cd	14 a	66 a
Sturdy	96 a	93 ab	91 a	86 a	32 b	0 b	66 a
KanKing	92 a	93 ab	87 a	83 a	38 b	0 b	65 a
David	95 a	93 ab	90 a	28 c	13 d	0 b	53 b

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

days (Table III) David showed the lowest germination under 9 and 12 atm while Triumph 64, Payne, Sturdy, and KanKing had the highest germination under 9 atmospheres, but the cultivar Rall showed the highest germination under 12 atmospheres.

The analysis of variance (Table IV) indicated that genotypic effects, mannitol concentrations (moisture tensions), and genotype by mannitol concentration interactions were highly significant at the 0.01 probability level for germinated seeds.

Second Experiment

The analyses of variance (Table V) indicated that mannitol concentrations and genotypic effects were highly significant at the 0.01 probability level for germinated seeds. Percent seed germination of the six wheat cultivars is presented in Tables VI, VII, and VIII. The differences among cultivars were at a maximum under 9 and 11 atm. Again the genotype by mannitol concentration interaction was highly significant. Under 9 atm, KanKing showed the highest percent germination, while David showed the lowest ability to germinate after 7 days. After 14 days, David had the lowest ability to germinate, while Payne had the highest germination under 9 and 11 atmospheres.

Total germination percentages, in both experiments, were largely inhibited by high moisture tension of mannitol solutions. This result was similar to that found by other investigators (9, 14, and 36). Seeds of all cultivars germinated quickly at low moisture tension. Knipe and Herbel (14) reported that germination was not delayed under low moisture stress. If enough time was given to the seeds, relatively high germination rates were obtained with higher mannitol concentrations.

TABLE IV

ANALYSIS OF VARIANCE AMONG SIX WHEAT CULTIVARS FOR GERMINATION PERCENTAGE IN SIX CONCENTRATIONS OF D-MANNITOL

Source	df	Mean Squares		
		1st Count	2nd Count	Total Count
Rep	3	48.17*	40.49	171.36**
Genotype	5	120.14***	140.88**	157.69***
Error A (Rep * GE)	15	21.90	24.79	13.33
M_1 (Linear)	1	43993.46***	0.02	43934.53***
M_2 (Qud.)	1	10709.41***	12632.51***	79.36
M-Level (Res.)	3	335.11***	1097.60***	444.83***
GE * M_1	5	11.66	38.68	38.22
GE * M_2	5	76.98**	237.68***	267.17***
GE * M-Level	15	63.64***	112.78***	96.61***
Error B	90	18.84	42.35	30.02

* Significant at the 5% level
** Significant at the 1% level
*** Significant at the 0.1% level

TABLE V

ANALYSIS OF VARIANCE AMONG SIX WHEAT CULTIVARS FOR GERMINATION PERCENTAGE IN FIVE CONCENTRATIONS OF D-MANNITOL

Source	df	Mean Squares		
		1st Count	2nd Count	Total Count
Rep	3	14.94	31.22	88.05***
Genotype	5	123.39***	131.19***	372.14***
Error A (Rep * GE)	15	6.87	34.15	29.86*
M_1 (Linear)	1	31735.12***	182.67***	36733.23***
M_2 (Qud.)	1	5952.77***	12848.30***	1310.16***
M-Level (Res.)	2	59.49***	843.04***	583.70***
GE * M_1	5	21.62**	22.37	30.41
GE * M_2	5	206.09***	117.89***	432.43***
GE * M-Level	10	138.14***	173.57***	40.19**
Error B	72	6.92	19.91	15.79

* Significant at the 5% level
** Significant at the 1% level
*** Significant at the 0.1% level

TABLE VI

THE PERCENTAGE GERMINATION FOR SIX WHEAT CULTIVARS AT FIVE LEVELS OF MOISTURE TENSION AFTER 7 DAYS (FIRST COUNT)

Cultivar	Moisture Tension (Atm)					Average
	0	9	11	13	14	
Rall	91 b*	2 d	0 c	0.0 a	0.0 a	19 c
Triumph 64	95 a	5 c	1 c	0.0 a	0.0 a	20 c
Payne	94 a	46 b	6 a	0.0 a	0.0 a	29 a
Sturdy	94 a	45 b	3 b	0.0 a	0.0 a	28 ab
KanKing	85 c	51 a	1 c	0.0 a	0.0 a	27 b
David	95 a	0 e	0 c	0.0 a	0.0 a	19 c

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

TABLE VII

THE PERCENTAGE GERMINATION FOR SIX WHEAT CULTIVARS AT FIVE LEVELS OF MOISTURE TENSION FROM DAY 7 TO DAY 14 (SECOND COUNT)

Cultivar	Moisture Tension (Atm)					Average
	0	9	11	13	14	
Rall	1 a*	74 a	44 c	2 c	1 b	24 a
Triumph 64	1 a	48 b	41 c	6 b	3 ab	20 b
Payne	1 a	44 cd	67 a	6 b	2 b	24 a
Sturdy	1 a	42 d	58 b	2 c	1 b	21 ab
KanKing	3 a	33 f	67 a	12 a	5 a	24 a
David	0 a	39 e	16 d	0 c	0 b	11 c

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

TABLE VIII

THE PERCENTAGE GERMINATION FOR SIX WHEAT CULTIVARS AT FIVE LEVELS OF MOISTURE TENSION AFTER 14 DAYS (TOTAL COUNT)

Cultivar	Moisture Tension (Atm)					Average
	0	9	11	13	14	
Rall	92 b*	76 c	44 d	2 c	1 bc	43 c
Triumph 64	96 a	53 d	42 d	6 b	3 ab	40 d
Payne	95 a	90 a	73 a	6 b	2 b	53 a
Sturdy	95 a	86 b	60 c	2 c	1 b	49 b
KanKing	87 c	84 b	68 b	12 a	5 a	51 ab
David	95 a	39 e	16 e	0 c	0 c	30 e

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

Moisture Stress Study

Transpiration and Transpiration Rates

According to the analysis of variance for transpiration and transpiration rate (Table IX), the differences among cultivars were not significant. This is probably due to the fact that total leaf area is related to the amount of water transpired during the five consecutive days. Significant differences were found among days at the 0.01 level of probability. There was a significant interaction between stress by day at the 0.01 level of probability, but no interaction between cultivar by day. This indicates that cultivars follow the same pattern during the five consecutive days.

Diffusion Resistance

The stomatal diffusion resistance values increased gradually near the end of the five-day period, indicating that moisture stress was increased from day to day as shown in Table X. It was concluded that plants close their stomata on the upper leaf surfaces, when exposed to moisture stress.

The values of diffusion resistance in the first day were higher than those in the second and the third days. This was due to the light effect because in the first day the light was off until 10:00 a.m. and the measurements were taken at 11:30 a.m. every day. Therefore, at least some stomata were closed due to the light stress when the measurements were taken.

The differences among cultivars occurred only in the fifth day as shown in Figure 1. Table X shows that Payne was significantly different

TABLE IX

ANALYSIS OF VARIANCE AMONG FOUR WHEAT CULTIVARS FOR TRANSPIRATION, TRANSPIRATION RATE, AND STOMATAL DIFFUSION RESISTANCE UNDER TWO MOISTURE LEVELS

Source	df	Mean Squares		
		Transpiration	Transpiration Rates	Diffusion Resistance
Rep	5	52.56	0.0029	21.28
Genotype	3	17.67	0.0003	78.10*
Stress	1	1079.08**	0.0899**	408.33**
GE Stress	3	5.35	0.0021	35.30
Error A (R * V/X)	35	12.43	0.0009	22.60
Day	4	1611.99**	0.1453**	772.38**
GE * Day	12	5.95	0.0008	27.24
Stress * Day	4	308.65**	0.0281**	242.17**
GE * Stress * Day	12	2.33	0.0003	24.06
Error B (R*D+R*D*G|S)	160	9.85	0.0010	23.77

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.

TABLE X

DAILY STOMATAL DIFFUSION RESISTANCE
OF FOUR WHEAT VARIETIES UNDER
MOISTURE STRESS

Cultivar	Diffusion Resistance (Sec/cm)					
	Days of Moisture Stress					
	1	2	3	4	5	Average
Rall	5.68 a*	2.46 a	2.23 a	4.68 a	13.64 ab	5.74 a
Payne	4.76 a	2.67 a	2.49 a	4.14 a	16.00 a	6.17 a
KanKing	3.51 a	2.07 a	1.94 a	3.38 a	7.34 b	3.65 a
David	3.53 a	2.07 a	2.50 a	3.89 a	10.96 b	4.59 a

* Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range test.

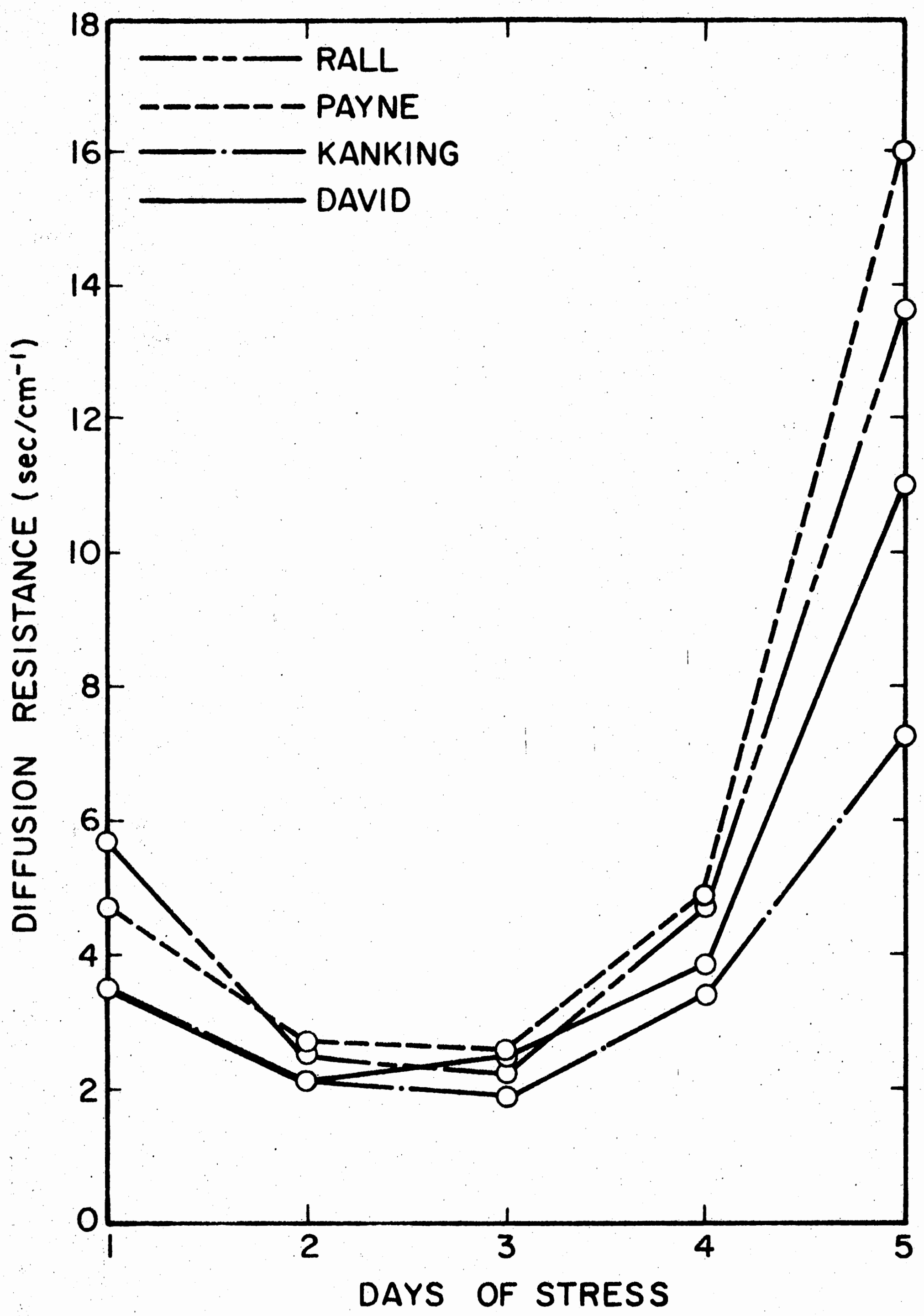

Figure 1. Mean Diffusive Resistance of Four Wheat Cultivars through Five Consecutive Days Under Moisture Stress.

from KanKing and David at the 0.01 level of confidence (Duncan's Multiple Range test). The order of cultivars from highest to lowest stomatal diffusion resistance at five days was as follows: Payne, Rall, David, and KanKing. The diffusion resistance values were respectively 16.00, 13.64, 10.96, and 7.34 sec cm^{-1}.

The analysis of variance for stomatal diffusion resistance (Table IX) showed that there were significant differences among moisture stress levels at 0.01 level of probability. There were also significant differences among days at the 0.01 level of probability. The interaction between stress by day was significant at the 0.01 level of confidence. No interaction between cultivar by day was observed. This indicates that cultivars follow the same pattern during the five consecutive days.

Fresh and Dry Weights

The data on fresh and dry weights of four wheat cultivars at two moisture levels are given in Tables XI and XII. These data indicate that green weight and dry weight are affected by soil moisture stress.

Duncan's Multiple Range Test at the 0.05 level in Tables XI and XII showed that there were significant differences among cultivars under Stress treatment 1 and Stress treatment 2. Payne had the highest fresh weight under the two moisture levels, while KanKing had the lowest fresh weight (Figure 2). In the case of dry weight Payne and Rall had the highest values, while KanKing had the lowest dry weight (Figure 3). Fresh and dry weights reflected the increased dryness under Stress treatment 2. The analysis of variance (Table XIII indicates that there were significant differences among cultivars and moisture levels.

TABLE XI

AVERAGE MEANS OF FRESH WEIGHT OF FOUR WHEAT CULTIVARS UNDER TWO MOISTURE LEVELS

Cultivar	Fresh Weight (gms)		
	Stress 1	Stress 2	Average
Rall	2.4 bc*	3.3 b	2.3 bc
Payne	2.9 a	2.6 a	2.7 a
KanKing	2.1 c	1.9 b	2.0 c
David	2.6 b	2.2 b	2.4 b

* Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

TABLE XII

AVERAGE MEANS OF DRY WEIGHT OF FOUR WHEAT CULTIVARS UNDER TWO MOISTURE LEVELS

Cultivar	Dry Weight (gms)		
	Stress 1	Stress 2	Average
Rall	0.396 bc*	0.408 a	0.402 b
Payne	0.481 a	0.430 a	0.456 a
KanKing	0.375 c	0.356 b	0.366 c
David	0.442 ab	0.390 ab	0.416 b

* Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

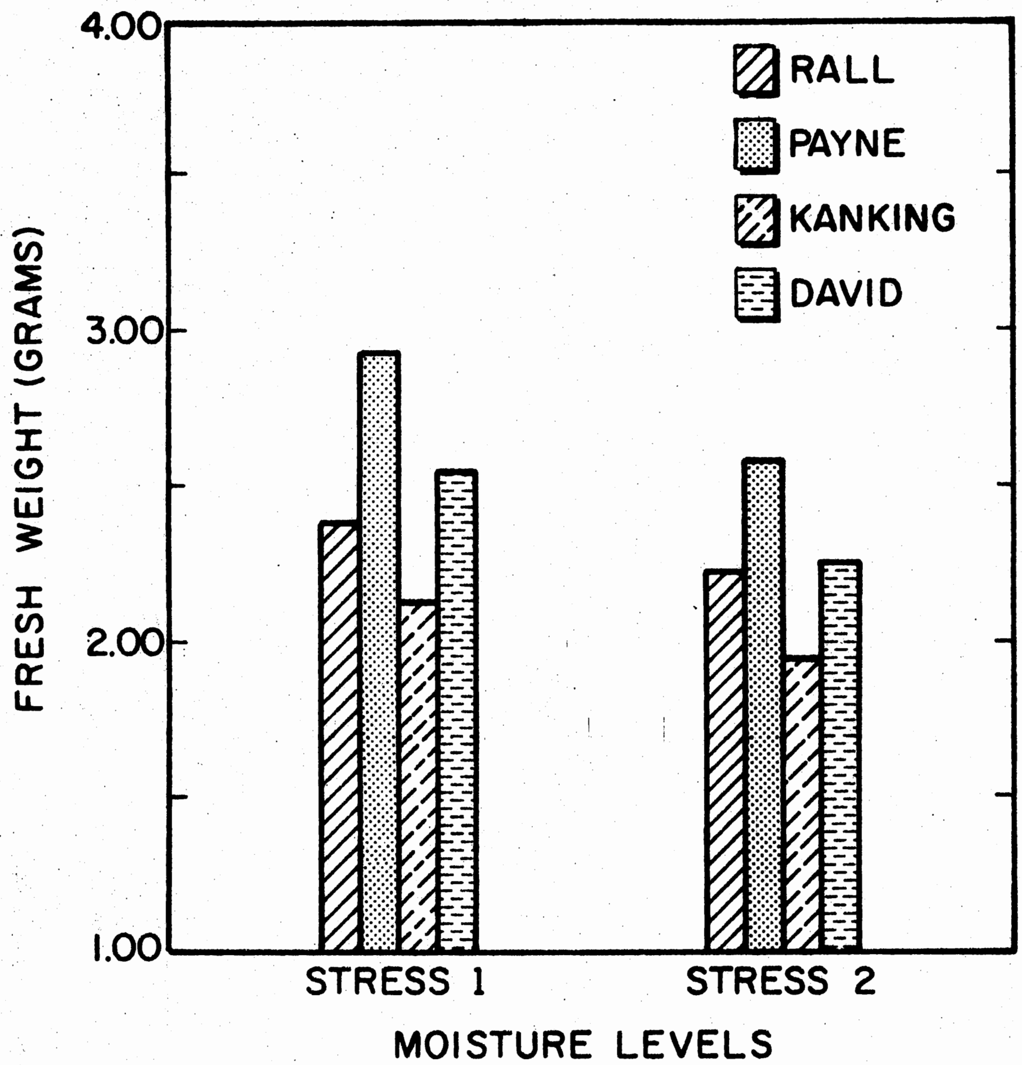

Figure 2. Fresh Weight of Four Cultivars Under Two Moisture Levels.

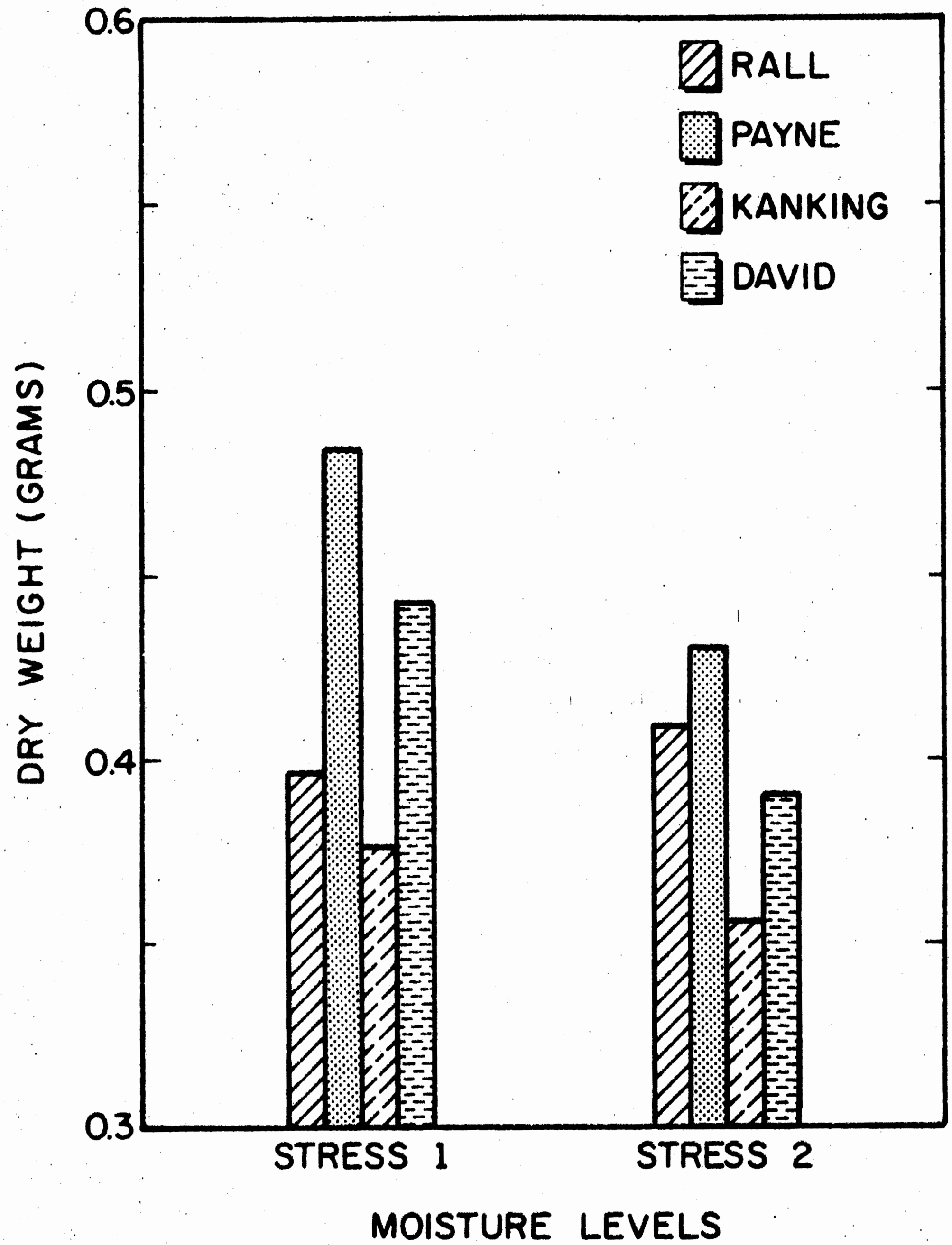

Figure 3. Dry Weight of Four Wheat Cultivars Under Two Moisture Levels.

TABLE XIII

ANALYSIS OF VARIANCE AMONG FOUR WHEAT CULTIVARS FOR FRESH WEIGHT, DRY WEIGHT, AND LEAF AREA UNDER TWO MOISTURE LEVELS

Source	df	Mean Squares		
		Fresh Weight	Dry Weight	Leaf Area
Rep	5	0.5688	0.0177	409.7610
Genotype	3	1.0122***	0.0165***	880.7127*
Stress	1	0.6491**	0.0090*	307.5975
GE * Stress	3	0.0210	0.0028	467.1643
Error (R*V|S)	35	0.0726	0.0022	237.1761

* Significant at 5% level
** Significant at 1% level
*** Significant at 0.1% level

Leaf Area

Duncan's Multiple Range Test at the 0.05 probability level in Table XIV indicated that there were significant differences among cultivars under Stress treatment 1. The differences among cultivars under Stress treatment 2 were not significant. This indicates that the differences which occurred under Stress treatment 1 were not due to moisture stress effect. It may be due to genetic makeup differences or certain environmental factors such as light and temperature. In Stress treatment 2, the results were expected because moisture stress during the five-day period, or actually the last three days, should not affect the leaf area.

TABLE XIV

AVERAGE MEANS OF LEAF AREA OF FOUR WHEAT CULTIVARS UNDER TWO MOISTURE LEVELS

Cultivar	Leaf Area (cm^2)		
	Stress 1	Stress 2	Average
Rall	97.66b	104.77a	101.22a
Payne	128.50a	110.47a	119.49a
KanKing	102.25b	106.25a	104.25a
David	108.81b	95.47a	102.14a

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

Survival Study

This study indicated that the older leaves died first, followed by the younger leaves. This indicates that water may move from the older leaves to the younger ones in the individual plant when wilting occurs. It was observed that when the shoot meristem died the recovery from drought was not possible.

Survival Percentage

Data presented in Table XV show a continuous reduction in percentage survival with each successive drought period. This result agreed with the results presented by Todd and Webster (35). The reduction in number of plants was not the same in all the cultivars (Figure 4). The average percentage survival of four drought cycles for Rall, Payne,

TABLE XV

SURVIVAL OF FOUR WHEAT CULTIVARS
FOR FOUR DROUGHT CYCLES

Cultivars	Percent Survival of Four Cycles			
	I	II	III	IV
Rall	75.00a	55.63a	46.56a	30.63a
Payne	77.81a	41.25b	32.50bc	25.31ab
KanKing	58.75b	47.81ab	37.50ab	29.69a
David	64.06b	29.69c	25.94c	22.50b

*Cultivars followed by the same letter were not significantly different at the 5% level using Duncan's Multiple Range Test.

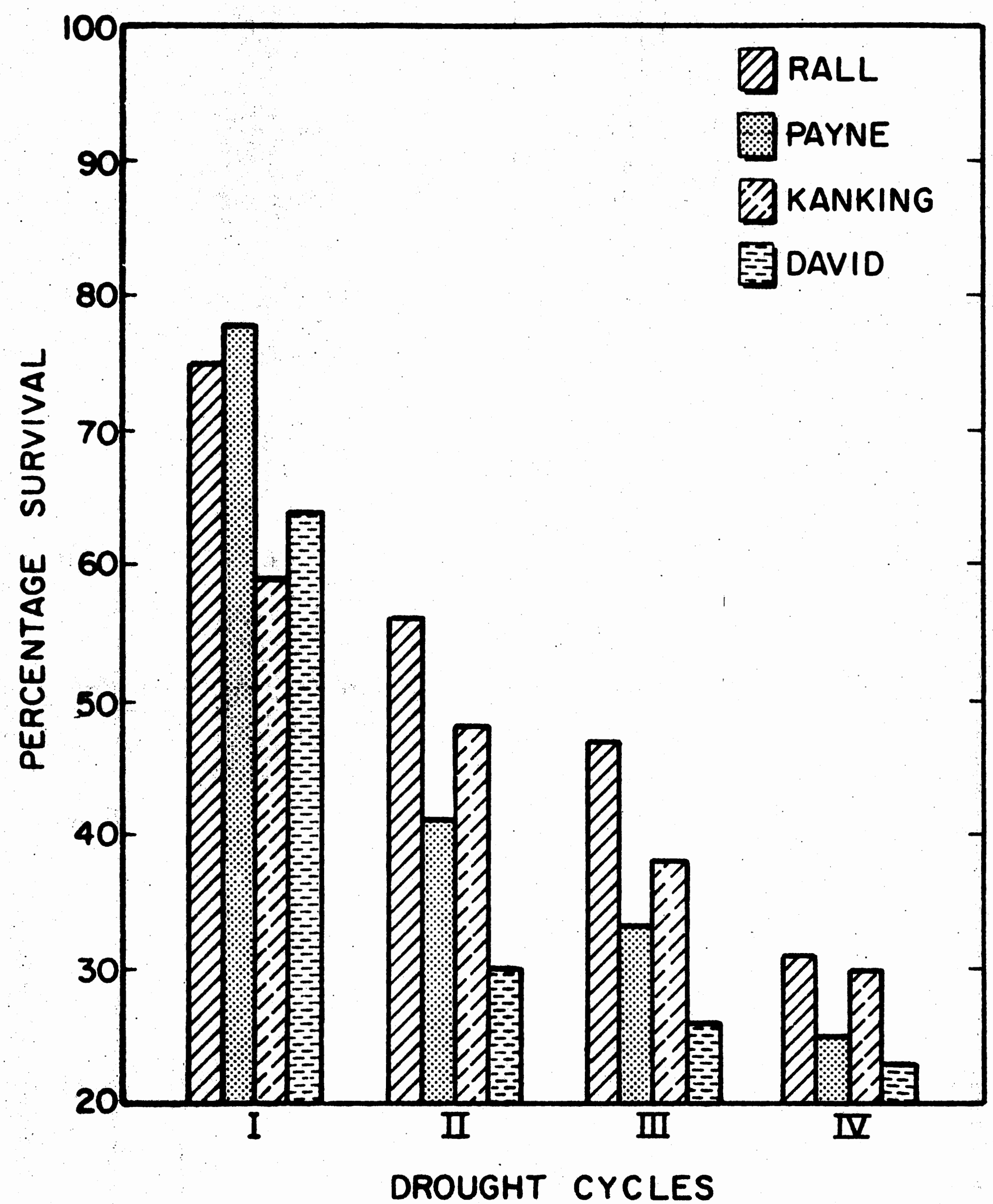

Figure 4. Mean Survival % of Four Cultivars after Exposure to Four Successive Drought Cycles.

KanKing, and David was 51.95, 44.22, 43.44, and 35.55%, respectively. Rall and Payne had the highest percentage survival, while David and KanKing had the lowest percentage under Stress treatment 2. In the case of Stress treatment 1, Rall, Payne, and KanKing had the highest percentage survival, while David had the lowest percentage.

The Multiple Range Test (Table XV) on percentage survival, in the first drought cycle showed that cultivars could be separated into two groups. In the second cycle, only David was separated, but in the third and fourth cycle, the cultivars were not distinctly separated from one another as indicated by the overlapping of the ranges.

The analysis of variance for percentage survival (Table XVI) indicated that significant differences among cultivars were observed in drought cycles I, II, III, and IV at different probability levels. The differences among moisture levels were significant at the 0.001 probability level in the whole drought cycles. The interaction of cultivar by stress was observed only in the first drought cycle at 0.01 probability level.

The results of the survival study were in conformity with other results, which were obtained from germination in mannitol solutions and diffusion resistance.

There were no significant differences in row and column effects in the survival study (Table XVI). Also the data indicated that the variation within the growth chambers that were used was low. The Latin square design was selected because previous research had shown much variation within the growth chamber.

In the first run, where the moisture stress was not enough to kill the plants, leaves of the cultivar David remained green much longer

TABLE XVI

ANALYSIS OF VARIANCE AMONG FOUR WHEAT CULTIVARS FOR PERCENTAGE SURVIVAL FOR 4 DROUGHT CYCLES

Source	df	Mean Squares			
		Cycle I	Cycle II	Cycle III	Cycle IV
Row	7	1283.71	1481.03	755.36	198.88
Col	7	457.81	426.56	451.79	305.13
Genotype	3	1296.35***	1927.60***	1209.38***	231.77*
Stress	1	23639.06***	27225.00***	31506.25***	18906.25***
GE * Stress	3	767.19**	78.13	105.21	101.04
Error	42	191.74	199.48	166.07	89.36

* Significant at 5% level
** Significant at 1% level
*** Significant at 0.1% level

than those of the other cultivars. But in the second run, where moisture was more severe, this difference was not obvious. Similar responses in other vegetative characters were noted for Payne, Rall, and KanKing. The differences in their root pattern may be very important, but it was not included in this study.

CHAPTER V

SUMMARY AND CONCLUSIONS

The purpose of this study was to (a) characterize the ability of wheat seeds to germinate in mannitol solutions of different moisture tensions; (b) study the ability of wheat seedlings to survive under repeated drought cycles; and (c) investigate transpiration and diffusion resistance of different wheat cultivars.

In the d-mannitol experiments, the seeds of six wheat cultivars: Rall, Triumph 64, Payne, David, Sturdy and KanKing, were germinated in different mannitol concentrations, from 0 to 15 atmospheres, for 14 days. The percentage seed germination was determined. The results indicated that percentage seed germination decreased by increasing moisture tensions. Seeds of all cultivars germinated quickly at low moisture tensions. Significant differences among cultivars were observed at higher tension levels.

The moisture stress study involved the use of potted seedlings of four of the cultivars of wheat for studying their diffusion resistance, their growth rate, in terms of leaf area, fresh weight, and dry weight and their transpiration patterns, in a controlled growth chamber. The differences among cultivars in stomatal diffusion resistance were significant. The values of diffusion resistance increased from one day to the next near the end of the 5-day period. Significant differences were found among cultivars in terms of leaf area, fresh and dry weights. The data presented in this study showed that fresh weight and dry weight were affected by soil moisture stress. The results indicated that the differences in transpiration and transpiration rates were not significant among the cultivars tested.

In the survival experiment, seedlings were grown in plastic pots and subjected to four weekly repeated drought cycles under two moisture levels followed by rewatering at the end of each cycle. The results of this study indicated that there was a continuous loss of plants in successive drought periods. The analysis of variance showed significant varietal differences in percentage survival for each of the four cycles.

From the above results some conclusions may be summarized as follows: (1) germination of wheat cultivars under different moisture tensions generally resulted in a decrease in the percentage germination in all cultivars tested. Moisture tensions of 9 and 11 atm were most effective for identifying the cultivars with highest and lowest germination under limited moisture conditions; (2) transpiration and diffusion resistance evaluation are more effective during the period before the plants reached the permanent wilting. Fresh weight and dry weight showed clear differences between cultivars tested; (3) the use of survival technique on wheat seedlings allowed differences among cultivars to be observed. This technique of screening seems to be easy and effective for drought resistance among unknown genotypes, especially for genotypes that have high percentage survival in the seedling stage. They would also tend to have high percentage of survival in the later stages of plant development; (4) in this study, the cultivars Rall and KanKing were selected as drought resistant cultivars; Triumph 64 and Payne were selected as intermediate for drought resistance while Sturdy and David were selected as drought susceptible cultivars. The overall conclusion from this study is that Payne had the highest general response for drought tolerance while David had the lowest. In fact, David was the only cultivar that can be considered as intolerant to moisture stress. The response of other cultivars were not consistent, and it was not possible to give them a ranking for drought resistance in this study; (5) this study suggested that the measurements of diffusion resistance should be taken from the upper and the lower leaf surfaces and from more than one leaf per each plant. Transpiration and diffusion resistance measurements should be taken from plants under moderate moisture stress; (6) the response of wheat cultivars should be tested in different stages of growth from germination to maturity; (7) the cultivar or cultivars that show high response by using different evaluation techniques at different growth stages may be able to withstand drought conditions.

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