An evaluation of plant drought stress parameters in spring wheat
by Katim Seringe Touray

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

Abstract:

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Soil moisture content, and soil moisture depletion, were measured and, from these parameters and precipitation measurements, evapotranspiration was computed. In addition, leaf water potential, leaf relative water content, stomatal mass flow resistance, crop canopy temperature, and canopy-air temperature difference were measured.

Results from the analyses of variance did not show significant accession differences in soil moisture content or in their relative water content, canopy temperature, canopy-air temperature difference and stomatal mass flow resistance. However, significant accession differences were found in soil moisture depletion, evapotranspiration, and leaf water potential.

Regression analysis gave good correlations (R^2 = 0.99) between canopy-air temperature difference and canopy temperature. Also, canopy temperature was found to be a linear function of stomatal mass flow resistance.

The results obtained suggest that the use of canopy temperature and canopy-air temperature difference as plant drought stress indicators is justifiable in some instances. However, there were indications that caution is warranted in the use of these parameters, especially as a means of screening crops for drought tolerance.

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Katim Seringe Touray

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Abbreviation or Symbol	Meaning
B	A composite constant
C_p	Volumetric heat capacity of air
C_s	Stomatal conductance (cm/sec)
CWSI	Crop Water Stress Index (dimensionless)
D	Soil moisture depletion (cm)
E	Transpiration (mm)
E_t	Evapotranspiration (mm)
f(u)	A function of wind speed, u
G	Soil heat flux (W m^{-2} sec^{-1})
I	Irrigation (mm)
IR	Infrared
LAI	Leaf Area Index (dimensionless)
LWP	Leaf Water Potential (MPa)
P	Precipitation (mm)
r_a	Boundary layer resistance (sec/cm)
r_c	Leaf cuticular diffusive resistance (sec/cm)
r_i	Leaf intercellular space diffusive resistance (sec/cm)
r_L	Leaf internal diffusive resistance (sec/cm)
r_{mf} (SMFR)	Stomatal mass flow resistance (sec/cm)
r_s	Stomatal diffusive resistance (sec/cm)

Abbreviation or Symbol	Meaning
r_w	Cell wall diffusive resistance in the leaf (sec/cm)
R	Radiation emitted from the crop canopy (W m^{-2} sec^{-1})
R_e	Rainfall (excluding run-off) (mm)
R_n	Net solar radiation (W m^{-2} sec^{-1})
R_p	Resistance to water flow from the roots to the evaporating surface in the leaves
R_{rs}	Mean resistance to water flow within the roots
RWC	Relative Water Content (%)
SDD	Stress Degree Day (°C)
SMC	Soil Moisture Content (cm)
SPD	Saturation Pressure Deficit (MPa)
T_a	Air temperature (°C)
T_c	Canopy temperature (°C)
T_c-T_a	Canopy-air temperature difference (°C)
u	Wind speed (m sec^{-1})
W_d	Drainage from the root zone (mm)
ψ_L	Mean leaf water potential (MPa)
ψ_m	Matrix potential (MPa)
ψ_p	Pressure potential (MPa)
ψ_{plant}	Whole-plant water potential (MPa)
ψ_s	Solute (osmotic) potential (MPa)
ψ_{soil}	Mean Soil Water potential (MPa)

Abbreviation or Symbol	Meaning
ϵ	Emissivity of crop canopy (dimensionless)
σ	Stefan-Boltzmann constant (5.674×10^{-8} W m^{-2} K^{-4})

ABSTRACT

Five spring wheat (Triticum aestivum L.) accessions were planted in the Summer of 1986 near Manhattan, Montana, to assess the relations between various plant drought stress parameters using a line-source sprinkler irrigation system (Hanks et. al., 1976).

Soil moisture content, and soil moisture depletion, were measured and, from these parameters and precipitation measurements, evapotranspiration was computed. In addition, leaf water potential, leaf relative water content, stomatal mass flow resistance, crop canopy temperature, and canopy-air temperature difference were measured.

Results from the analyses of variance did not show significant accession differences in soil moisture content or in their relative water content, canopy temperature, canopy-air temperature difference and stomatal mass flow resistance. However, significant accession differences were found in soil moisture depletion, evapotranspiration, and leaf water potential.

Regression analysis gave good correlations ($R^2 = 0.99$) between canopy-air temperature difference and canopy temperature. Also, canopy temperature was found to be a linear function of stomatal mass flow resistance.

The results obtained suggest that the use of canopy temperature and canopy-air temperature difference as plant drought stress indicators is justifiable in some instances. However, there were indications that caution is warranted in the use of these parameters, especially as a means of screening crops for drought tolerance.

INTRODUCTION

Water is a major component of all plants and, is essential for the production of crops. Unfortunately, the importance of water is seldom matched by its availability for agriculture.

As a consequence, modern agriculture has come to rely significantly on the judicious use of limited water resources. In this connection, the quest for efficient means of harnessing, conveying, and applying irrigation water has received considerable time and effort in the last few decades. In areas where irrigation is not common, the maximization of the crop production from available precipitation has been of paramount importance.

Increased efficiency in water use for crop production is beneficial in reducing the amounts of water that would otherwise have been wasted. It is also beneficial in reducing the hazards to the environment posed by the increased use of fertilizers under irrigated agriculture has posed. Contaminated ground water, increased salinity, and toxicity levels in soils are all testimonies to the problems attendant to the inefficient use of irrigation water.

For these reasons, various methods and techniques have been devised to aid in the achievement of better irrigation management practices. The various methods have aimed, with varying degrees of success and acceptance, at finding convenient and economic means of detecting crop water stress, estimating crop water requirements, and achieving efficient irrigation scheduling. Most of the methods developed for estimation of evapotranspiration, and hence the prediction of crop water requirements, are not very suitable for use by an individual farmer. This is because of the scale (in both time and space) and instrumentation factors entailed in the use of these techniques.

Therefore, there has been an increased effort recently to develop methods of crop water stress detection that are fast, economical, and reliable enough to assure that crops would neither be unduly stressed nor would irrigation water requirements be overestimated. For these reasons, crop water parameters that are easily measurable and correlate well with more difficult to measure but reliable water stress indicators, have been used.

Two such parameters, crop canopy temperature and its' difference from air temperature have received enthusiastic support from some researchers. These parameters have been studied in conjunction with other crop water stress parameters such as leaf water potential, leaf relative water content, stomatatal mass flow resistance, and soil moisture depletion.

This study aimed to investigate the relation between these drought parameters in five varieties of spring wheat under four levels of irrigation. Also, the study aimed to assess the efficacy of the use of these parameters in the detection of crop water stress and, explore the potential use of these parameters for irrigation scheduling.

LITERATURE REVIEW

Moisture uptake and use by plants is determined by a wide variety of factors. The factors governing evaporative flux from crops can be grouped into three classes (Reggie, 1971):

a) soil factors;
b) micrometeorological factors;
c) plant factors.

These factors consequently influence various aspects of soil water management, including irrigation scheduling.

Various methods for scheduling irrigation have been proposed, and they can be grouped into three broad classes (Jackson, 1982):

a) soil based;
b) meteorologically based;
c) plant based.

Quite commonly, combinations of the three are used for irrigation scheduling.

Soil based irrigation scheduling techniques rely on the measurement or monitoring of soil moisture content (Gear et al., 1977). The information thus obtained is used with a pre-defined refill point (the point at which irrigation should occur) and a full point to schedule irrigations. The full point is defined as the total soil water holding capacity of a specified depth expressed as depth of water per unit depth of soil after initial drainage has removed some of the water.

Meteorological methods of irrigation scheduling (e.g. Pierce, 1960; Jensen and Haise, 1963) make use of meteorological factors such as air temperature, net radiation, relative humidity and windspeed as inputs in models used for the calculation of evapotranspiration in a given time.

Plant-based methods of scheduling irrigation rely on the evaluation of plant drought stress parameters, e.g. leaf water potential (Scholander et al., 1965), leaf or canopy temperatures (Stone and Horton, 1974), or leaf diffusive resistance (Kanemasu and Tanner, 1969). These techniques are particularly attractive because they provide a diagnostic tool for detecting impending or actual plant water stress from the plant itself. This obviates the need for gathering precise information on available soil moisture content, root distribution and atmospheric evaporative demand (Pinter, Jr., and Reginato, 1982). However, the problem encountered in using plant parameters for scheduling irrigations is that it is a time-consuming method, requiring numerous measurements for the characterization of a field (Jackson, 1982).

The foregoing discussion indicates the complex nature of the interactions between the various factors involved in soil water management for efficient plant production. These factors viz: soil moisture content, evapotranspiration, and plant drought stress parameters have received the attention of researchers during the past couple of decades.

Soil Water Content

Soil water has both direct and indirect influences on plant growth. Soil water directly affects plant growth through its effect on plant water status. For example, soil water potential influences leaf water potential (Campbell and Campbell, 1982) in a manner given by the relationship:

$$\psi_L = \psi_{soil} - E (R_{rs} + R_p) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

where:

ψ_L = mean leaf water potential;

ψ_{soil} = mean soil water potential;

E = transpiration;

R_{rs} = mean resistance to water flow in the roots;

R_p = resistance to water flow from the roots to the evaporation surface in the leaves.

Ehrler et al. (1978) have also found changes in ψ_{plant} (potential measured on the whole plant) to be determined by changes in volumetric soil moisture content.

Indirectly, soil water acts on other plant growth factors such as soil temperature, soil aeration, and nutrient availability. Consequently, soil moisture conditions that lead to the minimization of plant water stress may result in unfavorable soil temperature or aeration, or may leach nutrients required for plant growth (Campbell and Campbell, 1982).

Often, it is the rate of movement of water within the soil, not water content or potential, which determines the availability of water for plant use, and hence, the need for irrigation (Hillel, 1972). The rate of movement of water within the soil-plant-atmosphere continuum has been explained with the aid of electrical resistance analogs (e.g. Cowan, 1965); which assign resistances to various components of the continuum. The significance of each of component toward the determination of the rate of water movement depends on its contribution to the total resistance of the system.

Soil water content is a dynamic parameter, in that it is not constant. One of the factors contributing to changes in soil water content is soil water depletion, which in turn is dependent on a variety of soil, environmental and management factors. For example, Jensen et al. (1971) have expressed soil moisture depletion (D) as:

$$D = \sum_{i=1}^{n} (E_t - R_e - I + W_d) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

where:

E_t = evapotranspiration;

R_e = rainfall (excluding run-off);

I = irrigation water applied;

W_d = drainage from the root zone.

In the above relation, $D=0$, and $i=1$ after a thorough irrigation, and the terms on the right are daily totals.

Equations (1) and (2) both indicate the importance of evapotranspiration in soil-plant-atmosphere continuum, especially as related to its water economy. Evapotranspiration has very intimate, complex and frequently recursive relationships with other plant water stress parameters. For example, Millar et al. (1970) found that transpiration rates of barley decreased with decreasing leaf relative water content (RWC). When RWC reached about 85%, there was a reduction of approximately 50% in actual transpiration recorded. Yang and de Jong (1972) found a similar pattern in the relationship between the two parameters. Thus, transpiration rate dropped rapidly as RWC decreased from 98 to 90%. The decline of transpiration rate became more gradual after RWC reached 90% until a constant transpiration rate of 0.05 g cm^{-2} day^{-1} was reached at about 50% RWC.

Leaf water potential (LWP) has also been found by Yang and de Jong (1972), to decrease with increased evaporative demand (which determines the potential evapotranspiration rate). This is only because leaf water deficits, which determines LWP, are caused by temporary imbalances in the rates of transpiration and water absorption. These imbalances can be caused by either a sudden increase in evaporative demand or by a lowering of water absorption (Ehrler et al., 1966). Furthermore, reduced evapotranspiration rate, by increasing leaf temperature, leads to increased leaf resistance to evaporation (van Bavel et al., 1965).

The transpiration of water from plant leaves leads to a lowering of leaf temperatures by virtue of the latent heat of vaporization of water relative to the heat capacity of plant tissue (Brown and Escombe, 1905). For given conditions, this depression of temperature should be proportional to the transpiration rate (Martin, 1943). Thus, Gates (1964a) found that for bur oak, <u>Quercus macrocorpa</u>, the effective radiation load on the leaf decreased by 0.10 cal cm^{-2} min^{-1} for each

1.7×10^{-4} g cm^{-1} min^{-1} increase in transpiration rate. This increase in transpiration rate was calculated to drop leaf temperature below that which would occur in the absence of transpiration.

Leaf Water Potential

Leaf water potential (LWP) has come to be a standard parameter for quantifying plant water stress. LWP is the chemical potential of water, defined as the algebraic sum of the potential components due to the pressure (ψ_p), solutes (ψ_s) and matrix (ψ_m) of the plant leaf (Hsiao, 1973). The importance of these components in determining LWP depends on the leaf water status. For example, in fully turgid tissue (Hsiao, 1973), large decreases in LWP are due mainly to changes in ψ_p. Furthermore, leaf age also has a significant influence on LWP irrespective of the plant water status (Kippling, 1967).

Given the complex nature of the interactions within a plant, LWP also influences other plant water stress parameters. Thus, the stomatal resistance of soy beans (Glycine max) has been reported by Kanemasu and Tanner (1969) to increase rapidly as LWP drops below -1.11 MPa. Duniway (1971) and Jordan and Ritchie (1971) found that leaf resistance increased sharply, beyond the threshold LWP for stomatal closure; increasing 20- to 30-fold for a drop in LWP of less than 0.5 MPa.

LWP has a significant bearing on evapotranspiration by its' direct influence on the moisture concentration gradient between the leaf and the ambient air. This is illustrated by the findings of Kirkham et al. (1985), which show that Sunflower had a high ET at high water potentials.

Ehrler, et al., (1978) have reported ψ_{plant} to influence the difference between canopy temperature and air temperature (T_c-T_a). Thus when ψ_{plant} decreased to -1.9 MPa, (T_c-T_a) was zero and when ψ_{plant} was -4.8 MPa, (T_c-T_a) rose to 4.8°C. Data from Kirkham et al. (1985) also indicate there is a tendency for crops with high potentials to have low (T_c-T_a) values and vice versa.

Leaf Relative Water Content

Leaf relative water content (RWC) is another commonly used index of plant water stress. Sometimes called water saturation deficit (WSD), RWC is used as an indicator of the state of water balance of a plant because it expresses the amount of water which the plant leaf requires to reach full saturation (Catsky, 1974). For this reason, RWC has some bearing, direct or indirectly, on other plant water stress indices.

Thus, Wiegland and Namken (1966) found that a decrease in RWC from 83% to 59% resulted in a 3.6°C increase in leaf temperature. Also, leaf reflectance in the 1.45 and 1.93 μ water absorption bands have been found to be significantly (p = 0.01) related to the relative water content in an inverse manner (Thomas et al. 1971). For cotton (Gossypium hirsutum L.), the changes in reflectance were found to occur when RWC fell below 70%. Carlson et al. (1971) also found significant relationships between RWC and the spectral properties of leaves of corn (Zea mays), soybean (Glycine max), and sorghum (Sorghum biocolor), over the wavelength region 800-2600 mμ. For example, for sorghum leaves, reflectivity decreased with increasing RWC at both 2200 mμ and 1950 mμ wavelengths. In addition, at a given RWC, reflectivity at 2200 mμ was higher than at 1950 mμ.

RWC has also been found to influence LWP. For example, Yang and de Jong (1972) found that as the RWC dropped in wheat plants, LWP dropped also, with a drastic change in the slope of the curve when RWC was between 93 and 97%. Millar et al. (1970) found a similar change in the slope of the curve for barley and observed that the change coincided with a change in the elasticity of the leaves. However, because variations in the environment can cause changes in RWC, the usefulness of RWC as on index of LWP is significantly reduced (Yang and de Jong, 1972).

Also, a change of a few MPa of LWP in nearly saturated tissue corresponds to a change of several percentage points in RWC (Hsiao, 1973). This is about the size of the random measurement error for RWC in many studies (Barrs, 1968). It is perhaps for this reason that RWC did not show significant changes in some studies even when other physiological processes were affected by mild stress (Hsiao, 1970, and Huffaker et al., 1970).

In studies where RWC was used as an index of leaf water status, the threshold value above which leaf diffusive resistance remains constant (i.e. open stomata) was found to be about 80 to 85% RWC for cotton (Troughton, 1969) and beans (Duniway and Durbin, 1971); suggesting that RWC is a poor indicator of mild stress. However, this conclusion probably cannot be generalized since there are some indications to the sensitivity of stomata of other species to mild stress (Boyer, 1970; El-Sharkany and Heskelt, 1964).

Leaf Diffusive Resistance and Stomatal Mass Flow Resistance

Leaf diffusive resistance is a measure of the resistance to the movement of water from the inside of the leaf to the ambient air. It is a single but important component in the network of resistances along the path of water in the soil-plant atmosphere continum.

The total internal leaf resistance r_L is given (Milthorpe, 1961) by:

$$\frac{1}{r_L} = \frac{1}{r_c} + \frac{1}{r_s + r_i + r_w} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3)$$

where:

r_c, r_s, r_i, and r_w are the resistances to diffusion of water vapor through the cuticle, stomata, intercellular spaces in the leaf, and the cell walls of the leaf, respectively.

Different components of r_L have varying significances, depending on a host of leaf and environmental conditions (Slatyer, 1967). In most cases, r_c far exceeds r_s when the stomata is open.

Since stomata control only one part of the total resistance, the magnitude of the effect of this change will depend on the importance of r_s relative to that of the boundary layer resistance (r_a), and r_c (Hsiao, 1970). Stomatal aperture in plant leaves is dependent to a large extent on the water status of and light intensity on plants (Slatyer, 1967). In well watered plants, stomatal aperture is determined by the illumination (Ehrler and van Bavel, 1967).

Various theories have been advanced to give the sequence of events leading to the closing of stomata in the event of water stress. One presumed sequence of events begins with the disparity between transpiration and absorption of water, which causes the development of a leaf water deficit and, subsequently, stomatal closure (van Bavel, 1965).

The effect of water stress on stomatal closure is probably similar to that of most other inhibitors; acting partly by causing changes in internal CO_2 concentration, thus mediating respiration and photosynthetic processes, and partly by influencing processes concerned with energy flow and guard cell turgor (Slatyer, 1967).

Of all the factors involved in plant water dynamics, evapotranspiration is perhaps the factor which is most influenced by stomatal closure. Thus, Holmgren et al., (1965); and Rijtema, (1965) found that transpiration rate is increased by increased evaporative demand (which determines transpiration) irrespective of LWP, probably due to stomatal and cuticular resistance to water movement.

However, the influence of r_s on transpiration is often significantly tempered by environmental factors. For example, in still air with the stomata open, {i.e. r_c (or r_s) << r_a }, Bange (1953) found little stomatal control of transpiration until stomatal aperture was significantly reduced. Under moving air conditions though, r_a is substantially reduced and, hence, stomatal control of transpiration is effective throughout the entire range of apertures.

One other drawback of using r_s as an index of plant water stress lies in the lack of correlation between values obtained on single leaves and those for crop canopies, since there is no simple relationship between crop and single leaf values of r_L (Slatyer, 1967). Further, given that leaf area index (LAI) for a good canopy normally exceeds 1, effective r_L values for crop canopies can be expected to be less than for a single leaf; declining as LAI decreases. This is because the resistances due to the individual leaves are connected in parallel.

The relationship between stomatal diffusive resistance r_s and stomatal mass flow (or viscous) resistance is somewhat complicated (Shimshi, 1977; Waggoner, 1965). One reason for this is that in amphistomatous leaves, the resistance measured by viscous flow porometers is the sum of the resistances of both epidermises with stomata and that of the intercellular system of the mesophyll (Slavik, 1974).

However, various power functions have been proposed to describe the relationship. For example, Darwin (1916), has related r_{mf} to r_s by:

$$r_s = r_{mf}^y \quad \text{......} \quad (4)$$

where y = 0.50.

A similar relationship was obtained empirically by Milthorpe and Penman (1965; cited in Waggoner, 1965), with y having a value of 0.44.

Canopy Temperature

Surface temperature data have been used in the study of many and varied natural processes. For example surface temperatures have been used as a means of estimating evaporative losses from large bodies of water (Richards and Irbe, 1969; Webb, 1970), bare soil (Conway and van Bavel, 1966, 1967), as well as vegetation (Blad and Rosenberg, 1975; Stone and Horton, 1974). Furthermore through the use of infrared photography, surface temperatures have been used to detect genetic variations in sorghum drought avoidance (Blum et al., 1978; Blum, 1975).

Canopy temperatures, in particular, have been found to be useful indicators of both matric and osmotic stress in cotton plants (Howell et al., 1984). Both contact and non-contact methods of measuring plant temperatures are in use. For large areas, non-contact methods (e.g. infrared thermometry) are more convenient than contact methods (e.g. thermocouples) since thermocouples are limited to ground use and individual leaves (Ehrler et al., 1978). Also, since thermocouples must be attached to or inserted in the plant (generally the leaf), they can cause changes in the condition of the plant part whose temperatures are to be measured (Blad and Rosenberg, 1976).

Monteith and Szeicz (1962) and Tanner (1963) were among the first researchers to use infrared (IR) radiometers for the measurement of plant temperatures. Tanner (1963) used IR thermometers to detect moisture stress in plants under different water regimes. He pointed out that Even though the temperature measurements so obtained are weighted toward the upper part of the plant, it is these portions of the plant canopy which participate most actively in transpiration, heat exchange and assimilation.

The principle behind the IR measurement of canopy temperature is the well-known Stephan-Boltzman law:

$$R = \varepsilon \sigma T_c^4 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (5)$$

where:

R = the radiation emitted from the canopy (Wm^{-2})

ε = the emissivity of the canopy

σ = Stefan-Boltzman constant (5.674×10^{-8} Wm^{-2} K^{-4}).

T_c = Canopy temperature (K)

IR thermometers measure the factor R in the Equation (4) above and relate this to T_c.

In the 8-14 μm band (where most hand-held IR thermometers operate) water vapor can have a significant influence on canopy temperature measurements, especially when distances between the target and sensor are great. However, Lorenz (1968) found that this effect is negligible when the distance to the target is less than 154m.

Emissivities of most plant surfaces have been reported (Jackson, 1982) to be in the range 0.95 to 1.00. Gates (1964b) found most plant leaves to have a long-wave emittance of 0.97 to 0.98.

Canopy temperatures have been found to vary both between and within plant species. For example, corn was found during one growing season to have a consistently warmer canopy than alfalfa (Blad and Rosenberg, 1976). Ehrler (1973) found significant and consistent differences in leaf temperatures of different cotton varieties. In particular, the differences observed were more pronounced in stands growing in dry soil, and explained by the fact that the leaves of warmer varieties were positioned nearly normal to sunlight. This contrasted with the drooping leaves of the cooler variety; a leaf position that leads to absorption of comparatively less shortwave energy.

In contrast to the findings of Ehrler (1973), Singh and Kanemasu (1983), working with pearl millet found greater differences in leaf temperatures of different genotypes when they were growing under irrigated conditions than under non-irrigated conditions; a difference attributed to differences in genetic make-up with a bearing on the energy transfer characteristics of the plants. However, Idso et al., (1984) found no significant differences among the canopy temperatures of six wheat (Triticum aestivum L.) cultures.

The differences in the results obtained in the above-mentioned experiments demonstrate the complexity of the relationship between various factors affecting leaf and canopy temperatures. Among these factors are the sensible heat exchange as dictated by the wind and crop geometry, net radiant energy absorbed, and the evaporative cooling which is dependent on wind and vapor pressure gradient (Ehrler and van Bavel, 1967).

Leaf temperature is determined by changes in any or all of these factors, as Raschke (1962), has shown quantitatively for single leaves. These factors influence canopy temperatures by virtue of their influence on the balance of sensitive and latent heat exchanges between the crop canopy and the atmosphere (Hatfield et al., 1985).

Canopy-Air Temperature Difference

Closely related to crop canopy temperature (T_c) is its difference from air temperature (T_a), i.e. the quantity (T_c-T_a). This parameter has been found to be a promising technique for monitoring plant water stress in wheat, given its significant response to changes in plant water potential occasioned by changes in soil moisture content (Ehrler et al., 1978).

Also, Ehrler (1973) has found (T_L-T_a) (the difference between leaf and air temperatures) to be a sensitive indicator of changes in r_s. Furthermore, even under conditions of severe drought, (T_L-T_a) correlated well with leaf diffusive resistance despite changes in the saturation deficit of the air.

The ability of (T_c-T_a) to indicate plant water stress has led to the development of models relating it to evapotranspiration. One such model (Brown and Rosenberg, 1973) is:

$$E_t = R_n - G - f(u)\ C_p\ (T_c-T_a) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (6)$$

where:

E_t = evapotranspiration

R_n = net solar radiation

G = soil heat flux

$f(u)$ = a function of wind speed

C_p = volumetric heat capacity of air.

Subsequent publications have discussed equation (6) in detail and have found it to be a reliable predictor of E_t (Stone and Horton, 1974; Blad and Rosenberg, 1976).

However, for practical situations, equation (6) is not easy to use since f(u) is rather tedious to determine and dependent upon crop type and location. Consequently, Jackson et al. (1977) made some simplifying assumptions:

a) for 24-hour periods, G is negligible

b) f(u) = 1, under still air conditions

Thus, equation (6) becomes reduced to:

$$E_t = R_n - B\ (T_c-T_a) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (7)$$

where:

B is a composite constant that can be determined experimentally.

Ehrler et al., (1978) found an inverse relationship between the stress degree day parameter (T_c-T_a) and xylem water potential of wheat. Later (1981 a), the stress degree day parameter (SDD) was refined by Idso et al., by taking the evaporative demand of the atmosphere into account. The transformed parameter was termed the crop water stress index (CWSI) and was found to correlate well with the xylem pressure potential of alfalfa plants subject to varying degrees of water stress (Idso et al., 1981 b). Pinter and Reginato (1982), Hatfield (1982) and Reginato (1983) have all proposed the use of the CWSI as a tool for irrigation scheduling.

MATERIALS AND METHODS

The experiment was carried out in the summer of 1986 on a Manhattan sandy loam (coarse-loamy, mixed, Typic calciborolls) located in the Gallatin Valley about 32 Km west of Bozeman, Montana.

The experiment used a line source sprinkler irrigation system along the lines of those proposed by Hanks et al., (1976); with the sprinkler line running down the middle of the experiment (Fig. 1). This way, a continuous gradient of soil water content is achieved in a direction perpendicular to the direction of the sprinkler line.

Five accessions {Newana, Fortuna, MT 7819 (Glenmann), MT 7836, and MT 8182)} of spring wheat (<u>Triticum aestivum</u> L.) were planted on May 15, 1986 in plots of 3.66 x 3.66m with a 30cm spacing between the rows.

The accessions were randomized within four replications with rows running perpendicular to the sprinkler line. Thus, each replication was split into two equal halves by the sprinkler line with irrigation treatments being high, medium, low and "dry", progressing away from the sprinkler line.

At the emergence stage of the plants, polyvinyl chloride (PVC) pipes were installed to a depth of about 2m for use as access tubes for neutron probe measurements of soil moisture. Also, a catch cup was installed in the center of each plot about 60cm above the ground on a wire frame to provide a means of measuring the amount of irrigation water applied on each plot.

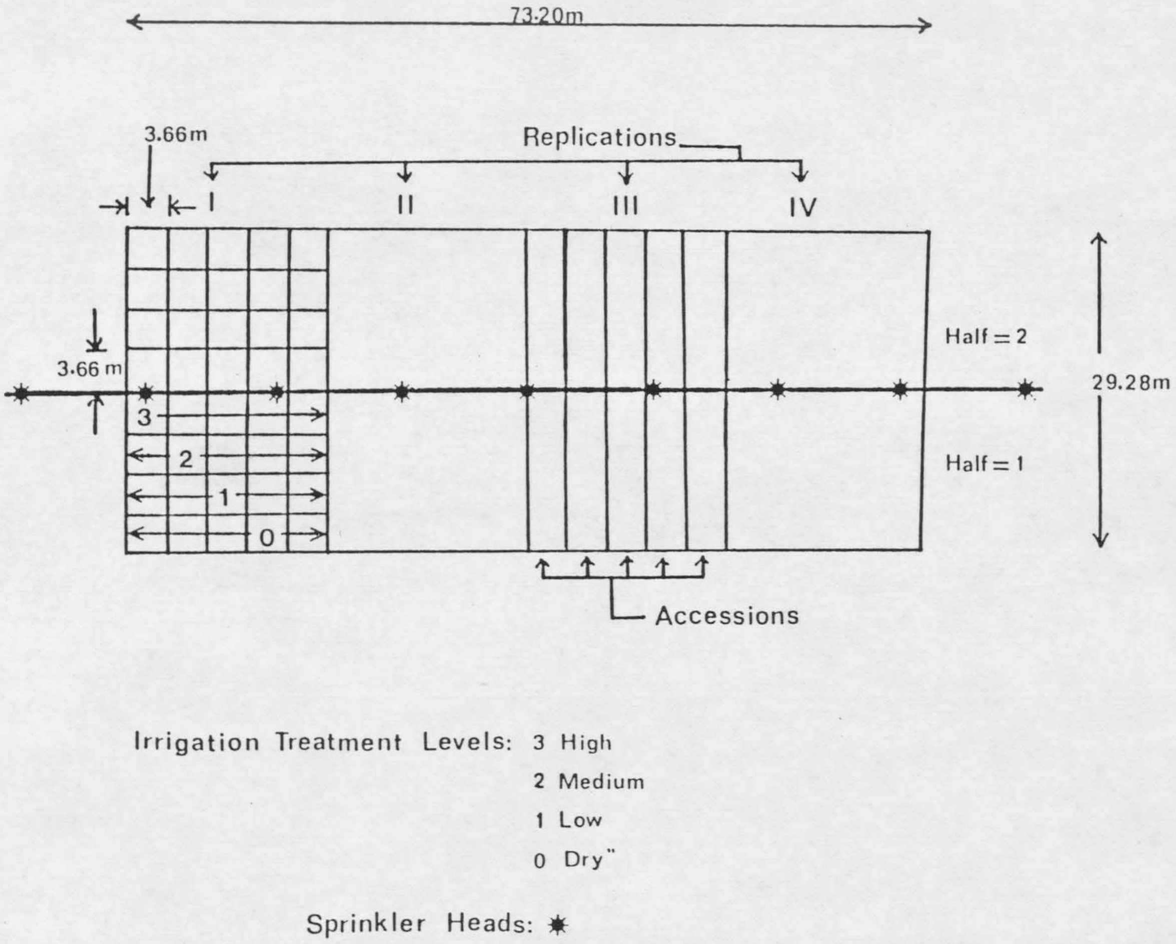

Figure 1. Experimental Layout.

The plots were irrigated on the 28th, 42nd and 82nd days after planting. The amounts of irrigation water applied on the different days and on each of the irrigation treatment levels is as shown in Figure 2. The plots were harvested at different dates, depending on how early the crop matured, beginning 110 days and ending 132 days after planting.

Measurement of Soil Moisture Content and Evapotranspiration

Soil moisture content determinations were made at 20cm intervals from a depth of 20cm to 140cm using a Campbell neutron probe. Days of moisture content measurements and irrigation events are as shown in Table 1. Using a previously constructed calibration curve, the neutron probe readings were converted to cm of water per cm of soil depth. The profile soil moisture content was obtained by summing the soil moisture content for each depth.

Table 1: Soil Moisture Content Measurements and Irrigation Events.

Days After Planting	Soil Moisture Content Measurement	Irrigation Event
18	Y	N
26	Y	N
28	N	Y
29	Y	N
40	Y	N
42	N	Y
44	Y	N
58	Y	N
74	Y	N
79	Y	N
82	N	Y
83	Y	N
88	Y	N
102	Y	N

Y = Yes
N = No

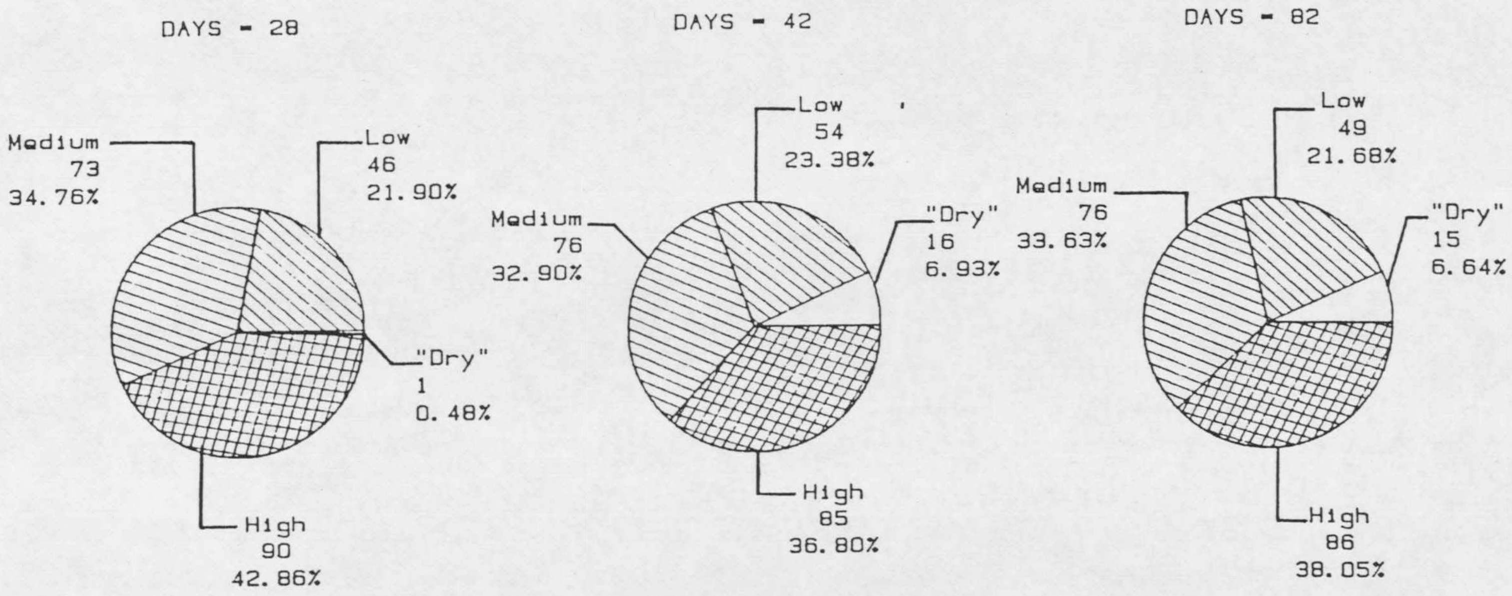

Figure 2. Irrigation water applied (in mm) at different days after planting.

Meteorological parameters used were precipitation and pan evaporation, both of which were recorded on a daily basis. For pan evaporation measurements, data obtained from two pans placed within the experiment were averaged to obtain a daily value.

The evapotranspiration from each plot between successive soil moisture content measurements was calculated using the following water balance formula:

$$E_t = I + P - D \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (8)$$

where:

E_t = evapotranspiration (mm)

I = amount of irrigation water applied (mm)

P = amount of precipitation (mm)

D = change in soil moisture between successive neutron probe measurements (mm).

Measurement of Plant Drought Stress Parameters

The plant drought stress parameters were measured from the 54th to the 93rd day after planting; after the attainment of practically full canopy. All parameter measurements on the plants were done between 1200 and 1600 hours (Mountain Daylight Time) to ensure maximum drought stress on the plants.

Irrigation applications were made on the 42nd and 82nd day after planting, allowing the monitoring of the parameters within both a drying and wetting cycle. The plant drought stress parameters measured were: leaf water potential, canopy temperature, canopy-air temperature difference, stomatal mass flow resistance, and leaf relative water content.

Leaf Water Potential

Plant leaf water potentials (LWP) were measured using the pressure chamber method (Scholander et al., 1965) using the flag leaf of the plant to avoid the disruptive effect of leaf aging on LWP (Millar et al., 1970).

Leaf Relative Water Content

Leaf relative water content (RWC) was determined on the flag leaf obtained for the LWP measurement. The method used for the determination of RWC was a modified version of that proposed by Stocker (1928). After determining LWP, the flag leaf was weighed and then placed in a test tube three quarters filled with distilled water. The test tube rack was then covered with a plastic sheet to prevent the drying of the exposed parts of the leaves. The leaves were left in the water to saturate overnight and then saturated weights measured.

The leaves were then oven-dried to a constant weight and RWC was then calculated according to the formula (Catsky, 1974):

$$\mathrm{RWC}(\%) = \frac{\text{Field Weight} - \text{Dry Weight}}{\text{Saturated Weight} - \text{Dry Weight}} \times 100 \qquad (9)$$

Stomatal Mass Flow Resistance

The stomatal mass flow resistances (SMFR) were measured (again, using flag leaves) using a porometer designed by Shimshi (1977). The porometer is essentially a portable version of that developed by Gregory and Pierce (1934).

Porometer readings which were in mm Hg were converted to stomatal conductances by using the calibration equations (Brown, 1987):

$$C_s = 117.7 - 0.8672*M_m + 0.001394*M_m^2 \text{ .... } (10)$$

when

$102 \leq M_m \leq 200$; and:

$$C_s = 295.5 - 4.936*M_m + 0.02419*M_m^2 \text{ .... } (11)$$

when

$M_m < 102$;

where:

C_s = stomatal conductance (cm sec^{-1})

M_m = porometer reading (mm Hg)

From the C_s values obtained, the SMFR (r_{mf}) were computed using the inverse relationship:

$$r_{mf} = \frac{1}{C_s} \text{ .... } (12)$$

Given the complications in relating r_{mf} to r_s pointed out earlier, the r_{mf} values obtained were not converted to r_s values. In addition, since the objective of the experiment was more toward using r_{mf} as an <u>index</u> of drought stress than measuring transpirational activity, the values obtained were used for the statistical analyses carried out.

Canopy Temperature and Canopy-Air Temperature Difference

Crop canopy temperatures (T_c) and canopy-air temperature differences (T_c-T_a) were measured using a hand-held infra-red thermometer with a 3° field of view and an 8-14 μm spectral band-pass filter. For the measurement of T_c, the thermometer was pointed obliquely to the crop canopy to avoid interference by exposed ground surface, and direct solar radiation (Singh and Kanemasu, 1983; Chandhuri et al., 1986). The emmisivity setting used for all canopy temperature measurements was 0.98 (Gates, 1964b). No corrections were made for humidity effects due to the short sensor-target distances involved (Lorenz, 1968) or for the sky radiant emittance since the thermometer was operating in the 8-14 μm bandwidth (Jackson, 1982).

RESULTS AND DISCUSSION

The data obtained were analyzed using the SAS Software package (SAS Institute Inc., 1982). Analysis of variance was done for soil moisture content, soil moisture depletion, evapotranspiration, and seasonal evapotranspiration. Data on plant water stress parameters were also analyzed using the analysis of variance procedure.

Hanks et al. (1980) have discussed the principles behind the statistical analysis of data obtained from a line source sprinkler experimental design. Because the irrigation treatments were not randomized, there is no valid estimate of error for the irrigation effect. However, the analysis of variance does provide valid error terms for testing the effects of other randomized variables as well as the effects of their interactions with irrigation treatment.

Varieties (factor C) were considered the main plots within each replication (R) and since the irrigation levels increase as the sprinkler line is approached from either side, the two halves of the experiment are mirror images of each other and as such are considered sub-plots (HA). Within these sub-plots, the irrigation treatment levels (T), were considered the sub-subplots. Since measurements were done over time, the weeks after an irrigation (WEEK) or days after planting (DAYS) were introduced as other factors in the analysis.

Regression analyses were also done to find the relationships between the plant water stress parameters and soil moisture content, evapotranspiration (both seasonal and periodic), and soil moisture depletion. Relationships between the plant water stress parameters themselves were also investigated using regression techniques.

Analysis of Variance Results

Soil Moisture Content

Results obtained from the analysis of variance of data on soil moisture content are shown in Table 2.

Table 2: Analysis of variance for soil moisture content (cm).

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE*
R	3	670.514	7.22	
C	4	256.817	2.08	NS
Error (C)	12	371.224		
HA	1	8.828	0.75	NV
C*HA	4	22.705	0.48	NS
Error (HA)	15	176.199		
T	3	8197.627	196.03	NV
C*T	12	152.124	0.91	NS
T*HA	3	71.895	1.72	NV
C*T*HA	12	62.958	0.38	NS
Error (T)	90	1254.533		
DAYS	10	53266.672	5562.14	* *
C*DAYS	40	82.986	2.17	* *
HA*DAYS	10	52.626	5.50	* *
T*DAYS	30	2433.335	84.70	* *
C*T*HA*DAYS	310	297.427	1.00	NS
Error (DAYS)	1200	1149.199		

Note:

* *	implies significance at the 1% level of significance;
*	implies significance at the 5% level of significance;
NS	denotes non-significance;
NV	signifies the non-validity of an F-test.

Cultivar (C) differences are not significant nor are the cultivar by irrigation treatment (C*T), and the (C*T*HA) interactions. Only days after planting (DAYS) and its interactions are significant.

Soil Moisture Depletion

Table 3 shows the analysis of variance results obtained for the depletion of soil moisture between successive neutron probe reading dates.

Table 3: Analysis of variance for soil moisture depletion (cm) between successive soil moisture content measurements.

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	0.844	1.46	
C	4	2.889	3.76	*
Error (c)	12	2.303		
HA	1	0.646	1.95	NV
C*HA	4	0.813	0.61	NS
Error (HA)	15	4.969		
T	3	36.550	56.33	NV
C*T	12	2.318	0.89	NS
T*HA	3	5.278	8.14	NV
C*T*HA	12	3.834	1.48	NS
Error (T)	90	19.465		
DAYS	9	10440.933	859.64	* *
C*DAYS	36	58.904	1.24	NS
HA*DAYS	9	110.599	9.11	* *
T*DAYS	27	2234.686	61.33	* *
C*T*HA*DAYS	279	301.116	0.80	NS
Error (DAYS)	1080	1457.488		

The cultivar factor is significant at the 5 % level and all interaction terms are non-significant except for the T*DAYS, and HA*DAYS terms.

Table 4 shows the results of the Tukeys' highest significant difference (HSD) test for cultivar differences in soil moisture depletion.

Table 4: Tukeys' HSD Test for cultivar differences in soil moisture depletion between successive soil moisture content measurements.

CULTIVAR	MEAN DEPLETION (cm)	GROUPING
MT 8182	1.22	A*
NEWANA	1.18	A B
FORTUNA	1.17	A B
MT 7836	1.11	A B
MT 7819 (Glenmann)	1.10	B

* Cultivars followed by the same letter are not significantly different.

Note:
probability (alpha) = 0.05
degrees of freedom (d.f) = 12
minimum significant difference (msd) = 0.11
mean square error (mse) = 0.19

As can be seen from Table 4, MT 8182 had a mean soil moisture depletion significantly higher than that of MT 7819 (Glenmann). The fact that there are significant cultivar differences in soil moisture depletion, even though there are no significant cultivar differences in soil moisture content is very interesting, primarily because soil moisture depletion is a function of soil moisture content.

Evapotranspiration

Table 5 shows the analysis of variance for the periodic (i.e. between successive soil moisture content measurements) evapotranspiration.

Table 5: Analysis of variance for evapotranspiration (mm)

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	48.011	1.63	
C	4	356.713	9.10	* *
Error (c)	12	117.619		
HA	1	10214.545	162.86	NV
C*HA	4	9.608	0.04	NS
Error (ha)	15	940.801		
T	3	58919.193	855.64	NV
C*T	12	249.233	0.90	NS
T*HA	3	4064.523	59.03	NV
C*T*HA	12	492.210	1.79	NS
Error (t)	90	2065.295		
DAYS	10	3122363.628	4058.50	* *
C*DAYS	40	3961.525	1.29	NS
HA*DAYS	10	140188.067	182.22	* *
T*DAYS	30	112481.194	48.73	* *
C*T*HA*DAYS	310	49731.176	2.09	* *
Error (D)	1200	92320.772		

Cultivar differences in evapotranspiration are highly significant. Also highly significant are the interaction terms HA*DAYS, T*DAYS, and C*T*HA*DAYS. Table 6 shows the results of the Tukeys' HSD test for cultivar differences in evapotranspiration. The cultivars Newana and MT 8182 have higher evapotranspiration than MT 7836 and MT 7819 (Glenmann).

Seasonal Evapotranspiration

The analysis of variance for the seasonal evapotranspiration data is shown in Table 7.

Table 6: Tukeys' HSD Test for cultivar differences in evapotranspiration.

CULTIVAR	MEAN EVAPOTRANSPIRATION (mm)	GROUPING
NEWANA	37.96	A
MT 8182	37.91	A
FORTUNA	37.45	A B
MT 7836	36.97	B
MT 7819 (Glenmann)	36.89	B

Note:
alpha = 0.05
d.f = 12
msd = 0.75
mse = 9.80

Table 7: Analysis of variance for seasonal evapotranspiration.

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	590.450	1.51	
C	4	9312.350	17.89	* *
Error (C)	12	1561.300		
HA	1	125104.225	286.37	NV
C*HA	4	232.900	0.13	NS
Error (HA)	15	6552.875		
T	3	1040366.450	1684.86	NV
C*T	12	3775.050	1.53	NS
T*HA	3	44384.425	71.88	NV
C*T*HA	12	2662.700	1.08	NS
Error (T)	90	18524.375		

Cultivar differences in seasonal evapotranspiration is highly significant. However, there are no significant C*HA, C*T, and C*T*HA effects. Results of the Tukeys' HSD means separation procedure for cultivar seasonal evapotranspiration are shown in Table 8.

Newana and MT 8182 had higher seasonal evapotranspiration than MT 7819, Fortuna, and MT 7836.

Table 8: Tukeys' HSD test for cultivar differences in seasonal evapotranspiration.

CULTIVAR	MEAN EVAPOTRANSPIRATION (mm)	GROUPING
NEWANA	456.91	A
MT 8182	456.84	A
MT 7819 (Glenmann)	442.28	B
FORTUNA	441.78	B
MT 7836	440.06	B

Note:

alpha = 0.05
d.f = 12
msd = 9.09
mse = 130.11

Relative Water Content

Results of the analysis of variance for leaf relative water content are tabulated in Table 9:

Table 9: Analysis of variance for leaf relative water content (%).

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	1	189.308	8.29	
C	4	357.804	3.92	NS
Error (C)	4	91.318		
T	3	84.149	1.26	NV
C*T	12	243.290	0.91	NS
Error (T)	15	334.804		
WEEK	1	12.038	0.12	NS
C*WEEK	4	290.871	0.75	NS
T*WEEK	3	88.972	0.31	NS
MODEL ERROR	19	1832.736		

The model Error term was used for the F-test of the C*WEEK and T*WEEK terms due to the fact that the R*C*T*WEEK term had zero degrees of freedom. In any event, these interaction terms turned out to be nonsignificant.

Results obtained from this analysis confirm the insensitivity of RWC as an index of plant moisture stress, as has been pointed out by Hsiao (1973). This is mostly due to variations in leaf water characteristics (including relative water content) which can be caused by changes in meteorological conditions (Yang and de Jong, 1972). Furthermore, given the fact that the RWC values obtained (Appendix 1) were relatively high (greater than 81%), the plants were not that stressed by the moisture regimes maintained for the duration of measurements of RWC.

Canopy Temperature and Canopy-Air Temperature Difference

Table 10 shows the analysis of variance results for the canopy temperature data.

Table 10: Analysis of variance for crop canopy temperature (^{o}C).

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	14.990	0.83	
C	4	18.269	0.76	NS
Error (C)	12	72.076		
HA	1	17.539	6.67	NV
C*HA	4	9.399	0.89	NS
Error (HA)	15	39.443		
T	3	438.089	104.03	NV
C*T	12	5.667	0.34	NS
T*HA	3	248.463	59.00	NV
C*T*HA	12	17.911	1.06	NS
Error (T)	90	126.334		
WEEK	3	2072.812	635.63	* *
C*WEEK	12	4.848	0.37	NS
HA*WEEK	1	283.831	261.11	* *
T*WEEK	6	0.000	0.00	NS
C*T*HA*WEEK	32	0.000	0.00	NS
Error (WEEK)	115	125.007		

The C factor proved to be insignificant, and the only significant interaction term is HA*WEEK.

The analysis of variance for the canopy-air temperature difference (T_c - T_a) is shown in Table 11.

Table 11: Analysis of variance for canopy-air temperature difference (°C).

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	27.199	1.86	
C	4	46.421	3.27	NS
Error (C)	12	58.639		
HA	1	0.123	0.03	NV
C*HA	4	2.847	0.20	NS
Error (HA)	15	54.705		
T	3	147.201	24.41	NV
C*T	12	20.483	0.85	NS
T*HA	3	38.763	6.43	NV
C*T*HA	12	18.830	0.78	NS
Error (T)	90	180.944		
WEEK	3	288.867	47.58	* *
C*WEEK	12	12.713	0.52	NS
HA*WEEK	1	10.823	5.35	*
T*WEEK	6	92.267	7.60	* *
C*T*HA*WEEK	32	48.597	0.75	NS
Error (WEEK)	115	132.750		

Again, there is no significant C effect, though there are very significant effects due to the WEEK term, and T*WEEK interaction term. The HA*WEEK interaction term is significant albeit only at the 5% level. All other terms are not significant.

Also, the significance of the interaction terms involving the WEEK factor point to the importance of the time lag between the measurement of T_c and (T_c - T_a). This is supported by the results obtained by Pinter, and Reginato (1982). Their research indicated that the parameter, crop water stress index (CWSI), which is based on (T_c - T_a), and hence, T_c, falls to a minimum value following an irrigation, and rises slowly again as the crop exhausts its supply of water.

The fact that there were no significant cultivar differences in canopy temperature-based drought stress parameters, as indicated in Tables 10 and 11 could also be due to the lack of significant differences in the soil water content of the irrigation treatments. Hatfield et al. (1984) have found T_c to be a useful indicator of crop water stress in cotton so it should not be unreasonable to expect cultivar differences in T_c and (T_c - T_a) under conditions of adequate moisture stress. Indeed, Blum et al. (1978) and Blum (1975) have used infra-red photography to successfully detect genotype-caused differences in sorghum drought tolerance.

Stomatal Mass Flow Resistance

Analysis of variance of stomatal mass flow resistance (SMFR) is shown in Table 12. Except for WEEK, all the main effects and interaction terms that can be validly tested are insignificant. These results are not surprising. Appendix 1 shows the mean SMFR for different cultivars at each irrigation treatment level. The resistances are all very low, even for the "dry" irrigation treatment levels. This implies that the stomata of the plants were open most of the time, indicating unstressed conditions. This, more than anything, explains why all the resistances obtained were below 1.0 sec cm^{-1}.

The effect of mild water stress on SMFR is probably mediated by other plant water stress parameters, like RWC, LWP, and T_c. As pointed out earlier, measured RWC values were relatively high, and T_c mean values obtained (Appendix 1) were relatively low. In fact, mean canopy

Table 12: Analysis of variance for stomatal mass flow resistance (sec cm^{-1}).

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	0.184	5.35	
C	4	0.005	0.10	NS
Error (C)	12	0.137		
HA	1	0.193	26.76	NV
C*HA	4	0.004	0.15	NS
Error (HA)	15	0.108		
T	3	0.375	19.34	NV
C*T	12	0.055	0.70	NS
T*HA	3	0.325	16.72	NV
C*T*HA	12	0.096	1.24	NS
Error (T)	90	0.583		
WEEK	3	1.433	47.89	* *
C*WEEK	12	0.101	0.84	NS
HA*WEEK	1	0.000	0.00	NS
T*WEEK	8	0.000	0.00	NS
C*T*HA*WEEK	40	0.164	0.41	NS
Error (WEEK)	75	0.748		

temperatures for all the cultivars and treatments were less than air temperature with (T_c-T_a) ranging from -4.7 to -2.1°C. This indicates significant transpirational activity (Gates, 1964; Wiegland and Namken, 1966).

Leaf Water Potential

Table 13 shows the results of the analysis of variance on the data for the plant leaf water potentials.

There were significant ($p = 0.05$) differences in accession leaf water potential. Other significant terms were the WEEK and the C*T*HA effects. Results of the Tukeys' HSD test for cultivar differences in LWP are as shown in Table 14.

Table 13: Analysis of variance for Leaf Water Potential (MPa):

SOURCE	D.F.	SUM OF SQUARES	F-VALUE	SIGNIFICANCE
R	3	6.183	22.59	
C	4	1.561	4.28	*
Error (C)	12	1.095		
HA	1	0.906	13.36	NV
C*HA	4	0.253	0.93	NS
Error (HA)	15	1.018		
T	3	1.675	8.42	NV
C*T	12	1.252	1.57	NS
T*HA	3	0.365	1.84	NS
C*T*HA	12	1.956	2.46	* *
Error (T)	90	5.964		
WEEK	4	5.218	3.01	*
C*WEEK	16	3.164	0.46	NS
T*WEEK	11	2.147	0.45	NS
C*T*HA*WEEK	25	6.437	0.59	NS
Error (WEEK)	35	15.162		

Table 14: Tukeys' HSD Test for cultivar differences absolute values of leaf water potential (MPa):

CULTIVAR	MEAN LWP	GROUPING	
MT 8182	1.76	A	
FORTUNA	1.64	A	B
MT 7819 (Glenmann)	1.63	A	B
MT 7836	1.60	A	B
NEWANA	1.55		B

Note:

alpha = 0.05
d.f = 12
msd = 0.17
mse = 0.09

MT 8182 had a mean LWP (-1.76 MPa) significantly lower than that of Newana (-1.55 MPa). This is not explained by the results obtained from the analysis of, for example, the accession differences in seasonal evapotranspiration (Table 8). From Table 8, it is seen that there are no significant differences between these accessions in their seasonal evapotranspiration means.

Relationships Between the Plant Drought Stress Parameters

The means of the plant drought stress parameters by accessions for each irrigation treatment are shown in Table 16. These values were used to carry out regressions on the parameters to find out relationships between them.

Stomatal Mass Flow Resistance and Leaf Relative Water Content

In plants not suffering from any drought stress, stomatal aperture is determined by illumination. However, once water supply to the plant becomes limited, stomatal aperture is determined by the degree of leaf water deficit developed in the plant tissue (Ehrler and van Bavel, 1967; Slatyer, 1967).

Consequently, the SMFR of plant leaves should be expected to be reduced with decreasing RWC, all things being equal. However, the relationship is not that simple, since most investigations (Hsiao, 1973) show a threshold value of RWC above which stomatal opening is constant.

Figure 3 shows a plot of SMFR versus RWC. No equation was fitted to the points but it is reasonable to conclude, on the basis of a visual inspection of the points, that there is a trend indicating a decrease in SMFR with an increase in RWC.

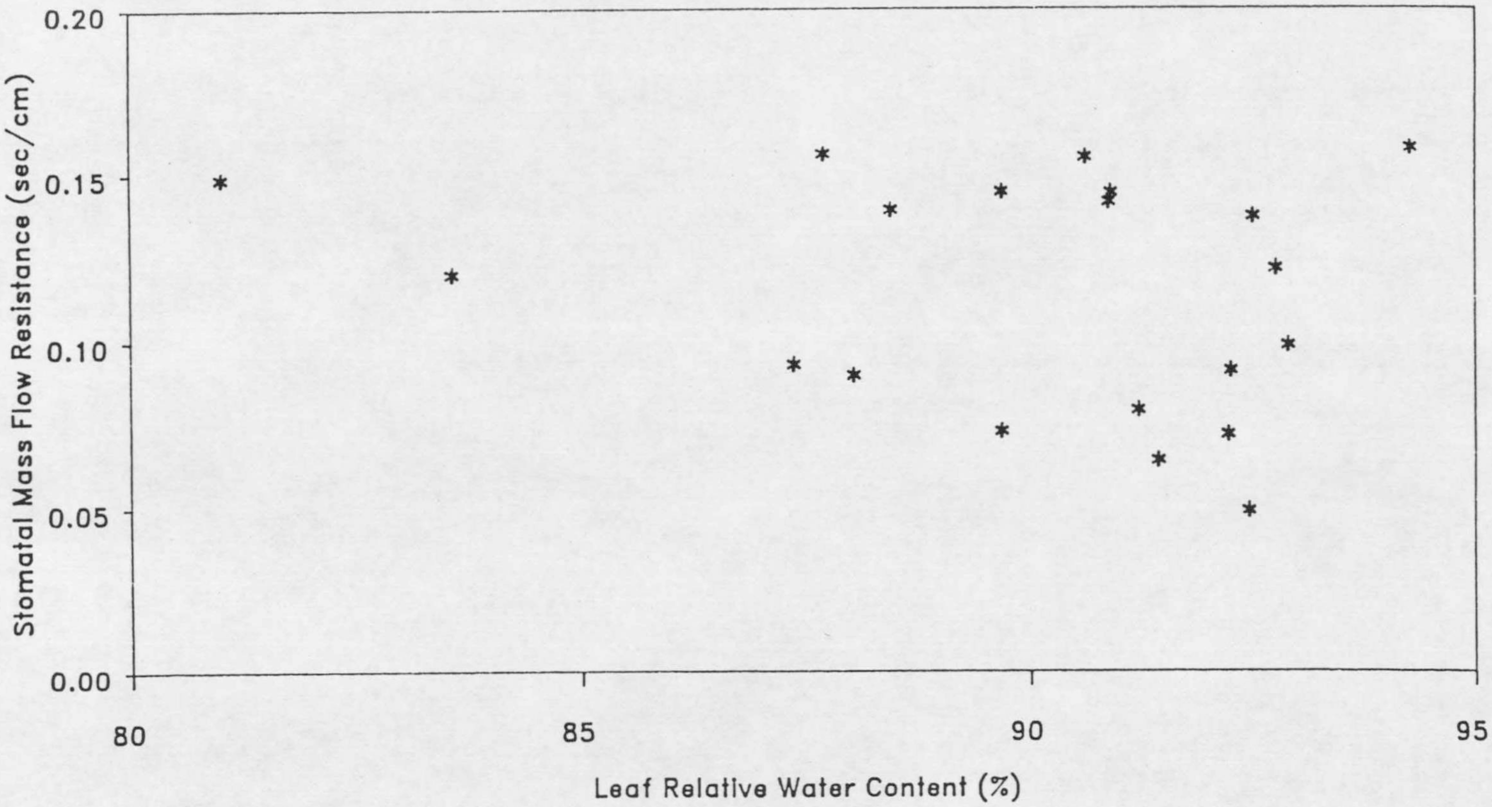

Figure 3. Plot of Stomatal Mass Flow Resistance versus Leaf Relative Water Content.

Canopy Temperature and Leaf Relative Water Content

Figure 4 shows a plot of T_c versus RWC, with no equation fitted to the points. Despite a lack of a fitted line, there is a trend in the points showing a decrease in T_c caused by increasing RWC. This is as expected since Weigland and Namken (1966) reported a 3.6°C increase in cotton leaf temperature when relative turgidity decreased from 83 to 59%.

Canopy Temperature and Stomatal Mass Flow Resistance

Canopy temperature depends to a large extent on transpiration rate. This is due to the large latent heat of vaporization of water. Thus, for a given set of conditions, canopy temperature should decrease proportionately to the increase in transpiration (Martin, 1943). Since transpiration rate is directly proportional to stomatal aperture, it is to be expected that canopy temperature should be related to stomatal aperture.

This is clearly indicated in Fig. 5, which shows a plot of canopy temperature versus stomatal mass flow resistance. When SMFR increases from 0.10 to 0.15 sec/cm, canopy temperature increases from 22.3 to 23.7°C. The intercept of the plot is at 19.5°C which indicates the temperature of the canopy under conditions of full stomatal opening and, by implication, no water stress. This is not necessarily a stable condition and most probably T_c, under conditions of no water stress, will be significantly dependent on environmental factors, e.g. solar radiation (Weigland and Namken, 1966).

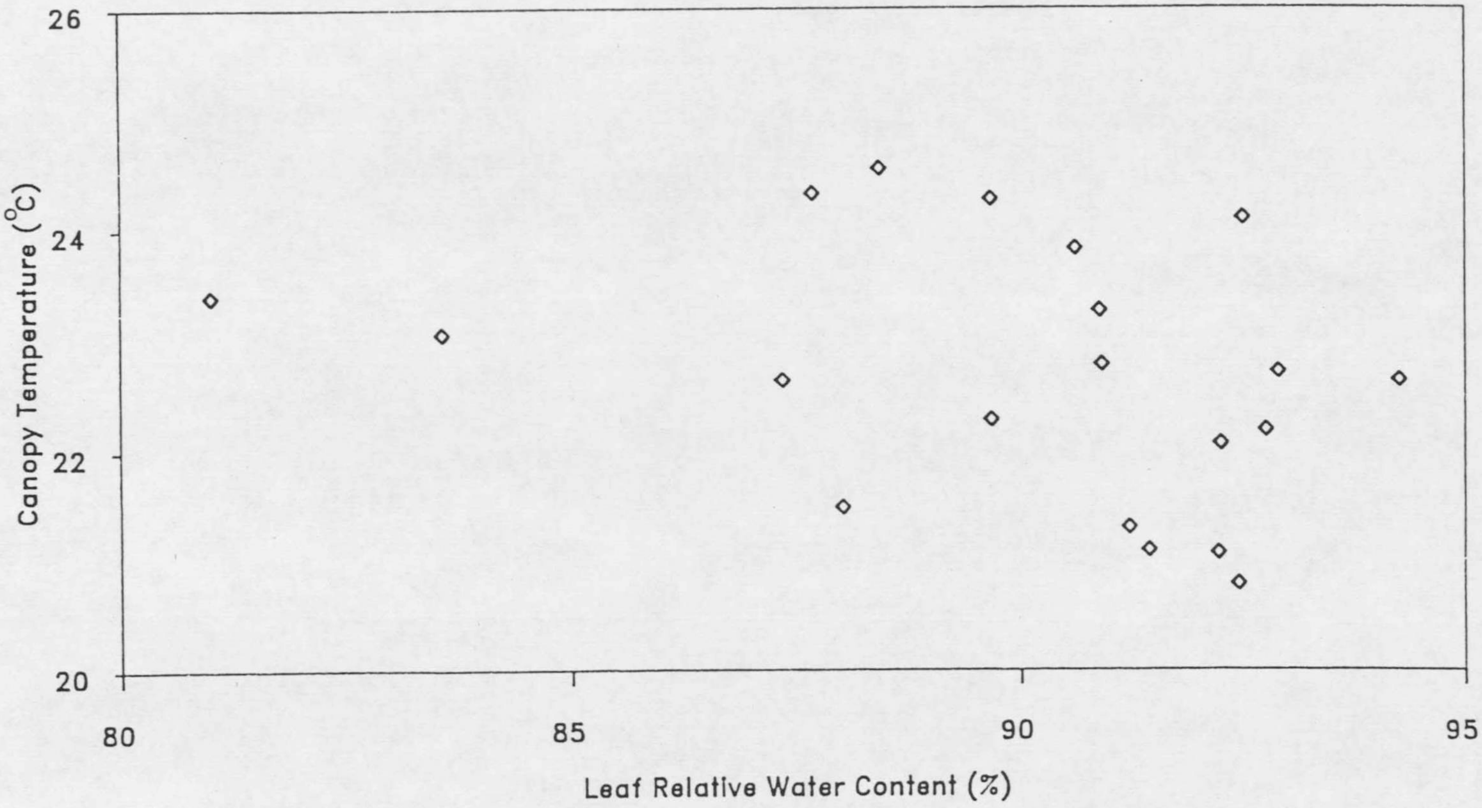

Figure 4. Plot of Canopy Temperature versus Leaf Relative Water Content.

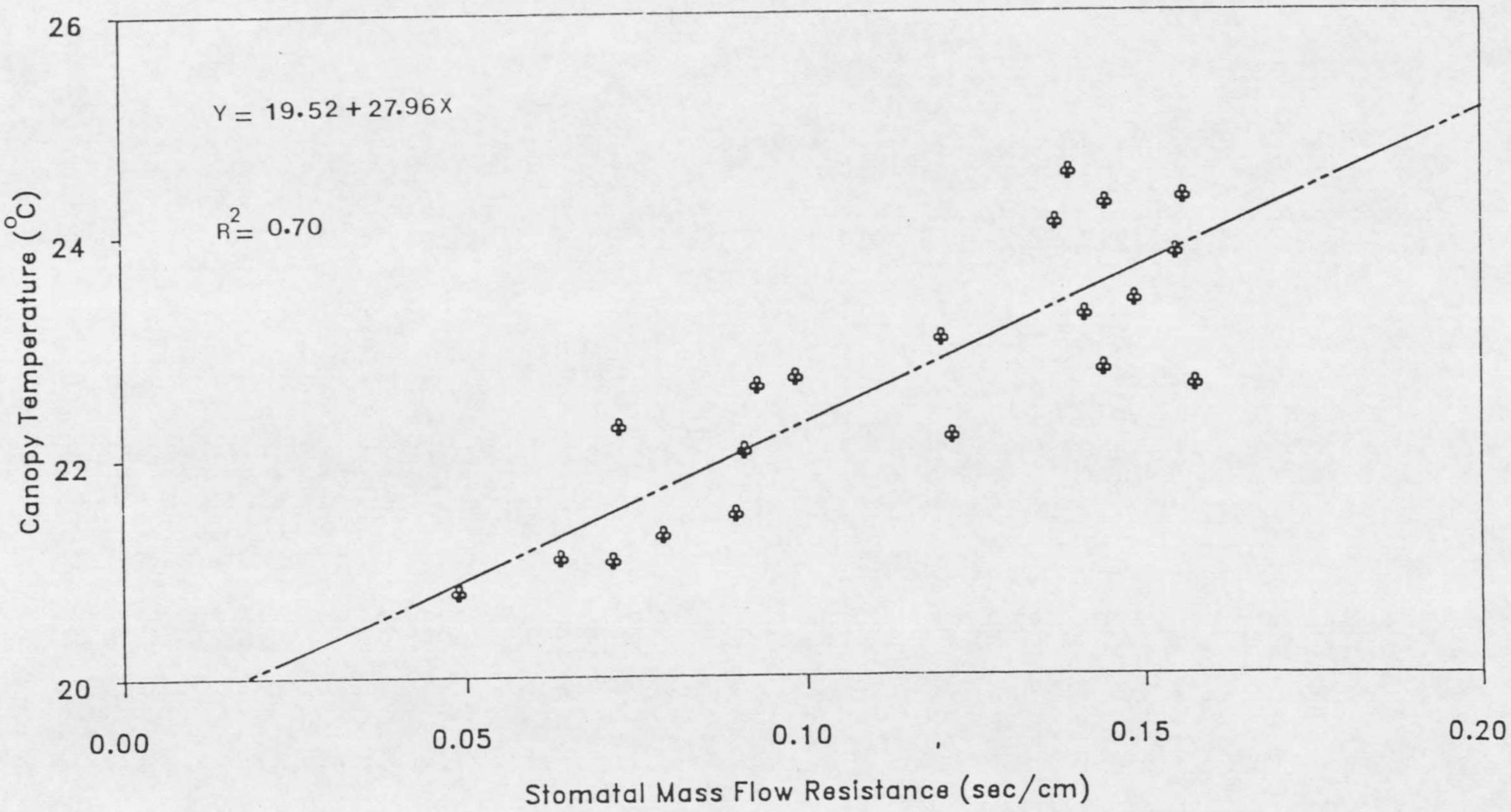

Figure 5. Plot of Canopy Temperature versus Stomatal Mass Flow Resistance.

Canopy-Air Temperature Difference and Canopy Temperature

The cubic plot of T_c-T_a versus T_c is as shown in Fig. 6. Even though the model fitted has a high correlation coefficient of 0.99 (R^2, — adjusted for the degrees of freedom), and the curve fits the points relatively well, as indicated by a coefficient of variation of - 10.3%.

Figure 6 has a point of inflection at a canopy temperature of about 22°C and a (T_c-T_a) value of - 4.3°C. Beyond a canopy temperature of 22°C, (T_c-T_a) increases with increasing T_c indicating a decrease in transpiration rate caused by stomatal closure (Ehrler, 1973). The decrease in (T_c-T_a) with increasing T_c below a T_c of 22°C could probably be due to the fact that (T_c-T_a) is influenced more by environmental factors than by transpiration rate (and hence, T_c) under conditions of low moisture stress.

Fluctuations of the Drought Stress Parameters

One unfortunate aspect of the experiment was that, due to the lack of manpower and time, most of the plant drought stress parameters could not measured simultaneously. Consequently, meaningful regressions could not be obtained for, say, SMFR versus LWP, RWC versus LWP, and T_c versus LWP. To skirt this problem, plots of the parameter means at different days after planting (Table 17) were constructed, as shown in Figs. 7 through 9.

Figure 7 shows a plot of LWP and SMFR versus the days after planting. Since there were irrigations on the 42nd and 82nd days, the plot shows the LWP changes within both a drying and wetting cycle. As can be seen from the plot, LWP fluctuates during the drying cycle (i.e between the 42nd and 82nd days), and this is without doubt due to

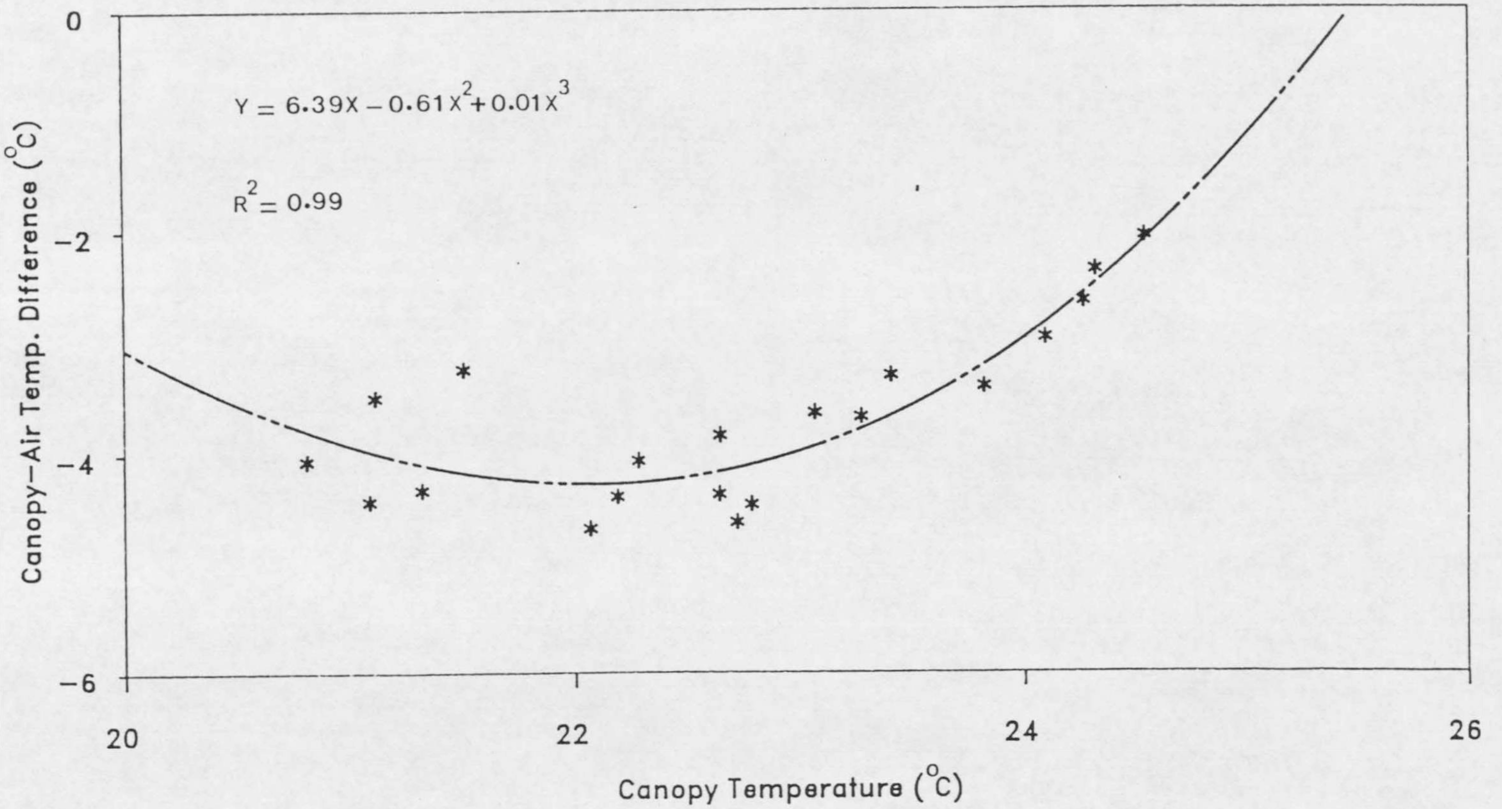

Figure 6. Cubic plot of Canopy-Air Temperature Difference versus Canopy Temperature.

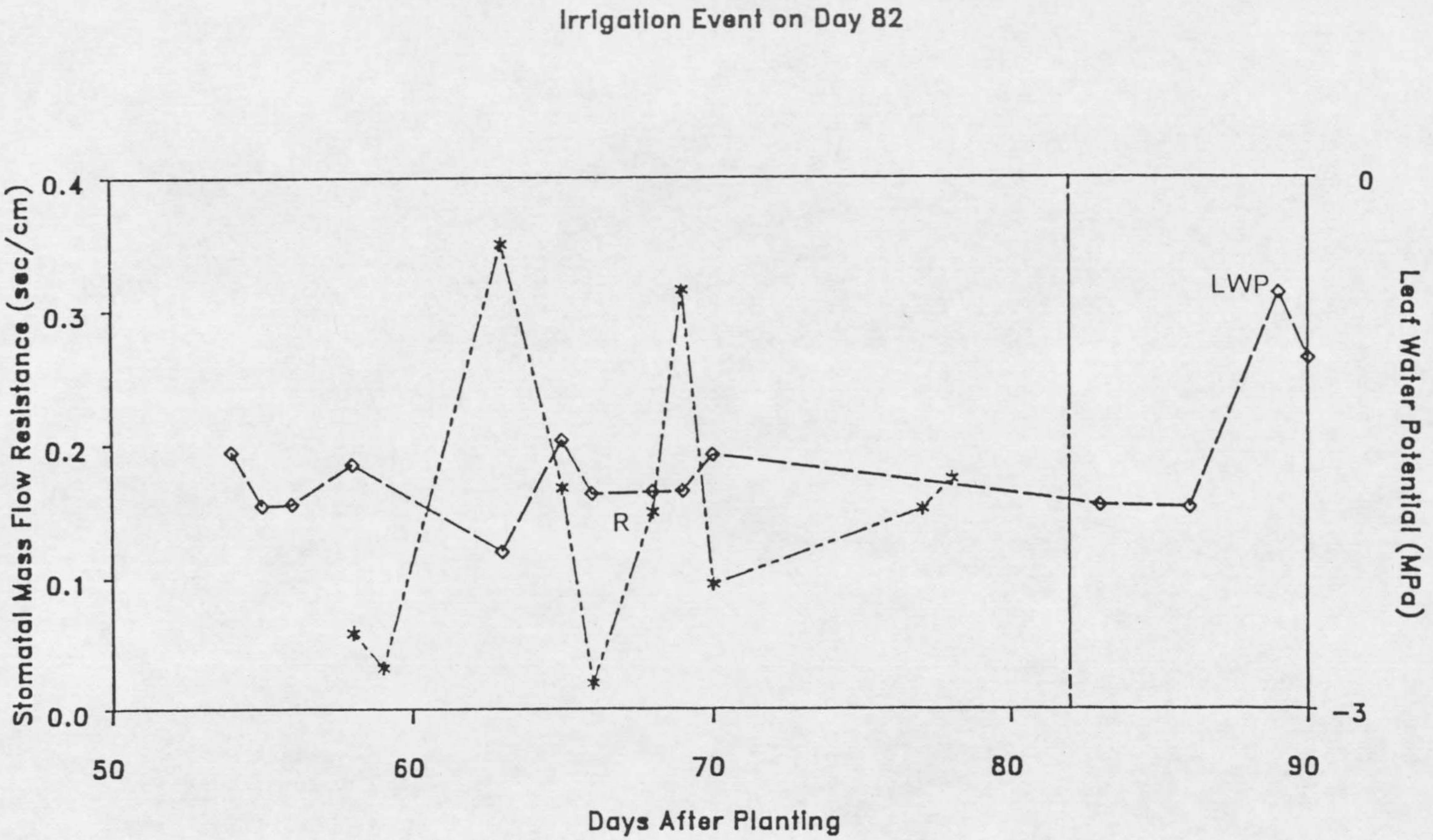

Figure 7. Plot of Stomatal Mass Flow and Leaf Water Potential Resistance at different days after planting.

extraneous events affecting soil moisture content, namely, precipitation. Worth noting is the fact that after an irrigation on the 82nd day, the LWP takes about 6 days to respond to the increase in moisture supply. This probably has more to do with the soil moisture-transport characteristics than any plant factor.

The stomatal mass flow resistances shown in Fig. 7 fluctuate even more than LWP. In addition to the precipitation factor, SMFR is also dependent on a gamut of environmental factors which act both singly and in concert. For this reason, changes in SMFR are hard to relate to soil moisture content alone. Furthermore, SMFR readings were not taken after the 78th day and as such, nothing can be said about its response to an irrigation.

Figure 8 shows the plots of the means of canopy temperature (T_c) and the canopy-air temperature difference (T_c-T_a) on different days after planting. Both curves show some relative stability between the 59th and 76th days. This is probably due more to the lack of data points between these days than to an expression of physical reality. This is indicated by the almost abrupt increase in T_c between the 76th and the 78th days.

Between the 59th and the 76th days, both curves have a slight positive slope indicating an increase in T_c with the drying of the soil profile (Figure 10). It is noteworthy that the (T_c-T_a) is shown to be increasing with increasing T_c.

Both canopy temperature and its difference from air temperature decreased after the irrigation on the 82nd day. However, the rate of decline of the parameters is not the same; canopy temperature declining

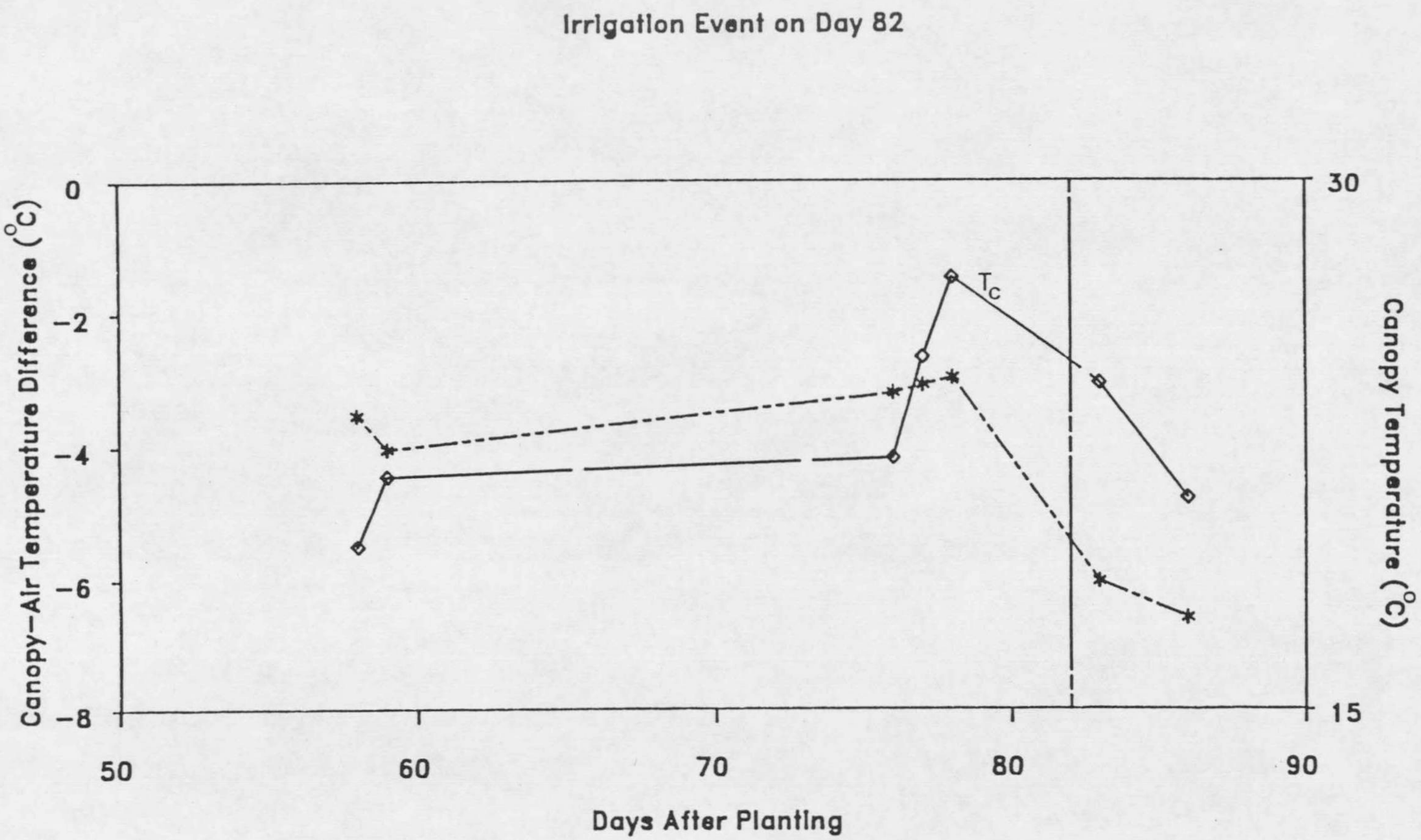

Figure 8. Canopy-Air Temperature Difference and Canopy Temperature at different days after planting.

at a faster rate than the canopy-air temperature difference. This suggests that in this case at least, the canopy-air temperature difference is not solely dependent on the canopy temperature.

Plots of the leaf RWC and LWP at different days after planting are as shown in Fig. 9. RWC was measured only within the period of 63 and 70 days after planting. The mean values obtained were variable, and further, changes in these values roughly reflect changes in LWP. For example, when RWC decreases from 91.7% on the 65th day to 78.8% on the 68th day, LWP decreased from -1.40 MPa to -1.77 MPa. When RWC increases from 78.8 to 90.6 % between the 68th and 70th days, LWP increases from -1.77 to -1.57 MPa.

These small changes in LWP in conjunction with large changes in RWC are in line with the conclusions of Hsiao (1973) since with nearly saturated tissue (as indicated by high RWC values), a small change in water content can significantly affect ψ_p (the pressure component of LWP).

Since soil moisture content was not measured simultaneously with the plant drought stress parameters, no regressions could be done to determine the relationships between soil moisture content and these parameters. However, as is shown in Figures 10 and 11 some of these parameters change in a manner roughly dependent on changes in soil moisture content.

Thus, from Fig. 10, which shows the soil moisture content and canopy temperature at different days after planting, it can be seen that as soil moisture content decreases from 20.8 to 18.6 cm from the 74th to the 79th day, canopy temperature increases from 22.1°C on the

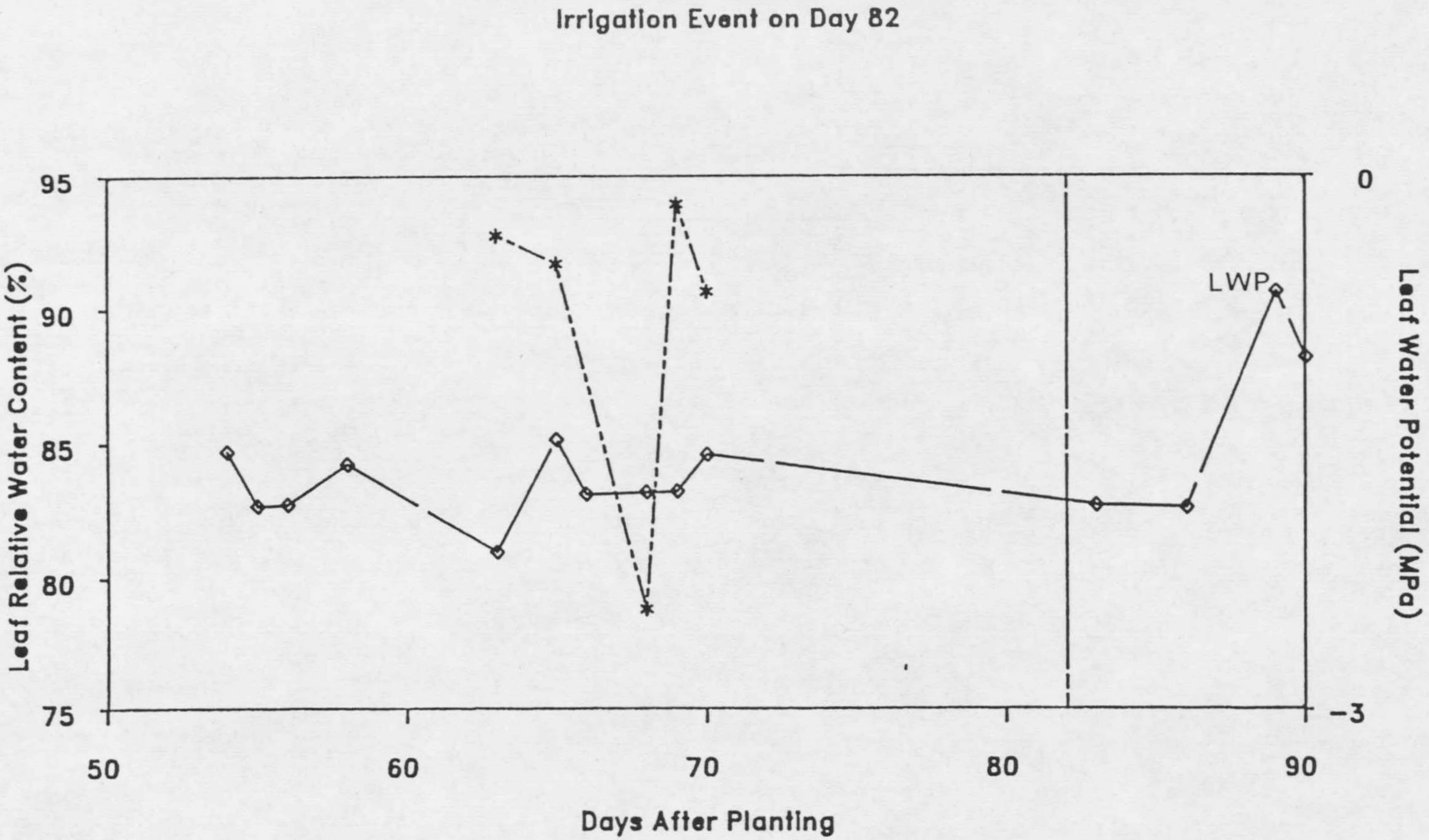

Figure 9. Leaf Relative Water Content and Leaf Water Potential at different days after planting.

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