

THE EFFECTS OF WATER STRESS ON THE DIFFUSIVE  
RESISTANCE, TRANSPIRATION, AND LEAF WATER  
POTENTIAL OF DIFFERENT SOYBEAN CULTIVARS

By

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## CHAPTER I

### INTRODUCTION

The problem of water stress is probably the most limiting factor in the expansion of soybean (Glycine max (L.) Merr.) production in Oklahoma. Total rainfall over the growing season is often low, with a wide year-to-year distribution. When applying supplemental irrigation water more information is needed on when to start application and how much water should be applied to meet the consumptive water use of the soybean crop at various physiological stages of growth, along with total consumptive water use requirements for producing soybeans in Oklahoma. The objective of good water management is to provide sufficient water to the soybean roots when needed by the plant to produce the most economical soybean yields. All varieties have a maximum yield potential that is genetically determined. This genetic yield potential is obtained only when environmental conditions are near perfect, but such growth conditions do not normally occur. In a field situation, nature provides the major portion of the environmental influence on soybean growth, development and yield; however, soybean producers can partially manipulate this environment with proven managerial practices.

Under most field conditions in Oklahoma an optimum water environment is seldom prevalent, and some degree of growth limiting water stress in soybeans is the rule rather than the exception. The soil system acts as a reservoir for water that permits transpiration

to continue day by day between periods of rainfall and irrigation. The maximum amount of water that can possibly be stored is determined by the soil depth and total volume of the voids or pore spaces. However, in the plant root zone this quantity may have little significance. Of more fundamental importance is the tenacity with which water is held in the soil by adsorption and capillary forces. This tenacity is expressed in terms of the potential energy of the water in the soil, usually with respect to free water. As the water content of the soil decreases, the potential energy of the remaining water decreases.

The soybean plant is most affected by moisture stress during the reproductive and pod filling stages of growth. With continuous water stress during the reproductive stages of growth: from flowering to pod set, there is a marked reduction in yield associated with decreased number of pods per plant. Water stress can also reduce the amount of nutrients absorbed from the soil by soybean plants, decrease the amount of leaf area and lower the photosynthetic potential of soybeans especially during the pod filling stages of growth, affect the rate of translocation in soybeans and its relationship to other processes, particularly source-sink relationships.

The objectives of this study were to determine the range in magnitudes of diffusive resistance, transpiration rate, and leaf water potentials of 15 soybean cultivars at different reproductive stages of growth and at different levels of water stress.

## CHAPTER II

### LITERATURE REVIEW

#### Soil Physical Properties Affecting Water Availability For Soybean Production

The inherent physical characteristics of soil affect root distribution and the ability of that soil to intercept, store, and release water for plant growth (Winter and Pendleton, 1968; Raper and Barber, 1970). Plant available water holding capacity is generally greater for medium to fine compared to coarse and very fine textured soils. Gardner et al. (1985) reported that a clay loam soil would hold about 20% of its weight as available moisture, whereas fine sand would hold about 7%. They further estimated that on a soil volume basis, the clay loam at field capacity would hold about 17 cm available water per meter of soil depth whereas the fine sand would hold less than 8 cm.

Texture, structure, layering, and depth of soil are primary in determining the capacity for entry, transmission, and storage of plant available water (Mitchell and Russell, 1971). In addition, these factors are very important in determining the change in soil moisture content and the magnitude of water stress as conditioned by plant growth and the atmospheric demands that take place over time (Brady, 1974). Nelson et al. (1975) emphasized that soils with severe compaction problems are not recommended for maximum soybean (Glycine max (L.) Merr.) production

because both plant and root growth can be restricted and yields reduced. The mechanical impedance of soil to root penetration can markedly affect root distribution and water uptake (Cassell, 1983). Under field conditions, sometimes bulk density is sufficiently high enough to preclude good root penetration (Brady, 1974). Hillel (1982) postulated that soil stratification and depth have an important bearing on the response of plants to soil moisture. Nelson and Larson (1984) reported that deep permeable soils thoroughly permeated with roots provided good water transfer contact between the soil and the plant. On the other hand, claypans, plow soles, sand layers, or bedrock may severely restrict the root zone and make the plant much more susceptible to drought. Howell (1960) emphasized that to produce maximum soybean yields, the soil must be able to provide water as it is needed especially during critical reproductive stages of growth.

#### Effects of Water Deficits on Growth, Development, and Yields of Soybeans

Water flows from the bulk of the soil to the root surface in response to a water potential gradient extending from the root surface outward (Kramer, 1983). The increase in total resistance, which corresponds to the decrease in transpiration flux, has been attributed to increased soil resistance to water flow and would become significant only at soil water contents near wilting point.

Plant resistance to water flow is defined as the resistance to liquid flow through the root, xylem, and leaf when soil resistance to water flow is not limiting (Jones et al., 1982). Predictions of plant

water relations and transpiration required estimates of resistances to water flow in the soil and in the plant and according to Jones et al. (1982), calculated plant resistance increased with transpiration flux in a non linear relationship. The dependence of plant resistance to water flow on transpiration flux implies that the relationship between the water potential gradient and the resulting flux through the plant is also non linear (Newman, 1972). For soybean plants, the change from vegetative growth to pod filling was accompanied by a decrease in the initial osmotic potential by  $-0.4\text{MPa}$  (Zur et al., 1982). Slatyer (1957, 1967) reported that plants usually wilt at a soil water potential of about  $-1.5\text{MPa}$  and permanent wilting occurred when the soil water potential decreased to the leaf water potential at which wilting occurred and leaves did not recover turgor at night. Boyer (1971) confirmed that there was a very high resistance ( $1.6 \times 10^6 \text{ s cm}^{-1}$ ) to water movement through soybean plants, which was probably why leaves showed wilting even in wet soil on days of very high evaporative demand.

#### Germination and root development

Amen (1963) defined germination as the resumption of active growth that resulted in rupture of the seed coat and emergence of the seedling. According to Toole et al. (1956), germination includes the following physiological and morphological events: (1) imbibition and absorption of water, (2) hydration of tissues, (3) absorption of  $\text{O}_2$ , (4) activation of enzymes and digestion, (5) transport of the hydrolyzed molecules to the embryo axis, (6) increases in respiration and assimilation, (7) initiation of cell division and enlargement, and (8)

embryo emergence. In the great majority of species, seed germination begins with the radicle (embryonic root) rather than epicotyl (shoot) protrusion through the seed coat (Berlyn, 1972).

Gardner et al. (1985) reported that a soil moisture level of field capacity was generally optimum for germination and germination proceeded at slower rates as soil moisture approached the wilting point. Hadas (1969) suggested that after the initial imbibition stage, there came a time when physiological changes were started and various biochemical reactions were triggered, culminating in germination. Several model studies (Collis-George and Sands, 1959, 1961, 1962) showed that the germination rate of oats, lucerne, and perennial ryegrass were apparently influenced by matric water potential (the attractive or binding force of soil for water), osmotic potential (due to solutes), and hydraulic conductivity. These model studies suggested that a decreasing matric potential, which occurred as soil lost water, represented an increasing amount of energy and time required by the seed to obtain a unit volume of water. Sedgley (1963) has suggested that the effect of matric potential on germination could be explained in terms of wetted area and not in terms of matric potential. Collis-George and Hector (1966) further reaffirmed their original concept of the significance of matric potential when they indicated that matric water potential was of great importance because of (1) its direct effect on the energy with which the water is held by the soil and the rate of water uptake by the seed, (2) its indirect effect on controlling the wetted area of contact between soil and seed, and (3) its effects on controlling the mechanical strength of the soil and compression of the

seed.

Grable and Danielson (1965) showed that the rate of root development of germinated soybean seeds was greater at  $-0.5$  bar than at  $-0.9$  bars of tension. Hanks and Thorp (1957) found that soil crust strength and soil moisture stress affected the emergence of soybean seedlings. They reported that at relatively low soil crust strengths, emergence decreased from approximately 90 to 70% as soil moisture decreased from field capacity to 25% available and at relatively high crust strengths, emergence decreased from 70 to 30% over the same change in moisture availability.

Root growth is exponentially and inversely related to soil bulk density (Davies and Runge, 1969). Gardner et al. (1985) reported that a resultant increase in bulk density increased impedance of roots and reduced  $O_2$  or the  $O_2/CO_2$  ratio, which adversely affected root growth. Gardner et al. (1985) reported that water was essential for root growth, evidenced by the fact that roots did not grow through dry soil layers. However, roots have what might be regarded as a water-stress adjustment mechanism whereby solutes accumulate in the tip and elevate the turgor pressure, which can sustain growth for a limited time (Sharp and Davis, 1979). Wright (1962) reported that soil moisture stress significantly reduced root weight of blue panicgrass (*Panicum antidotale* Retz.), and root length of soybean was significantly reduced (16%) by water potentials less than  $-2.0$  bars (Sivakumar et al., 1977). A moisture-deficient soil also modified soybean rooting patterns: to the extent that a smaller percentage of total roots were found in the surface layer (0-15 cm) compared to the percentage of roots found in

deeper soil strata (Mayaki et al., 1976).

Grimes et al. (1975) reported that the relationship between rooting density to absorption of soil water was linear. Machinery rolling between plant rows caused compaction and reduced water availability (Nelson et al., 1975). Esau (1965) reported that most of the root expansion evidently occurred in the region of the cell elongation immediately behind the meristematic region. Huck et al. (1970) has shown that primary root tissue might shrink as a result of water stress, especially before the cell walls have thickened sufficiently to give the tissue mechanical rigidity. Plant roots also remove water according to the needs of the plant and the location of the root system (Klepper et al., 1973). Lang and Gardner (1970) showed that as a root removed water from the thin layer of soil immediately adjacent to its surface, the rhizosphere layer rapidly decreased in conductivity.

#### Shoot growth and flower induction

The terminal meristem is always located at the tip of the stem and has primary responsibility for initiating leaves, developing axillary buds, and laying down nodes and internodes (Nelson and Larson, 1984). Vegetative organs (buds, leaves, and stems) have their origin in the apical and lateral buds of stems, starting with the embryo in the seed (Gardner et al., 1985). They reported that each subunit of structure, phytomer, had three components: (1) stem node and internode, (2) leaf, and (3) axillary bud. Gardner et al. (1985) defined growth as cell division (increase in number) and cell enlargement (increase in size) both requiring protein synthesis and were irreversible. They further



reported that dry weight accumulation was commonly used as a parameter for characterizing growth because it had the greatest economic importance.

The apical meristem of the shoot forms in the embryo and is the place where new leaves, branches, and floral parts originate (Salisbury and Ross, 1978). Salisbury and Ross (1978) also reported that increased stem diameter in gymnosperms and most dicots resulted from radial expansion of cells produced by the vascular cambium, just as in roots. In growing stems, cell division occurs in regions much farther from the tip than occurs in roots (Sachs, 1965). Salisbury and Ross (1978) reported that the earliest sign of leaf development in both gymnosperms and angiosperms consisted of divisions in one of the three outermost layers of cells near the surface of the shoot apex. They also reported that there was a competition for nutrients among vegetative and reproductive organs with young fruits possessing a large but unexplained "drawing power" for mineral salts, sugars, and amino acids. They also reported that factors which stimulated shoot growth retarded flower and fruit development.

Hsiao (1973) concluded that a threshold turgor in soybeans must be exceeded before any growth occurred, although pressure potential ( $\Psi_p$ ) might already be at a threshold value of 5 bars, additional pressure was needed for growth. He also reported that the growth rate of soybeans was very sensitive to the extent by which  $\Psi_p$  was raised above the turgor threshold, and growth stopped well before  $\Psi_p$  reached zero and before the tissues were wilted. Salisbury and Ross (1978) reported that a plant

required water as the driving force for growth, but continued water uptake required mineral salt absorption or sugars and other organic solutes provided by translocation or photosynthesis. Kramer (1983) attributed the development of moisture stress in soybeans during midday to a considerable resistance of water flow from the soil into the root xylem and when there was an appreciable volume of readily available water in the turgid parenchyma cells of the stems and leaves.

Subjecting soybeans to water stress during flower induction shortens the flowering period and causes flower abortion, whereas stress during pod filling reduces seed number and weight (Sionit and Kramer, 1977). They also reported that shoot growth was reduced more than root growth because more severe water deficits developed in the transpiring shoots and probably persisted longer. Green (1968) demonstrated that any change in turgor pressure effected on immediate growth rate change or cessation as turgor pressure changed from positive to negative. The delay in new root growth, which results in decreased translocation of nutrients and water to the shoot, imparts a significant stress in the shoot according to Arkin and Taylor (1981) and Fritter and Hay (1981). They also asserted that under such growth conditions, the plant could not approach its yield potential. When the supply of water and nutrients translocated to the shoot are severely limited, the shoot may slow its rate of terminal growth functions which include photosynthesis and assimilation, leaf expansion, and flower initiation or retention according to Howell (1960) and Levitt (1980). Sojka and Parsons (1983) reported that when significant water stress occurred during the vegetative stages of growth, complete canopy coverage was never achieved

for determinate soybean cultivars because vegetative growth tended to cease with flowering.

#### Leaf water potential and orientation

Leaf water potential measurements for plants can be valuable in evaluating plant water status because they integrate effects of crop species, plant age, soil moisture conditions, and atmospheric demand on plant water status (Stanley et al., 1981). They reported that when soil moisture was non limiting, atmospheric demand controlled leaf water potential responses. Linear relationships were found between temperature and water potential by Scott et al. (1981). They also found that leaf temperature of nonirrigated soybeans was more sensitive to changes in water potential than that of the irrigated soybeans and became more sensitive as drought progressed.

For soybeans, several studies have shown that water deficits led to lowered leaf water potentials and, consequently, to partial stomatal closure (Brady et al., 1975; Sionit and Kramer, 1977; Sivakumar and Shaw, 1978; Wien et al., 1979; Carlson et al., 1979; and Jung and Scott, 1980). Xylem pressure potential was very highly correlated with leaf vapor pressure deficit (Sojka and Parsons, 1983). However, plant water flux, especially in field grown plants, varies in response to solar radiation, atmospheric conditions, and the amount of water stored in the plant and rhizosphere and therefore is only rarely in a steady state (Reiscosky et al. 1982). They also postulated that for soybeans leaf water potential-evapotranspiration relationship seemed to be affected more by irrigation than by row spacing. Upper leaves were more exposed

than lower leaves and transpired more rapidly, lowering their water potential and causing water to move to them from the shaded lower leaves (Boyer et al., 1980). Boyer (1971) estimated that the soybean leaf water potential would have to decrease about twice as much to maintain water flow at the same rate; hence, soybeans might be under water stress more frequently and more severely than many other plants.

Prior to full ground cover, soybean leaf area is the most influential variable affecting water potential; thereafter, atmospheric demand is the principal controlling factor (Laing, 1966; Kato, 1967). Kato (1967) estimated the water requirement for soybeans to be  $580\text{g g}^{-1}$  dry matter produced. Stevenson and Shaw (1971a) reported that under water stress there was a preferential flow of water to upper leaves, because stomatal resistance of mid-canopy leaves increased with time more rapidly and to a greater extent than resistance of upper leaves on high-demand days. Under high water availability and low atmospheric demand conditions, Stevenson and Shaw (1971a) also found leaf resistance to be substantially less in upper than mid-canopy soybean leaves. Boyer (1970a, 1970b), working with whole soybean plants, has shown that leaf enlargement was the first process to respond to water deficit, followed by respiration, and then photosynthesis.

Leaflet reorientation in water-stressed soybeans may be a mechanism by which water loss is reduced while still maintaining some level of productivity (Meyer and Walker, 1981). They also reported that the inversion of the leaflets exposed the abaxial surface which maintained a higher level of diffuse conductance under water stress conditions than did the adaxial surface. The changes in leaf orientation or shape occur

as plant water status decreases (Begg and Torrsell, 1974; Shackel and Hall, 1979; Rawson, 1979; O'Toole and Cruz, 1980). Terminal leaflet inversion during midday appeared to be an early indicator of soybean plant water stress and was first observed when 60% of plant available water had been depleted (Meyer and Walker, 1981). Changes in leaf diffusive conductance also occur as plant water potential decreases (Meyer and Green, 1980). Boyer (1970a) reported that, for soybeans, the rate of change for leaf enlargement was very rapid at leaf water potentials greater than  $-4.0$  bars. Leaf water potential and turgor pressure within the developing cells of soybean are very important in determining rate of leaf enlargement and leaf area at full development (Lockhart, 1965).

#### Photosynthesis and water use efficiency

Soybean leaves are the principal light-intercepting and photosynthesizing organs on the plant with the leaf area being the best measure of the photosynthesizing capacity of the plant (Sakamoto and Shaw, 1967; Shaw and Weber, 1967). During early growth, soybean growth rate is nearly proportional to crop leaf area (Shibles and Weber, 1965). Optimal conditions for photosynthesis and good water-use efficiency exchange occur on clear days with air temperatures near  $30^{\circ}\text{C}$  and in the absence of sensible heat advection (Baldocchi et al., 1981). They reported that hot, clear days dominated by sensible heat advection limited  $\text{CO}_2$  exchange but increased latent heat flux. As a result, they concluded that carbon dioxide-water flux ratio (CWFR) was low.

Leaflets of upright display ( $10-15^{\circ}\text{C}$  to the vertical) have lower

temperature and lower stomatal diffusion resistance than those of horizontal, except on overcast days (Stevenson and Shaw, 1971b). Partial stomata closure in turn, lowers photosynthesis, transpiration, growth, and yield (Beardsell et al., 1973; Iljum, 1957). Stress in the shoot resulting from excessive temperature and evaporative demand or inadequate light which reduces photosynthetic activity not only slows shoot growth but, also limits photosynthate and assimilate translocation to the roots, thereby slowing the rate of root growth (Levitt, 1980). Water potentials below -11.0 bars inhibit photosynthesis in soybeans and any leaf water potential below -11.0 bars is considered a water deficit by Boyer et al. (1980).

Despite the obvious importance of photosynthesis to crop production, the relationship is not a direct one (Gifford and Evans, 1981). Leaf evolution has provided a structure that will withstand environmental rigors and yet provide both effective light absorption and rapid CO<sub>2</sub> uptake for photosynthesis (Gardner et al., 1985). They described the leaf as a photosynthetic organ because most crop leaves have (1) a large flat external surface; (2) upper and lower protective surfaces; (3) many stomata per unit area; (4) extensive internal surface and interconnecting air spaces; (5) an abundance of chloroplasts in each cell; and (6) a close relationship between the vascular and photosynthetic cells.

When compared to some other species, soybeans appeared to have a low leaf porosity (El-Sharkawy and Hesketh, 1965). Working with ryegrass (Lolium perenne L.), Wilson and Cooper (1967) found that CO<sub>2</sub> assimilation was positively correlated with the product of cell numbers

per unit volume x leaf thickness and with the intercellular volume of the leaf. For soybeans CO<sub>2</sub> assimilation is correlated with leaf density thickness (Dornhoff and Shibles, 1970).

### Transpiration

Gates (1968) reported that the water absorbed by soybean roots moved up in the xylem to the leaves where it is vaporized and released through the stomates in the atmosphere. As a result, plant water stress begins when transpiration water loss exceeds absorption by the roots. The amount and rate of water loss through plant leaves depend chiefly on leaf morphological characteristics and atmospheric conditions, whereas absorption of water by roots depend primarily on soil water conditions (Ritchie, 1974).

Shaw and Laing (1966) reported that the degree of stress which developed in soybeans depended on the lag between transpiration and absorption. According to Shaw and Laing (1966), transpiration is basically a passive process determined by: (1) the amount of energy input that supplies latent heat required for water evaporation, (2) the availability of water at the surfaces of the plant where evaporation occurs, and (3) the existence of a transfer mechanism to move the water vapor from the plant surfaces where evaporation occurs to the atmospheric sink. The driving force for transpiration is the difference in vapor pressure of water within the leaf and in the atmosphere beyond the boundary layer (Salisbury and Ross, 1978; Mederski et al., 1973). They reported that if the stomates were closed or nearly closed, resistance to transpiration could be very high; if they were opened,

resistance was very low. Mederski et al. (1973) also reported that the energy received by the leaf came from solar radiation, reradiation from soil and plant surfaces, and the transfer of sensible heat to the soybean leaf by air movement.

Transpiration accounts for 99% of the water used by plants; approximately 1% is used to hydrate the plant, maintain turgor pressure, and make growth possible (Gardner et al., 1985). The interrelationship between soil water and plant growth is affected by atmospheric factors that influence the rate of transpiration chiefly because of the high temperature and high vapor pressure deficit accompanying a high level of irradiance (Boyer et al., 1980; Kramer, 1983). Peters and Johnson (1960) using plastic cover irrigated plots assessed soybean transpiration to be about 129 mm from beginning bloom until maturity. Chin Choy and Kanemasu (1974) studied an evapotranspiration (ET) model for soybeans and sorghum in Kansas. They reported that the leaf area index (LAI) for sorghum was less than soybeans, which resulted in 13% greater ET from the soybean canopy than from grain sorghum because the latter had greater surface resistance.

### Yield

Adequate moisture is the major factor limiting yield in most areas where soybeans are grown. Soybeans are also more sensitive to water deficits during reproductive development than during vegetative growth stages (Brown et al., 1985; Salter and Goode, 1967; Thompson, 1975; Jung and Scott, 1980; Doss et al., 1974). They reported that pod filling was the critical period when soybean plants needed adequate water for



maximum yields. Their results showed that reductions in seed size and seed number were major components responsible for reduced yield in moisture stress treatments.

The sensitivity of soybeans to water stress measured in terms of yield reduction tended to increase dramatically as the crop advanced through its natural sequence of reproductive ontogeny (Kadhem et al., 1985). They reported that sensitivity increased to a maximum during the late pod elongation and subsequent seed enlargement stages. They also, suggested that the full pod (R4) stage was a critical "cross-over" point in reproductive ontogeny relative to irrigation timing and its effect on seed size.

Boyer et al. (1980) postulated that differences in midday water deficits between cultivars were only two to three bars at most, but these differences were associated with significant yield losses probably because of the sensitivity of photosynthesis and other processes to these water deficits. Stress during early flowering usually results in less than 10% yield reduction and flower and pod drop occur in the lower parts of the plant, but compensation in the form of more pods set on upper nodes almost negate the pod loss (Boyer, 1970b). The essence of good water management is to provide water to the soybean roots when needed by the plant to produce the most economical soybean yields.

## CHAPTER III

### MATERIALS AND METHODS

This experiment was conducted in the greenhouse using a Wynona silty clay loam soil (Cumulic Haplaquolls) diluted with sand to give a 3:1 soil-sand volume ratio. Sufficient quantity of this ratio was mixed in a concrete mixer for 30 minutes to ensure that the resulting soil texture of each experimental replication would represent a rooting medium with the same matric and osmotic water potentials. Soil test values showed phosphorus (P) and potassium (K) to be at 100% nutrient sufficiency levels as determined by the Oklahoma State University soil testing laboratory procedures and recommendations.

The experiment was conducted as a randomized block design with 15 treatments and 10 replications. One replication consisted of 3 pots, each 33 cm high with a diameter of 36 cm, containing 27.2 kg of the soil mixture in which 15 soybean cultivars were randomly planted. All soybean cultivars were inoculated with Rhizobium japonicum and planted at a depth of 2.5 cm on 5 June 1985 with three seeds of each cultivar planted per stand and five cultivars per pot. After two weeks plants were thinned to one plant of each cultivar per pot. Soybean treatment cultivars, maturity groups, and growth habits are shown in Table 1.

The growth and development periods of soybeans are referred to as vegetative and reproductive stages, respectively. These stages last different lengths of time and are influenced in different degrees by

internal and external factors. For soybeans, it has been convenient to divide each main stage (vegetative and reproductive) into substages. Although there is a major difference in plant development between indeterminate and determinate soybean varieties, these stage descriptions are unilaterally applied (Fehr and Caviness, 1977).

TABLE I

SOYBEAN TREATMENT CULTIVARS, MATURITY GROUPS,  
AND GROWTH HABITS

<u>Soybean treatment cultivar</u>	<u>Maturity groups</u>	<u>Growth Habit</u>
Weber	I	indeterminate
Lakota	I	indeterminate
Vinton 81	I	indeterminate
Gnome	II	determinate
Century 84	II	indeterminate
Platte	II	indeterminate
Hobbit	III	determinate
Williams 82	III	indeterminate
Douglas	IV	determinate
Crawford	IV	indeterminate
Pixie	IV	determinate
Forrest	V	determinate
Essex	V	determinate
Narow	V	determinate
Sohoma	VI	determinate

Vegetative stages are described by Fehr and Caviness (1977) as emergence, unfolding of the cotyledons, and then development of successive nodes on the main stem, beginning with the unifoliate nodes, taking into account nodes that have a fully developed leaf. Each stage description (Table II) is given a vegetative (V) stage designation and an abbreviated title to facilitate communication.

TABLE II

## DESCRIPTION OF VEGETATIVE STAGES

Stage No.	Abbreviated Stage Title	Description
VE	Emergence	Cotyledons above soil surface
VC	Cotyledon	Unifoliolate leaves unrolled sufficiently so the leaf edges are not touching
V1	First node	Fully developed leaves at unifoliolate nodes
V2	Second node	Fully developed trifoliolate leaf at node above unifoliolate nodes
V3	Third node	Three nodes on the main stem with fully developed leaves beginning with the unifoliolate nodes
.		
.		
.		$\eta$ number of nodes on the main stem with fully developed leaves beginning with the unifoliolate nodes, $\eta$ can be any number beginning with 1 for V1, first node stage
V( $\eta$ )		

Source: Fehr and Caviness (1977).

TABLE III  
DESCRIPTION OF REPRODUCTIVE STAGES

Stage No.	Abbreviated Stage Title	Description
R1	Beginning bloom	One open flower at any node on the main stem
R2	Full bloom	Open flower at one of the two uppermost nodes on the main stem with a fully developed leaf
R3	Beginning pod	Pod 5 mm (3/16") long at one of the four uppermost nodes on the main stem with a fully developed leaf
R4	Full pod	Pod 20 mm (3/4") long at one of the four uppermost nodes on the main stem with a fully developed leaf
R5	Beginning seed	Seed 3 mm (1/8") long in a pod at one of the four uppermost nodes on the main stem with fully developed leaf
R6	Full seed	Pod containing a green seed that fills the pod cavity at one of the four uppermost nodes on the main stem with a fully developed leaf
R7	Beginning maturity	One normal pod on the main stem that has reached their mature pod color. Five to 10 days of drying weather are required after R8 before the soybeans have less than 15% moisture
R8	Full maturity	Ninety-five percent of the pods have reached their mature pod color

Source: Fehr and Caviness (1977).

Description of the reproductive stages is made using the main stem. These stages are based on flowering, pod development, seed development, and plant maturation (Fehr and Caviness, 1977). Each stage description is given a reproductive (R) stage number and an abbreviated title (Table III).

Equal watering of the plants in each pot was ensured throughout the growth stages with 250 ml of water per pot being applied each day for the first four weeks of growth. The volume of water was increased to 500 ml each day per pot up to blooming time when it was increased to 1000 ml each day per pot. At different physiological stages of growth, water stress was induced by withholding water from pots for varying periods of time. Under different magnitudes of water stress diffusive resistance ( $\text{sec cm}^{-1}$ ) and transpiration ( $\mu\text{g cm}^{-2}\text{s}^{-1}$ ) were measured on all soybean cultivars with a Licor LI-1600 autoporometer. Leaf water potentials were also determined using leaf cutter thermocouple psychrometers as described by Johnson et al. (1984). Sampling was restricted to fully expanded trifoliolate leaves in the terminal part of the soybean plants. All measurements were made between 1000 and 1200 hours CDT on stress level dates.

Plants were harvested at maturity and the following agronomic characteristics were evaluated: (1) mature pods (with seeds) per plant, (2) immature pods (without seeds) per plant, (3) number of total pods on plant, (4) total seeds per plant, and (5) total dry weight (13 % moisture) of seeds per plant.

## CHAPTER IV

### RESULTS AND DISCUSSION

#### Soybean Water Stress Periods

Previous research has shown that soybean yields were drastically lowered if water stressed during reproductive stages of growth. All 15 soybean cultivars were allowed to grow under nonstressed mineral nutrition and water conditions until reproductive growth stages were reached. Water stress levels were induced by withholding water from the plants for a given period at which time diffusive resistance and transpiration were determined using the autoporometer. Leaf water potentials were also determined at the same time using leaf cutter thermocouple psychrometers.

The magnitude of stress (medium, high, and very high) were observed wilting condition of the soybean plants. Medium stress was where upper leaves of the soybean plant had started to wilt and curl with the terminal buds and 50 percent of the older leaves in the basal part of the plant still turgid. High stress was where all soybean leaves had wilted with the terminal buds and axillary buds still upright. Leaves were rolled and inversion was in progress; however, the soybean plants were still erect. Very high stress was where all leaves were wilted, rolled, inverted, with drooping of the terminal buds and apical portion of the foliage. The loss of water from the pots due to evapotranspiration over a given time period varied in the greenhouse

depending upon temperature, amount of cloud cover, and soybean growth stage.

#### 26 July 1985 Stress Level

Qualitatively this stress level was considered to be medium in magnitude. Diffusive resistance (DR), transpiration (TR), and leaf water potential (LWP) values are shown in Table IV. DR values within Maturity Groups I, II, and III were not significantly different (0.05 level) with the exception of the Williams 82 cultivar. Other than Williams 82, the cultivars in these three maturity groups were lower in DR values compared to cultivars in Maturity Groups IV, V, and VI with the Pixie cultivar being the only exception (Table IV). DR values for Williams 82, Douglas, Crawford, Forrest, Essex, and Narrow were higher compared to the other eleven cultivars (Table IV).

The rate of TR ranged from a high of 8.75 to a low of 5.31  $\mu\text{g cm}^{-2}\text{s}^{-1}$  and as expected varied inversely in magnitude with DR values (Table IV). All cultivars in Maturity Groups I, II, and III (with the exception of Williams 82), along with Pixie (Maturity Group IV), and Sohoma (Maturity Group VI) transpired more than the cultivars in Maturity Groups IV and V (Table IV).

LWP ranged from a high of -1.08 to a low of -1.39 MPa for this stress level with no significant statistical difference (0.05 level) between cultivars (Table IV). These data suggest that indeed soybean cultivars with similar LWP transpire at different rates for a given water stress level and is due to differences in DR properties of the various soybean cultivars. At this water stress level no trend was



TABLE IV

MEANS FOR THE EFFECT OF WATER STRESS ON THE DIFFUSIVE  
RESISTANCE, TRANSPIRATION, AND LEAF WATER POTENTIAL  
OF SOYBEAN CULTIVARS AT DIFFERENT GROWTH STAGES  
ON 26 JULY 1985

Cultivar	Maturity group	Diffusive resistance	Transpiration	Leaf water potential	Growth stage
		sec cm <sup>-1</sup>	μg cm <sup>-2</sup> s <sup>-1</sup>	-MPa	
Weber	I	0.96	8.29	1.08	R5
Lakota	I	0.91	8.49	1.17	R5
Vinton 81	I	0.84	8.50	1.25	R5
Gnome	II	0.96	8.66	1.21	R5
Century 84	II	1.21	8.41	1.32	R5
Platte	II	1.01	8.75	1.19	R5
Hobbit	III	0.97	8.73	1.26	R5
Williams 82	III	1.96	6.45	1.32	R4
Douglas	IV	1.80	6.75	1.34	R3
Crawford	IV	2.24	5.31	1.25	R3
Pixie	IV	0.99	8.71	1.19	R3
Forrest	V	1.89	6.80	1.17	R2
Essex	V	1.92	5.09	1.39	R2
Narrow	V	2.09	5.76	1.21	R1
Sohoma	VI	1.66	7.73	1.17	R1
LSD (0.05)		0.79	1.71	NS	
LSD (0.01)		1.06	2.27	NS	

noticed for differences in DR, TR and LWP due to growth habit.

#### 2 August 1985 Stress Level

On a qualitative basis this stress level was considered to be high. At this high stress level DR values increased greatly in magnitude, compared to the 26 July stress level, and ranged from the 13.55 to 19.54 sec cm<sup>-1</sup> with no significant statistical differences (0.05 level) between treatment cultivars (Table V). Excluding Weber, Maturity Groups I and II had higher TR values when compared to the other cultivars. The Lakota, Vinton 81, and Gnome cultivars were higher compared to all cultivars in Maturity Groups III, IV, V and VI (Table V).

LWP range from -1.67 to -2.56 MPa indicating water stress in the leaves was of larger magnitude than the 26 July stress level. Under this high level of water stress it is interesting to note that there is a trend for lower leaf water potentials with the exception of the Weber and Gnome cultivars (Table V). This observation suggests that there may be less resistance to water uptake and movement of water through the plant and to the leaves of these two cultivars. Again, there appeared to be no associated differences between TR, DR, and LWP values and soybean growth habit.

#### 9 August 1985 Stress Level

This stress level was also considered to be high on a qualitative scale. DR values were similar to those recorded on the 2 August high stress level (Table VI). Platte, Hobbit and all cultivars in Maturity

TABLE V

MEANS FOR THE EFFECT OF WATER STRESS ON THE DIFFUSIVE RESISTANCE,  
 TRANSPIRATION, AND LEAF WATER POTENTIAL OF SOYBEAN CULTIVARS  
 AT DIFFERENT GROWTH STAGES ON 2 AUGUST 1985

Cultivar	Maturity group	Diffusive resistance	Transpiration	Leaf water potential	Growth stage
		sec cm <sup>-1</sup>	μg cm <sup>-2</sup> s <sup>-1</sup>	-MPa	
Weber	I	19.40	0.42	1.67	R5
Lakota	I	14.64	0.62	2.06	R5
Vinton 81	I	13.55	0.54	2.10	R5
Gnome	II	14.30	0.54	1.73	R5
Century 84	II	17.44	0.48	2.00	R5
Platte	II	16.37	0.48	2.53	R5
Hobbit	III	18.95	0.38	2.30	R5
Williams 82	III	15.80	0.37	2.17	R4
Douglas	IV	15.30	0.40	2.21	R4
Crawford	IV	14.24	0.41	2.22	R4
Pixie	IV	19.54	0.41	2.51	R4
Forrest	V	18.16	0.35	2.51	R3
Essex	V	16.58	0.36	2.56	R3
Narrow	V	17.06	0.33	2.56	R2
Sohoma	VI	16.80	0.39	2.45	R2
LSD (0.05)		6.05	0.20	0.47	
LSD (0.01)		8.06	0.26	0.62	

TABLE VI

MEANS FOR THE EFFECT OF WATER STRESS ON THE DIFFUSIVE  
RESISTANCE, TRANSPIRATION, AND LEAF WATER POTENTIAL  
OF SOYBEAN CULTIVARS AT DIFFERENT GROWTH STAGES ON  
9 AUGUST 1985

Cultivar	Maturity group	Diffusive resistance	Transpiration	Leaf water potential	Growth stage
		sec cm <sup>-1</sup>	μg cm <sup>-2</sup> s <sup>-1</sup>	-MPa	
Weber	I	14.98	1.38	2.15	R6
Lakota	I	13.82	1.02	2.19	R6
Vinton 81	I	11.17	1.96	1.84	R6
Gnome	II	10.30	2.09	1.85	R6
Century 84	II	12.26	1.78	1.70	R6
Platte	II	17.24	0.81	2.53	R6
Hobbit	III	18.23	0.76	2.21	R5
Williams 82	III	13.60	0.98	2.50	R5
Douglas	IV	19.30	0.75	2.01	R5
Crawford	IV	15.75	0.93	2.06	R5
Pixie	IV	16.02	0.98	2.50	R5
Forrest	V	17.24	0.61	2.55	R2
Essex	V	19.40	0.56	2.74	R3
Narow	V	15.36	0.89	2.51	R2
Sohoma	VI	17.10	0.76	2.34	R2
LSD (0.05)		4.91	0.45	0.53	
LSD (0.01)		6.54	0.60	0.70	

Groups IV, V, and VI had higher DR values compared to Williams 82 and the rest of the cultivars in Maturity Groups I and II (Table VI). TR values had similar trends as the 2 August stress level with cultivars Vinton 81, Gnome, and Century 84 having higher TR rates compared to all other cultivars (Table VI). LWP were also on the same order of magnitude as the 2 August stress level. Platte, Williams 82, Pixie and all Maturity Group V and VI cultivars were lower in LWP compared to all other cultivars (Table VI). For these two high stress levels LWP values ranged from -1.67 to -2.74 MPa (Tables V and VI). Upon watering all cultivars recovered to what visually appeared to be normal turgid plants.

#### 23 August 1985 Stress Level

This stress level was considered to be very high on a qualitative scale and was initiated to test even further the limits of water stress and recovery of the 15 soybean cultivars. No measurements were made on the Platte cultivar because it was felt it was too far into maturation. DR values for all cultivars in Maturity Groups I and II were significantly lower (0.05 level) compared to cultivars Hobbit, Williams 82, and all cultivars in Maturity Groups IV, V, and V (Table VII). TR values for all cultivars in Maturity Groups I and II were significantly statistically higher (0.01 level) compared to all cultivars in the other Maturity Groups (Table VII). Leaf water potentials were significantly statistically higher (0.01 level) for all cultivars in Maturity Groups I and II compared to the cultivars in all other maturity groups. These data suggest that with increased maturity there is less resistance to

Table VII

MEANS FOR THE EFFECT OF WATER STRESS ON THE DIFFUSIVE  
RESISTANCE, TRANSPIRATION, AND LEAF WATER POTENTIAL OF  
SOYBEAN CULTIVARS AT DIFFERENT GROWTH STAGES ON  
23 AUGUST 1985

Cultivar	Maturity group	Diffusive resistance	Transpiration	Leaf water potential	Growth stage
		sec cm <sup>-1</sup>	μg cm <sup>-2</sup> s <sup>-1</sup>	-MPa	
Weber	I	6.97	2.07	1.97	R8
Lakota	I	3.75	2.41	2.06	R7
Vinton 81	I	5.06	2.14	1.90	R8
Gnome	II	4.29	1.98	1.97	R6
Century 84	II	3.67	1.97	1.54	R7
Platte	II	---	---	---	--
Hobbit	III	10.95	0.86	4.03	R7
Williams 82	III	10.54	0.88	3.89	R5
Douglas	IV	8.91	1.03	3.12	R5
Crawford	IV	10.90	0.82	3.81	R5
Pixie	IV	12.10	0.72	4.05	R5
Forrest	V	10.43	0.94	3.93	R4
Essex	V	11.22	0.88	4.43	R4
Narrow	V	11.70	0.81	4.38	R2
Sohoma	VI	11.56	0.78	4.36	R3
LSD (0.05)		2.29	0.54	0.68	
LSD (0.01)		3.05	0.72	0.90	

water uptake and movement of water to leaves or maturation in Maturity Groups I and II may have begun to play a role in LWP values. Upon watering, recovery to turgid normal plants was slow, however, all plants for all cultivar replications did recover.

#### 30 August 1985 Stress Level

For these measurements the water stress level was considered to be qualitatively high. All cultivars in Maturity Groups I, II, and III with the exception of Williams 82 were considered too mature for further valid DR, TR, and LWP measurements. DR values were significantly statistically lower (0.05 level) for the Douglas and Crawford cultivars compared to all other cultivars in Maturity Groups IV, V and VI (Table VIII). The DR value for Williams 82 was larger, but not significant from the Douglas and Crawford cultivars. As expected TR values for Williams 82, Douglas, and Crawford were significantly statistically higher (0.05 level) compared to all other cultivars (Table VIII).

LWP ranged from a high of  $-1.96$  to a low of  $-3.07$  MPa (Table VIII). The highest LWP were for cultivars Williams 82, Crawford, and Sohoma. Pixie had the lowest LWP, significant at the 0.01 level, with the rest of the cultivars falling into the intermediate range ( $-2.13$  to  $-2.30$  MPa) for this stress level.

#### 6 September 1985 Stress Level

The last measurements of TR, DR and LWP were made at a high qualitative stress level. DR values were on the similar order of magnitude as those measured on 30 August (Table IX). The Williams 82,

Table VIII. Means for the effect of water stress on the diffusive resistance, transpiration, and leaf water potential of soybean cultivars at different growth stages on 30 August 1985.

Cultivar	Maturity group	Diffusive resistance	Transpiration	Leaf water potential	Growth stages
		sec cm <sup>-1</sup>	μg cm <sup>-2</sup> s <sup>-1</sup>	-MPa	
Williams 82	III	8.78	2.60	1.96	R6
Douglas	IV	6.34	3.24	2.13	R6
Crawford	IV	6.59	3.02	1.76	R6
Pixie	IV	14.87	1.08	3.07	R6
Forrest	V	15.28	1.17	2.05	R5
Essex	V	16.18	0.95	2.30	R5
Narrow	V	13.22	1.20	2.14	R4
Sohoma	VI	12.39	1.53	1.90	R4
LSD (0.05)		3.77	0.99	0.43	
LSD (0.01)		5.09	1.33	0.58	

Table IX. Means for the effect of water stress on the diffusive resistance, transpiration, and leaf water potential of soybean cultivars at different growth stages on 6 September 1985.

Cultivar	Maturity group	Diffusive resistance	Transpiration	Leaf water potential	Growth stages
		sec cm <sup>-1</sup>	μg cm <sup>-2</sup> s <sup>-1</sup>	-MPa	
Williams 82	III	6.25	2.10	2.07	R8
Douglas	IV	4.74	2.94	2.12	R7
Crawford	IV	4.52	2.84	2.35	R6
Pixie	IV	10.44	0.54	2.95	R8
Forrest	V	14.02	0.43	3.30	R5
Essex	V	13.02	0.53	3.50	R5
Narrow	V	14.16	0.52	3.13	R5
Sohoma	VI	13.10	0.57	1.86	R5
LSD (0.05)		3.67	0.72	0.42	
LSD (0.01)		4.95	0.97	0.56	



Douglas, and Crawford cultivars were again significantly statistically lower (0.01 level) compared to Pixie, Forrest, Essex, Narow, and Sohoma cultivars. Values of TR were higher for the Williams 82, Douglas, and Crawford (Table IX). The inverse relationship between DR and TR values also followed similar trends as those obtained on 30 August. LWP were significantly higher (0.05 level) for the Williams 82, Douglas, Crawford, and Sohoma compared to Pixie, Forrest, Essex, and Narow cultivars (Table IX).

#### Pods, Total Seeds and Seed Weight Per Plant

For the six qualitative water stress levels studied over various reproductive stages of growth immature pod formation was significantly higher (0.01 level) for the Hobbit and Pixie compared to the other 13 cultivars (Table X). All other cultivars ranged from a low of 0.4 to a high 1.8 immature pods/plant. In general the formation of mature pods decreased as immature pod production increased for the Hobbit and Pixie cultivars, however, this relationship was not evident for the rest of the cultivars (Table X). Mature pods production for Forrest>Sohoma>Gnome>Essex>Crawford>Century 84 and represents the six top mature pod producing cultivars. The other cultivars were similar in the number of mature pods produced (Table X). Cultivars Gnome, Crawford, and Forrest were the three highest in total seeds produced with the Weber, Lakota, Vinton, Hobbit, Pixie, and Narow being the six low seed producing cultivars (Table X).

Seed weight/plant was significantly higher (0.01 level) for the Crawford compared to the next three highest (Forrest, Essex, and Sohoma)

TABLE X

MEANS FOR THE EFFECTS OF WATER STRESS ON THE NUMBER  
OF IMMATURE, MATURE, AND TOTAL PODS; TOTAL SEEDS; AND  
SEED WEIGHT PER PLANT

Cultivar	Maturity group	Immature pods	Mature pods	Total pods	Total seeds	Seed† weight --g--
Weber	I	0.9	7.0	7.9	15.4	1.25
Lakota	I	0.7	8.0	8.7	18.0	2.01
Vinton 81	I	0.6	9.3	9.9	17.6	2.66
Gnome	II	0.8	12.3	13.1	26.3	3.18
Century 84	II	0.4	10.3	10.7	22.6	3.37
Platte	II	1.6	8.9	10.5	20.9	1.95
Hobbit	III	3.7	8.1	11.8	18.0	1.77
Williams 82	III	0.3	8.7	9.0	19.7	2.70
Douglas	IV	0.3	9.0	9.3	21.2	3.06
Crawford	IV	0.5	11.5	12.0	28.0	4.86
Pixie	IV	4.9	8.1	13.0	17.4	1.37
Forrest	V	1.8	15.3	17.1	30.3	4.18
Essex	V	1.1	12.0	13.3	24.2	3.84
Narow	V	1.2	8.3	9.7	16.3	3.07
Sohoma	VI	0.8	13.4	14.2	24.2	3.85
LSD (0.05)		0.72	1.47	1.64	3.01	0.47
LSD (0.01)		0.95	1.94	2.17	3.98	0.62

†Adjusted to 13% moisture.

yielding cultivars. Vinton 81 (Maturity Group I), Century 84 (Maturity Group II), Williams 82 (Maturity Group III), Crawford (Maturity Group IV), Forrest and Essex (Maturity Group V), and Sohoma (Maturity Group VI) were the highest yielding cultivars after being subjected to all six water stress levels during reproductive stages of growth.

## CHAPTER V

### SUMMARY AND CONCLUSIONS

Fifteen soybean cultivars ranging from I to VI in Maturity Groups were subjected to induced water stress levels during reproductive stages of growth. Diffusive resistance, transpiration rates, and leaf water potential values were measured on six different water stress dates. Over the six water stress dates measured diffusive resistance values ranged from 0.84 (Table IV) to 19.54 (Table V)  $\text{sec cm}^{-1}$  and varied inversely at different degrees of magnitude with transpiration rates that ranged from 0.33 (Table V) to 8.75 (Table IV)  $\mu\text{g cm}^{-2}\text{s}^{-1}$ . Leaf water potentials ranged from -1.08 (Table IV) to -4.43 (Table VII) MPa.

A range in magnitude of leaf water potentials were related to visually described qualitative water stress levels. Qualitatively medium stressed soybeans had leaf water potentials of  $<-1.4$  MPa compared to a range between -1.7 to -3.0, and  $>-3.0$  MPa for high and very high qualitatively described water stress levels, respectively. There was a trend for leaf water potentials to be lower for soybean plants in the early compared to the later reproductive stages of growth at a given water stress level. These data suggest that there is less resistance to movement of water from the rooting medium, across root membranes, into the xylem, and movement up through the vascular system to the leaves as soybean cultivars proceed through reproductive growth stages.

Diffusive resistance and transpiration rates varied inversely with

considerable differences between cultivars in the same Maturity Group having similar leaf water potentials. This suggests differences in the rate of loss of water from the walls of the mesophyll cells, differences in movement of water vapor in the intercellular spaces to and through the stomates, and away from the outer air boundary.

The pod formation, total seeds, and seed weight data should be interpreted with great caution in that these agronomic characteristics were a result of six predetermined qualitative water stress levels for 15 different cultivars at different reproductive stages of growth. Newly designed experiments are required to ascertain the cause and effect relationships between the above mentioned production parameters.

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