



A screening technique for evaluating drought resistance of barley (*Hordeum vulgare* L.) lines
by Mohammad Abdul Martin

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in
Crop and Soil Science
Montana State University
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Abstract:

Barley is the world's fourth most important cereal crop after wheat, maize and rice. Much of the world's barley is produced in regions with climates unfavorable for production of other major cereals. It has persisted as a major cereal crop through so many centuries because of broad ecological adaptation; it is valued as a feed and food grain.

In many arid and semi-arid regions, drought is the most important environmental stress limiting production. In such areas maximum economic production per unit of applied water is essential. In this study, drought-resistant and drought-susceptible barley lines have been examined with the objective of evaluating parameters that may be indicators of drought tolerance under limited water supply.

Four cultivars of barley were grown in the field experiment during 1982. Line source irrigation was used to control the moisture gradient. Diurnal determinations of leaf water, osmotic and turgor potentials were made at early heading, late heading and flowering growth stages. Results indicate susceptible cultivars developed greater internal water stress compared to resistant lines. A series of greenhouse studies was carried out during 1984 and 1985 to observe the behavior of root osmotic, leaf water, leaf osmotic and leaf turgor potentials under watering and subsequent drying cycles on three-week-old plants. Resistant cultivars consistently developed higher potentials and quick recovery after watering. Susceptible cultivars reached zero turgor at least one day earlier than resistant ones.

Upon analyses of the results of 1982, 1984 and 1985, an intensive greenhouse study was conducted during 1986 on three-week-old plants using ten two-rowed and ten six-rowed barley lines chosen on the basis of resistance or susceptibility to drought. Predawn leaf water potential, relative water content (RWC) and morning and afternoon stomatal diffusion resistance were measured. Predawn leaf total water potential and RWC under stress differentiated resistant cultivars from susceptible ones. These data suggest that the internal water status measurements may be useful selection tools in developing drought-resistant varieties.

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OF BARLEY (HORDEUM VULGARE L.) LINES

by
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A thesis submitted in partial fulfillment
of the requirements for the degree

of
Doctor of Philosophy
in
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APPROVAL

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This thesis has been read by each member of the author's graduate 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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*Dedicated to my wife, Shamsun Naher Matin (Hena),
our son, Mahedi, our parents, our brothers and
sisters whose wishes are fulfilled and who share
their happiness with me.*

VITA

The author, Mohammad Abdul Matin, is the son of Mohammad Seraj Miah Molla and Zubeda Khaton. He was born on February 16, 1952, in Comilla, Bangladesh. He received his elementary and secondary education in his home town of Homna. In 1973, he obtained his B. Sc. Ag. degree, with honors, from Bangladesh Agricultural University, Mymensingh. He earned his M. Sc. Ag. (Soil Fertility) degree in soil science from Bangladesh Agricultural University, Mymensingh, Bangladesh, in 1976.

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ABSTRACT

Barley is the world's fourth most important cereal crop after wheat, maize and rice. Much of the world's barley is produced in regions with climates unfavorable for production of other major cereals. It has persisted as a major cereal crop through so many centuries because of broad ecological adaptation; it is valued as a feed and food grain.

In many arid and semi-arid regions, drought is the most important environmental stress limiting production. In such areas maximum economic production per unit of applied water is essential. In this study, drought-resistant and drought-susceptible barley lines have been examined with the objective of evaluating parameters that may be indicators of drought tolerance under limited water supply.

Four cultivars of barley were grown in the field experiment during 1982. Line source irrigation was used to control the moisture gradient. Diurnal determinations of leaf water, osmotic and turgor potentials were made at early heading, late heading and flowering growth stages. Results indicate susceptible cultivars developed greater internal water stress compared to resistant lines. A series of greenhouse studies was carried out during 1984 and 1985 to observe the behavior of root osmotic, leaf water, leaf osmotic and leaf turgor potentials under watering and subsequent drying cycles on three-week-old plants. Resistant cultivars consistently developed higher potentials and quick recovery after watering. Susceptible cultivars reached zero turgor at least one day earlier than resistant ones.

Upon analyses of the results of 1982, 1984 and 1985, an intensive greenhouse study was conducted during 1986 on three-week-old plants using ten two-rowed and ten six-rowed barley lines chosen on the basis of resistance or susceptibility to drought. Predawn leaf water potential, relative water content (RWC) and morning and afternoon stomatal diffusion resistance were measured. Predawn leaf total water potential and RWC under stress differentiated resistant cultivars from susceptible ones. These data suggest that the internal water status measurements may be useful selection tools in developing drought-resistant varieties.

CHAPTER 1

INTRODUCTION

Barley (Hordeum vulgare L.) is the world's fourth most important cereal crop after wheat, maize and rice. Much of the world's barley is produced in regions with climates unfavorable for production of other major cereals. Barley originated in the Eastern Mediterranean area. It has persisted as a major cereal crop through so many centuries because of broad ecological adaptation.

Water is a particularly critical part of the plant environment. It is, of course, essential for plant growth, and is used by plants in a number of familiar ways: as a chemical substrate for photosynthesis, in transpirational cooling of plant tissue, as a medium for transport of substances within the plant, as the medium for biochemical processes and in the maintenance of turgor.

Hurd (1974) describes most of the arable land of the world as semi-arid and consequently, "lack of moisture is the main limiting factor to increasing production." Chief among the climatic limitations is the water shortage. Drought is at least a periodic, if not common, occurrence over most of the agricultural areas on earth.

Drought stress commonly affects plant growth and development. In crop plants, this stress can reduce yield, particularly if the stress occurs near anthesis when reproductive structures can be damaged. A successful effort to improve the drought resistance of barley by plant

breeding techniques requires both selection criteria and a reliable screening procedure to verify the presence of variation for the traits.

Screening for yielding ability under drought is an obvious procedure in breeding for barley drought resistance. Screening for yielding ability is a labor-intensive and time-consuming method. Also, by simply measuring grain yield, the selection of desirable physiological components can be overlooked. The incorporation of desirable traits such as drought tolerance or avoidance (Levitt, 1980) into cultivars requires indexes which directly reflect those traits. Therefore, it may be valuable to screen material under laboratory conditions using seedlings as test material. The success of this approach requires evidence that the performance of barley seedlings adequately reflects the performance of the mature plant when subjected to drought stress. Such information relative to this species is limited.

A one-year study was conducted in the field under differential soil moisture deficits and then several intensive greenhouse experiments were carried out under induced water stress. The objectives of this research were: (1) to compare several plant water status measurements on barley cultivars known to differ in drought tolerance during development of water stress and (2) if differences in (1) existed, to develop rapid screening techniques for potential drought tolerance of barley using seedlings.

CHAPTER 2

LITERATURE REVIEW

Leaf Total Water Potential as a Screening
Procedure for Drought Resistance

A decrease in leaf total water potential (Ψ_{TL}) because of high evaporative demand or decreased soil water availability results in a reduction of photosynthetic activity and growth of plants (Acevedo et al., 1971; Boyer, 1968; Watts, 1974; Bunce, 1977). Drought tolerant plants are apparently able to continue photosynthesizing at relatively low Ψ_{TL} (Beedle et al., 1973; Sullivan and Eastin, 1974). They found higher photosynthetic rates in sorghum (a drought-resistant crop) compared to maize (a drought-susceptible crop) both in the greenhouse and field studies at the same soil moisture deficit.

Levitt (1972) describes the ability of a plant to maintain relatively high Ψ_{TL} (closer to zero) as a drought avoidance mechanism (see Figure 13, Appendix B). Sammons et al. (1978) conducted a greenhouse experiment under differential soil moisture deficit and measured Ψ_{TL} on 20 soybean cultivars. They separated drought-resistant soybeans on the basis of high Ψ_{TL} .

Components of leaf water potential (Ψ_{TL}) of two contrasting soybeans were determined (Cortes and Sinclair, 1986a) from pressure-volume curves obtained with a pressure chamber. Their data showed that the Ψ_{TL} in the drought-susceptible line was as much as 0.9 MPa (9 bars) lower

than the drought-tolerant cultivar. In their study, maintenance of high turgor was associated with maintenance of high Ψ_{TL} .

Hanson et al. (1977) conducted experiments using two barley cultivars differing in drought susceptibility in the field and greenhouse. They found significant varietal differences in the leaf water potential (Ψ_{TL}). Drought-resistant barley maintained higher Ψ_{TL} than drought-susceptible barley.

In a field experiment, Blum (1974) withheld water from 14 sorghum lines and measured leaf water potential (Ψ_{TL}). He found differences in water potential among the genotypes and concluded that resistant lines maintained higher Ψ_{TL} . Ackerson et al. (1977) conducted an experiment using differential soil moisture stress to compare the differences in the water relations of sorghum and cotton. The magnitude of diurnal change in Ψ_{TL} was greater in cotton than in sorghum at equivalent soil water potentials. They found that early morning and midday Ψ_{TL} in cotton was three to four bars lower than sorghum. They also reported a decrease in Ψ_{TL} between the vegetative and reproductive growth stage.

Quarrie and Jones (1979) found genotypic variations in the Ψ_{TL} of leaves of field-grown spring wheat subjected to water stress. They reported that some cultivars were drought-avoidant as indicated by their relatively high Ψ_{TL} . Jones (1977 and 1979) measured Ψ_{TL} of wheat cultivars in a field experiment by imposing irrigation treatments. He observed cultivars differed significantly in Ψ_{TL} and irrigated plants consistently maintained higher potentials.

Turk et al. (1980) reported that predawn leaf water potential (Ψ_{TL}) of cowpeas was more consistently related to soil water deficits than

afternoon values. Afternoon values of Ψ_{TL} are dependent upon evaporative demand but predawn values of Ψ_{TL} would be influenced much less by variations in evaporative demand. They also observed day-to-day variations with well watered plants that were greater than effects due to soil moisture deficit. They concluded that measurements of Ψ_{TL} might be useful for scheduling irrigation. Working with cowpeas, Shouse et al. (1980) also found that predawn Ψ_{TL} was a better indicator of crop water stress than that of midday as measured by pressure bomb technique. Similar results were reported by Wien et al. (1979) using several cultivars of cowpeas under field conditions at Riverside, California and in Nigeria.

Novero et al. (1985) conducted an experiment using a line source sprinkler system in the field. They measured leaf water potential (Ψ_{TL}) on two contrasting rice (I R 20 and I R 36) cultivars. The more drought-resistant rice (I R 20) cultivar was apparently able to maintain higher Ψ_{TL} and lower canopy temperature because of its superior ability to extract water from the soil profile. Significant differences were detected (O'Toole and Moya, 1978) among rice genotypes by Ψ_{TL} . They were able to identify drought resistant genotypes based on the degree of higher Ψ_{TL} maintenance. Peak et al. (1975) demonstrated differences in dawn and afternoon Ψ_{TL} among three pasture plants. They did not classify the plants as drought-resistant or susceptible on the basis of their Ψ_{TL} data.

Ekanayake et al. (1985) measured midday Ψ_{TL} in 13 rice populations in an effort to select populations for drought resistance in a glasshouse experiment. The Ψ_{TL} ranged from -1.7 to -3.5 MPa and showed

significant variations among the lines. They concluded that drought-resistant cultivars maintained higher Ψ_{TL} ; thus, higher Ψ_{TL} is an indicator of drought avoidance.

Osmotic Potential and Drought Tolerance

It has been known for many years and recent data give confirmation (Turner et al., 1978; Ludlaw, 1980; Morgan, 1980b; Blum, 1974; Hsiao et al., 1976; Turner and Begg, 1977) that water stress results in lowering of the osmotic potential of plants. This decrease in osmotic potential (osmoregulation) is an adaptive response and survival mechanism that helps maintain high or positive turgor and presumably more normal metabolic activity. Osmotic adjustment occurs because of a net increase in concentration of solutes caused by some combination of increase or change in types of solutes and loss of water from cells. Examples are that Cutler et al. (1977) found no change in the concentration of K^+ or other inorganic osmotica associated with changes in osmotic potential but found that changes in soluble carbohydrates (a sum of sucrose, glucose and fructose) and malate did occur. Meyer and Boyer (1972) suggest that import of organics, especially in immature tissue, might be the cause of increased concentration of solutes.

The osmotic potential of plant material is easily measured with the thermocouple psychrometer. However, it must be realized that this measurement has the potential to be in error because of the mixing of apoplastic water with cell sap. The apoplastic water dilutes the symplastic water that contains solutes when membranes are destroyed due to freezing and thawing of plant tissues. Campbell et al. (1979) showed

that this mixing might cause psychrometric determinations to be much higher than actual osmotic potential of tissue. It is possible but difficult to correct for this mixing. Few of the reports in the literature dealing with attempts to use osmotic potential or osmotic adjustment to differentiate between drought-resistant and susceptible plants contain corrections.

Campbell et al. (1979) determined the osmotic potential of leaves ($\Psi_{\pi L}$) from pressure volume curves (a procedure that does not involve apoplastic water mixing with symplastic water) of three winter wheat cultivars grown under moderately high and low soil moisture conditions. Significant cultivar differences were found in $\Psi_{\pi L}$. They also reported that the $\Psi_{\pi L}$ from the drier location was five bars or more lower than the leaves from the moist site.

Kirkham and Smith (1978) found that the osmotic potential of winter wheat cultivars did not differ significantly by cultivar. In their experiment, sufficient rainfall was received so that genotypes did not experience water stress and the turgor pressure was positive. Working with glasshouse-grown plants, Morgan (1977, 1980a) has shown that substantial differences in osmoregulation exist among wheat genotypes selected from widely differing backgrounds.

Yield differences between two sorghum cultivars were correlated with differences in osmoregulation when measured in both glasshouse and field studies (Wright et al., 1983). Jones and Turner (1978) determined the relationship among water potential (Ψ_{TL}), osmotic potential ($\Psi_{\pi L}$), turgor potential (Ψ_{PL}) and relative water content for leaves of sorghum using three different levels of water stress. No significant differences

in osmotic adjustment or tissue water relations were observed between the two cultivars. The $\Psi_{\pi L}$ at full turgor in the control sorghum was -0.7 MPa; stress treatment significantly lowered the $\Psi_{\pi L}$ to -1.6 MPa. As a result of this osmotic adjustment, Ψ_{PL} at a given value of Ψ_{TL} increased to allow physiological processes to continue.

A study of field-grown maize and sorghum by Fereres et al. (1978) has provided an indication of drought-induced seasonal and diurnal osmotic regulation in leaves. This is because of the maintenance of a minimum level of turgor by lowering osmotic potential in leaves such that leaf growth may be sustained despite large fluctuations in leaf water potential.

Osmotic adjustment is determined from the lowering of osmotic potential ($\Psi_{\pi L}$) at full turgor; its influence on leaf rolling and leaf death was assessed in lowland rice in both the greenhouse and field by Hsiao et al. (1984). The degree of osmotic adjustment varied with the degree and duration of stress but was usually 0.5 to 0.6 MPa under severe water stress conditions. In leaves in which osmotic adjustment was 0.5 to 0.6 MPa, leaf rolling and leaf death occurred at lower leaf water potentials in adjusted than in nonadjusted leaves. It was concluded that osmotic adjustment aids in the drought resistance of rice by delaying leaf rolling, thereby maintaining gas exchange and by delaying leaf death.

Working with barley, Irvine et al. (1980) reported that the osmotic potential of the last fully developed leaf did not differ between genotypes within a given environment on a particular day. There were differences in the osmotic potential of the last fully developed leaf

between environments but there was no genotype by environment interaction for this parameter. In their study, they found that the osmotic potential of the leaf declined over the season in all environments indicating that osmotic adjustment could be occurring. Fink (1979) reported that osmotic potential of the leaf was not a promising test because of its unreliability and the inability to significantly differentiate between cultivars.

Cortes and Sinclair (1986a) determined the leaf osmotic potential ($\Psi_{\pi L}$) of field grown soybeans differing in drought response. They reported that leaf turgor potential was not preserved by lowering $\Psi_{\pi L}$ because of larger decrease in leaf total water potential under stressful conditions during the day. It appears from their study that $\Psi_{\pi L}$ was not a good indicator of drought susceptibility. In another experiment, Cortes and Sinclair (1986b) found that drought susceptibility was more related to Ψ_{TL} than $\Psi_{\pi L}$.

Osmotic adjustment (lowering of osmotic potential during development of stress) helps to maintain high, or at least positive, turgor. However, this adjustment is limited, so turgor is not always maintained. Turgor was not maintained in orchard grass when leaf water potential decreased below -20 bars (Gavande and Taylor, 1967; Morgan, 1977 and 1980a). The osmotic adjustment was noted in the range of five to eight bars. When fully expanded leaves of sorghum and sunflower are subjected to water deficits, they have a limited capacity to maintain leaf turgor potential by osmotic adjustment (Jones and Turner, 1980; Turner et al., 1978). Wenkert et al. (1978) found seasonal osmotic adjustment in

soybeans by lowering of osmotic potential of about four bars over a two month period.

Turgor Pressure, Its Influence on Growth and as
a Screening Test for Drought Resistance

Turgor pressure is essential with respect to cell enlargement, plant growth and stomatal function. Thus, reliable estimates of turgor pressure are desirable. It is usually calculated from the difference between water potential and osmotic potential. It varies from zero at incipient plasmolysis to a value equal to that of the osmotic potential in a fully turgid cell when water potential (Ψ_{TL}) approaches zero. Numerous authors state that cell expansion is caused by turgor pressure acting on the cell wall (Thimann and Schneider, 1938; Burstrom, 1953; Cleland, 1959; Green et al., 1971). Cleland (1971) showed for Avena coleoptiles that cell elongation only occurs when turgor pressure (TP) is in excess of a critical value (CV) and that the rate of cell elongation is proportional to the amount by which TP exceeds CV.

Growth rate is promoted by an increase in turgor (Ray et al., 1972; Loescher and Nevins, 1973). They also reported that plants that are able to maintain relatively high turgor over a wide range of water stress will also maintain growth rate over that same stress range. Lockhart (1965a,b) suggested that turgor pressure (Ψ_p) must be above some threshold for growth to occur. He developed an equation expressing growth rate as being proportional to Ψ_p above a threshold level:

$$\frac{dV}{Vdt} = Eg(\Psi_p - \Psi_{p,th}) \quad [1]$$

Here enlargement rate is given relative to the total cell volume V , and t denotes time; E_g is gross extensibility and $\Psi_{p,th}$ is the threshold turgor below which the cell wall does not yield. It follows that a drop of a few tenths of an MPa in tissue water potential can reduce Ψ_p to the threshold level and stop growth. Equation [1] adequately describes the growth data of *Nitella* (Green et al., 1971), pea roots (Greacen and Oh, 1972) and radish cotyledons (Kirkham et al., 1972).

Stomatal closing and opening are important for CO_2 absorption for photosynthesis. A low moisture level in the leaf (low Ψ_{TL}) causes guard cells to lose their turgor, resulting in stomatal closure that affects photosynthesis. Ghorashy et al. (1971) measured apparent photosynthesis (AP) of soybean leaves in a field experiment. They found that rate of AP decreased when leaf turgor pressure became negative. Loss of turgor pressure resulted in wilting.

It has been recognized that turgor pressure (Ψ_p) of a plant cell decreases and the cell's water potential becomes more negative as the cell dehydrates in air or osmoticum. A question is posed: Does the Ψ_p remain zero or does negative Ψ_p develop? A negative Ψ_p would mean that the water in the protoplasm and vacuole is under tension in the transpiring plants. Mixing of apoplastic water with cell sap when membranes are destroyed results in high apparent osmotic potential (Tyree, 1976). This may result in calculated values of Ψ_p being negative since osmotic potential may not decrease as much as the apparent total potential (Ackerson et al., 1977). Negative turgor potential may seem unlikely but it has been reported in a wide range of species (Kreeb, 1963; Hellmuth, 1969; Grieve, 1961; Slatyer, 1957 and

1960; Noy-Meir and Ginzburg, 1967; Wilson, 1967a, 1967b and 1967c; Sojka et al., 1977; Luxmore, 1975; Oerti et al., 1975).

Ackerson et al. (1977) determined leaf turgor potentials (ψ_{PL}) of sorghum and cotton in a field experiment under differential soil moisture stress. Sorghum ψ_{PL} exhibited a much more distinctive and constant pattern than was characteristic of cotton. They reported that sorghum ψ_{PL} was generally greater than that observed in cotton. Working with sorghum and maize in a greenhouse experiment, Sanchez-Diaz and Kramer (1971) found that sorghum maintained higher ψ_{PL} compared to maize.

Turgor potential (ψ_{PL}) of leaves was examined (Johnson and Brown, 1977) over a wide range of species, including maize, in a greenhouse study. They found varietal differences and also noted that drought-resistant lines maintained higher ψ_{PL} . Findings of their greenhouse study on ψ_{PL} agreed closely with field observations. They concluded that the ability of their technique to distinguish differences in turgor response between hybrids with a common parent suggests that the technique may be useful for screening plant materials for superior resistance to water stress.

Quisenberry et al. (1985) measured leaf water potential (ψ_{TL}), leaf osmotic potential ($\psi_{\pi L}$) and turgor potential (ψ_{PL}) in a field experiment using two contrasting cotton cultivars. They found that resistant cultivars always maintained higher ψ_{TL} and ψ_{PL} both under irrigated and dry-land conditions. They concluded that observed variability in leaf turgidity under water deficit field conditions might be useful in selecting germplasm with enhanced drought tolerance.

Brown (1974) examined the turgor response (Ψ_{PL}) of Bromus inermis and Agropyron intermedium under differential soil moisture. He observed no significant differences in Ψ_{PL} . However, Johnson and Caldwell (1976) observed differences in Ψ_{PL} between two alpine tundra plant species. They did not classify the species as drought-resistant or susceptible with respect to Ψ_{PL} .

Effects of Water Stress on Root Water Potential and Osmotic Potential

While a plant transpires, water moves along a path of decreasing potential energy from the soil through the roots, stem, leaves, and into the atmosphere. So, the study of water transport phenomena in soil plant-atmosphere systems requires the measurement of water potential in the various parts of the system. Since water enters a plant through the roots, root function is crucial to an understanding of cultivar drought response and particularly drought avoidance. The water deficit shows up as a lowered leaf water potential which, when transmitted along the plant through various resistances, forms a potential gradient from the soil to the leaves. Soil water, if available, moves along this gradient to the various plant parts. In recent years a number of attempts have been made to deal with the soil-plant potential gradient and the associated resistances (Begg and Turner, 1970; Boyer, 1969; Cary and Fisher, 1971; Jensen et al., 1961; Wiebe et al., 1970).

To date, little attention has been given to the possibility that, in plants growing in drying soil, solutes are partitioned to roots, so that osmotic potential, turgor and root growth may be maintained. Sharp

et al. (1979) measured root water potential, root osmotic potential and the growth from potted maize seedlings after imposing water stress. They found a significant decrease of osmotic potential of the root. Root growth of the unwatered plants was maintained as the severity of water stress increased. They suggested that this growth characteristic may be a function of the capacity of a plant to lower osmotic potential and maintain turgor in its roots when subjected to a soil drying cycle. Similar results were also reported by Sharp et al. (1979) in sorghum.

Many authors discuss leaf osmotic potential and the importance of osmotic adjustment as an adaptational mechanism for plants to survive water deficits. This is because of the simplicity of the measurements. Difficulties, however, arise for water status measurements of roots due to problems of sample collection and measurement techniques.

Very young seedlings appear to have a greater capacity for osmotic adjustment in response to limited water. It has been suggested that roots adjust osmotically to a greater extent than the shoots of many species (Hsiao, 1973). Roots of three- to five-day-old pea seedlings were shown to adjust osmotic potential from -2.8 to -8.3 bars (Greacen and Oh, 1972).

In some cases water stress appears to enhance root growth. Hsiao and Acevedo (1973) have proposed that this increased growth of roots under stress may be due to the capacity of the roots to adjust osmotically (lower $\Psi_{\pi R}$). The lowering of $\Psi_{\pi R}$ may result in maintenance of the same or even greater root turgor and, thus, greater root growth. This would constitute an adaptive mechanism for growth and survival in

that a more extensive root system would make more soil water available to the plant.

The effects of different levels of water stress on osmotic and water potentials of roots and shoots of germinating tomato were examined (Taylor et al., 1982). As water stress increased, root osmotic potential decreased, thereby indicating that osmotic adjustment was taking place.

Silk and Wagner (1980) found a relationship between growth rate and water potential of corn roots. They found a decreased potential in the root that made more water available as a result of high potential gradient. Working with corn, Fiscus (1972) reported that the root water potential decreased to -10.3 bars during the first drying cycle. A second drying cycle gave similar results.

Osonubi and Davis (1978) studied root osmotic potential ($\Psi_{\pi R}$) of English oak and silver birch by imposing consecutive water stress cycles. Their results showed solute accumulation in roots as a result of stress as indicated by the development of a $\Psi_{\pi R}$ of -10 bars.

Sammons et al. (1978) measured root water potential of 20 soybean cultivars under differential soil moisture stress. They found significant differences in root water potential among the soybean genotypes. Soybean genotypes were separated into resistant and susceptible groups. Any cultivar able to avoid a significant decrease in root water potential as soil moisture stress increases likely avoids the effects of declining soil water potential on root tissue, and thus is classified as drought-resistant (using Levitt's definition, 1972).

Diffusion Resistance as a Screening Mechanism

Efficient use of water under limited water supply is an important factor in drought tolerance of crops. Stomatal response is a major factor controlling water loss from plant leaves; it is easily determined by measuring leaf diffusion resistance. Stomatal diffusion resistance appears to be a reasonable screening technique because it does seem to be an excellent criterion for estimating the water deficit in plants. Hence it may be used as a tool by which the soil-water-plant relationships can be predicted (Tarique and Bierhuizen, 1971). Genotype differences in stomatal sensitivity and diffusion resistance of different crop species have been reported by numerous authors (Boyer, 1970; Glover, 1959; Pallas and Bertrand, 1966; Sullivan and Blum, 1970; Teare and Kanemasu, 1972).

Henzell et al. (1976) determined the leaf diffusive resistance of nine sorghum lines under differential moisture stress in a growth chamber. They found that stomatal sensitivity varied significantly among the entries during progressive development of water deficit. At leaf water potential of -15 bars, leaf diffusive resistance differed nearly 100 percent between sensitive and insensitive genotypes. Also working with 14 genotypes of sorghum in a field experiment, Blum (1974) found significant differences among sorghum lines. He reported that the susceptible genotypes developed lower water potentials and relatively higher leaf diffusion resistance.

Jones (1974) reported differences in the stomatal conductance of two spring wheat cultivars. He suggested that stomatal control of water

loss appeared to provide a useful method for determining varietal differences in the control of leaf water potential. Quarrie and Jones (1979) also found genotypic differences in the reduction of stomatal conductances per unit change in water potential of wheat.

However, Jones (1978) points out that because of the sensitivity of stomatal response to environmental conditions and because of the difficulty of obtaining accurate measurements with sufficient replication, diffusion resistance measurements have been of little value in screening genotypes for drought tolerance.

Relative Water Content as a Screening Tool for Drought Resistance

A considerable amount of water is present in the cell and cell walls that acts as a buffering system during periods of water stress. Water is the medium for biochemical reaction in plants and helps in transpirational cooling during hot days. Drought resistance in plant species undoubtedly involves a multiplicity of factors, acting to conserve water. Sunken stomata, thick cuticle and special water storage systems all may contribute to the water economy of plants. These factors assist, to a limited degree, in slowing the initial stages of dehydration. The importance of plant water for the maintenance of turgidity as a survival means has been reported in the literature by various authors (Carr and Gaff, 1961; Gaff and Carr, 1961; May and Milthrope, 1962; Lemee, 1946).

The relationship between the amount of water and its energy status in plant leaves is considered to indicate a measure of drought resistance. It has been shown (Connor and Tunstall, 1968; Jarvis and Jarvis,

1963; Sanchez-Diaz and Kramer, 1971; Slatyer, 1960; Weatherly and Slatyer, 1951) that drought-resistant plants have relatively smaller water deficit per unit decrease in leaf water potential than more drought-susceptible plants. Levitt (1972) pointed out that a relatively smaller water deficit per unit reduction in leaf water potential is a measure of dehydration avoidance.

Excised-leaf water retention capability appears to be a characteristic of some drought-resistant wheat cultivars (Kirkham et al., 1980; Salim et al., 1969). The excised-leaf water retention trait can be determined relatively easily and may be of use in programs for breeding drought-resistant wheat (Clarke and McCaig, 1982). According to these authors, the retention differences were expressed better in stressed than in unstressed environments. Bayles et al. (1937) found differences in rate of water loss by excised plants of several spring wheat cultivars. Excised plants of drought-resistant winter wheat cultivars lost water more slowly than less resistant cultivars (Sandhu and Laude, 1958).

Clarke (1983) studied the water retention capability of excised leaves of wheat genotypes both in the field and in a controlled environment. Changes in leaf water content from 0 to 24 h were used for the plants grown in a controlled environment while changes from 0 to 10 h were used for the field material. He found genotypic differences in water retention capabilities. Using wheat, Clarke and Townley-Smith (1986) found a positive relationship between the water retention capability and yield. Jaradat and Konzak (1983) also reported similar results with wheat genotypes.

Relative saturation deficit, water content and water retention ability of wheat leaves were investigated by Dedio (1975) as possible tests for drought resistance. He suggests that rate of water loss from excised leaves has some promise for differentiating drought resistance among wheat cultivars, but that leaf water content measurement was the best differentiator of drought resistance.

The effects of differential soil water availability on leaf water potential and relative water content were examined (Ackerson et al., 1977) to compare the water relations of cotton and sorghum. The relationship between leaf water potential and relative water content was determined for each species. The change in relative water content per unit change in leaf water potential was greater in cotton than in sorghum. Similar results were found by Namken (1964) and Sanchez-Diaz and Kramer (1971).

Carter and Patterson (1985) evaluated response to drought stress of 20 soybean genotypes in the field. Stress was imposed with specially designed rain exclusion shelters at two reproductive stages. Leaf water and osmotic potentials, relative water content (RWC) and seed yield were measured for each genotype. Genotypes which experienced the least leaf dessication were generally the highest yielding for the stress treatments. They reported that RWC was the best discriminator of genotypes for drought tolerance. Repeatability was higher for RWC than for other traits.

Seedlings as a Screening Test Material
for Drought Resistance

Screening for yielding ability under drought is an obvious selection procedure for drought resistance. However, such a procedure requires full-season field data and is expensive. Therefore, it would be advantageous to be able to screen material under greenhouse conditions using seedlings as test material. The success of this approach requires evidence that the performance of seedlings adequately reflects the performance of the mature plant when subjected to drought stress.

Drought tolerance of plants often varies through the growth cycle. Tolerance tends to be greatest during early seedling development and decreases through later stages of development. Greater tolerance during the seedling stage assists in the establishment of plants adapted to arid areas. As the plant grows older, avoidance mechanisms such as more extensive root systems help to offset the decline in tolerance (Clarke and Durely, 1981).

Relatively few reports are available in the literature of successful efforts to screen seedlings of crop species for drought resistance under controlled environments. Morgan (1983) described a method in which measurements of osmoregulation made on glasshouse-grown wheat plants were used to select lines which yield higher under conditions of water deficit in the field. On the basis of his results it seems possible to screen against poor osmoregulation by using potted plants grown in the glasshouse. Even though glasshouse plants are known to differ from field-grown plants in their water relations (Slatyer, 1963),

it seems that in wheat the differences among cultivars (Morgan, 1977 and 1980a) or breeding lines are still observable and these differences correlate well with field performance measured as turgor or grain yields. Furthermore, the method of measuring osmoregulation in the controlled environment requires only a small number of leaf samples upon which relatively simple measurements are made. While osmotic potential ($\psi_{\pi L}$) was measured using thermocouple psychrometers, other techniques for measuring $\psi_{\pi L}$ may also be suitable or total potential may be measured as a substitute, possibly by other techniques which correlate well with psychrometers such as pressure bomb. Morgan finally concluded that the technique may therefore be suitable for screening moderate numbers of advanced breeding lines and parents.

Water retention and survival values were determined (Salim et al., 1969) on seven wheat, five barley and four oat cultivars after either whole plants or cut leaf sections were dried over either CaCl_2 or glycerol solutions at known relative humidities. They reported that water retention measurement provided a fair means of identifying drought-resistant cultivars.

Researchers have suggested exposure to high temperature as a screening tool for drought resistance of crop plants. Eight lines of maize ranging in drought reaction from susceptible to resistant under field conditions for several seasons were chosen (Hunter et al., 1936) for laboratory tests. They kept 14-day-old seedlings for 6.5 hours in a chamber with temperature controlled at 140°F and relative humidity of about 30 percent. The plants which survived after the test were rated as drought-tolerant. Essentially the same order of relative

resistance was obtained with the seedlings as was noted for the plants in the field. Also using maize in a controlled environment, Heyne and Brunson (1940) successfully differentiated between resistant and susceptible groups comparing heat injury of 20-day-old seedlings.

Williams et al. (1967) used three methods for measuring drought tolerance of 52 corn genotypes of 20-day-old seedlings. They were: exposing corn seedlings to 52°C for six hours followed by counting survivors; germinating corn seed in mannitol solution of 15 atm osmotic potential and selecting genotypes showing the highest percent germination; and subjecting corn seedlings to a 14-day permanent wilting period in a greenhouse followed by wilting ratings. Any one of the three methods was found to be effective as a screening technique for drought tolerance. Results were supported by observation from successive field plantings, one subjected to drought and one receiving normal rainfall.

Kilen and Andrew (1969) conducted a greenhouse experiment using 12 corn lines differing in drought response in the field. Plants at the four-leaf stage were exposed to a temperature of 54.5°C for five hours and a leaf firing scale (0 to 5 scale, with 0 indicating an entire dead leaf) was determined for the lines. They also performed chlorophyll stability tests on leaf tissue. The heat test was found to be the best separator in identifying drought-resistant lines. They concluded that the heat test of seedlings may be of greatest value in screening for drought-resistant genotypes since it can be applied to large numbers of plants and is rapid and inexpensive. Their greenhouse results supported the field results with respect to drought resistance.

Wright and Jordan (1970) performed a greenhouse trial for selection of seedling drought tolerance in boer lovegrass. Environmental stress included high temperature, low humidity, erratic distribution of rainfall and frequent drought. Surviving seedlings were counted. Their findings supported the use of controlled environment for seedling drought-tolerance evaluation. They found that resistant seedlings separated in the greenhouse were also superior genotypes for the natural environments in the field.

Sammons et al. (1978) studied the effects of soil moisture stress on root and shoot water potential using three-week-old potted soybean seedlings. The results suggest that soybean seedlings differ in drought response. They separated drought-resistant cultivars on the basis of development of higher root and shoot water potentials.

Sprinkler irrigation gradient systems were used (Rumbaugh et al., 1984) in screening of alfalfa seedlings for drought resistance. They identified drought-resistant seedlings by measuring stand densities and shoot dry weights.

Selection of Drought-Resistant Cultivars Using Water Status Measurements as Selection Techniques

A problem in the assessment of plant water status measurements as selection techniques for drought tolerance of cultivars is the lack of test materials with known drought resistance to test the techniques. Knowledge of the relative drought resistance or susceptibility of a cultivar is extremely important in order to test selection techniques that may be used to develop or sort out genetic lines resistant to drought. Finlay and Wilkinson (1963) and Eslick et al. (1972) used

regression techniques to evaluate the relative response of a large number of cultivars to environmental conditions. Findlay and Wilkinson (1963) used the yield data on logarithmic scales in generating regression lines. Eslick et al. (1972) plotted the yields of individual cultivars against the mean yields of all cultivars grown together in individual yield trials over a wide range of environments from adverse to favorable conditions. They suggested that drought-resistant cultivars are characterized by regression coefficients (slopes) of less than one and susceptible cultivars by coefficients greater than one. Analyses of their data indicate resistant cultivars perform relatively better under adverse conditions but not so well in favorable environments. In semi-arid areas low mean yields of crops nearly always result from drought; thus, the relatively higher yield level of a cultivar at low mean yield levels of all cultivars should be an indication of the drought-tolerance of that cultivar. The regression technique requires a large number of years of study in order to obtain the range of environmental conditions needed. Fink (1979) utilized barley yield data collected over a 40-year period for cultivars grown in the Northern Great Plains and analyzed by Professor Eslick (Montana State University) to generate regression lines as described above for 49 cultivars. He reported the mean yield levels of all cultivars by 10 bushel yield increments from 10 to 120 bu/a (independent values). In addition to using regression coefficients, he classified drought-resistant cultivars on the basis of the relatively higher yield produced by the cultivar at the low (10 bu/a) yield levels (e.g., drought years) of all cultivars.

CHAPTER 3

MATERIALS AND METHODS

Water Status (Ψ_{TL} , $\Psi_{\pi L}$, Ψ_{PL}) of Field Grown Barley
Cultivars Under Different Irrigation Levels

Effects of differential moisture levels on the water status of leaves of four two-rowed barley cultivars were evaluated in a field experiment at the Montana State University Horticultural Farm, Bozeman, Montana. The cultivars used in the study were Clark, Hector, Klages and New Moravian. The experiment was on a Bozeman silt-loam, fine-silty, mixed, Argic Pachic Cryoborolls. The depth of soil over gravel was approximately 70 cm.

A complete factorial in a completely randomized design was utilized in the experiment. Two irrigation treatments with decreasing moisture level from a line-source irrigation system were: (1) irrigation (a three-meter distance from the source) and (2) no irrigation. Irrigation treatments were fixed because of the nature of the experiment and cannot be statistically tested by analysis of variance (Hanks et al., 1980). Main treatment cultivars were randomized in each replication. Four replications were used in the experiment. Plots were irrigated prior to water status measurements.

Seed was planted 28 May 1982, 2.5 cm deep, in four-row plots with a coneseeder. Row spacings were 30 cm apart with 10 gram of seed per meter. Seeds were sized to minimize seedling variations.

Growing season precipitation, temperature, humidity and solar radiation were recorded daily with standard weather instruments. They are summarized in Table 48 (Appendix).

Water status measurements were taken at 0500, 0700, 0900 and 1200 hour (h) 30 July, 1982 at the early heading growth stage on four neighboring plants from irrigation treatment. On 4 August (late heading stage) measurement times were at 0500 and 1300 h and on 10 August (flowering stage) at 0500 and 0900 h, respectively. Three neighboring plants from irrigation and no irrigation treatments were used at the two latter stages.

The following measurements were made on plants:

- (1) Total water potential of leaves (ψ_{TL}): The ψ_{TL} was measured using a pressure chamber (PMS Instrument Co., Corvallis, Oregon). The pressure chamber was lined with a moist filter paper. Fully expanded leaves (immediately below the flag leaf) were cut with a razor blade and immediately placed between moistened cardboard sheets to avoid moisture loss from the leaf during transport. The leaf was then inserted through a split rubber stopper and placed in the pressure chamber. Pressure was increased slowly until the sap began to exude (examined by microscope) from the cut end.
- (2) Osmotic potential of leaves ($\psi_{\pi L}$): Immediately after ψ_{TL} measurement, the leaf was sealed in a latex tube 15 cm in length and with an inside diameter of 1 cm. The

tubes with the leaves were frozen on dry ice for about six hours and thawed for an hour. The sap was extracted with a steel roller. The sap was absorbed on a filter paper disc and $\psi_{\pi L}$ was determined using a model C-52 Wescor psychrometer sample chamber coupled to a Wescor HR-33T microvoltmeter operating in the dew point mode. Thirty minutes were allowed for vapor and temperature equilibrium. Five-minute equilibration intervals were allowed between each sample. The readings were recorded in microvolts and converted to $\psi_{\pi L}$ using a regression equation. The psychrometer was frequently checked by measuring microvolt readings of standard NaCl solutions.

- (3) Turgor potential of leaves (ψ_{PL}): The ψ_{PL} was calculated from the difference between ψ_{TL} and $\psi_{\pi L}$, that is,

$$\psi_{PL} = \psi_{TL} - \psi_{\pi L} \quad [2]$$

Water Status (ψ_{TL} , $\psi_{\pi L}$, ψ_{PL} , $\psi_{\pi R}$) of Greenhouse Grown Barley Cultivars as a Function of Water Stress

A series of greenhouse experiments (1984 and 1985) was carried out to observe the behavior of internal water status of barley seedlings as they were subjected to water stress.

Plastic tubs (78 cm long x 38 cm wide x 28 cm deep) with inlet-outlet tubes on the bottom and side were filled with 2.0 to 3.0 mm gravel. The gravel had been thoroughly washed to remove all soluble materials and fine materials. By using the inlet-outlet tubes, the

water level in the tubs could be maintained at any desired level and could be adjusted rapidly.

Plants were grown in soil-filled plastic cone-tainers, 2.5 cm diameter and 12.3 cm long, with holes in the bottom plugged with cheesecloth so that soil was retained but roots could emerge. Twelve days after emergence of plants in the cone-tainer, the cone-tainers were transferred to the tubs by pushing the bottom of the cone-tainers into the gravel so that the holes were in the capillary fringe above the water table. A rack held the cone-tainers so that all were the same level above the water table. Roots emerging from the holes were thus supplied with water at essentially zero stress. By removing water from the tubs, a water stress could be rapidly imposed on the plants since the large pores between the grains held little capillary water. Likewise, stress could be rapidly removed by resupplying water to the tubs. The entire process took place in the greenhouse with no control of humidity and at normal greenhouse temperatures.

In this work the following plant water status measurements were made at 10:00 AM daily from 1984 and 1985 experiments:

- (1) Total water potential of leaves: A fully expanded third leaf of the three-week-old plant was cut near the stem with a razor blade. The Ψ_{TL} was measured immediately after excision with a pressure chamber (Soil Moisture Equipment Corporation).
- (2) Osmotic potential of leaves: Following Ψ_{TL} measurement, the leaf was inserted into a latex tube. Freezing, thawing and sap extraction were done in accordance with

the procedure adopted during the field experiment. The $\psi_{\pi L}$ was determined using a model SC-10 Decagon sample chamber coupled to a Wescor HR-33T microvoltmeter operating in the dew point mode. Measurement techniques and precautions taken in the field experiment were also applied here.

- (3) Turgor potential of leaves: This was calculated using equation [2].
- (4) Osmotic potential of roots ($\psi_{\pi R}$): The cone-tainers were gently removed from the gravel leaving roots protruding through the holes in the bottom. Gravel was removed from the roots by gentle shaking and a soft brush. Roots were then excised with a razor blade and placed inside the sample cup. The cups, sealed with rubber stoppers, were frozen on dry ice for an hour and thawed for two hours. The cups were then transferred into the thermocouple sample chamber (SC-10) and allowed to equilibrate for another two hours. Fifteen-minute equilibration intervals were allowed between each sample reading. The $\psi_{\pi R}$ determination was similar to $\psi_{\pi L}$.

Two identical experiments, growing seedlings in one tub, were conducted 24 and 31 August 1984 using Clark, Hector and Klages as test crops. The seedlings were arranged in a complete factorial in a completely randomized design with three replications. Immediately after measurement of ψ_{TL} and root sample collection for $\psi_{\pi R}$ measurement under

no stress conditions, water was drained from the tub to induce stress. The Ψ_{TL} measurement and root sample collection and measurement continued as stress developed for five days. The plants were rewatered after the fifth day Ψ_{TL} measurement and root samples were collected. After elimination of stress, Ψ_{TL} measurement and root sample collection continued for an additional two days.

On 9 October 1984 a trial was carried out in two tubs. The seedlings were arranged in a complete factorial in a completely randomized design with two replications using Clark and Klages as test crops in each tub. The determinations of Ψ_{TL} and $\Psi_{\pi R}$ were continued for six days supplying water to plants constantly in one tub. This situation was designated as the nonstress condition. Imposition of water stress and rewatering of plants were done in the other tub as in the August 24 and 31 experiments. This situation was termed the stress condition. The Ψ_{TL} measurement and root sample collection for the $\Psi_{\pi R}$ measurement were also performed under the stress condition.

Another experiment was conducted 17 and 23 August 1985 in two tubs. This experiment was similar to the 9 October 1984 trial but a stress cycle (stress, release stress, stress, release stress) was imposed again on plants in the stressed tub. The experiments performed on 17 and 23 August 1985 were designated as the first-cycle and second-cycle experiments, respectively. The measurements of Ψ_{TL} , $\Psi_{\pi L}$, Ψ_{PL} and $\Psi_{\pi R}$ were continued for six and seven days from the first- and second-cycle experiments, respectively.

Thermocouple Psychrometer Calibration Technique

The thermocouple psychrometer can only give accurate measurements of water potential if it is properly calibrated. The calibration was done using NaCl solutions of known molality. During this study, five solutions were used at concentrations of 0.1, 0.3, 0.5, 0.7 and 1.0 molal. A filter paper disc soaked with NaCl solution for C-52 and six drops of NaCl solution for SC-10 were placed in the sample cups. The cups were then placed in the psychrometer sample chamber and 30 minutes were allowed for temperature and vapor equilibrium. The sample chamber was coupled to a Wescor HR-33T microvoltmeter operating in the dew point mode and output readings were recorded in microvolts. The sample cups and chamber were always kept clean for accurate measurements. A regression equation and calibration curve were made to convert microvolt readings into water potential. Since psychrometer calibrations can change quickly, the instruments were calibrated as necessary.

Water Status (Ψ_{TL} , R_S , RWC) of Greenhouse Grown Barley Cultivars as a Function of Water Stress

Seedlings were grown similarly as for the intensive greenhouse experiment of 1984 and 1985. The cultivars were arranged in a randomized complete block with five replications in one tub. Ten two-rowed and ten six-rowed barley cultivars were used in the study. Regression lines were generated regressing the predicted yield levels of individual cultivars (dependent values) against the mean yield levels of all cultivars by 10 bu/a yield increments from 10 to 120 bu/a (independent values) as described by Fink (1979). He used mean yield levels of 80

bu/a and above to predict individual cultivar yields at a mean yield level of 90 bu/a. He also used mean yield levels below 40 bu/a to predict individual cultivar yields at a mean yield level of 30 bu/a. Selection of the above cultivars was accomplished by observing the relatively higher yield of the cultivar at the low (10 bu/a, e.g., drought years) mean yield levels of all cultivars. The slope values and drought response of 19 barley cultivars are presented in Table 1. Clark, a drought-resistant cultivar recommended by breeders, is also included in this study (Table 1).

The following measurements were made on three-week-old plants:

- (1) Total water potential of leaves: The Ψ_{TL} was measured at predawn as before under nonstress conditions only.
- (2) Stomatal diffusion resistance (R_s): Following the Ψ_{TL} measurement, stress was imposed on plants by draining water from the tub. The R_s was measured using a Li-Cor model 700 autoporometer at 10:00 AM and 1:00 PM daily and continued for three days as stress developed. The readings were recorded in seconds. Stomatal diffusion resistance (scm^{-1}) was calculated using a regression equation made following the standard procedure of calibration of the porometer.
- (3) Relative water content (RWC): The RWC of stressed leaves was determined using the following equation:

$$\text{RWC} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

[3]

Table 1. Barley cultivar name, number of rows in head, slopes and drought response.

Cultivar	Rows	Slopes	Drought Response*	
Clark	2		Resistant (R)	
Compana	2	0.84	"	"
Dekap	2	0.86	"	"
Hector	2	1.04	"	"
New Moravian	2	0.77	"	"
Briggs	6	0.76	"	"
Larker	6	0.86	"	"
Trebi	6	0.89	"	"
Titan	6	0.86	"	"
Glacier	6	0.99	"	"
Georgie	2	1.08	Susceptible (S)	
Ingrid	2	1.05	"	"
Klages	2	1.04	"	"
Maris Mink	2	1.50	"	"
Zephyr	2	1.12	"	"
Hiland	6	1.14	"	"
Steveland	6	1.09	"	"
Bonneville	6	1.04	"	"
Vantage	6	1.06	"	"
Unitan	6	1.09	"	"

*Drought response was determined by Eslick et al. (1972); see Fink (1979).

RWC = relative water content, FW = fresh weight of leaf, TW = turgid weight of leaf and DW = dry weight of leaf. Relative water content was determined after three days water stress and expressed as a percentage. Following PM readings of diffusion resistance on day three, leaves were excised and weighed on an electronic balance to obtain fresh weight of the leaf. After weighing, the cut end of each leaf was inserted into distilled water in a glass test tube of 2.5 cm diameter and 20 cm in length. The test tubes were stoppered with cotton balls to prevent evaporation and kept under low light conditions in the laboratory. The leaves were allowed to absorb water for about five hours to attain turgid condition. Surface water was blotted from the leaves and they were reweighed to obtain turgid weight. After drying overnight at 70°C, dry weight of the leaves was determined.

Statistical Methods

The MSUSTAT computer program developed by Lund (1979) was used for all statistical analyses. Data were analyzed on the plant and soil science Discovery Computer System. Because of the nature of the design in the field (1982) and tub experiments (1984 and 1985), water relations parameters were analyzed using a subsampling technique. A Least Significant Difference (LSD) test was performed on the pooled variance

of analyses to detect the cultivar effect. For 1986 tub experimental results, LSD test for cultivar effect and orthogonal comparison test for resistant vs. susceptible were done using varying lengths of water stress treatments.

CHAPTER 4

RESULTS AND DISCUSSION

Water Status (Ψ_{TL} , $\Psi_{\pi L}$, Ψ_{PL}) of Field Grown Barley
Cultivars Under Different Irrigation Levels

Analysis of variance for leaf total water, leaf osmotic and leaf turgor potentials of the field-grown barley cultivars for one day at the early heading growth stage is shown in Table 2. Over the four measurements in irrigated plots, cultivars did not differ in Ψ_{TL} . As expected, Ψ_{TL} differed significantly with time of measurement. Also, there was a highly significant cultivar x time interaction indicating that cultivars responded differently to the stress developed due to radiation heat load during the day. Table 3 shows the mean values of Ψ_{TL} of the cultivars at the four time periods. At the time of minimum stress (0500) the two more resistant cultivars, Clark and Hector, had the higher Ψ_{TL} , with Hector being significantly higher, than the two susceptible cultivars. By 0700 only Hector had changed significantly and developed a lower Ψ_{TL} than Klages. At both 0900 and 1200 there were no differences among cultivars as tested by LSD, but Ψ_{TL} was much lower at 1200. New Moravian developed more negative Ψ_{TL} at 0500 than Hector. Osmotic potential of leaves showed no cultivar and cultivar x time interaction, but did change significantly with time of determinations (Table 2). Variety means for $\Psi_{\pi L}$ did not differ significantly at any time of the day (Table 4). There were no significant differences in Ψ_{PL} among

cultivars (Table 2), but there were highly significant time and cultivar x time interactions. Turgor potential decreased as the day progressed, becoming negative for Clark and Klages at 0900 and for all cultivars at 1200 (Table 5). This negative turgor is probably an artifact of the measurement technique as was discussed in the literature review. The significant cultivar x time interaction of Ψ_{PL} is the result of the rapid drop of Ψ_{TL} of Hector at the 0700 reading and probably is

Table 2. Analysis of variance for water status of four two-rowed barley cultivars at the early heading growth stage (irrigated), July 30, 1982.

Source of Variation	df	Mean Squares		
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}
Cultivars (C)	3	5.023	1.483	6.393
Time (T)	3	512.800**	31.170**	300.800**
C x T	9	12.540**	0.239	12.480**
Error	48	3.805	1.204	3.194

**Denotes significance at 1% level.

Table 3. Mean values of Ψ_{TL} of four two-rowed barley cultivars at different times of the day at the early heading growth stage (irrigated), July 30, 1982.

Cultivar	Times of the Day (Hours)			
	0500	0700	0900	1200
	----- MPa -----			
Clark	-0.59	-0.46	-1.46	-1.77
Hector	-0.45	-1.04	-1.30	-1.71
Klages	-0.72	-0.73	-1.55	-1.84
New Moravian	-0.77	-0.53	-1.32	-1.87
LSD .05	0.24	0.36	NS	NS

Table 4. Mean values of $\Psi_{\pi L}$ of four two-rowed barley cultivars at different times of the day at the early heading growth stage (irrigated), July 30, 1982.

Cultivar	Times of the Day (Hours)			
	0500	0700	0900	1200
	----- MPa -----			
Clark	-1.22	-1.23	-1.32	-1.49
Hector	-1.29	-1.28	-1.41	-1.55
Klages	-1.23	-1.20	-1.36	-1.53
New Moravian	-1.25	-1.26	-1.34	-1.59
LSD .05	NS	NS	NS	NS

Table 5. Mean values of Ψ_{PI} of four two-rowed barley cultivars at different times of the day at the early heading growth stage (irrigated), July 30, 1982.

Cultivar	Times of the Day (Hours)			
	0500	0700	0900	1200
	----- MPa -----			
Clark	0.62	0.76	-0.14	-0.27
Hector	0.84	0.24	0.11	-0.16
Klages	0.51	0.48	-0.19	-0.31
New Moravian	0.48	0.73	0.01	-0.28
LSD .05	NS	0.28	NS	NS

of little consequence. The LSD (Table 5) test indicates cultivar significance only at the 0700 reading.

An irrigation treatment was imposed on the crops prior to measurements made at the late heading growth stage. A valid statistical test was not possible for the irrigation effect because it was systematically

imposed and not randomized. However, since the cultivars were randomized, a valid statistical test is possible to test water status parameter differences of cultivars and irrigation by cultivar interaction (Hanks et al., 1980).

The analysis of variance (Table 6) indicates significant differences in Ψ_{TL} among cultivars, time of reading, cultivar x irrigation and time x irrigation. The cultivar significance in Ψ_{TL} of the pooled data are of interest in separating cultivars according to drought response. Table 7 shows means as tested by LSD among the cultivars at the 0500 reading in the non-irrigated treatment. The similarity between the rank of the cultivars at the 0700 (Table 3) and 0500 readings with no irrigation (Table 7) is striking. Hector and Klages appear to respond rapidly with applied stress compared to the other varieties (Table 3). The Ψ_{TL} of all cultivars were higher at 0500 with irrigation as would be expected; there was little difference between the irrigation treatments at 1300. Again, there are indications, not significant, that the two more resistant cultivars maintained higher potentials under well-watered conditions. Leaf osmotic potentials did not differ among cultivars nor were they influenced by irrigation treatments or times of the day (Tables 6 and 8). Turgor potential did not differ between cultivars (Tables 6 and 9). There was a significant decrease in Ψ_{PL} with time as would be expected considering the large change in Ψ_{TL} and small change in $\Psi_{\pi L}$. Although differences cannot be analyzed because of the nature of the experimental design, non-irrigated plots had what appear to be lower Ψ_{PL} than irrigated plots at both times.

Table 6. Analysis of variance for water status of four two-rowed barley cultivars at the late heading growth stage, August 4, 1982.

Source of Variation	df	Mean Squares		
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}
Cultivars (C)	3	9.991**	1.228	4.549
Time (T)	1	1459.000**	2.709	1336.000**
C x T	3	1.271	0.305	2.807
Irrigation (I)	1	18.750 NV	23.240 NV	83.740 NV
C x I	3	7.387*	1.236	3.517
T x I	1	12.200**	0.120	9.910*
C x T x I	3	1.815	1.294	2.305
Error	32	1.716	1.898	2.305

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

NV = Probability statements are not valid because treatments were not randomized.

Table 7. Mean values of Ψ_{TL} of four two-rowed barley cultivars under different irrigation levels and times of the day at the late heading growth stage, August 4, 1982.

Cultivar	Irrigation Level	Times of the Day (Hours)	
		0500	1300
----- MPa -----			
Clark	Irrigation	-0.45	-1.67
Hector	" "	-0.40	-1.65
Klages	" "	-0.70	-1.81
New Moravian	" "	-0.53	-1.77
LSD .05		NS	NS
Clark	No irrigation	-0.54	-1.67
Hector	" "	-0.97	-1.79
Klages	" "	-0.85	-1.85
New Moravian	" "	-0.63	-1.68
LSD .05		NS	NS

Table 8. Mean values of $\Psi_{\pi L}$ of four two-rowed barley cultivars under different irrigation levels and times of the day at the late heading growth stage, August 4, 1982.

Cultivar	Irrigation Level	Times of the Day (Hours)	
		0500	1300
----- MPa -----			
Clark	Irrigation	-1.59	-1.66
Hector	" "	-1.61	-1.64
Klages	" "	-1.71	-1.74
New Moravian	" "	-1.60	-1.69
LSD .05		NS	NS
Clark	No irrigation	-1.51	-1.47
Hector	" "	-1.51	-1.63
Klages	" "	-1.46	-1.59
New Moravian	" "	-1.50	-1.45
LSD .05		NS	NS

Table 9. Mean values of $\Psi_{\pi L}$ of four two-rowed barley cultivars under different irrigation levels and times of the day at the late heading growth stage, August 4, 1982.

Cultivar	Irrigation Level	Times of the Day (Hours)	
		0500	1300
----- MPa -----			
Clark	Irrigation	1.13	-0.01
Hector	" "	1.21	-0.02
Klages	" "	1.01	-0.07
New Moravian	" "	1.06	-0.07
LSD .05		NS	NS
Clark	No irrigation	0.97	-0.21
Hector	" "	0.54	-0.16
Klages	" "	0.61	-0.26
New Moravian	" "	0.87	-0.23
LSD .05		NS	NS

Analysis of variance for the measured variables at the flowering growth stage is presented in Table 10. This analysis indicates that there is a significant difference in Ψ_{TL} for cultivars, times of the day and cultivar x irrigation interaction. Table 11 gives mean values of Ψ_{TL} ; based on the LSD test there were no differences among cultivars, but at the time of minimum stress (0500 and irrigated) there are indications that Clark and Hector maintained higher leaf total water potential. The significant differences of cultivars in Table 10 occurred when these data were averaged across irrigation and time, whereas Table 11 data were within irrigation treatment. Leaf total water potential was consistently lower under non-irrigated treatments and for the mid-morning period. Only time (Table 10) influenced the $\Psi_{\pi L}$ and this occurred only in the non-irrigated plot (Table 12). There was no significant difference (Table 10) between cultivars in turgor potential, as was true at the other two growth stages, but the two less tolerant cultivars were the only ones to develop negative Ψ_{PL} (Table 13).

Inspection of the data on the variables of water status parameters from three growth stages indicated no consistent change during the day and with the age of the plants. However, if such a change had occurred, one would expect it to be expressed with irrigation and at 0500 hours. The significant cultivar differences were observed for leaf total water potential under nonstress conditions (Tables 6 and 10). Similar results were also reported by Hanson et al. (1977) with barley and Cortes and Sinclair (1986) with soybeans. The predawn Ψ_{TL} was a better indicator of stress response than afternoon values and these results agreed with the findings of Turk et al. (1980) and Wein et al. (1979) with cowpeas.

Table 10. Analysis of variance for water status of four two-rowed barley cultivars at the flowering growth stage, August 10, 1982.

Source of Variation	df	Mean Squares		
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}
Cultivars (C)	3	72.160**	18.760	22.240
Time (T)	1	613.500**	87.480**	237.600**
C x T	3	1.940	3.310	4.930
Irrigation (I)	1	1964.000 NV	863.600 NV	222.700 NV
C x I	3	29.340*	5.530	11.040
T x I	1	10.270	29.940	67.210**
C x T x I	3	5.506	7.584	4.591
Error	32	8.090	8.928	8.598

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

NV = Probability statements are not valid because treatments were not randomized.

Table 11. Mean values of Ψ_{TL} of four two-rowed barley cultivars under different irrigation levels and times of the day at the flowering growth stage, August 10, 1982.

Cultivar	Irrigation Level	Times of the Day (Hours)	
		0500	0900
----- MPa -----			
Clark	Irrigation	-0.39	-1.34
Hector	" "	-0.57	-1.36
Klages	" "	-0.80	-1.63
New Moravian	" "	-0.77	-1.43
LSD .05		NS	NS
Clark	No irrigation	-2.16	-2.52
Hector	" "	-1.41	-2.14
Klages	" "	-2.29	-3.02
New Moravian	" "	-2.15	-2.82
LSD .05		NS	NS

Table 12. Mean values of $\Psi_{\pi L}$ of four two-rowed barley cultivars under different irrigation levels and times of the day at the flowering growth stage, August 10, 1982.

Cultivar	Irrigation Level	Times of the Day (Hours)	
		0500	0900
----- MPa -----			
Clark	Irrigation	-1.35	-1.71
Hector	" "	-1.43	-1.45
Klages	" "	-1.58	-1.60
New Moravian	" "	-1.44	-1.54
LSD .05		NS	NS
Clark	No irrigation	-2.24	-2.54
Hector	" "	-1.97	-2.22
Klages	" "	-2.19	-2.91
New Moravian	" "	-2.21	-2.60
LSD .05		NS	NS

Table 13. Mean values of Ψ_{PI} of four two-rowed barley cultivars under different irrigation levels and times of the day at the flowering growth stage, August 10, 1982.

Cultivar	Irrigation Level	Times of the Day (Hours)	
		0500	0900
----- MPa -----			
Clark	Irrigation	0.96	0.37
Hector	" "	0.86	0.01
Klages	" "	0.78	-0.03
New Moravian	" "	0.67	0.11
LSD .05		NS	NS
Clark	No irrigation	0.08	0.02
Hector	" "	0.56	0.08
Klages	" "	-0.11	-0.11
New Moravian	" "	0.06	-0.21
LSD .05		NS	NS

Irrigation treatment resulted in higher Ψ_{TL} and this is similar to results obtained for wheat (Jones, 1977 and 1979). In general, the Ψ_{TL} was higher in resistant cultivars compared to susceptible ones under nonstress condition. No cultivar differences in leaf osmotic potentials were found from any of the three growth stages. Only time of measurement affected $\Psi_{\pi L}$ at the early heading and flowering growth stages. This pattern may indicate that as the day progressed, solute concentration increased from dehydration or active accumulation to lower $\Psi_{\pi L}$. The analyses of variance for Ψ_{PL} did not show any significant cultivar differences but LSD did (Table 5). Although Ψ_{PL} was not significantly different among cultivars, there is an indication that resistant cultivars, Clark and Hector, maintained higher turgor potential. The high or positive Ψ_{PL} did not result from the osmotic adjustment in response to radiation heat load or soil moisture deficit during the day. Ackerson et al. (1977) also noted a similar effect. In all three growth stages, it was found that higher or positive turgor maintenance was associated with the higher leaf total water potential for the resistant cultivars. This supports the results of Cortes and Sinclair (1986).

Intensive greenhouse studies were undertaken (1984) to observe the behavior of Ψ_{TL} , $\Psi_{\pi L}$, Ψ_{PL} and $\Psi_{\pi R}$ of three-week-old seedlings of three barley cultivars as they went from nonstress to stress and back to nonstress conditions. The plants were grown without stress until three weeks old when measurements were begun. After the first-day measurements of water status parameters from leaves and roots, stress was imposed by draining water from the tubs and measurements were made

each day for a four-day period. Stress was then removed and measurements were made on the recovering plants for an additional two days.

Analyses of variance for two runs, August 24 and 31, are given in Tables 14 and 15, respectively. Significance of variables measured are identical in these two runs. There was significance among cultivars and stress days (number of days after tub drainage) for ψ_{TL} , among stress days for ψ_{TL} , and among cultivars and stress days for ψ_{PL} and ψ_{PR} .

Mean values of ψ_{TL} for the two runs are given in Tables 16 and 17. Differences between cultivars with days are generally nonsignificant. Significance was found on only four days in the two runs. Clark had higher ψ_{TL} than Klages every measurement day; statistically so three times (Table 16). Hector had higher ψ_{TL} than Klages on all but one date (Tables 16 and 17) but these cultivars differed significantly only on the last recovery day of the second run. Hector was also consistently lower in ψ_{TL} than Clark, statistically so on two dates in the first run. Leaf total water potential decreased with days of stress for all of the cultivars and then increased as stress was relieved. Klages tended to recover less rapidly than the other cultivars (Tables 16 and 17).

Osmotic potential means of leaves of the two runs are given in Tables 18 and 19. The LSD analyses indicate general nonsignificant differences among the cultivars except on the first water stress day (Table 19). By subtracting the mean ψ_{TL} on day zero from the ψ_{TL} of the replicates on subsequent days, an estimate of osmotic adjustments was obtained. The LSD for this adjustment is shown in Tables 18 and 19. Although there are indications of significant differences on one date of each run, the lack of a consistent pattern in these data indicates no

Table 14. Analysis of variance for water status of three two-rowed barley cultivars in greenhouse experiment, August 24, 1984.

Source of Variation	df	Mean Squares			
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}	$\Psi_{\pi R}$
Cultivars (C)	2	30.970**	2.308	18.030**	27.070**
S-days (S)	6	129.700**	25.390**	48.230**	139.900**
C x S	12	1.447	0.735	0.859	1.578
Error	42	1.801	2.544	1.863	1.554

**Denotes significance at the 1% level.
S-days = stress days.

Table 15. Analysis of variance for water status of three two-rowed barley cultivars in greenhouse experiment, August 31, 1984.

Source of Variation	df	Mean Squares			
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}	$\Psi_{\pi R}$
Cultivars (C)	2	13.360**	0.341	13.260**	11.490**
S-days (S)	6	176.100**	51.690**	43.520**	84.230**
C x S	12	1.194	1.126	1.316	1.594
Error	42	1.710	1.065	1.675	1.490

**Denotes significance at the 1% level.
S-days = stress days.

Table 16. Mean values of Ψ_{TL} of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 24, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	-0.30	-0.70	-0.80	-1.21	-1.54	-0.94	-0.74
Hector	-0.51	-0.81	-1.04	-1.37	-1.66	-0.89	-0.81
Klages	-0.57	-0.86	-1.12	-1.40	-1.72	-1.17	-1.11
LSD .05	0.17	NS	0.15	NS	NS	NS	0.27

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

Table 17. Mean values of Ψ_{TL} of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 31, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	-0.57	-0.72	-1.20	-1.58	-1.76	-0.99	-0.71
Hector	-0.51	-0.93	-1.25	-1.55	-1.65	-1.00	-0.60
Klages	-0.66	-0.92	-1.41	-1.66	-1.80	-1.22	-0.80
LSD .05	NS	NS	NS	NS	NS	NS	0.14

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

Table 18. Mean values of $\Psi_{\pi L}$ of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 24, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	-0.99	-1.24	-1.33	-1.47	-1.51	-1.17	-1.10
Hector	-1.12	-1.14	-1.37	-1.47	-1.52	-1.12	-1.11
Klages	-1.13	-1.22	-1.34	-1.48	-1.54	-1.31	-1.22
LSD .05 (means)	NS	NS	NS	NS	NS	NS	NS
LSD .05 (adjustment)	--	NS	NS	NS	NS	0.15	NS

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

Table 19. Mean values of $\Psi_{\pi L}$ of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 31, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	-1.02	-1.04	-1.50	-1.52	-1.65	-1.28	-1.03
Hector	-1.05	-1.21	-1.43	-1.47	-1.56	-1.44	-1.05
Klages	-1.07	-1.10	-1.41	-1.52	-1.68	-1.38	-1.00
LSD .05 (means)	NS	0.11	NS	NS	NS	NS	NS
LSD .05 (adjustment)	--	0.11	NS	NS	NS	NS	NS

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

real difference among the cultivars. The mean differences of ψ_{PL} for three cultivars as tested by LSD are given in Tables 20 and 21, i.e., for the first run, cultivars differed significantly at the fourth water stress day (Table 20) when the seedlings experienced the severe water deficits in the study (Table 15) and developed negative ψ_{PL} in all three cultivars. Results in Table 21 revealed that Klages developed negative ψ_{PL} one day earlier than Clark and Hector. Again there is little indication that Klages tends to develop lower ψ_{PL} as stress is imposed compared to the other two varieties.

More rapid and greater osmotic potential adjustments of roots have been proposed as a drought-tolerance mechanism; such adjustments might allow for greater potential differences between roots and soil and also more relative root development under stress (Hsiao and Acevedo, 1973). Analyses in Tables 14 and 15 indicate significant cultivar differences in root osmotic potentials, but LSD comparisons of means (Tables 22 and 23) indicate only two cases of significance among the cultivars in the two runs. There is a tendency for Klages to have lower values than the two more tolerant cultivars. This possibility of separating resistant from susceptible cultivars by measurement of $\psi_{\pi R}$ should be further investigated. Osmotic adjustment LSD showed scattered cases of significant differences but no consistent pattern. An alternative inference is that the drought-susceptible line had lower $\psi_{\pi R}$ values.

Significant changes did occur in the variables measured over time of stress and during recovery in the two runs. Significant cultivar differences were found on the pooled data when averaged across all days from the two runs. These differences suggest the existence of species

Table 20. Mean values of Ψ_{PL} of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 24, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	0.69	0.54	0.53	0.26	-0.04	0.23	0.37
Hector	0.62	0.33	0.32	0.08	-0.13	0.24	0.31
Klages	0.56	0.36	0.22	0.08	-0.18	0.14	0.12
LSD .05	NS	NS	NS	NS	0.08	NS	NS

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

Table 21. Mean values of Ψ_{PL} of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 31, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	0.49	0.33	0.30	-0.06	-0.11	0.29	0.33
Hector	0.54	0.28	0.19	-0.08	-0.09	0.44	0.45
Klages	0.42	0.17	-0.03	-0.14	-0.12	0.16	0.21
LSD .05	NS	NS	NS	NS	NS	NS	0.09

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

Table 22. Mean values of $\Psi_{\pi R}$ of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 24, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	-0.58	-0.71	-0.84	-1.31	-1.50	-0.75	-0.67
Hector	-0.68	-0.71	-0.92	-1.47	-1.88	-0.89	-0.75
Klages	-0.93	-0.83	-0.99	-1.58	-1.77	-0.96	-0.87
LSD .05 (means)	0.15	NS	NS	NS	NS	NS	NS
LSD .05 (adjustment)	--	0.21	0.16	NS	NS	NS	0.14

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

Table 23. Mean values of $\Psi_{\pi R}$ of three two-rowed barley cultivars under differential water stress of three-week-old plants, August 31, 1984.

Cultivar	Water Stress Days						
	0	1	2	3	4	5 ⁺	6 ⁺⁺
	----- MPa -----						
Clark	-0.73	-0.62	-0.80	-0.98	-1.54	-0.79	-0.64
Hector	-0.69	-0.51	-0.84	-0.92	-1.31	-0.83	-0.70
Klages	-0.82	-0.64	-0.90	-1.17	-1.69	-0.84	-0.75
LSD .05 (means)	NS	NS	NS	NS	0.24	NS	NS
LSD .05 (adjustment)	--	NS	NS	NS	0.25	NS	NS

+ = Plants were rewatered for 24 hours.

++ = Plants were rewatered for 48 hours.

differences between cultivars with respect to drought response. In general, Clark and Hector had the greater ψ_{TL} compared to Klages throughout the measurement periods. The apparent drought-resistant cultivars, Clark and Hector, tended to avoid imposed drought stress by maintaining higher leaf potentials (ψ_{TL}). This is similar to results reported by Hanson et al. (1977) with barley, Sammons et al. (1978) with soybeans, and Novero et al. (1985) and Ekanayake (1985) with rice plants. Osmotic potential adjustment was slower than total potential in both this greenhouse study and the field study (see Tables 3, 4, 16, 17, 18 and 19). Total potential adjusted significantly within a day; whereas osmotic potential generally did not adjust significantly within a day but did over several days. Leaf osmotic potential recovery was, however, as rapid as total potential recovery. The cultivars did not differ statistically for $\psi_{\pi L}$. The lack of significant differences among cultivars indicates it may not be possible to differentiate cultivars using $\psi_{\pi L}$. Irvine et al. (1980) and Fink (1979) did not find varietal differences in barley on the measured $\psi_{\pi L}$.

Examination of ψ_{PL} data indicate that drought-susceptible cultivar Klages consistently reached zero turgor at least one day earlier than the resistant cultivars. Cultivar significant differences were found from the two runs. The drought-resistant cultivars maintained greater ψ_{PL} ; this agreed well with the results obtained by Ackerson et al. (1977), Johnson and Brown (1977) and Quisenberry et al. (1985).

The $\psi_{\pi R}$ declined significantly for all three cultivars over stress days. Similar results were also recorded by Osonubi and Davis (1978) and Taylor et al. (1982).

Water Status (ψ_{TL} , $\psi_{\pi L}$, ψ_{PL} , $\psi_{\pi R}$) of Greenhouse Grown
Barley Cultivars as a Function of Water Stress

In another series of experiments plants were grown simultaneously in two different tubs; one of them was drained after the first day measurements to impose stress and the other was not drained so that water was always readily available for the plants. Only two cultivars, Clark (resistant) and Klages (susceptible) were used to study the behavior of ψ_{TL} , $\psi_{\pi L}$, ψ_{PL} and $\psi_{\pi R}$.

The analysis of variance of the data is shown in Table 24 and graphical representations of the variables over time are given in Figures 1, 2, 3 and 4. There was a highly significant difference among cultivars and stress levels for ψ_{TL} , ψ_{PL} and $\psi_{\pi R}$. All of the variables were statistically different as a function of stress days. There was a significant stress days x stress level interaction as would be expected. Figure 1 indicates that Clark had higher total potential prior to the application of stress and maintained that position throughout stress and stress recovery. On day two in the non-stressed tub Klages developed lower ψ_{TL} than Clark. It should be emphasized that this experiment was conducted in the greenhouse with considerable day time heat load. Thus the well-watered plants did develop some stress and this accounts for the downward trend in the non-stressed plants over time. Osmotic potential of leaves was not significantly different in cultivars or as a function of stress levels but did drop with stress days (Table 24 and Figure 2). Under stress, turgor potential dropped significantly with stress days (Figure 3) and after day three was lower with Klages than

Clark. There was a strong tendency for the root osmotic potential of Klages to be lower than Clark (Figure 4). Under stress the difference was slight, but was considerably greater on days two and three under non-stress conditions.

Table 24. Analysis of variance for water status of two two-rowed barley cultivars in greenhouse experiment, October 9, 1984.

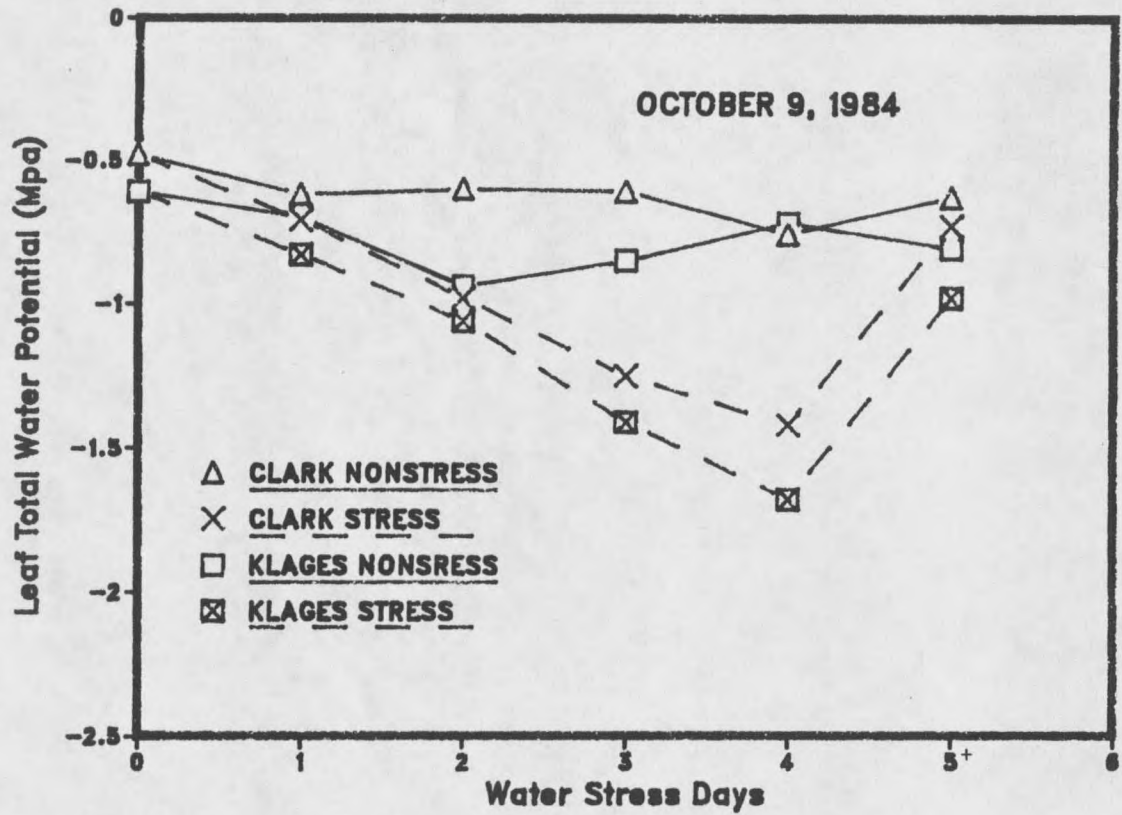
Source of Variation	df	Mean Squares			
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}	$\Psi_{\pi R}$
Cultivars (C)	1	30.400**	0.935	20.670**	24.800**
S-Levels (L)	1	117.800**	5.535	72.280**	47.800**
C x L	1	0.083	0.200	0.025	0.227
S-days (S)	5	38.010**	11.180**	12.110**	8.769**
C x S	5	0.593	1.669	1.762	0.456
L x S	5	20.710**	6.400	16.250**	7.542**
C x L x S	5	1.775	0.620	1.322	0.422
Error	24	1.269	2.580	1.386	0.544

**Denotes significance at the 1% level.

S-levels = stress levels.

S-days = stress days.

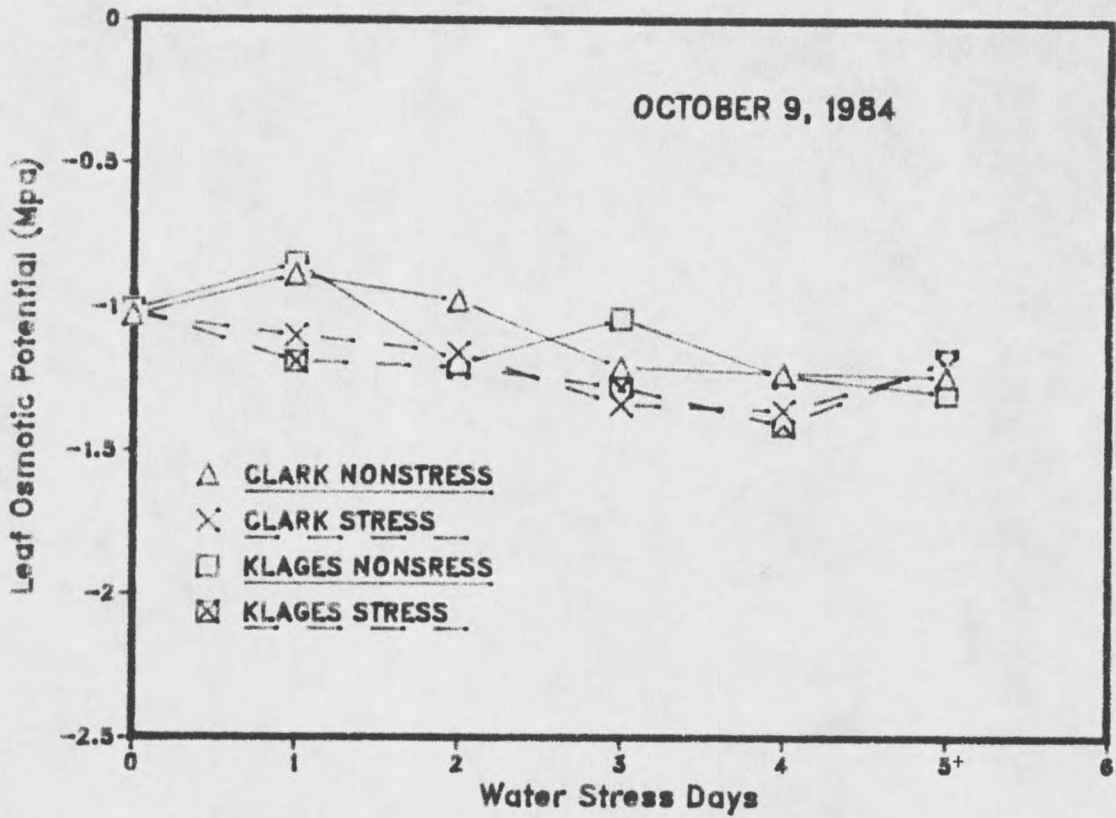
A two-tub experiment was also conducted in 1985, again using Clark and Klages as test crops. This experiment was similar to the 1984 two-tub experiment, but plants were exposed to two water stress cycles. In the first cycle, plants went from no-stress to stress and back to no-stress in one tub. We then imposed stress (no-stress, stress, relief of stress) in the stressed tub for the second cycle. Plants in the second tub were not stressed. The measurements of water status parameters were



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

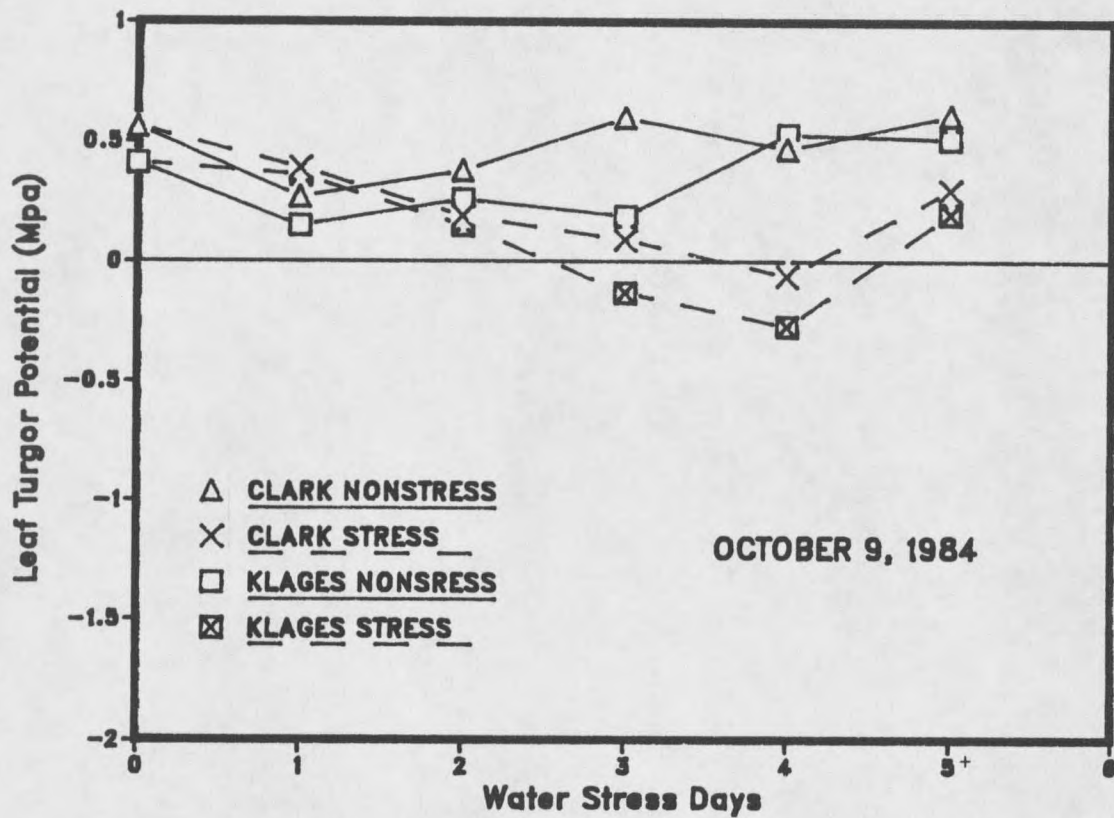
Figure 1. Effect of differential water stress on the Ψ_{TL} of two two-rowed barley cultivars of three-week-old plants.



Data points = the means of two replicate samples

+ = measurements were taken after 24 hours rewatering.

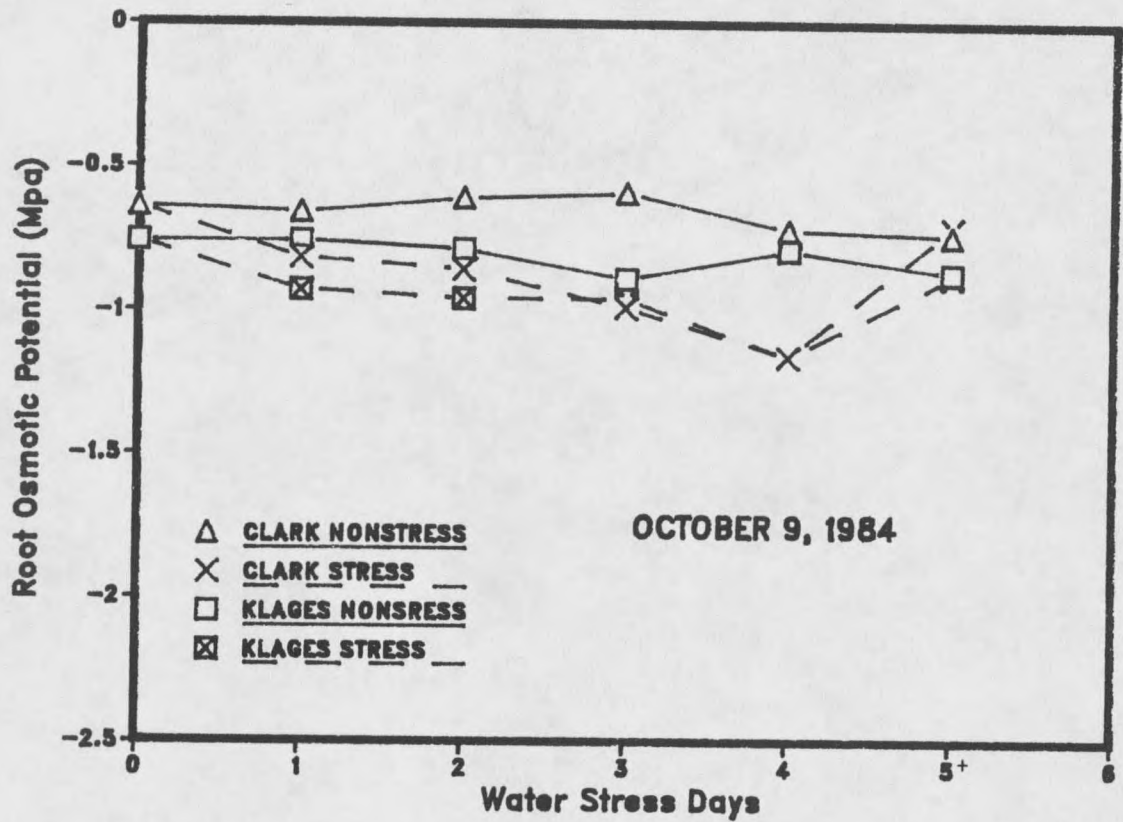
Figure 2. Effect of differential water stress on the $\Psi_{\pi L}$ of two two-rowed barley cultivars of three-week-old plants.



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

Figure 3. Effect of differential water stress on the ψ_{PL} of two two-rowed barley cultivars of three-week-old plants.



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

Figure 4. Effect of differential water stress on the $\Psi_{\pi R}$ of two two-rowed barley cultivars of three-week-old plants.

continued for six and seven days from the first and second cycle experiments, respectively.

The analysis of variance for the variables measured is presented in Table 25 (A and B). The results are shown graphically as a function of water stress days in Figures 5, 6, 7, 8, 9, 10, 11 and 12. In the first cycle (Table 25A), statistically significant differences were found in cultivars, stress levels and stress level x stress days interaction for ψ_{TL} , ψ_{PL} and $\psi_{\pi R}$. Only $\psi_{\pi R}$ differed significantly over stress days. In the second cycle (Table 25B), significant differences were observed between cultivars and stress levels as tested by ψ_{TL} and $\psi_{\pi R}$. Results in Table 25B indicate significant differences of ψ_{PL} for stress levels, stress days and stress level x stress days interaction. No significant differences of $\psi_{\pi L}$ were observed for any factor studied in either cycle.

Clark always maintained higher ψ_{TL} than Klages, both under non-stress and stress conditions (Figures 5 and 6). During the first cycle, on days 0, 1 and 3, Klages developed significantly lower ψ_{TL} in the non-stressed tub (Figure 5). Water stress did not cause a large reduction in total potential of the plants in the first cycle, but a substantial reduction was found in the second cycle (Figure 6). Lower ψ_{TL} for Klages suggests that the internal dehydration was greater in this cultivar. Very little decline of $\psi_{\pi L}$ was observed after three days water stress (Figures 7 and 8).

In the first cycle (Figure 9), no cultivar developed zero or negative ψ_{PL} , but a significant drop of ψ_{PL} was found in the second cycle (Figure 10). On day 4 and after relief of water stress, Clark developed significantly higher turgor potential under nonstress

conditions (Figure 9). Klages developed negative Ψ_{PL} one day earlier, as shown in Figure 10.

Table 25. Analysis of variance for water status of two two-rowed barley cultivars in greenhouse experiment, August 17 and 23, 1985.

Source of Variation	df	Mean Squares			
		Ψ_{TL}	$\Psi_{\pi L}$	Ψ_{PL}	$\Psi_{\pi R}$
A. First Cycle (August 17, 1985):					
Cultivars (C)	1	31.850**	0.009	31.360**	28.520**
S-Levels (L)	1	25.380**	0.152	29.450**	36.050**
C x L	1	0.110	0.130	0.008	5.210*
S-days (S)	5	0.660	2.782	2.266	10.180**
C x S	5	0.360	0.476	0.951	0.592
L x S	5	7.209**	1.723	4.005**	8.390**
C x L x S	5	0.099	0.692	0.641	0.306
Error	24	0.557	1.260	0.877	0.858

B. Second Cycle (August 23, 1985):					
Cultivars (C)	1	12.920**	1.858	4.980	14.500*
S-Levels (L)	1	154.100**	0.003	155.400**	75.210**
C x L	1	0.172	0.026	0.064	0.540
S-days (S)	6	19.240	3.233	7.752*	16.230**
C x S	6	0.416	0.484	0.468	0.927
L x S	6	16.680	2.215	8.610*	11.990**
C x L x S	6	0.095	0.441	0.340	0.571
Error	28	1.616	1.767	2.716	1.609

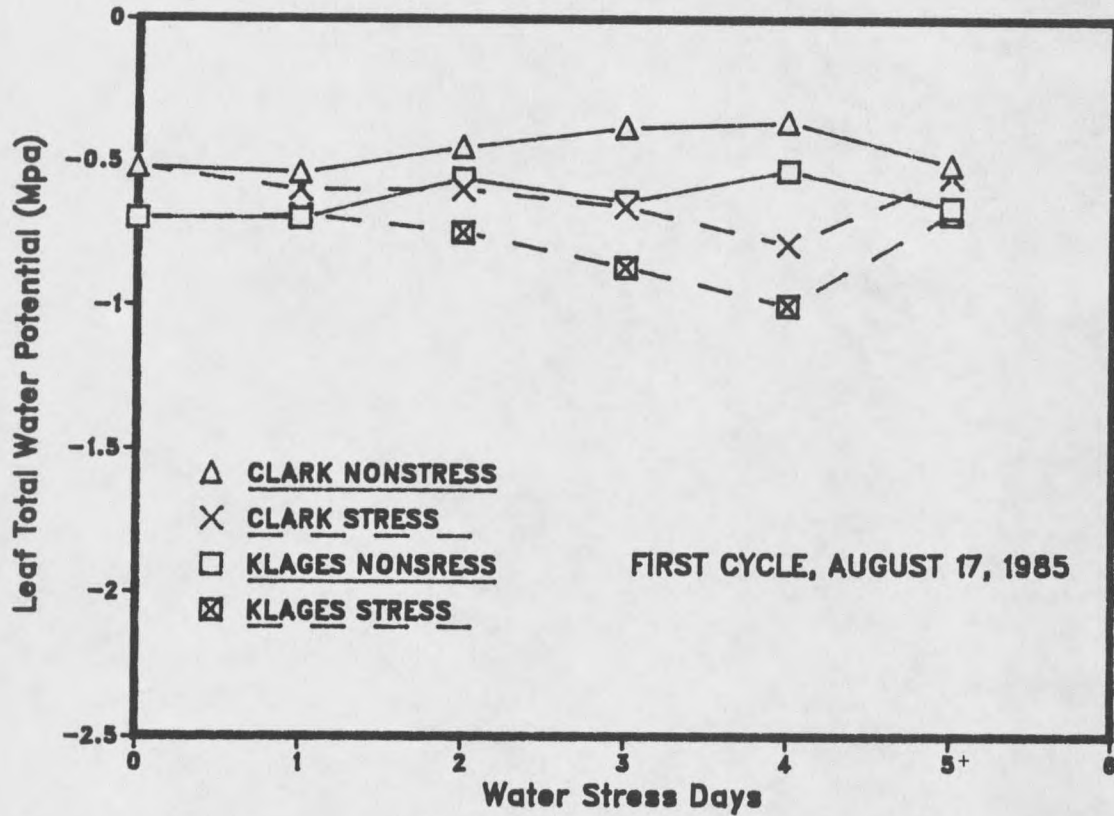
*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

S-levels = stress levels.

S-days = stress days.

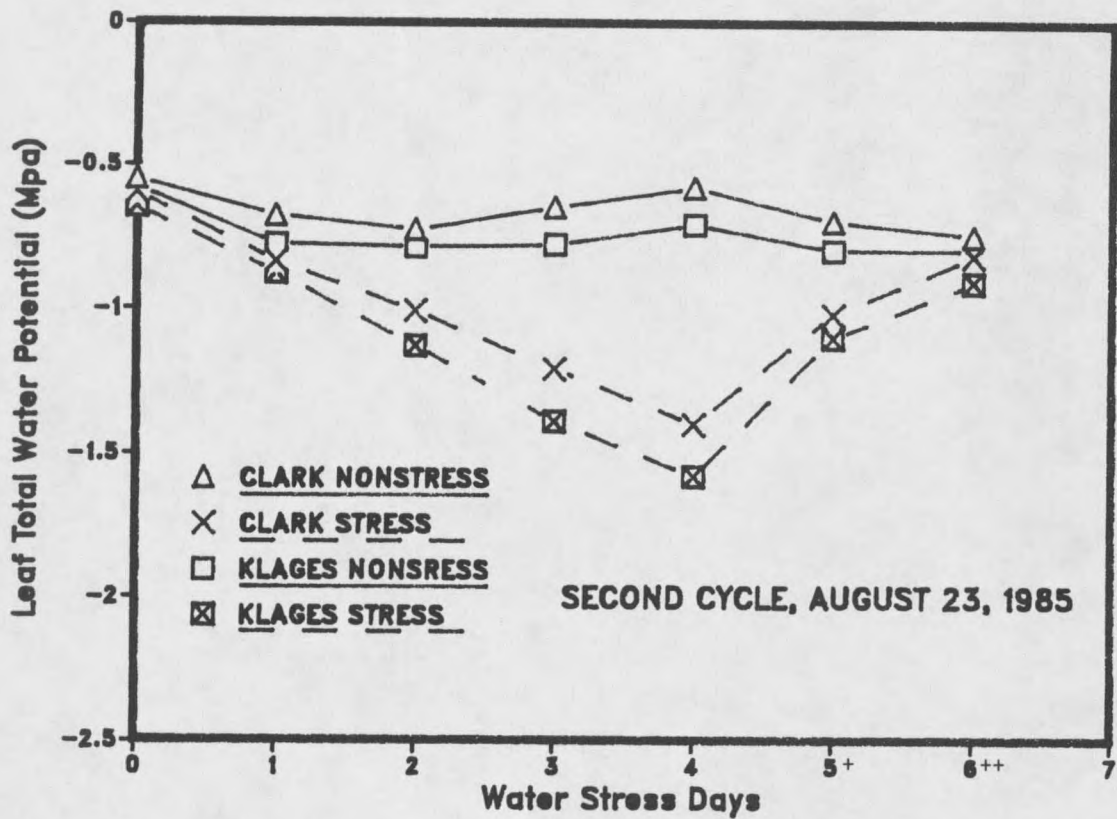
Figures 11 and 12 indicate that Clark had higher $\Psi_{\pi R}$ at the first measurement day and maintained this position throughout stress and stress recovery. On days 3 and 4 and after rewatering in the first cycle (Figure 11), and on day 2 and after relief of water stress in the



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

Figure 5. Effect of differential water stress on the Ψ_{TL} of two two-rowed barley cultivars of three-week-old plants (first cycle).

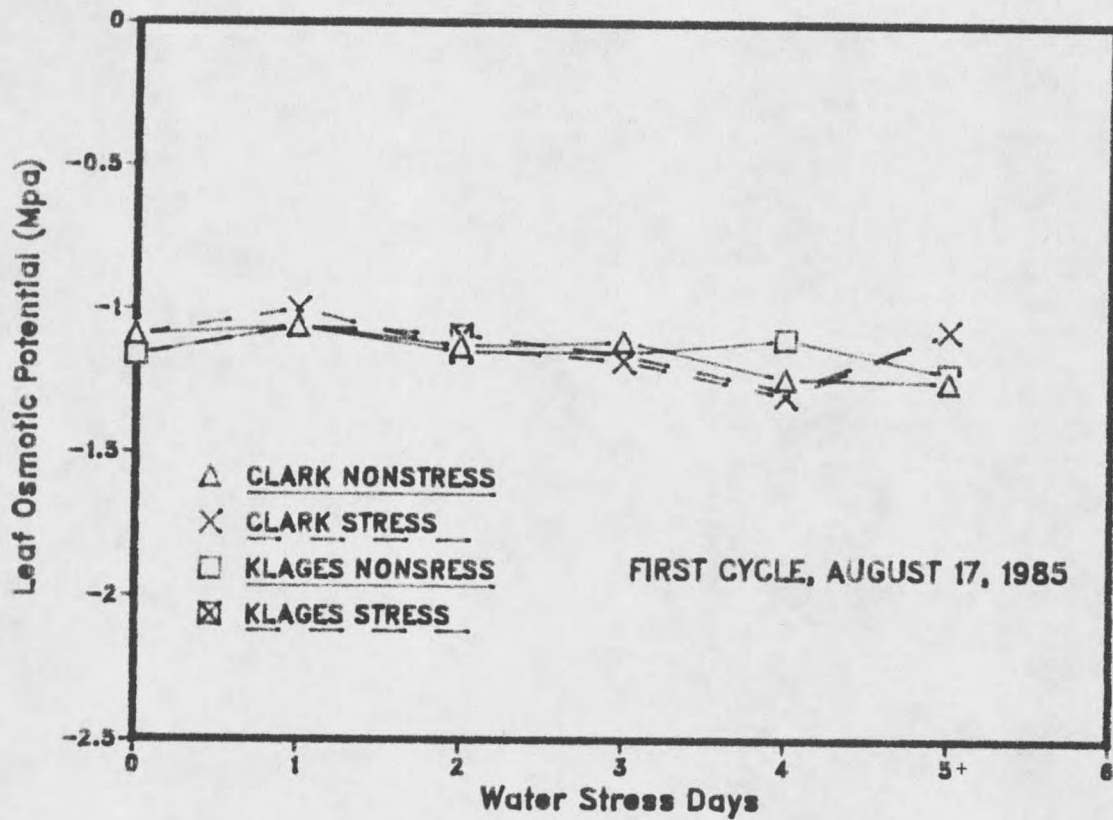


Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

++ = measurements were taken after 48 hours rewatering.

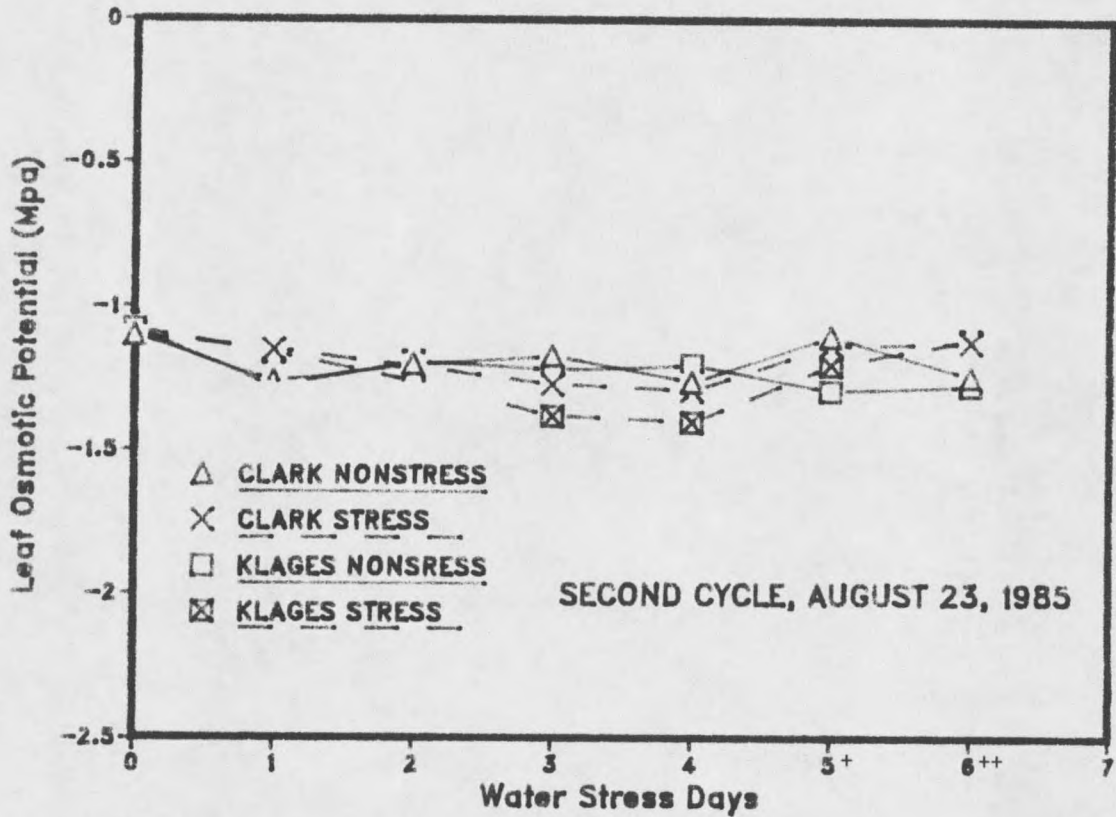
Figure 6. Effect of differential water stress on the Ψ_{TL} of two two-rowed barley cultivars of three-week-old plants (second cycle).



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

Figure 7. Effect of differential water stress on the $\psi_{\pi L}$ of two two-rowed barley cultivars of three-week-old plants (first cycle).

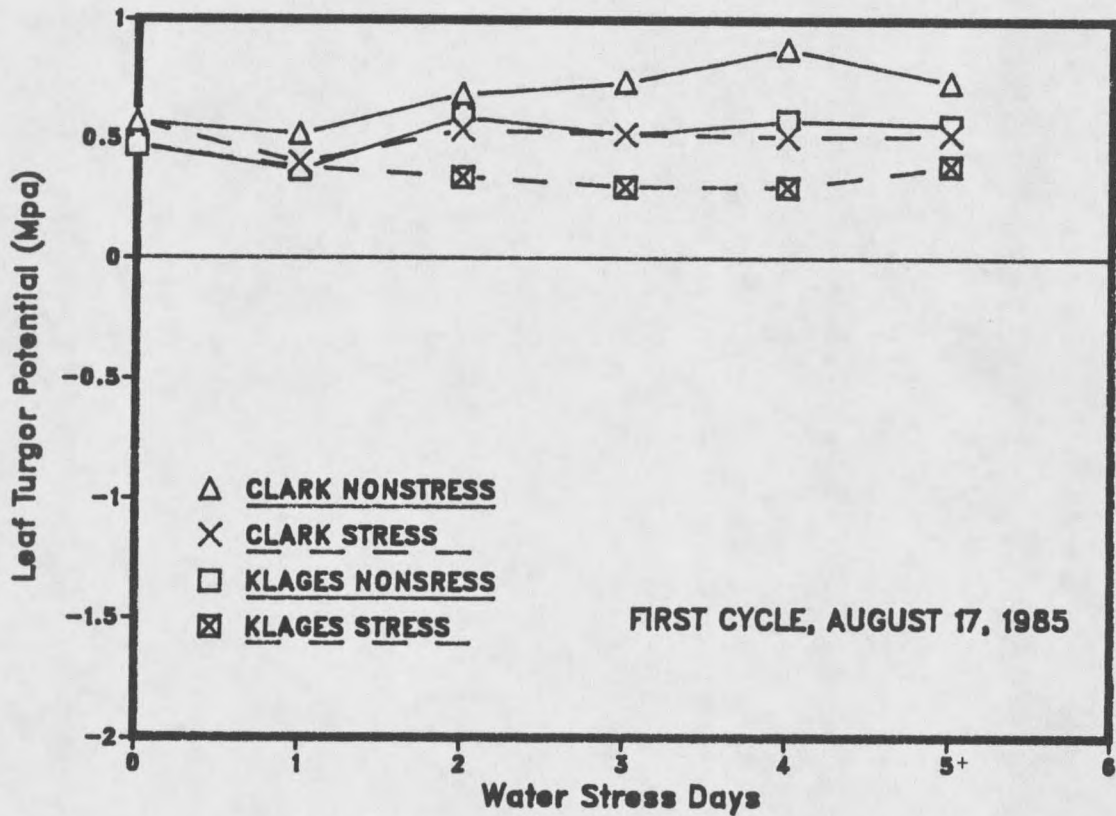


Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

++ = measurements were taken after 48 hours rewatering.

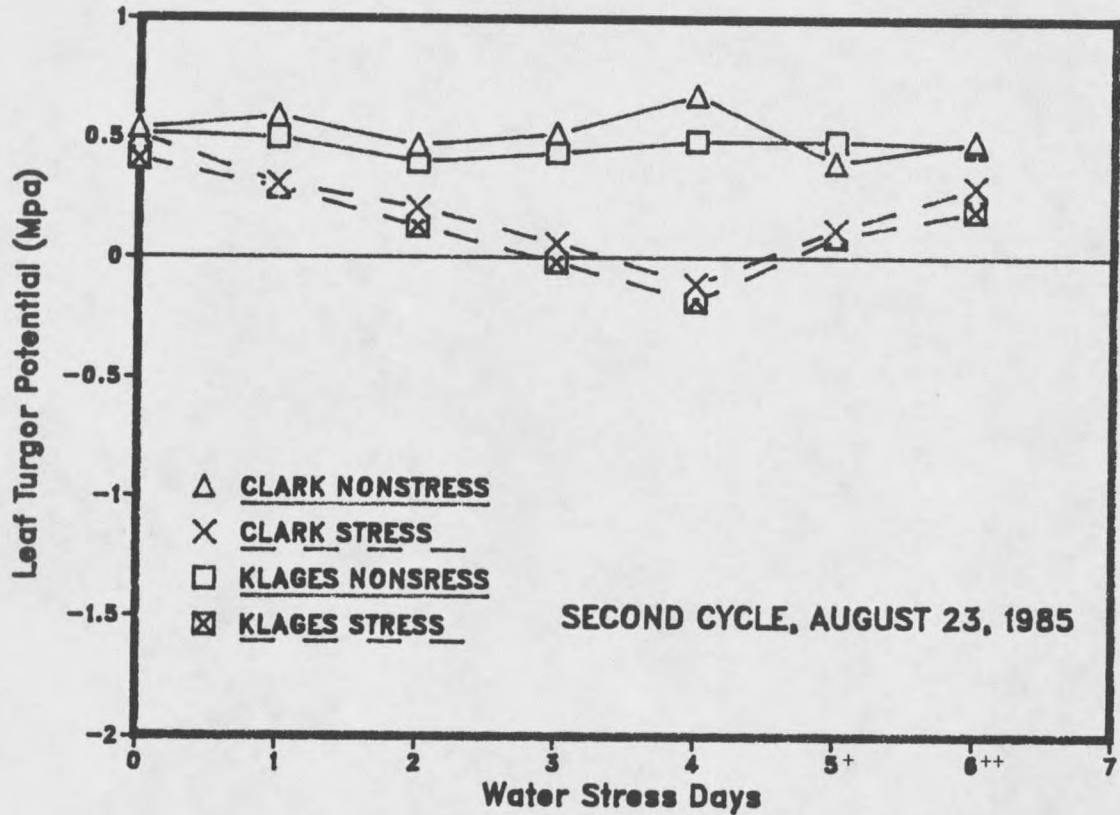
Figure 8. Effect of differential water stress on the $\Psi_{\pi L}$ of two two-rowed barley cultivars of three-week-old plants (second cycle).



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

Figure 9. Effect of differential water stress on the ψ_{PL} of two two-rowed barley cultivars of three-week-old plants (first cycle).

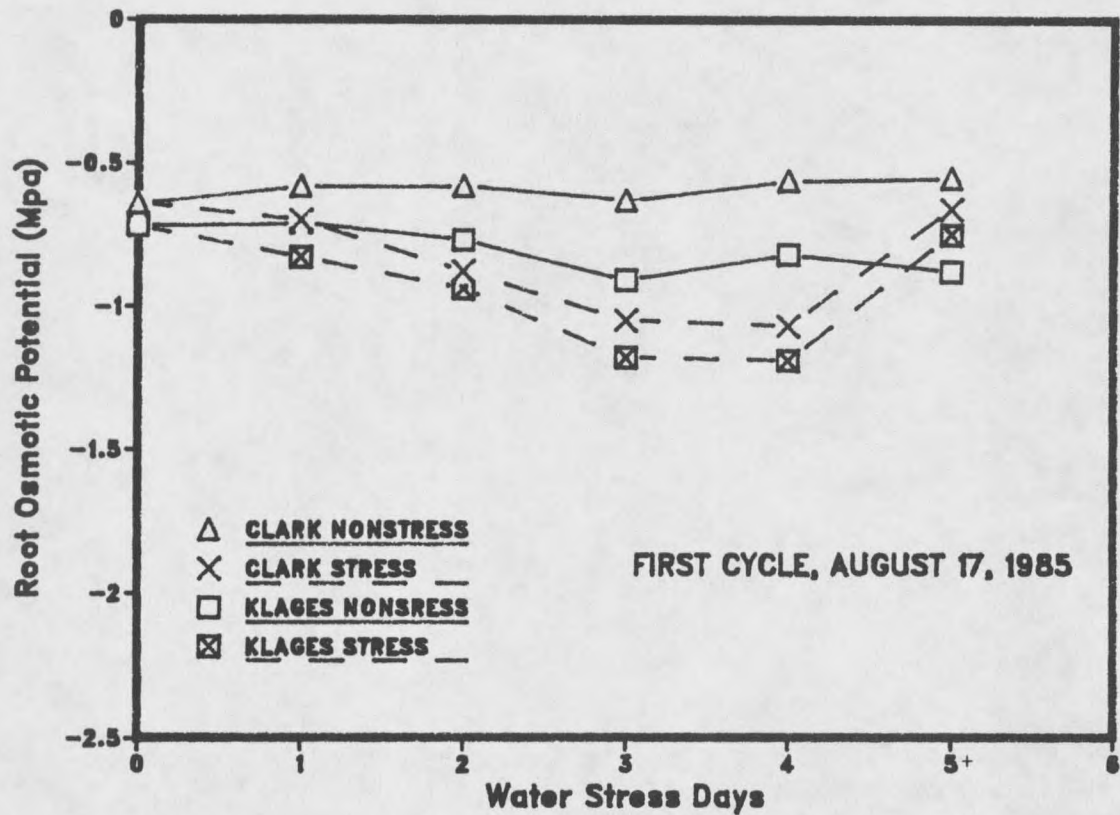


Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

++ = measurements were taken after 48 hours rewatering.

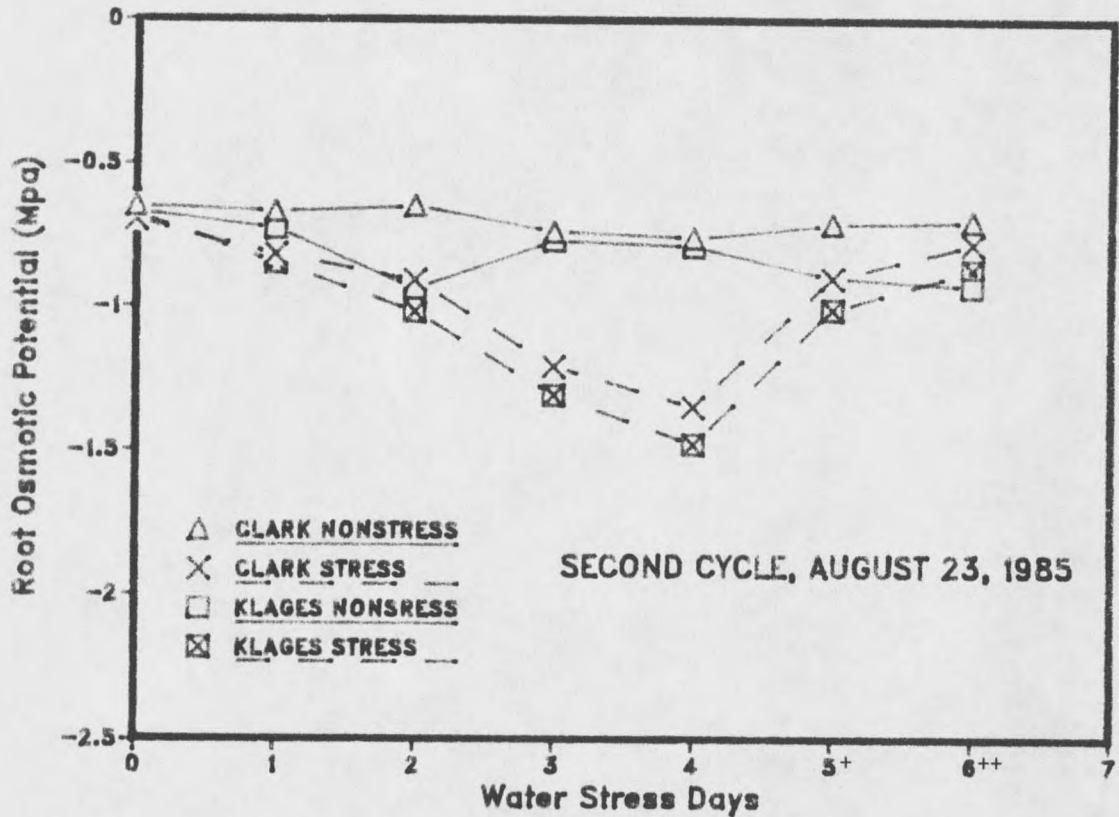
Figure 10. Effect of differential water stress on the Ψ_{PL} of two two-rowed barley cultivars of three-week-old plants (second cycle).



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

Figure 11. Effect of differential water stress on the $\Psi_{\pi R}$ of two two-rowed barley cultivars of three-week-old plants (first cycle).



Data points = the means of two replicate samples.

+ = measurements were taken after 24 hours rewatering.

++ = measurements were taken after 48 hours rewatering.

Figure 12. Effect of differential water stress on the $\Psi_{\pi R}$ of two two-rowed barley cultivars of three-week-old plants (second cycle).

second cycle (Figure 12), Clark developed significantly higher $\psi_{\pi R}$ in the nonstressed tubs.

Clark is, in our experience, considerably more drought-tolerant than Klages and in the earlier work there appeared to be a general difference in the way the two responded to the treatments made. These results are consistent with those of field (1982) and previous greenhouse experiments (1984). Examination of the results suggests that ψ_{TL} , ψ_{PL} and $\psi_{\pi R}$ may be good indicators of internal plant moisture stress. Clark avoided a significant decrease of $\psi_{\pi R}$ as soil moisture deficits increased in the study. Lower $\psi_{\pi R}$ in Klages indicates that the roots have dehydrated more or accumulated more solutes than Clark at the equivalent soil moisture stress.

Water Status (ψ_{TL} , RS, RWC) of Five Resistant and Five
Susceptible Cultivars of Two- and Six-Rowed
Barley Grown in the Greenhouse

Careful study of the results of the field (1982) and several greenhouse studies (1984 and 1985) indicated that cultivars believed to be more drought resistant consistently maintained higher ψ_{TL} under non-stress conditions than more drought susceptible cultivars. Based on this indication, experiments utilizing ten two- and six-rowed cultivars were conducted. Five drought-tolerant and five drought-susceptible cultivars were selected from each head type; measurements were then taken of predawn ψ_{TL} , stomatal diffusion resistance as stress developed and relative water content of leaves at maximum diffusion resistance.

Analyses of variance for ψ_{TL} of two- and six-rowed barley are presented in Tables 26 and 27. Significant block differences were

found for Ψ_{TL} of January 14 and March 15 (Tables 26 and 27). Cultivars differed highly significantly in all trials as shown in Tables 26 and 27. Although the block differences cannot be explained, they did not affect cultivar differences. The contrast comparison was performed to detect the group variation between resistant (R) and susceptible (S) cultivars. Highly significant R vs. S differences were found in all

Table 26. Analysis of variance and contrast comparison predawn leaf total water potential of resistant vs. susceptible groups for ten two-rowed barley cultivars in greenhouse experiment, January 1986.

Source of Variation	df	Mean Squares		
		January 8	January 14	January 20
Blocks	4	0.0632	0.5487**	0.1583
Cultivars	9	1.7750**	0.7246**	1.7960**
R vs. S+	1	12.6000**	4.3220**	12.7000**
Error	36	0.2009	0.1357	0.2956

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 27. Analysis of variance and contrast comparison of predawn leaf total water potential of resistant vs. susceptible groups for ten six-rowed barley cultivars in greenhouse experiment, March 1986.

Source of Variation	df	Mean Squares		
		March 2	March 8	March 15
Blocks	4	0.5137	0.0847	1.0640**
Cultivars	9	1.6590**	1.8050**	1.8590**
R vs. S+	1	7.7620**	9.8570**	10.0400**
Error	36	0.2968	0.1378	0.2415

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

experiments (Tables 26 and 27) indicating that the original choice of resistant and susceptible cultivars was valid.

Analysis of variance over dates (Table 28) indicates significant differences in ψ_{TL} among two- and six-rowed cultivars. There are also significant differences among dates and cultivar x date interaction for the measured ψ_{TL} for two- and six-rowed barley, respectively. Blocks did not differ for ψ_{TL} either for two- or six-rowed barley.

Table 28. Analysis of variance over dates of predawn leaf total water potential for ten two- and six-rowed barley cultivars in greenhouse experiment, 1986.

Source of Variation	df	Mean Squares	
		Two-Row	Six-Row
Blocks	4	0.0025	0.0031
Cultivars (C)	9	0.0346**	0.0380**
Dates (D)	2	0.0165**	0.0028
C x D	18	0.0042	0.0076**
Error	116	0.0022	0.0026

**Denotes significance at the 1% level.

The mean differences of the two- and six-rowed barley from the individual experiment and for the combined data over dates were tested by LSD and are reported in Tables 29 and 30. There were highly significant differences of ψ_{TL} in all experiments. Although the contrast comparisons between resistant and susceptible cultivars are highly significant at all trials (Tables 26 and 27) in comparing between cultivars across dates, there are obvious inconsistencies. With the two-rowed cultivars, Clark had higher ψ_{TL} in all three trials, whereas New Moravian was high in the first trial but relatively low on the

Table 29. Predawn mean values of Ψ_{TL} for ten two-rowed barley cultivars, January 1986.

Cultivar	Leaf Total Water Potential			
	January 8	January 14	January 20	Over Dates
	----- MPa -----			
Clark (R)	-0.14	-0.13	-0.13	-0.13
Compana (R)	-0.18	-0.17	-0.15	-0.17
Dekap (R)	-0.16	-0.13	-0.14	-0.14
Hector (R)	-0.17	-0.12	-0.17	-0.15
New Moravian (R)	-0.12	-0.18	-0.21	-0.17
Georgie (S)	-0.24	-0.19	-0.23	-0.22
Ingrid (S)	-0.24	-0.19	-0.30	-0.24
Klages (S)	-0.26	-0.24	-0.25	-0.25
Maris Mink (S)	-0.23	-0.20	-0.25	-0.22
Zephyr (S)	-0.31	-0.20	-0.27	-0.26

LSD .05	0.05	0.04	0.07	0.03

Table 30. Predawn mean values of Ψ_{TL} for ten six-rowed barley cultivars, March 1986.

Cultivar	Leaf Total Water Potential			
	March 2	March 8	March 15	Over Dates
	----- MPa -----			
Briggs (R)	-0.12	-0.13	-0.13	-0.13
Larker (R)	-0.18	-0.12	-0.17	-0.16
Trebi (R)	-0.19	-0.15	-0.14	-0.16
Titan (R)	-0.17	-0.18	-0.19	-0.18
Glacier (R)	-0.20	-0.18	-0.19	-0.19
Hiland (S)	-0.25	-0.19	-0.22	-0.22
Steveland (S)	-0.21	-0.26	-0.29	-0.25
Bonneville (S)	-0.25	-0.20	-0.32	-0.25
Vantage (S)	-0.33	-0.32	-0.20	-0.28
Unitan (S)	-0.21	-0.25	-0.25	-0.23

LSD .05	0.07	0.05	0.06	0.04

second and third trials. There were similar occurrences in the susceptible lines. Klages had relatively low Ψ_{TL} at all three trials but Zephyr had a relatively high Ψ_{TL} on the second trial and low values on trials of January 8 and 20. The same type of inconsistencies were found with the six-rowed cultivars (Table 30).

Clearly a single run is not adequate to separate cultivars within the resistant-susceptible groups or even clearly between the groups, in spite of the highly significant contrast comparison. However, analysis of the combined data from the three runs greatly improved the confidence for separating resistant and susceptible groups as well as separation within the groups. Based on the LSD value (0.03) from the combined data set, every resistant cultivar had higher Ψ_{TL} than any of the susceptible cultivars in the two-rowed types. Also, there are strong indications of differences within resistant or susceptible groups. Clark had higher Ψ_{TL} than Compana and New Moravian in the resistant set and Zephyr had lower Ψ_{TL} than Georgie and Maris Mink in the susceptible set.

Similar results were obtained with the six-rowed cultivars. However, in spite of the highly significant contrast comparison between the two groups, on an individual trial basis there were no differences between some of the resistant and susceptible cultivars. For instance, Titan and Glacier (resistant) are not statistically different from Hiland and Unitan (susceptible). Apparently the differentiation between the resistant and susceptible cultivars, based on Eslick's method E (1978) approach, is not as valid for the six-rowed as for the two-rowed cultivars; but with both head types, data combined over three runs allow

clear separation of some of these lines into resistant and susceptible groups that do agree well with Eslick's analysis.

The measured predawn ψ_{TL} results are consistent with those of field (0500 h readings) and nonstress of previous greenhouse experimental findings. Cultivars differed highly significantly as investigated by predawn ψ_{TL} . These results agree well with those obtained by Shouse et al. (1980) and Turk et al. (1980) with cowpeas. However, they did not specify their cultivars as drought resistant or susceptible prior to making measurements. They just reported that the measured predawn ψ_{TL} appeared to be a better indicator of internal plant moisture stress than the afternoon ψ_{TL} with respect to drought-avoiding characteristics. Boyer (1970) pointed out ψ_{TL} values obtained by use of pressure chamber are relative values useful in making comparisons, which is also desired here.

Tables 31, 32 and 33 summarize the analyses of variance and contrast comparisons for two-rowed barley stomatal diffusive resistance (R_s). Significant block differences were found in the PM recorded R_s for 0 water stress day (Table 31). Results in Table 32 also indicate that there are block differences for R_s in the PM, AM and PM of 0 and day 1, respectively, probably due to rapid changes in water stress with time. Cultivars differed significantly for the measured R_s in the AM of 0 and day 1 and PM of day 2 (Tables 31 and 32) due to water stress effects. There is no block difference for R_s in any water stress day of the third run, as shown in Table 33. Mean squares presented in Table 33 reveal that R_s differs statistically only at PM and AM measurements after first and second day water stress effects, respectively. Highly

Table 31. Analysis of variance and contrast comparison of stomatal diffusive resistance of resistant vs. susceptible groups for ten two-rowed barley cultivars in greenhouse experiment, January 8, 1986.

Source of Variation	df	Water Stress Days					
		0		1		2	
		AM	PM	AM	PM	AM	PM
----- Mean Squares -----							
Blocks	4	0.9252	7.4440**	0.4470	0.4743	0.4628	2.6260
Cultivars	9	2.1550**	0.1591	1.3310*	1.3320	1.3480	6.0200**
R vs. S+	1	16.5900**	0.9522	11.6200**	11.4200*	10.3100**	53.2500**
Error	36	0.4085	0.7513	0.5260	1.5860	0.9565	2.1120

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 32. Analysis of variance and contrast comparison of stomatal diffusive resistance of resistant vs. susceptible groups for ten two-rowed barley cultivars in greenhouse experiment, January 14, 1986.

		Water Stress Days					
Source of Variation	df	0		1		2	
		AM	PM	AM	PM	AM	PM
----- Mean Squares -----							
Blocks	4	0.6093	6.0540**	1.1280*	1.8150*	1.3650	0.9998
Cultivars	9	2.3400**	0.1783	3.6050**	1.0980	0.3049	5.0320**
R vs. S+	1	19.8400**	1.2480	30.2600**	8.4050**	1.8820	34.7800**
Error	36	0.4223	0.8968	0.3167	0.5883	0.8959	0.9559

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 33. Analysis of variance and contrast comparison of stomatal diffusive resistance of resistant vs. susceptible groups for ten two-rowed barley cultivars in greenhouse experiment, January 20, 1986.

Source of Variation	df	Water Stress Days					
		0		1		2	
		AM	PM	AM	PM	AM	PM
----- Mean Squares -----							
Blocks	4	0.2085	0.5687	0.2385	0.4452	0.4607	1.8830
Cultivars	9	0.1966	0.2148	0.2867	2.3790**	1.2370**	2.0330
R vs. S+	1	1.2480*	1.4790*	1.4800*	20.6100**	10.1200**	16.7000**
Error	36	0.2480	0.3223	0.2363	0.3228	0.3207	2.1440

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

significant differences were found between resistant and susceptible groups as tested by contrast comparison in most of the AM and PM measured Rs (Tables 31, 32 and 33).

Mean differences were tested by LSD, as shown in Tables 34, 35 and 36. Significant differences were observed for the measured Rs at 0 and after day 1 water stress in the AM and also at day 2 PM (Table 34). A similar pattern for Rs was established for the January 14 trial (Table 35). Results in Table 36 indicate that in the third run barley cultivars differed only in the PM and AM measured Rs after one and two days water stress, respectively.

The analyses of variance and contrast comparison of six-rowed barley cultivars for stomatal diffusive resistance (Rs) are reported in Tables 37, 38 and 39. As indicated in Tables 37, 38 and 39, there were

Table 34. Mean values of stomatal diffusive resistance for ten two-rowed barley cultivars as a function of water stress days and time of day, January 8, 1986.

Cultivar	Water Stress Days					
	0		1		2	
	AM	PM	AM	PM	AM	PM
	----- sec/cm -----					
Clark	1.4	3.2	1.9	6.9	4.6	12.6
Compana	1.2	3.4	1.8	7.1	5.0	12.5
Dekap	1.0	3.4	2.0	6.9	4.8	12.3
Hector	1.2	3.3	1.9	7.1	4.4	12.3
New Moravian	1.4	3.6	2.1	6.8	4.7	12.2
Georgie	2.2	3.2	3.0	6.1	5.3	10.4
Ingrid	2.1	3.1	2.8	5.9	5.5	10.2
Klages	2.3	3.1	2.9	6.0	5.9	10.5
Maris Mink	2.9	3.2	2.9	6.2	5.7	10.4
Zephyr	2.6	3.0	2.9	6.0	5.7	10.2
LSD .05	0.8	NS	0.9	NS	NS	1.9

Table 35. Mean values of stomatal diffusive resistance for ten two-rowed barley cultivars as a function of water stress days and time of day, January 14, 1986.

Cultivar	Water Stress Days					
	0		1		2	
	AM	PM	AM	PM	AM	PM
	----- sec/cm -----					
Clark	0.7	3.6	1.9	6.5	4.4	11.6
Compana	1.0	3.5	1.9	6.5	4.8	11.4
Dekap	0.8	3.4	2.1	6.4	4.7	11.9
Hector	1.0	3.7	1.8	6.3	4.6	12.2
New Moravian	0.8	3.6	2.0	6.6	4.9	10.8
Georgie	1.9	3.2	3.2	5.5	4.9	9.3
Ingrid	2.3	3.2	3.8	5.7	5.2	10.5
Klages	2.4	3.3	3.8	6.0	5.1	10.2
Maris Mink	2.0	3.3	3.4	5.3	5.1	9.6
Zephyr	2.1	3.3	3.2	5.7	4.9	9.9
LSD .05	0.8	NS	0.7	NS	NS	1.3

Table 36. Mean values of stomatal diffusive resistance for ten two-rowed barley cultivars as a function of water stress days and time of day, January 20, 1986.

Cultivar	Water Stress Days					
	0		1		2	
	AM	PM	AM	PM	AM	PM
	----- sec/cm -----					
Clark	1.3	3.8	2.3	7.9	4.8	12.9
Compana	1.1	4.0	2.4	7.8	4.6	12.5
Dekap	1.2	3.9	2.2	7.7	4.7	12.9
Hector	1.4	4.0	2.3	7.6	5.0	12.6
New Moravian	1.2	3.9	2.5	7.7	4.9	12.5
Georgie	1.5	3.6	2.5	6.6	5.6	11.7
Ingrid	1.7	3.7	2.7	6.7	5.5	11.5
Klages	1.4	3.5	2.6	6.4	5.6	11.7
Maris Mink	1.5	3.7	2.6	6.3	5.7	11.2
Zephyr	1.5	3.4	3.0	6.5	5.9	11.4
LSD .05	NS	NS	NS	0.7	0.7	NS

Table 37. Analysis of variance and contrast comparison of stomatal diffusive resistance of resistant vs. susceptible groups for ten six-rowed barley cultivars in greenhouse experiment, March 2, 1986.

		Water Stress Days					
Source of Variation	df	0		1		2	
		AM	PM	AM	PM	AM	PM
----- Mean Squares -----							
Blocks	4	0.3097	2.0020	0.4677	2.2130	1.3130	0.7003
Cultivars	9	1.7780**	0.2008	0.7774	2.1210	0.1556	1.7190
R vs. S+	1	13.2100**	1.3450	4.6210	16.5900**	0.9800	10.2100*
Error	36	0.4694	1.3550	0.4879*	1.3710	1.6590	1.7900

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 38. Analysis of variance and contrast comparison of stomatal diffusive resistance of resistant vs. susceptible groups for ten six-rowed barley cultivars in greenhouse experiment, March 8, 1986.

Source of Variation	df	Water Stress Days					
		0		1		2	
		AM	PM	AM	PM	AM	PM
----- Mean Squares -----							
Blocks	4	0.4060	1.6740	2.1610	1.8400	1.2900	2.2190
Cultivars	9	1.8100**	0.2286	1.8510	2.2960*	1.0380	4.4630
R vs. S+	1	13.1100**	1.4450	16.0200**	16.7000**	6.4800*	36.6400**
Error	36	0.3769	1.3900	1.1390	1.0760	0.9164	2.1760

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 39. Analysis of variance and contrast comparison of stomatal diffusive resistance of resistant vs. susceptible groups for ten six-rowed barley cultivars in greenhouse experiment, March 15, 1986.

Source of Variation	df	Water Stress Days					
		0		1		2	
		AM	PM	AM	PM	AM	PM
		----- Mean Squares -----					
Blocks	4	0.4117	2.0380	0.6832	0.5797	0.4322	2.1350
Cultivars	9	1.4500**	0.2721	0.6691	1.0080	1.2130	1.5650
R vs. S+	1	10.8600**	1.4790	5.4450*	5.7800**	8.1610**	10.3100*
Error	36	0.3708	1.3480	0.7583	0.7613	0.9309	2.2090

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

no block differences for Rs. Significant cultivar differences were found only in the AM measured Rs, as shown in Tables 37 and 39. There were also significant differences for cultivars at 0 and after day 1 water stress in the AM and PM, respectively, as indicated by Rs (Table 38). Contrast comparison tests indicate that resistant groups differed significantly in most of the AM and PM measurements of Rs (Tables 37, 38 and 39).

The mean differences of Rs were tested by LSD and are given in Tables 40, 41 and 42. The significant differences in Rs were found at 0 water stress day in the AM for all dates (Tables 40, 41 and 42). Cultivars also differed in Rs at day 1 water stress in the PM (Table 41).

Results on stomatal diffusion resistance for the two head types are somewhat confusing and inconsistent. However, there are general trends that are very interesting and that may help explain the problems encountered in the past of the use of diffusion resistance to separate between resistant and susceptible lines (Tables 34, 35, 36, 40, 41 and 42). Under no-stress conditions (AM of 0-day), diffusion resistance of resistant lines was consistently lower than for susceptible lines. As stress developed after this first Rs measurement, there was a consistent increase in diffusion resistance of all lines; but the general pattern of stress development was confusing. However, by the PM of the third day, resistant lines had developed generally greater diffusion resistance than the susceptible lines. Thus, there was a general reversal of diffusion resistance between the resistant and susceptible lines in going from no-stress to high-stress conditions and between these two

Table 40. Mean values of stomatal diffusive resistance for ten six-rowed barley cultivars as a function of water stress days and time of day, March 2, 1986.

Cultivar	Water Stress Days					
	0		1		2	
	AM	PM	AM	PM	AM	PM
	----- sec/cm -----					
Briggs	1.1	3.4	1.9	7.6	5.3	12.8
Larker	1.5	3.3	2.0	7.8	5.3	13.0
Trebi	1.3	3.5	1.9	7.0	5.5	12.5
Titan	1.5	3.2	1.7	7.4	5.5	13.3
Glacier	1.2	3.4	2.1	7.2	5.3	12.8
Hiland	2.3	3.1	2.9	6.3	5.5	12.4
Steveland	2.1	3.0	2.2	6.3	5.7	11.8
Bonneville	2.9	3.2	2.5	5.9	5.7	11.6
Vantage	2.5	3.0	2.8	6.2	5.7	11.6
Unitan	2.0	3.1	2.3	6.4	5.6	12.4
LSD .05	0.8	NS	NS	NS	NS	NS

Table 41. Mean values of stomatal diffusive resistance for ten six-rowed barley cultivars as a function of water stress days and time of day, March 8, 1986.

Cultivar	Water Stress Days					
	0		1		2	
	AM	PM	AM	PM	AM	PM
	----- sec/cm -----					
Briggs	1.2	3.4	2.3	7.4	5.2	12.4
Larker	1.2	3.3	2.1	8.1	4.8	11.9
Trebi	1.5	3.3	2.0	7.4	5.1	12.2
Titan	1.0	3.5	2.2	7.7	4.6	11.5
Glacier	1.4	3.7	2.2	7.5	4.5	12.2
Hiland	2.2	3.0	3.4	6.3	5.3	10.3
Steveland	2.6	3.2	3.2	6.3	5.6	10.3
Bonneville	2.1	3.1	3.2	6.2	5.4	10.2
Vantage	1.9	3.1	3.5	7.0	5.9	10.8
Unitan	2.7	3.1	3.3	6.5	5.5	10.0
LSD .05	0.8	NS	NS	1.3	NS	NS

Table 42. Mean values of stomatal diffusive resistance for ten six-rowed barley cultivars as a function of water stress days and time of day, March 15, 1986.

Cultivar	Water Stress Days					
	0		1		2	
	AM	PM	AM	PM	AM	PM
	----- sec/cm -----					
Briggs	1.5	3.3	2.0	7.5	4.4	11.8
Larker	1.2	3.5	1.9	6.9	4.8	11.3
Trebi	1.1	3.3	2.1	7.2	5.1	12.3
Titan	1.1	3.6	1.7	6.7	4.7	11.6
Glacier	1.4	3.2	2.0	6.9	4.9	11.7
Hiland	2.1	2.9	2.5	6.6	5.7	11.1
Steveland	2.5	3.0	2.7	6.3	5.7	10.8
Bonneville	2.4	3.2	2.5	6.7	5.1	10.4
Vantage	2.2	3.1	2.6	6.2	5.8	10.9
Unitan	1.7	3.1	2.7	6.0	5.6	11.0
LSD .05	0.8	NS	NS	NS	NS	NS

extremes the results are generally unpredictable. This pattern of results may partially explain the problems encountered in the past in using diffusion resistance as a separator between lines. Resistant lines apparently have low resistance under no-stress and high resistance at high stress; the reversal is true for susceptible lines. Data obtained between these two extremes are difficult to define and may lead to conflicting conclusions. These data may have been improved with more replications; Jones (1978) points out the need for a large number of replications in diffusion resistance measurements. With the number of replications used, R_s could not be used to separate within groups and often not between groups. Only the generalizations given above could be drawn. Blum (1974) measured R_s only in the afternoon on resistant and

susceptible sorghum lines. At this time (PM) the lines were stressed and he reported that susceptible lines had high Rs. This disagrees with our data with barley which indicates that resistant lines have higher Rs under stress (PM). Quarrie and Jones (1979) found genotypic variations of Rs of wheat, but they did not specify from their experience whether some of their cultivars were drought-resistant or susceptible lines prior to Rs investigation.

The analyses of variance and contrast comparison for two- and six-rowed barley relative water content (RWC) are given in Tables 43 and 44. There were block differences in the two-rowed trials (January 8 and 14) and six-rowed trials (March 8 and 15) for the measured RWC (Tables 43 and 44), but they did not mask the cultivar differences. Highly significant differences in RWC were found in two- and six-rowed barley cultivars. Results indicated that there were highly significant differences in RWC of resistant vs. susceptible groups of both head types at every date, as tested by contrast comparison tests (Tables 43 and 44). Analysis of variance (Table 45) over dates indicates significant differences of RWC for blocks among cultivars and dates for the two- and six-rowed barley.

The LSD analyses of RWC for the two- and six-rowed barley lines for all trials and for the combined data are shown in Tables 46 and 47. The resistant cultivars consistently had higher RWC than did the susceptible lines; this agrees with the diffusion resistance data which showed higher resistance to water loss in the resistant sets under high stress. This higher water content under high stress of the resistant lines may allow metabolic processes (Gaff and Carr, 1961; May and Milthrope, 1962)

to continue under stress. Resistant two-rowed lines, with few exceptions, had significantly higher RWC than any of the susceptible lines. When analyzed over dates (Tables 46 and 47), all resistant lines had higher RWC than any of the susceptible lines, but no separation was possible within the resistant or susceptible groups. However, the total

Table 43. Analysis of variance and contrast comparison of relative water content of resistant vs. susceptible groups for ten two-rowed barley cultivars in greenhouse experiment, January 1986.

Source of Variation	df	Mean Squares		
		January 8	January 14	January 20
Blocks	4	336.10**	173.00**	34.17
Cultivars	9	235.30**	213.50**	165.40**
R vs. S+	1	1978.00**	1670.00**	1205.00**
Error	36	76.97	33.73	34.52

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 44. Analysis of variance and contrast comparison of relative water content of resistant vs. susceptible groups for ten six-rowed barley cultivars in greenhouse experiment, March 1986.

Source of Variation	df	Mean Squares		
		March 2	March 8	March 15
Blocks	4	44.94	18.73**	14.77*
Cultivars	9	162.30**	61.62**	105.70**
R vs. S+	1	1186.00**	320.50**	678.60**
Error	36	45.54	2.63	5.20

**Denotes significance at the 1% level.

R vs. S+ = drought resistant vs. drought susceptible.

Table 45. Analysis of variance over dates for relative water content of ten two- and six-rowed barley cultivars in greenhouse experiment, 1986.

Source of Variation	df	Mean Squares	
		Two-Row	Six-Row
Blocks	4	390.70**	68.43**
Cultivars (C)	9	560.10**	249.40**
Dates (D)	2	354.10**	65.00*
C x D	18	27.07	30.09
Error	116	50.33	16.91

*Denotes significance at the 5% level.

**Denotes significance at the 1% level.

Table 46. Mean values of relative water content of ten two-rowed barley cultivars after three days water stress, January 1986.

Cultivar	Relative Water Content			
	January 8	January 14	January 20	Over Dates
	----- % -----			
Clark	96.3	91.0	86.5	91.3
Compana	92.3	90.0	88.8	90.3
Dekap	95.6	93.5	84.5	91.2
Hector	94.9	89.0	92.7	92.2
New Moravian	91.5	86.6	85.2	87.8
Georgie	80.4	82.3	78.7	80.5
Ingrid	81.2	78.4	75.8	78.5
Klages	84.3	78.9	77.1	80.1
Maris Mink	81.1	76.6	76.6	78.1
Zephyr	80.7	76.0	80.3	79.0
LSD .05	5.6	3.7	7.5	5.1

Table 47. Mean values of relative water content of ten six-rowed barley cultivars after three days water stress, March 1986.

Cultivar	Relative Water Content			
	March 2	March 8	March 15	Over Dates
	----- % -----			
Briggs	93.7	97.2	93.2	94.8
Larker	95.9	92.5	91.1	93.2
Trebi	93.2	93.9	95.8	94.3
Titan	97.8	90.7	89.3	92.6
Glacier	90.1	92.2	91.6	91.4
Hiland	85.4	89.4	88.4	87.8
Steveland	82.5	88.0	86.7	85.8
Bonneville	87.0	84.3	81.9	84.4
Vantage	81.5	90.4	85.0	85.7
Unitan	85.6	89.1	82.3	85.7

LSD .05	8.6	2.0	2.9	4.5

potential (ψ_{TL}) measurements did allow separation within groups (Table 29). The results for RWC are less clear-cut for the six-rowed lines (Table 47), just as they were for ψ_{TL} (Table 30). Over the three runs, Glacier (resistant) could not be separated from Hiland (susceptible); all other resistant and susceptible lines were different, but no separation could be made within any of the groups.

After being subjected to approximately two days water stress, the resistant cultivars retained a higher percentage of water in their leaves. These results support the findings obtained by Dedio (1975) with wheat and Carter and Patterson (1985) with soybeans. They proposed using RWC to separate between resistant and susceptible cultivars with respect to drought response.

CHAPTER 5

SUMMARY AND CONCLUSIONS

An attempt was made to classify barley cultivars as to relative drought resistance or susceptibility by estimating several internal plant water status parameters. The cultivars were grown for one season in the field (1982) under a line source sprinkler irrigation system. A series of greenhouse studies was then carried out under watering and subsequent drying cycles on three-week-old plants. The plant water status estimates from the field experiment included total water, osmotic and turgor potentials of leaves for three different growth stages. The behavior of root osmotic-, leaf total-, leaf osmotic-, leaf turgor potentials, stomatal diffusive resistance and relative water content of leaves was examined in greenhouse studies. Specific cultivar differences for the above parameters are of interest because of the possibility of using them to screen for drought resistance.

The plant water measurement data of the field experiment are confounded by the fact that soil depth over gravel was shallow and differed significantly and randomly throughout the plant area. For this reason, the data obtained in the field must be used with caution. However, it appears that there was no difference in osmotic potential or osmotic adjustment of the cultivars; but there are indications that the leaf total water potential of more drought-tolerant cultivars was slightly higher under low stress conditions and that these cultivars

maintained slightly higher turgor potentials. The leaf total water potential differed among cultivars (0500 h readings) and appeared to be a good indicator of internal plant moisture stress.

Field study is labor-intensive, time-consuming, and requires full-season data. Therefore, a greenhouse methodology was developed (1984 and 1985) for a rapid screening technique of barley cultivars using seedlings as test material. The results obtained are somewhat similar to field experimental data. Clark (resistant) consistently maintained higher leaf total water potential than Klages (susceptible) under non-stress conditions. Klages consistently approached zero turgor at least one day earlier than Clark. The osmotic potential of roots showed much the same pattern of results through stress cycles as the leaf total water potential. However, osmotic potential was lower in Klages than in Clark and maintained the same relative position through stress cycles. Osmotic potential of roots and leaves and adjustments in total water potential during stress cycles were higher in Clark than Klages. An early stress cycle did not modify the pattern of leaf total water potential and osmotic adjustment in subsequent stress cycles. The leaf total water potential measurement on three-week-old plants appeared to be a promising method for identifying drought-resistant cultivars under nonstress conditions. Therefore, studies were extended to more cultivars of both two- and six-rowed barley to provide enough evidence to differentiate cultivars as to drought resistance or susceptibility. The predawn leaf total water potential, stomatal diffusive resistance as stress developed and relative water content of leaves after being

subjected to water stress were then studied in the intensive greenhouse experiments (1986) on two- and six-rowed barley cultivars.

Drought-resistant cultivars consistently maintained higher predawn leaf total water potential than drought-susceptible cultivars. In the morning, resistant cultivars had lower stomatal diffusive resistance compared to susceptible cultivars; but in the afternoon and as stress developed over days, higher stomatal diffusive resistance was found for the resistant cultivars. Inconsistencies in diffusion resistance measurement made data difficult to interpret. This pattern of stomatal behavior for resistant cultivars may help to conserve more water for future use. With stress, a significantly higher relative water content was found in resistant cultivars.

Plant internal water stress is best expressed by the leaf total water potential under nonstress conditions. The present findings and other reports in the literature (Hanson et al., 1977; Sammons et al., 1978) support the use of leaf total water potential determined by pressure chamber as a valid selection technique of drought-resistant cultivars. For ease of determination, relative water content was found to be a good differentiator as to drought resistance between resistant and susceptible groups but could not be used to differentiate within groups. The system of using Ψ_{TL} , R_s and RWC appears promising in rapid screening of a large number of populations. These results suggest the use of Ψ_{TL} and RWC for drought selection in plant breeding programs.

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APPENDICES

APPENDIX A

TABLE 48: DAILY ENVIRONMENTAL DATA FOR FIELD EXPERIMENT
FOR HORTICULTURAL FARM AT BOZEMAN, MT, 1982

Table 48. Daily environmental data for field experiment for horticultural farm at Bozeman, MT, 1982.

Date	Precip	Temperature			Humidity		Solar Radiation
		High	Low	Mean	High	Low	
	-- mm --	----- °C -----			---- % ----		-- Wm ⁻² --
July							
7/14	11.8	24	12	18	83	36	8,027
7/15	0.0	24	6	15	78	35	7,957
7/16	T*	18	6	12	71	31	6,771
7/17	0.0	22	3	13	80	29	8,097
7/18	0.0	25	7	16	78	24	8,167
7/19	0.0	29	9	19	62	20	8,585
7/20	T	30	10	20	70	19	7,818
7/21	0.0	31	12	22	69	21	8,027
7/22	T	26	13	20	68	28	6,212
7/23	2.0	28	12	20	84	31	6,701
7/24	T	24	15	20	84	43	4,467
7/25	2.0	26	14	20	92	16	8,167
7/26	0.0	28	14	21	58	11	7,538
7/27	0.0	28	14	21	62	34	8,167
7/28	0.0	25	16	21	61	37	6,142
7/29	0.0	27	9	18	82	22	7,608
7/30	0.0	29	9	19	76	22	7,887
7/31	2.3	29	14	22	82	28	7,538
August							
8/1	2.4	31	12	22	81	19	7,189
8/2	0.0	25	7	16	82	22	8,167
8/3	0.3	25	6	16	75	23	7,259
8/4	0.0	27	6	17	79	25	8,027
8/5	0.0	28	8	18	83	24	6,980
8/6	0.0	29	9	19	79	19	8,029
8/7	0.0	29	11	20	70	25	7,887
8/8	0.3	21	17	19	66	36	4,397
8/9	0.8	27	13	20	88	28	7,189
8/10	0.0	28	12	20	83	29	6,980
8/11	0.0	30	10	20	73	13	7,818
8/12	0.0	26	6	16	81	18	7,957
8/13	0.0	29	6	18	77	15	7,818
8/14	0.5	27	10	19	65	21	3,839
8/15	1.3	27	8	18	82	26	5,514
8/16	2.3	28	9	19	83	24	6,701
8/17	0.0	30	9	20	83	24	6,142
8/18	0.8	28	9	19	86	27	5,375

Table 48--continued

Date	Precip	Temperature			Humidity		Solar Radiation
		High	Low	Mean	High	Low	
	-- mm --	----- °C -----			----- % -----		-- Wm ⁻² --
8/19	1.0	28	12	20	88	22	7,259
8/20	0.0	30	12	21	74	23	6,910
8/21	1.8	29	12	21	88	21	7,329
8/22	9.6	25	13	19	94	36	6,142
8/23	T	24	8	16	93	28	6,352
8/24	T	25	6	16	92	20	7,399
8/25	0.0	28	7	18	72	16	6,980
8/26	0.0	26	8	17	64	17	6,910
8/27	T	28	7	18	72	23	6,073
8/28	0.0	30	10	20	66	12	6,175
8/29	T	26	9	18	87	27	5,165
8/30	4.6	19	11	15	91	50	4,118
8/31	T	22	6	14	89	20	6,841
September							
9/1	0.0	24	6	15	77	21	6,422

T* = trace

APPENDIX B

FIGURE 13: SCHEMATIC REPRESENTATION OF WATER RELATIONS
OF DROUGHT AVOIDANT AND SUSCEPTIBLE CROPS AS A
FUNCTION OF WATER STRESS DEVELOPMENT

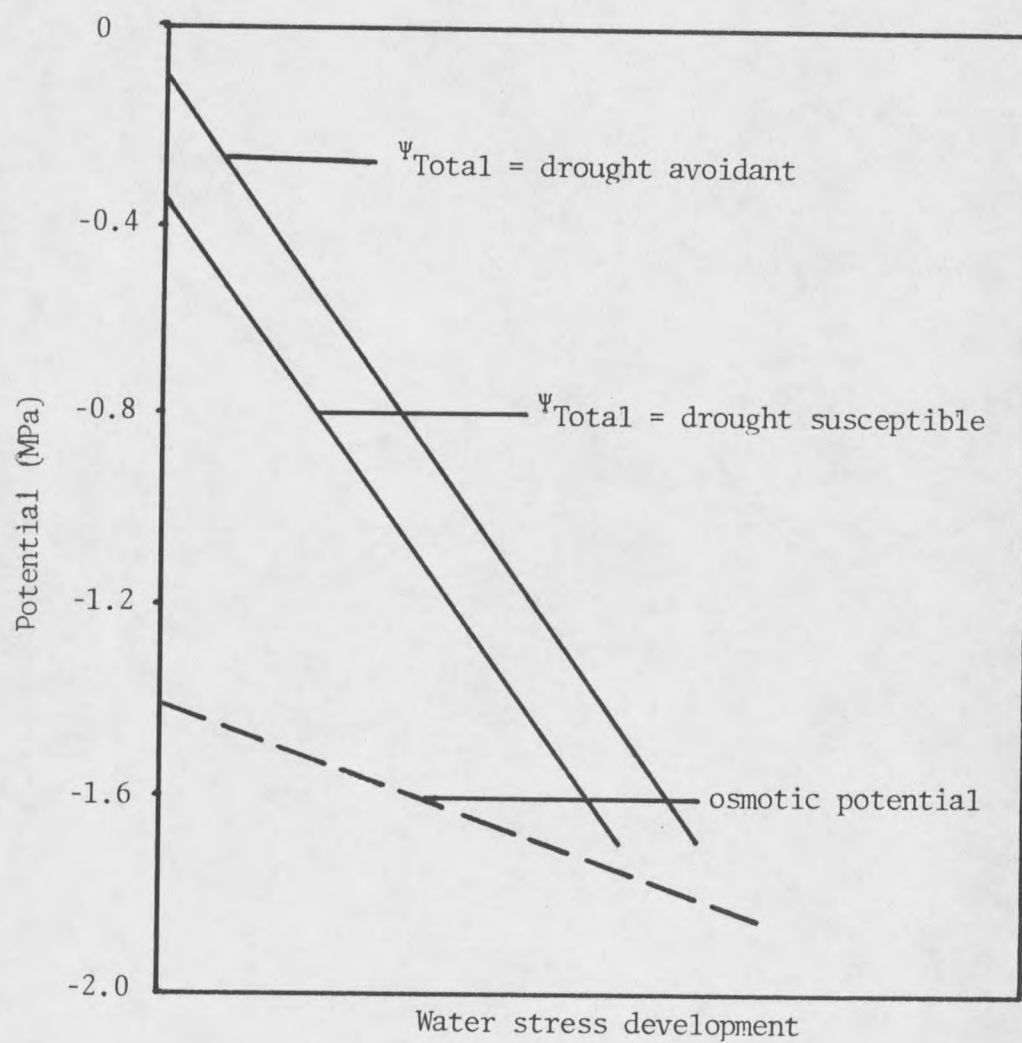


Figure 13. Schematic representation of water relations of drought avoidant and susceptible crops as a function of water stress development.

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