



Physiological measurements of drought stress on spring wheat (*Triticum aestivum* L.)
by Abdulkadir Ahmed Elmi

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Agronomy
Montana State University
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Abstract:

Six spring wheat (*Triticum aestivum* L.) cultivars were studied for characteristics associated with drought resistance under dryland in 1986 and 1987. Three of them were hypothesized to be resistant and three susceptible to drought on the basis of regression analysis. Leaf water saturation deficit, leaf diffusive resistance, plant canopy temperature, leaf water potential and soil water depletion were measured. Cultivars differed in leaf diffusive resistance, water saturation deficit, grain yield, kernel weight and kernel number. Leaf diffusive resistance was higher while water saturation deficit was lower for the resistant cultivars. Leaf diffusive resistance and water saturation deficit have some potential for differentiation between drought resistant and susceptible cultivars. Both are feasible, non-destructive and efficient methods that are useful in screening large numbers of genotypes for their resistance to drought.

Leaf desiccation with 2% sodium chlorate was also used to simulate drought stress. Plants were sprayed at booting, heading or flowering stages. Reductions in resistant and susceptible cultivars were similar. In 1986 reductions by the desiccant for grain yield, kernel weight and kernel number were 24.2, 21.1 and 19.4% in resistant cultivars and 26.4, 21.6 and 22.6% in susceptible cultivars, respectively. In 1987 reductions for grain yield, kernel weight and kernel number were 24.9, 22.0 and 23.3% in the resistant cultivars and 26.4, 24.2 and 26.0% in the susceptible cultivars, respectively. Leaf desiccation from sodium chlorate appears to simulate some aspects of drought stress.

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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LIST OF ABBREVIATIONS AND SYMBOLS

ψ_T	=	leaf total water potential
WSD	=	water saturation deficit
Rs	=	leaf diffusive resistance
MPa	=	Mega-pascals
s	=	seconds
Tc	=	canopy temperature
Ta	=	ambient or air temperature
Tl	=	leaf temperature
h	=	hour
yrs	=	years
a	=	intercept
Cult	=	cultivar
Date	=	date of sampling
R	=	resistant
S	=	susceptible
Res	=	residual
*	=	denotes significant LSD at 0.05

ABSTRACT

Six spring wheat (*Triticum aestivum* L.) cultivars were studied for characteristics associated with drought resistance under dryland in 1986 and 1987. Three of them were hypothesized to be resistant and three susceptible to drought on the basis of regression analysis. Leaf water saturation deficit, leaf diffusive resistance, plant canopy temperature, leaf water potential and soil water depletion were measured. Cultivars differed in leaf diffusive resistance, water saturation deficit, grain yield, kernel weight and kernel number. Leaf diffusive resistance was higher while water saturation deficit was lower for the resistant cultivars. Leaf diffusive resistance and water saturation deficit have some potential for differentiation between drought resistant and susceptible cultivars. Both are feasible, non-destructive and efficient methods that are useful in screening large numbers of genotypes for their resistance to drought.

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INTRODUCTION

Growth is the integrated effect of many factors in plants, any of which may restrict it. Decreased water supply to plants, for example, generally leads to decreased leaf water potential (ψ_T), increased stomatal diffusion resistance (R_s), and thus reduced growth. The degree of stress that reduces growth varies among plant species. Plant breeders screening for improved drought resistance need methods of assessing water stress that are both rapid and capable of detecting real genotypic differences. The availability of commercial instruments for measurement of leaf diffusive resistance, leaf temperature and leaf water potential has facilitated the routine measurement of these characteristics.

Adjei and Kirkham (1980) found that a drought resistant winter wheat cultivar had higher stomatal resistance than a drought susceptible cultivar for part of the growth cycle. Ehrler et al. (1978) found that wheat canopy temperatures provided a good indication of differences in the plant water potential. Lower leaf water potential resulted in increased canopy temperature. Water loss rate from excised leaves often differentiated between drought resistant and susceptible wheat cultivars.

The objectives of the present study were:

1. To evaluate the physiological characteristics of six spring wheat cultivars for drought resistance using different

commercially available instruments.

2. To examine tolerance of spring wheat to drought stress induced by a chemical desiccant.

LITERATURE REVIEW

Many techniques have been used to measure water stress in wheat (Triticum spp.) plants. These techniques include measurement of leaf water content or saturation deficit (Dedio, 1975), leaf diffusive resistance (Jones, 1977), water potential (Kaul, 1969), temperature (Ehrler et al., 1978), and artificially induced drought (Blum et al., 1983a and b).

Soil moisture availability often limits productivity in dryland wheat culture. As a consequence, considerable research effort has been focused on increasing yield performance under sub-optimum moisture conditions through selective pressure on the gene pool. Hanson and Nelson (1980) examined agronomic, physiological and biochemical approaches that could be used in a breeding program for assessing genotypic sensitivity to drought. They suggested that an ideal screening test be:

1. Rapid, accurate, and able to handle large numbers of samples during the season.
2. Applicable early in the development of the plant.
3. Nondestructive.

Species and genotypic differences in response to drought stress have been identified with respect to several physiological and morphological characteristics. Although numerous authors have examined the responses of wheat plants to water stress and suggested

various mechanisms that may result in improved drought resistance, there is no clear understanding of the morphological and physiological characteristics that are responsible for differential responses to stress.

Water Saturation Deficit (WSD)

Plants are designed to extract water from the soil and maintain an optimum water status. The dynamic water content of plants is the difference between transpiration and root uptake; therefore, plants that can survive in very dry areas must have efficient systems both to extract water and prevent unnecessary loss.

Water loss rate from excised leaves has shown promise for characterizing drought resistance of wheat genotypes. Bayles et al. (1937) were the first to use the water loss from excised leaves to evaluate drought tolerance in wheat. Clark and McCaig (1982) found that differences between cultivars in water retention were expressed better for plants grown in stressed than in non-stressed environments. Kirkham et al. (1980) concluded that the stage of growth and position of sampled leaves affect the water retention ability. It is necessary that leaves from the same position and plants of the same physiological age be used for comparing water retention ability.

Results obtained by Bayles et al. (1937) and Clark and McCaig (1982) showed that more drought tolerant wheat cultivars had greater water retention than drought susceptible cultivars. Dedio (1975) showed that the cultivar Pitic 62 had higher water retention

capability, while, among cultivars grown in the field, Clark and McCaig (1982) found Pitic 62 to have relatively low retention capability.

Several studies have indicated that water status of intact (Schonfeld et al., 1986) or excised (Dedio, 1975; Kirkham et al., 1980; Jaradat and Konzak, 1983; Clark and McCaig, 1982) leaves may be related to drought resistance. These techniques are often labor intensive and not well suited to large scale breeding programs. Partial automation using microcomputers significantly decreased the measurement time (Clark and McCaig, 1982); and complete automation allowed even more detailed study (McCaig, 1986).

Leaf Diffusive Resistance (R_s)

Stomatal diffusive resistance has long been recognized as a key variable influencing leaf gas exchange through its regulation of water vapor and CO_2 diffusion. Many researchers have shown severe plant water deficits are associated with increases in stomatal resistance. However, much less data exist to describe stomatal response during relatively mild plant water deficits, especially under field conditions.

Fischer et al. (1977) suggested that at least 10 autoporometer diffusive resistance readings per genotype are needed to detect cultivar differences in wheat because of high standard deviation. (Newer instruments may be better.) Both Fischer et al. (1977) and Sojka et al. (1979) found that the stability of leaf permeability or

diffusive resistance over several hours during the midday period allow large numbers of determinations to be made in one day. In a controlled environment experiment, Adjei and Kirkham (1980) found that a drought resistant cultivar had higher stomatal resistance than a drought sensitive cultivar for part of the growth cycle. However, interpretation of leaf diffusive resistance results is dependent upon both environment and plant age.

To quantify the response of stomata with changes in plant water status, many attempts were made to relate stomatal resistance to the thermodynamic state of leaf water. However, Sinclair and Ludlow (1985) suggested that relative water content might be a better indicator of leaf water status than the thermodynamic state variables.

Research on numerous crop species has correlated stomatal resistance and leaf water status. Generally, stomatal resistance increases only after a threshold leaf water or turgor potential is attained (Baldochi et al., 1985; Brown and Jordan, 1976; Hsiao and Acevedo, 1974; Jordan et al., 1975; Markhart, 1985; Radin and Ackerson, 1981; Teare et al., 1982; Turner, 1974).

Under well watered conditions, Shimshi and Ephrat (1975) found that leaf diffusive resistance was negatively correlated with yield. Fischer and Wood (1979) found few significant correlations between yield and diffusive resistance. It appears that interpretation of leaf diffusive resistance results is dependent upon both environment and plant age.

Leaf Water Potential (ψ_T)

Pressure chamber techniques are widely used to measure water potential of leaves in physiological, agronomical and ecological studies (Ritchie and Hinckley, 1975). The technique measures the water potential of the xylem sap (Ritchie and Hinckley, 1975). If osmotic potential of the apoplastic water is close to zero, enough time is taken to degrade any gradients of leaf water potential in the leaf, and transpiration is small or nonexistent, then the water potential of the xylem sap as measured by the pressure chamber should be close to the water potential of the leaf cells. Total water potential measured by the pressure chamber usually agrees with results from the thermocouple psychrometer (Ritchie and Hinckley, 1975). A recent report, however, has suggested that there can be discrepancies, particularly when the leaves are transpiring rapidly (Ishihara and Hirasawa, 1978).

Ritchie and Hinckley (1975) have described a number of possible sources of error in the estimation of water potentials by pressure chambers. These include the loss of water, and the consequent lowering of water potential, after excision (Baughn and Tanner, 1976). Water loss from excision is reported to lower the water potential by 0.1-0.2 MPa in a range of species (Goode, 1968; Jordan, 1970, Gandar and Tanner, 1976). Reducing the time between excision and placing the leaf in the chamber to less than 30s and reducing water loss in the chamber itself by lining the chamber with wet filter paper minimizes the errors from water loss after excision.

In spite of these minor technical problems, many studies have shown that ψ_T plays a direct role in controlling plant growth (Boyer, 1968; Acevedo et al., 1971). Boyer (1970) reported that leaf enlargement of corn (Zea mays L.), soybeans [Glycine max (L.) Merr.] and sunflower (Helianthus spp.) was inhibited when ψ_T dropped below -4 bars. After these plants were rewatered, their rate of enlargement was not equal to that of control plants. Acevedo, Hsiao and Henderson (1971) noted that corn leaf elongation decreased gradually to zero over a range of -2.8 to -7.0 bar ψ_T , but upon relief of stress, rapid growth completely compensated for reduced growth during the stress period. They concluded stress severe enough to reduce corn growth had no adverse effect on subsequent metabolic processes. Also, Dube et al. (1974) found that more drought resistant lines of corn (Zea mays L.) were capable of maintaining higher leaf water potentials further into the stress period.

Canopy Temperatures

Energy exchange by radiation, convection and transpiration determines leaf and canopy temperatures of crop plants. Many environmental variables, including wind speed, solar radiation, soil moisture availability, and ambient air temperatures influence the leaf temperature of a given plant type.

It has been shown that transpiration reduces leaf temperature considerably (Tanner, 1963; Gates, 1964; Pallas et al., 1967; Van Bavel and Ehrler, 1968; Slatyer and Bierhuizen, 1964). When water

deficits develop in the leaves, stomates close progressively, transpiration is reduced, and hence leaf temperature rises.

Canopy temperatures measured with a remote infrared thermometer have been used to predict yields for a number of years. Idso et al. (1977), for example, showed that the cumulative sum of midday canopy (T_c) minus air temperature (T_a) values over the grain filling period was inversely correlated with final grain yield of a durum wheat, Triticum produra Desf. Leaf minus air temperature ($T_l - T_a$) was correlated with plant-water stress (Ehrler and Van Bavel, 1967; Blad and Rosenberg, 1976). Ehrler et al. (1978) reported that maximum values of $T_l - T_a$ or $T_c - T_a$ are obtained in the afternoon at 1400 h and that measurements taken at that time represent the whole day of plant-water stress. In durum wheat (Triticum durum Desf.) Ehrler et al. (1978) found that ($T_c - T_a$) and plant-water potential were significantly correlated. For barley (Hordeum vulgare L.) and soybeans [Glycine max (L.) Merr.] Millar et al. (1971) and Carlson et al. (1972), respectively, showed a significant correlation between leaf temperature and water saturation deficit of leaves. Similarly, Wiegand and Namken (1966) reported that a decrease in relative turgidity of cotton (Gossypium hirsutum L.) leaves from 83 to 59% resulted in a 3.6°C increase in leaf temperature and a 2.7 to 3.7°C increase in $T_l - T_a$ when air temperature and solar radiation were approximately constant. Plants with inadequate moisture supplies had less water for evapotranspiration, resulting in higher canopy temperatures and depressed yields. Recent studies have revealed

similar relationships for a wide spectrum of agricultural crops [review by Jackson et al. (1986)]. Reports concerning the response of different genotypes within a species vary. Mtui et al. (1981) examined several lines of corn (Zea mays L.) noting that the hybrids had cooler temperatures and used more water than their inbred parental lines. The hybrids also had higher water use efficiencies and yields.

Since a significant correlation exists between level of water stress in a plant and its leaf or canopy temperatures, it seems possible that leaf or canopy temperatures could be used as criteria to screen genotypes of a species for their crop yields and susceptibility to drought.

Kirkham et al. (1984) reported that inbred lines of drought resistant corn growing under well watered conditions had about 0.5°C higher average canopy temperatures during the growing season than drought sensitive inbreds. Hatfield et al. (1987) demonstrated that canopy temperatures could be used to identify water conservation in commercial and exotic strains of cotton. They found that strains which were warmer earlier in the season had a reduced rate of soil water use, hence remained cooler towards the later part of the season. The warmer strains under irrigated conditions also had the highest relative biomass under dryland field tests.

Singh and Kanemasu (1983) found as much as 5°C difference in afternoon canopy temperatures among 10 pearl millet (Pennisetum americanum L.) genotypes growing in a non-stressed environment. Since the warmer genotypes had higher relative yields, they suggested that

canopy temperatures could be used to screen genotypes for their response to water stress.

Soil Water Content (Depletion)

Since the pioneering work of Gardner and Kirkham (1952) and Van Bavel (1958, 1962, 1963) the neutron-scattering method is now classically and extensively used in field studies for measuring volumetric soil water content, soil water storage, and their changes with time. Although several new technologies for direct or indirect soil moisture assessment have recently become available (e.g., time domain reflectometry, Topp et al., 1983; thermal radiometry, Jackson et al., 1980), the neutron probe is possibly the most well known procedure for soil moisture status assessment (Holmes et al., 1967). The use of the neutron probe requires attention to the associated errors. Hewlett et al. (1964) investigated the several sources of error resulting from the use of a neutron probe. Instrumentation, timing and location variances were identified as the different components of the total variance of an individual water content estimate.

As Hawerkamp et al. (1984) demonstrated, the calibration equation of a neutron probe can be represented by the following equation.

$$\theta = a_0 + a_1 n + e$$

where θ is the volumetric water content corresponding to a count rate ratio n , a_0 and a_1 are, respectively, the Y intercept and the slope of the regression line, and n is usually given by the ratio between the

mean count rate \bar{N} (counts per second) of p replications, N_i , recorded at the same depth during a count time of T_c sec, and the mean count rate \bar{N}_s of g replications, N_{si} , in a standard absorber (water or paraffin block) during a counting time of T_c sec. In the above equation, e is a stochastic disturbance term, which accounts for the deviation from the exact linear model, as well as for measurement errors involved in volumetric water content (θ) and count rate ratio determinations. Thus, the accuracy of the neutron probe data is highly dependent upon an accurate calibration equation.

Artificially Induced Drought

Drought is a very important factor in limiting spring wheat production. The ability of wheat plants to produce grain under drought conditions might be due to various phenomena, and the limiting factor may differ among cultivars. Therefore, it is important to determine whether wheat cultivars differ in their drought responses. An older review of literature (Aamodt, 1935) described the construction of a drought chamber to determine the relative resistance of wheat varieties. Aamodt and Johnston (1936) compared drought resistance of several spring wheat varieties using this drought chamber. They found that drought-resistant varieties possessed a more highly branched primary root system than susceptible varieties. Also Krasnosel'skaia-Maksimova and Kondo (1933) in Russia, studied the effect of drought at different stages of plant development by using a drought chamber with controlled temperature, humidity and air

velocity. They found that the occurrence of drought during the period from shooting to the end of flowering was most injurious to cereal plants.

Blum et al. (1983a) showed that when cereal crop plants are subjected to post-anthesis stress (such as drought), kernel growth is increasingly supported by the mobilization of plant reserves, relative to transient photosynthesis, and that genetic variation exists for this trait. Another study (Blum et al., 1983b) evaluated the total destruction of the plant's photosynthetic source, by spraying the crop with a chemical desiccant (magnesium chlorate) after anthesis, as a means of revealing genetic variations in translocation-based kernel growth. He found that chemical desiccation, 14 days after anthesis, induced earlier mobilization of stem reserves in some wheat strains but not in others. Post-anthesis chemical desiccation of wheat was found to be a potentially useful method for differentiating among wheat genotype abilities to use stem reserves during post-anthesis stress of the photosynthetic system, such as drought might impose.

Assimilates for grain growth in the temperate cereals are largely derived from photosynthesis during grain filling. Wardlaw and Porter (1967) found that reserves from the stem contribute at most only 5-10% of final grain weight. The role of stem reserves may be greater when severe stress occurs during grain development, as indicated by the results of Asana and Basu (1963), Asana and Joseph (1964) and Yu et al. (1964). These stem reserves may also be greater in cultivars adapted to short growing seasons, as Stoy (1965) has suggested.

MATERIALS AND METHODS

Six cultivars of spring wheat (Triticum aestivum L.) were planted in the field May 4, 1986 and April 29, 1987 in single dryland areas (northwest of Bozeman). Before sowing, 60-20-10 kg/ha of NPK was added to the soil. Soil type was a coarse-silt, mixed (Borollic Calciorthids Aridosols) in 1986 and coarse-loamy, carbonatic (Borollic Calciorthids Aridosols) in 1987. Neutron access tubes were installed at the center of each plot for soil water depletion measurement. A 20 cm diameter rain gauge was installed in 1987.

The experiment was arranged in a split plot design with four replications, varieties being the main plots and time of sampling the subplots. Each of the 24 plots consisted of 8 rows each 20' long with 14" row spacing in 1986, and 12" spacing in 1987. Four rows were used for yield determinations. Grasshopper infestation late in the 1986 growing season resulted in significant defoliation.

For an artificially created drought stress study on the same cultivars, similar plots without the access tubes were planted in a randomized complete block design. In 1986 two replications were used as a preliminary study, while in 1987 four replications were used after the preliminary study showed encouraging results.

Cultivar Selection

The cultivars used in this study were chosen according to their yield performance and stability at 6-8 Montana dryland locations (sites) in 1982, 1983, 1984 and 1985 by regression analysis done by J. Brown using data supplied by L. Alexander at Montana State University (unpublished Annual Wheat Reports from 1982-1985) (Table 15, Appendix). In 1938 Yates and Cochran proposed that the regression of a single cultivar's yield on the mean yield of all other cultivars at a given location could provide a useful parameter for studying genotypes. Finlay and Wilkinson (1963) extended the idea and interpreted a regression coefficient (b) of zero to represent "absolute" phenotypic stability. A slope of 1 represented average stability, while $b < 1$ represented less than average response to the environment. Eberhart and Russell (1966) obtained their environmental index by subtracting the site mean from the grand mean over all environments. Plaisted and Peterson (1959), using a combined analysis of variance with pairs of cultivars, suggested that the line with the smallest cultivar by location interaction was the most "stable" cultivar.

As the review of literature indicates, the term "stability" is subject to different interpretations. Finlay and Wilkinson (1963) related the term to the slope of the logarithmic regression line, while Eberhart and Russell (1966) suggest that it should refer to the deviations from regression, and Schmidt et al. (1973) and Eslick et al. (1972) use the coefficient of determination and the slope to

measure cultivar response. All three techniques show promise of describing or predicting cultivar response over a series of environments, but the cultivars used in this study were selected on the basis of the slope of the regression line, Y intercept and R^2 . Three of the cultivars used in the experiment showed slopes greater than one and three had slopes less than one when yields were compared to site means (Table 15, Appendix). The cultivars with higher slopes are expected to be less environmentally stable and, therefore, "susceptible" to drought, while the cultivars with lower slopes are expected to exhibit drought "resistance" (Finlay and Wilkinson, 1963). Based on the regression analysis, Owens, McKay and Cando were hypothesized to be "susceptible" to drought and Fortuna, Lew and Thatcher to be "resistant" to drought.

Water Saturation Deficit (WSD)

Leaf sampling started at the 3- to 4-leaf stage and continued until 3/4 of the leaves senesced in both years. The newest fully expanded leaf was sampled randomly from each plot in the early afternoon. The leaves were excised, wrapped in Parafilm and then in aluminum foil to prevent water loss. Transport to the laboratory was done as quickly as possible on ice in a cooler. Fresh weight was determined, freshly cut surfaces of leaves were placed in individual test tubes containing 5 ml of distilled water at 4°C for 24 hours in the dark, and turgid weights were determined. Drying was at 65°C for

24 hours. Water saturation deficit (%) was calculated as suggested by Weatherly (1956):

$$\text{WSD} = \frac{\text{Turgid weight} - \text{Fresh weight}}{\text{Turgid weight} - \text{Dry weight}} \times 100$$

Leaf Diffusive Resistance (Rs)

Leaf diffusive resistance was measured with a Licor Model LI-700 steady state diffusion porometer (Lambda Instrument Corp., Lincoln, Nebraska) in 1986, and a Delta T-Device (Cambridge, England) was used in 1987. Values of Rs for the two years cannot be compared directly because of the different instruments used.

Measurements were started at about the four-leaf stage and continued weekly until flag leaf senescence started. The measurements were made on three different intact, randomly chosen leaves per plot. The newest fully expanded leaves were used in each case. Samples were taken at 0900-1000 h and 1100-1200 h once a week.

Canopy Temperatures

Canopy temperature was measured with a hand held infrared thermometer (Everest Interscience Model 110). Measurements were made at 1000-1100 h or 1100-1200 h when wind and clouds were absent. The thermometer had a nominal 8° field-of-view and 8-14 μm bandpass range. It was pointed obliquely at the wheat canopies and away from the sun, at an angle of about 30° from the horizontal. The canopy

temperatures and the differential canopy-air temperature ($T_c - T_a$) were recorded for each plot.

Leaf Water Potential (ψ_T)

Leaf water potential was measured with a pressure chamber similar to the one described by Scholander et al. (1964). Standardization of the procedures of leaf water potential determinations is essential for reproducible results (Ritchie and Hinckley, 1975). The leaf that is used and the position on the leaf where the measurement is made are critical. In this study well-exposed top leaves ("youngest mature" leaves) were randomly selected, excised, and placed in the pressure chamber. Approximately 5 mm of the leaf was kept external to the chamber rubber stopper and a pressurization rate of about 0.3 MPa min^{-1} was used as recommended by Tyree et al. (1978). The time from cutting to pressurization was minimized, and the chamber was lined with wet towel, particularly when temperatures were high.

Soil Water Depletion Measurement

Soil moisture was measured with a neutron-scattering depth moisture gauge model 2651 (Troxler Laboratories) according to the methods of Gardner and Kirkham (1952). Plastic access tubes with an inside diameter of 4.0 cm were placed in the center of each plot. The tubes extended 200 cm into the soil profile in 1986 and only 75 cm in 1987 because of a hard carbonate layer. The tubes were installed with hydraulic probe mounted on a pickup truck. Percentage moisture

by volume was determined beginning 22.5 cm below the soil surface at 30 cm depth intervals in 1986 and at 15 cm intervals in 1987. Standard counts were made prior to and after measuring the plots. Plot counts were then converted to volumetric water percentages using a dBase II computer program developed by Mark Kingstad. A 20 cm diameter rain gauge was installed at the plots in 1987. A layer of mineral oil was added to prevent evaporation. Rainfall recorded weekly throughout the year is shown in Table 16 (Appendix).

Artificial Drought

The same six cultivars of spring wheat were used for this experiment in 1986 and 1987. Two replications in 1986 and four in 1987 were arranged in randomized complete block designs. A 2% sodium chlorate solution was sprayed on 10 ft of row of each plot at the booting stage, the heading stage and the flowering stage. The sodium chlorate was received from Dr. G. Allan Taylor and S. Sabry. A spraying rate of 16.6 ml/sec was used. The spraying dates were 6/13, 7/4 and 7/12 in 1986 and 6/27, 7/2 and 7/9 in 1987 corresponding to the booting, heading and flowering stages respectively in the two years.

RESULTS AND DISCUSSION

The data obtained during the summers of 1986 and 1987 were analyzed using the General Linear Models (GLM) procedure of the Statistical Analysis System (SAS Institute, Inc., 1982). Analysis of variance was done for leaf water saturation deficit, leaf diffusive resistance, canopy temperatures, leaf water potential, soil moisture depletion and chemical desiccation (artificially induced drought). These parameters were compared using LSD for the six cultivars and contrasts to compare the two groups (resistant vs. susceptible). In the artificially induced drought experiment, plants sprayed at different growth stages were compared to each other and to the non-sprayed control in each year. Individual cultivars and resistant versus susceptible cultivar groups were compared. Yield and yield components were determined both years, plant height in 1986 and bundle weight in 1987.

Water Saturation Deficit (WSD)

Results of analysis of variance for the leaf WSD are shown in Table 1 for the two years, 1986 and 1987. Both years there were significant effects of cultivar, drought (resistant versus susceptible) and date. In 1986, date x cultivar, date x drought (Dro), and date x residual (Res) were significant, while in 1987 date x drought was the only significant interaction.

Table 1. Mean squares for leaf water saturation deficit (WSD in %) in 1986 and 1987.

Source	DF	1986	DF	1987
Blocks	3	3.84	3	14.77
Cultivar (Cult)	5	277.15 **	5	81.56 **
Dro (R vs S)	1	1144.31 **	1	381.80 **
Residual (Res)	4	60.36 NS	4	6.50 NS
Error (a)	15	21.85	15	4.85
Date (D)	7	766.81 **	7	71.38 **
Cult x D	35	33.91 **	35	7.42 NS
Dro x D	7	48.80 *	7	13.84 *
Res x D	28	30.18 *	28	5.82 NS
Error (b)	126	14.87	126	5.87

In both years the three resistant cultivars had significantly lower WSD than the susceptible cultivars (Table 17, Appendix). Perhaps WSD is related to roots. Wheats with more extensive root systems may provide more water to the leaves and, all other factors being equal, allow those wheats to maintain higher water content. Hurd's (1975) excellent research on rooting patterns has demonstrated that Pelissier and Pitic both have very extensive root systems compared to other tetraploid and hexaploid wheats, especially under dryland conditions.

Leaf water saturation deficit as a function of weeks after emergence is shown in Figs. 1 and 2 for the years 1986 and 1987. Although there is variation of the WSD due to rain, there is increasing WSD as the season progressed in 1986. In 1987 there is no clear increase of WSD except in the last week, just before full maturity. Generally the WSD of the most recent fully-expanded leaves increased

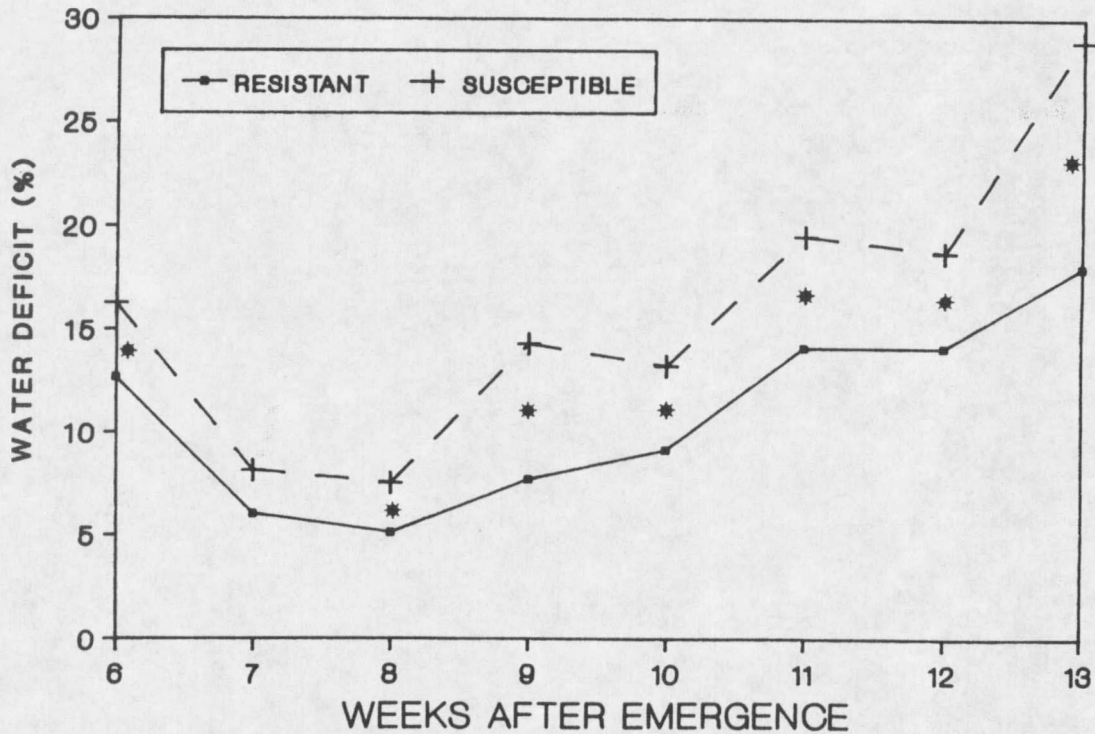


Fig. 1. Leaf water saturation deficit versus weeks after seedling emergence in 1986.

regularly throughout the season in 1986, while in 1987 more rain and an almost impermeable layer of carbonate at about 75 cm depth in the soil profile reduced WSD below 1986 levels.

The resistant cultivars had significantly lower WSD than the susceptible cultivars (Figs. 1 and 2), except for the seventh week of 1986 and the sixth week after emergence of 1987. These dates correspond to the lower leaf diffusive resistance for early sample dates, especially in 1986 (Figs. 3 and 4). Significantly lower WSD in the resistant cultivars than for the susceptible ones could be due to more rapid stomatal closure of resistant cultivars in response to

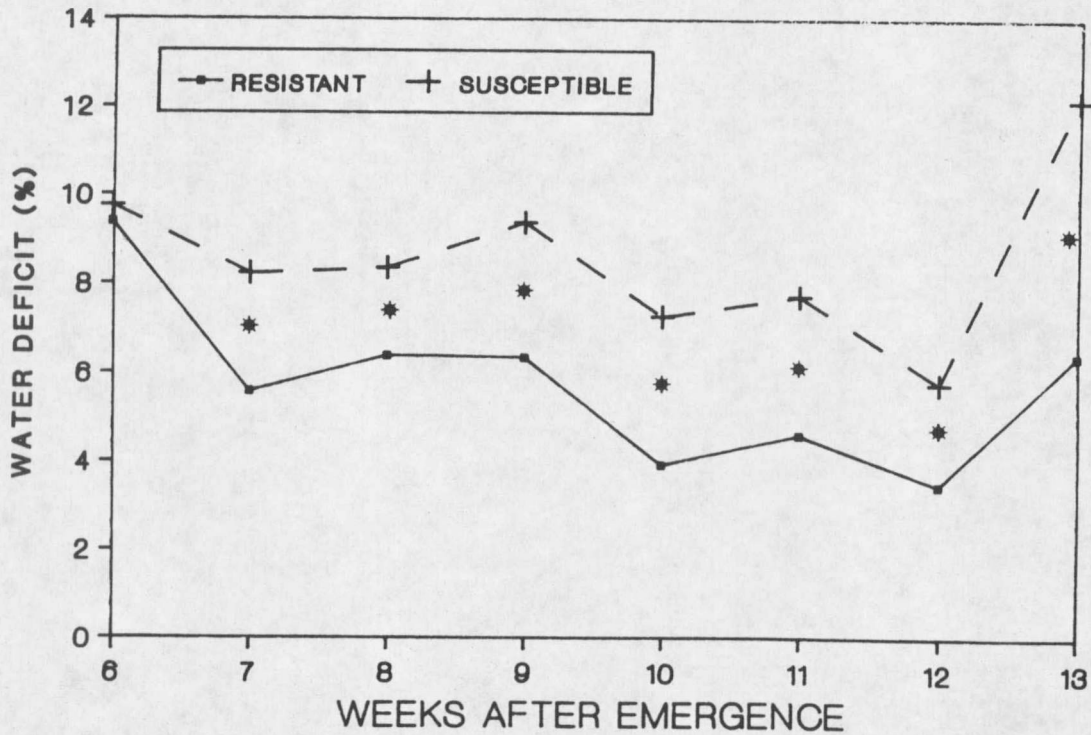


Fig. 2. Leaf water saturation deficit versus weeks after seedling emergence in 1987.

stress (Frank et al., 1973). Salim et al. (1969) also found that drought-hardy wheat cultivars had better water retention by excised leaves than did less hardy cultivars.

Leaf Stomatal Diffusive Resistance (R_s)

In both years the differences in R_s between cultivars, drought and date were highly significant (Table 2). Date x cultivar and date x drought interactions were also significant both years.

The resistant cultivars had significantly higher R_s than the susceptible cultivars in both years (Table 18, Appendix). Lew had the

Table 2. Mean squares for leaf diffusive resistance (Rs) in 1986 and 1987 (s/cm).

Source	DF	1986	DF	1987
Blocks	3	64.69	3	0.59
Cultivar (Cult)	5	658.14 **	5	10.12 **
Dro (R vs S)	1	3093.24 **	1	49.70 **
Residual (Res)	4	49.37 NS	4	0.23
Error (a)	15	8.24	15	0.19
Date (D)	7	1262.41 **	5	1.22 **
Cult x D	35	190.92 **	25	0.51 *
Dro x D	7	931.43 **	5	1.65 *
Res x D	28	5.79 NS	20	0.23 NS
Error (b)	126	5.88	90	0.193

highest mean Rs, while McKay had the lowest in 1986. In 1987 Lew also had the highest mean Rs, but Owens had the lowest Rs. This is consistent with the results of Adjei and Kirkham (1980), who found that a drought resistant cultivar had higher stomatal resistance than a drought sensitive cultivar for part of the growth cycle.

The two groups (resistant and susceptible) differed significantly most of the season for Rs. At seven weeks after emergence in 1986 the resistant cultivars had significantly lower Rs than the susceptible ones (Fig. 3), with adequate soil moisture in the soil. As the season progressed and stress developed in both years, resistant cultivars had significantly higher Rs than the susceptible group. Similar results were reported by other authors who concluded that stomatal resistance increases after a threshold leaf water turgor potential is attained (Baldocchi et al., 1985; Brown and Jordan, 1976; Jordan et al., 1975;

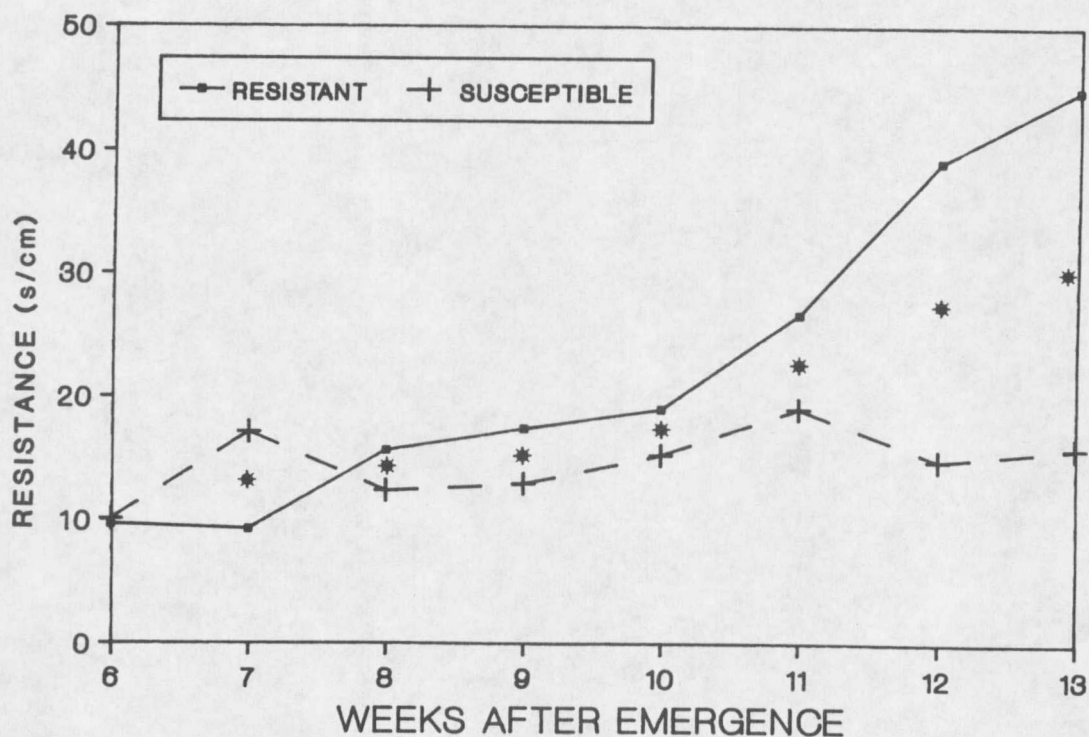


Fig. 3. Leaf stomatal diffusive resistance (R_s) versus weeks after seedling emergence in 1986.

Markhart, 1985; Radin and Ackerson, 1981; Teare et al., 1982; Turner, 1974).

This difference in R_s could be due to the lower leaf water saturation deficit observed in the resistant cultivars (Figs. 1 and 2). Decreased leaf water deficit (WSD) could result in increased plant water content and may cause changes in R_s which are probably related to cell extensibility. According to Stålfelt (1966), if the osmotic potential of the epidermal cells rises, water is sucked from the guard cells, whose uptake of water by suction is decreased, promoting stomatal closure (higher stomatal resistance). As stomatal

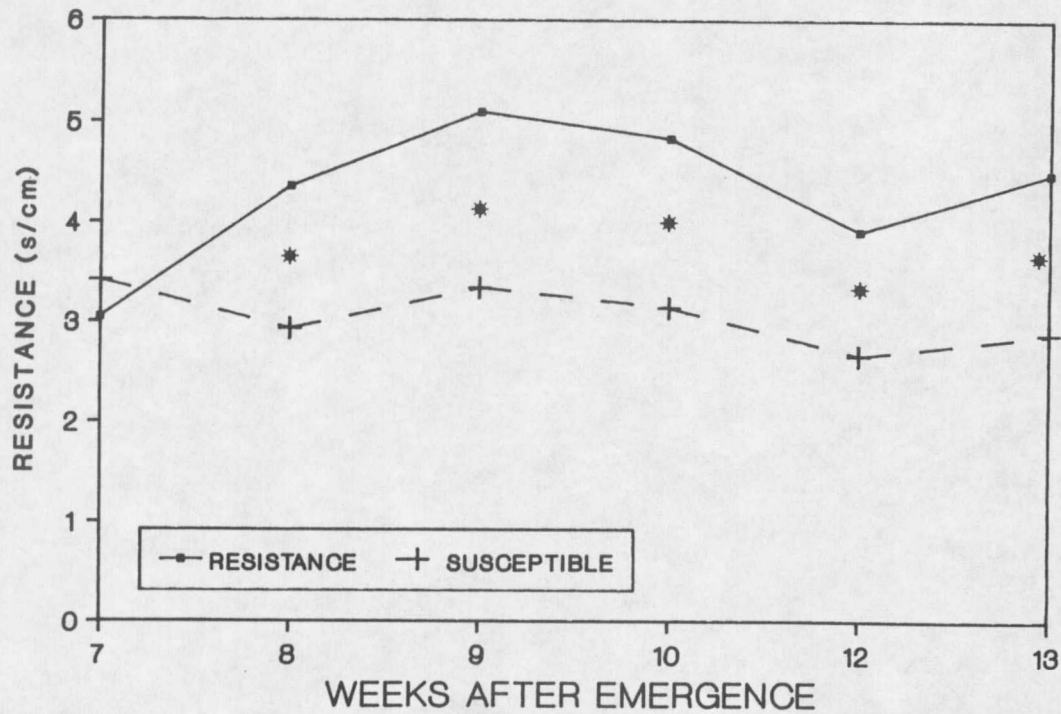


Fig. 4. Leaf stomatal diffusive resistance (R_s) versus weeks after seedling emergence in 1987.

aperture decreases, water loss decreases and subsequently plant water content increases. In dryland conditions these could result in an increased canopy temperature.

Sunrise Leaf Water Potential (ψ_T)

During the 1986/1987 summers sunrise leaf water potential failed to indicate any difference between the cultivars used (Table 3). Date was the only variable that differed. Also, no differences were obtained between the resistant and susceptible cultivars throughout the two seasons (Table 19, Appendix). As transpiration is greatly

Table 3. Mean squares for leaf water potential (ψ_T) near sunrise in 1986 and 1987 (MPa).

Source	DF	1986	DF	1987
Blocks	3	0.43	3	0.03
Cultivar (Cult)	5	0.10 NS	5	0.02 NS
Dro (R vs S)	1	0.10 NS	1	0.02 NS
Residual (Res)	4	0.10 NS	4	0.02 NS
Error (a)	15	0.068	15	0.01
Date (D)	7	13.52 **	5	1.73 **
Cult x D	35	0.06 NS	25	0.01 NS
Dro x D	7	0.12 NS	5	0.01 NS
Res x D	28	0.07 NS	20	0.01 NS
Error (b)	126	0.086	90	0.017

reduced or even eliminated at night, the tissue refills with water until dawn (Hsiao et al., 1980). At that time, leaf water potential approaches equilibrium with the soil water potential and hence is indicative of the soil water status in the rhizosphere. So we were expecting that sunrise leaf water potential would show some difference between the genotypes. Boedt and Laker (1985) found the pre-dawn water potentials to be suitable indicators of soil induced plant water stress, but under very hot, dry summer conditions in South Africa the method failed to indicate the onset of soil induced plant water stress. Several mechanisms could cause the lack of significant cultivar differences. Firstly, under high evaporative demand the available water in the rhizosphere may be depleted quickly, resulting in an extremely dry soil layer around the root. In an average dry soil the hydraulic conductivity from the rest of the soil to the rhizosphere may be so low that it takes more than 24 hours to reach

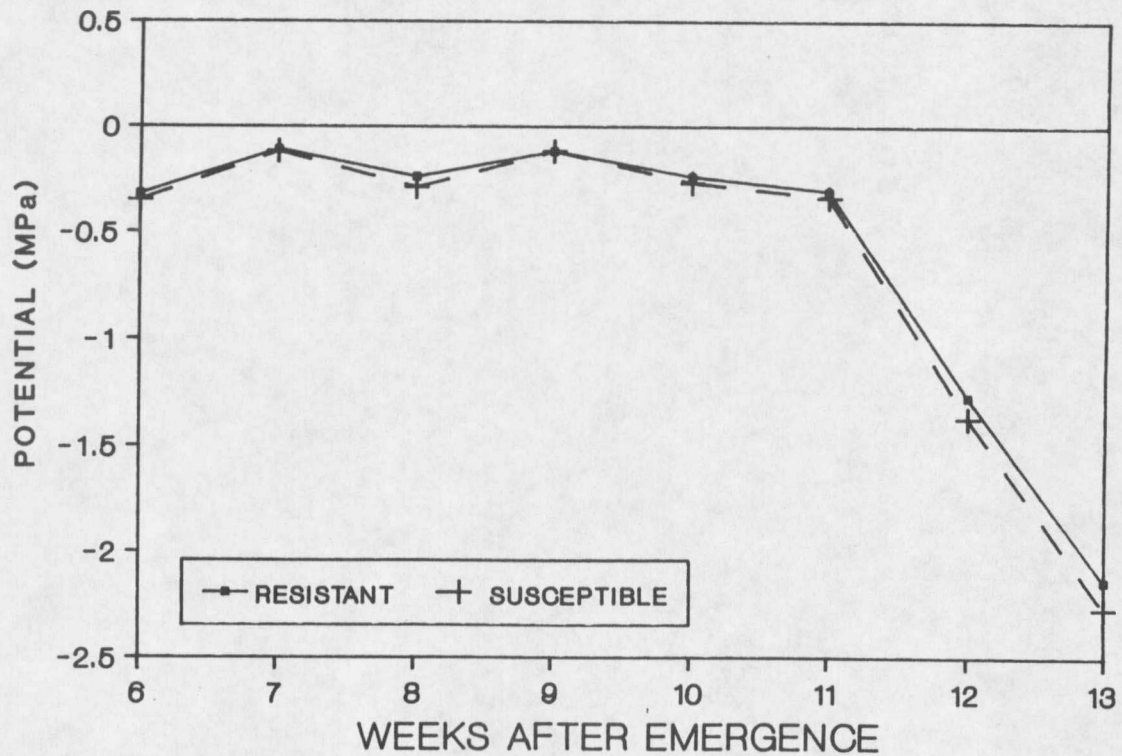


Fig. 5. Leaf water potential near sunrise versus weeks after seedling emergence in 1986 (MPa).

equilibrium with the adjacent soil layers. Secondly, Larcher (1980) and Klepper (1983) reported shrinkage of the root diameter under very high evaporative demand. This could result in a loss of contact between the root surface and the soil. Therefore, the roots may require a long time to regain their original diameter. Under these conditions it is possible that the plant may fail to equilibrate with soil water overnight. The reason for the failure to obtain cultivar differences in sunrise (ψ_T) is not known, but it could be partially due to rapid changes from pre-dawn microclimatological conditions at sunrise. The leaf water potential monitored near noon did not show

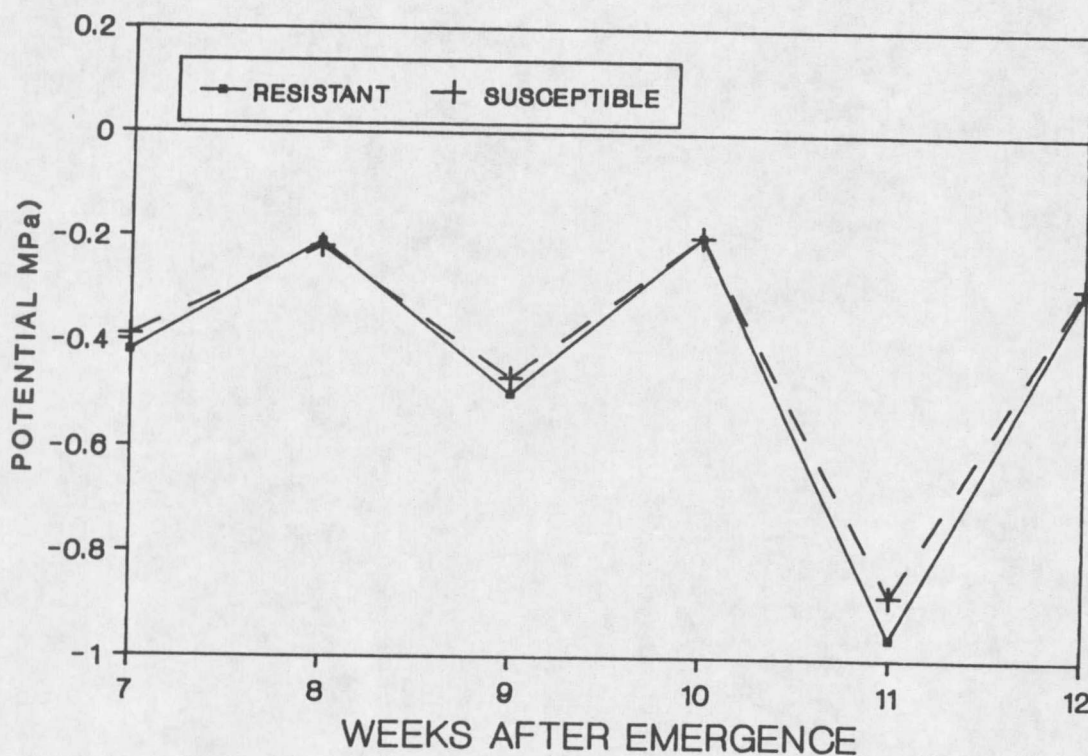


Fig. 6. Leaf water potential near sunrise versus weeks after seedling emergence in 1987 (MPa).

Table 4. Mean squares for leaf water potential (ψ_T) near solar noon in 1986 and 1987 (MPa).

Source	DF	1986	DF	1987
Blocks	3	0.12	3	0.04
Cultivar (Cult)	5	0.10 NS	5	0.04 NS
Dro (R vs S)	1	0.09 NS	1	0.08 NS
Residual (Res)	4	0.11 NS	4	0.13 NS
Error (a)	15	0.05	15	0.05
Date (D)	5	2.10 **	4	2.41 **
Cult x D	25	0.04 NS	20	0.03 NS
Dro x D	5	0.43 NS	4	0.01 NS
Res x D	20	0.07 NS	16	0.03 NS
Error (b)	90	0.05	72	0.03

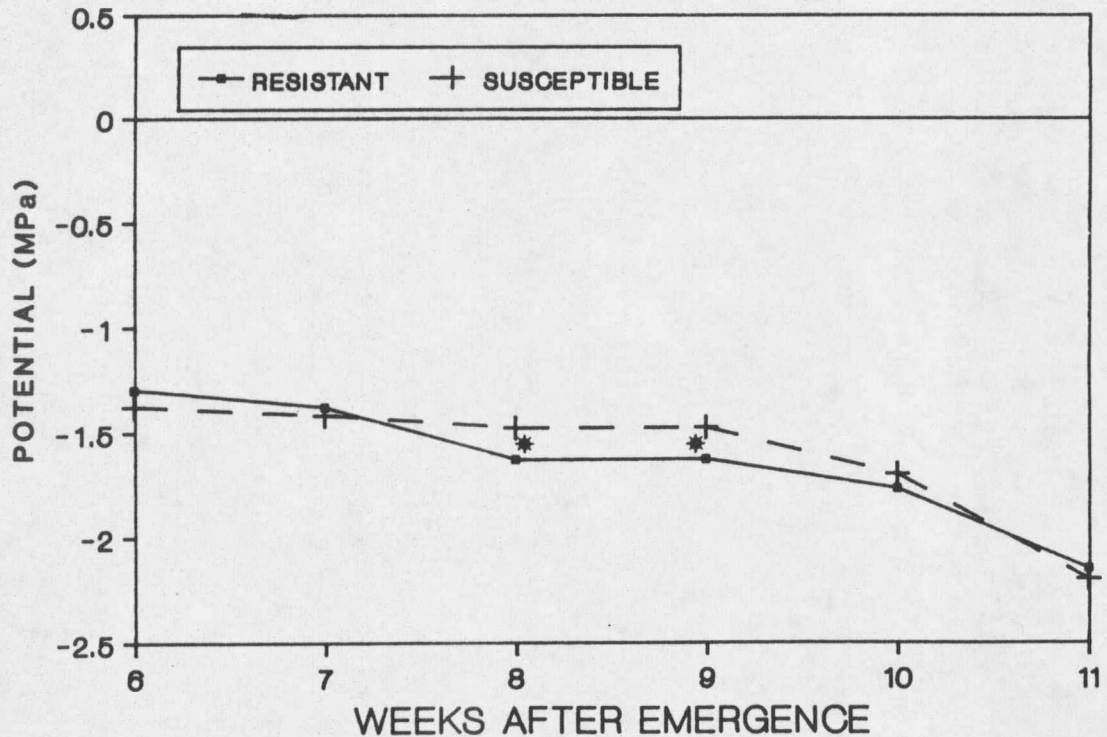


Fig. 7. Leaf water potential near solar noon versus weeks after seedling emergence in 1986 (MPa).

any differences except for date in both years (Table 4). Only Thatcher had significantly higher ψ_T near solar noon than Cando, Lew and Owens in 1986 (Table 20, Appendix).

Solar noon until 1400h is expected to be the maximum stress period in dryland areas. But differences in noon ψ_T were shown only for two sampling dates (8 and 9 weeks after emergence) in 1986 (Fig. 7). During those two weeks the resistant cultivars had lower ψ_T than the susceptible cultivars. Maintenance of lower (high absolute value) ψ_T , although not common in this study, has often been suggested as a drought resistance mechanism in plants (O'Toole and

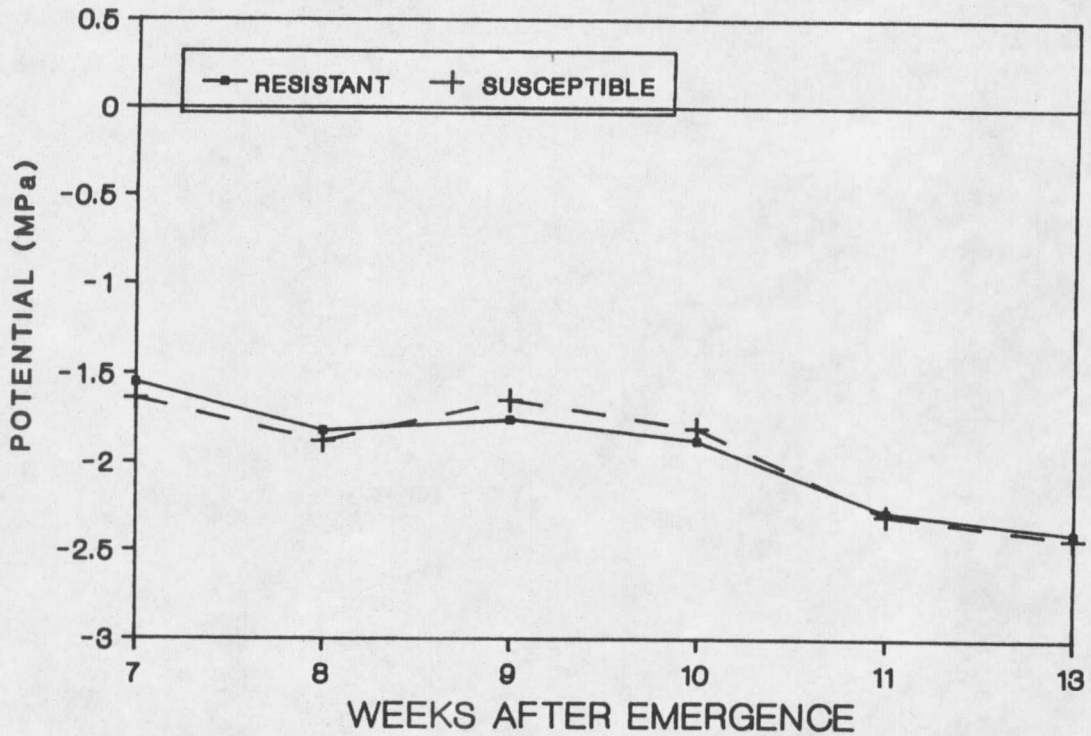


Fig. 8. Leaf water potential near solar noon versus weeks after seedling emergence in 1987 (MPa).

O'Toole and Cruz, 1980; Kramer, 1983). No differences were obtained for the ψ_T monitored at solar noon in 1987 (Fig. 8).

Our results agree with the conclusions of Lorens et al. (1987). Since ψ_{op} (osmotic potentials) were not measured in this study, it is not certain whether the lower ψ_T observed during these two weeks was due to accumulation of solutes, the concentration of solutes as a result of water loss from cells during dehydration, or a combination of both factors.

Canopy and Air Temperature Difference (Tc-Ta)

In 1986 Tc-Ta of cultivars at midmorning did not differ, but the two groups (resistant and susceptible) and date differed significantly (Table 5). In 1987 the differences between cultivars, drought and date were highly significant for Tc-Ta, and date x cultivar and date x drought interactions were also significant at midmorning.

Table 5. Mean squares for differential canopy temperature (Tc-Ta) in 1986 and 1987 at midmorning ($^{\circ}\text{C}$).

Source	DF	1986	DF	1987
Blocks	3	6.12	3	0.79
Cultivar (Cult)	5	1.01 NS	5	7.08 **
Dro (R vs S)	1	4.95 *	1	131.37 **
Residual (Res)	4	0.03 NS	4	1.01 NS
Error (a)	15	0.71	15	0.77
Date (D)	7	60.37 **	6	42.60 **
Cult x D	35	0.49 NS	30	1.64 *
Dro x D	7	0.87 NS	6	4.39 *
Res x D	28	0.40 NS	24	0.92 NS
Error (b)	114	1.47	108	0.83

As shown in Table 21 (Appendix), there were no significant differences in midmorning differential canopy temperatures between the resistant and the susceptible cultivars in 1986. However, the two groups differed significantly in 1987. The two resistant cultivars, Lew and Fortuna, were significantly warmer ($.96^{\circ}\text{C}$) than the three susceptible cultivars during the season. Similar results were found by Singh and Kanemasu (1983), Kirkham et al. (1984), and Hatfield et al. (1987). Conflicting results were found by Mtui et al. (1981) on

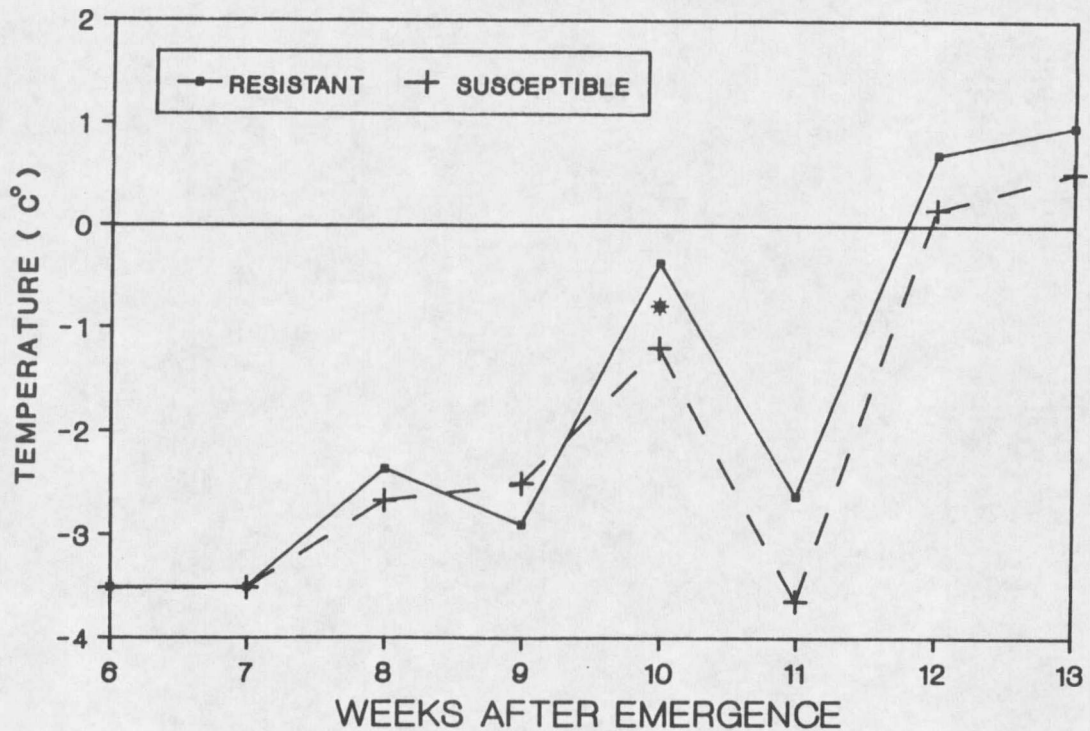


Fig. 9. Differential canopy-air temperature at midmorning versus weeks after seedling emergence in 1986 (°C).

corn (*Zea mays* L.). Working in a high moisture environment, they noted that the hybrids they used had cooler canopy temperatures and used more water than their inbred parental lines. The hybrids they used also had higher yields and water use efficiencies.

Weekly $T_c - T_a$ values for the two years are presented in Figs. 9 and 10. The fluctuation of increasing and decreasing $T_c - T_a$ values in 1986 reflect genotype and environment interaction, which in turn could be determined by the soil and plant resistance to flow of water.

