DROUGHT STRESS INFLUENCE ON SOME PHYSIOLOGICAL PROCESSES IN WINTER WHEAT (*TRITICUM AESTIVUM* L.)

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CHAPTER I

INTRODUCTION

This dissertation is divided into four main chapters. Each chapter is a separate paper prepared for publication in a professional journal.

The exposure of wheat and other cereal crops to drought during their life cycle is a problem in most of the arid and semi-arid regions of the world. These regions need high yielding genotypes which are tolerant of drought stress conditions, not only because rainfall is often inadequate, but also because irrigation is becoming limited or very expensive. For these reasons, interest in greater drought resistance in wheat is widespread and has been the subject of much research including that reported in this dissertation.

Increased yield potential has always been of basic importance in physiology, breeding, management and production programs. Thus understanding the effect of drought on physiological processes becomes very important and would help breeders develop cultivars with a high level of drought resistance, as well as high yield.

The agronomist interested in plant response to drought is always faced with the problem of identifying which method or methods to use for the greatest advantage in conducting research. One of the areas of wheat research in which the agronomists are interested is the possible differences in the rates of photosynthesis among cultivars and to see if these differences may be related to yield.

Nitrogen is a constituent of enzymes and nucleoproteins, and these play a major role in plant growth processes. Nitrate reductase governs the rate and the amount of nitrate utilization. The activity of this enzyme is often reduced when the plant undergoes water and temperature stress. Therefore, it is important that plants be able to maintain the activity of this enzyme since high nitrate reductase activity is one factor associated with high grain yield and protein.

The development of wheat cultivars with greater resistance to adverse environmental conditions, such as drought stress, offers considerable promise for increasing crop production under such conditions throughout the world.

The major objective of this research was to find the relationship between drought resistance and some physiological responses and the relation of such responses to yield under drought stress.

CHAPTER II

DROUGHT RESISTANCE AT THE SEEDLING STAGE OF WINTER WHEAT IN RELATION TO NITRATE REDUCTASE ACTIVITY AND WATER RELATIONS

Abstract

The purpose of this study was to examine the relationship of drought resistance of winter wheat to nitrate reductase (NR) activity and water relations using two moisture stress levels. Ten winter wheat cultivars were evaluated. The plants were subjected to treatments at four weeks of age. Treatments 1 and 2 received 100 and 60 ml of tap water, respectively. Then, water was withheld for one week during which measurements were taken at two dates; the second and the seventh day of stress.

Data obtained from this study indicated that nitrate reductase activity was greatly reduced by moisture stress. The cultivars Cheyenne, Red Chief, Turkey, and KanKing maintained higher NR level than Goens, Ponca, and Sturdy under stress conditions. Percent reduction in NR activity ranged from 7 to 56%. With respect to internal water balance measurements, moisture stress increased the degree

of dehydration and slightly reduced the water retention capacity. Under moisture stress 2, relative water content (RWC) and NR activity was reduced by 10 and 33%, respectively.

Introduction and Literature Review

Nitrate Reductase Under Water Stress

Nitrate reductase (NR) is the enzyme responsible for the first step in the reduction of nitrate to ammonia. Activity of this enzyme varied under the influence of CO_2 levels, light intensity and water availability, temperature and nitrate supply (6, 12).

The relationship of nitrate reductase and drought stress have received some attention. Beevers and Hageman (3) suggested that NR might be related to heat (drought) resistance. Mattas and Pauli (12) and Huffaker et al. (8) indicated that corn and barley plants exposed to drought conditions had a significant decrease in NR activity. Todd (16) pointed out that under severe water deficit, activities of most enzymes decreased. Reduction in NR activity under water stress may be due to one or more of the following: (a) a lower rate of enzyme synthesis or increased rate of dehydration leading to a new equilibrium between the two processes of synthesis and degradation (1); (b) the enzyme is inactivated under water stress possibly as a result of a partial denaturation of the enzyme due to dessication (14);

and (c) a fraction of NR may be located in the cytoplasm and activity lost during stress as the result of the inhibition of protein synthesis (15).

Internal Water Balance

Emphasis has been placed on the importance of the internal water balance in plant-water relations because of its relationship to the rates of physiological processes that control plant growth (13). Kramer (9) considers drought to be a soil moisture deficit sufficient to produce internal water deficits which reduce growth in plants. Leaf water maintenance may be the most important factor in many plants for surviving drought. There were differences among species in moisture levels to which they could be reduced and stay alive (9). A distinct reduction in enzyme activity occurred when relative water content declined by 10 to 20% in leaves of maize seedlings (1, 11) and in wheat seedlings (14) as a result of water stress.

Blum (4) studied the relationship between leaf water saturation deficit (WSD) and leaf water potential in ten sorghum genotypes under stress conditions. He indicated that the leaf water potential, at which exponential increases in WSD appeared, varied among the genotypes studied. Levitt (10) pointed out that a relatively small increase in WSD per unit reduction in leaf water potential is a measure of dehydration avoidance. Neither relative water content (RWC) nor WSD seems to have any decisive advantage, but both will probably continue in use (2). Barrs (2) indicated that either leaf discs or whole leaves with their petioles standing in water in closed container may be used to measure internal water balance.

The objectives of this research were: (a) to study the relation of drought resistance among cultivars of wheat to NR activity and water relations; and (b) to investigate the stability of NR activity in wheat seedlings under drought stress conditions.

Materials and Methods

This experiment was conducted in a growth chamber at the Controlled Environmental Center, Oklahoma State University, Stillwater, Oklahoma. The light at plant level inside the chamber was 460 μE M^{-2} sec^{-1} and the temperatures were 18/13° C day/night with 12 hour light period. Ten cultivars of winter wheat, Cheyenne, Red Chief, Turkey, KanKing, Blue Jacket, Blue Boy, Ponca, Ashkof, Sturdy, and Goens were evaluated. These cultivars are believed to have different levels of drought resistance.

A split plot design with 4 replications was used. Each replication was divided into two moisture levels. Pots (one liter size) were filled with a mixture of three parts per volume of soil and one part of vermiculite. Fifteen seeds were planted in each pot and seedlings were thinned to ten per pot seven days after emergence. From this time through

4 weeks of age all pots received 100 ml tap water every other day.

At four weeks of age, the plants were subjected to treatments for one week. Treatments 1 and 2 received 100 and 60 ml tap water, respectively on the first day of the week. Then, water was withheld for a one week period for both treatments during which time measurements were taken 2 and 7 days after the withholding of water.

Nitrate Reductase

The NR level was measured using the *in vitro* method of Hageman and Flesher (7) and modified by Croy and Hageman (5). Samples were taken from leaf tissue of two random plants in each pot. Leaves were cut into small pieces. Then, one gm of plant tissue was ground for 30 seconds with a Brinkmann Polytron ST 20 homogenizer at 3/4 speed in 7 ml of an extraction medium of pH 9.0 containing 25 mM K_2HPO_4, 5 mM disodium ethylene diamine tetraacetate, 10 mM cysteine. The extracts were centrifuged for 15 minutes at 20,000 XG. Samples were kept in an ice bath throughout the entire extraction process. Aliquots (0.2 ml) of plant extracts were placed in a buffered solution of pH 7.5 which contained the substrate, nitrate, and a reducing agent ($NADH_2$). The temperature was maintained at the optimum for the enzyme (30° C) during the incubation period. At the end of 15 minutes reactions were terminated with 1% sulfanilamide reagent in 3 N HCl and 0.02% N-{1-napthyl) ethylene diamine

HCl (1:1 ratio) and absorbance read at 540 nm after 20 minutes. NR activity was determined at two different dates during the week of stress, one early and the other at the end of stress period. The percent of reduction was determined using the difference between moisture level 1 and 2 on the early date of sampling (date 1) as shown in the following formula:

$$\% \text{ of reduction in NR activity} = \frac{ML1 - ML2}{ML1} \times 100$$

where: ML1 = NR under moisture level 1
ML2 = NR under moisture level 2.

Internal Water Balance

At the end of a week of stress leaf samples were collected. The second whole leaf from the top of a plant from each pot was cut, immediately weighed to obtain fresh weight and then kept in distilled water in a closed test tube for 4 hours away from light to obtain turgid weight. After turgid weight was obtained, the dry weight was determined by drying 2 days in the oven at 70° C. Water saturation deficit and relative saturation deficit were calculated using the following formulas to determine the dehydration of plant tissue.

$$\text{Water Saturation Deficit (WSD)} = \frac{(TW - FW)}{(TW - DW)} \times 100$$

$$\text{Relative Saturation Deficit (RSD)} = \frac{(TW - FW)}{TW} \times 100$$

Where:
TW = Turgid weight,
FW = Fresh weight,
DW = Dry weight.

On the other hand, relative water content was calculated using the following formula to determine the ability of plant tissue to hold water under stress conditions.

$$\text{Relative Water Content (RWC)} = ((FW - DW)/(TW - DW)) \times 100$$

Leaf area was determined for each leaf by the use of a LI - COR Leaf Area Meter (Model LI-3000 A, Lambda Instrument Corp., Lincoln, Nebraska).

At the end of the experiment, five plants were harvested from each pot and dried 4 days in the oven at 70° C to determine dry weight.

Results and Discussion

Nitrate Reductase Under Moisture Stress

The data presented in Table I showed a reduction in the NR activity as the plants were subjected to moisture stress. The difference between dates was significant at 0.01% level of probability. Using Duncan's Multiple Range Test at 5% level of probability, the differences among cultivars were significant in moisture level 1 in both dates but in moisture level 2 only in date 1.

Percent of reduction in the NR activity (Table II) ranged from 7 to 56%. The cultivars Turkey, Red Chief, Cheyenne, and KanKing had the lowest percentage NR reduction, while Ashkof, Goens, Sturdy, and Ponca showed the highest percent reduction under moisture stress conditions on the early date of sampling (date 1).

NR activity was reduced by moisture stress and the reduction in activity under stress seems to be related to drought resistance of the cultivars. The same relationship has been found with corn seedlings (3). Thus, it appears feasible to use this technique in studying the relation of drought resistance to NR activity.

Internal Water Balance

It is essential to know the moisture content which exists within plant tissue when physiological processes such as NR activity is measured to determine the relationship with water deficit or moisture tension present in plant tissue.

Means of WSD, RWC, and RSD at two moisture levels determined on the whole leaf of winter wheat are given in Table III. There were no significant differences among cultivars under moisture level 1, whereas under moisture level 2 the differences were significant at 5% level.

However, the degree of dehydration increased while the water-retention capacity was reduced under stress conditions as indicated by water saturation deficit and relative water content, respectively (Table IV). Sturdy, Ponca, and Blue Jacket had the lowest WSD and the highest RWC among the cultivars tested under relatively severe stress (Table III). But, Turkey and Red Chief possessed higher WSD and lower RWC. This indicates that the cultivars which were believed to be drought sensitive such as Sturdy and Ponca tend to absorb water faster probably to balance the environmental demand, while the ones believed to be drought resistant take up water from the soil in lower rate to balance this demand. Thus, these data lead to the conclusion that the drought resistance cultivars lose water slower than do the sensitive ones through the transpiration processes.

When relative water content (RWC) under moisture level 2 was reduced by 10% in leaves of wheat seedlings, the NR activity was reduced by 33% relative to moisture level 1. These results are similar to those reported by others (1, 2, 15). Partial correlations (Table V) showed that NR activity and internal water balance values were not strongly related.

Dry weight values are presented in Table VI. There were no differences among cultivars under moisture levell, while the differences were significant under moisture level 2. Cultivars Ashkof, Cheyenne, Red Chief, and Turkey had the lowest dry weight whereas Sturdy had the highest dry weight.

Summary

1. NR activity and RWC decreased by increasing moisture stress, while the degree of dehydration,

as indicated by WSD, increased.

2. NR and internal water balance measurements did not separate cultivars tested into drought resistance and drought susceptible categories as expected. This was probably due to the fact that water stress was not enough to permit cultivars to express their degree of resistance.
3. This study suggests that even though the drought resistance cultivars retain less water and expressed more leaf tissue dehydration, they maintained higher NR activity under moisture stress conditions than those believed to be drought susceptible.

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TABLE I

NITRATE REDUCTASE ACTIVITY OF 10 WINTER WHEAT CULTIVARS

	Date 1		Date 2	
Cultivar	Moisture Level 1	Moisture Level 2	Moisture Level 1	Moisture Level 2
	μMoles NO_2^-/gm. fr. wt./hr			
Cheyenne	11.0 a*	8.2 a	2.0 abc	0.2 a
Red Chief	10.3 ab	8.0 a	2.7 a	0.3 a
Turkey	8.5 ab	7.9 a	2.6 ab	0.4 a
KanKing	8.8 ab	6.5 ab	2.1 abc	0.2 a
Blue Jacket	8.9 ab	5.8 abc	0.8 c	0.1 a
Blue Boy	8.8 ab	5.4 abc	1.0 bc	0.2 a
Ponca	7.5 bc	4.4 bcd	1.4 abc	0.1 a
Ashkof	9.6 ab	4.2 bcd	2.3 abc	0.1 a
Sturdy	5.6 cd	3.2 cd	1.6 abc	0.1 a
Goens	3.6 d	1.9 d	0.7 c	0.2 a

*Means within columns followed by the same letter are not significantly different at 5% level using Duncan's Multiple Range Test.

TABLE II

PERCENT REDUCTION IN NITRATE REDUCTASE (NR) ACTIVITY BY INCREASING MOISTURE STRESS ON DATE 1

Cultivar	Moisture Level 1	Difference Between Moisture Level 1 and 2	% of Reduction NR Activity
	μMoles NO_2^-/gm. fr. wt./hr		
Cheyenne	11.0	2.8	26
Red Chief	10.3	2.3	22
Turkey	8.5	0.6	7
KanKing	8.8	2.3	26
Blue Jacket	8.9	3.1	35
Blue Boy	8.8	3.4	39
Ponca	7.5	3.1	41
Ashkof	9.6	2.4	43
Sturdy	5.6	5.4	56
Goens	3.6	1.7	47

TABLE III

WATER SATURATION DEFICIT (WSD), RELATIVE WATER CONTENT (RWC), AND RELATIVE SATURATION DEFICIT (RSD) MEANS OF 10 WINTER WHEAT CULTIVARS UNDER TWO MOISTURE LEVELS (ML1 AND ML2)

	WSD(%)		RWC(%)		RSD(%)	
Cultivar	ML1	ML2	ML1	ML2	ML1	ML2
Turkey	13	33	87	67	12	29
Red Chief	10	25	90	75	9	22
Goens	12	22	88	78	10	19
KanKing	9	19	91	81	8	16
Blue Boy	8	19	92	81	7	17
Cheyenne	14	18	86	82	12	16
Ashkof	11	17	89	83	9	15
Blue Jacket	9	16	91	84	8	14
Sturdy	9	13	91	87	8	11
Ponca	11	13	89	87	10	11
$LSD_{0.05}$	NS	8	NS	8	NS	8
C. V. %	38	38	9	5	39	39

NS = not significant at 5% level.

TABLE IV

NITRATE REDUCTASE, NITRATE, WATER SATURATION DEFICIT, RELATIVE WATER CONTENT, AND RELATIVE SATURATION DEFICIT AVERAGED OVER 10 CULTIVARS UNDER TWO MOISTURE LEVELS

Measurements	Moisture Level 1	Moisture Level 2
Nitrate Reductase uMoles NO_2^-/gm fr. wt/hr	8.3	5.6
Nitrate mg NO_3^-/gm fr. wt	7.3	9.4
Water Saturation Deficit, %	10.5	19.4
Relative Water Content, %	89.5	80.6
Relative Saturation Deficit, %	9.3	17.0

TABLE V

PARTIAL CORRELATION COEFFICIENTS BETWEEN NITRATE REDUCTASE ACTIVITY AND FOUR OTHER VARIABLES UNDER MOISTURE STRESS

Variables	Nitrate Reductase Activity
Nitrate (NO_3^-)	-0.395*
Water Saturation Deficit (WSD)	-0.235
Relative Water Content (RWC)	0.235
Relative Saturation Deficit (RSD)	-0.244

*Significant at 5% level.

TABLE VI

DRY WEIGHT OF 10 WINTER WHEAT CULTIVARS UNDER TWO MOISTURE LEVELS AT THE END OF STRESS

Cultivar	Moisture Level 1 Dry Weight (mg)	Moisture Level 2 Dry Weight (mg)
Sturdy	408 a*	593 a
Ponca	388 a	547 ab
Blue Boy	394 a	546 ab
Blue Jacket	400 a	543 ab
Goens	398 a	540 ab
KanKing	378 a	526 ab
Ashkof	366 a	514 b
Cheyenne	394 a	500 b
Red Chief	364 a	488 b
Turkey	354 a	480 b

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

CHAPTER III

NITRATE REDUCTASE, PHOTOSYNTHESIS, AND STOMATAL RESISTANCE IN RELATION TO DROUGHT RESISTANCE IN WINTER WHEAT

Abstract

This research was conducted under controlled environmental conditions to study nitrate reductase at the seedling stage and photosynthesis and stomatal diffusive resistance after head emergence. Ten winter wheat (*Triticum aestivum* L.) cultivars were evaluated in this study. These cultivars are believed to have different degrees of drought resistance. At four weeks of age, the plants were subjected to water stress for seven days during which nitrate reductase (NR) activity was determined for 3 dates. After head emergence the plants were exposed again to a week of water stress during which net carbon dioxide exchange (NCE) as a measure of photosynthesis and stomatal diffusive resistance (R_s) were measured every other day.

The results showed a sharp decrease in NR activity when the plants were subjected to water stress. The percent of NRA stability after 7 days of stress ranged from 23% for cv

Payne to 51% for cv Cheyenne. With respect to photosynthesis and stomatal diffusive resistance, the data revealed a decline in net carbon dioxide exchange and an increase in R_s. Net carbon dioxide exchange was negatively correlated with stomatal resistance and positively correlated with yield components.

Water potential, Ψ_w showed no differences among cultivars. However, the water potential, was decreased (more negative) by water stress. It can be concluded from this study that wheat cultivars which maintain high water potential (less negative), high stability of nitrate reductase, less reduction of photosynthesis and high stomatal resistance under water stress have a greater capacity for the tolerance of such stress.

Introduction and Literature Review

Limited soil moisture affects growth and yield through a number of physiological processes including enzyme activity, photosynthetic activity and stomatal action.

Nitrate Reductase (NR) and Water Potential Ψ_w

Nitrate reductase (NR) activity is sensitive to changes in the water status of plants and declines when the plant water potential decreases. Shaner and Boyer (12) conducted experiments to determine whether the nitrate flux to the leaves or the nitrate content of the leaves regulated the NR activity in leaves of intact maize (Zea mays L.). Their results showed that in seedlings dessicated slowly, the nitrate flux, leaf nitrate content, and NR activity decreased as Ψ_w decreased. Beevers and Hageman (1) proposed that NR activity was related to heat (drought) tolerance. Heuer et al. (6) studied the effect of different types of water stress on nitrate and nitrite reductase of wheat (Triticum vulgare L. cv Mivhor) leaves. Their data showed that NR was more sensitive to water stress than nitrite reductase.

Croy (3) found that when cv Ponca was grown at 12.8/23.8 C and 20/29.4 C (day/night), the leaves contained significantly more extractable nitrate reductase than did leaves of the cv Monon grown under comparable conditions. This difference was not significant when the plants were grown at higher and lower temperature regimes. A study was conducted to evaluate NR activity of ten winter wheat cultivars at four weeks of age under moisture stress conditions (16). Data of this study indicate that cv Cheyenne, Red Chief, Turkey, and KanKing maintained higher NR level than cv Goens, Ponca, and Sturdy, The percent of reduction in NR activity ranged from 7 to 56%.

The pressure bomb is now extensively used to estimate Ψ_w in plant-water relations. This technique involves measuring xylem pressure potential. Stems and leaves of plants are used in this procedure to measure their potential. It is assumed certain plants have the same response of potential as their stems (15). This technique determines the water stress of a plant by measuring the pressure necessary to force water out of the cut stem surface.

Photosynthetic Activity and Stomatal Action in Relation to Yield

In any research program designed to achieve increased yields, a knowledge of the photosynthetic rate, photosynthetic area, yield components and their relationships to yield in response to the different environmental conditions such as moisture and temperature stress should be taken into consideration by both plant breeders and crop physiologists. Frank et al. (4) and Todd and Webster (14) indicated that photosynthesis in wheat leaves declined as the drought stress increased. The rates of photosynthesis (P_n) are inversely proportional to the total diffusive resistance to CO_2 from the air to the site of fixation (5). Research by McCree (11) indicated that water stress reduced the rate of photosynthesis both by the closing of the stomata and other means.

Heritable variation in assimilate formation for grain filling of wheat cultivars grown under rapidly increasing water stress seems to be restricted to the last phase of their life cycle (9). The relative yield performance of five wheat cultivars grown in the field under continuously increasing water deficits was predictable from the integrated net photosynthetic potential of their flag leaves (9). Kaul and Crowle (10) measured potential net photosynthesis (P_N) in the third to seventh leaves of moderately drought-stressed wheat. They found that the ranking of cultivars for grain yield was related to integrated net photosynthetic potential readings.

The development and use of an easy and rapid procedure for measuring photosynthesis will be helpful to study the response of large numbers of plants under stress condition. The syringe method developed by Sullivan et al. (13) and modified by Huber (7) and Bruns (2) permit photosynthetic measurements of many plants within a reasonable time.

A number of empirical tests have been used which differentiate among drought resistant cereal plants. These tests include heat tolerance, chlorophyll stability, enzyme activity, stomatal resistance and photosynthetic activity. Even though considerable data are available, the physiological basis for drought resistance is not fully understood yet. Therefore, the purposes of this research were: (a) to investigate the NR level under water stress during the seedling stage and its relation to water potential; and (b) to study the effect of water stress on photosynthesis and stomatal diffusive resistance and their relations to yield components.

Materials and Methods

This research was initiated in 1980 in a growth chamber at the Controlled Environment Research Laboratory, Oklahoma State University, Stillwater, Oklahoma. Ten winter wheat genotypes were selected for this study. These cultivars are believed to have different degrees of drought resistance. The cultivars include Cheyenne, Ponca, Red Chief, Goens, KanKing, Sturdy, Blue Boy, David, Blue Jacket, and Payne. A randomized block design with 4 replications was used in this research. Each replication was placed in a wood box with dimensions of 60 cm length, 28 cm width, and 23 cm depth. These boxes were filled up to 18 cm depth with a mixture of soil, sand, vermiculite and peatmoss (4:1:2:1) respectively.

Cultivars were planted in rows at random in each box. Twenty seeds from each cultivar were planted in rows spaced 5 cm apart. The seedlings were thinned to 12 per row, six days after emergence.

Four weeks after emergence the plants were subjected to water stress for seven days by withholding water. NR activity was measured on 3 dates; the second, the fourth, and the seventh day of stress. The procedure for measuring NR level was described in the previous chapter except 0.5 g leaf tissue was used instead of 1 g. During these three periods of sampling NR, water potentials were determined following the Waring and Clary (15) procedure to determine the relation between enzyme activity and internal water stress. The growth chamber temperatures were 18/13° C day/night with light of 350 μE m^{-2} sec^{-1} at plant level, as measured by a LI-COR quanitum meter with sensor, and 12-hour light period.

After 7 days of water stress during which NR levels were determined, the boxes were irrigated every other day. One week later the plants were exposed to cold treatment with temperatures 7/1° C day/night with 8-hour light period for vernalization. After 46 days of vernalization, the boxes were moved to a controlled environmental chamber. A half strength Hoagland solution was added to the boxes once a week and plants were watered every other day with a uniform amount of water until they reached head emergence. Temperatures were 20/14° C day/night with light of 550 μE m^{-2} sec^{-1} at plant level and 15-hour light period.

During head emergence the plants were exposed to water stress for seven days after which plants were returned to adequate moisture. Through the period of stress, photosynthesis, and stomatal diffusive resistance were measured every other day on the same flag leaf. A Beckman Model 865 infra-red gas analyzer was used to determine net carbon dioxide exchange (NCE) as a measure of photosynthesis. The syringe method developed by Sullivan et al. (13) and modified by Huber (7) and Bruns (2), was used. The measurements were taken from the flag leaf. A gas sample of 6 to 7 cc was withdrawn using a hypodermic syringe at zero time. The leaf was then exposed to light for 60 seconds after which a second sample was taken. These two samples were adjusted to 5 cc and then injected into the infra-red gas analyzer to determine carbon dioxide concentrations. Apparent photosynthesis was determined by the rate of net carbon dioxide exchange (NCE) per unit leaf area. Since the measurements were taken each time from the same flag leaf, a non-destructive procedure was used to determine the leaf segment area that was used for photosynthesis.

Leaf area (LA) = L x W x C.F.

where: L = Length of leaf chamber,
W = Width of flag leaf,
C. F. = Correction factor (0.97)[1] to correct for the leaf segment shape.

The net carbon dioxide exchange (NCE) for leaf segment was calculated using the formula described by Bruns (2).

Stomatal resistance (R_s) was measured by a Lambda LI-65 S diffusive resistance meter made by Lambda equipment Corporation, Lincoln, Nebraska, and a LI-20 S sensor calibrated according to methods of Kanemasu et al. (8). The measurements were taken from the upper surface of the same flag leaf used for photosynthetic measurements.

When ripe, plants were harvested for yield components and plant height was determined for the tillers used to

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[1] Osmanzai M. (Unpublished data).

collect previous data on photosynthesis and stomatal resistance. In addition four other uniform tillers were selected to be averaged with those used for photosynthesis and stomatal resistance for a total of 5 tillers.

Results and Discussion

Nitrate Reductase (NR) and Water Potential, Ψ_w

Nitrate reductase (NR) activity was reduced while Ψ_w decreased (more negative) when plants were subjected to a week of water stress at 4 weeks of age (Table I). This period of stress reduced NR levels in winter wheat genotypes from 49% to 77% of the initial level. Differences among cultivars and periods of sampling were significant at 0.01% level. However, the water potential, Ψ_w differences were not significant among the cultivars. This probably occurred because stress as measured by water potential of -11.5 bars was not enough to distinguish between cultivars (Table I). No interactions were observed between cultivars and periods of sampling for NR and Ψ_w.

Percent of NR stability was calculated using the following formula:

$$\text{\% of NR Stability} = \frac{\text{Final Rate of NR at the End of Stress}}{\text{Initial Rate of NR at the Beginning of Stress}} \times 100.$$

The data showed that the percent of NR stability after

7 days of water stress ranged from 23% in cv Payne up to 51% in cv Cheyenne (Table II). These data indicated that even though the initial NR activity of the cultivars, Blue Boy and Cheyenne, was very close, Cheyenne maintained a higher enzyme level than Blue Boy did under stress. By the same token, the cultivars David and Blue Boy had almost the same percentage of NR stability after 7 days of water stress, but their initial enzyme levels were very different, 6.1 and 14.7 μmoles NO_2^- per gm fresh weight per hour, respectively (Table II). These results show that both the initial and the final levels should be considered in order to study the effect of water stress on NR activity.

The correlation coefficient between nitrate reductase and nitrate was -0.491** (Table III). Figure 1 illustrated that NR was reduced by decreasing water potential (more negative), while NO_3^- increased under such conditions. This negative relation indicated that the reduction in enzyme activity was accompanied by accumulation of nitrate (Table I). Since the enzyme is substrate inducible, it appeared to be the rate limiting step in nitrogen reduction as indicated by nitrate accumulation under water stress as a result of lower nitrate reduction. The reduction in NR activity under stress conditions probably leads to the reduction of ammonical forms required for protein synthesis; however, water soluble protein was not different among cultivars during the stress period. On the other hand, water soluble protein was not correlated with either NR activity or nitrate (Table III). This is probably true in this study because the stress was during a short period and the water soluble protein was the result of NR levels a few days before stress. In other words, the effect of water stress on water soluble protein can be observed if such stress for a longer period of time.

Photosynthetic Activity and Stomatal Resistance in Relation to Yield

Net carbon dioxide exchange (NCE) and stomatal diffusive resistance (R_s) were measured after ear emergence. The data indicated that photosynthesis in wheat flag leaves declined (Table IV) as the drought stress increased and stomatal diffusive resistance increased (Table V).

The differences between periods of sampling NCE were highly significant at 0.01% level of probability. Using Duncan's Multiple Range Test (Table IV), the cultivars could not be separated from each other as the result of their overlapping. The differences among cultivars, using the average of all samplings, were significant at 0.01% level. No interactions between sampling periods and cultivars were observed.

The stomata largely controls water loss from the plant. They tend to close when subjected to water stress, and, at the same time, this closure causes a reduction in photosynthetic rate. Therefore, an optimum balance between the degree of closure and CO_2 exchange is desirable to reduce water loss without severe reduction in photosynthesis. The percent of NCE reduction and the change in stomatal resistance were presented in Table VI. The percent of NCE reduction per unit change in R_s ranges from 3.7 for Sturdy to 18.9 for David. This suggests that some cultivars have a lower percentage of reduction in NCE per unit change in R_s.

Payne, David, Sturdy, and Blue Boy are the short cultivars in the experiment. Yield component data on weight per head, kernel numbers per head and kernel weight showed significant differences among cultivars (Table VII). Payne, Sturdy, and Blue Boy had the lowest yield component, while Cheyenne, David and Goens had the highest. The kernels per head were not related to kernel weight. This suggests that the environmental effect of yield and yield components differ from one stage to the other. Stress conditions at anthesis reduced the number of kernels per head, while stress during grain filling reduced kernel weight. However, all yield components are considered to be sensitive to water stress. But, drought stress at a certain period will affect some of these components more severely than the others.

Kernels per head showed a relatively high positive correlation ($r = 0.79^{****}$) with weight per head, whereas the correlation coefficient between kernel weight and weight per head was 0.60^{****} (Table VIII). Plant height was positively correlated with kernels and weight per head and with NCE, but not with stomatal resistance.

Summary

NCE was negatively correlated with R_s and positively correlated with yield components. The negative relation between photosynthesis and stomtal resistance indicates that the selection for one will lead to the reduction of the other. However, it is logical to expect grain yield to be related to the photosynthetic activity. If this conclusion is true, such data may provide a basis for plant breeders to screen for high-yielding cultivars by measuring photosynthetic activity particularly if such correlation between NCE and yield exists under field conditions.

It can be concluded from this study that wheat cultivars which maintain high nitrate reductase stability and less reduction in photosynthetic activity with high stomatal resistance under water stress have a greater capacity for the tolerance of such stress.

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FIGURE

TABLE I

WATER POTENTIAL, NITRATE REDUCTASE, AND NITRATE IN ALL WHEAT CULTIVARS AT 4 WEEKS OF AGE UNDER MOISTURE STRESS

Variables	Day 2	Day 4	Day 7
Water Potential, bars	-1.6	-6.0	-11.5
Nitrate Reductase[1]	10.7	6.3	4.0
Nitrate[2]	3.8	4.7	7.1

[1] Nitrate Reductase (μmoles NO_2^- gm. fr. wt.$^{-1}$ hr^{-1}).

[2] Nitrate (mg NO_3^- gm. fr. wt.$^{-1}$).

TABLE II

PERCENT OF NITRATE REDUCTASE (NR) STABILITY IN WHEAT AT 4 WEEKS OF AGE COMPARED TO THE INITIAL AND THE FINAL RATE OF NITRATE REDUCTASE (NR) ACTIVITY UNDER 7 DAYS OF MOISTURE STRESS

Cultivar	Nitrate Reductase µmoles NO_2^- gm. fr. wt.$^{-1}$ hr.$^{-1}$		% of NR Stability
	Initial Rate	Final Rate	
Cheyenne	13.5 ab*	6.9 a	51
Ponca	10.0 cd	4.2 abc	42
Red Chief	11.5 bcd	4.7 abc	41
Goens	8.7 de	3.5 bc	40
KanKing	10.8 bcd	4.1 abc	38
Sturdy	9.4 cd	3.5 bc	37
Blue Boy	14.7 a	5.2 ab	35
David	6.1 e	2.0 c	33
Blue Jacket	11.9 bc	3.6 bc	30
Payne	10.7 bcd	2.5 bc	23

*Means with the same letter are not significantly different at 5% level using Duncan's Multiple Range Test.

TABLE III

SIMPLE CORRELATION COEFFICIENTS BETWEEN NITRATE REDUCTASE, NITRATE, WATER SOLUBLE PROTEIN, AND WATER POTENTIAL UNDER 7 DAYS OF WATER STRESS

Variables	2	3	4
1. Nitrate reductase	-0.49****	-0.16	-0.38****
2. Nitrate		0.08	0.51****
3. Water soluble protein			0.21*
4. Water potential			

*Significant at 5% level.

****Significant at 0.01% level.

TABLE IV

NET CARBON DIOXIDE EXCHANGE IN 10 WINTER WHEAT CULTIVARS AFTER EAR EMERGENCE DURING A WEEK OF MOISTURE STRESS

Cultivar	Initial Rate	Rate After 7 Days of Stress
	-----mg CO_2 dm.$^{-2}$ hr.$^{-1}$-----	
Blue Jacket	7.3 a*	4.7 a
KanKing	6.9 a	4.0 a
Goens	5.7 ab	4.2 a
David	7.1 a	2.5 a
Red Chief	6.1 ab	4.2 a
Cheyenne	7.0 a	1.9 a
Ponca	6.3 ab	3.4 a
Blue Boy	4.4 bc	2.7 a
Payne	4.2 bc	2.6 a
Sturdy	3.0 c	2.5 a
C.V. %	24.5	55.2

*Means with the same letter within columns are not significantly different at 5% level using Duncan's Multiple Range Test.

TABLE V

STOMATAL DIFFUSIVE RESISTANCE AFTER EAR EMERGENCE IN 10 WINTER WHEAT CULTIVARS DURING A WEEK OF MOISTURE STRESS

Cultivar	Initial Rate	Rate After 7 Days of Stress	Average Over Whole Week
	-----------------sec. cm	-------------------	-------------------
Ponca	6.2 a*	14.4 a	8.2 a
Blue Boy	5.0 abc	12.5 ab	7.2 ab
Cheyenne	6.1 ab	11.3 ab	7.1 abc
Goens	5.2 abc	9.2 ab	6.4 bcd
Sturdy	4.6 bc	9.0 ab	6.0 cde
KanKing	4.0 c	10.0 ab	6.0 de
Red Chief	4.3 c	9.9 ab	6.9 de
David	4.6 bc	8.0 b	5.6 de
Blue Jacket	4.5 c	7.9 b	5.5 de
Payne	4.2 c	6.8 b	5.2 e
C.V. %	18.7	32.5	24.5

*Means with the same letter within columns are not significantly different at 5% level using Duncan's Multiple Range Test.

TABLE VI

PERCENT OF NET CARBON DIOXIDE EXCHANGE (NCE) REDUCTION AND THE CHANGE IN STOMATAL RESISTANCE (R_S) AFTER EAR EMERGENCE IN 10 WINTER WHEAT CULTIVARS DURING A WEEK OF MOISTURE STRESS

Cultivar	% Reduction[1] in NCE	Change in R_s (Sec/Cm)	% Change in NCE Per Unit Change in R_s
David	64.1	3.4	18.9
Payne	37.4	2.7	13.9
Cheyenne	72.2	5.2	13.9
Blue Jacket	35.5	3.5	10.1
KanKing	42.3	6.0	7.1
Goens	26.1	4.1	6.4
Ponca	46.1	8.2	5.6
Red Chief	30.1	5.6	5.4
Blue Boy	39.2	7.4	5.3
Sturdy	16.3	4.4	3.7

[1] Calculated from Table IV as [(initial rate - rate after 7 days of stress)/initial rate] X 100.

TABLE VII

MEANS OF HEIGHT, NUMBER OF KERNELS AND WEIGHT PER HEAD AND KERNEL WEIGHT IN WHEAT CULTIVARS

Cultivar	Height (cm)	Kernels/ Head	Weight/ Head (g)	Kernel Weight (mg)
David	69 b*	40 a	1.77 a	44.3 a
Red Chief	75 ab	26 bc	1.09 bcd	41.6 ab
Goens	78 ab	30 ab	1.19 b	39.6 ab
Blue Jacket	83 a	29 bc	1.11 bc	38.4 bc
KanKing	73 ab	26 bc	0.97 bcd	37.8 bc
Ponca	75 ab	26 bc	0.96 bc	37.4 bc
Cheyenne	76 ab	34 ab	1.17 b	34.6 c
Sturdy	47 c	18 c	0.51 e	28.2 d
Payne	48 c	26 bc	0.72 cde	27.9 d
Blue Boy	57 c	33 ab	0.71 de	22.5 e
C.V. %	12.3	23.8	26.5	10.6

*Means with the same letter are not significantly different at 5% level using Duncan's Multiple Range Test.

TABLE VIII

SIMPLE CORRELATION COEFFICIENTS FOR SIX PLANT CHARACTERS

Plant Character	1	2	3	4	5	6
1. Height		0.41	0.58	0.44	0.40	0.05
2. Kernels/Head			0.79	0.03	0.21	-0.04
3. Weight/Head				0.60	0.35	-0.05
4. Kernel Weight					0.34	-0.11
5. Net Carbon Dioxide Exchange						-0.47
6. Stomatal Resistance						

Values from 0.21 and above are significant at 1% level.

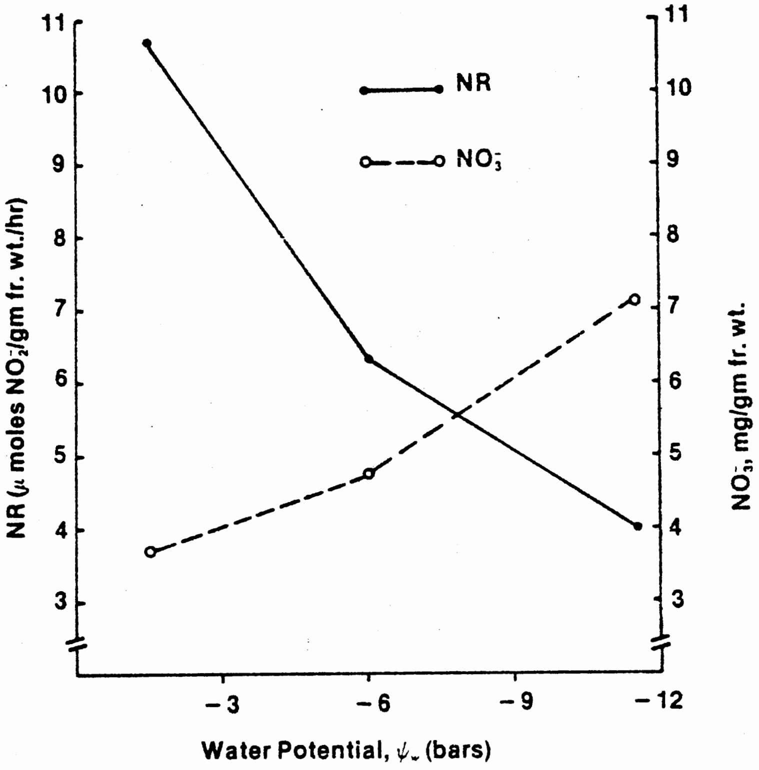

Figure 1. Nitrate Reductase (NR) and Nitrate (NO_3^-) and Their Relation with Water Potential, Ψ w

CHAPTER IV

THE EFFECT OF WATER STRESS ON PHOTOSYNTHETIC ACTIVITY AND STOMATAL ACTION AND THEIR RELATIONSHIP WITH YIELD COMPONENTS UNDER FIELD CONDITIONS

Abstract

This study was performed in 1980-1981 season on Stillwater Agronomy Research Station to examine the effects of water stress on photosynthesis and stomatal resistance. Five winter wheat cultivars were selected on the basis of previous research. Thirty liter containers were used to conduct this experiment. The stress treatment did not receive supplemental water except when necessary to prevent plants from wilting.

From booting stage until maturity, photosynthetic activity and stomatal resistance (R_s) were measured at selected dates. At the end of the study, the plants were harvested to determine yield components and some other morphological characteristics.

The results of this research show a general pattern of

reduction in NCE by moisture stress. The reduction ranged from 0.01 to 4.39 mg CO_2 dm^{-2} hr^{-1}. These data also show an increase in R_s as the result of stress condition. The change in R_s values vary from 7.41 to 20.38 sec cm^{-1}. The percent of reduction in NCE per unit change of R_s was much higher in cv Ponca than the other cultivars. This suggests that such cultivar cannot maintain enough assimilate to keep it surviving under stress conditions. Generally, the cultivars that developed more stomatal resistance reflected more reduction in their NCE and vice versa. This suggests that the reduction of water loss through stomates by increasing their resistance to water movement was at the expense of CO_2 exchange through these openings. NCE and R_s traits showed a nonsignificant negative relation using partial correlation. On the other hand yield components, particularly yield per plant, were positively related with NCE and negatively associated with R_s.

Morphological characteristics and yield data express wide differences among the cultivars tested. Such morphological characteristics and yield components were reduced by moisture stress. The percent of reduction in these traits varies from none to 39%. Peduncle length and NCE were the most severely reduced by stress, while sheath length, weight per head, kernel weight and number of heads per plant showed the least reduction under such conditions. The cultivar Sturdy had the greatest reduction in each trait measured.

Introduction and Literature Review

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 CO_2 into the leaf through stomata is decreased. Sullivan (14) reported that when the stomata close under moisture stress, severe dessication may be avoided, but diffusive resistance to CO_2 exchange increases, photosynthesis decreases and yield is reduced. The ability of wheat plants to produce grain under drought conditions might be related to the ability of their root systems to absorb water as fast as or faster than the amount of water lost by transpiration. On the other hand, the ability of these plants to limit transpiration and to continue the process of photosynthesis and assimilation under high evaporative demands might be related to the ability of wheat plants to produce grain under drought conditions. Hurd (5) 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. However, the ability of a crop species or genotype to grow and yield satisfactory in areas subjected to periodic water deficits has been termed its drought resistance (16). Laing and Fischer (11) have shown that lines selected for high yield under adequate water supply in general yield well under a limited water supply. This indicates that the yield potential of a cultivar under favorable conditions is important in determining its yielding ability when the water supply is limited.

Work by McPherson and Boyer (12) identifies some of the physiological mechanisms responsible for yield reduction under drought. Their data indicate that photosynthesis is inhibited to a greater extent by drought imposed during grain filling than translocation. The yielding ability for several winter cultivars were evaluated under severe soil moisture stress and for general dryland adaptation (9). Two cultivars, Wanser and Yamhill, were found to be highly drought resistant but differed greatly from each other in several morphological traits. This suggests that the ability of cultivars to yield well under drought conditions may be controlled by different physiological and morphological characteristics. Chinoy (1) and Derera et al. (2) point out that drought resistance or high yield in germplasm under drought stress could be attributed to earliness. Escape traits such as early maturity allow the plant to complete its life cycle before the onset of severe moisture stress. On the other hand, Keim and Kronstad (8) indicated that drought escape was ruled out as a factor in contributing to yield under drought stress.

It has been claimed that the stomata, exercise less control over photosynthesis than over transpiration (10).

However, if this is true, the stomatal closure functions more in the reduction of water loss than in the reduction of CO_2 exchange. Hsiao (3) proposed that there are nonstomatal effects of stress involved in suppressing photosynthesis in addition to the stomatal effect, at least in some species when stress is sufficiently severe. The basis for these effects may lie in altered transport parameters for CO_2 from the intercellular space to the chloroplasts or in altered ability of chloroplasts to photosynthesize (4). Much of the rationale for selection for stomatal characters is based on their use in control of either plant water status or crop transpiration and photosynthetic rates. These characters are likely to have more direct relevance to yield under drought than does stomatal conductance itself (13). It has been suggested that it is better to concentrate on transpiration and photosynthetic rates which are more directly related to drought resistance than stomatal behavior (6). Hence, the stomata represent a smaller portion of the total resistance to CO_2 than to water vapor diffusion. If this is true a partial closure of the stomata should reduce transpiration more than it reduces photosynthesis (15).

Wilting was not observed in field-grown cotton plants for water potentials down to -27 bar but did occur in container-grown plants at water potentials near -15 bar (7). These results and the growth chamber data that is presented in the previous chapters indicate the presence of variances between field tests and growth chamber tests. This suggests the need of studying the plant response to water stress in the field under natural conditions. The difference between field and growth chamber data is probably due to the fact that light inside the chamber ranges from 1/4 to 1/2 of full sunlight plus the lack of diurnal variation. On the other hand, plants grown in small containers do not have enough volume of soil for normal growth. Thus, this study was designed to overcome these two major limitations by using few plants in large containers for more realistic root development in volume and depth and by locating these containers in the field to provide higher light.

The reduction of photosynthesis and the development of stomatal resistance under water stress conditions are well documented (10, 13, 14, 15). However, little research has been devoted to the relation of photosynthesis and stomatal resistance to yield under such conditions. Therefore, this study was conducted to examine the effects of water stress on photosynthesis and stomatal resistance in winter wheat plants. Also, the relation of these two traits to yield and yield components under field conditons were investigated.

Materials and Methods

This study was performed in 1980-1981 season by subjecting five winter wheat (*Triticum aestivum* L.) cultivars to water stress under field conditions. Large basket containers of 30 liter size were used to conduct this experiment. Each container was filled with a soil taken from the field surface 0-12 cm depth. One hundred gm of 18-46-0 ($N-P_2O_5-K_2O$) chemical fertilizer was mixed with the soil before planting in each basket. A randomized block design with 3 replications was conducted on Stillwater Agronomy Research Station. Each replication consisted of two baskets to represent two different moisture levels, namely stress and non-stress treatments. Five winter wheat cultivars were selected on the basis of previous studies to represent different levels of drought resistance. These cultivars were Cheyenne, KanKing, Sturdy, Goens, and Ponca.

Three seeds were planted from each cultivar in each basket on November 28th, 1980. The seedlings were thinned to two per cultivar 20 days after emergence and then to one after the freezing period passed. The baskets were surrounded with straw and soil to protect the roots from freezing effect. The rainfall was not enough to provide sufficient moisture and prevent water stress. Thus, both moisture level treatments received supplemental irrigation to avoid excessive stress between rainfall periods. The stressed baskets received only half of the water applied to the non-stress treatment when it was necessary to water to prevent plants from wilting.

From the booting through the grain filling stage, stomatal resistance and photosynthetic activity were measured. The samples were collected at selected dates from random flag leaves, one sample per plant using the same procedures describe in Chapter III. The sunlight during the measurements ranged from 1800 to 2200 uE m^{-2} sec^{-1} during the sampling period.

At the end of the study, the plants were harvested to determine number of tillers, plant height, peduncle length, sheath length, number of kernels per head, head weight, kernel weight, and yield per plant.

Results and Discussion

Figure 1 shows a general pattern of reduction in NCE and an increase in R_s as the result of moisture stress. This pattern was more pronounced on April 29 as the result of low light intensity during that day. NCE reduction ranged from 0.01 to 4.39 mg CO_2 dm^{-2} hr^{-1} whereas the changes in R_s varied from 7.41 to 20.38 sec cm^{-1}. The NCE and R_s differences among cultivars were not significant under the two moisture levels. However, the differences between moisture levels were significant at 0.01 and 0.09 levels in case of NCE and R_s, respectively, averaged over eight sampling dates.

Generally, the cultivars that developed more stomatal resistance reflected more reduction in their net carbon dioxide exchange rate and vice versa (Table II). This indicates that the reduction of water loss through stomates by increasing their resistance to water movement was at the expense of CO_2 exchange through these openings.

The percent of reduction in NCE was determined using the following formula:

$$\% \text{ of NCE Reduction} = \frac{NS - ST}{NS} \times 100$$

where: NS = NCE under non-stress,
ST = NCE under moisture stress.

Then, percent of reduction for each cultivar in NCE under the effect of moisture stress per unit change in R_s was calculated by dividing the percent of reduction by increasing values of R_s. The percent of reduction in Ponca was almost two times that of KanKing and Sturdy and more than 200 times of Goens. These results indicate that cultivars such as Goens can maintain high NCE relative to R_s. This may be a desirable character and suggests that this kind of cultivar continues to produce enough photosynthetic assimilate under stress conditions to help them survive such conditions. On the other hand, cultivars such as Ponca cannot maintain enough assimilate under severe stress to survive under such adverse conditions.

Morphological characteristics and yield data of the five cultivars studied are presented in Table III. These data show wide differences among cultivars in morphological characteristics and some yield components. Even though the number of tillers per plant was significantly different among cultivars, the yield per plant was not different. Cultivars with few tillers tended to have similar grain yield per plant to ones that had larger number of tillers. Therefore, the production of more tillers in the second group was at the expense of yield. Cultivars such as Goens, KanKing and Sturdy which produced less tillers than Ponca and Cheyenne probably consumed less water to produce the same yield per plant.

It can be concluded that cultivars with higher potential for tillering probably transpire more and this leads to their suffering a greater degree of water stress than the ones with lower potential for tillering. On the other hand, it is possible that cultivars with a few large tillers having a high rate of survival should be able to achieve relatively high yields in drought conditions without sacrificing yield potential under non-drought conditions (7).

The percent of reduction of each trait by moisture stress was calculated using the average across the five cultivars studied under the two moisture treatments. The results of this calculation are presented in Table IV. The percent of reduction among the listed traits ranges from zero to 39%. The traits peduncle length and NCE were the most severely reduced by stress whereas sheath length, weight per head, kernel weight, and number of tillers showed the least reduction. With respect to the reduction in those traits among cultivars, Sturdy expressed the most pronounced reduction of many of the traits. The reduction of traits in this cultivar was 24, 26, 50, 50, and 61% in weight per head, number of kernels per head, number of tillers per plant, NCE, and yield per plant, respectively.

In the current study partial correlations (Table V) were determined between traits measured from random tillers. There was non-significant negative relation between NCE and R_s. Yield components were positively correlated with NCE and negatively correlated with R_s. This relation was significant only on the basis of yield per plant. Grain yield per plant was highly correlated with weight per head, height, peduncle and sheath length with values of 0.804, 0.836, 0.576, and 0.650, respectively. The relationships between the morphological characters (height, peduncle ahd sheath lengths) measured and yield components were relatively high. There was no relation between sheath and peduncle lengths. These two characters were highly correlated with height. Weight per kernel was significantly related to weight per head and yield per plant, 0.810 and 0.493, respectively.

Summary

Several observations can be summarized from this study:

1. The reduction of water loss through stomates by increasing their resistance to water movement was at the expense of CO_2 exchange through these openings.
2. Generally, there was a reduction in NCE and an

increase in R_s under moisture stress conditions.

3. Morphological characteristics and yield components were reduced by moisture stress.
4. NCE and R_s traits showed a nonsignificant negative relationship using partial correlation.
5. Yield and yield components were positively related with NCE and negatively associated with R_s.
6. The Cultivar Sturdy expressed the most pronounced reduction in nearly every trait measured.

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TABLE I

NET CARBON DIOXIDE EXCHANGE (NCE) AND STOMATAL RESISTANCE (R_s) OF FIVE WHEAT CULTIVARS AVERAGED OVER 8 SAMPLING DATES UNDER TWO MOISTURE LEVELS

Cultivar	Non-Stress	Moisture Stress	Difference
	------------NCE (mg CO_2 dm^{-2} hr^{-1})----------		
Goens	7.17	7.16	-0.01
Cheyenne	7.01	5.56	-1.45
KanKing	8.74	6.44	-2.30
Ponca	8.67	4.38	-4.29
Sturdy	8.74	4.35	-4.39
CV %	11.85	27.24	
	----------------R_s (Sec cm^{-1})--------------		
Goens	16.95	24.36	7.41
Cheyenne	21.03	34.71	13.68
KanKing	15.30	26.25	10.95
Ponca	18.08	27.79	9.71
Sturdy	12.92	33.30	20.38
CV%	24.12	28.71	

TABLE II

PERCENT OF NET CARBON DIOXIDE EXCHANGE (NCE) REDUCTION AND THE CHANGE IN STOMATAL RESISTANCE (R_s) IN 5 WINTER WHEAT CULTIVARS AS THE RESULT OF MOISTURE STRESS

	% Reduction in NCE	Change in R_s (sec cm^{-1})	% Reduction in NCE Per Unit Change in R_s
Goens	0.14	7.41	0.02
Cheyenne	20.69	13.68	1.51
KanKing	26.32	10.95	2.40
Sturdy	50.23	20.38	2.46
Ponca	49.48	9.71	5.10

TABLE III

MORPHOLOGICAL CHARACTERISTICS, YIELD AND YIELD COMPONENTS OF FIVE WHEAT CULTIVARS ACROSS TWO MOISTURE LEVELS

	Morphological Characteristics			
Cultivar	Height (cm)	Peduncle Length (cm)	Sheath Length (cm)	No. of Tillers Per Plant
Goens	69 a*	7 b	21 a	4.0 c
KanKing	66 ab	14 a	16 b	5.3 bc
Ponca	64 bc	14 a	16 b	9.8 a
Cheyenne	61 c	15 a	16 b	7.5 ab
Sturdy	41 d	4 c	15 c	5.5 bc
CV %	9.3	24.8	7.9	44.5

	Yield and Yield Components			
Cultivar	Yield/Plant (g)	Kernels Per Head	Weight/Head (g)	Kernel Weight (mg)
Goens	2.6 a	32 a	0.75 c	23 d
Cheyenne	4.7 a	31 a	0.83 abc	27 c
Ponca	5.8 a	31 a	0.92 ab	30 b
Sturdy	4.5 a	30 a	0.99 a	33 a
Kanking	3.3 a	28 a	0.77 bc	27 c
CV %	56.0	20.6	29.0	14.0

*Means with the same letter are not significantly different at 5% level using Multiple Range Test.

TABLE IV

AVERAGE OF DIFFERENT TRAITS UNDER TWO MOISTURE LEVELS AND THE PERCENT OF REDUCTION IN THESE TRAITS BY STRESS ACROSS FIVE WINTER WHEAT CULTIVARS

Trait	Non Stress	Moisture Stress	Percent of Reduction
No. of Kernels per Head	30.3	30.3	0
Weight per Head (mg)	880.0	820.0	7
Kernel Weight (mg)	29.0	27.0	7
Yield per Plant (g)	4.7	3.7	21
No. of Tillers per Plant	6.7	6.2	8
Height (cm)	64.0	56.0	13
Peduncle Length (cm)	13.0	8.0	39
Sheath Length (cm)	17.0	16.0	6
NCE (mg CO_2 dm^{-2} hr^{-1})	8.1	5.6	31

TABLE V

PARTIAL CORRELATION OF EIGHT PLANT TRAITS AMONG FIVE WINTER WHEAT CULTIVARS

Trait	Plant Traits						
	2	3	4	5	6	7	8
1. NCE (mg CO_2 dm^{-2} hr^{-1})	-0.243	0.318	0.268	0.475*	0.527**	0.541**	0.283
2. Stomatal Res. (sec/cm)		-0.252	-0.049	-0.351^{+}	-0.179	-0.021	-0.463*
3. Weight per Head (gm)			0.810****	0.804****	0.735****	0.466*	0.534**
4. Weight per Kernel (mg)				0.493*	0.621***	0.451*	0.246
5. Yield per Plant (gm)					0.836****	0.576**	0.650**
6. Height (cm)						0.576**	0.633**
7. Peduncle Length (cm)							0.179
8. Sheath Length (cm)							

[1] Correlation obtained on mean of the cultivars under two moisture levels (21 degrees of freedom).

+, *, **, ***, **** Denotes significance at 10%, 5%, 1%, 0.1%, and 0.01% levels, respectively.

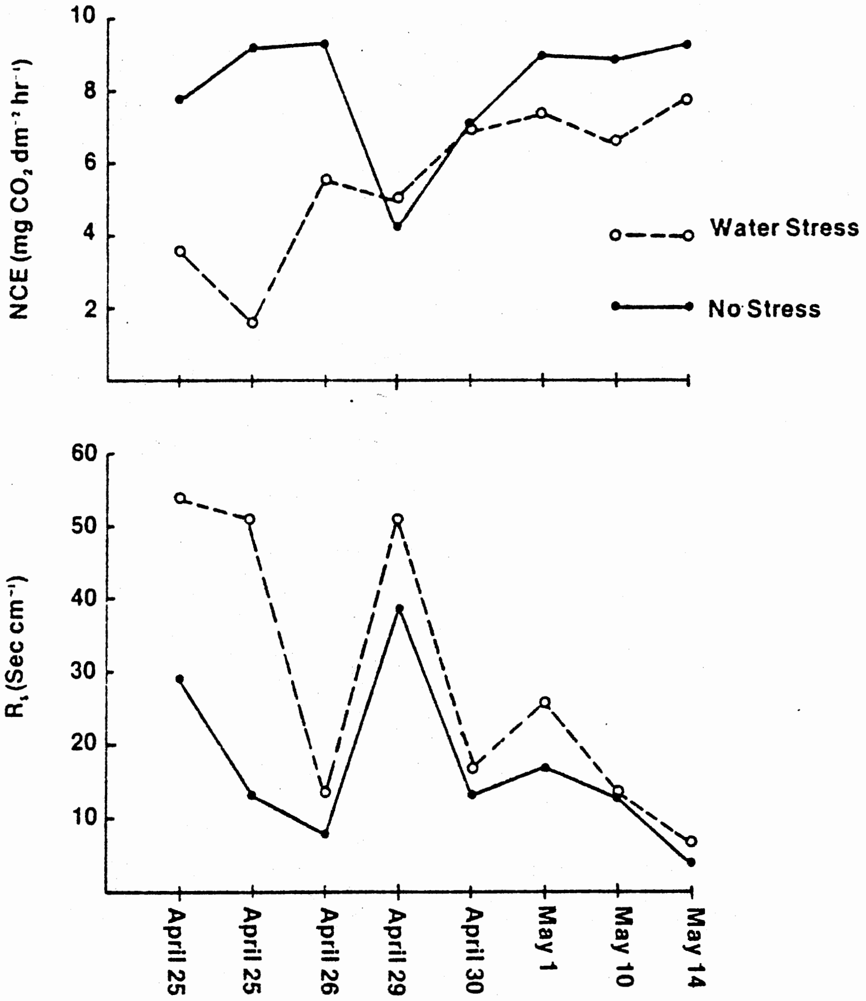

Figure 1. Net Carbon Dioxide Exchange (NCE) and Stomatal Resistance (R_S) During Eight Sampling Dates

CHAPTER V

NITRATE REDUCTASE AND YIELD EVALUATION OF 36 CULTIVARS AND SELECTIONS UNDER FIELD CONDITIONS

Abstract

The major objective of this research was to evaluate 36 entries for nitrate reductase (NR), yield, and yield components. The study was conducted in 1980-1981 season on the Agronomy Research Station, Stillwater, Oklahoma. NR activity of 36 winter wheat genotypes was measured at intervals throughout the spring season. Yield and yield components were determined at the end of the season. Statistical analyses were carried out on several variables to meet the objectives.

Small significant differences in level of NR activity was observed among entries. Differences in yield and yield components among these entries were highly significant.

All yield components were positively associated with grain yield. The phenotypic correlation indicated that number of tillers per unit area, weight per seed, and weight per head were the most closely related to grain yield. Seed weight was significantly and negatively related to the

number of seeds and spikelets per head. However, the number of seeds and spikelets per head were very closely associated ($r = 0.681^{**}$).

Introduction and Literature Review

Nitrate Reductase and Its Relation With Yield

Plant growth and yield are the result of a series of biochemical reactions present in the plant each of which is catalyzed by specific enzymes (9). If such enzymes can be isolated and their control mechanism determined, then selection for cultivars superior for a particular enzyme would hasten development of superior cultivars with complex traits. High nitrate reductase activity (NR) is one factor associated with high grain yield and protein. The nitrate reductase system is an example of a physiological process which may be limiting wheat yield under certain environmental conditions. It is believed that this system can be altered through physiological research and plant breeding programs to enhance productivity.

Nitrate reductase is an enzyme whose study could produce valuable insight into the complex metabolism involved in grain protein production. This enzyme is related to total reduced nitrogen accumulated in the plant (20); associated with increased protein formation and decreased nitrate content (8); and linearly related to total grain protein production within a genotype (4). Harper and Paulsen (10) obtained a positive correlation coefficient of 0.856 between nitrate reductase activity and water soluble protein content in winter wheat. They also showed that NR activity decreased with approaching maturity. A significant positive relation was obtained between input of reduced nitrogen and the amount of protein accumulated in grains in two wheat cultivars (4). Hageman and Flesher (8) found that the diurnal variation in NR was correlated positively with WSP content and negatively with nitrate content. Johnson et al. (12) stated that high grain protein was not associated with differential nitrogen uptake or nitrogen accumulation in the plant. On the other hand, Zieserl and Hageman (21), evaluating 47 inbred lines of corn, found significant differences in NR activity, WSP content, and nitrate, but no positive correlation was found between NR activity and WSP content or negative relation between NR activity and nitrate content.

Croy (3) stated that higher NR activity and WSP content appeared to be associated with increased yield and grain protein production per acre. He also pointed out that increasing NR levels and nitrogen reduction whether by genotype or fertility and water management should provide potential and lead to higher yields and greater protein production per acre. Eilrich and Hageman (7) observed seasonal NR activity was correlated significantly and positively with grain yields. Deckard et al. (6) found significant positive correlations between NR activity and grain yield. Several studies indicated that NR assays could be a useful predictive selection criterion for grain yield (4, 5, 7). Blackwood and Hallam (2) believed that with careful choice of leaf tissue good correlations between spot determinations of nitrate reductase activity and yield can be achieved for more than one cultivar of wheat in a variety of growth situations.

Yield and Yield Components and Their Relation to Each Other

Grain yield in wheat is determined by three major components of yield: tiller number per plant or per unit area, the average number of kernels per spike, and the average kernel weight. It has been suggested that indirect selection for yield based on the components of yield might be more effective than direct selection for yield itself (11, 20, 21). Thus, knowledge of the interrelations among yield and the yield components is necessary for effective selection to increase yield.

Yield components are considered as the units from which high yield might be developed. On the other hand, selection on the basis of these components did not lead to the yield increase as expected due to the biological limitations and compensation among such yield components. The increase in one yield component usually cause a decrease in one or more of the components. Osmanzai (18) and Assadian (1) found that kernel weight was the only yield component which had a significant correlation with yield. They believed that kernel weight was the most important yield component in terms of its influence on grain yield under conditions where tiller number and head size have reached an optimum for yield. It has been concluded that indirect selection based on kernel weight would be an effective procedure to increase yield (15, 18). The results of two wheat cultivars showed that spikes per plant and kernel per head were more closely related to yield per plant than kernel weight (17). McNeal et al. (16) showed that in wheat varieties, grain yield was more associated with fertile tillers per unit area than with kernels per spike or kernel weight. Scott et al. (19) indicated that grain yield was more closely related to grain number per unit area using simple correlation coefficients.

Under field conditions, the success of newly developed dwarf cultivars may in part be due to a greater tiller population per unit area than with the older taller cultivars. Jones and Kirby (13) studied the effect of several detillering treatments on dry-matter production and grain yield in barley. Their results indicated that the plants with few tillers tended to have greater grain yield than plants permitted to tiller freely. Furthermore, when these tillers are developing they compete with the other developing shoots for assimilate, thus reducing the size of these shoots and their potential yield (14).

The objectives of this study were: (1) to determine the relationship between grain yield and yield components; and (2) to evaluate 36 winter wheat entries for NR and yield components.

Materials and Methods

This study was conducted in 1980-1981 season on the Agronomy Research Station, Stillwater, Oklahoma. Such material has been under screening processes for desirable morphological and physiological characters including yield potential and drought resistance. This experiment was designed to subject plants to water stress, but no stress treatments were applied.

Field plots were arranged in a randomized block design with nine replicatitons containing 36 entries each. Three out of the nine replications were used to collect leaf samples for nitrate reductase measurements. The other six replications were used to collect yield data. The seeds were planted on October 29, 1980. Guard rows were planted around the blocks to reduce border effect. The plots were fertilized with the equivalent of 224 kg ha^{-1} of 10-20-10 ($N-P_2O_5-K_2O$) preplant.

Leaf samples were collected between 9-10 A.M. throughout the 1981 spring growing season from late March to the first week of May. Due to the number of samples involved,it was possible to take measurements from only one replication per day. Leaves were cut into short sections, discarding tips and bases. Then 0.5 g of plant tissue was used to determine NR activity following the same procedure described in previous chapters.

After maturity, data were collected on yield per plot, tiller number per unit area, yield per tiller, spikelets per head and number of seeds per head. Yield per plot was determined on the weight of the threshed and cleaned grain harvested from each 3000 cm^{-2} of plot and was expressed in grams per plot and also converted into Kg ha^{-1}. Tiller count was based on the number of fertile tillers in a 30 cm length row. Two observations were collected at random from each row before plot yield was obtained. Heads of six random tillers from each plot were harvested and utilized for study of yield components.

Statistical analysis were carried out on nitrate reductase, number of tillers per 30 cm length of row, yield per plot, yield per tiller, spikelets per head, seeds per head, and seed weight. Analysis of variance for each trait was performed on 36 entries. Phenotypic and genotypic correlations were computed among traits.

Results and Discussion

The entries are given a numerical listing from 1 to 36 to refer to in the results and discussion of this chapter. These entries and their associated numbers are listed in Table I.

Precipitation and temperature data are presented in Table II as recorded by the U.S. Weather Bureau official reporting station at Stillwater.

Nitrate Reductase and Yield Relationship

The potential of plants to utilize more nitrogen and change it to reduced forms can be determined by measuring the NR levels of plant tissue. Nitrate reductase average over all the spring growing season and the grain yield of the 36 entries are presented in Table III. Figure 1 shows that nitrate reductase (NR) level reached its maximum April 22 and then started to decline by approaching maturity. Others have shown similar results (10). Differences in level of NR activity was observed among entries. In fact, some of the differences in NR activity were confounded with replications as the result of sampling. These observations appear to support the view presented by Croy and Hageman (4). They believed that their results suggests the presence of a relatively narrow genetic base. The results of this study also indicated that the NR differences among entries were not as pronounced as grain yield (Table III).

Yield and Yield Components

The overall mean of the grain yield for 36 entries was 2064.9 kg/ha and yields ranged from 939.1 to 2870.5 kg/ha. The four top high yielding entries were 1, 31, 3, and 5.

Analysis of variance presented in Table IV showed that there were highly significant differences at 0.01% level among entries for yield and yield components (tillers per unit area, spikelets per head, seeds per head, weight per head, and weight per seed). Number of tillers and grain yield (Table IV) show a relatively high coefficient of variability (C.V.), 21 and 33%, respectively compared to weight per seed (C.V. = 6.8%).

With respect to the number of fertile tillers per plot (Table V), entries 11, 34, 26, and 29 ranked first, second, third, and fourth. These entries ranked 14th, 26th, 13th, and 6th, respectively in their grain yield.

The phenotypic and genotypic correlation coefficients between yield and yield components variables are presented in Table VI. The relation between grain yield and number of tillers was positively significant ($r = 0.461^{**}$). Figure 2 also illustrates such positive association. Some other workers have showed a negative correlation between these two traits (1, 18).

The weight per head was highly correlated with spikelets per head, seeds per head, and weight per seed. The correlation coefficients were 0.457^{**}, 0.626^{**}, and 0.571^{**}, respectively (Table VI). On the other hand the weight per head and grain yield were positively and significantly correlated ($r = 0.423^{**}$). Spikelets and seeds per head were nonsignificant and positively correlated with grain yield. It is interesting to see the genotypic correlation coefficients of such traits were relatively high and negative. This suggests that the use of phenotypic or simple correlation may hide the genotypic relation of yield components to each other. Therefore, it is desirable to apply the phenotypic and the genotypic association. This also indicates that the environment may lead to the change in the direction of such relation. It seems that if the correlated traits are highly heritable the genotypic correlation may be considered as a useful estimate of their relation.

A significant negative relation ($r = -0.269^{**}$) between weight per seed and number of seeds per head was observed, indicating that simultaneous improvement of these two traits may be difficult. Number of spikelets and seeds per head were highly and positively correlated ($r = 0.681^{**}$). But, the seed weight was negatively related to number of spikelets per head ($r = -0.171^{*}$). On the other hand, Table VI and figure 3 showed a high positive relationship between seed weight and grain yield. Other workers obtained similar results (1, 18).

Summary

1. The differences in NR activity among entries studied were not as pronounced as their grain yield and yield components.
2. All yield components were positively associated with grain yield. The number of tillers per unit area, weight per seed, and weight per head were the most closely related to grain yield.
3. The correlation coefficients suggest that the use of phenotypic correlation under some environments may hide the genotypic association of yield components to each other.

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TABLE I

ENTRY NUMBER, NAME, C. I. NUMBER

Entry No.	Entry	C. I. Number
1	Triumph	12132
2	A12	10206
3	Red Chief	12109
4	Unknown	8530
5	Blue Jacket	12502
6	No. 2681	9550
7	Hope/TK/Cnn	13182
8	Triplet	5408
9	Sturdy	13684
10	Turkey Sel	11984
11	Turkey Sel	10096
12	Ponca	12128
13	No. 2697	9551
14	TK/Fn/GO/FR/Oro Sel 2715	12250
15	Ashkof	6680
16	Ganderbal	7288
17	Hope/Turkey	11966
18	Unknown	13898
19	Royal D85	12588
20	Cheyenne	8885
21	NB67786	14061
22	Akakawa Aka	Unknown
23	Unknown	7126
24	Cnn/Tenmarq	11972
25	Blue Boy II	15281
26	Turkey 1069/Cnn	11983
27	Shen Chow 2387	8339
28	Clark R169	12556
29	Cheyenne Sel.	8885
30	Goens	4857
31	Tam W-101	15324
32	Sonowar 139	7285
33	Newsar	12530
34	N6	11056
35	KanKing	12719
36	Centurk	15075

TABLE II

MONTHLY CLIMATOLOGICAL DATA FOR 1980-1981 SEASON AT THE AGRONOMY RESEARCH STATION, STILLWATER

		Temperature °C			Rainfall (mm)		
Year	Month	Mean	Min	Max	Received	Long Term Mean	Deviation
1980	Aug.	29	18	41	88	82	6
	Sept.	20	9	38	36	86	-50
	Oct.	16	-3	34	43	71	-28
	Nov.	13	-6	31	10	47	-37
	Dec.	6	-13	23	41	34	7
1981	Jan.	3	-13	26	2	29	-27
	Feb.	6	-18	30	27	34	-7
	Mar.	10	-2	24	57	47	10
	Apr.	20	1	32	23	73	-50
	May	18	3	32	162	117	45
	June	26	12	36	122	108	14

TABLE III

NITRATE REDUCTASE (NR) AND GRAIN YIELD FOR 36 ENTRIES GROWN IN FIELD 1980-1981 SEASON

Entry	Nitrate Reductase (NR) (μmoles NO_2^- gm fr wt^{-1} hr^{-1})	NR Rank	Yield (g $Plot^{-1}$)	Grain Yield Rank
1	8.24	(31)	86.2	(1)
31	11.80	(1)	85.8	(2)
3	9.10	(19)	80.8	(3)
5	9.08	(21)	80.0	(4)
21	8.27	(30)	77.5	(5)
29	11.77	(2)	77.3	(6)
35	9.30	(14)	76.0	(7)
36	9.25	(16)	75.8	(8)
18	7.16	(36)	74.3	(9)
12	9.10	(18)	72.2	(10)
25	8.90	(23)	71.3	(11)
30	9.69	(9)	70.8	(12)
26	7.88	(35)	64.7	(13)
10	8.22	(32)	63.2	(14)
11	10.16	(5)	63.2	(14)
6	8.73	(27)	63.0	(16)
13	9.90	(7)	62.7	(17)
27	9.53	(10)	62.3	(18)
7	10.34	(3)	62.0	(19)
20	8.05	(34)	61.7	(20)
33	8.99	(22)	61.7	(20)
16	9.09	(20)	61.5	(22)
23	8.83	(26)	58.5	(23)
32	9.24	(17)	58.5	(23)
28	8.46	(28)	55.2	(25)
17	9.34	(13)	52.0	(26)
34	8.90	(24)	51.3	(27)
24	10.04	(6)	51.2	(28)
19	8.07	(33)	51.0	(29)
14	9.42	(12)	49.7	(30)
8	9.80	(8)	48.0	(31)
22	8.89	(25)	48.0	(31)
2	9.27	(15)	46.0	(33)
9	10.21	(4)	44.3	(34)
4	9.44	(11)	36.5	(35)
15	8.35	(29)	28.2	(36)
$LSD_{0.05}$	1.55		23.3	
C.V. %	25.66		33.00	

TABLE IV

MEAN SQUARE FOR YIELD AND YIELD COMPONENTS OF 36 WHEAT ENTRIES GROWN UNDER FIELD CONDITIONS 1980-81 SEASON

Source	Degree of Freedom	Tillers Plot^{-1}	Spikelets Head^{-1}	Seeds Head^{-1}	Weight Head^{-1}	Weight Seed^{-1}	Grain Yield
Rep	5	166.7	6.8	22.9	0.05	0.009	812.0***
Entry	35	219.4***	11.1***	104.6***	0.14***	0.135***	1124.1***
Error	175	66.1	1.5	15.9	0.02	0.005	418.8
C.V. %		21.24	8.19	12.24	13.65	6.82	33.00

***Denotes significance at 0.01% level.

TABLE V

NUMBER OF TILLERS AND SOME OTHER YIELD COMPONENTS OF 36 WHEAT ENTRIES GROWN 1980-81 SEASON

Entry	Tillers/ Plot	Spikelets/ Head	Seeds/ Head	Head Weight (g)	Seed Weight (mg)	Grain Yield (Kg/ha)
1	43.6	11.5	24.9	1.02	41.0	2870.5
2	34.9	15.2	37.6	1.06	28.2	1531.8
3	39.3	15.3	28.8	1.09	37.6	2674.1
4	29.5	1.6	32.5	0.97	29.2	1215.5
5	42.3	15.9	32.8	1.12	33.9	2664.0
6	42.6	16.1	36.3	0.99	27.2	2097.9
7	37.8	14.5	30.1	1.00	33.2	2064.6
8	33.7	17.9	42.3	1.10	25.9	1598.4
9	28.7	15.1	35.4	0.96	26.7	1475.2
10	43.1	14.1	28.5	0.88	31.3	2104.6
11	55.4	13.5	27.5	0.77	28.2	2104.6
12	41.6	13.6	29.5	1.02	34.5	2404.3
13	42.7	15.4	37.8	0.98	25.9	2087.9
14	31.3	17.4	36.5	1.01	27.8	1655.0
15	35.2	15.4	27.5	0.71	25.3	939.1
16	33.8	14.4	32.4	1.09	33.7	2048.1
17	42.7	12.5	27.1	0.82	30.3	1731.6
18	35.5	15.0	35.0	1.37	39.2	2474.2
19	31.6	15.7	38.3	1.19	31.3	1698.3
20	43.3	14.1	31.7	1.02	32.4	2054.6
21	32.3	16.3	34.4	1.26	36.9	2580.8
22	25.9	15.5	31.7	1.20	38.1	1598.4
23	34.1	14.6	32.6	1.05	32.1	1948.1
24	41.7	13.2	27.0	0.76	27.7	1705.1
25	33.8	15.6	38.8	1.22	31.3	2374.3
26	45.8	14.1	31.4	1.09	35.0	2154.5
27	39.8	16.6	35.8	1.06	29.3	2074.6
28	36.8	16.2	31.3	1.21	38.7	1838.2
29	44.8	14.4	32.4	1.06	32.7	2574.1
30	33.0	16.8	37.7	1.24	33.2	2357.6
31	42.3	12.7	29.5	1.21	41.2	2857.1
32	39.0	14.9	31.8	0.87	27.7	1948.1
33	35.0	14.3	25.8	0.921	35.8	2054.6
34	47.3	14.5	35.9	0.89	24.7	1708.3
35	37.4	15.6	29.7	1.17	39.3	2530.8
36	41.6	14.9	35.4	1.02	28.6	2524.1
$LSD_{0.05}$	9.3	1.4	4.5	0.16	2.5	775.9
$LSD_{0.01}$	12.2	1.8	6.1	0.21	3.3	1025.6

TABLE VI

PHENOTYPIC AND GENOTYPIC CORRELATIONS BETWEEN SIX YIELD TRAITS USING THE MEAN OF 36 WINTER WHEAT ENTRIES

	Grain Yield	Spikelets per Head	Seeds per Head	Head Weight	Seed Weight
1. Tiller Number	0.461[1,2]	-0.094	-0.124	-0.127	-0.021
	0.386	-0.553	-0.362	-0.404	-0.082
2. Grain Yield		0.089	0.078	0.423	0.444
		-0.297	-0.151	0.477	0.639
3. Spikelets/Head			0.681	0.457	-0.171
			0.713	0.350	-0.274
4. Seeds/Head				0.626	-0.269
				0.445	-0.402
5. Head Weight					0.571
					0.633

[1] The upper value is phenotypic or simple correlation coefficient based on total corrected sum of product and the lower is genetic correlation coeffficient bases on entry sum of product.

[2] Values above 0.269 are significant at 1% level of probability.

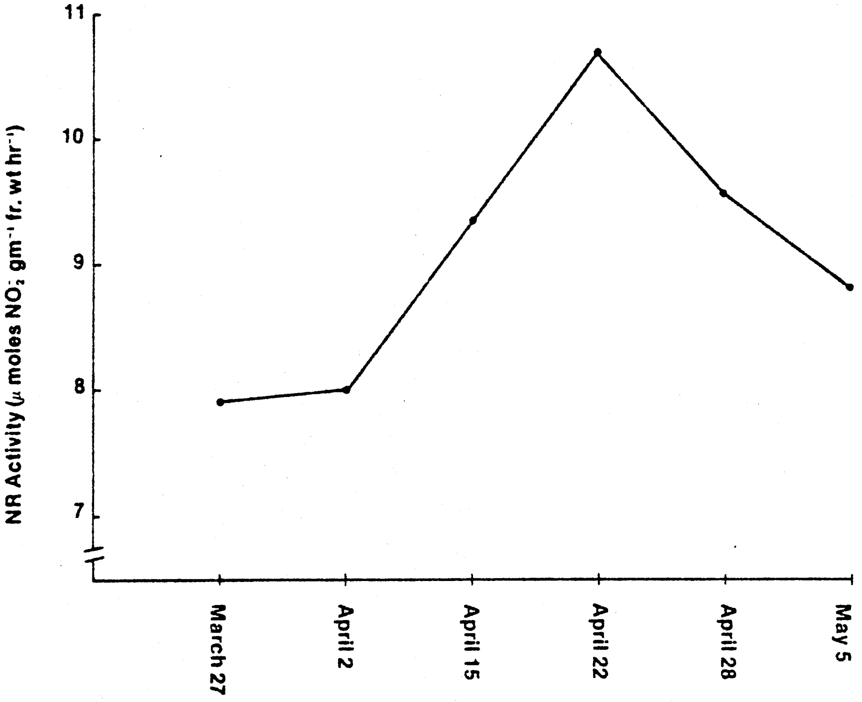

Figure 1. Changes in Nitrate Reductase (NR) Activity by Sampling Dates

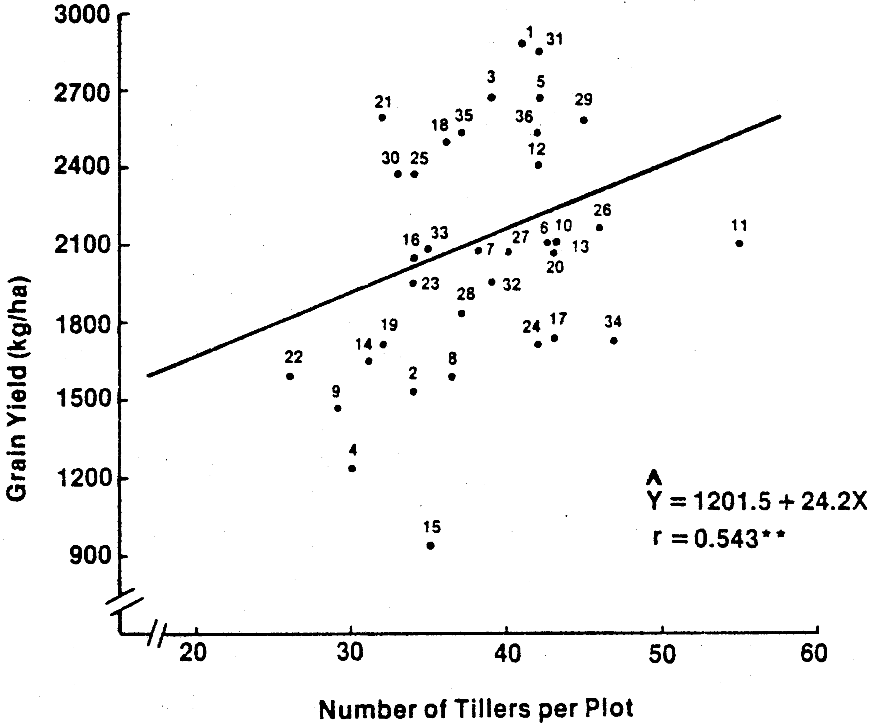

Figure 2. Regression of Grain Yield on Tillers

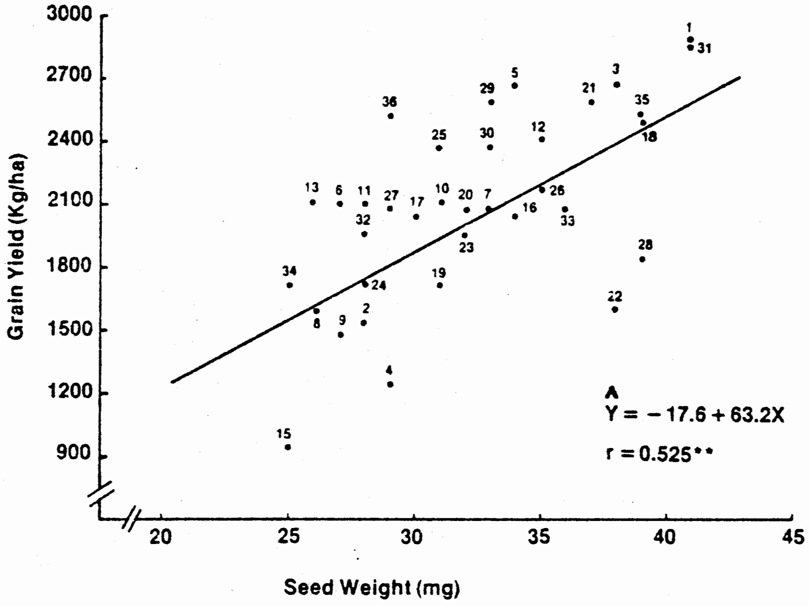

Figure 3. Regression of Grain Yield on Seed Weight

CHAPTER VI

SUMMARY AND CONCLUSIONS

The purposes of this research were: (a) to study the relationships among different physiological aspects under drought stress conditions; (b) to investigate the relation of these aspects to drought resistance; and (c) to evaluate different winter wheat cultivars in terms of their resistance to water stress. The research was carried out by conducting different experiments under different environmental conditions. Some of these studies were conducted in growth chambers, and others were performed under field conditions.

The physiological aspects evaluated were nitrate reductase (NR) activity, net carbon dioxide exchange (NCE), stomatal resistance (R_s), yield and yield components, and some other physiological and morphological characters.

The data obtained from this research indicated that NR activity was reduced when the plants were subjected to water stress. This reduction reached 50% in some cases. Such reduction in enzyme activity under water stress conditions was accompanied by the accumulation of nitrate (NO_3^-) as indicated by significant negative correlation between NR levels and NO_3^- content. The percent of enzyme stability was determined in one study. This percentage ranged from 23 to 51%. These results suggest that NR assay could be a useful technique to evaluate the capability of wheat cultivars to withstand drought stress conditions.

By the same token, net carbon dioxide exchange (NCE) data revealed a decline in this trait under water stress conditions. This reduction was accompanied by an increase in stomatal diffusive resistance (R_s). There was generally significant negative relation between these two physiological aspects. The cultivars that developed more R_s reflected more reduction in their NCE and vice versa. Such conclusion suggested that the reduction in water loss through stomates as the result of higher stomatal resistance was at the expense of carbon dioxide exchange through these openings. This negative relation between NCE and R_s also indicated that the selection for one of them will lead to the reduction of the other.

However, an optimum balance between the development of stomatal resistance and the reduction of carbon dioxide exchange was desirable in this situation. The crop physiologist should search for the cultivars that have the capability to increase their stomatal resistance with a minimum reduction in carbon dioxide exchange. The results of this research indicated that cultivars expressed different percentages of NCE reduction per unit change in stomatal resistance under water stress. As physiologists we should search for cultivars that show smaller reduction in NCE per unit change in R_s to reduce water loss through transpiration with less sacrifice in photosynthetic assimilate under drought stress conditions. On the other hand, there is a possibility that such relation between NCE and R_s does exist in some cultivars. If this is true, it will be valuable to use these cultivars in breeding for drought resistance.

It is very interesting to see that NCE is generally associated with yield and yield components. The results of this research showed a significant positive correlation between NCE and yield or yield components. Therefore, if this conclusion is true, such data may provide a basis for plant breeders to screen for high yielding cultivars or predict their yield by measuring the photosynthetic activity. The relation between R_s and yield or yield components was a nonsignificant negative relationship.

Morphological characteristics and yield components were reduced by water stress. Peduncle length and height were severely reduced by such stress. There was a significant positive correlation between morphological characteristics measured and yield or yield components.

Under normal field conditions, the differences in NR activity among entries studied were not as pronounced as their grain yield and yield components.

All yield components were positively associated with grain yield. The number of tillers per unit area, weight per seed, and weight per head were the most closely related to grain yield. Weight per seed was negatively and closely associated with the number of spikelets and seeds per head. The last two yield components were highly and positively related to each other.

Finally, it can be concluded from this research that wheat cultivars which would be able to maintain high NR activity and minimum reduction in photosynthesis with high stomatal resistance under drought conditions have a greater capacity to tolerate such stress. It also can be concluded from this research that no single trait measured has sufficient reliability to determine overall cultivar drought response in winter wheat.

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