DROUGHT SENSITIVITY IN WINTER WHEAT POPULATIONS UNDER FIELD CONDITIONS AND ELEVATED ATMOSPHERIC CO$_2$

By

MARIE ANTOINETTE SCHONFELD

Candidate in Agricultural Sciences
Agricultural University of Wageningen
Wageningen, the Netherlands
1976

Ingenieur in Agricultural Sciences
Agricultural University of Wageningen
Wageningen, the Netherlands
1982

Submitted to the Faculty of the
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Thesis Approved:

Richard C Johnson
Thesis Adviser

Eugene G. Krenzer Jr

Brett F Carver

Ronald W. McNew

Norman N. Durham
Dean of the Graduate College

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LIST OF SYMBOLS

A	Carbon Assimilation Rate
B1, B2	Backcross of F1 to P1 or P2, respectively
C_a	Ambient CO_2 Concentration
C_i	Intracellular CO_2 Concentration
CV	Coefficient of Variation
ϵ	Modulus of Elasticity
F1, F2	First and Second Filial Generation
g_sCO_2	Stomatal Conductance to CO_2
h^2	Narrow-Sense Heritability
L	Stomatal Limitation to Photosynthesis
P1, P2	Parents of a Cross Between Two Cultivars
PC	Pot Water Holding Capacity
PPFD	Photosynthetic Photon Flux Density
RWC	Relative Water Content
SP	Solute Potential
T	Transpiration Rate
TP	Turgor Potential
WP	Water Potential

CHAPTER I

INTRODUCTION

Drought stress is a severe problem in crop production worldwide. In the southern Great Plains of the U.S., winter wheat (Triticum aestivum L.) grain yield can be reduced by frequent droughts during fall or spring. In the coming decennia, the gradual depletion of the Ogallala Aquifer in this region will lead to a relative increase in the area of dryland wheat production (Warren et al., 1981).

In the coming decennia, a rapid increase in atmospheric CO_2 concentration will also occur. Atmospheric levels may double as early as 2025 (Gribbin, 1981). This rise could have beneficial effects on crop production, because plant photosynthesis is limited by the ambient CO_2 concentration, especially C_3 plants (Kimball, 1983). This rise could also lead to an increase in global temperature, due to the "greenhouse effect", resulting in increased drought stress in many areas. To anticipate the influence of increased CO_2 levels on crop production, it is important to gain insight into the possible interaction between CO_2 enrichment and drought stress.

Wheat cultivars are known to differ in drought resistance (Todd and Webster, 1965), but the mechanisms governing these differences are not well understood. Improved drought resistance has long been one of the major goals in crop breeding (Hurd, 1976). An increased understanding of the characteristics that control differences in drought resistance could lead to the use of more effective selection criteria in a breeding program.

The research described herein focuses on two aspects of drought sensitivity. The first project was a field study in two consecutive growing seasons. Drought stress was induced in the spring with a rain shelter, and several physiological and developmental traits were investigated while drought stress developed, to determine if genetic differences could be detected between winter wheat cultivars differing in drought resistance. The traits considered were tillering pattern, water potential (WP), WP components (turgor potential, TP, and solute potential, SP), and relative water content (RWC). Yield and yield components were determined at maturity. If any of these traits exhibited such differences, their genetic control was further investigated.

The effects of CO_2-enrichment and prolonged dehydration stress on growth, development, and photosynthesis of vegetative winter wheat plants was investigated in a controlled-environment study. Seedlings in pots were placed in growth chambers where the atmosphere was maintained at either the ambient or double the ambient CO_2 concentration. When the plants were well established, three levels of water supply were established by controlling the amount of water supplied: well-watered, medium drought-stressed, and severely drought-stressed. During several weeks of this regime, plant developmental stages were recorded daily. Steady-state gas exchange measurements were made, and WP, RWC, and dry matter production were determined. The interaction of CO_2 enrichment and drought stress was determined from these data.

The two parts of this dissertation are separate and complete manuscripts to be submitted for publication. The format of each manuscript conforms to the style of <u>Crop Science</u>.

CHAPTER II

WATER RELATIONS IN WINTER WHEAT AS DROUGHT RESISTANCE INDICATORS

Manette Schönfeld, Richard C. Johnson,
Brett F. Carver, and Dolores W. Mornhinweg

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Former graduate research assistant (now research associate, University of Idaho Research and Extension Center, Aberdeen, ID 83210), associate and assistant professor, and research associate, respectively. Agronomy Department, Oklahoma State Univ., Stillwater, OK 74078

ABSTRACT

Grain yield of winter wheat (Triticum aestivum L.) is severely limited by drought stress in the southern Great Plains. In 1984-85 and 1985-86, field experiments were conducted in Stillwater, OK, to determine potential drought resistance parameters and their inheritance in winter wheat. Single plants of the cultivars 'TAM W-101' and 'Sturdy', their F1 and F2 progeny, and the backcrosses of the F1 to each of the parents were evaluated under a rain shelter. Tiller number was recorded throughout the growing season. While stress developed during reproductive development, measurements of water potential (WP), solute potential (SP), turgor potential (TP), and relative water content (RWC) were taken at seven- to ten-day intervals on single leaves until flag leaf senescence. Tiller number and growth rate were similar among the six populations. Water potential, WP components, and RWC declined with increasing drought stress, but no significant differences among populations were found in WP, SP or TP. Relative water content, however, differed significantly between the parents under increasing drought stress. TAM W-101 maintained a higher RWC under drought conditions than Sturdy, and this was associated with a longer grain filling period. Comparison of the RWC values among populations indicated that differences were controlled predominantly by genes with additive effects. Narrow-sense heritability (h^2) of RWC increased as drought stress intensified and reached a maximum value of 0.64 one week prior to flag leaf senescence. With this high h^2, RWC shows promise as a selection criterion for drought resistance in winter wheat.

Additional index words: *Triticum aestivum* L., Relative water content, Tillering, Water potential, Generation-means analysis.

INTRODUCTION

Drought stress is one of the most limiting factors to crop production worldwide. In the central and southern Great Plains of the USA, drought is often a serious wheat (Triticum aestivum L.) production problem. Fall droughts often occur which can reduce tillering and leaf production important for grazing cattle and potential grain yield (Johnson and Kanemasu, 1982). Spring droughts also occur frequently and can seriously reduce grain yield.

Wheat cultivars are known to differ in drought resistance (Todd and Webster, 1965), but the mechanisms controlling these differences are not well understood. Improved drought resistance has been one of the major goals in crop breeding (Hurd, 1976). To be successful, selection criteria must be identified which are associated with improved yield under conditions of drought stress, have a high heritability, and can be measured feasibly and accurately in large populations. An improved understanding of the basis for differences in drought resistance could lead to the use of these characteristics as selection criteria.

Various physiological and developmental traits were investigated to determine if differences between winter wheat cultivars could be determined under drought stress. The traits studied were tillering pattern, water potential (WP), WP components (solute potential, SP, and turgor potential, TP), and leaf relative water content (RWC). Tillering pattern was considered because previous experiments (unpublished data) indicated that a genotype which produces a large number of tillers, thus accumulating a large biomass, might deplete soil moisture earlier in the spring than a genotype with less prolific tillering. Water potential components were investigated because WP is generally considered a reliable measurement of the water status of plant tissue. Recently, RWC was proposed as a better indicator of water status than WP (Sinclair and Ludlow, 1985) because RWC may more closely reflect the balance between water supply to the leaf and transpiration rate. In addition, RWC can be measured more feasibly than WP without expensive equipment.

The first objective of this study was to determine if differences in tillering, WP, WP components, and RWC could be determined under drought stress between winter wheat populations differing in drought resistance. The second objective was to determine the genetic control of such differences.

MATERIALS AND METHODS

The experiment was conducted during two growing seasons between October 1984 and June 1986 at the Agronomy Research Station in Stillwater, Oklahoma. The soil type was a Kirkland silt loam (fine, mixed, thermic Udertic Paleustolls). Nitrogen was applied as ammonium diphosphate (50 kg N per ha) before planting.

The experimental material was comprised of two cultivars of hard red winter wheat 'TAM W-101' and 'Sturdy', their F1 and F2 progenies, and the backcross progenies of the F1 to TAM W-101 and Sturdy (B1 and B2, respectively). TAM W-101 has reportedly more drought resistance under field conditions than Sturdy (O. Merkle, K. Porter, personal communication). Because segregating populations (F2, B1, and B2) required more sampling than nonsegregating populations (parents and F1), the number of plants representing each population differed. Four rows of F2 plants and two rows of B1 and B2 plants were planted for each row of parent and F1 plants. Apart from this modification, the experimental design was a randomized complete block with four replications in both years. For comparison with plants exposed to drought stress under a rain shelter, plants of the two parental genotypes were planted in a well-watered area outside the shelter in 1984-85 and underneath the shelter in 1985-86. The experimental design followed that of the drought-stressed plots in all details of row spacing, fertilization, and replication. The same experimental data were collected on the same sampling dates.

Seedlings with two to three leaves were transplanted on 12 Oct. 1984 and on 25 Oct. 1985. Six plants were spaced 0.10 m apart within 0.50 m rows, and rows were spaced 0.30 m apart. The plots were surrounded on all sides with wheat, and all rows within the plots were separated by border rows of the cultivar 'TAM 105'. During the fall, plots were watered as needed to prevent drought stress. From 13 Mar. 1985 (day 73 from 1 January) and from 3 Mar. 1986 (day 62 from 1 January) until harvest was completed, the plot area was covered with a rain shelter to simulate drought conditions. The shelter consisted of an open-ended 9 x 14.4 m greenhouse (Columbine, Nexus Greenhouse Corp., Northglenn, CO), with open sides 0.5 m from the ground. The shelter was covered with a double layer of polyethylene film, which allowed passage of 70 to 75% of the photosynthetic photon flux density. On any given day, the average air temperature at the top of the canopy and 0.5 m above the canopy was no more than 2°C higher inside the shelter than outside the shelter. These relatively small differences in light and temperature did not have any visual effect on plant growth and development compared to plants outside the shelter. Developmental stages were determined according to the improved Feekes scale (Zadoks et al., 1974).

During the first year, tiller emergence was recorded every other day until approximately 15 tillers had appeared (day 320 of 1984). Individual tillers were identified according to the system developed by Klepper et al., (1982), and marked with color-coded rings as they emerged from the leaf sheath of the supporting leaf. Subsequently, the number of tillers per plant was counted every six to eight weeks. In the first year, tiller emergence and tiller number were recorded for the central three plants in each row. In the second year, total tiller number was recorded approximately every two months on the central four plants per row, beginning when the plants had developed three to four tillers (day 309 in 1985).

After the plot area was covered in March, the development of drought stress was monitored with periodic measurements of WP, WP components, and RWC between 1100 h and 1300 h. It has been shown that WP is reasonably stable during that period (Fischer and Sanchez, 1979). In 1985, two samples were taken at random from the central four plants in each row at approximately 10-day intervals. In 1986, one sample was taken at 7-day intervals from each of the four central plants per row to enable estimation of genetic effects. The final measurements were taken when the flag leaf had senesced on approximately one-third of the plants (day 127 in 1985 and day 120 in 1986). Water potential was measured using leaf cutter psychrometers (Morrill Specialty Inc., Logan, UT) as described by Johnson et al., (1983). The youngest, fully expanded leaf (with auricles clasping the next leaf or the stem) on a randomly chosen tiller was sampled; care was taken that no tiller was sampled on consecutive sampling dates. One disc of 0.24 cm^2 was cut from the center of the leaf and used for water potential readings. Psychrometers were equilibrated for two hours in a water bath at 30°C, and readings for total WP were made. Thermocouples with samples inside were then frozen overnight at -20°C to disrupt cell membranes. After thawing and equilibrating at 30°C in the water bath, SP was measured in the same manner as WP, and TP was calculated from the equation:

$$WP = SP + TP.$$

After WP samples were taken, the same leaves were used to determine RWC. Immediately after cutting at the base of the lamina, leaves were wrapped in aluminum foil, sealed inside a plastic bag, and placed in a cooler. Fresh weight was determined within 2 h after excision. Turgid weight was obtained after soaking the leaves for 16 to 18 h in distilled water at room temperature (ca. 20°C). Preliminary tests indicated no further increase in leaf weight after this time period. After soaking, leaves were quickly and carefully blotted dry with tissue paper prior to determination of turgid weight. Dry weight was obtained after oven drying the leaf samples for 72 h at 70°C. Relative water content was calculated from the equation:

$$\text{RWC (\%)} = \frac{\text{fresh weight - dry weight}}{\text{turgid weight - dry weight}} \times 100$$

Physiological maturity (hard dough stage) was reached on day 149 for TAM W-101 and on day 143 for Sturdy in 1985, and on day 140 for TAM W-101 and day 131 for Sturdy in 1986.

The plants were harvested on day 157 in 1985 and on day 154 in 1986. Above-ground biomass, grain yield, yield components (number of heads per plant, number of kernels per head, and kernel weight), and harvest index were determined on each of the four central plants of each row in both years.

Data analysis was performed using the GLM (General Linear Models) procedure in SAS (SAS Institute,Inc, 1985). Linear orthogonal contrasts were made between population means (Steel and Torrie, 1980). The comparisons considered were TAM W-101 vs. Sturdy, F1 vs. the mid-parent, B1 vs. B2, and F2 vs. the mid-backcross. Narrow-sense heritability (h^2) was calculated based on the variation within each population pooled over replications; negative estimates of h^2 are reported as 0 (Wright, 1968). Genetic hypotheses were tested by generation-means analysis (Bulmer, 1980). The contribution of additive, dominance, and digenic epistatic effects to variation among population means was determined under a six-parameter model (Hayman, 1958). A weighted analysis of variance was performed on the data, with reciprocals of variances of the population means as weights. Using matrix algebra operations to simplify computations (Rowe and Alexander, 1980), genetic effects were tested in the following sequential order: m, mid-parent value of the drought sensitive and drought resistant parents; a, additive effects pooled over loci; d, pooled dominance effects; aa, pooled additive x additive epistatic effects; ad, pooled additive x dominance epistatic effects; and dd, pooled dominance x dominance epistatic effects. The sequential fitting of data was terminated (i.e. a particular model was considered to provide a good fit for the data) when the residual mean square no longer exceeded ($P < 0.05$) the experimental error mean square from the analysis of variance. Because well-watered and drought-stressed plots were not randomized with respect to each other, statistical tests for water treatment effects and genotype x water treatment interaction were not made.

RESULTS

In both years, leaf rolling and wilting became visible around the boot stage in April (day 110 in 1985 and day 99 in 1986) and increased in intensity over time. Neither wilting nor leaf rolling occurred in the well-watered plots. Spring in 1986 was warmer than in the previous year and the plants developed faster. However, the rain shelter was covered 10 days earlier in the second year, so that visible drought symptoms appeared at approximately the same developmental stage in both years.

The decline in WP started at approximately day 108 in 1985 and day 92 in 1986 (Fig. 1), before leaf rolling and wilting became visible. The average WP over all populations had dropped to -1.25 MPa by the time visible drought symptoms became apparent and continued to decrease throughout the growing season. The lowest values were -2.20 MPa in 1985 and -2.75 MPa in 1986, just prior to complete flag leaf senescence. Plants in the well-watered plots maintained a WP greater than -1.3 MPa up to flag leaf senescence. Although visible leaf wilting and yellowing were more rapid and severe in the Sturdy plants than in the TAM W-101 plants, this was never reflected as statistical differences ($P < 0.05$) in WP. As with WP, SP and TP declined over time with increasing drought stress (Figs. 2 and 3); SP and TP also failed to show significant ($P < 0.05$) differences among populations. The lowest values for SP were -2.52 and -2.81 MPa in 1985 and 1986, resectively, and 0.31 and 0.06 MPa for

TP in both years.

Relative water content decreased with increasing drought stress, and showed significant differences among populations (Fig. 4). A consistently higher RWC was maintained in TAM W-101 than in Sturdy under drought. Significant differences between the parents also occurred under well-watered conditions, but the magnitude of the difference was much smaller than observed under drought. The slope of the decline in RWC was 38 to 89% greater for Sturdy than for TAM W-101 (Table 1). The slope for the F1 was intermediate to TAM W-101 and Sturdy, and the slopes for B1 and B2 approached the corresponding recurrent parent value.

As drought stress intensified, the difference in RWC between the parents and between the backcrosses increased (Table 2). The F1 did not differ significantly from the midparent value on any given day. Narrow-sense heritability for RWC was high, and increased with increasing drought stress until one week prior to complete flag leaf senescence. In the first season the stress developed later, so there were fewer sampling dates available for analysis. However, the same pattern appeared in both years.

Generation-means analysis was applied to the 1986 data for the two sampling dates that resulted in a high narrow-sense heritability. χ^2-tests performed on the various models indicated that additive gene action alone did not provide a complete explanation for the inheritance of RWC (Table 3). Dominance and additive x additive epistasis were required to provide an adequate fit of the model; however, these effects did not differ from 0 at the 5% level of significance according to Student's t-test.

Tillering was prolific in both years and continued until March, when the plants had developed 36.1 ± 0.4 tillers. Plant spacing was wide both within and between rows, thus allowing individual plants to develop a relatively large number of tillers. Number of tillers was similar among the populations at any point in time (not shown). The maximum number of tillers was reached in mid-March before the onset of drought stress. Over all populations, 80% of the grain bearing heads produced under drought stress resulted from the earliest formed tillers (those developed before mid-November, day 320 in 1984). Tiller abortion was more extreme in the presence of drought stress than under well-watered conditions. In TAM W-101, 57% of the tillers produced grain-bearing heads under well-watered conditions; under drought, only 43% of the tillers produced grain-bearing heads. In Sturdy, these percentages were 47 and 33% under well-watered and drought-stressed conditions, respectively.

Because year x population interactions were not significant, the yield data were pooled over both years (Table 4). TAM W-101 had a significantly higher biomass, grain yield, number of heads per plant, and kernel weight than Sturdy, both under drought-stressed and well-watered conditions. The difference between the backcrosses was significant for kernel weight. Narrow-sense heritability under drought stress was 35.5% for kernel weight, 9.2% for number of heads per plant, and 0% for grain yield.

Comparison of the drought-stressed and the well-watered parents showed that drought caused reductions in biomass, grain yield, number of heads per plant, kernel weight, and harvest index. Under well-watered conditions, grain yield of Sturdy was 74.5% that of TAM W-101; under drought, the yield of Sturdy was only 62% that of TAM W-101 (Table 4). To a lesser extent, the same pattern was observed for yield components and harvest index. Biomass of well-watered Sturdy plants was unexpectedly low, which was associated with an overall poor growth performance of these plants, especially in the second year. For both cultivars, yield reduction under drought conditions was attributable to the combined reduction in number of heads per plant and kernel weight.

DISCUSSION

Early generative development and maturity are generally considered as stress escape mechanisms, which allow a plant to complete its life cycle prior to the onset of an environmental stress (Blum, 1985). Thus, escape is not considered to be part of stress resistance. The lower sensitivity of TAM W-101 to drought relative to Sturdy was not associated with a difference in maturity, because TAM W-101 did not develop or mature earlier than Sturdy. On the contrary, under well-watered conditions, TAM W-101 was five to seven days later than Sturdy at every stage of reproductive development beginning at the double-ridge stage. Under drought, this difference diminished to approximately three days for booting, heading, and anthesis, but physiological maturity in TAM W-101 was extended six to ten days beyond that of Sturdy.

In previous experiments using pressure volume curves to determine water relations in controlled environments, TAM W-101 showed a greater capacity for osmotic adjustment than Sturdy (Johnson et al., 1984). The lack of significance in differences among populations in WP, SP, or TP in this study may be due to the relatively large experimental error associated with water potential measurements. In a study of variance in water potential measurements under controlled conditions, a minimum of 12 samples per treatment was necessary to obtain a 95% confidence interval of ± 0.5 MPa for WP means in stressed treatments (Johnson et al., 1986).

This difference is large compared to the small differences that were found among 53 cultivars of wheat, barley, and triticale (Fischer and Sanchez, 1979). Real differences in WP, SP, or TP may have been present, but we were unable to detect these in our experiment, possibly due to the experimental error associated with the available methods of measuring water potential.

Differences in TP were even more difficult to detect than differences in WP or SP. The variance of the TP was similar in magnitude when compared to WP and SP; however, due to cell dehydration, the absolute value of TP decreased with increasing stress duration, whereas the absolute value of WP and SP increased. As a result, the coefficient of variation (CV) for TP increased sharply as drought stress increased, compared to the CV for WP and SP. The CV for TP, which was 35% before the onset of drought stress, reached values on the final sampling dates of 128% in 1985 and 327% in 1986; respective values in both years were 18 and 20% for SP, and 32 and 27% for WP. Thus, even if important differences for TP existed under severe stress, it would have been very difficult to detect them.

The differences in RWC found among populations may have obscured differences in SP resulting from osmotic adjustment. Osmotic change reflects changes in the solute level and/or changes in the water content (Wenkert et al., 1978). TAM W-101 has been shown to adjust osmotically to a greater extent than Sturdy (Johnson et al., 1984). Thus, the larger concentration of solutes (lower SP) would tend to result in a higher RWC due to osmotic movement of water into the cells (Morgan, 1984). With a given amount of solutes, however, a larger RWC implies that the solutes are more diluted, and a lower solute concentration would then be reflected in a higher SP. Therefore, if two genotypes have the same SP but differ in RWC, it may be inferred that osmotic adjustment occurred in the genotype with the higher RWC. If osmotic adjustment leads to a higher RWC, then a higher TP should also result. As stated above, however, significant differences in TP were difficult to detect under severe stress.

Differences in RWC may also arise from differences in cell wall elasticity, as observed previously for TAM W-101 and Sturdy (Johnson et al., 1984). TAM W-101 had a higher tissue rigidity (higher modulus of elasticity, ϵ) than Sturdy, resulting in a higher RWC at zero TP. With leaf dehydration, a greater reduction in TP and WP is expected when cell walls are rigid (Morgan, 1980; Coyne et al., 1982). TAM W-101 leaves would thus develop a steeper WP gradient from leaf to soil at a given RWC than Sturdy, and thus lose less water to develop the necessary gradient to extract water from a drying soil (Coyne et al., 1982). Osmotic adjustment and low tissue elasticity could both contribute to drought resistance, but osmotic adjustment lowers the RWC at zero TP, and low elasticity tends to raise the RWC at zero TP.

The slower phenological development of TAM W-101 may have contributed to the longer retention of tissue water in

TAM W-101 than in Sturdy. The difference in developmental characters between the two genotypes, with the exception of physiological maturity, was approximately three days under drought stress. The developmental differences were not the sole cause for the RWC differences observed, because TAM W-101 reached any specific RWC level 10 to 14 days later than Sturdy (Fig. 4). The apparent drought resistance of TAM W-101 was associated with a higher RWC and longer retention of chlorophyllic tissue. TAM W-101 may have had a higher stomatal conductance than Sturdy, leading to a higher RWC. However, measurements on days 110 and 113 of 1986 did not show differences in stomatal conductance under drought conditions between TAM W-101 and Sturdy (data not shown). Thus, we believe that the differences in RWC resulted from differences in osmotic adjustment and/or tissue elasticity, as observed in a previous laboratory study (Johnson et al., 1984).

The difference in RWC between the parent populations and between the backcrosses increased as stress became more severe (Table 2). The phenotypic distribution in the F2 and the backcrosses .indicated that RWC was quantitatively inherited and not under control of one or two major genes. The RWC of the F1 did not differ significantly from the mid-parent value (Table 2), indicating that additive gene action was involved in the genetic control of RWC. This was supported by the high h^2 for RWC.

The number of tillers and the rate of tiller development throughout the growing season were similar in all populations studied. This indicates that the difference in drought resistance between TAM W-101 and Sturdy was not caused by a difference in tiller formation. The hypothesis that a more drought sensitive cultivar would form a greater biomass and thereby deplete soil moisture at an earlier point in time could therefore not be tested.

The h^2 for RWC was much higher than that for yield or any of the yield components. The values for yield and for kernel weight were low compared to values found in the literature (Smith, 1976; Alexander et al., 1984). These discrepancies may be explained in part by study conditions. In our study, the determinination of the h^2 estimate was done under conditions of severe drought stress, whereas other estimates were made under more optimal growing conditions.

Based on the greater reduction in yield in response to drought of Sturdy than of TAM W-101, TAM W-101 appeared more drought resistant than Sturdy. We have shown that significant genetic variation for leaf RWC exists in winter wheat. No genetic variation was found for tillering pattern or water potential components. The high h^2 for RWC indicates that RWC is more amenable to selection in drought-stressed environments than yield or yield components.

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Table 1. Linear change b[†] in relative water content (RWC) for six winter wheat populations under increasing drought stress.

Population/Contrast	1985	1986
Population	% day^{-1}	
TAM W-101	-0.68	-0.77
Sturdy	-1.27	-1.06
F1	-0.92	-0.94
F2	-0.72	-0.78
Backcross 1	-0.53	-0.83
Backcross 2	-1.06	-1.02
Contrast	level of significance	
P1 vs. P2[‡]	*	**
F1 vs. MidP	NS	NS
B1 vs. B2	**	**
F2 vs. MidB	NS	*

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*,** Significant at 0.05 and 0.01 level, respectively.

[†] b was computed over the last 3 sampling dates in 1985 and the last 5 sampling dates in 1986.

[‡] P1 and P2 are the cultivars TAM W-101 and Sturdy, respectively; MidP is the mid-parent value; B1 and B2 are the backcrosses of the F1 to TAM W-101 and Sturdy, respectively; and MidB is the mid-backcross value.

Table 2. Partitioning of variation and narrow-sense heritability (h^2) of relative water content (RWC) among six winter wheat populations as drought stress increased during generative development in 1986.

Source	df	99	106	113	120
		Day of the year			
		Mean square			
Generation	5	97.7*	154.0**	236.0**	504.4**
P1 vs. P2†	1	293.3**	359.3**	455.9**	784.3**
F1 vs. MidP	1	8.9	25.1	3.7	17.0
B1 vs. B2	1	93.8	196.9**	488.0**	578.1**
F2 vs. MidB	1	59.6	144.4**	110.7	1001.2**
Error	15	23.2	14.7	45.6	33.7
h^2 (%) ± SE		5.1 ± 28.9	63.0 ± 13.0	64.4 ± 14.4	0.0‡

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*,** Significant at 0.05 and 0.01 level, respectively.

† P1 and P2 are the cultivars TAM W-101 and Sturdy, respectively; MidP is the mid-parent value; B1 and B2 are the backcrosses of the F1 to TAM W-101 and Sturdy, respectively; and MidB is the mid-backcross value.

‡ Estimated value was -45.1 ± 44.8

Table 3. Generation-means analysis for relative water content (RWC) on two sampling dates in 1986 in TAM W-101 and Sturdy winter wheat.

Genetic effects	Day 106	day 113
	mean ± SE	mean ± SE
Additive (a)	3.46 ± 0.66*	4.16 ± 0.50*
Dominance (d)	-6.13 ± 2.07†	-6.61 ± 2.14†
Epistasis (a x a)	-4.59 ± 1.72	-6.14 ± 1.58†
χ^2‡	2.00	1.38

* Significantly different from 0 at 0.05 level.

† Significantly different from 0 at 0.10 level.

‡ χ^2 (2 df) for model (with a, d, and a x a) which provided a good fit (P > 0.05).

Table 4. Average biomass, yield, yield components, and harvest index of six winter wheat populations under drought stress and of TAM W-101 and Sturdy under well-watered conditions over two years[†](1984-85 and 1985-86).

Treatment	B[‡]	Y	H/P	K/H	Kwt	HI
Drought stressed	g		No.		mg	%
TAM W-101	39.7	11.6	16.0	21.7	31.8	27.9
Sturdy	30.8	7.2	12.1	25.2	22.6	22.6
F1	39.4	11.2	14.2	26.0	29.6	27.9
F2	36.0	9.8	14.6	22.8	27.2	25.7
Backcross 1	33.1	9.6	13.0	23.3	29.7	27.4
Backcross 2	36.2	9.9	13.6	25.4	25.6	25.7
P1 vs. P2[§]	*	**	*	NS	**	NS
Well watered						
TAM W-101	52.2	15.7	21.3	21.1	34.3	29.5
Sturdy	41.3	11.7	17.3	26.3	26.2	27.8
P1 vs. P2[§]	*	**	**	NS	**	NS

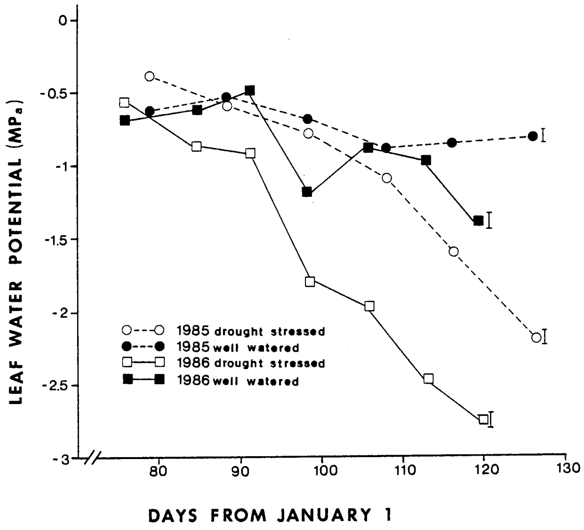
*, ** Significant at 0.05 and 0.01 level, respectively.

[†] Population x year interactions were not significant, (P > 0.20).

[‡] B, above ground biomass per plant; Y, grain yield per plant ; H/P, heads per plant; K/H, kernels per head; Kwt, kernel weight; and HI, harvest index.

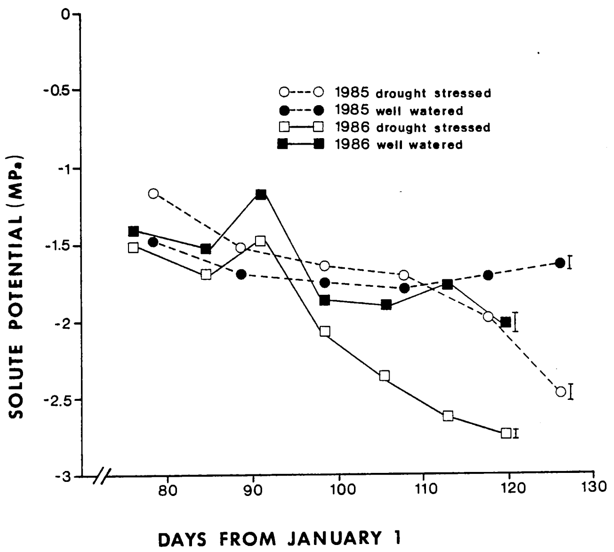
[§] Comparison between the means of TAM W-101 and Sturdy; the other contrasts did not show significant differences for any of the parameters, except kernel weight.

Fig. 1. Leaf water potential in winter wheat under increasing drought stress and well-watered conditions in 1985 and 1986. Points are averages over six populations (drought-stressed) and two populations (well-watered).[†] Vertical bars represent the pooled standard error of the mean for each line.



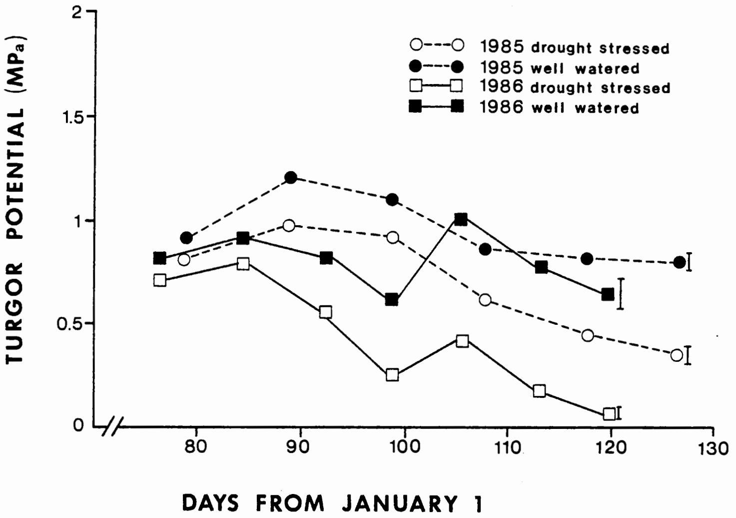
[†] Differences between populations were not significant, (P > 0.05).

Fig. 2. Solute potential in winter wheat under increasing drought stress and well-watered conditions in 1985 and 1986. Points are averages over six populations (drought-stressed) and two populations (well-watered).[†] Vertical bars represent the pooled standard error of the mean for each line.



[†] Differences between populations were not significant, (P > 0.05).

Fig. 3. Turgor potential in winter wheat under increasing drought stress and well-watered conditions in 1985 and 1986. Points are averages over six populations (drought-stressed) and two populations (well-watered).† Vertical bars represent the pooled standard error of the mean for each line.



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† Differences between populations were not significant, (P > 0.05).

Fig. 4. Leaf relative water content (RWC) in two winter wheat cultivars (P1: TAM W-101; P2: Sturdy) under increasing drought stress and well watered in 1985 (a) and in 1986 (b). Vertical bars represent the pooled standard error of the mean for each line.

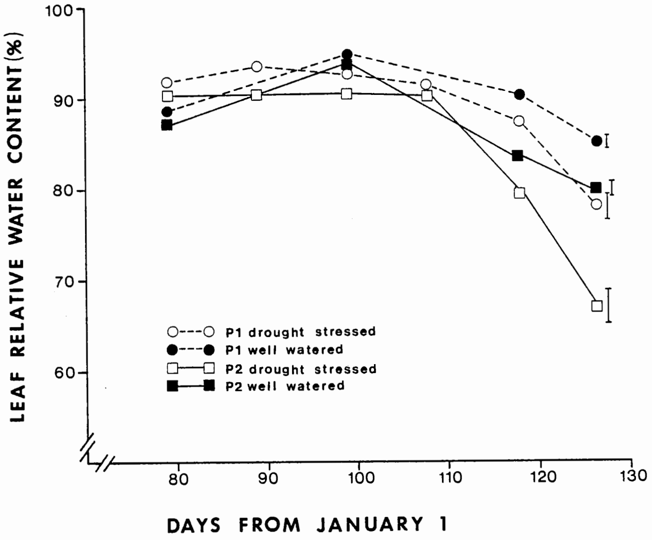
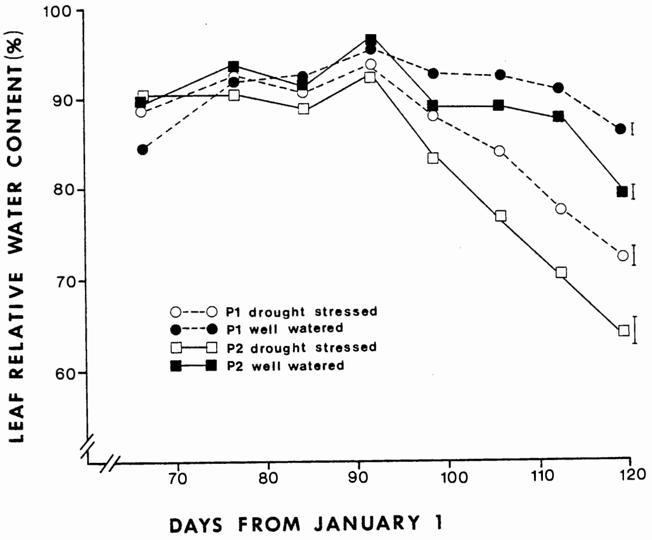


Fig. 4b.


LEAF RELATIVE WATER CONTENT (%)
100
90
80
70
60
○---○ P1 drought stressed
●---● P1 well watered
□—□ P2 drought stressed
■—■ P2 well watered
70
80
90
100
110
120
DAYS FROM JANUARY 1

CHAPTER III

DEVELOPMENT AND PHOTOSYNTHESIS OF WINTER WHEAT SEEDLINGS IN RESPONSE TO INCREASED ATMOSPHERIC CO_2 AND WATER LIMITATION

Manette Schönfeld, Richard C. Johnson
and David M. Ferris

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Former graduate research assistant (now research associate, Univ. of Idaho Research and Extension Center, Aberdeen, ID 83210), associate professor, and senior agriculturist, Agronomy Department, Oklahoma State University, Stillwater, OK 74078

ABSTRACT

Atmospheric CO_2 concentrations are increasing worldwide and are expected to double within the next century. This study was conducted to determine the combined effects of CO_2 enrichment and dehydration stress on growth and photosynthesis of 'TAM W-101' winter wheat (*Triticum aestivum*. L.) seedlings. Seedlings (one per pot) were placed in growth chambers maintained at 350 (ambient) or 700 (enriched) $\mu L\ L^{-1}$ CO_2. Main stem leaf number (MSL) was recorded daily. For stress treatments, water was limited to 28% of pot capacity (PC) (medium stress), or 22% PC (severe stress), from MSL three (16 days from emergence) until the end of the experiment (40 days from emergence). Water potential (WP) and relative water content (RWC) of the plants were determined at 40 days. At that time, gas exchange characteristics were determined in one replication, and leaf CO_2 assimilation (A) vs. internal leaf CO_2 concentration (C_i) response curves were developed. Leaf area and dry wt were determined for each plant, and water use efficiency (WUE) in g dry wt L^{-1} water used, root:shoot ratio, and specific leaf weight (SLW) were calculated. Elevated CO_2 caused only a slight increase in MSL at each water level. Dry matter production at 700 $\mu L\ L^{-1}$ CO_2 was increased by 23% under well-watered conditions and by 51% and 30% under medium and severe dehydration stress, respectively. Specific leaf weight and WUE were significantly higher for plants grown under enriched CO_2. Carbon assimilation vs C_i response curves were similar between plants grown at the different CO_2 levels. At 700 $\mu L\ L^{-1}$ CO_2, A was 17% higher than at 350 $\mu L\ L^{-1}$ for all plants grown under well-watered conditions, and 27% and 8% higher for plants under medium and severe dehydration stress, respectively. Although CO_2 enrichment had positive effects on growth and photosynthesis of winter wheat seedlings, these effects were counterbalanced by the debilitating effects of limited water.

Additional index words: Carbon assimilation, Dehydration stress, Specific leaf weight, *Triticum aestivum* L., Water potential, Water use efficiency.

INTRODUCTION

The atmospheric level of CO_2 is increasing rapidly due, in part, to the burning of fossil fuel. It is expected to double within the next century (Gribbin, 1981). This rise may be beneficial to crop production because of the relationship to photosynthesis, which is limited by current ambient atmospheric CO_2 levels (Kimball, 1983). At the same time, there is a concern that the increasing CO_2 levels may lead to a global temperature rise because CO_2 would trap increased long-wave radiation (Fleagle and Businger, 1963), which could lead to increased drought and heat stress in many areas of the world.

Although this temperature rise may be much smaller than was previously predicted (Idso, 1982, 1984), drought stress is still one of the major limitations to crop production worldwide and may become more prevalent in certain areas as atmospheric CO_2-enrichment continues. Winter wheat (_Triticum aestivum_ L.) is an important crop in the Central and Southern Great Plains where the depletion of the Ogallala Aquifer is expected to lead to an increase in the area of dryland wheat production in the coming decennia (Warren et al., 1981).

Kimball (1983) concluded that a doubling of the atmospheric CO_2 concentration would increase agricultural yields by 25 to 43%. Krenzer and Moss (1975) showed an increase in wheat grain yield of 15 to 37% both in the field and at higher growth temperatures in growth chambers when CO_2 enrichment was applied during floral development or during grain development; however, no effect on grain yield was observed when enrichment was applied before floral development or at any growth stage under a low temperature regime. Similarly, Fischer and Aguilar (1976) found that CO_2 fertilization at any growth stage during spring wheat development increased dry matter production, but grain yield was increased significantly (up to 23%) only when CO_2 enrichment was applied during the growth stage at which the number of grains per area was determined. Neales and Nicholls (1978), found that the age effect was much larger than the CO_2 effect. For example, relative growth rate of 10-day-old wheat seedlings was increased by 35% when the CO_2 level increased from 200 to 800 $\mu L\ L^{-1}$. In 24-day-old seedlings it was reduced by 44% over the same interval of CO_2 concentration. They concluded that large interactions between plant age and CO_2 concentration could account for the relatively small enhancement by CO_2 of total plant biomass.

The objectives of this study were to determine the effect of CO_2-enrichment and prolonged dehydration stress on vegetative growth and development of winter wheat plants, and to determine photosynthetic characteristics under those conditions.

MATERIALS AND METHODS

Winter wheat 'TAM W-101' seeds were germinated in petri dishes on a double layer of Whatman no.2 filter paper. Uniform seedlings (coleoptile length approximately 1 cm) were transplanted to square (0.1 x 0.1 x 0.1 m^3) plastic pots containing approximately 1 kg sand. The single plants were placed in growth chambers under controlled conditions of temperature, light, and CO_2 concentration. Temperature was maintained at 20°C during the day and 16°C during the night. Light was approximately 600 μmol m^{-2} s^{-1} quanta photosynthetic photon flux density (PPFD) maximum during the day at the top of the plants and was provided by a combination of fluorescent and incandescent lights. Total day length was 14 h; light intensity was gradually increased from darkness to full light intensity over a 2 h period in the morning, and gradually decreased over 2 h at night.

The concentration of CO_2 in the growth chambers was 350 $\pm$ 10 μL L^{-1} (ambient), or 700 $\pm$ 15 μL L^{-1} (enriched). The CO_2 level was increased by bleeding CO_2 gas (ultra high purity) from cylinders into the growth chamber's air distribution system. Any ethylene present in the bottled CO_2 gas was removed by passing the humidified gas through a column filled with perlite, soaked in a saturated solution of potassium permanganate (Morison and Gifford, 1984). The air in the chambers was monitored every minute with an infrared gas analyzer, and the CO_2 level was adjusted automatically when it deviated more than 1.5% from the desired concentration.

Since only two growth chambers were available (one for each CO_2 level), the experiment was replicated twice over time. Level of CO_2 was randomized over growth chambers. Planting was staggered over time to permit gas exchange measurements on plants of the same age. Treatment combinations were applied in a split-plot arrangement. Main plot treatment was CO_2 level, and sub-plot treatment was water level with six plants per treatment, completely randomized within the chamber.

All plants were kept well-watered for the first 16 days after transplanting. Pots were weighed daily and soil moisture was replenished to 85% of pot water holding capacity (PC) with 25% strength Hoagland's nutrient solution. Evaporation was kept minimal (below 4% per day at 85% PC) by covering the soil surface with styrofoam beads after transplanting. The primary purpose of the soil cover was to allow for a gradual implementation of water deficits. Pot weight data were used to calculate water use efficiency (WUE) as g dry wt L^{-1} water used over the total growth period. Main stem leaf (MSL) number (Haun, 1973) was recorded daily for each plant, and newly formed tillers were counted and marked with color-coded rings according to main tiller groups (T0, T1, etc.; Klepper et al., 1982). When the plants had reached a MSL of three (16 days after transplanting), dehydration stress treatments were initiated. Three water levels were established: well watered (85% PC);

intermediate drought stress (28% PC); and severe drought stress (22% PC). These levels were chosen empirically, based on preliminary experiments with sand from the same source.

The experiment was terminated after the stress treatments had been continued about four weeks. Severely stressed plants had developed a MSL number of six to seven at that time, and well-watered plants had a MSL number of eight to nine. One plant from each of the six treatment combinations was removed each day for measurements and harvest; the order in which those six plants were measured was randomized. The youngest, fully expanded leaf (with auricles clasping the next leaf) on the main stem was used for measurements of light-saturated, steady-state gas exchange characteristics in the second replication only. A stirred, temperature and humidity controlled reaction chamber (cuvette) was used, described in detail by Bingham et al. (1980) and Coyne et al. (1982). Humidity was measured inside the chamber with a condensation dew-point hygrometer (General Eastern 1100DP, Watertown, MA), and CO_2 was measured by passing chamber exhaust through a differential CO_2 gas analyzer (Horiba PIR 2000, R, Irvine, CA). Measurements were made at gradually increasing ambient CO_2 levels (C_a) from near 0 to about 700 $\mu L\ L^{-1}$ at steps of about 80 $\mu L\ L^{-1}$. Measurements were also made on each plant at C_a = 350 $\mu L\ L^{-1}$ and at C_a = 700 $\mu L\ L^{-1}$, the growing conditions of the plants. Carbon assimilation rate (A) and transpiration rate (T) were calculated from the amount of CO_2-free dry air and CO_2-enriched dry air required to keep desired steady-state conditions inside the chamber. Stomatal conductance to CO_2 (g_sCO_2), along with internal CO_2 concentration (C_i), and steady-state WUE (A/T) were then calculated (Gaasstra, 1959; Farquhar and Sharkey, 1982).

The protocol for determining the stomatal limitation to A was that outlined by Farquhar and Sharkey (1982). They defined a 'demand' function as the rate of change of A in response to a change in the C_i and defined a 'supply' function as the rate of change of C_i allowed by the g_sCO_2 and the C_a. By exposing a leaf to a range of C_a's and simultaneously measuring A and C_i, one can estimate what A would be when C_i=350 $\mu L\ L^{-1}$ (near current atmospheric CO_2 concentration), and this would be the theoretical maximum A if there were no stomatal limitation to CO_2 exchange. Theoretically, the same can be determined at C_i=700 for the plants grown under elevated CO_2 concentration; however, this point was not reached because A reached a maximum at C_i<700 in all treatments. By comparing the theoretical maximum A to A at ambient conditions, one can calculate the stomatal limitation (L) to photosynthesis:

$$L = \frac{A(C_i=350\ \mu L\ L^{-1}) - A(C_a=350\ \mu L\ L^{-1})}{A(C_i=350\ \mu L\ L^{-1})}$$

After the CO_2 response curve was developed, three punches of 0.24 cm^2 were taken from the same leaf for chlorophyll concentration determination, according to the method developed by Inskeep and Bloom (1985). Total chlorophyll, and the ratio of chlorophyll a to b, were measured.

In both replications, the water status of each plant was then determined on the same leaf with water potential (WP) and relative water content (RWC) measurements. Water potential was measured using leaf cutter psychrometers (Morrill Specialty Inc., Logan, UT) as described by Johnson et al. (1986). One disc of 0.24 cm² was cut from the center of the leaf and used for WP readings. Psychrometers were equilibrated for two hours in a water bath at 30°C, and readings for total WP were made. Thermocouples with samples inside were then frozen overnight at -20°C to disrupt cell membranes. After thawing and equilibrating at 30°C in the water bath, SP was measured in the same manner as WP, and TP was calculated from the equation:

$$WP = SP + TP.$$

After chlorophyll and WP samples were taken, the same leaf was used to determine RWC. Immediately after cutting at the base of the leaf lamina, fresh weight was determined. Turgid weight was obtained by soaking the leaves for 16 to 18 h in distilled water at room temperature (ca. 20°C). Preliminary tests indicated no further increase in leaf weight after this time. After equilibration, the leaves were quickly and carefully blotted dry with tissue paper prior to determination of turgid weight. Dry weight was obtained after oven drying the leaf samples for 48 h at 70°C. Relative water content was calculated from the equation:

$$\text{RWC (\%)} = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \times 100$$

Total leaf area per plant was determined, using a LI-3000 portable area meter (Li-Cor, Lincoln, NE). Finally, the leaves and the pseudostem were dried for 48 hours at 70°C to obtain dry wt, and the roots were carefully rinsed and dried to determine root dry weight. From these measurements, the root:shoot ratio and the ratio of leaf dry wt to leaf area (specific leaf weight, SLW) were calculated.

Data that were available from both replications were analyzed using the GLM (General Linear Models) procedure in SAS (SAS Institute, Inc., 1985). Linear orthogonal comparisons were made between treatment means (Steel and Torrie, 1980). The contrasts considered were ambient vs. enriched CO_2 level, well-watered vs. drought-stressed plants, and medium vs. severe drought stress level. Gas exchange measurements, for which no replication of CO_2 level was available, were analyzed as randomized complete blocks with six sub-samples, with growth chambers (CO_2 levels) as blocks. When blocking had a significant effect, it was considered to be an effect of CO_2 enrichment. The replicated growth data suggested that any significant difference between plants in different growth chambers could be attributed to the CO_2 level.

RESULTS

Plant development, as expressed in MSL stage, was slightly faster under CO_2-enriched than under ambient CO_2 conditions, although the difference was not significant until 25 days after emergence (Fig. 1). Dehydration stress affected MSL number more strongly than CO_2 enrichment. Stress did not become apparent until day 24, when the difference between the well-watered and the stressed treatments became significant. Water had been limited since day 16, but it took approximately one week for the pot soil to become sufficiently dry to influence plant development. The difference in leaf numbers between the intermediate and severe stress levels was significant after day 30 (not shown).

Plant water status at the end of the experiment did not show significant differences between CO_2 levels; therefore, the data were pooled over CO_2 levels. The difference between water levels was significant, with the well-watered plants having the higher values for RWC and for WP, SP, and TP (Table 1).

Because none of the plant growth variables had a significant interaction of CO_2 level and dehydration stress, the description of the results is limited to the main effects (Table 2). The total number of tillers developed was slightly greater under elevated CO_2 ($P = 0.057$). Similarly, the plant dry wt was larger, but not significant ($P = 0.153$). Water use efficiency over the total growth period was significantly higher for the plants grown under elevated CO_2. A large effect of CO_2-enrichment was also seen in the SLW. Carbon dioxide enrichment was associated with a higher SLW, indicating either thicker leaves, or leaves with heavier cell constituents. The effect of dehydration stress was much greater than the CO_2 enrichment effect on all yield variables, with the exception of WUE and SLW. Dehydration effect was significant for plant dry weight, SLW, and total tiller number. For WUE, it was only significant under CO_2 enrichment. It was also significant for root and for shoot dry wt, tillers of every sub-group, and leaf area (not shown). Root:shoot ratio did not differ significantly between well-watered and stressed plants; however, it increased with increasing stress levels, and was greater for plants grown under elevated than under ambient CO_2. The difference between the intermediate and severe stress levels was significant only for total number of tillers, and not for any of the tiller sub-groups. Although some of these variables did not show significant effects of CO_2-enrichment, the increases in MSL, tiller number, dry weight, and WUE due to CO_2-enrichment were consistent with two preliminary experiments, which included 'Sturdy' as well as TAM W-101 plants (unpublished data).

Because A and C_i did not show significant differences between the plants grown at ambient and enriched CO_2 concentrations, the CO_2 response curves at the different water levels were averaged over CO_2 levels during growth (Fig. 2).

The compensation point was approximately 25 $\mu L\ L^{-1}$ for the well-watered and mildly stressed plants, and 37 $\mu L\ L^{-1}$ for the severely stressed plants, but this difference was not significant. The initial slope of the curves was 0.091 $\mu mol\ m^{-2}\ s^{-1}\ (L\ L^{-1})^{-1}$ for the well-watered plants, 0.071 for the medium stressed plants, and 0.048 for the severely stressed plants. The difference in slope was significant at the 5% level between well-watered and stressed plants; between the two levels of stress it was significant at $\alpha = 0.10$. Stomatal limitation did not differ significantly between the water levels, ranging from 18% for the well-watered plants to 21% and 19% for the intermediate and the severe stress levels, respectively. Carbon assimilation rate was 17% higher at 700 than at 350 $\mu L\ L^{-1}$ for the well-watered plants from either CO_2 treatment. For the medium-stressed plants this increase was 27%, and for the severely-stressed plants the increase was only 8%. Maximum A at all water supply levels was reached well before C_a was 700 $\mu L\ L^{-1}$, and even decreased after C_i reached approximately 400 $\mu L\ L^{-1}$ under well-watered conditions. Under drought-stressed conditions, the maximum A was found at a higher C_i.

At both CO_2 concentrations, C_i decreased with increasing water supply (Tables 3 and 4). At 700 $\mu L\ L^{-1}$, the difference was not significant, probably due to the large variation at the high end of the curve, where photosynthesis was CO_2-saturated under the measuring conditions. Carbon assimilation increased significantly under well-watered conditions, and steady-state WUE also increased, but again, the differences between water levels were not significant at 700 $\mu L\ L^{-1}$. Stomatal conductance did not show significant differences at either ambient CO_2 level. However, g_sCO_2 was lower at 700 than at 350 $\mu L\ L^{-1}$, which can explain the higher WUE found over total growth for the plants grown under elevated CO_2. At both measuring points, g_sCO_2 was much higher for the well-watered than for the drought-stressed plants.

Total chlorophyll on basis of leaf area was significantly lower for leaves of plants grown at the elevated CO_2 level, as well as for the severely dehydration-stressed plants (Table 5). Consequently, the ratio of carbon assimilation to total chlorophyll (the specific photosynthetic activity of chlorophyll; Ryan et al., 1987) was significantly higher for the plants grown at high CO_2, especially under well-watered conditions. The CO_2 effect on total chlorophyll was larger than the effect of water levels. The ratio of chlorophyll a to b did not differ between CO_2 levels, but was higher in well-watered than in stressed plants.

DISCUSSION

The effect of increasing the ambient CO_2 concentration twofold on the characters studied varied from mild to fairly strong. Kimball (1983) cites an experiment in which a CO_2 increase to 1200 μL L^{-1} doubled the leaf dry wt production per plant at 30 days after germination. Early effects of CO_2 enrichment were associated with increased tiller numbers, rather than with increased leaf emergence rates (Gifford, 1977). In our study, the leaf emergence rate resulted in a 3% increase in MSL with CO_2 enrichment over all water levels. Under the same conditions, tiller numbers increased by 5% for the well-watered as well as for the stressed plants. These numbers are small compared to total dry wt under elevated CO_2, which at 40 days after emergence was increased by 23% for the well-watered and by 40% for the stressed plants. The variation in dry wt data was very large (CV's of 40 to 50%), which may explain why these differences were not significant. Gifford (1977) found a slight increase (less than 10%) in total dry wt at 40 days after emergence when CO_2 level was increased to 200 μL L^{-1} above ambient (which fluctuated in their growth chamber study). At 130 days (plant maturity), this difference increased to 30%.

The largest effect of CO_2-enrichment on plant development in this study was seen in the increased SLW, which was not associated with a reduced leaf area. This increase could be the result of increased leaf thickness, or increased starch accumulation in the cells (Sharkey, 1985). Neales and Nicholls (1978) found that increased SLW was accompanied by a reduced leaf area, which did not occur in our study. Increased SLW, whether accompanied by a decreased leaf area or not, is a common feature of C_3 plants grown under CO_2-enriched conditions (Ford and Thorne, 1967; Thomas and Harvey, 1983).

Differences in leaf morphology, such as in SLW, could be related to differences in photosynthetic behaviour. However, we found no difference in A, either at 350 or at 700 $\mu L\ L^{-1}$, between the plants grown at ambient and elevated CO_2. The previous growth conditions therefore did not seem to precondition the plants to a specific photosynthetic behavior, although we did not measure in situ. These results agree with the findings of Ford and Thorne (1967) and Gifford (1977) that the CO_2 exchange rate was related only to the immediate, as opposed to the preconditioning, CO_2 level.

CO_2-enrichment had no significant effect on the water relations of the plants. The effect of water limitation on these traits was much greater, as expected. Sionit et al. (1981) reported that plants grown at 1000 $\mu L\ L^{-1}$ maintained a higher turgor under drought stress than plants grown at ambient CO_2, possibly due to a decreased water loss associated with a lower g_sCO_2 at high CO_2. The same authors also reported the maintenance of a higher RWC under enriched CO_2, but we did not observe this.

Gas exchange measurements did not show that significant differences existed between plants grown in the two growth chambers at different CO_2 levels in their basic capacity for mesophyll photosynthesis. A complicating factor may have been that the light conditions in our growth chamber were relatively low; at 600 μmol quanta m^{-2} s^{-1} PPFD, photosynthesis is almost light saturated at a CO_2 concentration of 350 μL L^{-1}, but not at 700 μL L^{-1} (Stoy, 1965; Wong, 1979). However, A was 17% higher at 700 than at 350 μL L^{-1} CO_2 for the well-watered plants grown under either CO_2 concentration when measured under high light intensity (1800 μmol m^{-2} s^{-1}). The maximum A under well-watered conditions was reached at C_i of approximately 400 μL L^{-1} (Fig. 2); at C_i=700 μL L^{-1}, it was lower than at 400 μL L^{-1}. The relatively low light conditions in the growth chambers may provide a partial explanation for the limited effect of CO_2 enrichment on leaf emergence and on tiller production in our experiments.

The effect of water limitation on photosynthesis was much larger than that of CO_2 enrichment. The compensation point was higher under severe stress, as previously shown in wheat by Johnson et al. (1987), although it is not true for all species (Sharkey and Badger, 1982). However, in their study stress was induced osmotically (with PEG), which may affect the photosynthetic behavior differently than when water is withheld from pots. The initial slope, which has been termed the carboxylation efficiency (Ku and Edwards, 1977), decreased significantly with increasing water limitation, whereas the stomatal limitation remained steady, suggesting that mesophyll factors are responsible for the decreased photosynthesis under dehydration stress (Krieg, 1983). This decreasing slope is typical in winter wheat under water limitation (Johnson et al., 1987; Ryan et al., 1987); again, it is not seen with PEG-induced stress, or in all species (von Caemmerer and Farquhar, 1981; Sharkey and Badger, 1982; Sharkey, 1984).

In our experiment, C_i at ambient CO_2 concentrations of 350 and 700 $\mu L\ L^{-1}$ increased with increasing drought stress, whereas A, steady-state WUE, and g_sCO_2 decreased. Water use efficiency was higher at 700 $\mu L\ L^{-1}$ for all water levels, which agrees with the WUE, determined from dry wt production. The decrease with increasing water limitation in steady-state WUE indicates that drought stress reduced the plant's capacity to balance assimilation and transpiration by adjusting g_sCO_2. This contrasts with the WUE on dry wt basis, which was similar between water levels for plants grown at 350 $\mu L\ L^{-1}$ CO_2. The difference between the two measures for WUE can not be explained at this time; but one system provides a long-term measure in dry wt produced for a whole plant, whereas the other provides an instantaneous number for carbon fixation of one leaf of a specific developmental stage. In soybean, the g_sCO_2 of well-watered plants decreased with increasing CO_2 concentration, thus decreasing the water loss per plant (Rogers et al., 1984). This agrees with the higher direct WUE that we found for plants grown under enriched CO_2, and with our conductance values, which showed the same trend although the differences were not significant.

The activity of various carbon fixation enzymes decreases under enriched CO_2 conditions (Porter and Grodzinski, 1984; Wong, 1979). This may explain reports on reduction of photosynthesis under enriched CO_2 (Woo and Wong, 1983). In this context, the increased specific photosynthetic activity of chlorophyll was surprising, and can not be explained at this point. Further research of the biochemistry of photosynthesis under CO_2 enriched conditions is currently in progress.

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Table 1. Midday leaf water status of wheat plants grown at three levels of water supply averaged over two CO_2 levels.

Water level	RWC[†]	WP	SP	TP
	%		MPa	
Severe stress	79.8	−2.05	−2.35	0.30
Medium stress	81.4	−1.57	−2.10	0.53
Well watered	91.4	−0.78	−1.69	0.91
LSD (α = 0.05)	4.3	0.33	0.29	0.29

[†] RWC: relative water content; WP: water potential; SP: solute potential; TP: turgor.

Table 2. Dry matter production, root:shoot ratio, number of tillers per plant, specific leaf weight, and water use efficiency over the total growth period of wheat plants grown at ambient (350 μL L^{-1}) and at enriched (700 μL L^{-1}) CO_2 concentration, and at three levels of water supply.

Growing conditions	DW†	R/S	TIL	SLW	WUE
	g pl^{-1}		pl^{-1}	g m^{-2}	g L^{-1}
Ambient CO_2 level	3.2	0.81	16.7	5.5	4.7
Severe stress	1.9	0.93	11.4	5.8	4.7
Medium stress	2.2	0.84	13.0	5.7	4.7
Well watered	5.3	0.65	25.7	4.9	4.8
Enriched CO_2 level	4.2	0.93	17.6	6.7	7.0
Severe stress	2.5	1.02	11.7	7.4	7.5
Medium stress	3.4	1.05	14.2	6.8	7.3
Well watered	6.6	0.71	27.0	5.8	6.1
Contrasts‡	level of significance				
Amb vs. Enr CO_2	NS	NS	NS	*	**
Nostress vs. Stress	**	NS	**	NS	*
Med vs. Severe Stress	NS	NS	*	NS	NS

*, ** Significant at the 5% and 1% level, respectively.

†DW: dry weight; R/S: root:shoot ratio; TIL: number of tillers; SLW: specific leaf weight; and WUE: water use efficiency over the total growth period.

‡Contrasts: ambient vs. enriched CO_2 level, well-watered vs. drought-stressed plants, and medium vs. severe drought stress level.

Table 3. Steady-state gas exchange characteristics at an ambient concentration of 350 µL L^{-1} CO_2 of wheat plants grown at three levels of water supply, averaged over the growth CO_2 levels.

Water level	C_i†	A	WUE	g_sCO_2
	µL L^{-1}	µmol CO_2 m^{-2} h^{-1}	mmol CO_2 mol^{-1} H_2O	cm s^{-1}
Severe stress	268	7.0	2.7	0.08
Medium stress	251	10.0	3.3	0.09
Well watered	248	21.3	4.0	0.23
LSD (α = 0.05)	13	10.6	0.4	0.16

†C_i: intercellular CO_2 concentration; A: carbon assimilation rate; WUE: water use efficiency; and g_s CO_2: stomatal conductance to CO_2.

Table 4. Steady-state gas exchange characteristics at an ambient concentration of 700 µL L^{-1} CO_2 of wheat plants grown at three levels of water supply, averaged over the growth CO_2 levels.

Water level	C_i †	A	WUE	g_sCO_2
	µL L^{-1}	µmol CO_2 m^{-2} h^{-1}	mmol CO_2 mol^{-1} H_2O	cm s^{-1}
Severe stress	573	7.4	3.8	0.07
Medium stress	520	12.6	5.4	0.08
Well watered	496	25.7	6.9	0.15
LSD (α = 0.05)	89	12.9	2.7	0.11

† C_i: intercellular CO_2 concentration; A: carbon assimilation rate; WUE: water use efficiency; and g_sCO_2: stomatal conductance to CO_2.

Table 5. Leaf chlorophyll content and ratio of CO_2 assimilation to total chlorophyll of wheat plants grown at ambient and enriched CO_2 levels, and at three levels of water supply.

Growing conditions	ChlT†	a/b	A360/Chl	A700/Chl
Ambient CO_2 level	mmol m^{-2}		mmol CO_2 mol^{-1}	
Severe stress	0.53	4.2	13.6	14.03
Medium stress	0.55	4.2	16.1	24.86
Well watered	0.57	4.5	33.2	33.88
Enriched CO_2 level				
Severe stress	0.48	4.3	10.5	15.43
Medium stress	0.49	4.3	14.4	21.43
Well watered	0.52	4.5	43.7	57.87
LSD ($\alpha = 0.05$)	0.02	0.1	3.8	5.13

† ChlT: total chlorophyll; a/b: ratio of chlorophylls *a* and *b*; A360/Chl: ratio of CO_2 assimilation to total chlorophyll in an ambient CO_2 concentration of 350 μL L^{-1} CO_2; and A700/Chl: the same ratio at an ambient CO_2 concentration of 700 μL L^{-1} CO_2.

Fig. 1. Growth in number of main stem leaves of winter wheat plants grown under ambient (350 µL L^{-1}) or enriched (700 µL L^{-1}) atmospheric CO_2 concentration and under well-watered or water-limited conditions. Each line represents the average of twelve plants.

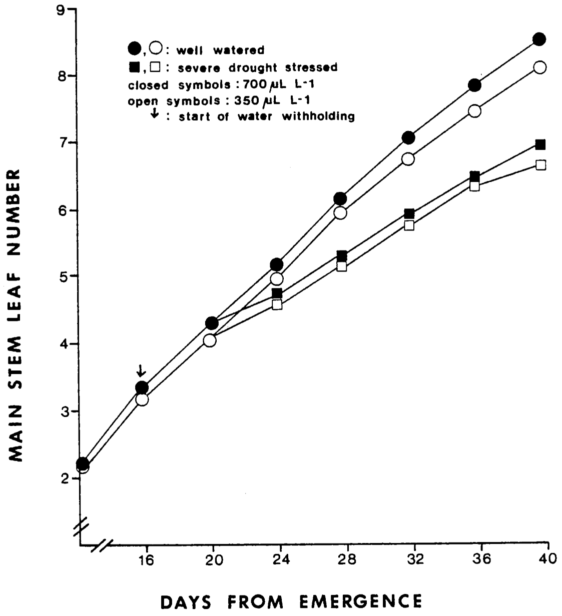
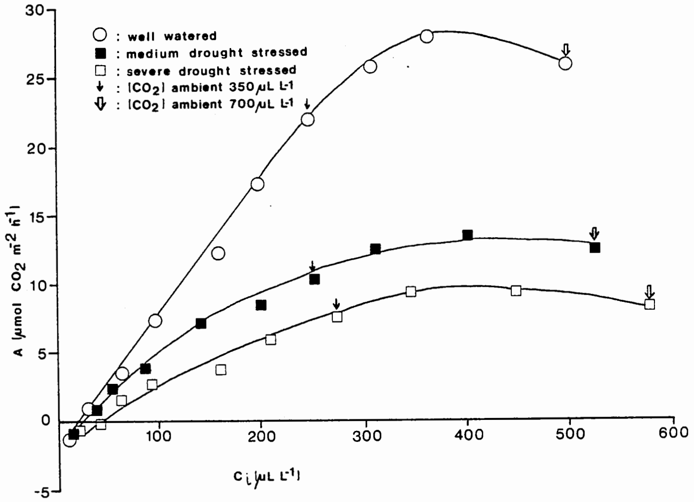


Fig. 2. Carbon assimilation rate (A) vs. internal CO_2 concentration (C_i) in wheat leaves grown under well-watered conditions and under two levels of dehydration stress. Values are averaged over CO_2 conditions during growth. Each line represents the average of nine to twelve plants.



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APPENDIXES

APPENDIX A

RESULTS OF SOIL MOISTURE DETERMINATIONS

Soil moisture was determined using a neutron probe with readings taken at 0.15 m intervals to a depth of 1.20 m. In each block of the drought-stressed plots at a randomly chosen place, and at three locations in the well-watered plots, tubes were installed and measurements were made approximately every two weeks. The neutron probe data in Tables 1 and 2 show the decrease in volumetric soil moisture in the spring, before and after the erection of the rain shelter (on day 73 in 1985, and day 62 in 1986). In 1985, soil moisture began to decrease in the top 0.15 m after day 87; in the 0.15 to 0.45 m layer decrease became apparent after day 100. In 1985, the plants did continue to extract water up to the harvest; between day 136 and 154 (the harvest date) there was still a large decrease, even in the deeper soil layers between 0.60 and 1.20 m. In 1986, with the earlier erection of the shelter and less spring rain, the top layer gradually dried out after day 30, and reached its maximum dryness by day 108. The decrease in the medium deep layers (0.15 to 0.60 m) was also earlier in the second year, and no further drying out occurred after day 127. Even in the deepest layers, from 0.60 to 1.20 m, little change occurred after day 100. The sharp decrease in the top 0.15 m and the more gradual decrease in the medium deep soil layers coincided in both years with the onset of visible stress symptoms in the plants.

Table 1. Volumetric water content (%) at increasing depth in the soil profile of wheat plots under drought-stressed (D) and well-watered (W) conditions in 1985.

Day	Water level	Depth (cm) 15	30	45	60	75	90	105	120
24	D	35	36	34	32	30	31	31	32
	W	36	37	37	35	34	31	31	34
77	D	36	35	35	34	33	34	33	33
	W	36	36	36	35	34	34	35	35
87	D	37	33	33	33	32	32	33	33
	W	--†	--	--	--	--	--	--	--
100	D	25	30	30	30	31	31	32	32
	W	32	34	33	33	33	33	34	34
108	D	25	28	28	28	28	30	31	32
	W	29	31	31	30	30	32	33	33
127	D	20	25	25	25	26	27	29	31
	W	31	31	31	30	29	31	32	34
136	D	17	23	24	24	25	26	28	31
	W	25	28	29	28	28	30	31	34
154	D	15	21	22	22	22	24	26	28
	W	24	27	27	26	25	27	28	32

† No data available.

Table 2. Volumetric water content (%) at increasing depth in the soil profile of wheat plots under drought-stressed (D) and well-watered (W) conditions in 1986.

Day	Water level	Depth (cm)							
		15	30	45	60	75	90	105	120
24	D	31	39	39	38	36	36	37	36
	W	26	38	38	38	38	36	38	38
77	D	25	35	36	37	36	36	36	37
	W	33	38	37	38	36	37	38	37
87	D	19	33	34	34	34	35	36	36
	W	28	37	37	36	35	36	37	37
100	D	16	30	31	31	32	33	34	35
	W	24	35	35	34	34	35	36	36
108	D	13	29	30	31	31	32	34	35
	W	20	34	34	34	34	35	36	36
127	D	13	27	29	29	30	31	32	34
	W	15	31	33	33	32	33	36	36
136	D	12	27	29	30	30	31	33	35
	W	17	27	33	33	33	33	35	37
154	D	12	27	29	29	30	32	33	35
	W	15	32	32	32	31	33	35	35

APPENDIX B

NUMBER OF TILLERS THROUGHOUT THE GROWING SEASON

Table 1. Number of tillers per plant in six wheat populations throughout two growing seasons.

	1984-85 growing season			
Day of the year	318	345	74	93
Generation				
P1	14.7	23.1	37.4	32.6
P2	13.3	21.6	40.7	32.4
F1	15.0	23.6	35.8	29.3
F2	14.4	22.9	37.5	31.8
B1	11.8	19.2	33.5	29.9
B2	14.3	23.2	38.9	32.8
Average	13.9	22.2	37.2	31.5
Standard Error	0.3	0.4	0.7	0.7

	1985-86 growing season			
Day of the year	309	1	57	87
Generation				
P1	3.2	15.3	37.4	27.6
P2	3.0	13.4	33.6	20.0
F1	2.9	14.9	36.8	24.3
F2	3.5	16.9	36.1	25.7
B1	2.0	9.4	30.0	22.3
B2	3.0	14.7	36.5	23.5
Average	3.0	14.5	35.0	24.2
Standard Error	0.1	0.4	0.7	0.6

VITA

Marie Antoinette Schönfeld

Candidate for the degree of

Doctor of Philosophy

Thesis: DROUGHT SENSITIVITY IN WINTER WHEAT POPULATIONS UNDER FIELD CONDITIONS AND ELEVATED ATMOSPHERIC CO_2

Major Field: Agronomy - Crop Science

Biographical:

Personal Data: Born in 's-Gravenhage (The Hague), The Netherlands, July 14, 1950, the daughter of Chris and Heleen Schönfeld.

Education: Graduated from Haags Montessori Lyceum, 's-Gravenhage, in May, 1967; received "kandidaats" degree in Agricultural Sciences from the Agricultural University of Wageningen, the Netherlands in June, 1976; graduated from the Pharmacy Technician School, Arnhem, The Netherlands, in May, 1978; received "ingenieurs" degree in Agricultural Sciences (Weed Science) from the Agricultural University of Wageningen, the Netherlands in June, 1982; completed requirements for the Doctor of Philosophy degree at Oklahoma State University in July, 1987.

Professional Experience: Pharmacy Technician, Ede, The Netherlands, January, 1978, to February, 1979; Research Assistant, ARC Weed Research Organization, Oxford, England, March to August, 1979; Teaching Assistant, Department of Weed Science, Department of Plant Physiology and Morphology, and Department of Agronomy, Agricultural University of Wageningen, June, 1981, to May, 1983; Research Assistant, Department of Agronomy, Oklahoma State University, August, 1983, to March, 1987.

Memberships: Agronomy Society of America, Crop Science Society of America, Weed Science Society of America, Netherlands Institute for Agricultural Science (NILI), Phi Kappa Phi, and Gamma Sigma Delta.