AN ABSTRACT OF THE THESIS OF

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Title: Physiological and Yield Responses of Snap Beans (Phaseolus vulgaris) to Water Availability

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Selected aspects of the water relations of snap beans (cv. "Oregon 1604") were investigated under contrasting water regimes in the field. These were coupled with studies of leaf growth, the Plastochron Index, stomatal behavior as related to dry matter and pod yield. The field experiments were conducted in 1980 and 1981 on deep, alluvial silty clay loam with a high water holding capacity. Fully expanded leaves had an average value of solute potential at full turgor ($\psi_{s,100}$) of -5.39 ± 0.34 and -6.72 ± 1.33 bars and an average value of solute potential at zero turgor ($\psi_{s,0}$) of -8.02 ± 0.53 and -10.66 ± 2.36 for the non-stressed (NS) and severely stressed (SS) treatments, respectively. The apoplastic water contents for the NS and SS treatment were 14.9 ± 2.5 and 23.7 ± 1.52 percent, respectively. The elastic modulus of elasticity (ε) increased linearly with increasing turgor pressure (ψ_p) from 0 to 3.0 bars. Results from the PI experiments indicated that the plastochron duration in the field of the NS and SS treatments were 42 ± 11.6 and 71 ± 8.8 hours, respectively. Plastochron duration in the growth chamber were 145 ± 3.3 and 230 ± 3.1 hours for NS and SS treatments, respectively.

The threshold leaf water potential (Ψ) for stomatal closure was estimated to range from -13.0 to -15.0 and from -10.5 to -12.5 bars for NS and SS treatments, respectively. Leaves of the NS treatment had higher (Ψ) than those of the SS treatment throughout the day. The osmotic potential (Ψ_s) at midday hours was generally lowest for the SS treatment and (Ψ_p) was maintained at values greater than those of the NS treatment. Evidences of osmotic adjustment were observed seasonally as well as diurnally. However, the observed turgor maintenance could not overcome the drastic effects of water deficit on plant growth and pod yield. Plants of treatments NS, GS and SS produced about 11.9, 11.5 and 5.5 pods per plant, respectively. The pod weights were 5.14, 4.06 and 2.47 grams per pod for the NS, GS and SS treatments, respectively. The pod yields were 33580, 21967, and 8278 Kg/ha for NS, GS and SS treatments, respectively.

Physiological and Yield Responses of Snap Beans (*Phaseolus vulgaris*) to Water Availability

by

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PHYSIOLOGICAL AND YIELD RESPONSES OF SNAP BEANS (*PHASEOLUS VULGARIS*) TO WATER AVAILABILITY

INTRODUCTION

Water is the earth's most abundant compound and it represents the most essential component of life. Water comprises approximately 90 percent of the total fresh weight in physiologically active herbaceous plants. The lack of water is the single most limiting factor to plant production throughout the world, especially in the arid and semi-arid areas.

The growth potential of a crop is ultimately determined by its genetic make-up. However, the environment plays a major role in determining the extent to which the growth potential is expressed. When soil water availability becomes limiting, plant water stress becomes increasingly pronounced. This water stress affects the biochemical and physiological processes and changes the conditions in plants. Reduction in plant productivity and crop yield are unavoidable consequences of exposing plants to severe water stress. Hsiao (1973) showed that plant water stress affects every aspect of plant growth and the worldwide losses in yield from water stress probably exceed the losses from all other causes combined (Kramer, 1980).

Field research on crop responses to variable water supply has been largely empirical, directed at quantifying yield to water use and water deficits at different crop growth stages. In recent years, interest has focused on specific physiological alterations in plants caused by water stress, specifically those related to the transpiration

and photosynthesis processes. Leaf growth and turgor mediated processes received much attention in the last two decades. Modeling and simulation techniques have advanced recently to the point that permits attempts to integrate diverse plant processes over time, which theoretically would allow long term prediction of crop growth. Most recently interests have focused on the importance of morphological and physiological mechanisms of adaptation to water stress, such as mechanism of osmotic adjustment and turgor maintenance.

In this study we will focus on some of the physiological changes that occur in the bean plants in response to water deficits. Special emphasis is given to analyzing the impact of water supply on the internal characteristics of bean leaves, the growth and development of leaves, and diurnal and seasonal changes of the plant water stress. An attempt will be made to identify mechanisms of adaptation to water stress and their possible role in maintaining the growth of the plant.

It is the author's belief that the breeding and the selection for adaptation of plants to water stress would be facilitated by a better knowledge of the physiological, morphological, and agronomical responses of the crop to water deficits.

LITERATURE REVIEW

General Aspects of Plant Water Relations

Concepts in Plant Water Relations

The plant may be considered as a water conducting system from a source, the soil system, to a sink, the atmosphere. Therefore the water transport through the plant must be dealt with as a continuum from the soil to the atmosphere through the plant. This is known as the soil-water-plant-atmosphere continuum. Transpiration in response to the evaporative demand of the atmosphere is the main driving force for the transport of most of the water through a plant. For the last three decades, it has been known that this loss due to transpiration develops a potential gradient between the source and the sink. Water movement is from regions of high water potential to regions of low water potential. Water moves in the direction of lowest energy levels. At any time, the water status of the plant depends on the rate of water uptake and the rate of water loss.

The rate of water uptake is given by

$$E = \frac{\Psi_r - \Psi_s}{r_r + r_s} , \qquad (1)$$

where Ψ_r and Ψ_s are, respectively, the water potentials at the root system and the soil around roots and r_r and r_s represent the resistances to water flow from the soil to the root xylem (Slatyer, 1967).

The transpiration rate is given by

$$T = \frac{C_{wv}^{l} - C_{wv}^{a}}{r_l + r_a} \quad , \qquad (2)$$

where C_{wv}^{l} and C_{wv}^{a}, are the water vapor concentrations inside the leaf cells and in the air, respectively, and r_l and r_a are the leaf and air resistances, respectively (Slatyer, 1967). Many climatic factors influence this equation. Some of these are light, air temperatures, air humidity, and wind speed. Plants take up huge amounts of water. One acre of a crop may transpire 2 to 3 acre-feet of water during a growing season. About 99% of this water merely passes through the plant, being quickly transpired to the atmosphere. Availability of water is extremely important to the well being of the plant. A high plant water status is essential for almost all of the plant's physiological processes.

Definition of Plant Water Status

The potential distribution in the soil-water-plant-atmosphere continuum is dynamic and constantly changing, making defining the plant water status very difficult. The water status of plant tissue can be defined by either the amount of water contained in the cells or by the energy status of that water (Barrs, 1968; Boyer, 1969; Slavik, 1974). The water content of plant tissues if expressed on a dry weight or fresh weight basis are unsatisfactory, because the tissue weight changes diurnally and seasonally (Barrs, 1968). Therefore, to avoid these problems, water content should be expressed on the basis of the water content at full turgor which is termed Relative Water Content

(RWC). It is defined as (Barrs, 1968)

$$RWC = \frac{\text{Water content at sampling}}{\text{Water content at full turgor}} \times 100 \ . \qquad (3)$$

The energy status of water can be expressed by its free or chemical energy which is termed total water potential, often denoted by (Ψ). Water potential is one variant of the fundamental thermodynamic parameter, chemical potential of water (μ_w) (Slatyer and Taylor, 1961). It is defined as the difference in free energy or chemical potential per unit molal volume between pure water and water in cells at the same temperature. It is expressed mathematically as:

$$\Psi = \frac{\mu_w^\circ - \mu_w}{\bar{v}_w} = -\frac{RT}{\bar{v}_w} \ln(e/e_s) \ , \qquad (4)$$

Where (e/e_s) is the ratio of the vapor pressure to the saturated vapor pressure, R is the universal gas constant, T is the absolute temperature (°K), μ_w° and μ_w, respectively, are the chemical potentials of pure water and that of cell at the same temperature, and $\bar{v}_w$ is the molal volume of water. The potential of pure water is set to zero ($\Psi = 0$), hence the potential of water in the cells and solutions is less than zero, or negative. This concept is superior to the one that was in use two decades ago, namely, the Diffusion Pressure Deficit (DPD). The water potential of a cell is numerically equal to the diffusion pressure deficit, but has a negative sign.

The water potential is the most commonly used indicator of the energy status of water in plant tissues (Kramer et al., 1966; Boyer, 1969; Hsiao, 1973). The total water potential is composed of four

main components,

$$\Psi = \Psi_p + \Psi_s + \Psi_m + \Psi_g \qquad (5)$$

where Ψ_p is the pressure potential, due to turgor, Ψ_s is the osmotic potential, due to solutes, Ψ_m is the matric potential, due to interaction of water with the tissue matrix, and Ψ_g is the gravitational potential, due to gravity.

In plant physiology literature, traditionally Ψ has been expressed in pressure units (bars) instead of energy units. Recently, the units of Mega Pascal (MPa) has been adopted (MPa = 10 bars). These energy units and pressure units are related since pressure (force per unit area) is equivalent to energy per unit volume.

Magnitude and Significance of Water Potential and Its Components

Within the cytoplasm, Ψ is a function of Ψ_s, Ψ_p, and Ψ_m. In the vacuole we expect Ψ_s to dominate and Ψ_p to be similar to that of the cytoplasm. The contribution of Ψ_m in the vacuole is negligible (Nobel, 1974). Within the wall of the plant cells, Ψ is primarily a function of Ψ_m. The water in the cell wall is called "apoplastic water" (Campbell et al., 1979) and also referred to as "bound water" (Wenkert et al., 1978). The gravitational potential, Ψ_g, is negligible except in tall trees. This is because Ψ_p and Ψ_s are normally so large that they dominate over Ψ_g.

The pressure potential, Ψ_p, represents the hydrostatic pressure that results from turgor. It is positive in the plant tissues and drops to zero at the point of incipient plasmolysis. Negative turgor

pressure is reported to occur only if the tissues are severely dehydrated. Slatyer (1967) argued against the concept of negative turgor pressure in plant cells. He attributed reports of negative turgor pressures to errors in measurements.

The osmotic potential Ψ_s reflects the presence of solute molecules on water potential

$$\Psi_s = \frac{RT}{\bar{v}_w} \ln a_w \ , \qquad (6)$$

where a_w is the activity of water in the cell, R is the universal gas constant, and T is the Kelvin temperature. This expression for osmotic potential is almost exact, the only approximation being that water is incompressible (Slatyer, 1967). Further simplification results in a linear relationship between osmotic potential and the molar concentration of the solution. This relationship is known as the Van't Hoff equation (Slatyer, 1967),

$$\Psi_s \simeq - cRT \ , \qquad (7)$$

where c is the molar concentration of the solutes in the cell. This formula estimates Ψ_s fairly well for dilute solutions. The concentration of the solutes in the plant cell is high, therefore, Ψ_s is low, e.g. Ψ_s can be - 10 bars or lower. In the vacuole, the concentration is relatively higher than that in the cytoplasm because the vacuole is used for storing the osmotically active organic and inorganic molecules. Matric potential, Ψ_m, is not usually taken into consideration when considering bulk tissues. However, it is very important within the cell walls. Campbell et al. (1979) estimated that about 5, 17,

and 30 percent of the plant water is bound by the cell walls for wheat, potato, and wheatgrass, respectively. Boyer (1967) concluded that Ψ_m arises primarily in the walls of the leaf cells and its significance decreases as tissues become turgid. His results showed that Ψ_m becomes more negative, decreases from -5 to -15 bars, as tissue water content of sunflower decreases to 20 percent. Recent measurements by Wenkert (1980) on corn showed that an 11 to 16 percent error in the measurement of osmotic potential was due to the contribution of Ψ_m of the cell walls.

Measurements of Plant Water Status

Many methods for measuring RWC are discussed by Barrs (1968) and Kramer (1969). Another review was completed by Catsky (1974). The most common method for determining RWC is by floating leaf discs or whole leaves on water until they regain full turgidity. The relative water content can be determined at any water content by

$$RWC = \frac{FW - DW}{TW - DW} \times 100 , \qquad (8)$$

where FW, DW, and TW are fresh weight, dry weight, and turgid weight of the tissues, respectively.

Many methods have been developed to measure Ψ in plant tissues. A review of most of these can be found in Kozlowski (1968) and Slavik (1974). The most commonly used method for measuring Ψ is the pressure chamber method that was introduced by Scholander et al. (1965). Exised leaves or other organs are sealed in a chamber with the cut end of the petiole protruding through a rubber stopper. The

pressure in the chamber is gradually increased, using N_2 gas, until the xylem sap returns to the exposed end of the organ. The applied pressure is assumed to be numerically identical to the xylem potential, which is assumed to be in equilibrium with leaf water potential. When xylem sap has a high concentration of solutes a correction may be needed. Several precautions have been suggested by Turner (1980) when using the pressure chamber technique. Water loss between sampling and measurement must be prevented by sampling in humid and shaded environments (Boyer, 1974). The chamber should be lined with wet paper towels to prevent water loss in the chamber itself (Slavik, 1974). The leaves should be placed in a plastic bag inside the chamber (Turner, 1980). Milar and Hansen (1975) discussed the error that resulted from leaving part of the sample protruding from the chamber. This excluded portion is not subject to the applied pressure, which leads to what is called the "exclusion error." The error can be minimized by leaving a minimum length outside the chamber. Pressurization should be slow. A rate of 0.03 to 0.05 bar/sec is recommended (Turner, 1980) and gas leakage from the chamber must be prevented. One of the difficulties with the technique is the determination of the real end point. In many species it is hard to see the exact point at which xylem sap just appears at the exposed cut. Drying the cut surface with a filter paper helps to prevent reading a false end point.

Many techniques are available for the measurement of osmotic potential, i.e., refractometric methods which depend on concentration of dissolved compounds and their relation to refractive index;

cryoscopic methods which depend on the change in the freezing point; the psychrometric method which depends on the change in the relative vapor pressure (Barrs, 1968; Slavik, 1974; Turner, 1981). The most common technique is to measure the water potential of the cell sap expressed from initially frozen and subsequently thawed tissues with a thermocouple psychrometer (Neuman et al., 1973; Campbell and Campbell, 1974; Acevedo, 1975; Fereres, 1976; and Turner, 1981). It is assumed that Ψ_p is atmospheric, Ψ_s is the same as that of the living tissues, and Ψ_m is maybe neglected. Recently, it has become more common to correct for the matric potential component by estimating the apoplastic water fraction with the pressure-volume technique or any other valid method. The correction factor makes it possible to obtain a better estimate of Ψ_s of the living tissues.

The most widely used method for obtaining turgor pressure is to estimate it from measurements for total water potential, Ψ, and osmotic potential, Ψ_s, corrected for the bound water fraction. Turgor pressure is obtained by difference ($\Psi - \Psi_s$). Green (1968) discussed the possibility of measuring turgor pressure directly. He measured the turgor pressure of a Nitalla cell to within 0.1 bar or less, by measuring the ability of the cell to compress gas trapped in the closed end of a capillary with the cell vacuole in the open end. Heathcote et al. (1979) have described a technique for estimating the average turgor pressure of leaves, based on the principle that the deformation of leaf tissues is affected by its turgor pressure. The deformation of a constrained area of the leaf under a fixed pressure is measured by sensitive strain gauges. Hammel (1968)

devised a direct method for measuring the turgor pressure in the secondary phloem sieve tubes of oak trees. He also described a method for estimating the average turgor pressure in cells of the leaves.

In situ measurement of plant water status has been the main goal of many investigators. Campbell and Campbell (1974) used psychrometers and hygrometers to measure Ψ in situ. Their results indicate that temperature gradients between leaf and thermocouple caused an error of about 0.4 bars. The results from the hygrometer procedure were compared with pressure chamber measurements. It was found that the average pressure chamber reading was 0.4 to 1.0 bars lower than that obtained with the leaf hygrometer. Baughn and Tanner (1976) have found that the pressure chamber gave lower Ψ than the hygrometer in the wet range and higher Ψ than the hygrometer in the dry range.

Indirect Estimations of Plant Water Status

Many of the accepted methods for evaluating the water status by means of measuring water potential or leaf water content are both labor intensive and tedious. Furthermore, they are subject to considerable experimental and sampling errors (Turner, 1981; Pinter et al., 1981). Recently, many studies were conducted to evaluate the water status indirectly. Infrared thermometry, for example, is being used to evaluate canopy or leaf and air temperature differences as indicators of water stress (Ehrler et al., 1978; Idso et al., 1981; and Jackson et al., 1981). Infrared photography has been used for the same

purpose (Blum, 1974). Stem diameter and leaf elongation rate have been measured by linear variable displacement transducers (LVDT) (Namken et al., 1969 and Barlow, 1979). A commonly used and accepted approach is the measurement of stomatal conductance or resistance with diffusion flow porometers (Kanemasu, 1975). The leaf resistance was measured directly and rapidly and with simple portable equipment by Van Bavel et al. (1965) and Kanemasu et al. (1969). They reported the use of diffusion porometers which permit estimating stomatal resistance. Results agreed well with results obtained by the leaf energy balance. Measurements of stomatal actions are thoroughly reviewed by Barrs (1968); Kanemasu (1975); and Raschke (1975).

Pressure - Volume Curves of Plant Tissues

To measure the osmotic potential of the cell sap, the pressure potential (turgor) is forced to be atmospheric, by killing the tissues. First freezing, and then thawing the tissues is the most common practice to accomplish this. The expressed solution is a mixture of apoplastic water (i.e. water in the walls and xylem external to the cells) and of the symplastic water (i.e. water from the cell vacuole and cytoplasm). Turner (1981) reports that the osmotic potential of apoplastic water is usually higher than -1.0 bar and often higher than -0.2 bars, whereas the osmotic potential of the symplastic water is usually -10 to -30 bars. Thus, the symplastic water is actually diluted by apoplastic water. A technique was developed, called the P-V curve technique, to estimate the dilution caused by mixing symplastic water with apoplastic water. The procedure was introduced

by Scholander et al. (1964) and reviewed by Boyer (1969).

Theory and Development of P-V Curves

The theory for the P-V relationships of plant tissues in the pressure chamber was introduced by Scholander et al. (1964), discussed by Boyer (1969), redeveloped by Tyree and Hammel (1972), refined by Tyree (1976), and later simplified by Turner (1981).

At equilibrium conditions, the leaf water potential is the same in the apoplastic and symplastic regions. In the apoplastic region, Ψ is mainly due to matric and osmotic effects. However, for the symplastic region the water potential is a result of the interaction of matric, osmotic, and pressure effects.

The simplest model for a symplastic water system involves certain assumptions, namely the matric potential Ψ_m is negligible, the osmotic pressure, π, is proportional to the inverse of the symplastic water volume and the turgor pressure, p, remains at zero once it becomes atmospheric.

The general expression for the total water potential is

$$\Psi = \Psi_s + \Psi_p + \Psi_m \,, \tag{9}$$

which can also be expressed as:

$$\Psi = -\pi + P + \Psi_m \,, \tag{10}$$

where P is the turgor pressure and π is the osmotic pressure. Assuming $\Psi_m = 0$, the turgor pressure is defined as the volume averaged turgor pressure and expressed as follows:

$$\overline{P}_v = \sum_i \frac{V_i}{V_s} P_i \ , \qquad (11)$$

where P_i is the turgor pressure of the i-th cell, V_i is the volume of the i-th cell and V_s is the volume of the symplasm at which $\overline{P}_v$ is evaluated. Define the osmotic pressure as the bulk averaged osmotic pressure given by:

$$\pi = \frac{RT}{V} \sum_i \left(n_i \right) = \frac{RT}{V} N_s \ , \qquad (12)$$

with

$$N_s = \sum_i \left(n_i \right) \ ,$$

where R is the universal gas constant, T is the absolute temperature, and n_i is the number of moles of dissolved solute in the i-th cell. Since $\overline{P}_v$ will fall to zero and remain zero, P = 0 and $\Psi = -\pi$. Therefore equation 12 will be

$$- \Psi = \frac{RT}{V} N_s \ , \qquad (13)$$

or

$$- \frac{1}{\Psi} = \frac{V}{RT\ N_s} \ ,$$

Since

$$V = V_s - V_e \ ,$$

$$- \frac{1}{\Psi} = \frac{V_s}{RTN_s} - \frac{V_e}{RTN_s} \ , \qquad (14)$$

where V_s is the symplastic volume at full turgor, $\Psi = 0$, which is

constant by hypothesis, and V_e is the volume of water lost from the symplasm.

Equation 14 predicts a linear relationship between $-\frac{1}{\Psi}$ and V_e with a slope equal to $-1/RTN_s$ and an intercept equal to V_s/RTN_s. This relationship is shown in Figure 1.

The relationship shown in Figure 1 can be obtained by placing the leaf in a pressure chamber. Pressure is applied until the sap appears at the exposed surface outside the chamber. The pressure at this point is numerically equal to the water potential of leaf cells before pressurization. Then, the leaf is over pressurized by 2 to 5 bars, and the sap expressed in this manner is collected. The procedure is repeated for a succession of pressure values until enough points have been obtained to characterize the curved and linear portions of the P-V curve. The pressure is then released and the leaf is dried to obtain the residual water content and dry weight.

Significance and Application of P-V Curves

·Point of Incipient Plasmolysis. This point is indicated by the inflection point on the curve (point A in Figure 1) where $\Psi_p = 0$ and $\Psi_s = \Psi$. The value of the osmotic potential at incipient plasmolysis, $\Psi_{s,0}$, sets a limit to the water potential above which positive turgor pressure occurs.

·Point of Full Turgidity. The osmotic potential at full turgidity $\Psi_{s,100}$ can be estimated by extrapolating the straight line part of the Y-axis. At $V_e = 0$, $\Psi = \Psi_{s,100}$ (point C on the graph in Figure 1). The

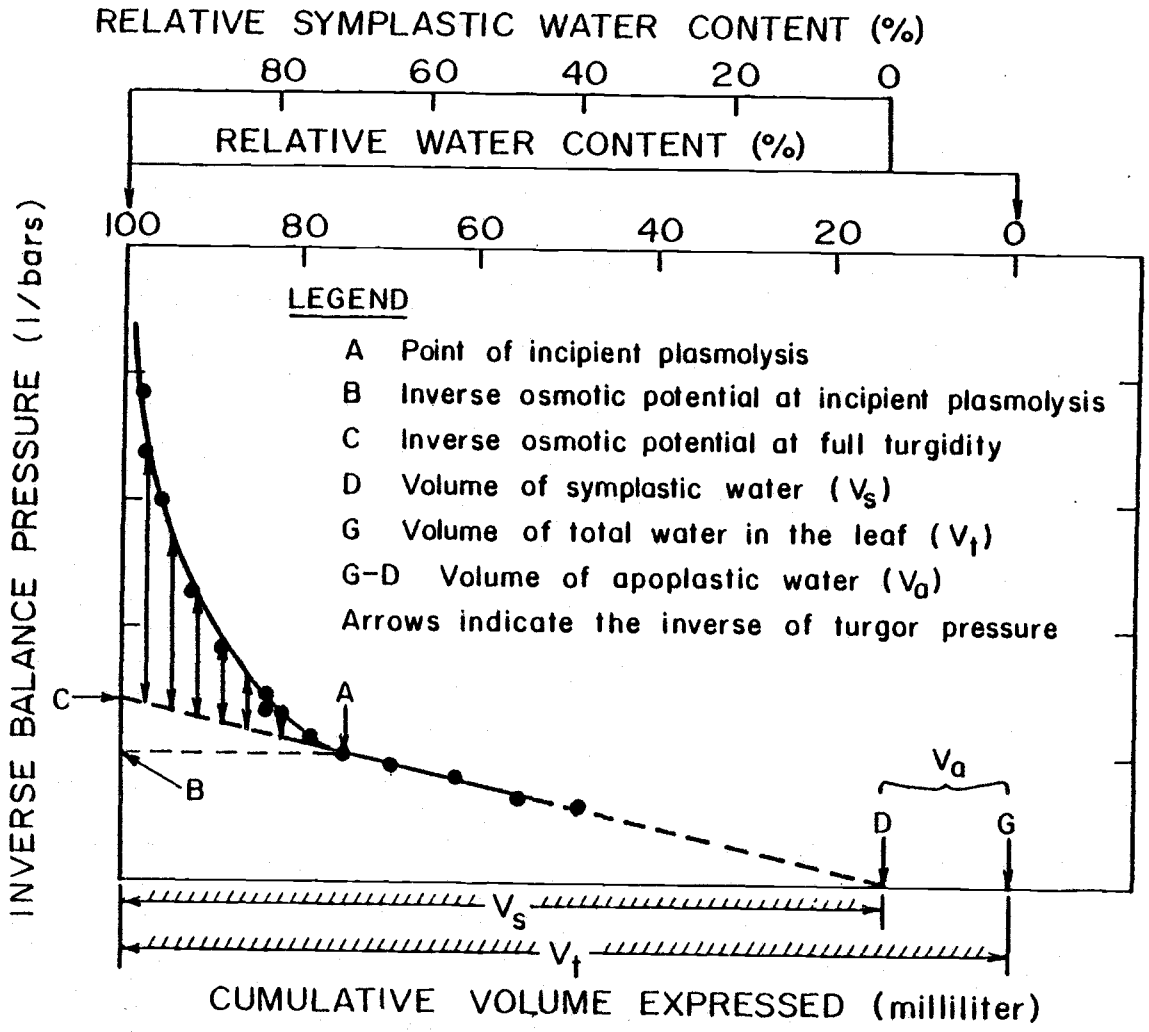

Figure 1. An idealized P-V relation of a single leaf. Adopted from Turner (1981).

value of $_{s,100}$ describes the amount of osmotic solutes a leaf contains per unit volume of symplastic water V_s.

·Symplastic Water Volume. The value of symplastic water content V_s can be obtained by extrapolating the straight line part of the P-V curve to the X-axis. At $-\frac{1}{\Psi} = 0$, $V_e = V_s$, indicated by point D on the graph. V_s is constant.

·Tissue Turgor Pressure. The inverse of the turgor pressure $1/\Psi_p$ at any level of turgidity is the difference between the $1/\Psi$ (curvilinear) and $1/\Psi_s$ (linear) parts of the P-V curve. Values are indicated by the arrows between the two lines in Figure 1.

·Total Water Volume of Tissues. The total volume V_t of water in the tissues can be estimated as follows:

$$V_t = V_r + \sum_{1}^{n} V_{ei} \,, \qquad (15)$$

where V_r is the volume of the residual water after the tissues have been dehydrated and become flaccid, V_{ei} is the volume of expressed water at the i-th pressure measurement (i = 1, 2, 3, ... , n), and V_t is the total water volume of the tissues, indicated by point G in Figure 1.

Assuming the density of the residual water is unity, then $V_r = W_r$. Where W_r is the weight of the residual water, determined by subtracting the dry weight (DW) of the tissues from the weight of the flaccid tissues (FLW).

·Relative Water Content. The relative water content (RWC) for each paired measurement can be calculated by

$$RWC_j = 1 - \frac{\sum_1^i V_{ei}}{V_t} , \qquad (16)$$

·The Relative Symplastic Water Content (RSWC). The relative symplastic water content for each paired measurement is given by

$$RSWC_i = 1 - \frac{\sum_1^i V_{ei}}{V_s} , \qquad (17)$$

·The Bulk Modulus of Elasticity. This parameter was derived by Tyree and Hammel (1972). Then Cheung et al. (1976) defined a bulk modulus of elasticity as

$$\varepsilon = \frac{d\overline{P}_v}{dF} , \qquad (18)$$

where $\overline{P}_v$ is the volume averaged turgor pressure and

$$F = \frac{V_s - V_p - V_e}{V_p} , \qquad (19)$$

where V_e is the volume of water expressed, V_s is the tissue symplast volume at $V_e = 0$, and V_p is the bulk volume at incipient plasmolysis. Turner (1981) reported another expression of ε, namely

$$\varepsilon_t = \frac{\Delta P}{\Delta RSWC} , \qquad (20)$$

Melkonian et al. (1982) argued that both Tyree and Cheung defined ε in

terms of derived, and in particular depend on the rather uncertain estimation of V_p. Melkonian et al. (1982) defined the tissue-water bulk modulus by

$$\varepsilon_m = V_t \frac{\Delta P}{\Delta V} \quad , \tag{21}$$

where V_t is the volume of water in the leaf at full hydration, and ΔV is the volume expressed between balance pressures differing by ΔP. In our analysis, we will use the definitions of both Turner (1981) with the symbol ε_t, and Melkonian et al. (1982) with the symbol ε_m as shown in equations 20 and 21, respectively.

·Apoplastic (Bound) Water Fraction. This fraction is that water which resides in the xylem and cell walls. It is given by

$$B = \frac{V_a}{V_t} \times 100 = \frac{V_t - V_s}{V_t} \times 100 \tag{22}$$

where V_a is the apoplastic water volume, B is the bound water fraction, and V_s and V_t are as previously defined.

·Correction Factor for Bound Water. The bound water fraction obtained from P-V techniques can be used for correcting Ψ_s values measured by the dew point hygrometer to account for the dilution effect of the apoplastic water, which occurs during the procedure for obtaining cell sap for measurement of Ψ_s. This measured value can be corrected according to the following procedure (Campbell et al., 1979),

$$\Psi_s \text{ corrected} = \Psi_s \text{ measured } \left(\frac{RWC}{RWC - B}\right) \tag{23}$$

where RWC is the relative water content and B is the bound water

fraction. Several precautions and viewpoints have been discussed by Tyree et al. (1978), Campbell et al. (1979), and Turner et al. (1981) to insure the success of this technique.

Plant Responses to Water Stress

Water has a crucial role in every place of the plant complex. It is involved directly or indirectly in almost all biochemical reactions that take place in a plant cell. Therefore, under conditions of water deficiency, almost all physiological and metabolic processes are altered to some degree. The growth of a plant under natural conditions is an expression resulting from the continuous interaction between the environment with the genetic make-up of the plant. Crop plants rarely attain their full genetic potential for yield because of limitations imposed by the environment, especially unfavorable temperatures and lack of water (Kramer, 1980). Water is the most widely limiting environmental factor for crop production (Loomis et al., 1971, and Hsiao, 1973).

Levitt (1980) defined two main components of water deficit, namely, "stress" and "strain." Biological stress is defined as any environmental factor (i.e. water) capable of inducing potentially injurious consequences in living organism, e.g. plants. However, "strain" is defined as any physical or chemical change produced by a stress. "Drought" is a more general and commonly used term to describe stress and is defined by Kramer (1980) as being an environmental stress of sufficient duration to produce a plant water deficit

or stress, which in turn causes disturbance of physiological processes.

In recent years, effects of water stress have been thoroughly reviewed (Slatyer, 1969; Hsiao, 1973; Stone, 1974; Kramer, 1974; Begg and Turner, 1976; Levitt, 1980; Kramer, 1980). The literature gives the impression that if the stress is severe and long enough almost every parameter is changed by water stress. The purpose of the following review is to describe the highlights of the effects of water stress on physiological processes that may be of great importance in the growth and yield of crop plants.

Effects of Water Stress on Internal Water Characteristics

The internal water characteristics of a leaf can be established by knowing the relationship between RWC and leaf Ψ. This relationship appears to change with cultivar (Blum, 1974), with age for dogwood trees (Knipling, 1967) and for barley (Millar et al., 1968). The relationship of RWC to Ψ is not constant for a given species but depends on growth stages, leaf number (Miller et al., 1970), and water deficit (Hsiao, 1973; Kramer, 1974; Kappen et al., 1975; Jones and Turner, 1978). Many changes in the water relations of the tissues have been attributed to long term changes in the anatomy of the cells (Kappen et al., 1975) and related to changes in solute content and cell wall elasticity (Knipling, 1967). Weatherly (1965) reported that tissues with elastic cell walls have a greater decrease in volume for a given decrease in Ψ_p than tissues with rigid walls. It was also found that the value of modulus of elasticity generally increases with increasing

Ψ_p (Hellkvist et al., 1974). Steudle et al. (1977) have found that ε of the cell depends strongly on Ψ_p and on cell volume. The importance of turgor pressure in the cell water relations was emphasized by Hsiao (1973). He concluded that in growing cells, changes in Ψ_p trigger alteration in the plant metabolism via changes in growth. Kramer (1974) suggested that changes in the spatial relations of macromolecules due to tissue dehydration may be of importance with respect to enzyme activity and may eventually contribute to the changes that occur within the cell system in response to water stress. It appears from these findings that the mechanisms by which water deficits cause metabolic changes in plant cells are not well understood. One of the difficulties in characterizing these changes is that they are so dynamic that they may occur during the same day. Acevedo (1975) and Fereres (1976) determined this relationship at two different times of the day and noted that in the afternoon a given RWC was associated with lower Ψ (more negative) than in early morning.

Many investigators have studied the effect of water stress on the physiological parameters, using the P-V technique as a way of characterizing the internal water relations of the tissues under water stress. Wilson et al. (1980) found that $\Psi_{s,100}$ and $\Psi_{s,0}$ of stressed leaves decreased by 2.5 to 4.0 bars and by 3 to 5 bars from the control treatments, respectively. However, these differences were largely lost within a few days of rewatering. Similar results were reported for sorghum (Jones and Turner, 1978), winter wheat (Campbell et al., 1979), and sunflower (Jones and Turner, 1980). Water stress preconditioning appeared to increase the proportion of bound water (B) slightly, and

also the relative water content at zero turgor (RWC_0) (Wilson et al., 1980). However, Jones and Turner (1978) reported that zero turgor of sorghum occurred at approximately the same value of RWC irrespective of previous stress history. Brown et al. (1976) and Elston et al. (1976) suggested that stress preconditioning alters the relationship between Ψ and Ψ_p so that plants with a previous history of water deficits have a lower Ψ at zero turgor. This physiologically important parameter is closely related to the point of stomatal closure (Turner, 1975). This observed lowering of Ψ for stomatol closure as a result of stress preconditioning in sorghum was attributed to lowering of Ψ_s by osmotic adjustment (McCree, 1974). Information on the effect of stress on the apoplastic water fraction and the volumetric modulus of elasticity is conflicting and limited. Tyree (1976) reported that the volume of apoplastic water (V_a) is relatively constant as the leaf dries and the dilution factor is slightly increased as RWC decreased. Elston et al. (1976) reported that elasticity increased in response to increased water deficit in field beans. This is opposite to what was found in sorghum by Jones and Turner (1978). Results for winter wheat showed that apoplastic water fraction B and modulus of elasticity ε were relatively insensitive to environment (Campbell et al., 1979). Turner (1975) reported that the prestressed treatment had higher Ψ_p at full turgidity which led to an increase in the volumetric elastic modulus. This increase in ε represents a decrease in tissue elasticity. High ε values indicate rigid cell walls and low values are associated with elastic cell walls (Wilson, 1977). Tissues with elastic cell walls have a greater decrease in volume for a given

decrease in Ψ_p than tissues with rigid walls (Weatherley, 1965). Modulus of elasticity is a function of Ψ_p and cell volume (Steudle et al., 1977) and increases linearly with turgor pressure (Wenkert et al., 1978). Therefore, the observed increase in ε induced by an increase of Ψ_p may be a result of osmotic adjustment and lowering of Ψ_s (Jones and Turner, 1978). The tissue volume at full turgor could also be influenced by osmotic adjustment which would result in a change of ε.

Hsiao et al. (1976) observed that osmotic adaptation of sorghum, based on lowering $\Psi_{s,0}$, did not arise from changes in ε but from an active adjustment in Ψ_s.

Effects of Water Stress on Leaf Growth

Growth is the result of a set of dynamic and complex interactions between soil water and atmospheric conditions expressing the genetic potential of the crop. Vegetative growth is highly sensitive to this complex of interactions. The growth of a plant organ is accomplished by cell division followed by cell expansion and differentiation of individual cells. However, for cell elongation to occur the increase in length of the cell wall must be irreversible. The driving force for this irreversible process is the turgor pressure (Lockhart, 1965). Many formulae were derived to describe the growth process. Green (1968) analyzed data of Nitella growth and gave a formula, relating growth rate to Ψ_p,

$$GR = Eg\ (\Psi_p - \Psi_{p,th})\ , \qquad (24)$$

where GR is the rate of cell expansion (growth) in cm/day^{-1}, Ψ_p is the pressure potential of the cell in bars, $\Psi_{p,th}$ is the threshold or minimum pressure potential (in bars) below which expansion will cease, and Eq is the extensibility coefficient in $cm \cdot day^{-1} \cdot bar^{-1}$.

Lockhart (1965) in an analysis of irreversible cell elongation gave a similar but more complex equation. Equation 24 indicates two important points. First is the high importance of turgor pressure in cell elongation. Second, is the fact that the absolute value of turgor pressure does not reflect the rate of expansion unless compared with a threshold value, which implies that the growth ceases before Ψ_p falls to zero. If $\Psi_{p,th}$ is relatively high, a small reduction in Ψ_p may reduce the expansion rate drastically. This agrees well with the idea, now generally accepted, that cell growth expansion is extremely sensitive to water deficit (Hsiao, 1973; Hsiao et al., 1976). Both cell division and cell expansion are very sensitive to water stress (Boyer, 1968, 1970a; Acevedo et al., 1971). However, Hsiao (1973) suggested that cell division and expansion are interrelated so that cell division may decrease as a result of decreased cell expansion. A study of short term growth under water stress in soybeans suggests that cell expansion is more sensitive than cell division to water deficits (Bunce, 1977; Wenkert et al., 1978a). Acevedo et al. (1971) reported that any reduction in tissue Ψ reduced growth of corn and was stopped completely when Ψ was lowered to -7.0 bars.

In maize grown in controlled environments, leaf expansion declined rapidly at Ψ lower than -2.0 bars and ceased at -7.0 to -9.0 bars (Boyer, 1970b). At the leaf water potential of -4 bars, leaf

enlargement was 0, 25, and 20 percent of the observed maximum for sunflower, soybean, and corn, respectively. The minimum turgor for leaf enlargement was equivalent to about 7 bars in corn, 8 bars in sunflower, and 6.5 bars in soybeans (Boyer, 1968, 1970). Leaf expansion rates were reduced drastically long before net photosynthesis rates were reduced in soybean and cotton (Bunce, 1978) and in corn, soybeans, and sunflower (Boyer, 1970). Watts (1974) reported that leaf expansion of Zea mays grown in the field was not as sensitive to water deficit as when grown in a controlled environment. When water stress develops and turgor is lowered, growth must decrease according to Equation 24. However, if E_g, Ψ_p and $\Psi_{p,th}$ are modified in the right direction in response to stress, growth will recover at least partially (Hsiao, 1973) while tissue Ψ remains at the lower value. Therefore, $\Psi_{p,th}$ and E_g are variable and dependent on other factors. Green (1968) argued that rapid changes in Ψ_p show that Ψ_g is not constant but has a value of zero unless the cell has 80% of normal turgor. Reported values of $\Psi_{p,th}$ range from 2 bars for sugar beet (Lawlor and Milford, 1973) to 8 bars for sunflower (Boyer, 1970). On the other hand, Green et al. (1971) has argued that $(\Psi_p - \Psi_{p,th})$ tends to be constant within certain limits of variation of Ψ_p for Nitella cells. Many evidences suggest that the growth rate of stressed plants recovers very quickly to the original rate after rewatering. Nitella cells recovered within a few minutes after releasing stress (Green et al., 1971), elongation of corn leaves resumed in less than a few seconds after rewatering (Acevedo et al., 1971), and soybean leaves recovered in an hour (Wenkert et al., 1978). The rate of recovery was more related

to the level of water stress than to current Ψ level (Ludlow and Ng, 1977).

The sensitivity of the leaf expansion rates to a decrease in turgor pressure led to the hypothesis that expansive growth occurs in the field mainly during the night when Ψ values are close to zero and that during the day very little growth should be expected due to the decrease in leaf Ψ observed especially at midday hours (Boyer, 1968; Jordan, 1970; Millar, 1971). Results with field grown maize showed leaf elongation rates unexpectedly high in early afternoon hours when leaf Ψ was near the daily minimum (Acevedo, 1975). Similar results for sorghum were found by Fereres (1976). These results could not be explained on the basis of Ψ_p alone. They explained the slow growth at night and early morning by the low temperatures. Osmotic adjustment enabled the stressed plants to maintain high Ψ_p despite the lowering of Ψ. This mechanism was responsible for the high growth rate observed at midday hours. Cutler et al. (1980) reported that leaf elongation rates were 15 to 30 percent greater during the day than during the night. The diurnal pattern of elongation was opposite to the patterns of bulk leaf turgor which was lower during the day than at night. They attributed these results to the fact that night temperature below 27°C limited the rate of elongation at night but when night temperatures exceeded 27°C, night elongation rates exceeded rates during the day. A recent study by Michelena and Boyer (1982) suggests that low water potential inhibits the growth of leaves of grasses for reasons other than loss of turgor or lack of substrate for the growth process.

Effects of Water Stress on Stomatal Movement

Stomata are the leaf openings which regulate both the loss of water vapor by transpiration and the inward movement of CO_2 for photosynthesis. Many evidences indicate that the mechanism of opening and closing of stomata is very complex and is related to a large variety of internal factors. This review will only emphasize the effects of water stress on the stomatal action of some species. For more details of general stomatal physiology, other references should be consulted (Stalfelt, 1966; Zelitch, 1969; Hsiao, 1973; Raschke, 1975; Begg and Turner, 1976).

It is now generally recognized that stomata does not respond to changes in leaf water potential or relative water content until a critical threshold level is reached, and that stomata close over a small range of leaf Ψ (Hsiao, 1973). This level varies with species and possibly with growing conditions. In many cases, the range is -8 to -16 bars of leaf Ψ. Reduction beyond the threshold level, even if only by 1 to 3 bars, causes pronounced stomatal closure.

Growth conditions or the previous history of stress is considered to be a factor contributing to the variability of Ψ at which stomata close. Lower stomates of preconditioned field-grown cotton remained open at lower leaf Ψ than those of nonstressed plants (Thomas et al., 1976). Preconditioning was found mostly to affect the abaxial surfaces (Brown et al., 1974). This is explained by the osmotic adjustment of the guard cells on the abaxial surface and the lack of that adjustment on the adaxial surfaces. These results are similar to the

differences observed between growth chamber and field grown plants (McCree, 1974). Ludlow and Ng (1976) argued that these differences are mainly because of differences in rates of stress development rather than differences in aerial environment between field and growth chamber. Jones and Rawson (1979) exposed sorghum to different rates of stress development and concluded that leaf conductance at a given Ψ_p was lowest at the fastest rate of stress development and highest at the lowest rate of stress development. Many results show that stomatal diffusion resistance recovers to prestress levels within a few hours (Fischer et al., 1970; Frank et al., 1973; Jones and Rawson, 1979). Many studies report that stomatal closure involves changes in turgor relations of the guard cells (Turner, 1974; Meidner and Edwards, 1975; Millar and Denmead, 1976; Jones and Rawson, 1979). The differences between plant species are attributed to the differences in osmotic adjustment of the guard cells (Millar and Denmead, 1976; Brown et al., 1976).

Threshold values of -10 to -12 bars have been reported for soybeans (Boyer, 1970b), -7 to -9 bars for tomato (Duniway, 1971), -17 bars for field grown sorghum (Turner, 1974), and -11 bars for abaxial surfaces and -8 bars for adaxial surfaces of snap beans (Kanemasu and Tanner, 1969). The relatively low values of threshold Ψ indicates that stomata may not be very sensitive to mild water stress (Hsiao, 1973). Data on cotton show that no single value of leaf Ψ will adequately represent a threshold level for stomatal closure (Jordan et al., 1975). Jones and Rawson (1979) concluded that stomatal closure of sorghum leaves occurs slowly over a wide range of leaf Ψ rather than at a

threshold point. This Ψ range is very much a function of the rate of stress development. Slower rates of stress development are associated with a wider range of Ψ for stomatal closure. The leaf position or age has been reported to contribute to this variation. When plants were subjected to increasing water stress, increases in stomatal resistance occurred first on the lower leaves and stomatal closure proceeded from lower or oldest leaves to the upper or youngest leaves as stress became more severe (Jordan et al., 1975). Similar conclusions were reported for spring wheat (Frank et al., 1973). Turner (1974) reported that, for corn, sorghum, and tobacco, the resistance of leaves in the upper canopy increased at more negative value of Ψ than those at the base of the canopy. Leaf senescence was suggested to be the main factor for this difference. Millar and Denmead (1976) argued that because of the different relationships between Ψ and Ψ_p for each leaf, the critical Ψ was lower for the upper leaves.

Stomatal opening and closing is reported to be affected by other factors. Accumulation of potassium ions in guard cells under light conditions is associated very strongly with stomatal opening. Loss of these ions from the guard cells in the dark contributes to stomatal closure (Humble and Rashke, 1971). Water stress is reported to affect ion uptake by plants (Gale et al., 1966), and translocation within the plant (Hartt, 1967; Brevedan and Hodges, 1973). Stomatal opening is also reported to be inhibited by accumulation of abscissic acid (Cummins et al., 1971) the concentration of which rises markedly in leaves subjected to severe water stress (Wright and Hiron, 1969).

Effects of Water Stress on Photosynthesis

The effects of water stress on assimilation processes, particularly photosynthesis have received considerable attention (Iljin, 1957; Brix, 1962; Slatyer, 1969; Boyer, 1970a, 1976; Hsiao, 1973; Sullivan and Eastin, 1974). Turner and Begg (1978, 1981) concluded that water stress results in large reductions in photosynthesis. Data show that this reduction is primarily due to increased stomatal diffusive resistance. Boyer (1976) attributed reduction in photosynthesis to a decrease in photosynthetic activity of the stressed leaf and a reduction in the rate of leaf area expansion. On the other hand, photosynthetic activities are affected by stomatal resistance increase and chloroplast activity decrease. Both are responses to water stress. The sensitivity of net photosynthesis is lower than that of leaf expansion. Hsiao (1973) reported that cell growth can be affected effectively if Ψ decreased from 0 to -3 bars. However, photosynthesis may be affected effectively only when Ψ drops to the range of -6 to -15 bars. Turner and Begg (1978) reported that the deficits required to influence the rate of net photosynthesis are usually more negative than those required to influence leaf elongation.

Popisilova et al. (1978) observed that a decrease in the photosynthetic rate was due to a reduction in both epidermal conductance and in intercellular conductance. Similar results were found by Ludlow and Ng (1976). They stated that at moderate stress the rate of photosynthesis was affected by increasing both stomatal and intercellular resistances. The internal conductance of CO_2 is less sensitive to

water stress and it was unaffected at Ψ levels required to close stomata of bean leaves (Moldau, 1973). Dark respiration is also affected by water stress. However, its decrease by water stress is less than that of photosynthesis at the same Ψ (Boyer, 1971). Changes in leaf photosynthesis with increasing water stress correspond to changes in transpiration rate measured at the same time (Boyer, 1970a; Catskey et al., 1973; Rawson et al., 1978). Many evidences of non-stomatal factors on the increase of stomatal resistance are discussed in the literature. Some of these are an increase of the compensation point at the threshold point of stomatal closure and a decrease of the activity of RUDB carboxylase enzyme at the same Ψ (O'Toole, 1975). It can be concluded that photosynthesis declines initially as a result of stomatal closure, but prolonged and severe water stress can lead to depression of chloroplast and enzyme activity and to nonstomatal effects on photosynthesis (Begg and Turner, 1976). Recovery of net photosynthesis upon rewatering seem to be related to recovery of stomatal diffusion resistance in wheat (Frank et al., 1973), in sorghum (Jones and Rawson, 1979), and in corn (Fischer et al., 1970).

Effects of Water Stress on Crop Productivity

The first prerequisite for high yield is a high production of total dry matter per unit area. The dry matter production depends on the effectiveness of photosynthesis of the crop.

Generally speaking, the effectiveness of photosynthesis is determined by the size and efficiency of the assimilating area, supply of energy, CO_2 concentration and environmental conditions (Arnon, 1981).

Water deficit or stress can affect photosynthesis in many ways depending on the timing and severity of the stress and the length of the stress period (Hsiao, 1973). Water stress during flowering determines the number of fruits which will be produced and stress during pod development determines the size of the bean seeds. However, stress during ripening only affects the length of the ripening period (Arnon, 1981). For a number of cereals and grasses it has been shown that most of the assimilate supplied to the grain comes from photosynthesis after anthesis (Thorne, 1966). In beans, this appears to be the case with insignificant effects on yield resulting from water stress during the vegetative period. However, stress during flowering reduced yield drastically (Hoffman et al., 1978). Therefore, there must be a close relation between weight of pods and rate of photosynthesis during pod enlargement. Sionit and Kramer (1977) reported that yield of soybeans as measured by weight of seeds was reduced most by stress during early formation and pod filling. Peet et al. (1977) concluded that the increase in rate of photosynthesis from flowering to pod set of some varieties of dry beans was correlated positively with its final seed yield. Bush beans are determinate in growth habit, that is stem elongation ceases and leaf production terminates when the terminal flower racemes have developed (Martin et al., 1976). The yield depends more on the development stages at which stress is applied and on sensitivity of that stage to stress. Slatyer et al. (1965) concluded that bean yields are not sensitive to drought at all developmental stages. However, inadequate water during flowering and early pod growth is especially damaging to productivity. Many researchers have

reported that relatively high sensitivity to water stress during the flowering stage in Vicia Faba (El-Nadi et al., 1969), in southern peas (Hiler et al., 1972), in soybeans (Doss et al., 1974), in field beans (Keatinge and Shaykewich, 1977), and in pinto beans (Hoffman et al., 1978). One of the most common mistakes in water stress studies in field experiments is that the stress period is not defined very well and sometimes the period is too long which makes the problem more complicated by introducing too many secondary and tertiary changes (Hsiao, 1973). The effects of water stress on growth stages other than flowering have been studied by many researchers. Dubetz and Mahalle (1969) reported that the total weight of green pods of bush beans were reduced 53 percent and 35 percent by water stress during preflowering and post flowering, respectively. Stress during early pod formation of soybeans caused the greatest reduction in number of pods and seeds at harvest (Sionit and Kramer, 1977). In another study on snap beans, Gonzalez and Williams (1979) reported that water stress significantly decreased yield and pod weight. Hiler et al. (1972) found that the pod development stage of southern peas was the least sensitive to water stress. Early pod formation and filling was reported to be the most important stage for weight of seeds (Sionit and Kramer, 1977). Stress during the vegetative growth period was the least significant contributor to yield reduction (El-Nadi et al., 1969; Hoffman et al., 1978). The quality of the seeds in terms of oil or protein content was not affected by water stress at any stage of growth (Sionit and Kramer, 1977).

Many results of the water stress effects on crop yield were

obtained empirically. These studies, however, fail to link the long term effects of water stress on growth or yield to some basic physiological effects of stress. In fact, many of the detailed observations that were made on changes in the morphological characteristics of plants under stress were not usually accompanied by an accurate estimate of water stress in the tissues. In this study we will try to avoid these errors.

Adaptation of Plants Under Water Deficit Conditions

Terminology

The soil-water-plant-atmosphere continuum is a very complex system and it becomes more complicated when studied in the field environment. Neither this environment nor the water status of the system is ever constant. The atmospheric conditions change continuously causing transient variations of the plant environment. The plants respond to water deficits in many ways, some of which were discussed previously. However, many of these observed responses of the plants under water stress tend to minimize the use of water that will eventually enhance plant survival under the adverse conditions. These reactions of the plant could be described as adaptive responses.

Levitt (1972) identifies adaptation as being a resistance to environmental stress by some sort of avoidance and tolerance mechanisms. A plant may avoid drought stress by maintaining high rates of root growth into a larger volume of soil. Or it may tolerate stress by decreasing its transpiration rate and survive despite the low

plant water potential. Levitt (1980) has a lengthy and thorough discussion of the different kinds of mechanisms that enable the plant to survive the adverse environmental conditions. He classified drought avoidance and tolerance as being drought resisting mechanisms which are different from drought escaping. The latter mechanism is a characteristic of Ephemerols - plants that complete their life cycle in arid habitats during the brief periods free of water stress.

Higher plants are classified as drought tolerant organisms which are capable of maintaining their turgor to some degree when exposed to an external water stress. Many reviews have been made that deal with drought resistant plants (Parker, 1968; Levitt, 1972; Turner, 1979; Turner and Jones, 1980; Arnon, 1981). In this review we will only focus on some of the mechanisms that lead to turgor maintenance of plant tissues under water stress.

Osmotic Adjustment In Higher Plants

Plants subjected to water stress or salinity stress dehydrate to varying degrees (Bernstein, 1961). This water loss will result in reducing Ψ and Ψ_p accordingly. The relationship $\Psi = \Psi_p + \Psi_s$ shows that if Ψ_p is to be maintained as Ψ decreases, then a decrease in Ψ_s must take place. In the literature, the terms osmoregulation, osmotic adjustment, turgor adaptation, and turgor maintenance have been used indiscriminately to describe the lowering of Ψ_s due to tissue dehydration, or due to accumulation of solutes in the cell or both.

Turner and Jones (1980) defined osmoregulation or turgor regulation as the regulation of the osmotic potential (Ψ_s) within a cell by

addition or removal of solutes from solution until the intercellular Ψ_s is approximately equal to the potential of the medium surrounding the cell. Osmotic adjustment, on the other hand, is defined (Turner and Jones, 1980) as the lowering of osmotic potential arising from the net accumulation of solutes in response to water deficit or salinity. They recommended to use osmoregulation for lower plants and microorganisms or for a decrease in cell solutes for higher plants. However, osmotic adjustment is recommended to be used only for accumulation of solutes in higher plants. This term has long been adopted by many workers (Lechtenberg et al., 1971; Acevedo, 1975; Fereres, 1976; Hsiao et al., 1976; Jones and Turner, 1978; Acevedo et al., 1979).

Recent studies of osmotic adjustment in response to water stress show that it occurs in the leaves (Hsiao et al., 1976), in the hypocotyl (Meyer et al., 1972), in the root (Acevedo, 1975), in the apex (Munns et al., 1979), and in reproductive organs, such as spikelets (Morgan, 1980), resulting in full or partial turgor maintenance of many crop species, including maize (Fereres, 1976), sorghum (Acevedo, 1975; Hsiao et al., 1976; Jones et al., 1980; Jones and Turner, 1978), wheat (Morgan, 1980; Campbell et al., 1979), sunflower (Turner et al., 1978), cotton (Cutler et al., 1977), soybeans (Turner et al., 1978). However, little information concerning the osmotic adjustment in beans (Lawlor, 1969) has been reported.

The lowering of osmotic potential alone is insufficient evidence of osmotic adjustment since, firstly, a decrease in the water content of the cells will in itself cause a passive increase in the concentration of cell solutes. Secondly, an increase in elasticity at a

constant water potential will also lower the osmotic potential without any net solute increase (Weatherley, 1970). However, Jones and Turner (1978) showed that sorghum exhibited a decrease in elasticity as a result of increasing water deficit. Many studies reported the concentration increase of many solutes, particularly sugars and free amino acids. Munns et al. (1979) concluded that the main contribution to the decline in Ψ_s (from -12 to -40 bars) in wheat leaves was an increase in the content of ethanol-soluble carbohydrate and of some amino acids, i.e. proline. Sugar and malate concentrations increases of 10 to 40 percent accounted for the diurnal changes in Ψ_s of field cotton (Cutler et al., 1977). Conversion of starch to other forms was reported to allow a further decrease in Ψ_s, starch concentration declined from 9.9 to 5.9 percent and sucrose increased from 1.2 to 6.6 percent of the dry herbage (Lechtenberg et al., 1973). Munns et al. (1979) reported an increase in the ratio of reducing to non-reducing sugars in the wheat apex which implies sucrose conversion allowing further decrease in Ψ_s without a change in total sugar content. Free ions are reported to increase in concentration accounting for osmotic adjustment in many crop species. Some of these ions are K^+, NO_3^-, and malate in cotton (Cutler et al., 1977), in tropical grasses (Ford and Wilson, 1981), and in sorghum (Jones et al., 1980). The contribution of Cl^- to osmotic adjustment in winter wheat was observed by Christensen et al. (1981).

Significance of Osmotic Adjustment to Plant Growth

Osmotic adjustment may serve as a mechanism enabling plants to tolerate water shortages and maintain growth and other turgor mediated processes leading to reasonable levels of plant performance and eventually improving yields. Many scientists concluded that growth was actually reduced but the reduction was much more drastic in the absence of osmotic adjustment (Meyer and Boyer, 1972). Acevedo (1975) reported that osmotic adjustment maintained root elongation of maize under stress. Jones and Rawson (1979) showed that adjustment of Ψ_s lowered the Ψ at which stomata close. Turner et al. (1978) showed similar effects of osmotic adjustment on stomatal adjustment. All of these effects of osmotic adjustment enable the plant to maintain a favorable rate of photosynthesis and to explore a greater soil volume under high levels of water stress. Turner and Jones (1980) concluded that the degree and presence of osmotic adjustment varies with species and varieties. However, further investigations are needed to provide information that would aid in the screening of a wide range of genotypes for osmotic adjustment. In this study we hope to assess some quantitative relationships between the degree of osmotic adjustment, if present, and the crop yield of snap beans.

MATERIALS AND METHODS

General Description Of The Experiments

Growth Chamber Experiment

The purpose of the experiment was to study the effects of water stress on the development of snap bean plants under controlled conditions. Five seeds of snap beans (Phaseolus vulgaris L. cv "Oregon 1604") were planted approximately 2 cm below the soil surface in a Xerollic Duragids Loam Soil (42.4% sand, 37.5% silt, and 20.1% clay) contained in medium size pots, 16 cm high with a 14.5 cm inside diameter. The pots were placed in a small growth chamber. A light intensity of 130 watts/m^2 at the top of the plants was provided by a combination of fluorescent and incandescant bulbs. Plants were exposed to 14 hours of daylight with day and night temperatures of 27°C and 21°C, respectively. A total of four pots were planted and watered on 8 April to be kept at favorable conditions for seed germination. Emergence of seeds occurred on 14 and 15 April. The pots were thinned to 3 plants per pot one week after planting. The non-stressed (NS) plants were watered at one to two day intervals. The stressed treatment (SS) plants received water at an interval of seven days. The amount of water applied at each watering averaged 200 cm^3 per pot. The total volume of water applied was 1400 cm^3 and 3800 cm^3 for the SS and NS treatments, respectively. The trifoliate leaves of the shoot, above the cotyledons, were identified with successive integers 1, 2, 3, ... , n, in order of their appearance. The age of the plant

is roughly designated by the number of leaves which have appeared.

Daily measurements were made at about 9:00 am of the length of the middle leaflet of each trifoliate leaf including the lamina and petiole on each plant of both treatments. Leaf length was measured to the nearest 1 mm with a plastic ruler. Cotyledons were omitted from the analysis because they were equal in length throughout their development. These measurements produced a family of growth curves for each plant.

Field Experiments

Two field experiments were conducted during the summers of 1980 and 1981. These experiments were performed at the farm of the Department of Horticulture at Oregon State University. A summary of the meterorological parameters measured during the summer months of the two years is presented in Table 1. The climate during the period from mid-June to mid-August is characterized by warm days and cool nights. The average maximum temperature for July 1980 was 27.00°C and the average minimum temperature was 11.33°C. The average rates of daily solar radiation were 501.2 and 505.4 Langley/day for July 1980 and 1981, respectively. However, several days of the summer of 1981 had a pattern of cloudy mornings and warm sunny afternoons. Very little precipitation occurred during the months of July and August. The recorded rainfall for the growing season were 2.26 and 2.79 cm for the years 1980 and 1981, respectively. The warm, dry weather conditions during the season resulted in severe moisture stress of the non-irrigated plants. Cultivar "Oregon 1604" was used in both

TABLE 1. Meteorological parameters during the 1980 and 1981 growing seasons measured at the field laboratory of the Department of Horticulture, Corvallis, Oregon.

Years	Months	Average Temperatures		Precipitation	Average 24-hour winds	Average solar radiation	Total pan evaporation
		Max.	Min.				
		°C	°C	(cm)	(km)	Langley/day	(cm)
1980	June	19.94	9.00	4.290	75.57	--	11.72
	July	27.00	11.33	0.588	97.68	501.2	20.10
	August	26.33	8.50	0.025	87.19	449.9	17.49
1981	June	21.24	9.04	6.321	72.83	--	12.30
	July	26.44	10.72	0.245	88.45	505.4	18.38
	August	29.33	11.22	0.025	69.24	434.0	18.48

experiments. Planting was during the second half of June in east-west rows spaced 90 cm apart. The average number of plants per meter of row was 30 which is equivalent to 300,000 plants/ha. The soil was deep alluvial, silty clay loam with a high water holding capacity, of the Chehalis soil series and classified as fine-silty, mixed, mesic cumulic ultic Haploxeroll. The plots were fertilized at planting time with a band application, 5 cm to the side of each row and 5 cm below the seed, of N-P-K at rates of 55 Kg N/ha, 75 Kg P/ha, and 45 Kg K/ha. Plots were thoroughly irrigated prior to planting to uniformly wet the soil throughout the root zone.

In 1980, the experiment was planted in a randomized block design with four replications of four irrigation treatments. For 1981, six irrigation treatments were used with four replications. However, only three treatments were considered in our study. Table 2 identifies the treatments of both experiments and describes each one briefly. Treatments NS of 1980 and 1981 were identical and were considered as the control treatments. Treatment GS of 1980 and 1981 were considered to be moderately stressed. These treatements were irrigated at four predetermined stages and described as follows: 1. Irrigated when the first trifoliate leaf expands, 2. Irrigated at the stage before flowering (pre-bloom), 3. Irrigated at the stage after flowering (post-bloom), and 4. Irrigated at the stage before harvesting (pre-harvest). Tables 3 and 4 show the dates and amounts of water applied to each plot during the 1980 and 1981 experiments, respectively. Each plot was 6.6 x 6.6 meters (20 feet x 20 feet) in size and was sprinkler irrigated. Two rows of different cultivars were grown on

TABLE 2. Identification and description of the irrigation treatments used during the 1980 and 1981 experiments.

Year	ID	Treatments
1980	NS	- Non-stressed. Irrigated when soil water potential reaches -0.6 bars.
	GS	- Moderately stressed. Irrigated at four pre-determined times: 1st irrigation when the first trifoliate leaf expanded. 2nd irrigation at a stage just before flowering. 3rd irrigation at a stage just after flowering . 4th irrigation at a stage just before harvesting.
	MS	- Moderately stressed. Irrigated when the soil water potential reaches -2.5 bars.
	SF	- Stressed during flowering - irrigated when the soil water potential reaches -0.6 bars through the periods before and after flowering, not irrigated during flowering stage.
1981	NS	- Same as 1980
	GS	- Same as 1980
	SS	- Severely stressed. Non-irrigated throughout the growing season, starting with a moist soil profile.

TABLE 3. Dates of irrigation and amounts of water applied to each plot of the treatments of 1980 experiment.

Dates	Irrigation Treatments			
	NS	MS	GS	SF
	mm			
8 July	22			22
15 July	22	29	29	22
24 July	27			
26 July		36	36	
29 July	27			
2 August		53		
4 August	31		53	
5 August				
7 August	36			36
9 August				
12 August		44	44	44
15 August	27			
Total	192	162	162	124

TABLE 4. Dates of irrigation and amounts of water applied to each plot of the treatments of 1981 experiment.

Dates	Irrigation Treatments		
	NS	GS	SS
	mm		
24 June	9	9	9
6 July	18		
13 July		18	
15 July	27		
23 July	27		
29 July	27	44	
3 August	31		
9 August	31		
11 August		53	
13 August	40		
18 August		35	
20 August	31		
Total	241	159	9

each side of the plots. The middle row of each plot was instrumented with gypsum blocks and tensiometers for soil water potential measurements. One access tube for neutron probe readings was installed at the center of the middle row in 1981. For the 1980 experiment, two access tubes were installed in replications I and II for each treatment. All instrumentations were installed between plants within the rows.

Methodology

Soil Water Content

Soil water content was measured with a neutron probe. In 1980 all plots from two replications were instrumented and two access tubes were installed in each plot. The neutron probe used was a Troxler Electronic Laboratories, Inc., Moisture Gauge Model No. 104A and Scaler Model 2601. In 1981, all plots from all replicates were instrumented and one access tube was installed in each plot. The neutron probe used was the Campbell Pacific Nuclear, CPN Model 503. Readings were taken at 15, 30, 45, 60, 90, and 120 cm depths in 1980. In 1981, depths of 150 and 180 cm were also monitored. Readings were taken the day before irrigation and the day after irrigation and at four to seven day intervals for the treatments with long irrigation cycles. Both neutron probes were calibrated in a nearby wheat field. Samples for bulk density determinations were taken to express results on a volume basis. The water content θ_v as a function of the ratio of the reading to the standard counts were found to be:

$$\Theta_v = 0.049 + 0.38\ P \quad (r = 0.896\ ;\ 41\ d.f.) \quad (1980)$$

$$\Theta_v = -0.236 + 0.38\ P \quad (r = 0.830\ ;\ 41\ d.f.) \quad (1981)$$

where Θ_v is the volumetric water content (cm^3/cm^3) and P is the ratio of the readings (R) to the standard counts.

Soil Water Potential

Soil matric potential for the wet treatments (NS) was monitored with tensiometers over the range from 0 to -0.8 bars. The tensiometers were installed in each plot of the treatment at depths of 15 to 30 cm. Gypsum blocks were used to monitor soil matric potential from 1.0 to 15.0 bars. Several gypsum units were chosen randomly for calibration and for uniformity. The units used were manufactured by Delmhorst Instrument Co.

Leaf Water Potential

Water potentials were measured using the pressure chamber technique (Scholander et al., 1965). During 1980, the measurements were made with the PMS type, PMS Instrument Co. The plant water status console Model 3005, Soil Moisture Equipment Corp., was used throughout the 1981 growing season. A young, fully expanded leaf from each replication was sampled. The leaf was placed in a plastic bag to minimize evaporation losses. On hot days, when Ψ was measured at midday hours, the chamber was lined with a wet filter paper to minimize developing large temperature gradients within the chamber. The leaf was sealed in the chamber with its petiole protruding from it through the rubber stopper. Pressure was applied slowly and the camlock was

tightened during pressurization if a leak developed around the rubber seal. The cut surface was often dried with soft filter paper (Kleenex) to prevent reading false end points. The pressure was slowly increased until the sap returned to the cut end of the petiole. This balance pressure was recorded, then the pressure was reduced by about 2 bars. The pressure was then increased again until the true end point was observed. This pressure is numerically equal to the water potential of the leaflet but of opposite sign.

Osmotic Potential

After the water potential was measured with the pressure chamber the leaflet was rolled and inserted into a labeled section of tygon tubing, sealed with rubber stoppers at both ends. The tygon tubing with the sample was put in a box with dry ice. The samples were transported to the laboratory in the dry ice where they were stored in a freezer at -5 to -10°C. Measurement of osmotic potentials were usually made 10 to 15 days after sampling. The samples were thawed at room temperature for 30 to 60 minutes. After thawing the sample in the tygon tubing was squeezed through a mechanical press composed of two steel rollers. This process was performed slowly to ensure rupturing of the cell walls and to obtain mixing of symplastic and apoplastic water. A filter paper disc with a diameter of 7 mm was used to absorb some of the expressed sap. The disc was transferred to a Wescor C-52 sample holder and readings were obtained with a Wescor HR-33T Dewpoint Microvoltmeter. Prior to the measurement, the cooling coefficient, π_v, of the hygrometer was set for the ambient temperature.

Sufficient time was allowed to reach thermal equilibrium, usually 3 to 5 minutes and the readings were recorded. Microvoltmeter readings were calibrated before each series of measurements against four known osmotic standards made up of KCl solutions. The measurements were made in a controlled temperature room at 25°C. Contamination of the sample holder and of the thermocouple junction was always checked carefully before measurement. Cleaning of the contaminated surface was conducted as described by Ekasingh (1982). The value of tissue osmotic potential obtained by this method may not be the true osmotic potential, because thawing and crushing of the tissues permits mixing of apoplastic and symplastic water which produces a dilution effect that increases the osmotic pressure and and a negative turgor pressure may result (Tyree, 1976). To correct for this error, an estimate of apoplastic water fraction and the relative water content of the tissue are required. The correction factor is calculated from:

$$CF = \frac{RWC}{RWC - B} \quad , \qquad (25)$$

where CF is the correction factor, RWC is the relative water content, and B is the apoplastic water function. The corrected value of osmotic potential is obtained by multiplying the value measured with the dew-point hygrometer by the correction factor.

Turgor Pressure or Pressure Potential

The turgor pressure or pressure potential is the algebraic difference between the water potential measured with the pressure chamber and the corrected value of osmotic potential.

Pressure - Volume Technique

The procedure for the construction of a P - V curve with the use of the pressure chamber was described by Tyree et al. (1978) and Turner (1981). Leaves obtained in the field were sampled and rehydrated by putting them in distilled water and leaving them overnight in the dark. The leaf to be used was dried with filter paper and wrapped in a plastic bag to minimize temperature fluctuations in the chamber. The pressure was applied slowly and the end point was determined as described for the water potential measurements. After recording the balance pressure, a pre-weighed sap collector consisting of a section of small tygon tubing stuffed with cotton wool was set over the cut end of the petiole. The chamber was then over-pressurized slowly to a pressure level ranging from 2 to 4 bars and left at that pressure for a period of 5 to 30 minutes, depending on the turgidity of the tissues. When equilibrium was established and no more sap was being expressed, the collected sap was weighed to determine the expressed volume at that pressure.

The pressure was then released to a pressure about half-way between the previous pressure and the new pressure. Time was allowed for the sap to be withdrawn into the bascular bundles and equilibrated with the pressure inside the pressure chamber. The pressure was increased again to the new balance pressure and the sap was collected and the procedure was repeated for the number of measurement pairs required for plotting the P-V curve.

Finally, at the end of the series of measurements, the residual fresh weight of the flaccid tissues was determined. Then the flaccid tissues were dried in an oven at 80°C for 48 hours to determine the dry weight (DW). The difference between FTW and DW is the residual weight or volume of water to be added to the volume of water expressed from the leaf. This technique was performed for several plants of both NS and SS treatments of the 1981 experiment.

Leaf and Canopy Temperatures

A Raynger II infrared thermometer (Raytek, Inc., Mode R2LT) with a response time of < 1.0 sec., accuracy of $\pm$ 0.5°C, and a resolution of $\pm$ 0.1°C was used to measure leaf temperature. The emissivity is set into the memory of the instrument and temperature is measured by aiming the instrument at the leaf from a distance of 10 to 100 cm depending on the size of the leaf and the percentage of ground coverage. Measurements were taken from different angles and the average of 4 measurements was recorded.

Leaf Diffusive Resistance

Measurement of diffusive resistance were taken during the 1980 experiment with a transient-state diffusion porometer (Kanemasu et al., 1969) manufactured by Lambda Instruments. The instrument used was a Model LI-65 equipped with horizontal sensor Model LI-20S. The instrument was calibrated at temperatures of 22, 27 and 30°C. Diffusive resistances at temperatures other than those used for the calibration were obtained by a linear interpolation procedure. In 1981, the

steady state porometer, Lambda Instruments, Model LI-1600, was used. This instrument was used to measure diffusive resistances, transpiration rates, relative humidities and leaf temperatures. These measurements were made on both sides of several leaflets. However, after establishing a correlation between lower and upper sides of the leaves, only the lower sides were considered.

Leaf Length

The length of the middle leaflet of trifoliate leaves were measured for the study of plastochron index. Three plants from each plot were chosen randomly a few days after emergence. The plants were considered to be morphologically similar at that time. A total of 36 plants were identified by inserting a long wooden stake in the soil a few inches on the side of the plant. These plants were monitored every other day, recording the leaflet position and its length. Length of the petiole of the middle leaflet including lamella was measured with a plastic ruler to the nearest 1.0 mm. The trifoliate leaves of the shoot, above the cotyledons, were identified with successive integers 1, 2, 3, ... , n, in the order of their appearances. These measurements continued throughout the growing season and produced a family of growth curves for each plant studied.

Seasonal Vegetative Growth

The seasonal vegetative growth was measured in terms of shoot fresh weight, shoot dry weight, and leaf area index. Weekly samples of 10 plants were harvested and brought to the laboratory immediately.

One row from each plot was used for this purpose. The roots were cut and the shoots were weighed fresh. The leaves were detached from the plants and leaves and stems were weighed separately. Later in the growing season the pods were detached and weighed. The plant materials were stored in labeled paper bags in a cool room until they were brought out for leaf area measurements with the Lambda Instruments, Inc., Model LI-3100 leaf area meter. The leaves were counted and data were recorded. The plant material was then transferred to an oven and dried at 70 to 80°C for at least 48 hours, and the dry weight of leaves, stems, and buds was obtained.

Yield and Yield Components

Most beans are harvested when 40 to 50 percent of the pods are sieve size 4 or under (Mansour, 1975). In this study the time of physiological maturity was defined as the time when 50 percent of the pods pass the No. 4 sieve size. During harvest, samples of 60 plants were harvested from one row in each plot. The pods were separated from the rest of the plant, pods of extremely small size were discarded. The rest were sieved for their size distribution and weighed, then they were transferred to the laboratory and dried in an oven at 70 to 80°C for 48 hours. Total yield is represented by the total fresh weight of the above ground biomass. The marketable yield is expressed by the fresh weight of the marketable size pods. Pods were counted and the average weight per pod was calculated.

RESULTS AND DISCUSSIONS

Leaf Water Characteristics of Snap Beans

Pressure - Volume Curves

Plants from each of the NS and SS treatments were sampled early in the evening. The pressure volume curves were obtained for three of the most recently matured leaves from each treatment according to the procedure described in Material and Methods. The P-V curves obtained are shown in Figures 2 through 7. These curves show the typical P-V curves as reported by Tyree et al. (1972), Cutler et al. (1979), Wilson et al. (1979), and Turner (1981). Linear regression analyses of the straight line portions yielded equations with r^2 values ranging from 0.984 to 0.993 and from 0.983 to 0.993 for NS and SS treatments, respectively. Comparison of these P-V curves requires the use of a relative basis for water status of the tissues. Curves were therefore constructed by plotting $-1/\Psi$ against RWC (Figures 8 through 13). The results of Figures 2 through 13 are summarized in Table 5. The mean values of osmotic potential at full turgor ($\Psi_{s,100}$) were -5.39 $\pm$ 0.34 and -6.72 $\pm$ 1.33 bars for NS and SS treatments, respectively. The leaves of plants grown in the controlled environment had a $\Psi_{s,100}$ value of -8.84 bars. Mean values of osmotic potential at zero turgor ($\Psi_{s,0}$) for NS, SS, and CE treatments were -8.02 $\pm$ 0.53, -10.66 $\pm$ 2.36, and -11.10 bars, respectively. Results from the controlled environment experiment represent only one P-V relationship for one leaf. Figures 14 and 15 represent the combined data obtained from the corresponding P-V curves of non-stressed (NS) and severely stressed (SS) treatments.

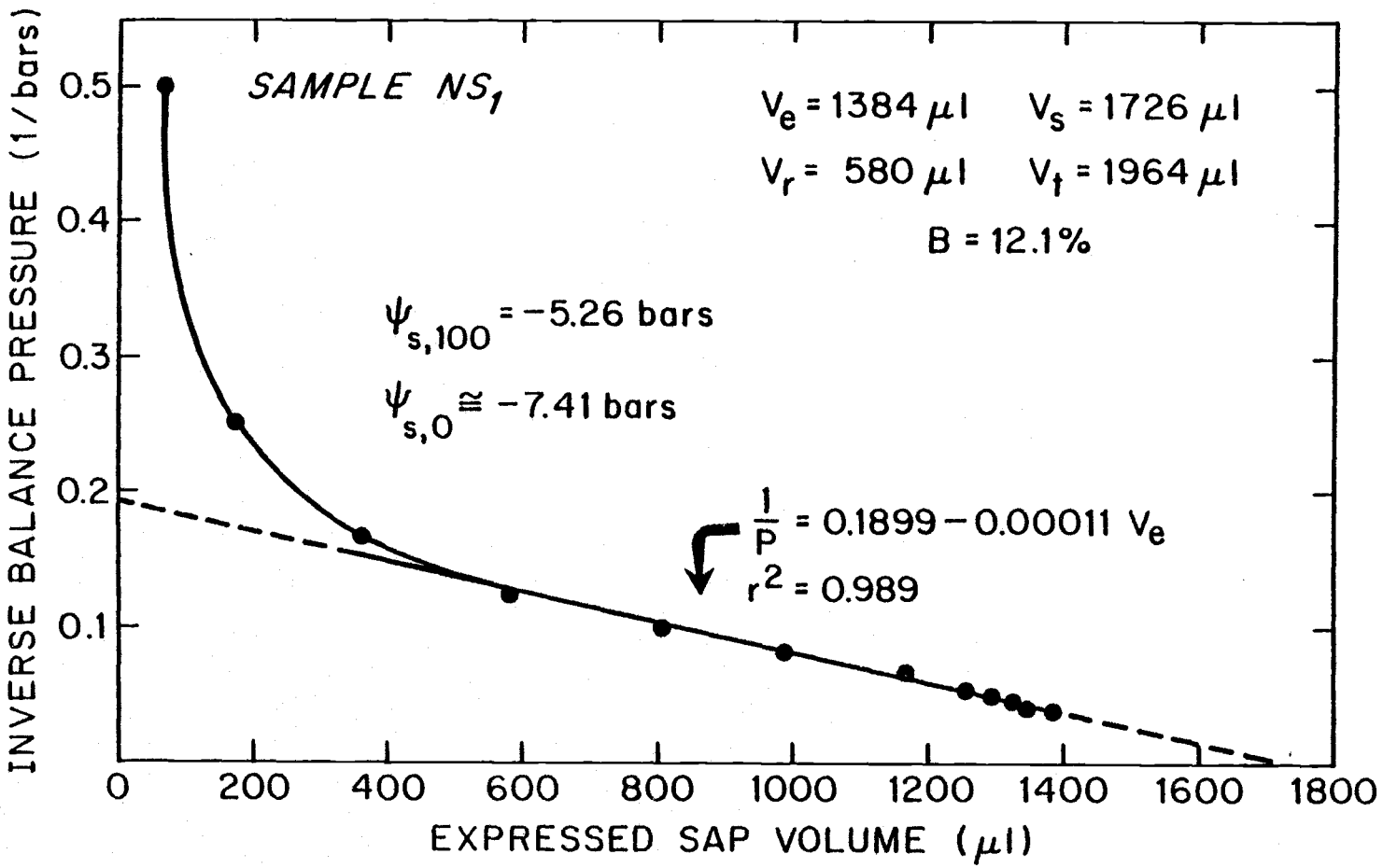

Figure 2. Pressure volume curve for a fully expanded trifoliate leaf from the NS treatment. Sample No. 1, 1981.

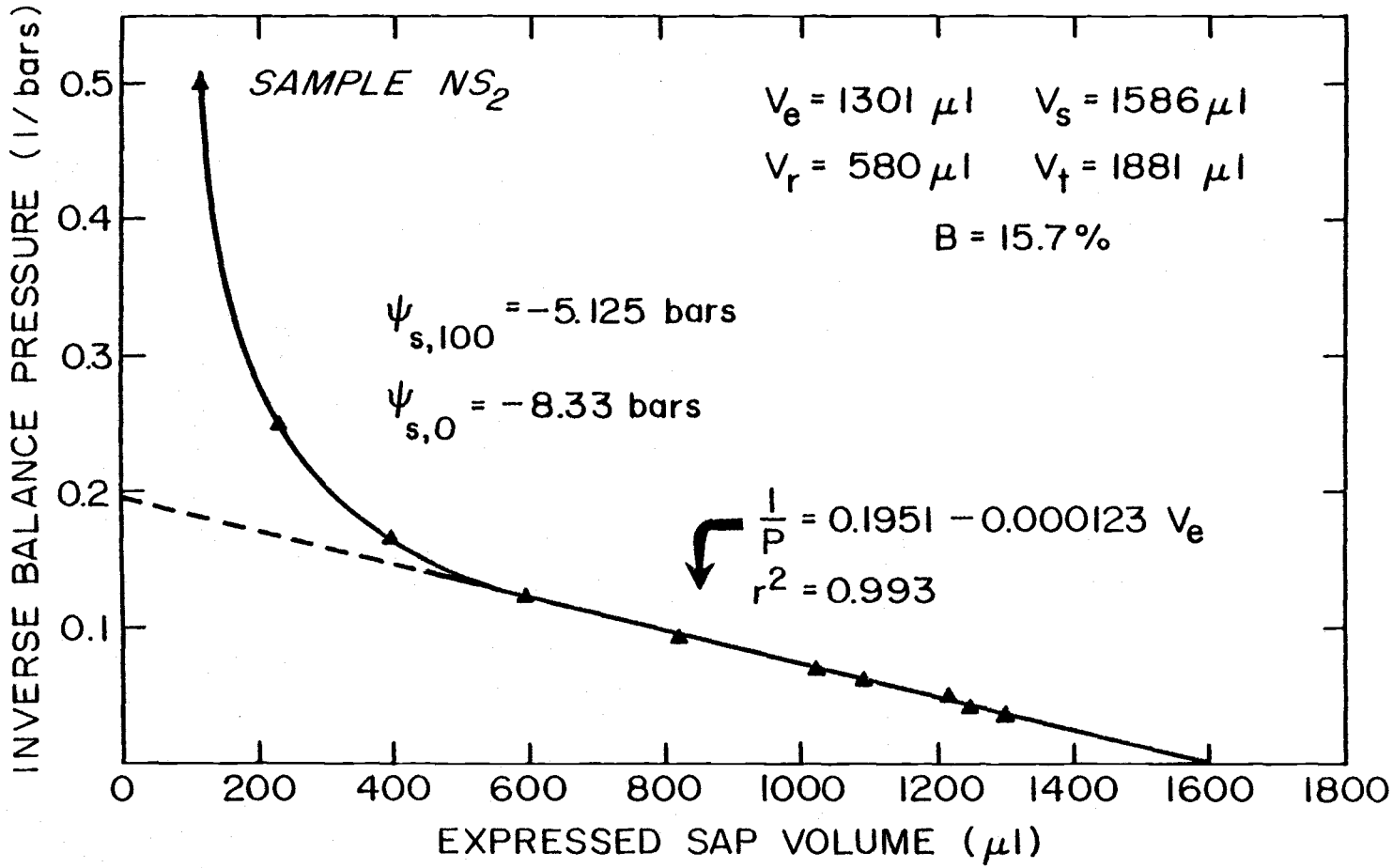

Figure 3. Pressure volume curve for a fully expanded trifoliate leaf from the NS treatment. Sample No. 2, 1981.

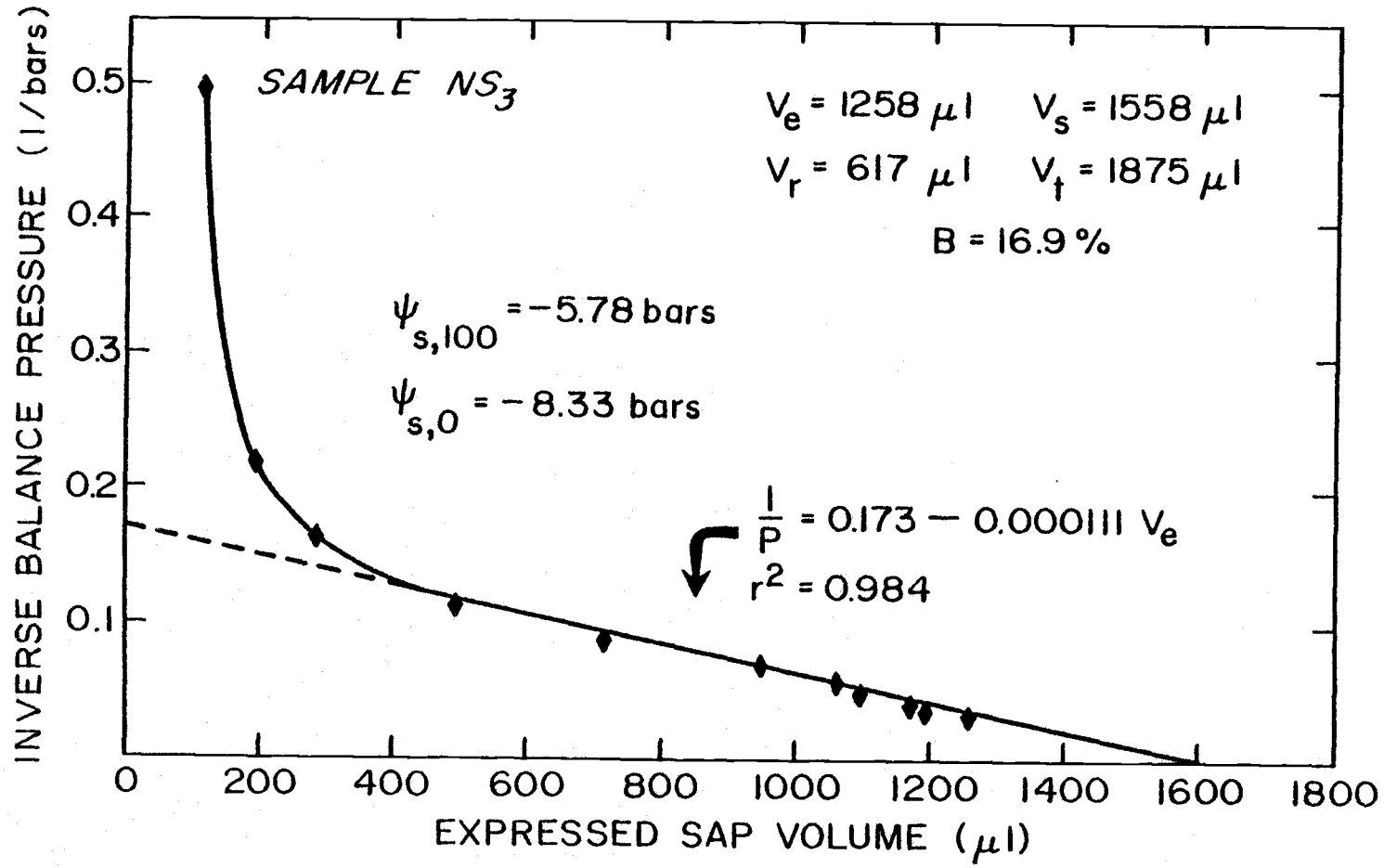

Figure 4. Pressure volume curve for a fully expanded trifoliate leaf from the NS treatment. Sample No. 3, 1981.

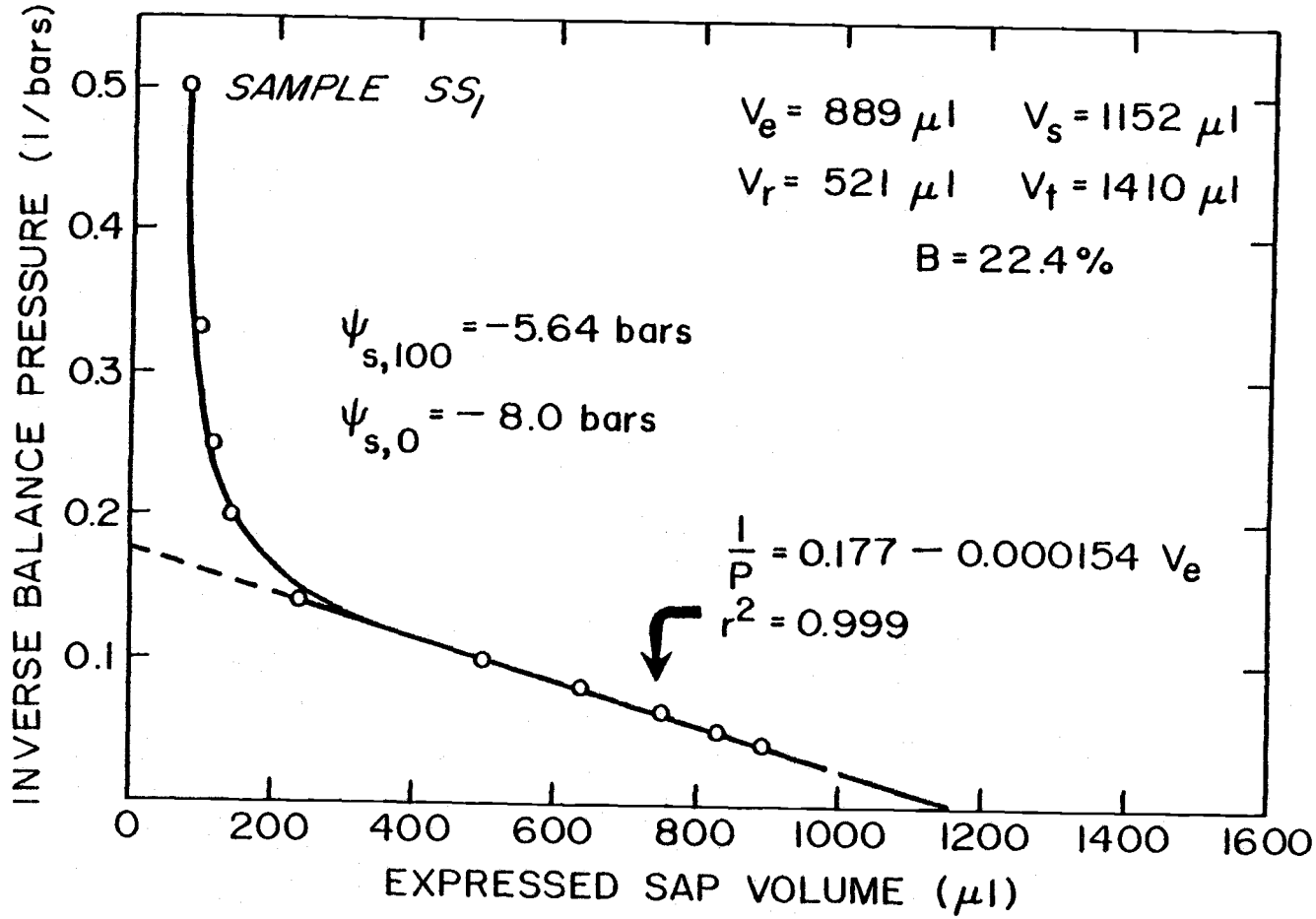

Figure 5. Pressure volume curve for a fully expanded trifoliate leaf from the SS treatment. Sample No. 1, 1981.

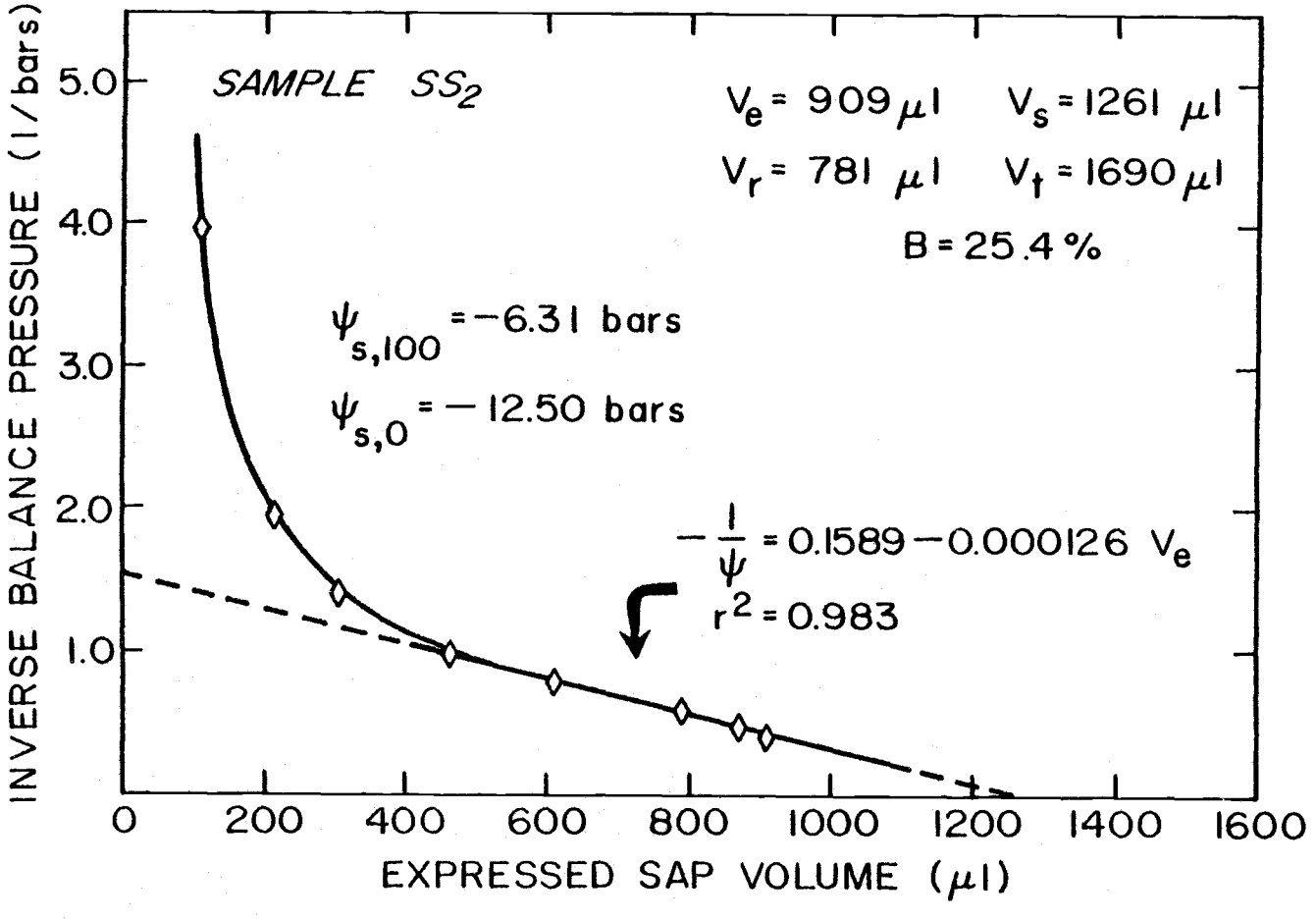

Figure 6. Pressure volume curve for a fully expanded trioliate leaf from the SS treatment. Sample No. 2, 1981.

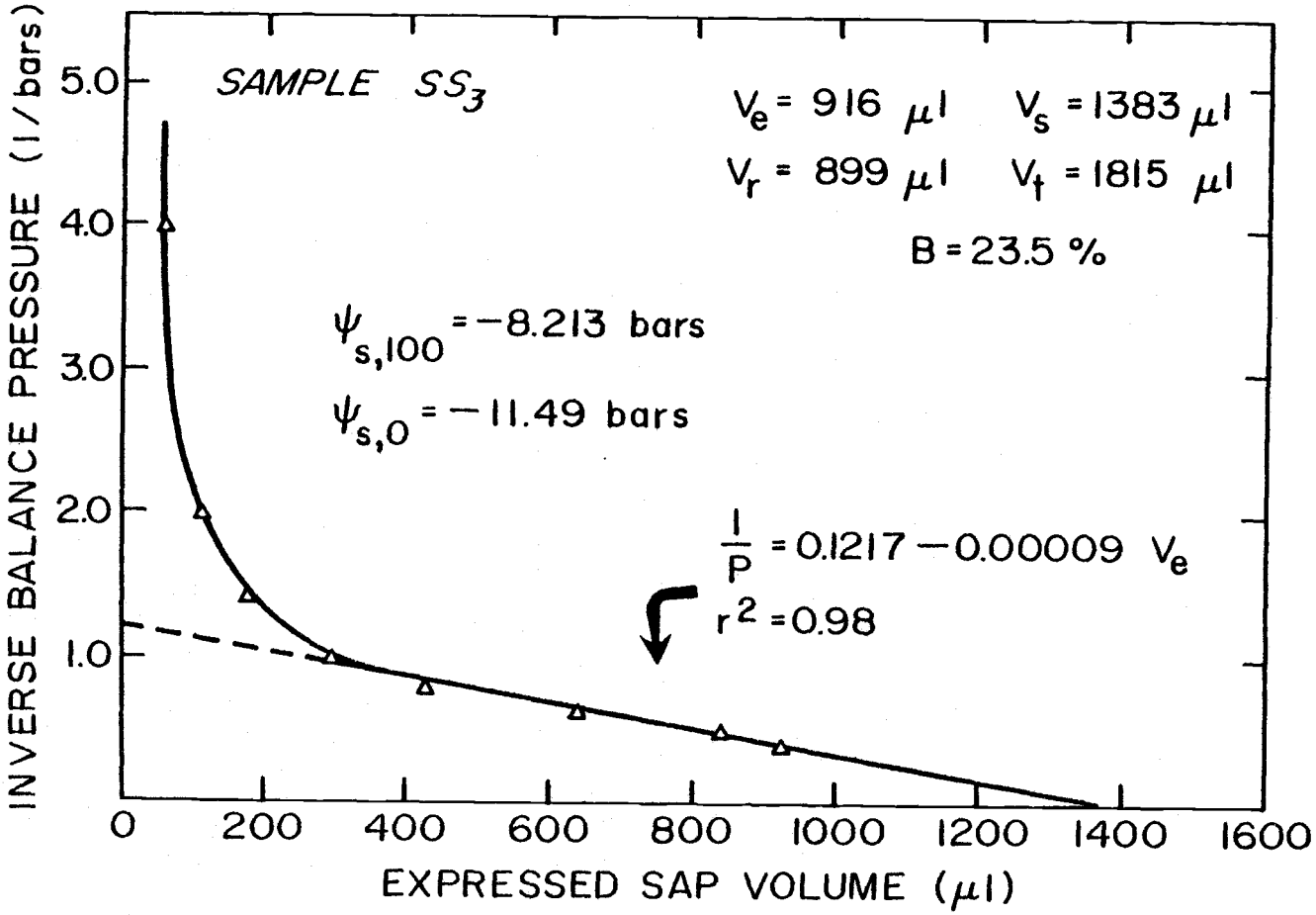

Figure 7. Pressure volume curve for a fully expanded trifoliate leaf from the SS treatment. Sample No. 3, 1981.

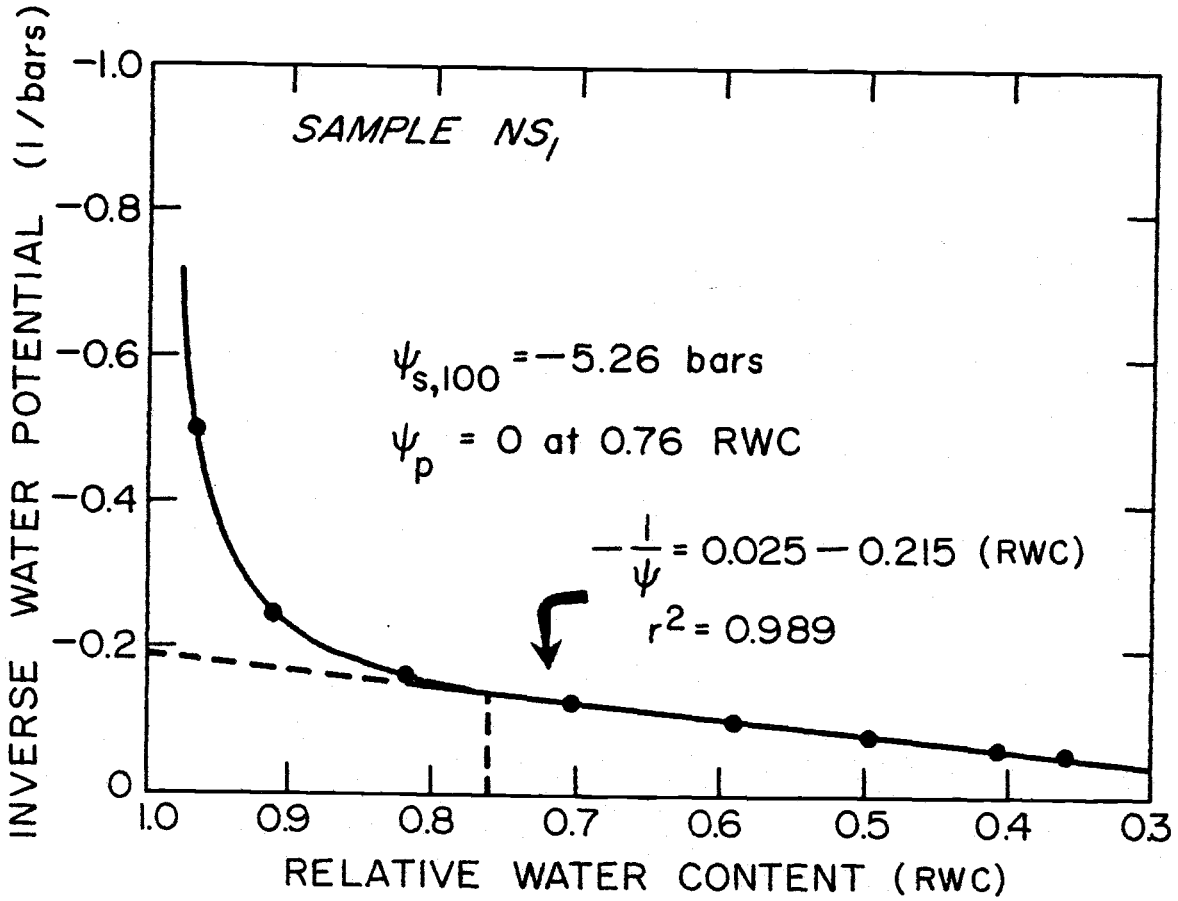

Figure 8. Water release curve of a fully expanded trifoliate leaf from the NS treatment. Sample No. 1.

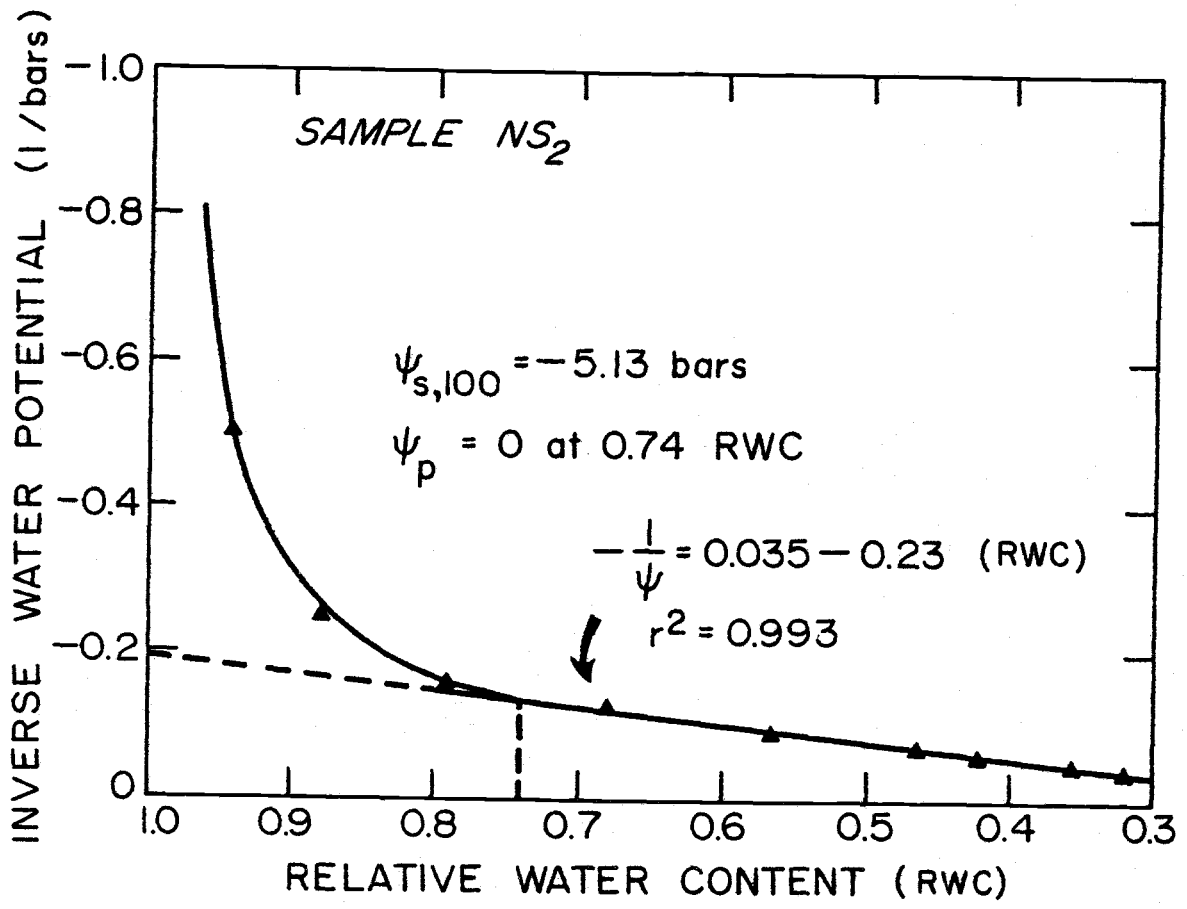

Figure 9. Water release curve of a fully expanded trifoliate leaf from the NS treatment. Sample No. 2.

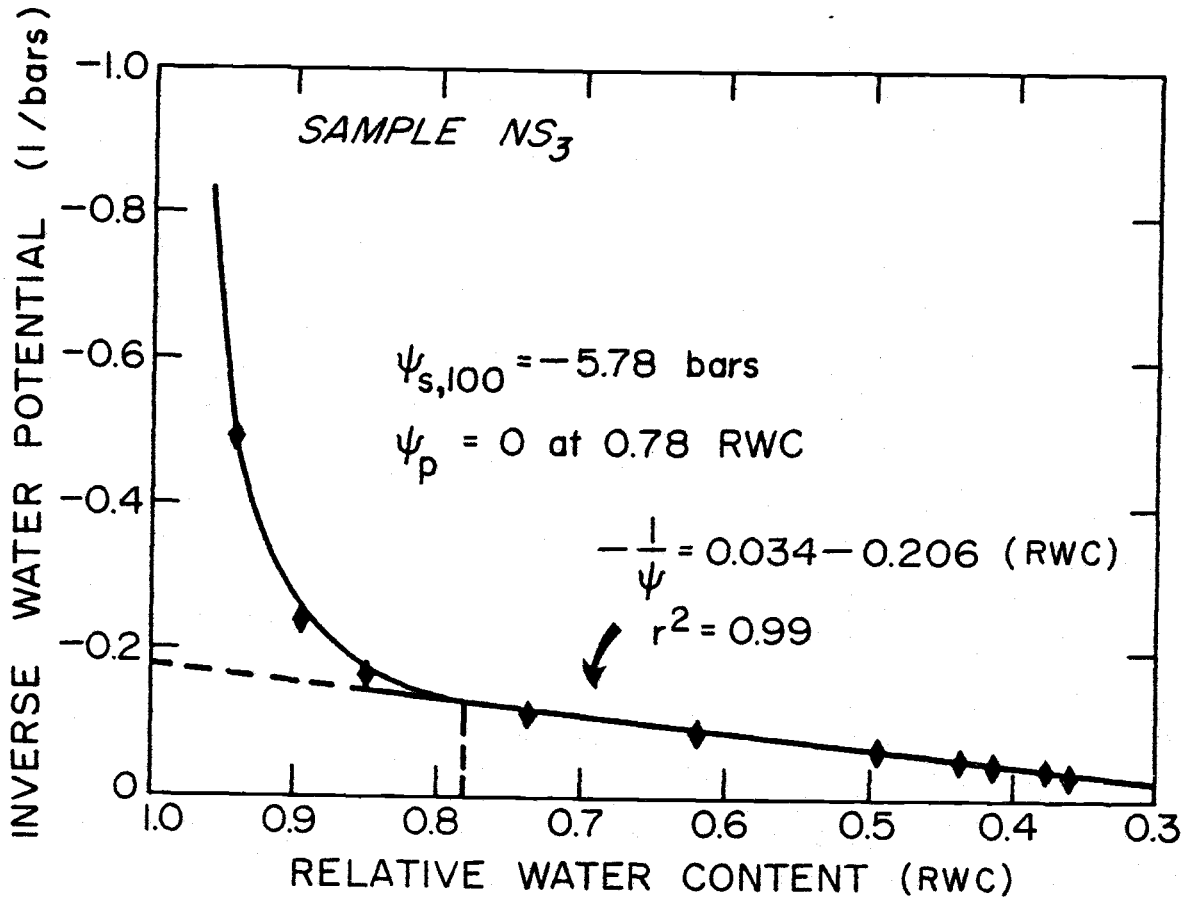

Figure 10. Water release curve of a fully expanded trifoliate leaf from the NS treatment. Sample No. 3.

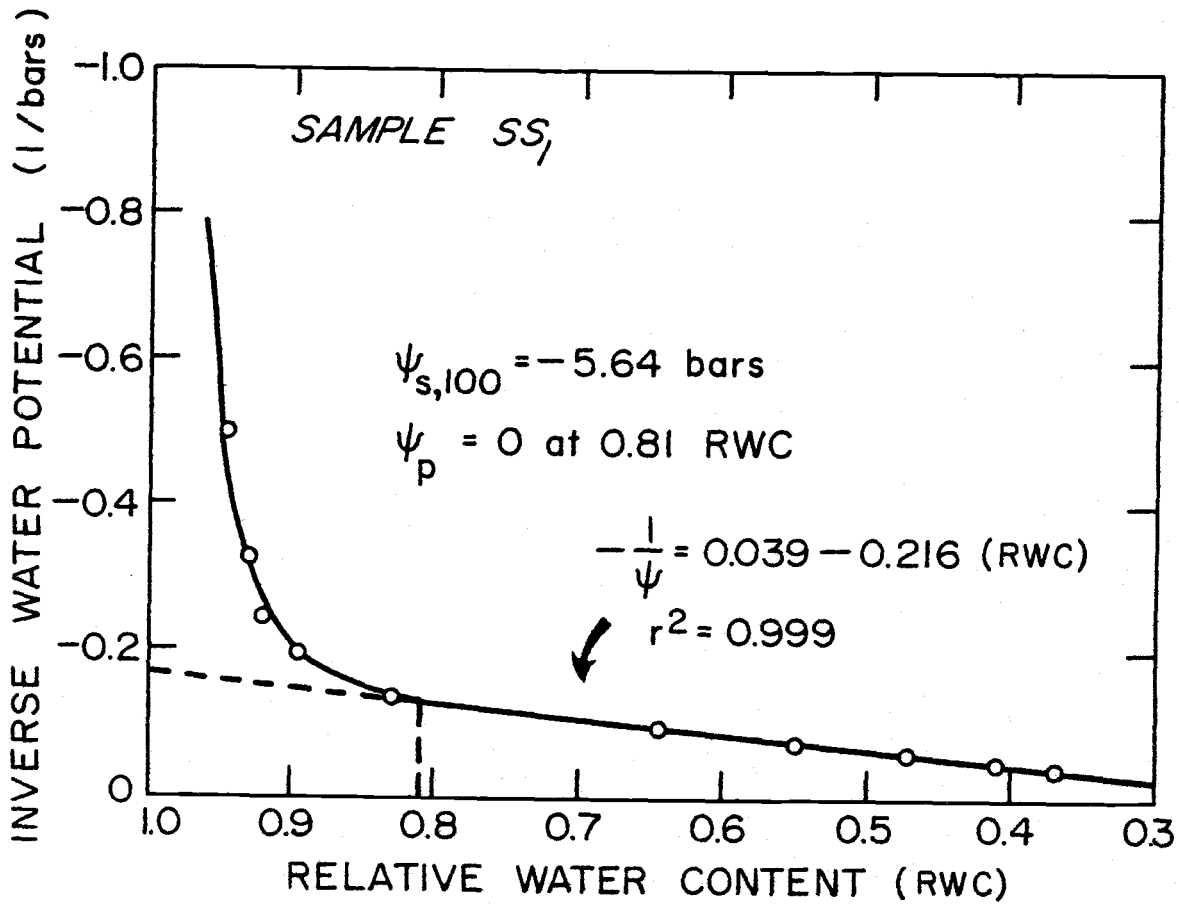

Figure 11. Water release curve of a fully expanded trifoliate leaf from the SS treatment. Sample No. 1.

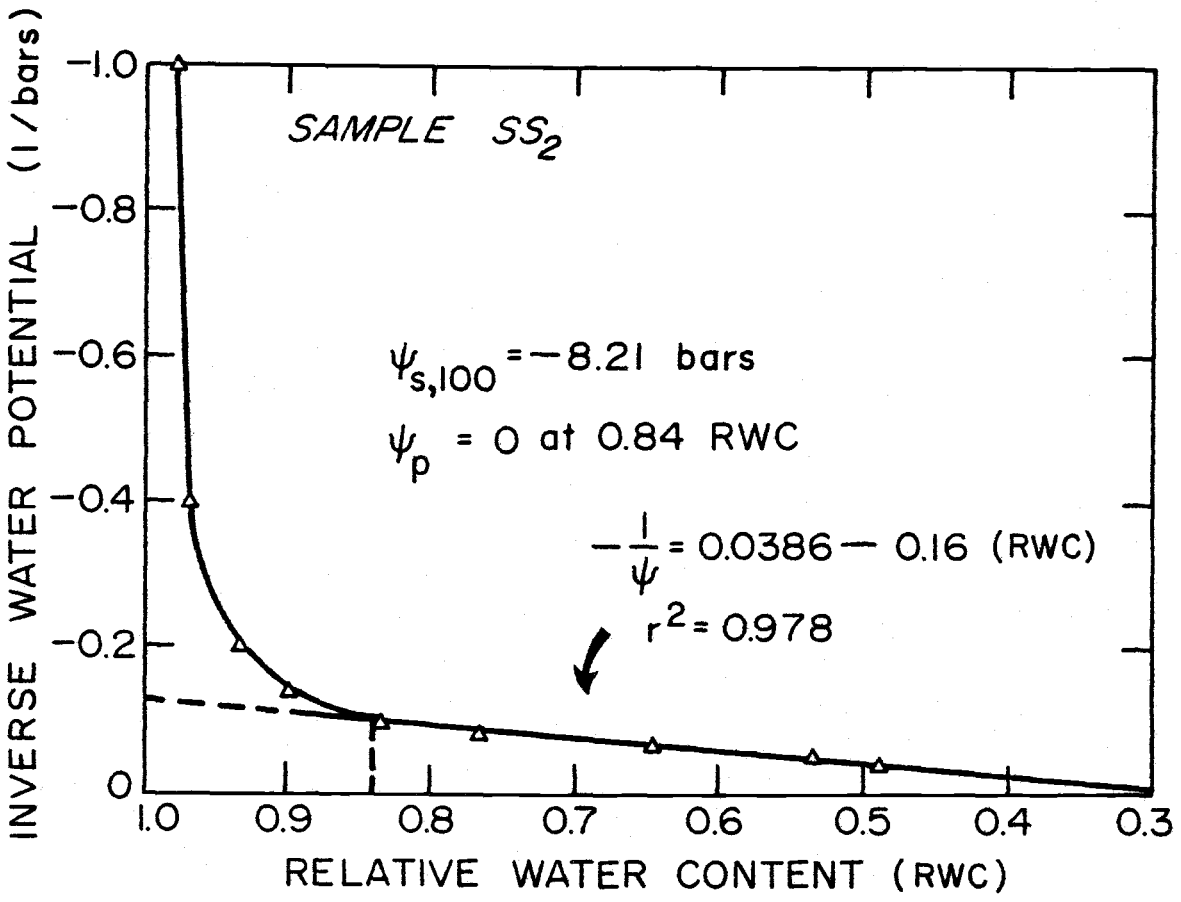

Figure 12. Water release curve of a fully expanded trifoliate leaf from the NS treatment. Sample No. 2.

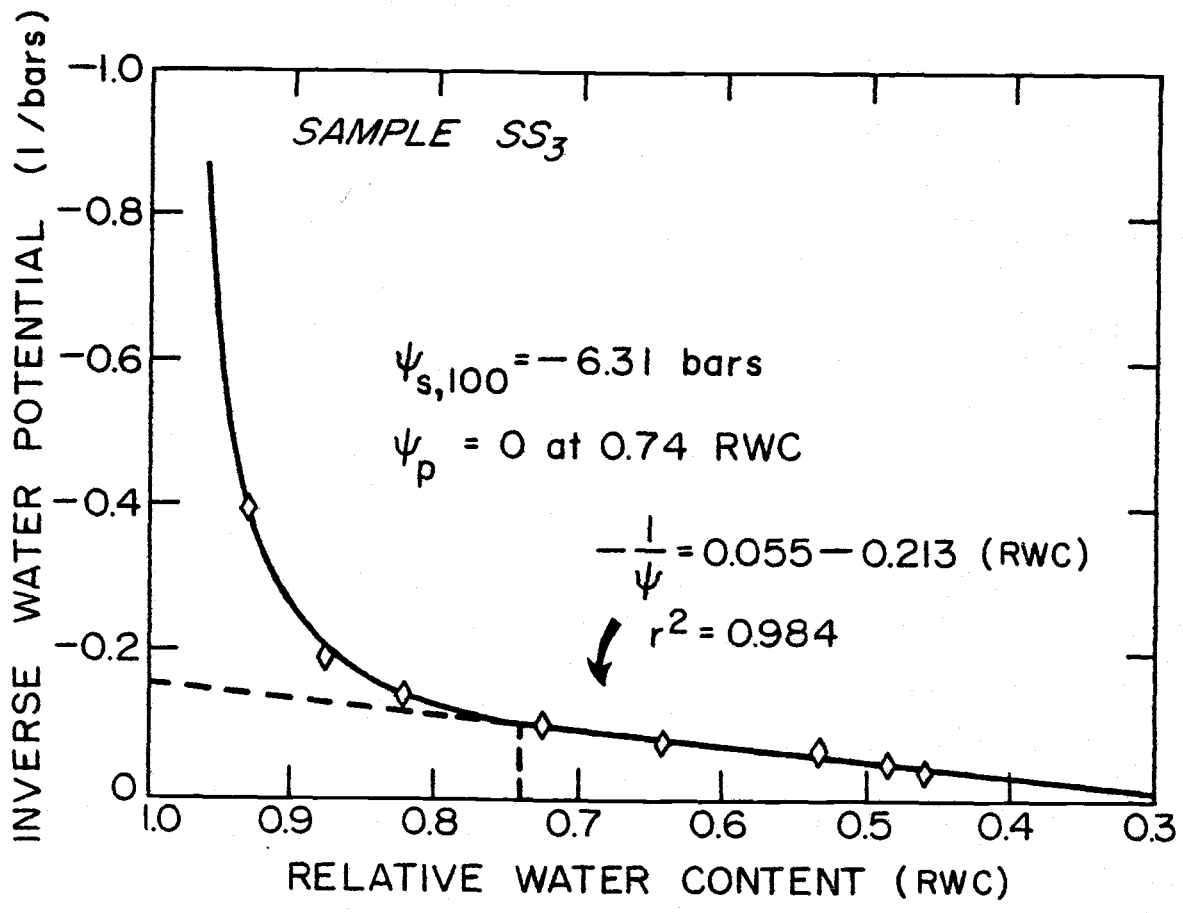

Figure 13. Water release curve of a fully expanded trifoliate leaf from the SS treatment. Sample No. 3.

TABLE 5. Summary of data obtained from the P-V curves for leaf samples of the controlled environment (CE) experiment and from the non-stressed (NS) and severely stressed (SS) treatments of the 1981 experiment.

Treatments	EFW[1]	$\psi_{s,100}$[2]	$\psi_{s,0}$[3]	RWC_o[4]	B[5]	V_s/V_t[6]	V_p/V_s[7]
	(mg)	(bar)	(bar)	(%)	(%)	(%)	(%)
Controlled environment	1057	-8.84	-11.10	82.5	9.9	90.1	77.1
Non-stressed							
NS_1	2474	-5.26	-7.41	76.0	12.1	87.9	69.3
NS_2	2343	-5.13	-8.33	74.0	15.7	84.4	61.5
NS_3	2629	-5.78	-8.33	78.0	16.9	83.1	64.2
$\overline{NS}$	2482	-5.39	-8.02	76.0	14.9	85.1	66.7
S.D.	±143	±0.34	±0.53	±2.0	±2.5	±2.5	±4.5
Severely stressed							
SS_1	2047	-5.64	-8.0	81.0	22.4	81.7	69.6
SS_2	2240	-8.21	-11.49	84.0	23.5	76.2	69.6
SS_3	2471	-6.31	-12.50	74.0	25.4	74.6	55.6
$\overline{SS}$	2251	-6.72	-10.66	79.7	23.7	77.5	64.9
S.D.	±212	±1.33	±2.36	±5.13	±1.52	±3.7	±8.1

[1] EFW is the extrapolated fresh weight at full turgor

[2] $\Psi_{s,100}$ is the osmotic potential at full turgor

[3] $\Psi_{s,0}$ is the osmotic potential at zero turgor

[4] RWC_o is the relative water content at zero turgor

[5] B is the bound water fraction

[6] V_s/V_t is the ratio of symplastic to total water volumes

[7] V_p/V_s is the ratio of symplastic water at zero and full turgor

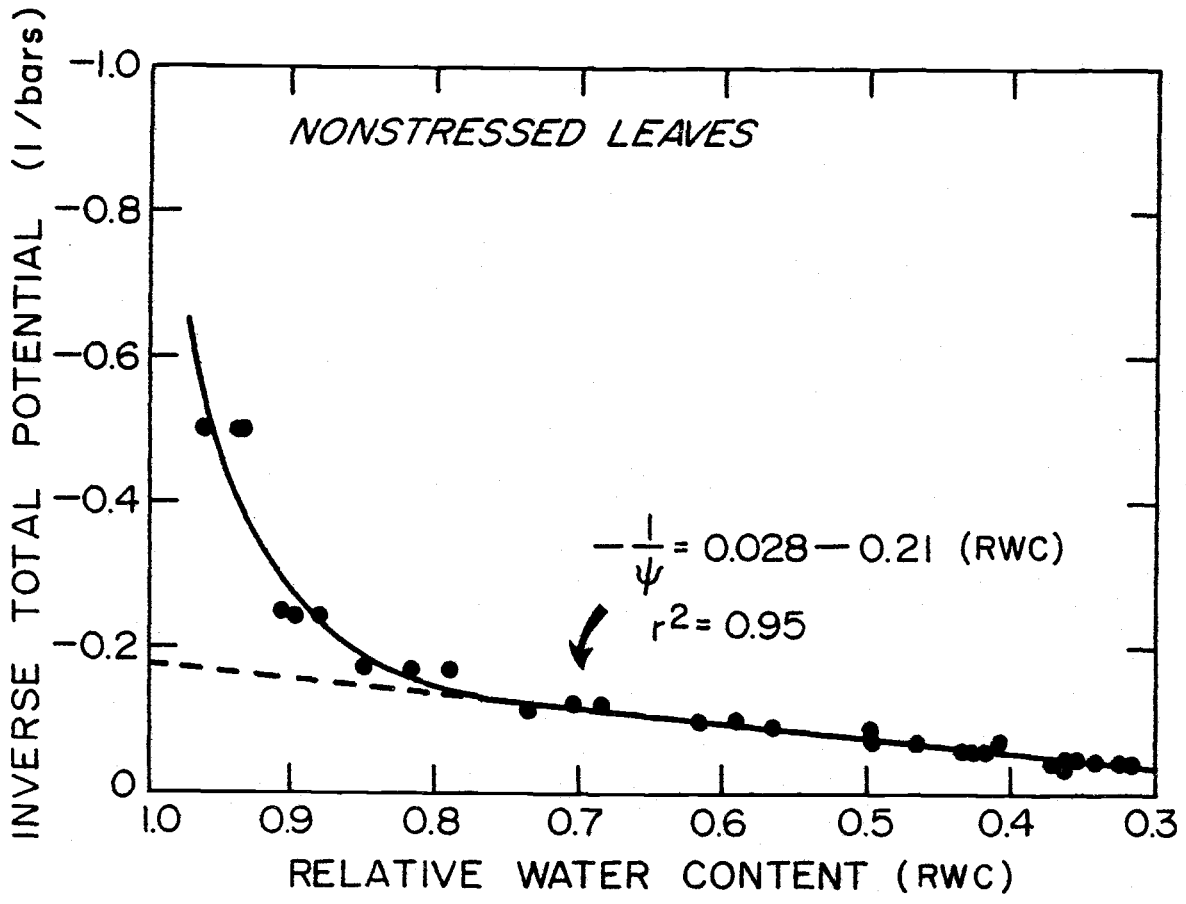

Figure 14. Water release curve of fully expanded trifoliate leaf from the NS treatment based on pooled data from Figures 8, 9, and 10.

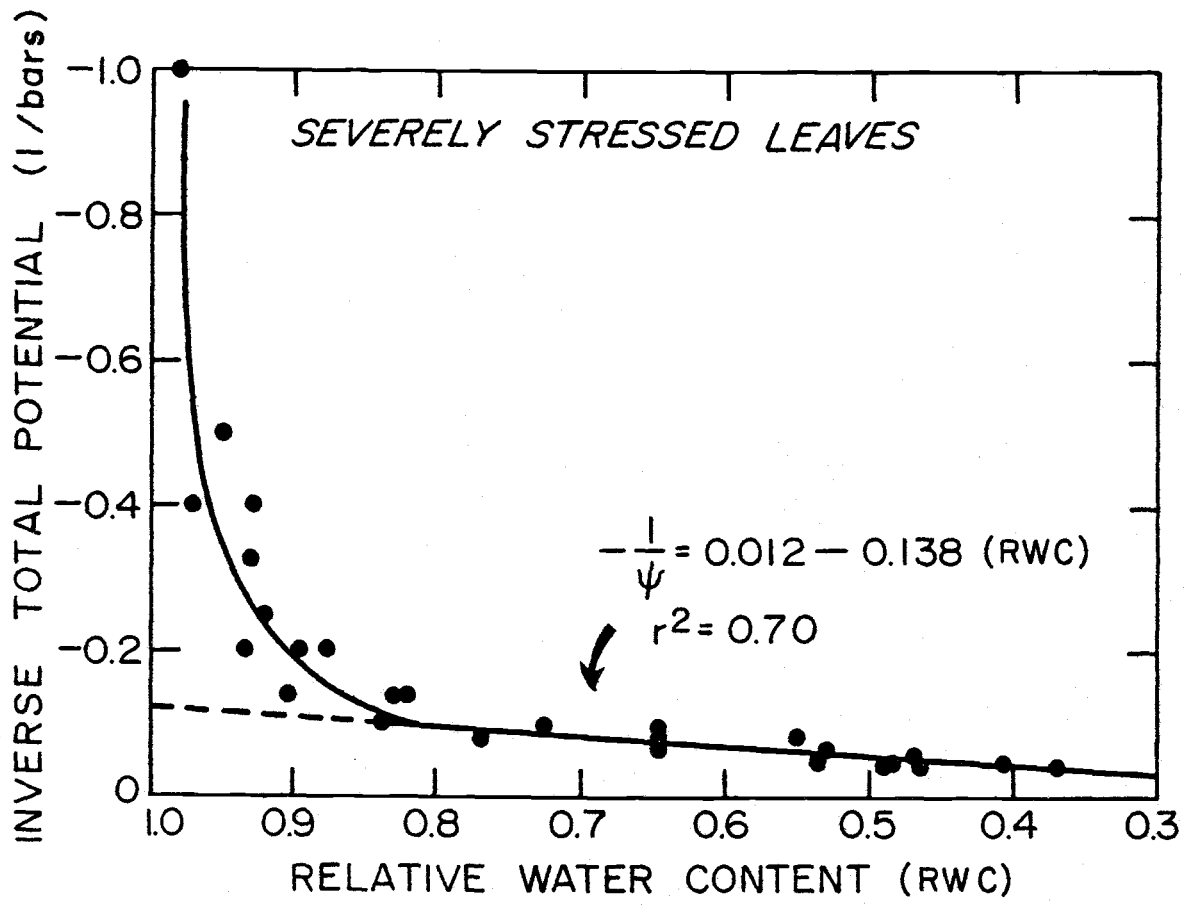

Figure 15. Water release curve of fully expanded trifoliate leaf from the SS treatment based on pooled data from Figures 11, 12, and 13.

Zero turgor pressure corresponds to mean relative water contents of 76.0 ± 2.0, 79.7 ± 5.1, and 82.5 percent for NS, SS, and CE treatments, respectively.

The amount of water held in the range of 0 to 1.0 bars were estimated by extrapolation of the first three to four readings to the Y-axis of the curve relating the balance pressure to the weight of the tissues at that pressure. The intercept point with the Y-axis is considered to be the fresh weight at full turgor. The mean values of the extrapolated fresh weights at full turgor are 2482 ± 143 and 2252 ± 212 mg for NS and SS treatments, respectively (Table 5).

The percentages of apoplastic water in the leaf tissues ranged from 12.1 to 16.9 percent of the total volume of water in the tissues with an average value of 14.9 ± 2.49 percent for the non-stressed treatment. For the severely stressed treatment these values ranged from 22.4 to 25.4 percent with a mean value of 23.7 ± 1.52 percent. Results for one leaf from a plant grown in the controlled environment show an apoplastic water fraction of only 9.9%. This value is much lower than the well watered treatment of the field experiment. These results indicate that the leaves grown under the conditions of the growth chamber have cells with thinner cell walls. Differences in the growing conditions and the rate of stress development between the field and the growth chamber might be considered. Plants grown in the growth chamber were exposed to much lower light intensity levels, lower temperatures, and their roots were exposed to smaller volumes of soil. These differences produce a totally different leaf from that of the field grown plants. This reflects the difficulty one

encounters when trying to extrapolate information from growth chamber experiments to field conditions where parameters that affect growth, such as nutrient supply, temperatures, and radiation intensities vary.

The differences between treatments due to water stress ranged from 0.5 to 3.0 bars and from 1.5 to 5.0 in $\Psi_{s,100}$, and $\Psi_{s,0}$, respectively. SS leaves being lower in $\Psi_{s,100}$ and $\Psi_{s,0}$ than NS leaves. The difference between $\Psi_{s,0}$ and $\Psi_{s,100}$ was about 1.5 to 3.0 bars in the NS treatment. However, in the SS treatment, the difference ($\Psi_{s,0}$-$\Psi_{s,100}$) increased to become 2.5 to 6.0 bars.

The percentage of the osmotic water in the tissues can be expressed on the basis of the volume of water at full turgor (V_s/V_t) as shown in Table 5. The ratios (V_s/V_t) were 77.5 $\pm$ 3.7 and 85.1 $\pm$ 2.5 for the SS and NS treatments, respectively. The difference may be due to the relatively greater volume of apoplastic water in the cell walls of the plants of the severely stressed treatment. The SS plants have an average apoplastic water fraction, B, of 23.7 percent while the corresponding value for the irrigated treatment, NS, was 14.9 percent. Another useful expression that can be studied is the ratio (V_p/V_s), where V_p is the volume of osmotic water at zero turgor (incipient plasmolysis), and V_s is the volume of osmotic (symplastic) water at full turgor. The mean values of V_p/V_s were 66.7 $\pm$ 4.5 and 64.9 $\pm$ 8.1 for NS and SS treatments, respectively. This insignificant difference may imply that the leaves did not respond to water stress in terms of retaining the osmotic water when dehydrated from full turgidity to incipient plasmolysis.

In other words, the severely stressed treatment retained more or less the same percentage of the symplastic water when dehydrated to incipient plasmolysis as compared to the behavior of the non-stressed treatment. This similarity may imply indirectly that the difference in the adjustment of the osmotic potential of the tissues between treatment could not be explained solely on the basis of differences in dehydration characteristics, rather the accumulation of solutes and increasing the concentration of the osmotically active solutes may play an important role in lowering the osmotic potential upon dehydration.

The bulk of modulus of elasticity ε is defined and calculated in different ways. In this study we use ε_t as defined by equation 20 and ε_m as given by equation 21. Figures 16a and 16b show the relationship between ε_t and turgor pressure of the tissues. Results indicate that ε_t increases approximately linearly with the turgor pressure over the range from 0.0 to 2.5 bars. There is an apparent decrease in ε_t near full turgor. The same observation was made for soybeans by Ekasingh (1982). He considered the drop of ε near full turgor to be an artifact which is caused by errors in extrapolation when obtaining the amount of water retained at full turgor. Cheung et al. (1976) also observed that there is a rapid decrease in turgor potential per unit amounts of water expressed near full turgor. Therefore, a large error in ε can be produced by a relatively small error in extrapolation. Wenkert et al. (1978c) reported that mature soybean leaves showed a linear decrease in ε with turgor, over a wide range of pressures in the field. Jones and Turner (1978) concluded that the change in ε may not arise from the

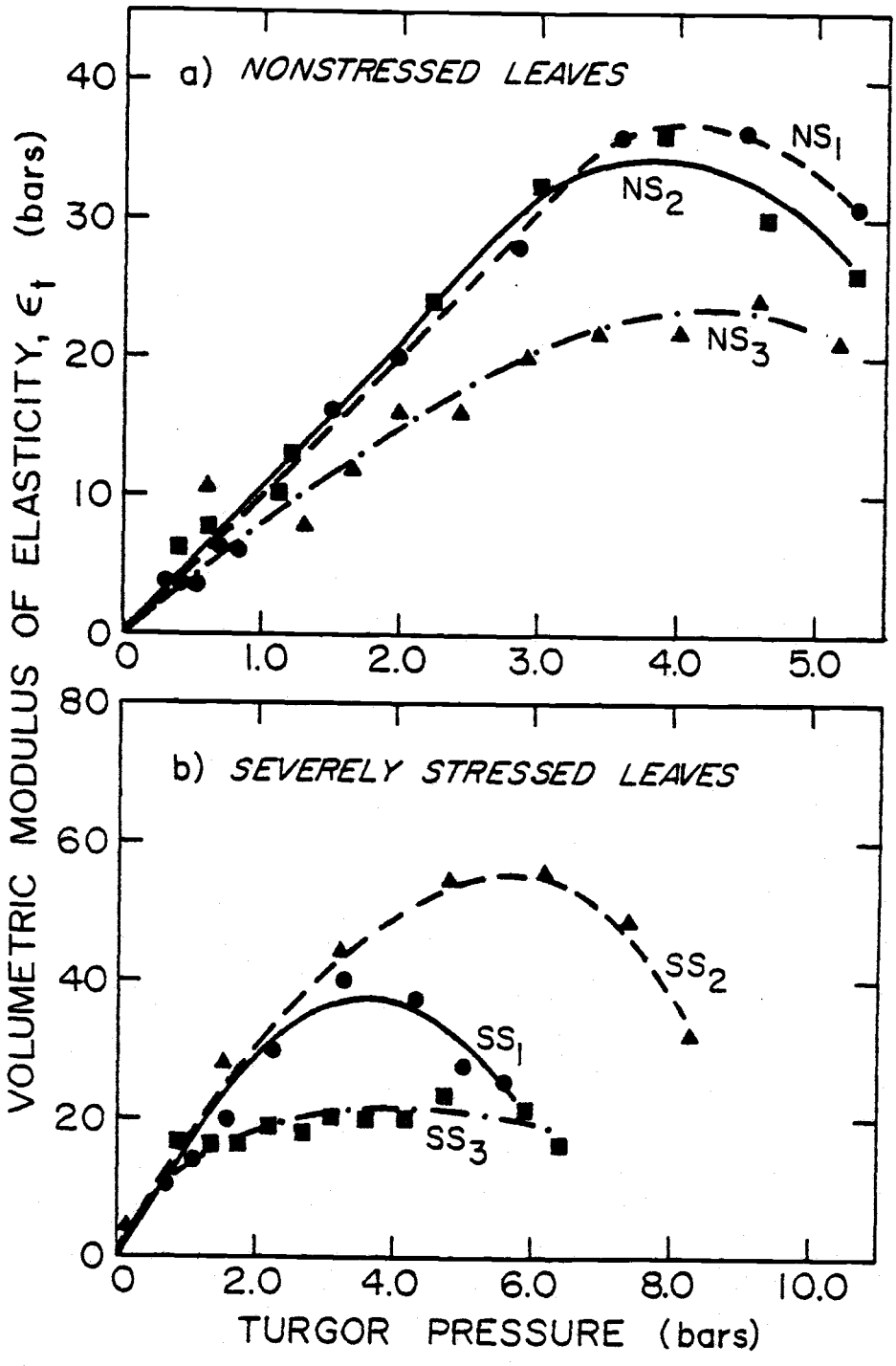

Figure 16. Volumetric modulus of elasticity (ε_T) as function of turgor pressure for non-stressed treatment (a) and severely stressed treatment (b).

change in Ψ_p alone. Steudle et al. (1977) reported that ε depends strongly on turgor pressure and on cell volume. This volume dependence was pronounced more in the high pressure range.

Figures 17a and 17b represent the relationship between the turgor pressure and the bulk modulus of elasticity as given by equation 21 (Melkonian et al., 1982). Data suggests an approximately linear relationship between ε_m and Ψ_p over the turgor pressure range from 0.0 2.0 bars. The data points for both treatments are highly scattered at higher turgor pressures. A recent study by Melkonian et al. (1982) showed that the modulus of elasticity, whether defined as ε_t (eq. 20) or ε_m (eq. 21), is independent of turgor pressure over the range of applied pressure from 0.0 to 8.0 bars. The results of our study and the conflicting reports in the literature led us to conclude that the modulus of elasticity is still an ambiguous parameter which needs to be defined more clearly. The changes and the variability observed in ε could be the result of changes in the mechanical properties of the cell wall, changes in cell size, or a combination of all these factors.

The modulus of elasticity ε could be very important in evaluating the effects of water stress on plant water relations since cell wall elasticity influences the relation between water content and water potential (Cheung et al., 1976). The effect of water stress on the value of ε is not clear and cannot be clarified by the data obtained by this experiment. Reports in the literature are also very conflicting and confusing. Researchers reported an increase of ε as a result of water stress in sorghum (Jones and Turner, 1978), and in wheat

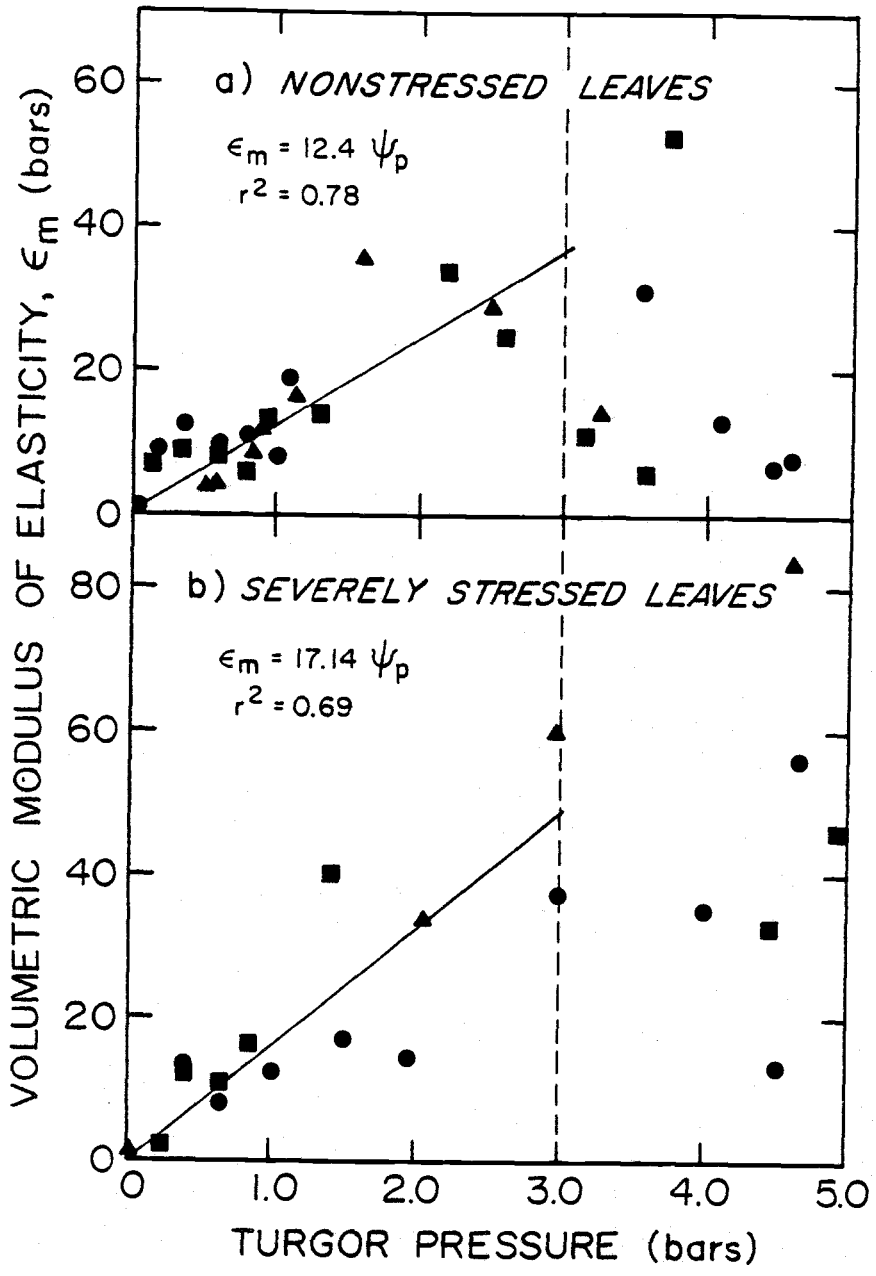

Figure 17. Volumetric modulus of elasticity (ε_m) as function of turgor pressure for non-stressed treatment (a) and severely stressed treatment (b).

(Melkonian et al., 1982), while others report that water stress decreased ε in field beans (Kassam and Elston, 1974; Elston et al., 1976). In contrast, no significant change in ε due to water stress was observed in either cotton (Hsiao et al., 1978), or sunflower (Jones and Turner, 1980).

The P-V technique seems to be very useful for characterizing water relations of plants. Analysis of the P-V curve provides information about several properties such as initial solute potential, solute potential at zero turgor, osmotic water content, bulk modulus of elasticity, and bound water fraction. This technique is useful for obtaining the apoplastic water content necessary for correcting osmotic potential data determined by the hygrometric method. However, the use of this technique in field measurements is restricted by the limited number of measurements which can be made.

The next section will be devoted to the analysis of the effects of water stress on the properties measured by the P-V curves.

Treatment Effects on Internal Water Relations of Leaves

One approach to comparing the two treatments is by plotting the RWC against the inverse of water potential (Figure 18). The combined P-V curves of the leaves for both NS and SS treatments are shown. Graphs were fitted by "eyeball technique." Figure 18 shows that as the RWC decreases from 0.96 to 0.90, the tissue water potential decreased from -1.92 to -3.70 bars and from -2.17 to -4.76 bars for NS and SS treatments, respectively. This decrease in water potential corresponded to a decrease of Ψ_p of 1.33 and 1.98 bars for the NS and

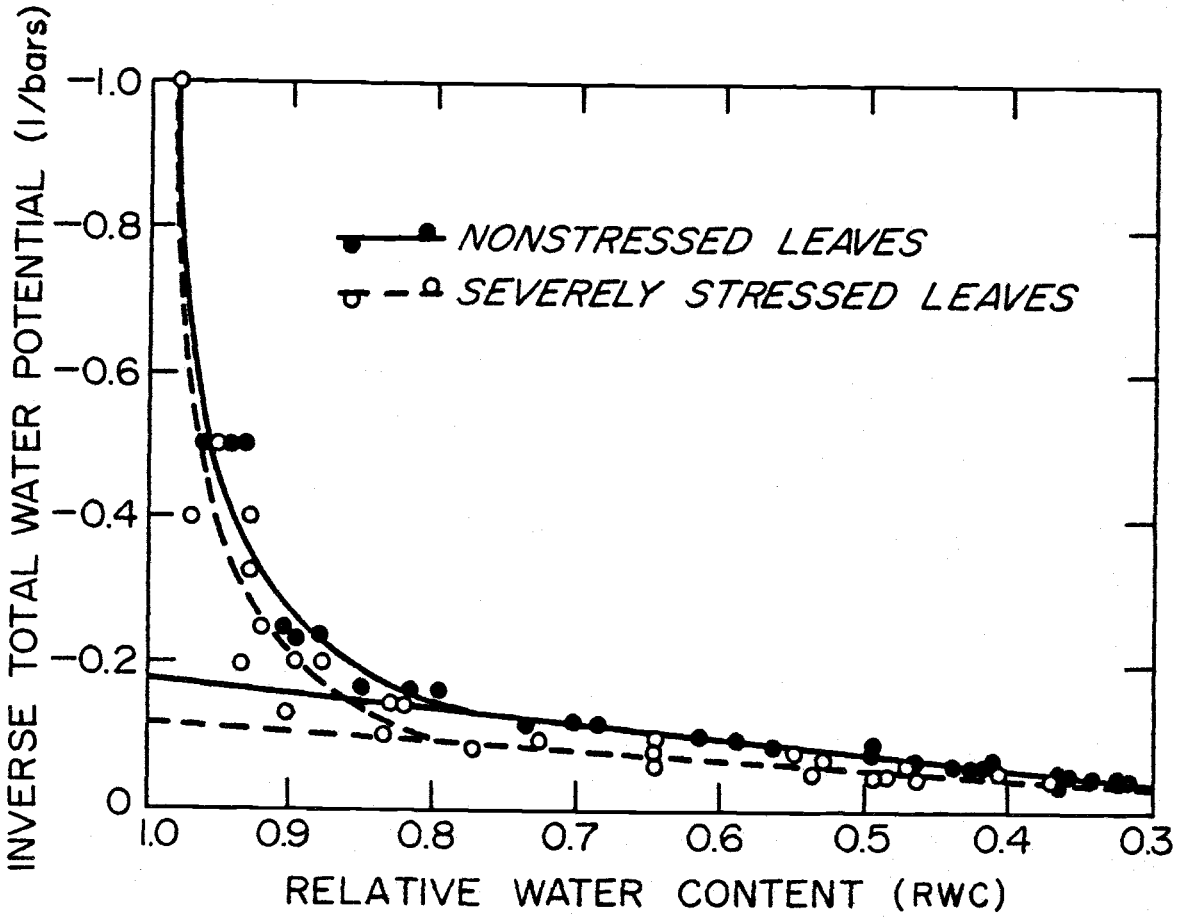

Figure 18. Relationship between water potential and relative water content for the non-stressed treatment and severely stressed treatment. Data obtained from P-V curves shown in Figures 14 and 15.

SS treatment, and a decrease of Ψ_s by 0.45 and 0.60 bars for the NS and SS treatments, respectively. These results indicate that for the same amount of reduction in RWC of the tissues, the stressed leaves respond differently from the non-stressed leaves. The stressed leaves lower their osmotic potential by a greater amount in the stressed leaves in comparison to those of the non-stressed leaves. This difference points out an evidence of osmotic adjustment as a response to water stress.

The linear portion of the P-V curve describes the change of Ψ with changing RWC, where the change is due only to the reduction of Ψ_s since Ψ_p remains zero. The linear parts are shown in Figure 19 on a larger scale. Linear regression analysis of these lines results in r^2 values of 0.95 and 0.70 for NS and SS treatments, respectively. Mean values of $\Psi_{s,100}$ obtained from the negative reciprocal of the intercepts where RWC = 1.0, these are -5.39 and -8.02 bars for NS and SS treatments, respectively. The graphs in Figure 19 indicate that at any level of hydration (RWC), the SS treatment has higher value of $-1/\Psi_s$ (less negative). Therefore, the SS treatment has a lower or a more negative Ψ_s. The lowering of Ψ_s in the tissues may be considered to be a way of regulating the turgor of the tissues as a response to water stress.

The linear function of $-1/\Psi_s$ vs. RWC enables us to estimate the rate of change of Ψ_s with respect to tissue hydration level (RWC). The derivative $\frac{d\Psi_s}{dRWC}$ can be derived as follows:

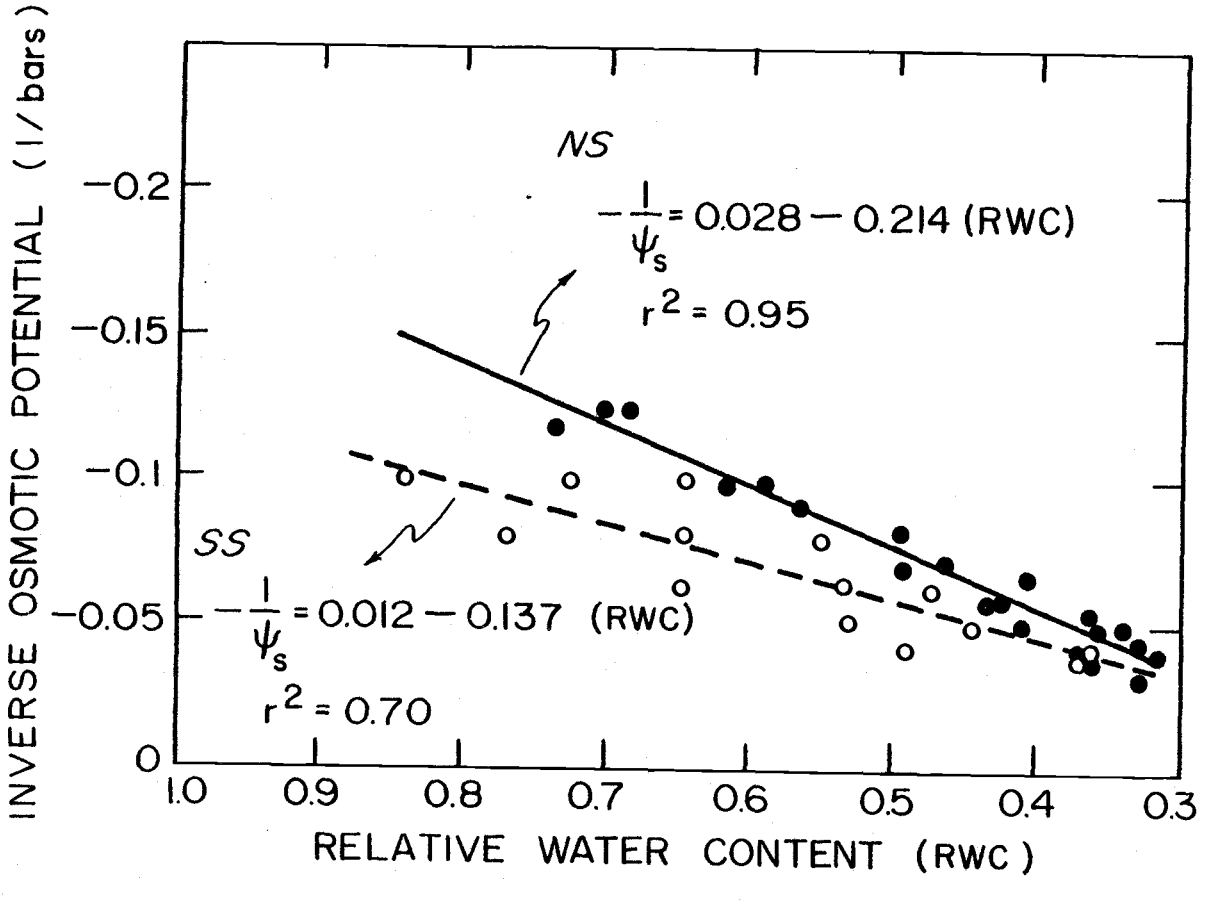

Figure 19. Comparison of water release curves of non-stressed treatment and severely stressed treatment. Diagram shows same data as shown in Figure 18, but on a larger scale.

$$-\frac{1}{\Psi_s} = a - b(RWC) ,$$

and

$$\Psi_s = -\frac{1}{a - b(RWC)} ,$$

so that

$$\frac{d\ s}{dRWC} = \frac{-b}{[a - b(RWC)]^2} . \qquad (26)$$

Figure 20 shows the change of $\frac{d\Psi_s}{dRWC}$ as a function of hydration level (RWC). Results indicate that there is no significant difference between treatments as far as $\frac{d\Psi_s}{dRWC}$ is concerned. It is interesting to observe that the slope of the curve Ψ_s vs RWC decreases with hydration reaching a constant value at the region near full turgidity. This observation points out that the change in the energy status of water in the region near full turgidity is mainly due to the change in the pressure potential component. The change in the osmotic component is negligible at that region of hydration. Dehydration beyond the point of incipient plasmolysis result in a lower water potential of the tissues which is due only to the change of the osmotic component. This discussion might help clarify the validity of the commonly made assumption of linearity between $-1/\Psi_s$ and RWC in the hydration range between incipient plasmolysis and full turgidity. In this experiment, the points of incipient plasmolysis were estimated to be about 0.76 and 0.79 RWC for NS and SS treatments, respectively. A thorough treatment of this point would require more detailed experimental measurements of the P-V curve over this region.

A closer look at the curvilinear portion of the P-V curve

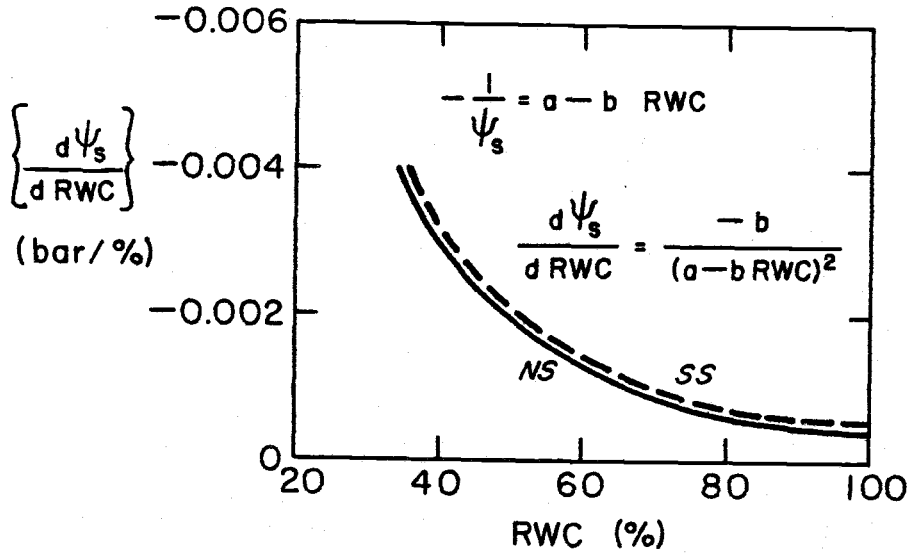

Figure 20. Relationships between the rate of ψ_s change with respect to change in RWC, $d\psi_s/dRWC$, and relative water content for both NS and SS treatments.

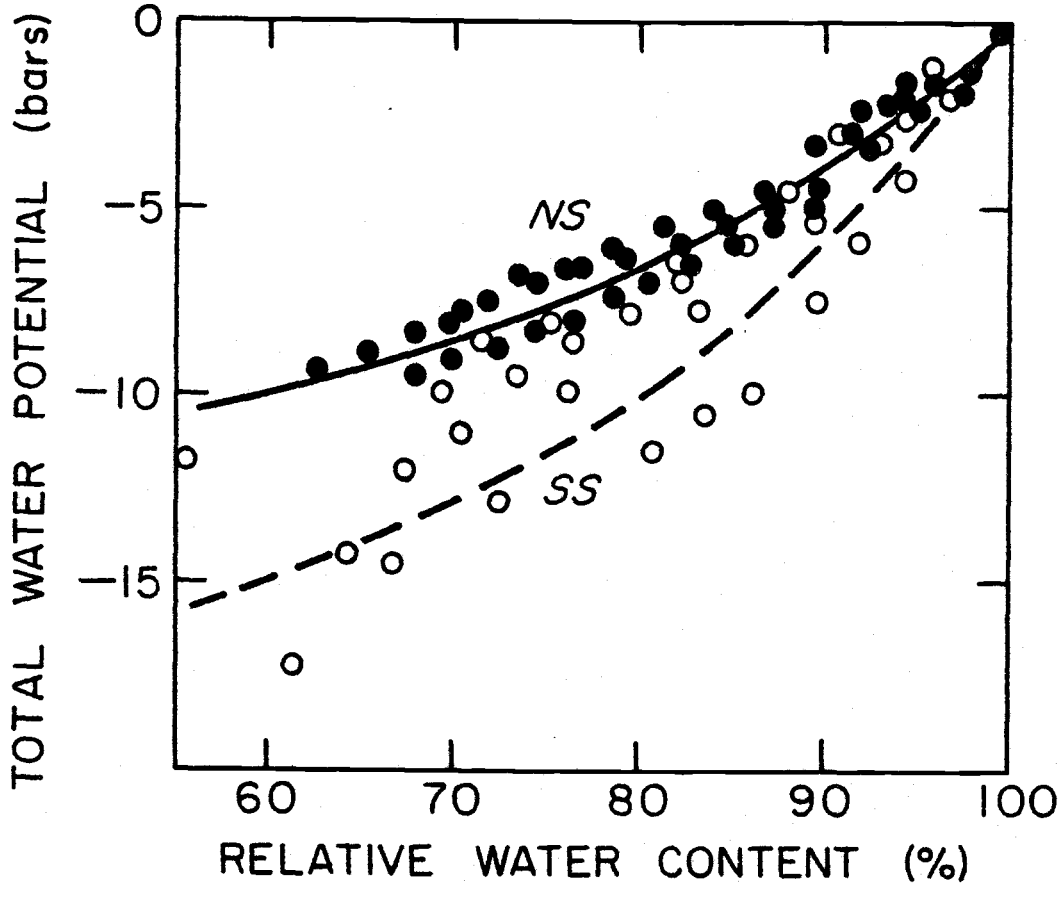

Figure 21. Water potential as a function of RWC for samples from non-stressed (NS) and severely stressed (SS) treatments. Data obtained from P-V curves shown in Figures 2 to 7.

(Figure 18) shows that the irrigation treatment altered the relationships between the energy status of the leaf cells expressed by the total water potential and the water content of the tissues expressed by relative water content. Figure 21 shows the relationships between Ψ and RWC for both NS and SS treatments. The data points were derived from the graphs shown in Figures 8 through 13. Figure 21 shows that non-irrigated (SS) plants had higher tissue water contents than irrigated plants (NS) at the same leaf water potentials. This indicates that the leaf water characteristic curve (Ψ vs. RWC) is not a unique one for the bulk tissues of the leaf. It changes in time and space. Water stress seems to shift this relationship so that leaf tissues maintain higher relative water content at lower water potential levels. At the same leaf water potential, the tissues of the severely stressed plants contain higher moisture content (higher RWC) which may be explained by higher bound water fraction (see Table 5). At the same hydration level (RWC) the non-stressed leaves have greater water potential than those of the severely stressed treatment. This shift in the leaf water characteristic curve (Ψ vs. RWC) enables the severely stressed tissues of lowering the water potential in a way that is favorable for maintaining greater potential gradient for water movement into the tissues.

Figures 22a and 22b describe the relationship between Ψ_s and RWC for the leaves of the NS and SS treatments, respectively. Results from all samples indicate a linear decrease in Ψ_s with dehydration especially in the region between full turgidity and the point of incipient plasmolysis.

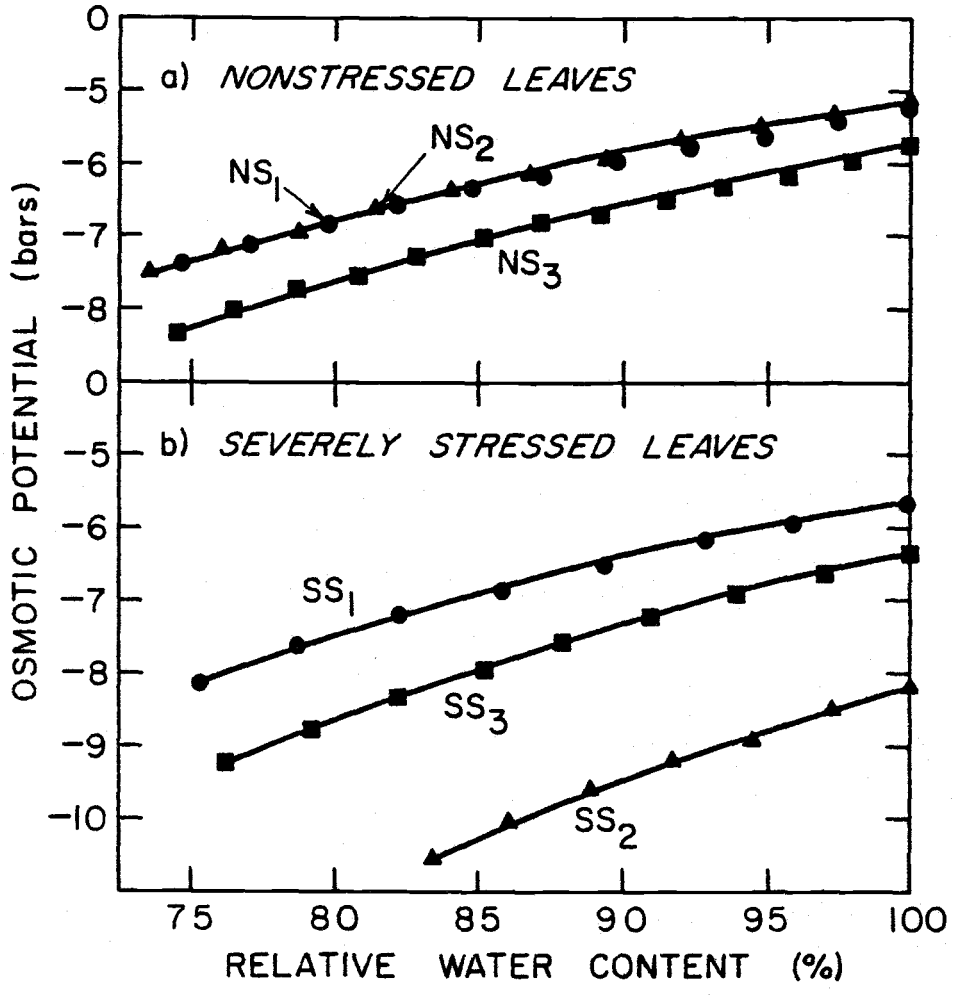

Figure 22. Relationships between osmotic potential Ψ_s and RWC for non-stressed leaves (a) and severely stressed leaves (b). Data obtained from P-V curves shown in Figures 2 to 7.

Similar results shown in Table 5 indicate that the osmotic potential of the leaves decreased by an average of 2.63 and 3.94 bars when the tissues dehydrated from full turgor to incipient plasmolysis for the NS and SS treatments, respectively. The reduction in RWC between full turgor and zero turgor were by 24.0 and 20.3 percent for NS and SS treatments, respectively. Thus, smaller decrease in RWC in the severely stressed treatments produced greater decrease in the osmotic potential which reflects the ability of the tissue to osmoregulate.

The ability of the tissues to adjust the osmotic potential component under stress condition may be reflected in the magnitude of turgor pressure maintenance at corresponding RWC. Figure 23 shows Ψ_p as a function of RWC. The plants of SS treatment were able to maintain higher turgor pressures at the same RWC, particularly in the range of 90 to 100 percent RWC. The difference between treatments disappears when the tissues dehydrate close to the point of incipient plasmolysis ($\simeq$ 80% RWC). Differences between treatments could be attributed to the previous discussions, namely the shift in the leaf water characteristic curve, the ability of the tissues in lowering the osmotic component, and the changes observed in the elasticity of the cell walls.

The main conclusions that can be drawn from the results of these experiments are that water stress decreased the osmotic potential at full turgor $\Psi_{s,100}$, and consequently the osmotic potential at zero turgor $\Psi_{s,0}$. The relative water content at zero turgor (RWC_0) appeared to increase only slightly with water stress. The bound water fraction

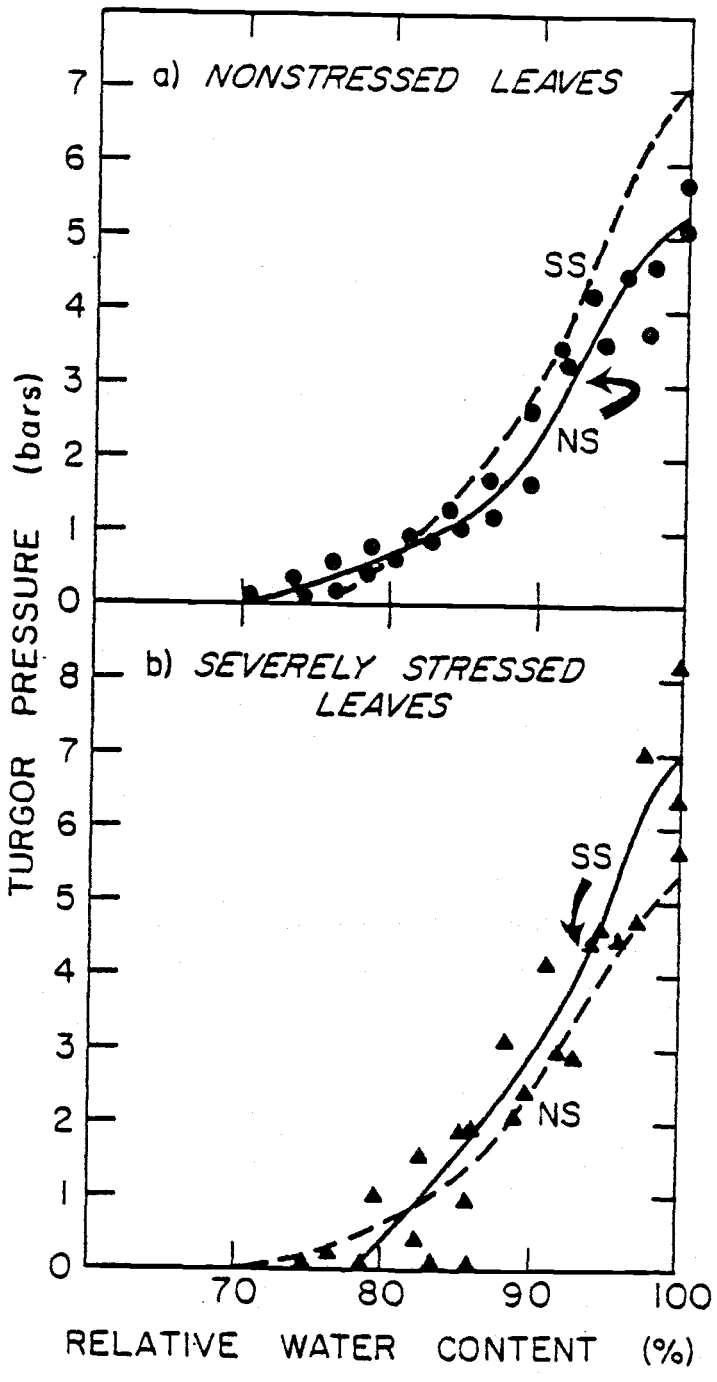

Figure 23. Turgor pressure as a function of RWC for samples from the non-stressed treatment (a) and severely stressed treatment (b). Data obtained from P-V curves shown in Figures 2 through 7. Both graphs shown on each figure for comparison.

seems to be increased by water stress.

Although the data was highly variable, the value of Ψ was not affected or altered by water stress. The modulus of elasticity appears to be related linearly to Ψ_p at values from incipient plasmolysis (zero turgor) to about 3 bars. The relationship becomes hysteric above that range which may be explained by the ability to make accurate measurement of the P-V curve at that range of hydration.

Results suggest that the osmotic potential at full turgor and that at zero turgor and cell wall elasticity may be closely related to the ability of the tissues to osmoregulate within a certain range of water potential.

Effects of Water Stress on Water Relations of Beans

Diurnal Changes of Leaf Water Potential (Ψ)

Changes in the water status are directly influenced by the environmental conditions for the plant, namely the soil water status and the atmospheric demand. Figure 24 shows the diurnal changes of leaf Ψ of the NS treatment on four typical days. The diurnal cycle of leaf Ψ follows the cycle in the incoming solar radiation. Leaf Ψ was about -4 bars at sunrise. As the sun rises, the rate of radiation increases and the transpiration rate starts to increase. Leaf Ψ starts to decrease, maintaining a water potential gradient from the soil to the leaves. A minimum value of -10 to -13 bars was reached during the period from 1230 to 1630 hours depending on the climatic conditions of the day. Late in the afternoon, as the rate of solar radiation -

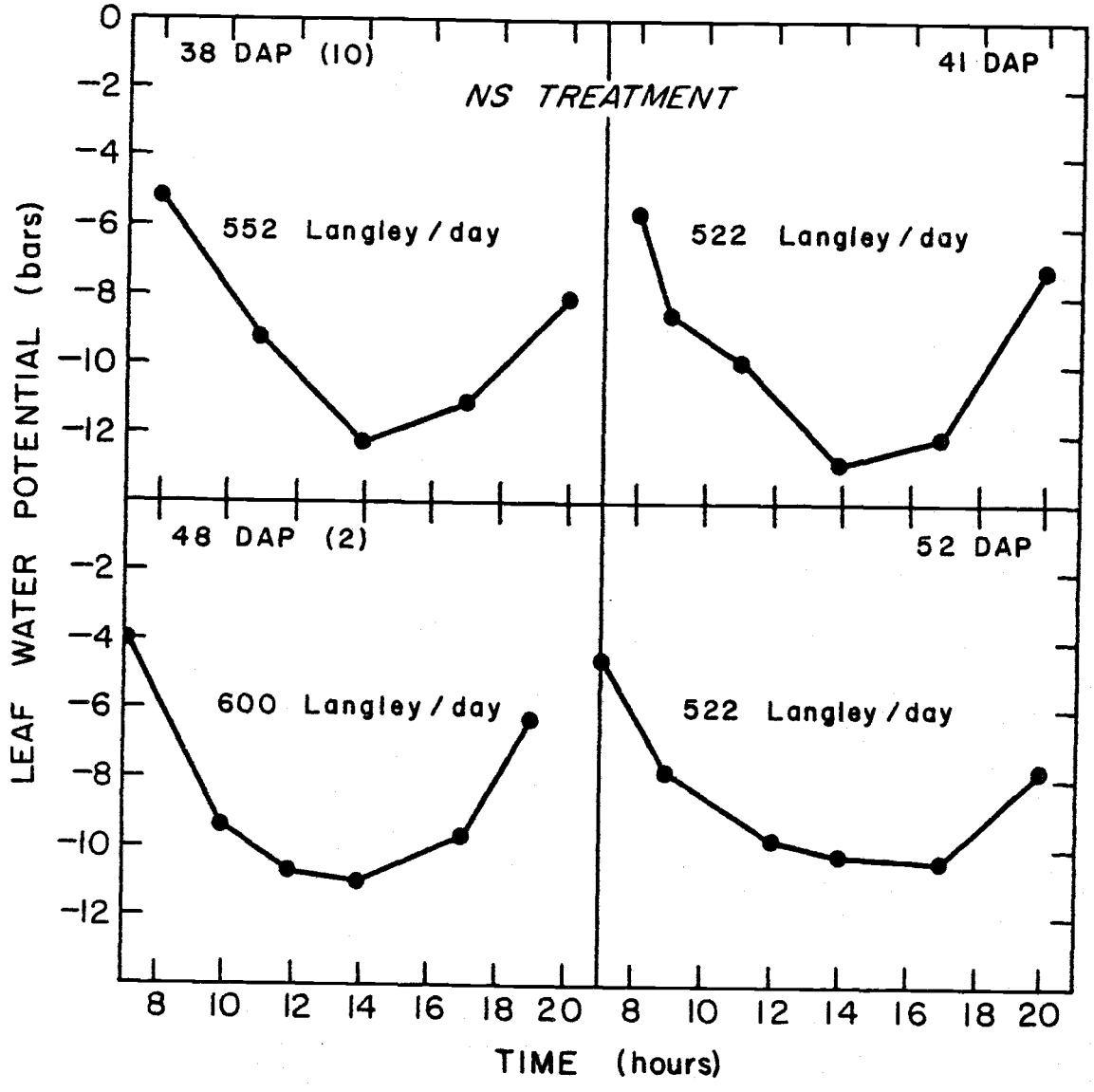

Figure 24. Leaf water potential as a function of time of the day, 1980, for the NS treatment at 38, 41, 48 and 52 days after planting. Each point is the average of 4 measurements. Incoming solar radiation is also indicated in the diagram. The numbers (10) and (2) indicate days after last irrigation.

decreases, leaf Ψ increases again, reaching a value ranging from -4 to -6 bars after sunset.

Daily totals of solar radiation are shown in Figure 24. Unfortunately, hourly records of incoming radiation were not taken for this experiment. However, measurements of solar radiation for Corvallis confirm that maximum rate of incoming radiation occurs during the period from 1300 to 1500 hours (Nagaraja et al., 1981). Figures 25a and 25b show the daily incoming solar radiation during the 1980 and 1981 experiments, respectively. Daily totals of solar radiation for days 38, 41, 48, and 52 after planting were 552, 522, 600, and 522 Langley/day, respectively. The amplitude of the Ψ oscillation depends on both the rate of incoming radiation and the soil water status. The effect of soil water status is seen in Figure 24. At higher soil water content, two days after irrigation (DAI), the mid-day depression of Ψ was down to -11 bars (Figures 24b). On the other hand, when soil water was limiting, 10 days after irrigation, the mid-day depression of Ψ was to -12.3 bars.

Figure 26 shows three daily cycles of Ψ during the 1980 growing season. The soil water distribution on the days measurement of Ψ was made are shown in Figures 27a, b and c. The stressed plants (SF treatment) were not irrigated during the flowering stage. The stress cycle lasted 22 days from Day 29 to 51. Leaf Ψ was more negative on the SF treatment during all days, especially during the mid-day hours. The differences between treatments were greatest on day 48, as much as 2.5 bars around 1400 hours. One would expect that the differences between treatments to be even greater on day 50 because of the greater

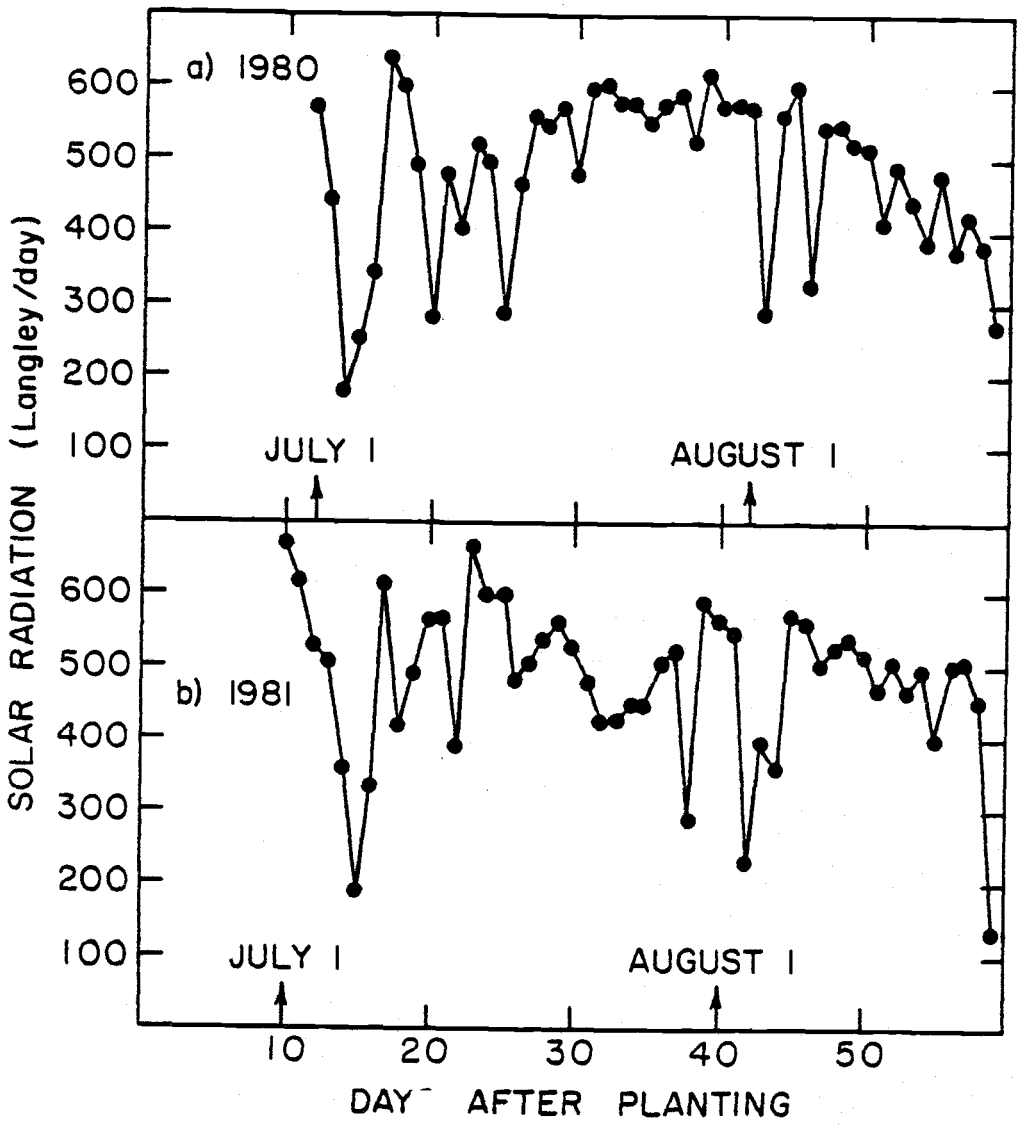

Figure 25. Daily totals of incoming solar radiation during (a) the 1980 experiment and (b) the 1981 experiment. Data obtained from C. R. Nagaraja Rao et al. (1980 and 1981). Measurements were made near the site of the experiments.

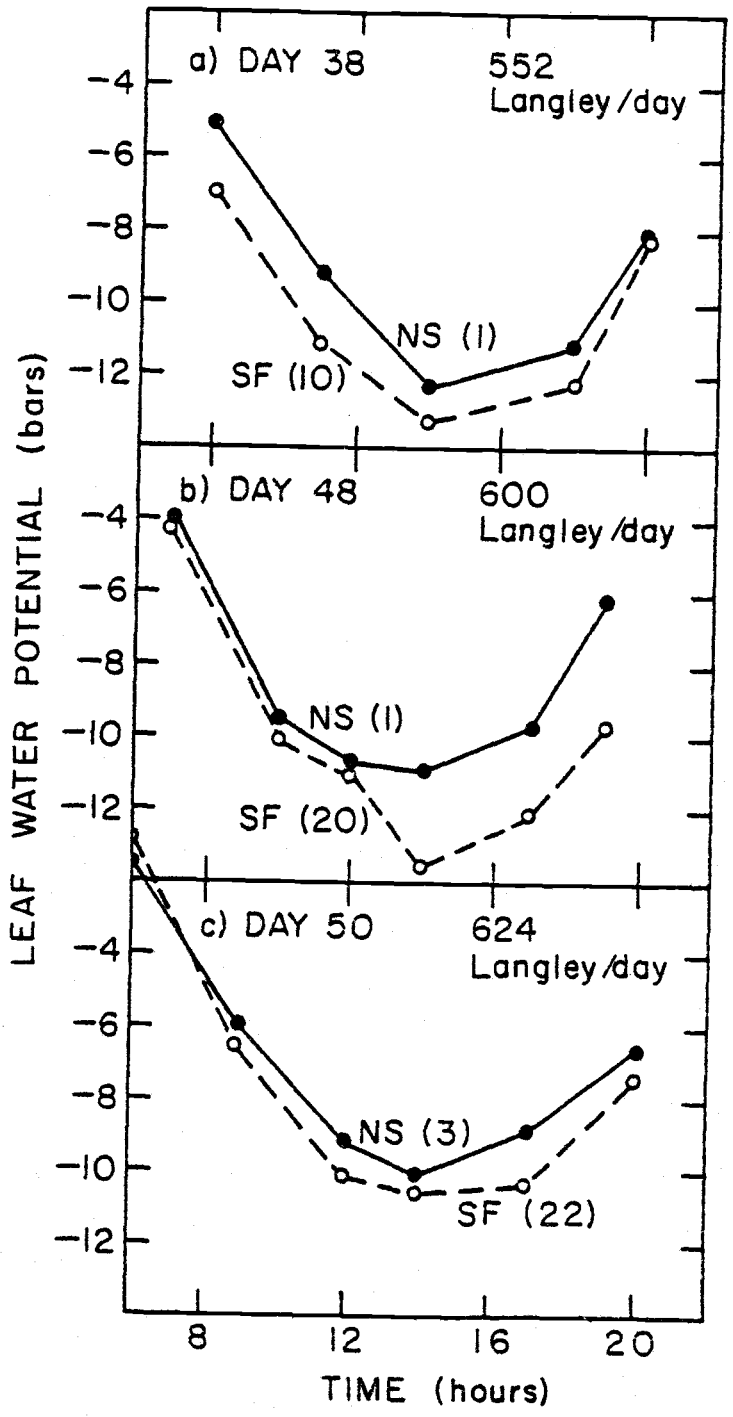

Figure 26. Leaf water potential as a function of time of the day for the NS and SF treatments at 38, 48, and 50 days after planting. Each point represents the average of at least three measurements of (a) fully exposed, recently matured or, (b and c) uppermost three leaves. Sampling dates indicated in the figures. Numbers in parenthesis indicate days after last irrigation.

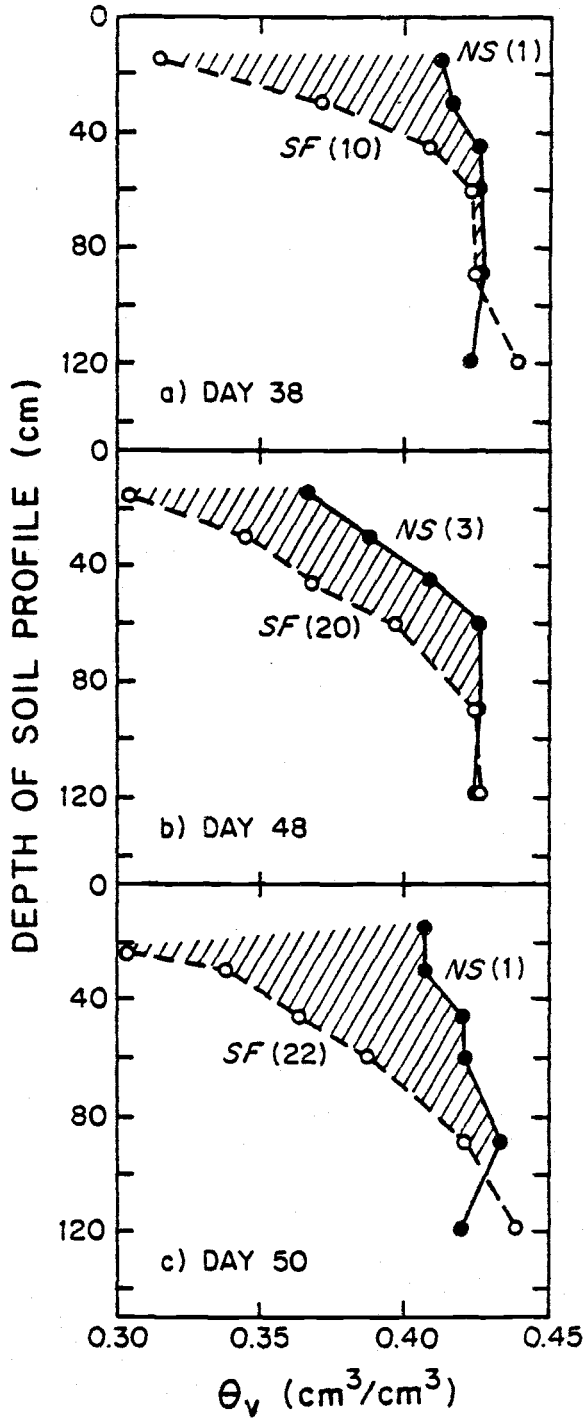

Figure 27. Soil water content as a function of soil depth for treatments NS and SF 38 days after planting (a), treatments NS and SF 48 days after planting (b), and treatments NS and SF 50 days after planting (c). Numbers in parenthesis indicate days since last irrigation. Shaded area indicates soil water depletion from the profile.

differences in soil water distribution (Figure 27c). Day 50 is the day after irrigating treatment NS and the day before irrigating SF treatment. This represents the beginning of the stress cycle of NS and the end of the cycle for SF treatment. Results show that the total water potential was not sensitive enough to indicate the differences due to the degree of stress in terms of the stress period. The oscillation in the water potential parameter is a result of the interaction of many factors, namely the soil water potential, the solar radiation, the evaporative demand, the degree of cloudiness, and the stress period. In our results, the measurements of Ψ were not consistent with the changes of the soil water potential, the solar radiation, and the stress period. These inconsistencies could not be explained on the basis of these limited observations.

The depression of Ψ in both treatments during all days of measurements are expected to have an effect on the growth during the hot part of the day. Unfortunately, hourly records of leaf enlargements or growth were not taken.

Diurnal Changes of Ψ_s and Ψ_p

Figures 28, 29, 30, and 31 represent the diurnal cycles of potential components, namely Ψ, Ψ_s, and Ψ_p, for treatments GS, NS, MS, and SF, respectively. This data was obtained during the 1980 experiment. Each graph represents three days of measurements (41, 43, and 48 days after planting) and each point represents the average of three measurements. In all cases, the water potential of the leaves changed during the day as discussed previously. Graphs of Ψ show the greatest

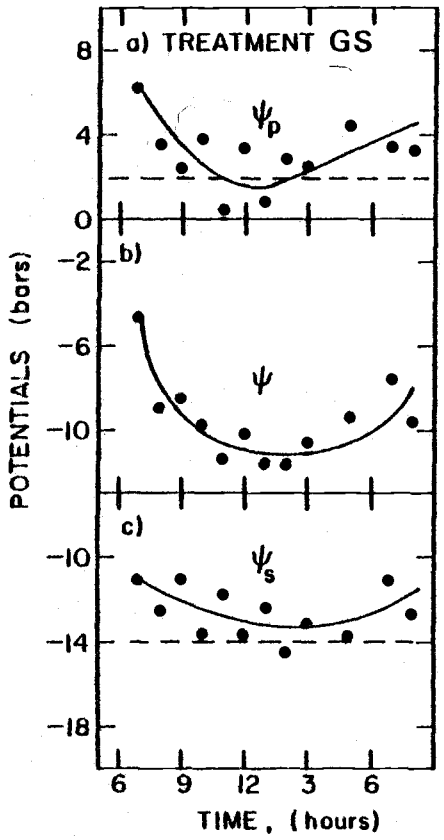

Figure 28. Diurnal changes of leaf Ψ, Ψ_s, and Ψ_p for treatment GS. Data points represent three days of measurements 31, 43, and 48 days after planting. Each point represents the average of three measurements.

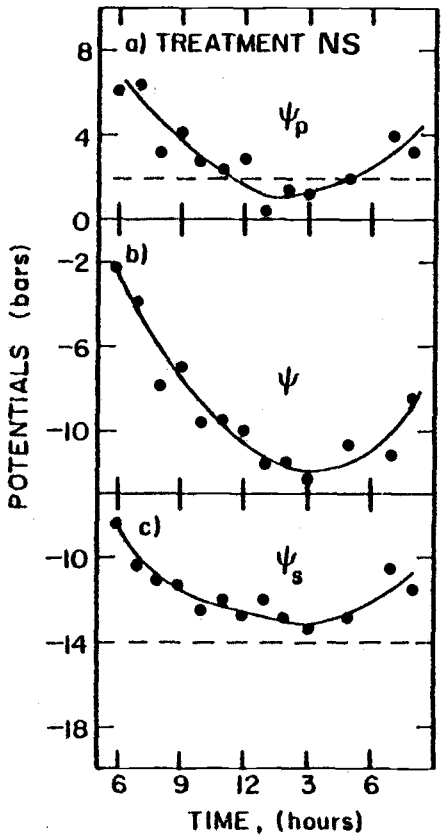

Figure 29. Diurnal changes of leaf Ψ, Ψ_s, and Ψ_p for treatment NS. Data points represent three days of measurements 41, 43, and 48 days after planting. Each point represents the average of three measurements.

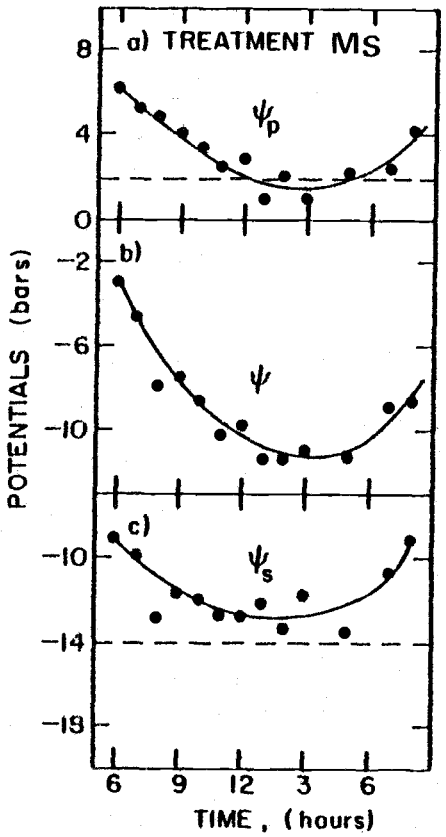

Figure 30. Diurnal changes of leaf Ψ, Ψ_s, and Ψ_p for treatment MS. Data pointes represent three days of measurements, 41, 43, and 48 days after planting. Each point represents the average of three measurements.

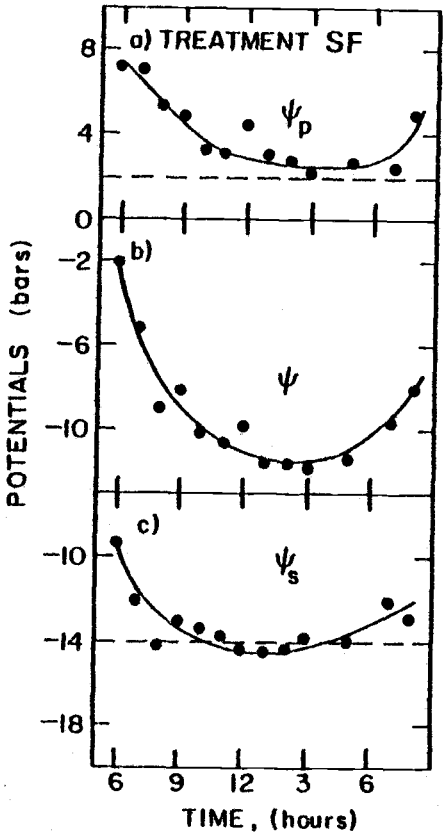

Figure 31. Diurnal changes of leaf Ψ, Ψ_s, and Ψ_p for treatments SF. Data points represent three days of measurements 41, 43, and 48 days after planting. Each point represents the average of three measurements.

amplitude in comparison with the potential components (Ψ_s, Ψ_p). The osmotic potential, Ψ_s, was not constant during the day. The changes in Ψ_s follow the changes in leaf Ψ. As the leaf Ψ decreases, Ψ_s also decreases but at a slower rate reaching its minimum value around noon. Turgor pressure was maintained positive as a result of the cycle in Ψ_s.

For better comparison between treatments, Figures 29 and 31 for treatments NS and SF were superimposed on each other and presented in Figure 32. In both treatments, the depression in Ψ_s at mid-day hours paralleled the decrease in leaf Ψ. Differences in leaf Ψ between treatments (Figure 32) were not significant throughout the day. However, the osmotic potential Ψ_s of the stressed treatment (SF) was lower throughout the daytime hours and, consequently, the pressure potential of SF treatment was maintained at a greater or equal value throughout most of the day. The greatest difference between treatments occurred during the midday hours. The greatest difference in Ψ_s between treatments was about 2.5 bars with the stressed treatment (SF) having the lower values.

The resultant difference in Ψ_p was about 1.5 bars, with the stressed treatment having the higher values of Ψ_p. These results imply that the leaves of the SF treatment were capable of maintaining the turgor of the tissues throughout most of the day and during midday hours in particular.

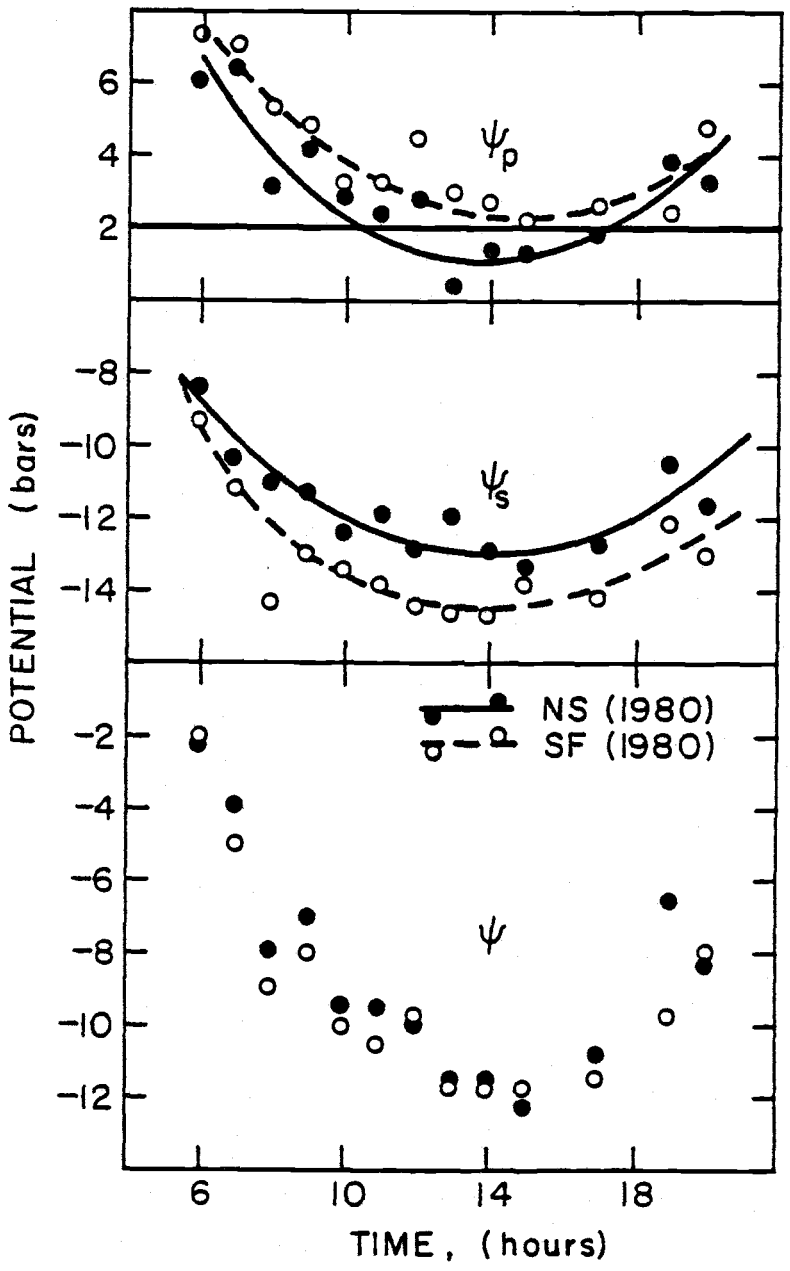

Figure 32. Diurnal cycles of Ψ, Ψ_s, and Ψ_p, 1980. Data obtained from Figures 29 and 31. Lines were eye fitted to experimental values for the NS treatment (solid line) and SF treatment (dashed line).

Diurnal Osmotic Adjustment

From the previous discussion we can see that under field conditions, turgor pressure decreases with decreasing Ψ. The rate of decline in Ψ_p is in part controlled by the ability of the leaves to lower Ψ_s. Figure 33 shows results from the 1981 experiment where young, fully expanded, leaves were measured every 2 to 3 hours for two consecutive days (29 and 30 days after planting). Results shown in Figure 34 compare a well watered treatment (NS) with a non-irrigated treatment (SS). The leaves of the well watered treatment had higher leaf Ψ than those of the severely stressed treatment (SS) throughout the day. However, the leaves of the SS treatment had a much lower Ψ_s values throughout the day and night. This indicates that lowering of the Ψ_s is the result of net accumulation of solutes rather than of tissue dehydration. As a result, turgor pressure was maintained at a reasonably high level on the SS treatment during these hours. These results might lead to the expectation to have similar rates of growth on both treatments. In our discussion of treatment effects on growth, we will try to explain this point in more detail.

Another view of the same aspect of maintenance of Ψ_p at reduced Ψ can be obtained by plotting Ψ_s as a function of Ψ, as shown in Figures 34 and 35 (Acevedo, 1975; Fereres, 1976). Figure 34 represents the relationship between Ψ_s and Ψ for treatments NS and SS. The diagonal line passing through the origin represents the line for which $\Psi = \Psi_s$. The data points fall below this line indicating that Ψ_s is always smaller than Ψ. Lines were drawn describing the relationship between Ψ and Ψ_s.

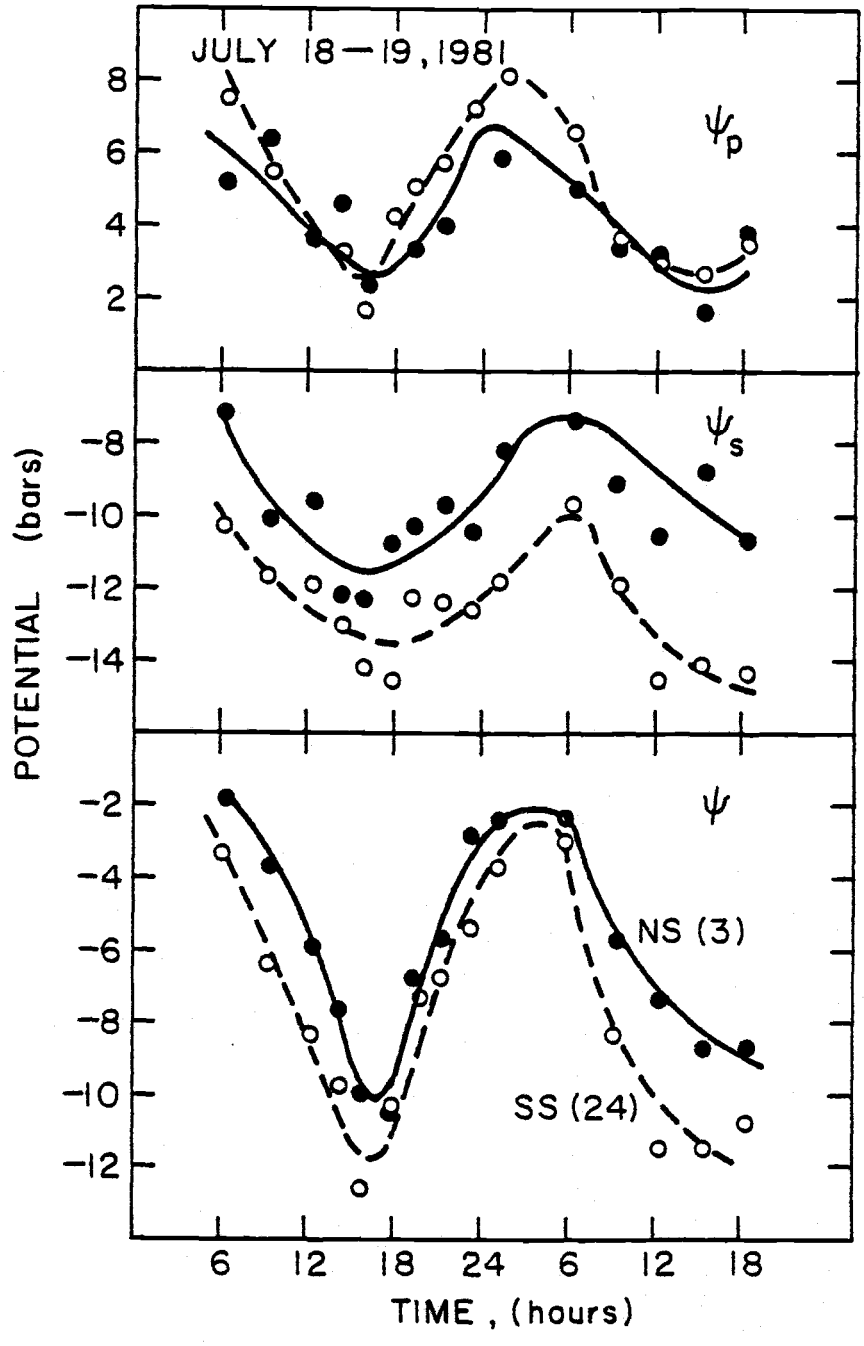

Figure 33. Daily course of leaf water potential (Ψ), osmotic potential (Ψ_s), and pressure potential (Ψ_p) in expanding leaves of non-stressed (solid lines) and severely stressed (dashed lines) treatments. Measurements were taken 29 and 30 days after planting. Lines were fitted by eye .

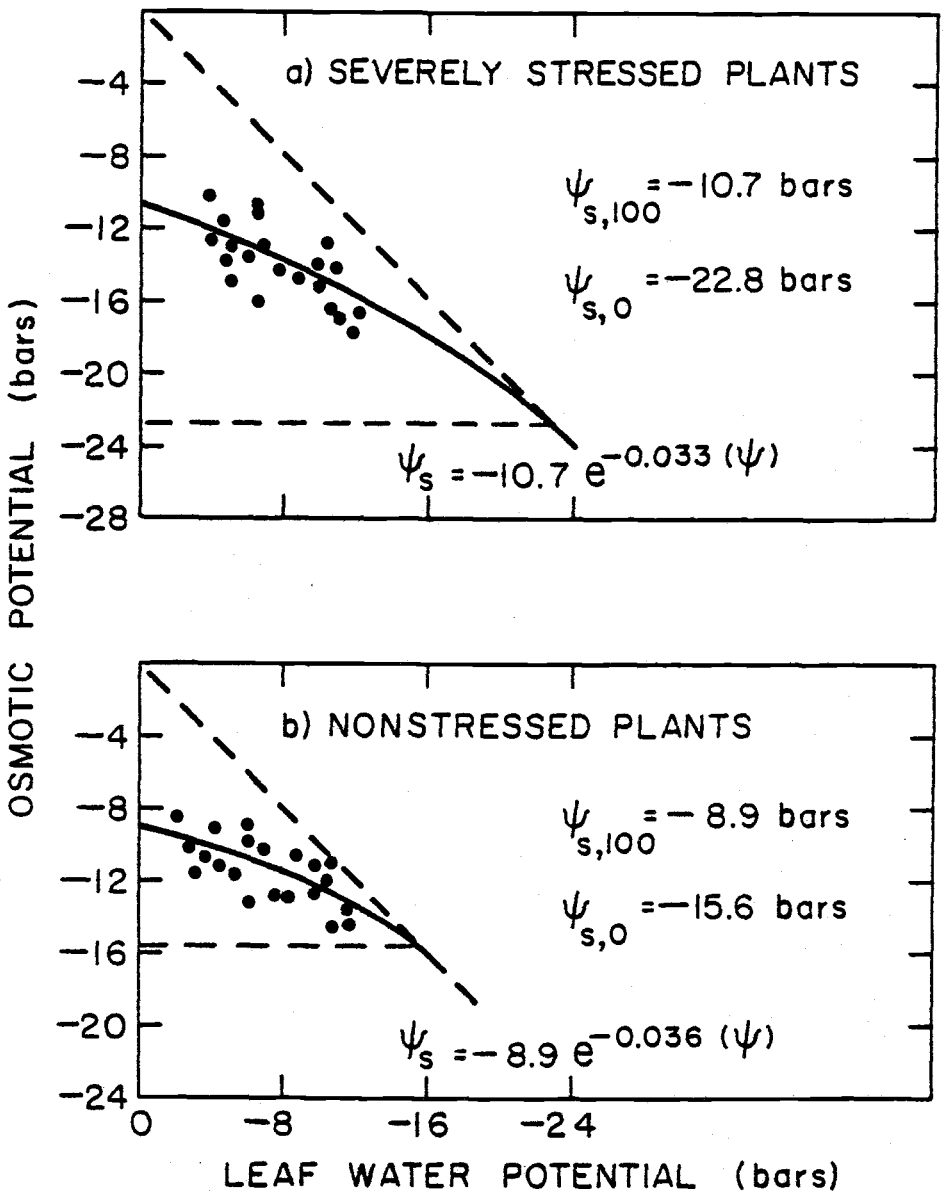

Figure 34. Relationships between Ψ and Ψ_s in recently matured leaves of severely stressed plants (a) and non-stressed plants (b). Data points represent single measurements taken on day 50 after planting.

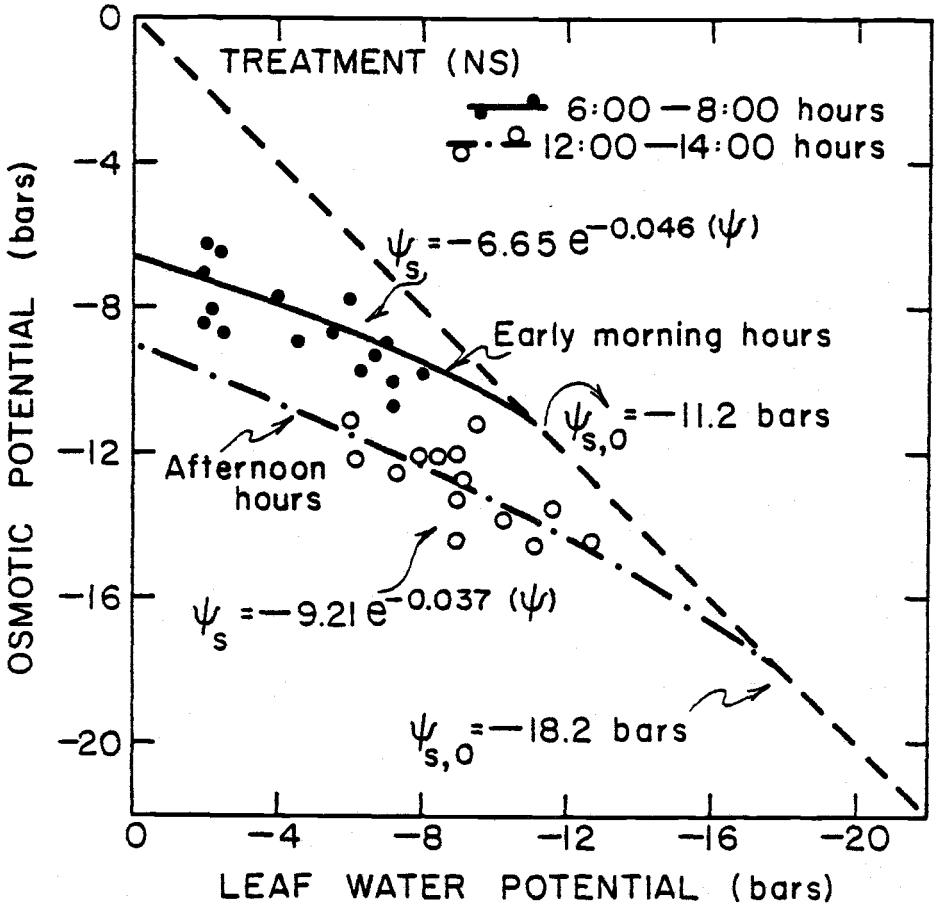

Figure 35. Relationships between ψ and ψ_s in recently matured leaves of non-stressed (NS) plants. Solid line represents samples taken during early morning hours (6:00-8:00 hours) and dashed line represents samples taken during late afternoon hours (12:00-14:00 hours).

The relationship between Ψ and Ψ_s intersects the diagonal line at the point of incipient plasmolysis where $\Psi = \Psi_s$ and $\Psi_p = 0$. The points of incipient plasmolysis were -15.6 and -22.8 bars for NS and SS treatments, respectively. The line of the relationship intersects the Y-axis at the point of full turgidity where $-\Psi_s = \Psi_p$ and $\Psi = 0$. The points of intersection represent the osmotic potential at full turgidity ($\Psi_{s,0}$). The value of $\Psi_{s,100}$ obtained from Figure 34 were -8.9 and -10.7 bars for NS and SS treatments, respectively. Clearly, values of both $\Psi_{s,0}$ and $\Psi_{s,100}$ are much lower for the SS treatment than for the NS treatment, which agrees well with the results obtained from the P-V curves results shown in Table 5. The magnitudes of $\Psi_{s,0}$ and $\Psi_{s,100}$ values obtained in the field were much lower (more negative) than those from the P-V curves. Differences in magnitude may be attributed to the effect of the rate of stress development. The leaves stressed in the field were exposed to a much slower rate of stress development but the P-V technique imposes a faster rate of dehydration in the pressure chamber. Slower rates of stress development imply that the cells have much longer time to respond and adapt to water stress which enabled these cells to accumulate greater concentrations of solutes and having lower values of $\Psi_{s,0}$ and $\Psi_{s,100}$.

The relationship between Ψ and Ψ_s is not constant, rather it changes during the day. Figure 35 describes the same relationship for the same treatment (NS) at two time periods of the day namely, the early morning (0600-0800) and the afternoon hours (1200-1400). Figure 35 indicates that the pressure potential becomes zero at Ψ = -18.2 bars in the samples taken during the afternoon but at

Ψ = -11.2 bars in the morning samples. These results indicate that the relationship between Ψ and Ψ_s changes during the day and points out the complexity of the system. This evidence strongly indicates that the plant is performing some mechanism to adjust the osmotic potential as a way of dealing with the stress conditions.

The degree of osmotic adjustment can be estimated by plotting Ψ_p versus Ψ and estimating the slope of the graph ($d\Psi_p/d\Psi$). Figure 36 shows the relationship between Ψ and Ψ_p. Data points represent an average of three measurements taken on day 50 after planting of the 1981 experiment. Linear relationships were found for both the SS and NS treatments with r^2 values of 0.82 and 0.93, respectively. The slope of these lines ($d\Psi_p/d\Psi$) represents the degree of change of Ψ_p per unit change Ψ, describing the degree of osmotic adjustment of the leaves (Ekasingh, 1982). A value approaching unity indicates that any drop in Ψ will produce the same change in Ψ_p, meaning no adjustment of Ψ_s has occurred. The further the value of the slope is from unity, the higher the ability to adjust osmotically. Figure 36 shows that very little adjustment occurred in the well watered leaves (slope = 0.74). The stressed (SS) leaves have a greater ability of osmotic adjustment (slope = 0.35). As a result, stressed leaves show greater turgor maintenance.

Diurnal Changes of Leaf Resistance and Leaf Temperature

As discussed in the literature review, leaf resistance and leaf temperature have been used in numerous studies (Kanemasu, 1975; Idso et al., 1981) to evaluate the water status of plants. These parameters

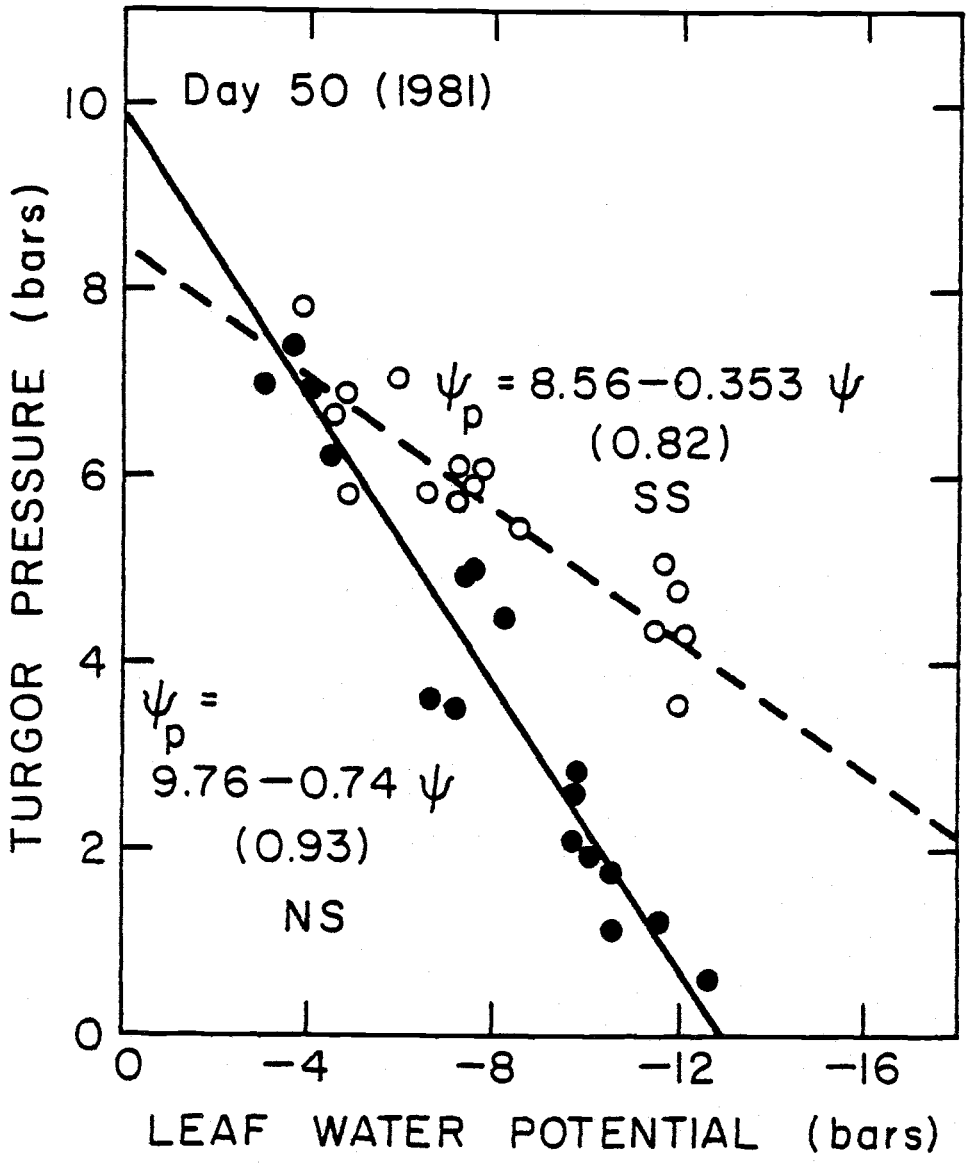

Figure 36. Relationships between leaf water potential and turgor pressure for fully expanded leaves sampled at 50 days after planting for treatment NS (solid line) and treatment SS (dashed line).

are also used to evaluate the effects of water stress on the performance of plants under adverse environmental conditions.

The stomata of leaves play an important role in controlling transpiration and photosynthesis. To compare the stomatal responses in the irrigated and non-irrigated treatment, daily fluctuations in stomatal openings as indicated by the diffusive resistance of the upper leaves in the canopy at various days after planting were measured.

Figure 37 shows the fluctuations in leaf diffusive resistance of three treatments during two days of the 1980 field experiment. The well watered treatment (NS) had relatively lower (r_L) than the stressed treatments, especially during mid-day hours. The higher resistance values observed around 1400 hours in SF on day 36, and both SF and MS treatments on day 41 represent evidence of partial closure of stomates during these hours. The variability of the data was high for the two field experiments. These variations were observed from day to day depending on the changes in the ambient conditions, especially light and CO_2 concentrations as well as the water status of the plants. It was observed on most days that although the average diffusive resistance was consistently higher for the SS treatment at mid-day, the differences were very small. Possible effects of these small differences on transpiration will be discussed in following sections.

Leaf temperature can also be used to indicate stomatal closure. Leaf energy balance considerations show that stomatal closure often results in smaller latent heat flux and greater sensible heat flux (Reicosky et al., 1980). If radiation balance and wind structure maintain the same conditions, the decrease in latent heat flux results in

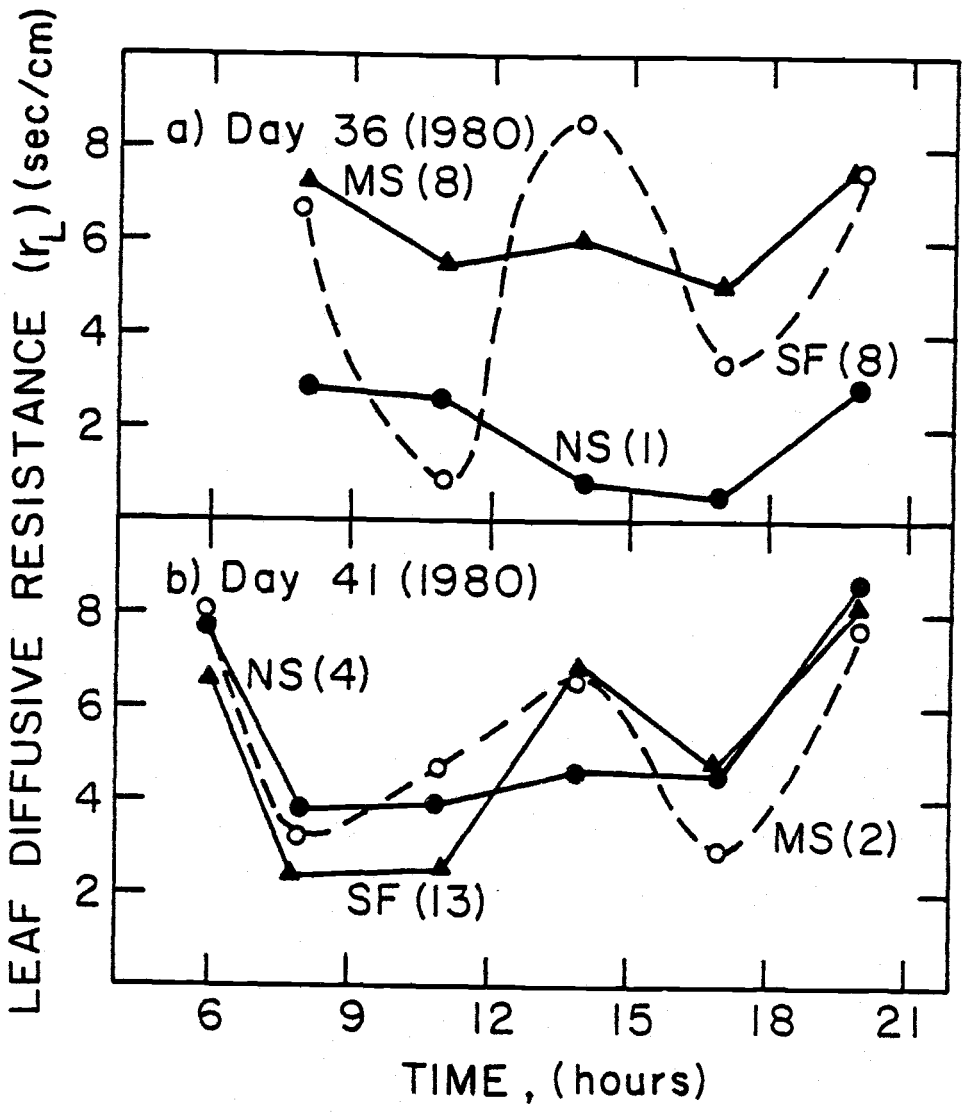

Figure 37. Diurnal trends of leaf diffusive resistance r_L of the MS, SF, and NS treatments, 36 days after planting (a) and 41 days after planting (b) in 1980. Each data point is an average of three measurements on fully expanded leaves. Numbers in brackets indicate days after last irrigation.

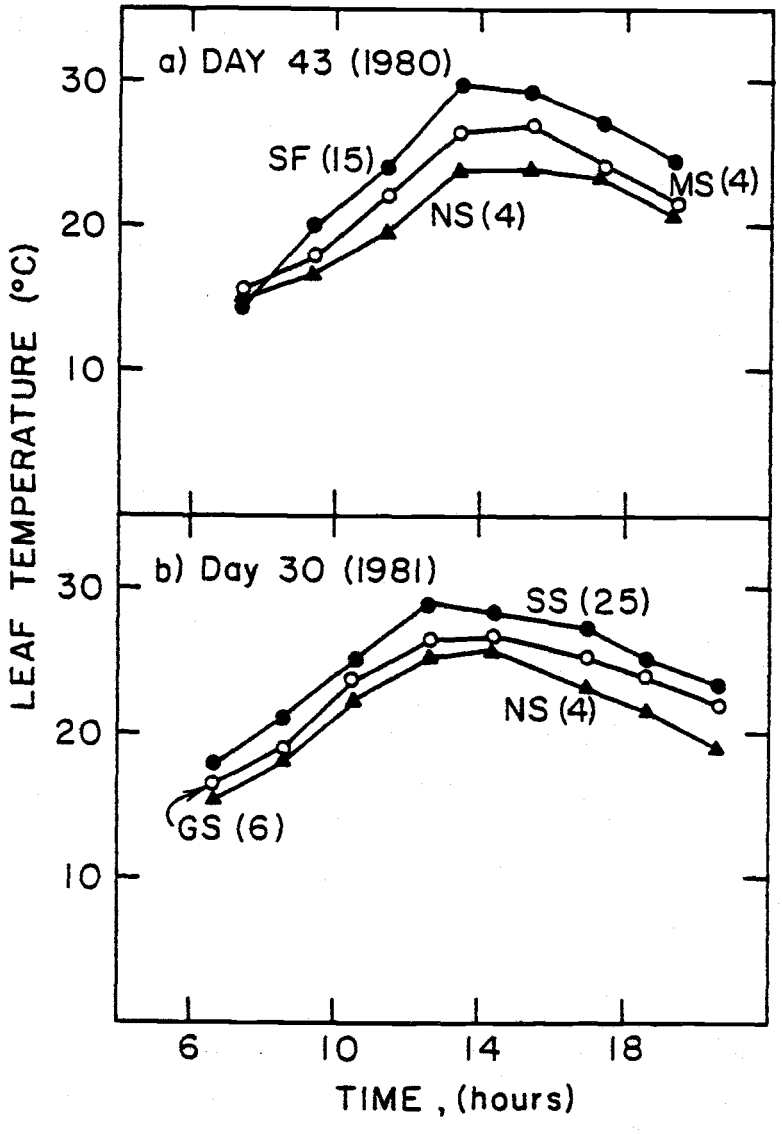

Figure 38. Diurnal trends of leaf temperature measured with an Infrared thermometer on the NS, MS and SF treatments 30 days after planting of the 1980 experiment (a) and on treatments NS, GS and SS, 43 days after planting of the 1981 experiment (b). Each point represents an average of four measurements for the 1980 experiments and eight measurements for the 1981 experiment. Numbers in parenthesis represent days since last irrigation of the corresponding treatment.

an increase of leaf temperature.

Figure 38 represents the course of leaf temperature as measured by an infrared thermometer (Raytek, Inc., Model R2LT). On day 43 of the experiment in 1980, leaf temperatures of the SF treatment were higher than those of the MS and NS treatments throughout most of the day. The stressed treatment (SF) was at the late stages of the stress period, 15 days after the last irrigation, as compared to the well watered treatment NS which was 4 days after the last irrigation. The leaf temperature profiles peak around the mid-day hours from 1200 to 1500, which coincides with the peak period of solar radiation and the mid-day depression of leaf Ψ. Similar results were obtained on day 30 of the 1981 experiment.

A linear relationship exists between leaf temperature (T_1) and leaf water potential (Ψ) (Figure 39) with r^2 value of 0.55 and 0.72 for SS and NS treatments, respectively. The slope ($dT_L/d\Psi$) represents the change in leaf temperature in response to a change in Ψ. The higher the slope the more sensitive the plant is to water stress. The SS treatment has a slightly smaller slope.

Figures 40 and 41 show the diurnal changes of Ψ, Ψ_s, Ψ_p, r_L, T_L and transpiration rates of the driest (SS) and wettest (NS) treatments. The leaf diffusive resistance of both treatments remained low until noon when a slight increase occurred. A decrease occurred in the afternoons followed by a rise at about 1800 hours. This oscillation in leaf diffusive resistance results in an increase in rate of transpiration after sunrise with a slight depression during mid-day hours and an obvious decrease in the afternoons. The leaf temperatures followed

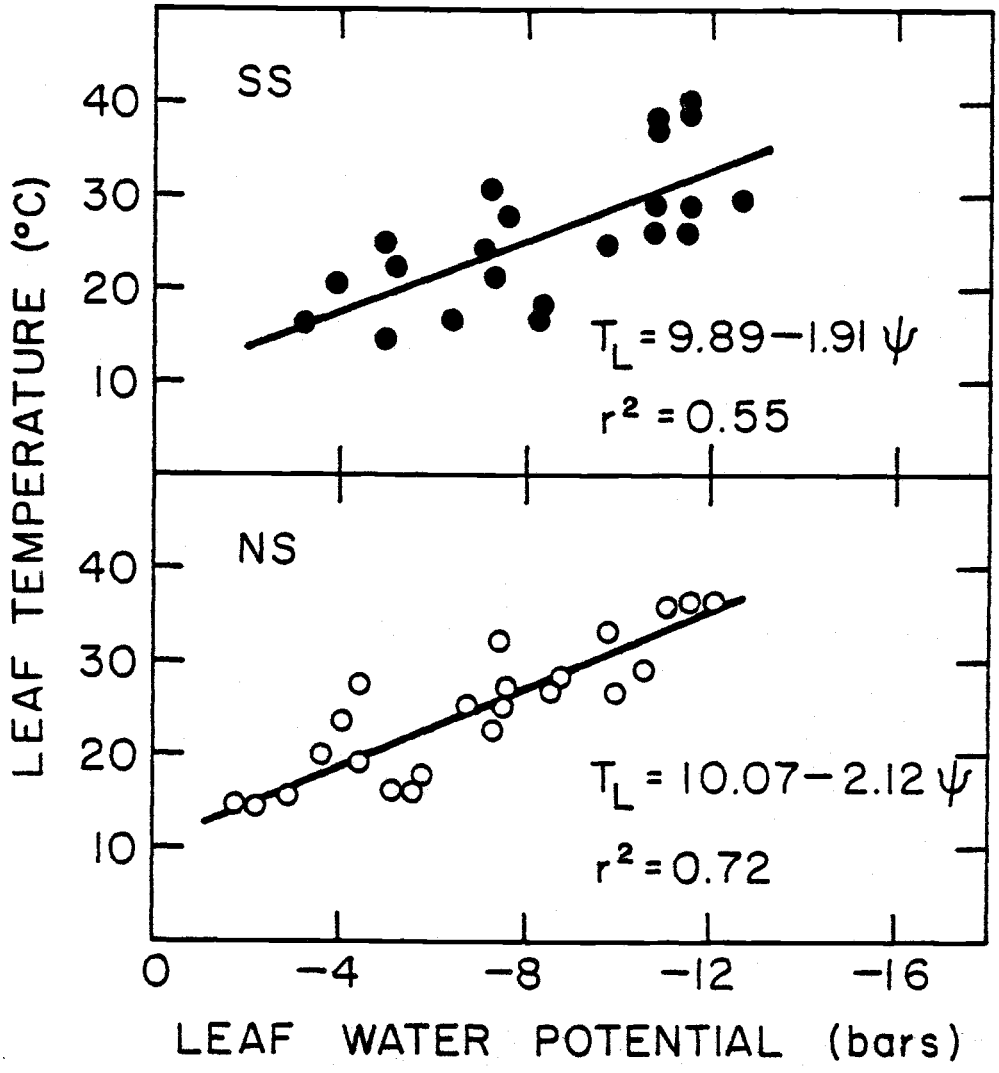

Figure 39. Relationships between leaf temperature and leaf ψ for the NS and SS treatments of the 1981 experiment.

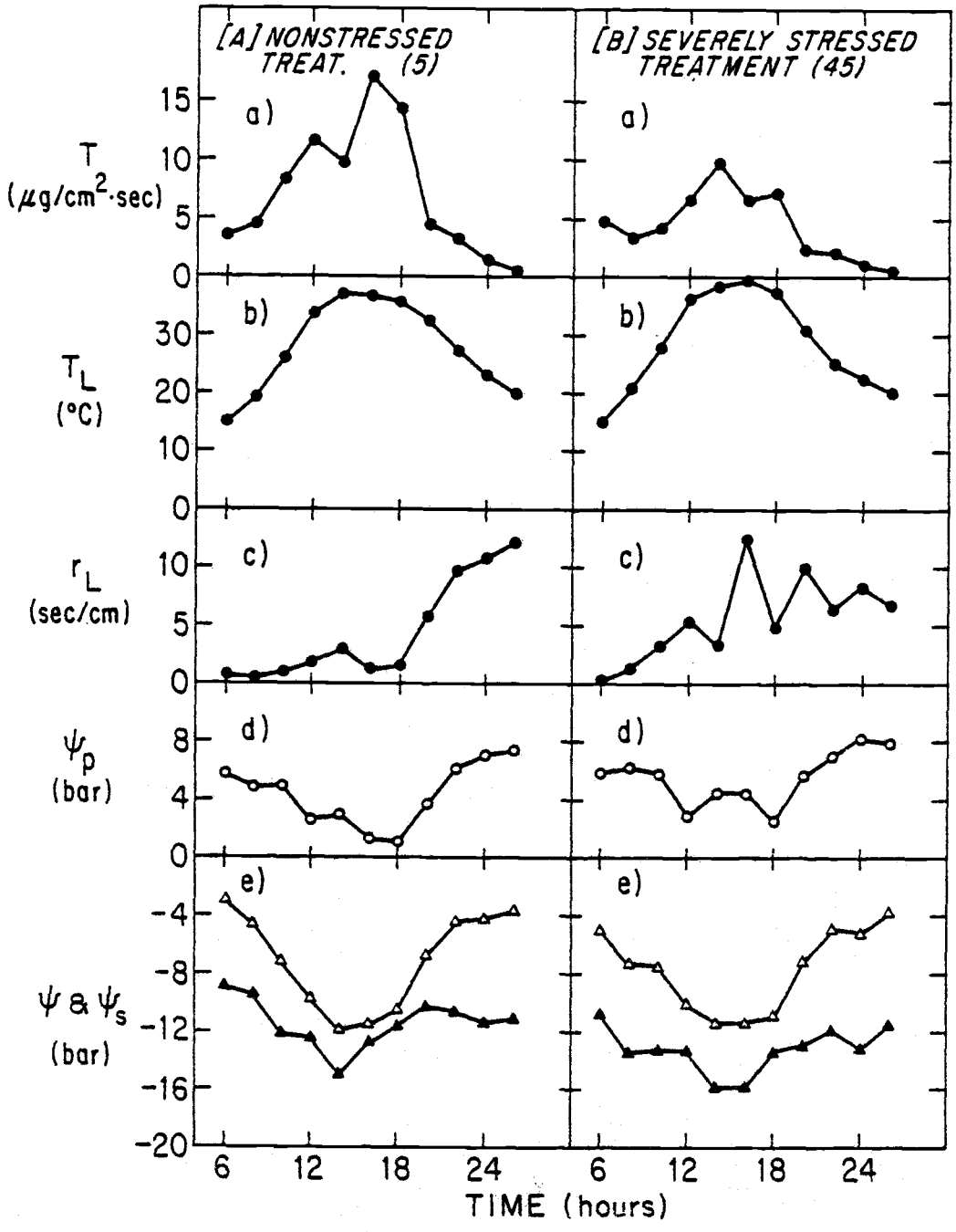

Figure 40. Diurnal course of the following parameters: (a) transpiration rates; (b) leaf temperature; (c) leaf diffusive resistance; (d) turgor pressure, and (e) leaf water potential ψ and osmotic potential ψ_s for the NS treatments five days after the last irrigation [A] and the SS treatment 45 days after irrigation [B]. Date were taken 50 days after planting of 1981 experiment.

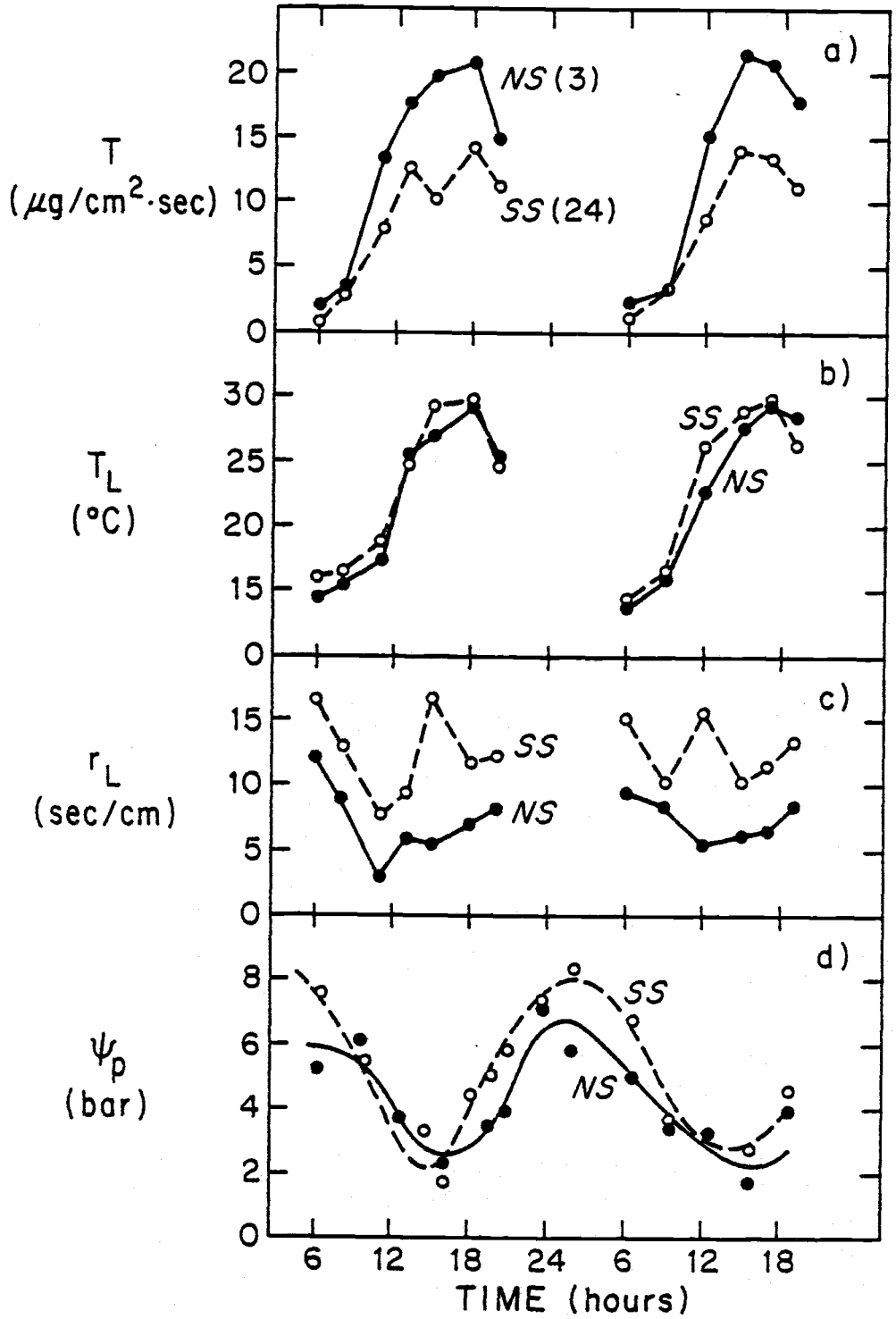

Figure 41. Diurnal course of the following parameters: (a) transpiration rate, (b) leaf temperature, (c) leaf resistance, (d) turgor pressure. Measurements were taken 29 days after planting of the NS treatment (solid line) and the SS treatment (dashed line) of 1981 experiment.

trends similar to those shown in Figure 38.

Due to the deposition of dew at dawn, the measurements of leaf diffusive resistance and other related parameters were only performed at sunrise. These parameters were not measured during the night as shown in Figure 41. Considering that the stomates were closed at night, there was no need for measuring these parameters. Treatment comparisons were made at mid-morning and early afternoon when the effects of different water supply conditions should be most evident. The leaf diffusive resistances were significantly higher for SS treatment at mid-day hours. However, transpiration rates for SS treatments were significantly lower during the early afternoon. There is a lag time of about two hours for the response of transpiration rate.

Leaf temperature profiles in Figures 40 and 41 show slight difference between treatments, with SS leaves slightly warmer for a few hours around noon. Leaf temperature (T_L) reaches a maximum in the period from 1400 to 1600 hours.

Results shown in Figures 37, 38, 40, and 41 emphasize the point discussed earlier of the ability of the stressed plants of adjusting the osmotic pressure component and maintaining turgor pressure at favorable level especially during the day. The maintenance of the turgor pressure in the SS treatment prevented the stomata from closing, keeping the process of exchange of CO_2 and water vapor with the atmosphere at a reasonable rate.

Relationships Between Leaf Resistance and Leaf Water Potentials

The previous discussion showed that the fully exposed leaflets never had extremely high values of r_L indicative of complete stomatal closure during the time course of the field experiments. However, in relative terms, the SS leaves had higher r_L values than those of the well watered treatments during most days. In order to drive stomates to closure, some plants were pulled and allowed to dehydrate. Measurements of Ψ, r_L, T_L and T were obtained every 5 to 10 minutes for a period of 2.5 hours. Leaf samples were collected for measurement of ψ_s as discussed earlier. Results are shown in Figure 42.

The values of leaf water potential remained comparable to those of field grown plants during mid-day hours for about two hours after detachment, then decreased rapidly to values lower than -20 bars. This result indicates low sensitivity of water potential to dehydration. The osmotic potential decreased for about 10 minutes then increased slowly to about 2 hours at which time a gradual decrease began. The immediate decrease in ψ_s can be explained by tissue dehydration that resulted in an increase of the concentration of the contained solutes. The gradual increase after that cannot be explained. The turgor pressure (Figure 42d) steadily decreased and approached zero about two hours after detachment. A few negative values for ψ_p were obtained. These can only be explained by the errors associated with measuring both ψ and ψ_s and also with estimating both the bound water fraction and the RWC of the tissues. There was an immediate and steady increase in leaf temperature and a sudden decrease in transpiration rate as

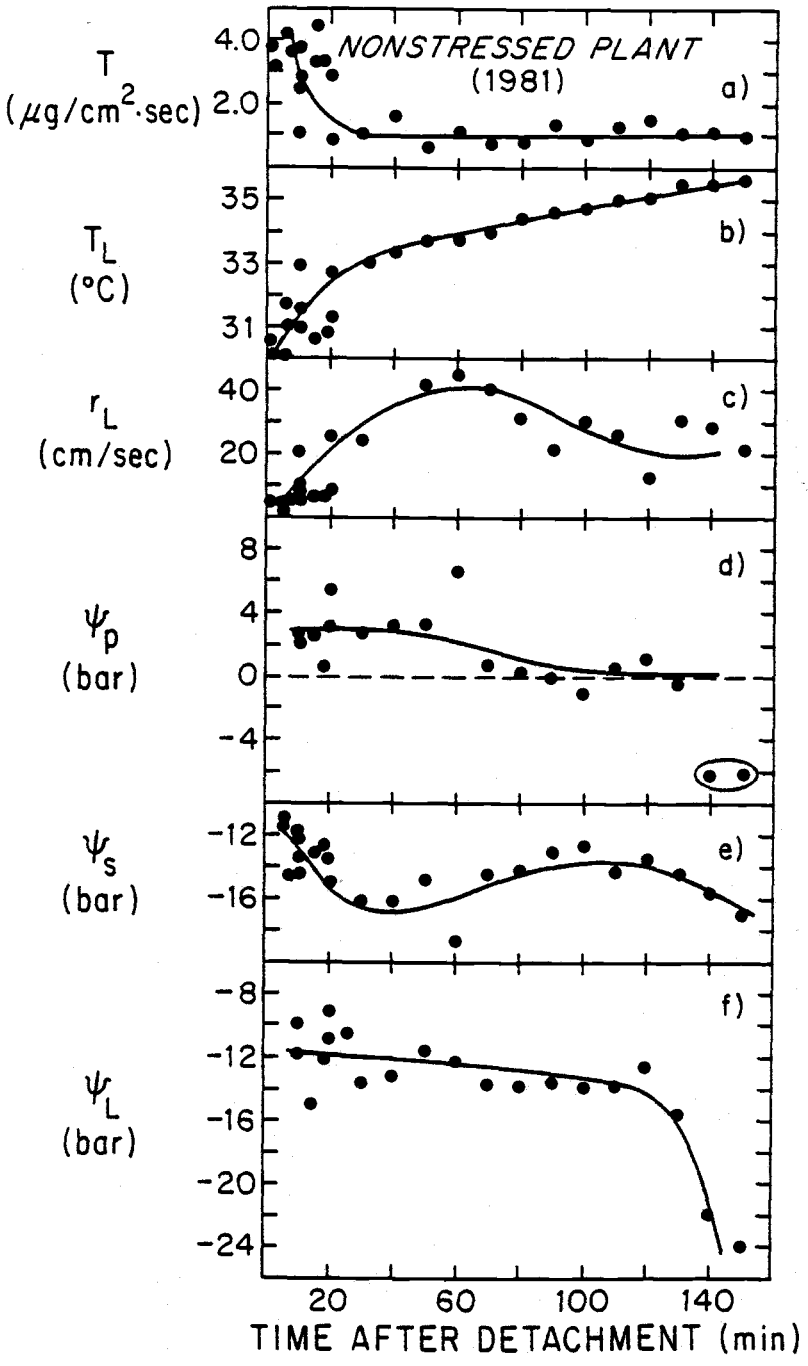

Figure 42. Transpiration rate (a), leaf temperature (b), leaf diffusive resistance (c), pressure potential (d), osmotic potential (e), and leaf water potential (f) as a function of time after detachment. Data points represent single measurements of treatment NS, 1981.

time of dehydration proceeded. The leaf resistance increased with time for about 10 minutes with later results during the period beginning about one hour after detachment showing great variability.

The data of stress experiment induced by cutting leaves from plants were plotted to estimate the threshold Ψ at which stomata close. Figures 43a and 43b show the relationships between leaf Ψ and r_L for treatments NS and SS, respectively. Data points represent both measurements from the stress induced experiment of Figure 42, represented by circles, and from the diurnal measurements, represented by triangles. Results indicate that for the upper, fully exposed leaves of snap beans grown under the conditions of this experiment, the threshold value of Ψ for stomatal closure is in the range from -10.5 to -12.5 and from -13.0 to -15.0 bars for the SS and NS treatments, respectively. Kanemasu and Tanner (1969) presented data for field grown snap beans showing a threshold value of -8.0 bars for adaxial (upper) surface stomata and a value of -12 bars for abaxial (lower) surface stomata. In our discussion we will only show the measurements for the lower (abaxial) surface of the leaf (as shown in Figure 43). Results of Figures 43a and b show that the SS treatment has slightly lower (more negative) threshold Ψ than that obtained for the NS treatment suggesting that prolonged stress preconditioned the plants. Thus, plants may be adapted to tolerate lower leaf Ψ without increasing leaf resistance. The threshold value of Ψ for stomatal closure can be changed by many factors. It varies with leaf age, growing conditions, stress history and with the rate of stress development (Brown, 1974; Jordan et al., 1975).

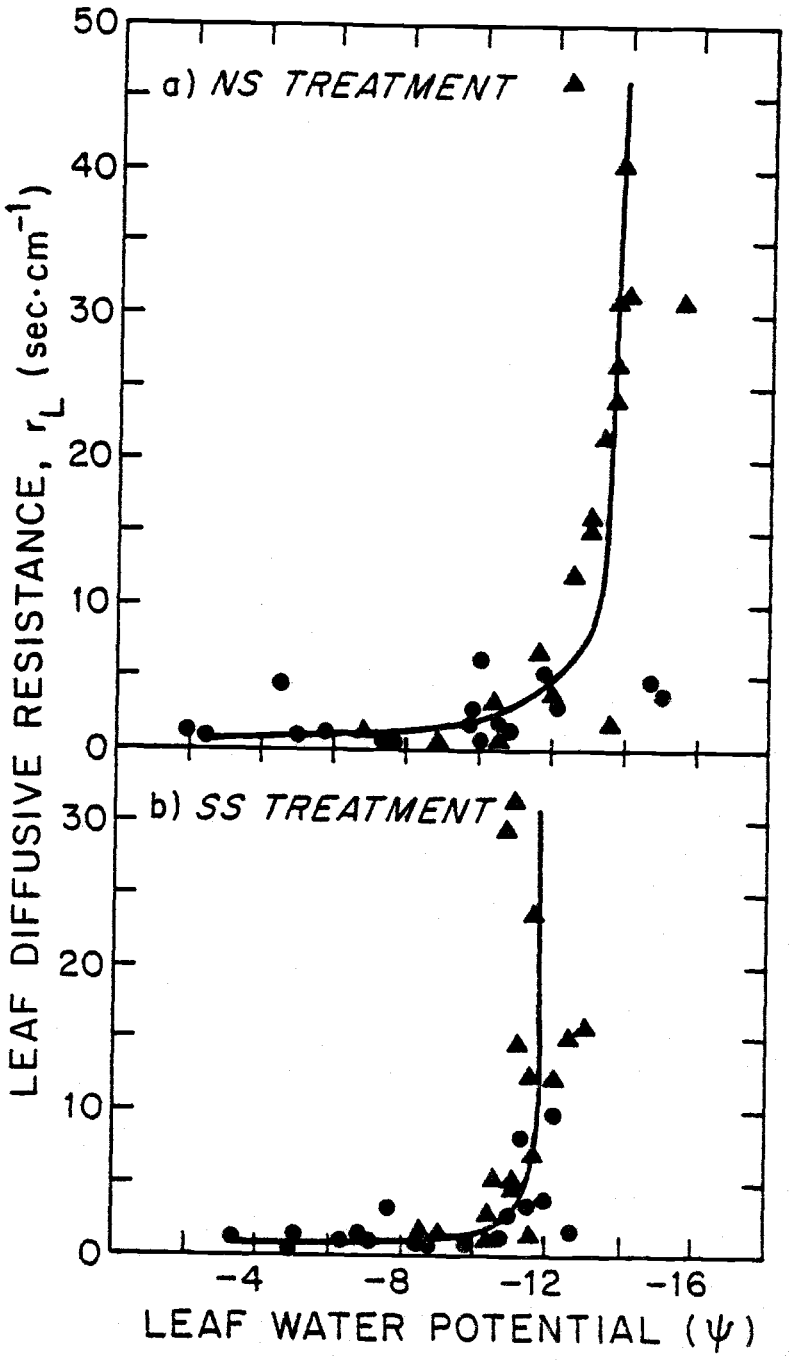

Figure 43. Relationships between leaf diffusive resistance r_L and leaf water potential Ψ for NS treatment (a) and SS treatment (b). Circles are data points obtained from field measurements and triangles are data points obtained from the experiment with detached leaves. Lines are fitted by eye.

Since stomatal opening and closing processes are related to the turgor differences between the guard cells and surrounding cells, Ψ_p may be a better parameter to be considered. Figure 44 shows the relationship between r_L and Ψ_p for both NS and SS treatments. Results show that correlation of Ψ_p with r_L is not simple. Variation is greater for the SS treatment. Figure 44 suggests that under the conditions of this experiment a turgor pressure of less than 2 bars was associated with stomatal closure. The variability of the correlation between Ψ_p and r_L is an indication of the error that is made in correlating the bulk leaf Ψ_p with stomatal closure. This averaging of Ψ_p of the leaf cells might be an over-simplification of a complex mechanism. These results lead us to conclude that the initiation of stomatal closure might not be limited to a fixed single value of Ψ_p or a narrow range of Ψ. This range might be affected by the ability of the leaf to adjust osmotically which modifies its turgor relations. In our experiment where stress was induced by detaching plants, leaves were stressed at a higher rate and were not allowed to adapt and adjust Ψ_s. Leaf resistance (r_L) increased dramatically at Ψ values of -12 bars and -14 bars, for SS and NS treatments, respectively (Figure 43). For field data the plants were exposed to slower rates of stress development and for longer periods of time. These plants, by lowering their Ψ_s of the exposed leaves, were able to maintain high Ψ_p values despite the low Ψ. This might have been the reason that stomatal closure was not observed. The transpiration rate is inversely proportional to the sum of leaf resistance and air boundary resistance and directly proportional to water vapor concentration difference between the cell and

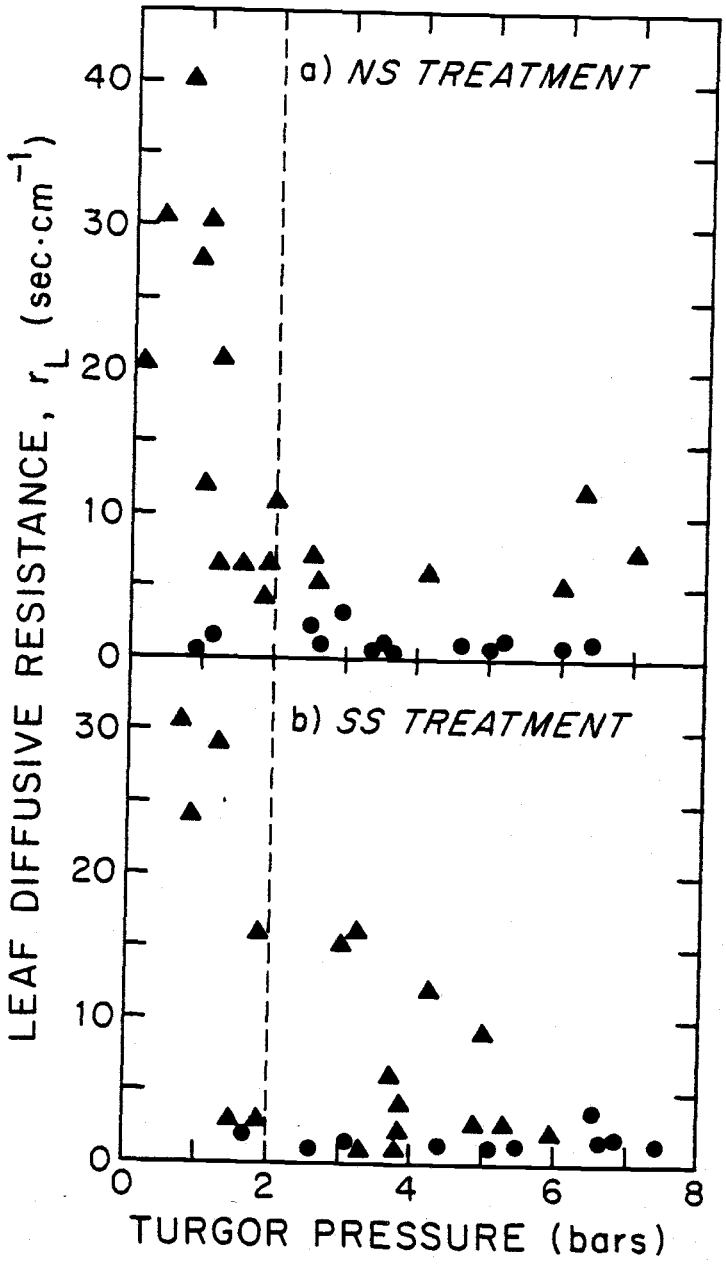

Figure 44. Diffusive resistance r_l as a function of turgor pressure Ψ_p for NS treatment (a) and for SS treatment (b). Data represent the same leaves as shown in Figure 43. Circles are data points obtained from field measurements and triangles are data points obtained from the experiment with detached leaves.

the air as given in Equation 2.

Figures 45a and b show the relationship between the transpiration rate and the leaf diffusive resistance measured by the steady state porometer. Data points represent leaf samples from the experiment of stress induced by detachment of leaves from plants. An exponential reduction of transpiration rate as the leaf diffusive resistance was found for both treatments. The response of transpiration rate was more pronounced for the SS treatment where at the same diffusive resistance of 10 $sec \cdot cm^{-1}$, the transpiration rates for SS and NS were 1.25 and 2.44 $\mu g \cdot cm^{-2} \cdot sec^{-1}$, respectively. The relationship described by equation 2 indicates that the same leaf diffusive resistance should give the same rate of transpiration if all other parameters are constant. Results shown in Figure 45a and b indicate that this relationship does not hold for the water stress treatments. These results could be explained by the fact the water stress in the severely stress treatment was long and severe enough to produce adverse effects on the configuration on the stomatal pore, the thickness of cell wall surrounding and the intercellular air spaces. Another important effect due to the severe water stress is the greater resistance of the mesophyll to the water in the liquid state which may become limiting to the process of evaporation of water molecules from the cell and eventually limit the process of transpiration.

Seasonal Changes of Plant Water Relations

The rate of water movement through the plant system is a function of a potential difference between the soil and the atmosphere. As the

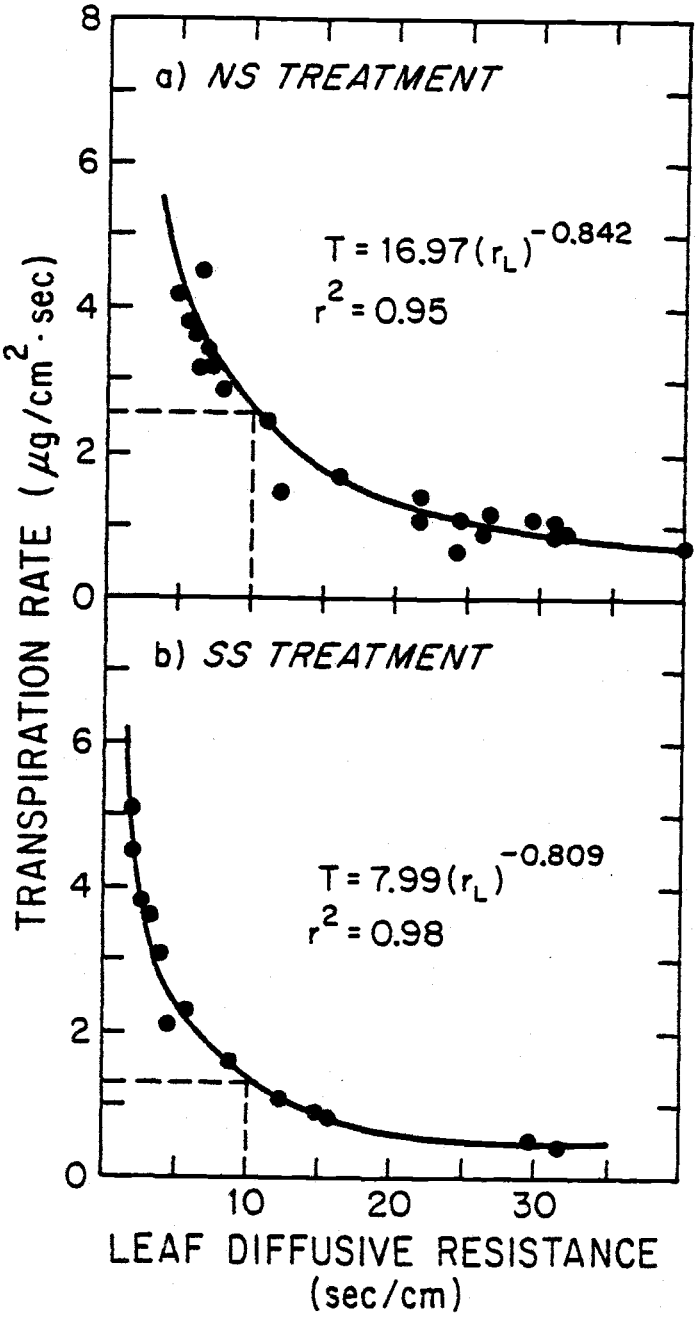

Figure 45. Transpiration rate as function of diffusive resistance based on data from the water stress induced experiment (detaching experiment) for NS treatment (a) and SS treatment (b).

plant grows, the distance that water has to move from the roots to the leaves increases. This implies that the gradient of water potential becomes steeper to meet evapotranspiration demand if constant resistance per unit length is assumed. According to this, leaf water potential (Ψ) may be expected to decrease as the season progresses. If no significant changes in the osmotic potential occur during the season, a loss of turgor will be certain.

As shown in Figures 32 and 33, minimum values of leaf Ψ occurred usually around mid-day hours in all treatments. Measurements were taken in young, fully expanded leaflets between noon and 1400 hours. These were averaged and plotted as a function of days from planting (Figures 46, 47, and 49). The diagrams show the mid-day average of Ψ, Ψ_s, and Ψ_p for NS, GS, and SS treatments, respectively. The curves for the three treatments indicate an initial increase in Ψ, as well as Ψ_s up to about 42 to 45 days after planting. This change is associated with the flowering stage which occurs at this time. The course of Ψ_s during the season allowed the plants to keep a positive turgor pressure in spite of the lower leaf Ψ. The physiological significance of this change during flowering is not clear.

Figure 49 shows a comparison between the irrigated (NS) and the non-irrigated (SS) treatments. Small differences were observed in leaf Ψ measurements. However, the variability is so great that it is impossible to make definitive conclusions. The seasonal mid-day Ψ_s values throughout the season with the maximum difference being at flowering. As a result, mid-day turgor pressure values were more or less constant throughout the season with more fluctuation late in the

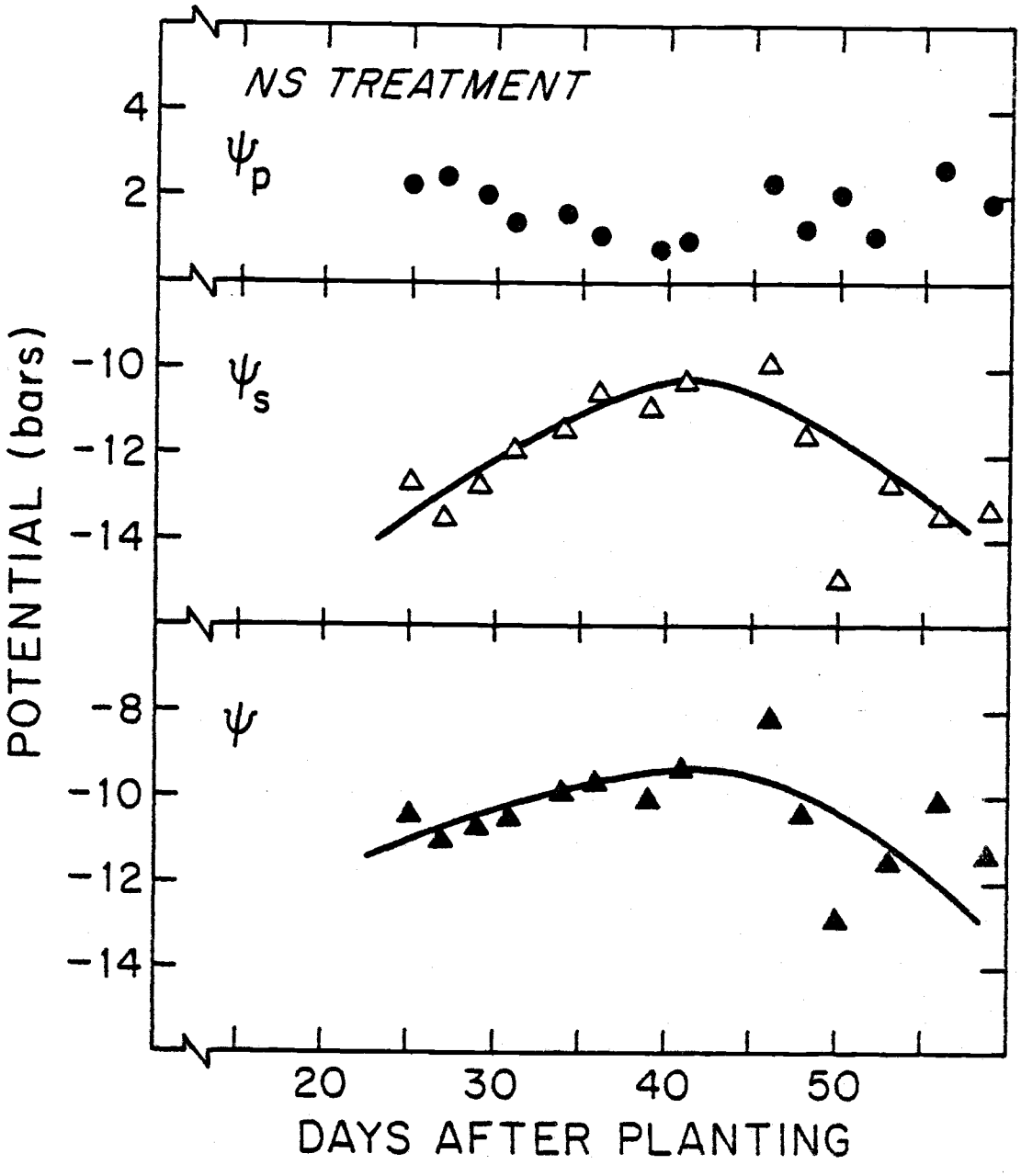

Figure 46. Seasonal trends of leaf Ψ, osmotic potential Ψ_s and pressure potential of the NS treatment. Each point is the average of 3 or 4 measurements on fully exposed leaves taken around mid-day (noon to 1500 hours).

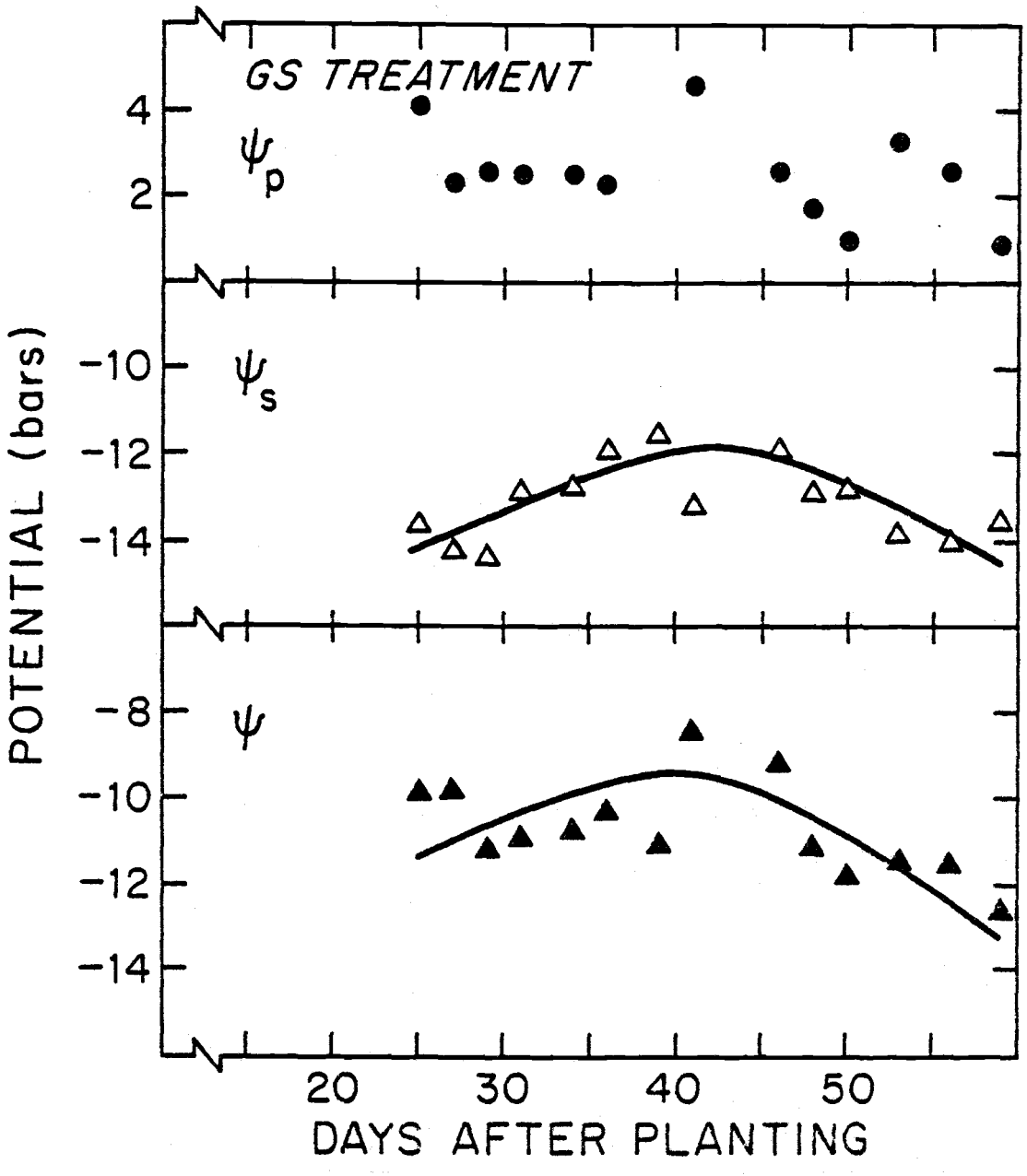

Figure 47. Seasonal trends of leaf Ψ, osmotic potential Ψ_s, and pressure potential of the GS treatment. Each point is the average of 3 or 4 measurements on fully exposed leaves taken around mid-day (noon to 1500 hours).

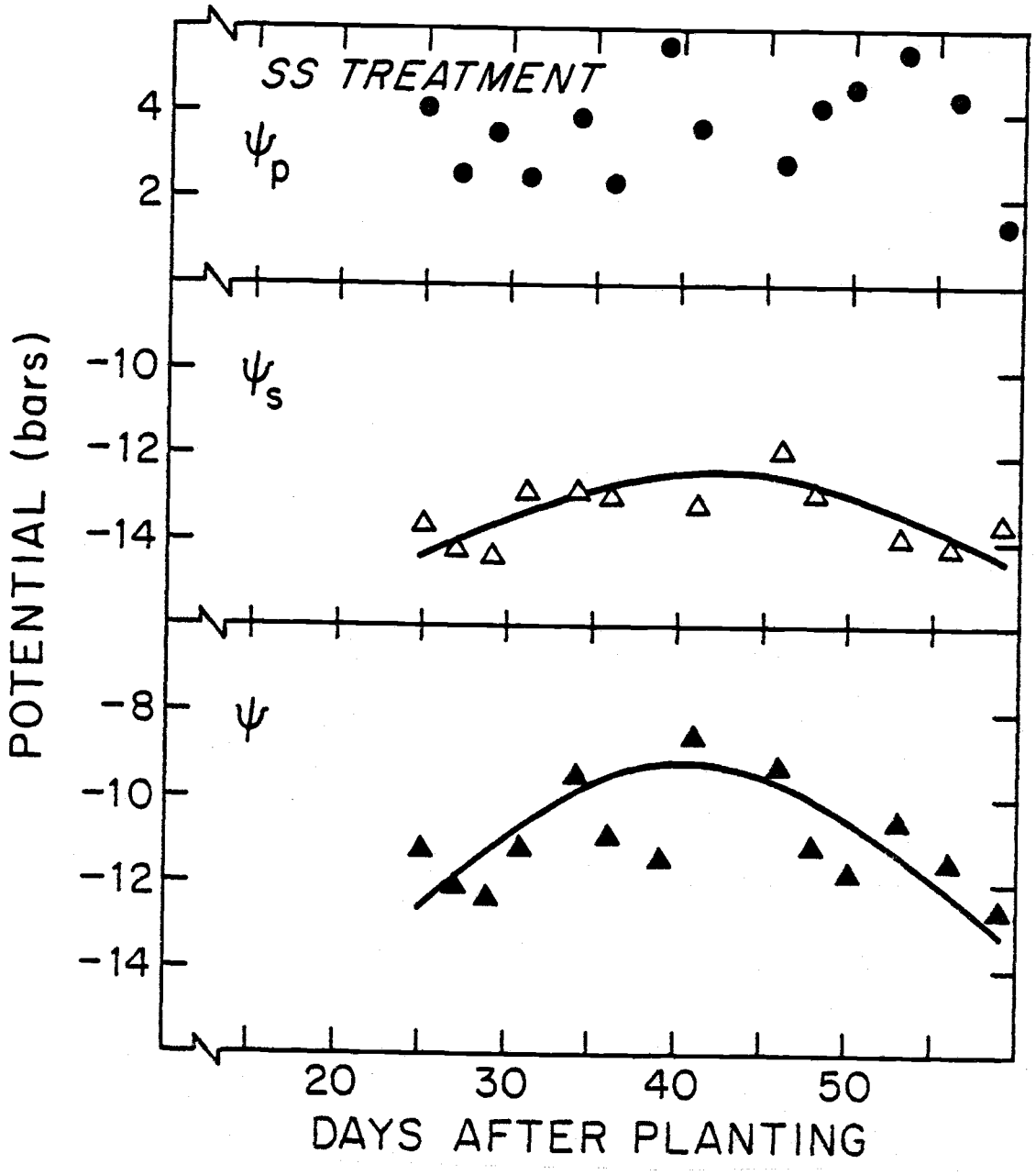

Figure 48. Seasonal trends of leaf Ψ, osmotic potential Ψ_s, and pressure potential of the SS treatment. Each point is the average of 3 or 4 measurements on fully exposed leaves taken around mid-day (noon to 1500 hours).

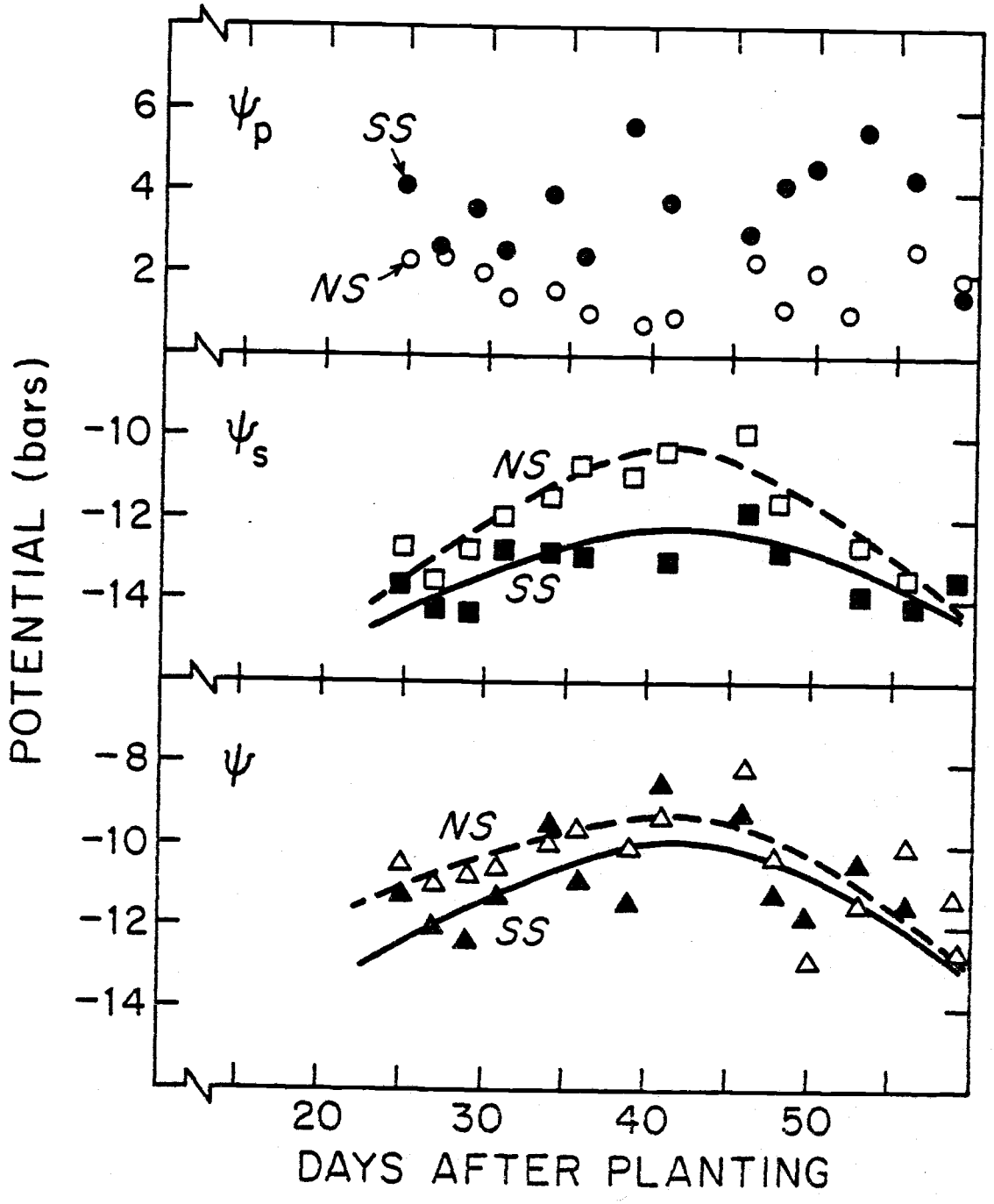

Figure 49. Treatment comparison of seasonal trends of Ψ, Ψ_s, and Ψ_p between NS and SS treatments. Data are the same as shown in Figures 46 and 48. Lines were fitted by eye.

season. The difference in the ability of Ψ_s adjustment with time may be responsible for the difference observed in the turgor pressure values. The SS treatment maintained on the average higher turgor pressure values at mid-day hours. Ψ_p value were varying between 0.8 and 2.6 and between 2.0 and 6.0 bars for NS and SS treatments, respectively.

Osmotic adjustment has been indicated as a mechanism for turgor maintenance on a daily basis. This data indicate that this adjustment is present and consistent throughout the season.

Effects of Water Stress on Crop Development and Yield

Plastochron Index as a Developmental Index

The leaf is a three dimensional structure that elongates, expands in area, and grows in thickness. This growth is the result of cell division, followed by cell expansion. Both of these processes depend on other related, vital events such as water and nutrient uptake, photosynthesis, synthesis of structural materials and metabolites, and transport of substances between cells. Water deficit is a critical factor in determining the rate of growth of leaves. Hsiao (1973) concluded that cell expansion and cell division are the most sensitive processes to water stress.

The leaf length has frequently been used in developmental studies, because it represents an important dimension of change in the morphology of the growing leaf and its change can be monitored with simple experimental procedures. A ruler or a caliper usually suffices for measurements of changes in length and width. A further advantage is

that these measurements can be repeated on the same leaf or plant without causing injury.

The use of chronological age as a time scale was of limited value in many of the developmental studies reported in the literature (Erickson, 1948; Erickson et al., 1957; and Michelini, 1958). These authors argue that individual plants are generally not genetically uniform and cannot be grown under the exact same growing conditions. Variability is usually so great that plants of the same age have reached quite different stages of development, while plants which are morphologically similar may be of quite different chronological ages. Erickson and Michelini (1957) suggested that these discrepancies can be minimized by using a developmental index as an indirect time scale. The "Plastochron Index" was then proposed to define a developmental stage of plants. They stated that:

> "A Plastochron is conventionally defined as the time interval between initiation of two successive leaves. It might be more broadly defined as the interval between corresponding stages of development of successive leaves, and one might choose initiation, maturity or any intermediate stage of development as the stage of reference."

The Plastochron Index for leaf length can be calculated according to an equation given by Erickson et al. (1957),

$$PI = n + \frac{\log L_n - \log L_r}{\log L_n - \log L_{n+1}}, \qquad (27)$$

where Pi is the Plastochron Index which is the age of the plant expressed in plastochrons, n is the serial number counting from the base of that leaf which is just longer than the reference length, L_r is the reference length in mm for which Erickson used 10 mm, L_n is the

length of leaf n which is just longer than L_r in mm, L_{n+1} is the length of leaf n+1 which is just shorter than L_r in mm, and log is the logarithm to the base 10. The natural logarithm could also be used.

The Plastochron Index of a plant can be estimated easily by counting the number of leaves on the same plant which are longer than L_r and measuring the lengths of leaves n and n+1, which are just longer and just shorter than L_r, respectively. The values so obtained are then substituted into equation 27. To simplify estimation of the fractional values of equation 27, Erickson (1960) developed a nomogram that utilizes the reference length of 10 mm. Other nomograms could be constructed for other reference lengths. Coleman et al. (1976) stated that the length to be chosen as the reference should be long enough for the leaf to be measured without causing injury. However, it should be limited to the range of the early stage of development, the exponential growth stage.

Erickson et al. (1957) also expressed the PI by

$$PI = \frac{\ln(Lo) - \ln(Lr)}{P} + \frac{r}{P} t , \qquad (28)$$

where r is the relative rate of elongation of a leaf (day^{-1}), P is the natural logarithm of the ratio of lengths of two successive leaves ($\ln \frac{Ln}{Ln+1}$). r/P is the slope of the PI vs. time, Lo is the length of the leaf at time zero, Lr is the reference length, and ln is the natural logarithm.

Equation 28 is a better and more useful expression because it indicates that PI can be related linearly to the chronological age of the plant with the value r/P as the slope and the ln(Lo) - ln(Lr)/P

as the intercept. The reciprocal of the slope indicate the value of P/r in units of days per plastochron which is an expression of the plastochron duration.

Erickson and Michelini (1957) also proposed a leaf plastochron index which is applicable to only one leaf. It is obtainable by subtracting the serial number of the leaf in question from the PI of the plant which bears it.

$$LPI = PI - a , \qquad (29)$$

where (a) is the serial number of the desired leaf. A leaf which is exactly equal in length to the reference length has a LPI of zero, leaves that are longer or shorter than the reference length have positive or negative plastochron ages, respectively.

Table 6 shows the leaf lengths, in mm, of successive leaves of a bean plant on indicated days after planting (DAP). The same information is shown in Figures 50 and 51 where the leaf length and log of leaf length are plotted against time. Each growth curve shown in Figures 50 and 51 applies to a single leaf. Figure 52 shows an idealized geometric representation of straight line portions of three growth curves from Figure 51. The diagonal lines represent parts of the leaf length curves and the solid horizontal line is the logarithm of the reference. A vertical line is drawn at time (t) when leaf n is longer and leaf n+1 is shorter than the established reference length. The PI at time t is equal to the leaf number n plus a fraction of the plastochron index. The value of this fraction must be determined.

Note in Figure 52, that for triangles ABD and CBE, AB/AC = DB/DE.

TABLE 6. Lengths of leaves in mm of a plant from the NS treatment during the period 14 to 60 days after planting. Measurements were taken around 7:00 to 9:00 a.m. with a plastic ruler to the nearest 1.0 mm.

DAP	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8	L_9	L_{10}	L_{11}	L_{12}	L_{13}	L_{14}	L_{15}	L_{16}	L_{17}	L_{18}	L_{19}	L_{20}
14	8																			
16	35	11																		
18	57	34	17																	
20	77	55	36	19																
22	95	74	58	38	23															
24	111	94	78	57	39	23														
26	126	112	99	75	53	38	21													
28	139	129	115	94	70	51	35	18	12											
30	150	142	133	110	86	69	54	31	24	16	10									
32	159	151	145	128	100	84	69	44	38	28	21	10								
34	165	156	157	140	113	98	85	58	52	41	36	24								
36	168	158	167	154	123	112	100	72	65	50	46	35	15							
38	170	160	174	163	132	124	110	84	77	60	55	43	25	17						
40	171	162	181	168	137	130	116	94	87	69	63	50	35	26	12					
42	172	162	184	171	141	134	120	99	93	76	69	56	44	34	19	9				
44	172	164	186	174	144	136	124	101	96	82	75	60	50	42	26	16				
48	173	165	188	177	150	140	128	104	100	90	82	68	59	53	37	28	16	7		
52	174	166	192	180	154	142	134	106	102	96	88	76	66	60	46	40	25	16	12	
56	176	168	194	183	159	146	138	108	104	98	94	81	74	68	57	50	40	28	24	12
60	176	169	196	186	162	148	142	109	105	101	98	88	80	74	69	60	55	46	42	32

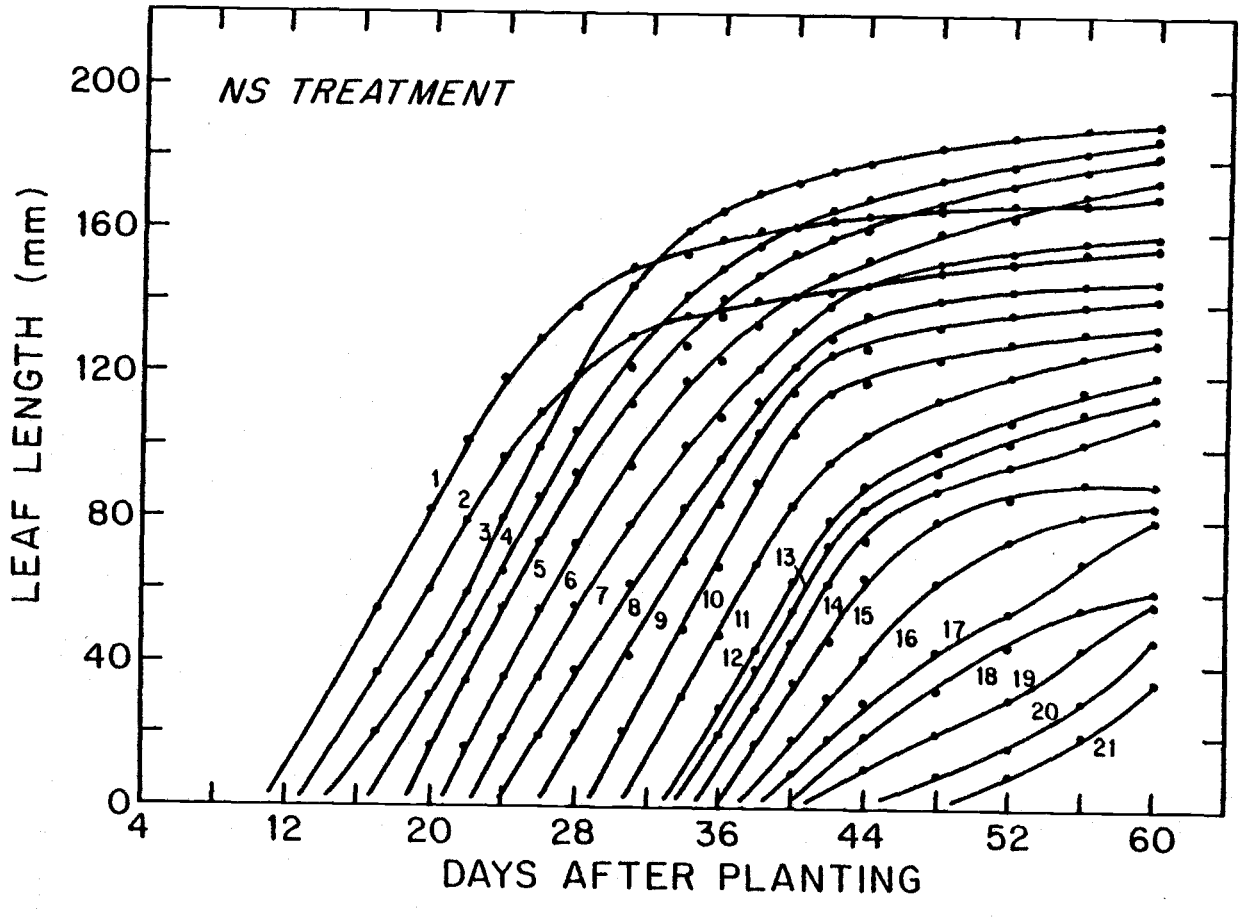

Figure 50. Lengths of successive leaves of a plant from the NS treatment plotted against days after planting. Each curve applies to a single leaf of the same plant. Serial number of leaves are indicated.

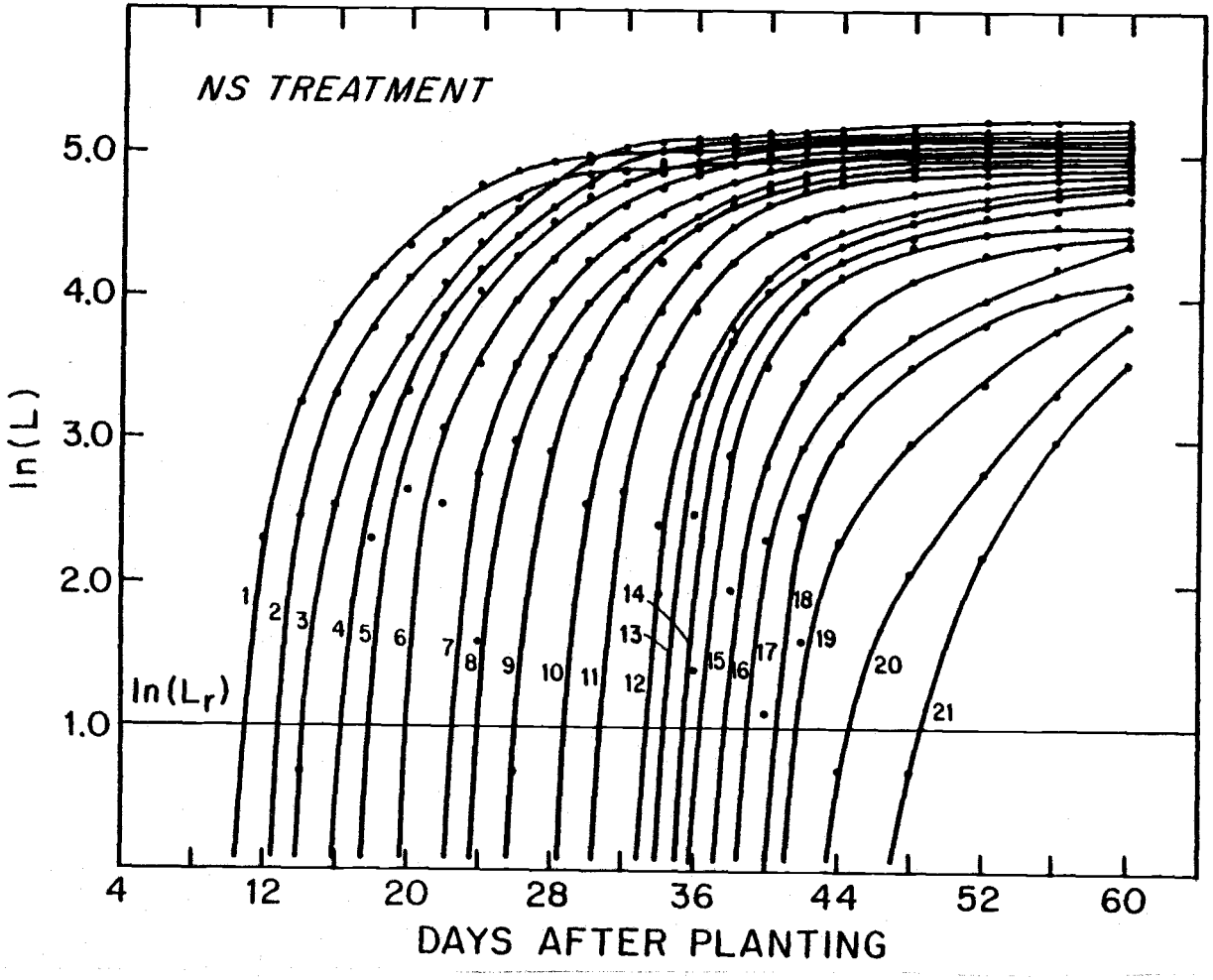

Figure 51. Logarithm of lengths of successive leaves of the sample plant shown in Figure 50, plotted against time. Each curve applies to a single leaf of the same plant. Serial numbers of the leaves are indicated.

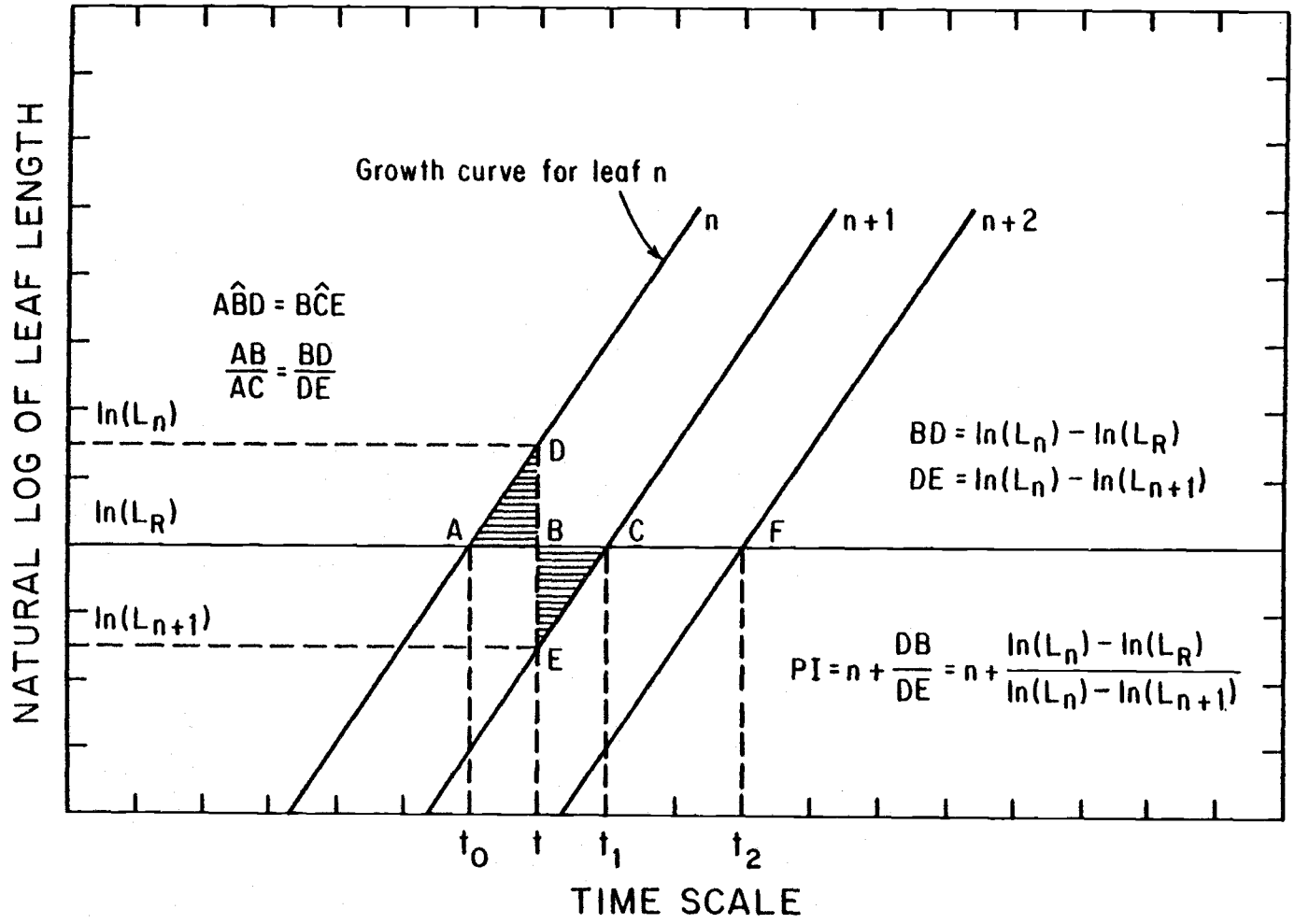

Figure 52. An idealized representation of the relationship between natural log of the leaf length and time for leaves from a single plant. Each diagonal line represents the growth of a single leaf. Three consecutive leaves are shown. The reference length is indicated by the solid horizontal line (ABCF).

Thus the value of the plastochron index of time (t) is equal to $n + \frac{AB}{AC}$. However, the ratio between the natural logarithms of the leaf lengths before and after the specified time, where DB equals $\ln(L_n) - \ln(L_r)$ and DE is $\ln(L_n) - \ln(L_{n+1})$. The fractional plastochron therefore can be given as:

$$PI = n + \frac{DB}{DE} = n + \frac{\ln(L_n) - \ln(L_r)}{\ln(L_n) - \ln(L_{n+1})}, \qquad (30)$$

This equation is equivalent to equation 27 and can be used to calculate the PI at any time throughout the growing season.

Computation of the PI

Consider day 28 after planting of the data shown in Table 4 and Figure 51. On this day the plant has 10 leaves that can be identified and measured, so that the plastochron index has a value slightly greater than 10. The value of $\ln(L_{10})$ on the day can be estimated from Figure 51 and is equal to 1.35. From the same diagram $\ln(L_{11}) = 0.70$, since $\ln(L_r) = 1.0$,

$$PI = 10 + \frac{1.35 - 1.00}{1.35 - 0.70} = 10.54.$$

Table 7 shows values of the PI during the period from 14 to 50 days after planting. Figure 53 shows the PI as a function of DAP. The PI seems to change linearly with time through most of the vegetative growth stage with a rate of 0.47 plastochrons per day. Starting about 37 DAP, the slope of the line of PI vs DAP seems to decrease slightly. This is the period during which flowering occurred.

TABLE 7. Values of the PI for one plant from the NS treatment. The PI was obtained by equation 30. Reference length - 2.72, $\ln(L_r) = 1.0$.

DAP	Serial number n	$\ln(L_n)$	$\ln(L_{n+1})$	PI
14	1	2.0	0.75	1.8
16	3	2.4	0.95	3.97
18	4	1.65	0.00	4.39
20	5	1.60	0.40	5.5
22	6	2.0	0.00	6.5
24	7	1.45	0.00	7.31
26	8	1.55	0.85	8.79
28	10	1.35	0.70	10.54
30	12	1.00	0.00	12.00
32	12	2.30	-0.10	12.54
34	13	1.30	0.50	13.38
36	14	1.95	1.00	14.49
38	15	1.30	-0.25	15.19
40	16	1.00	0.00	16.00
42	16	2.35	0.8	16.87
44	17	1.95	0.5	17.66
46	18	1.65	0.00	18.39
48	19	1.15	-1.15	19.08
50	19	2.05	-0.25	19.58

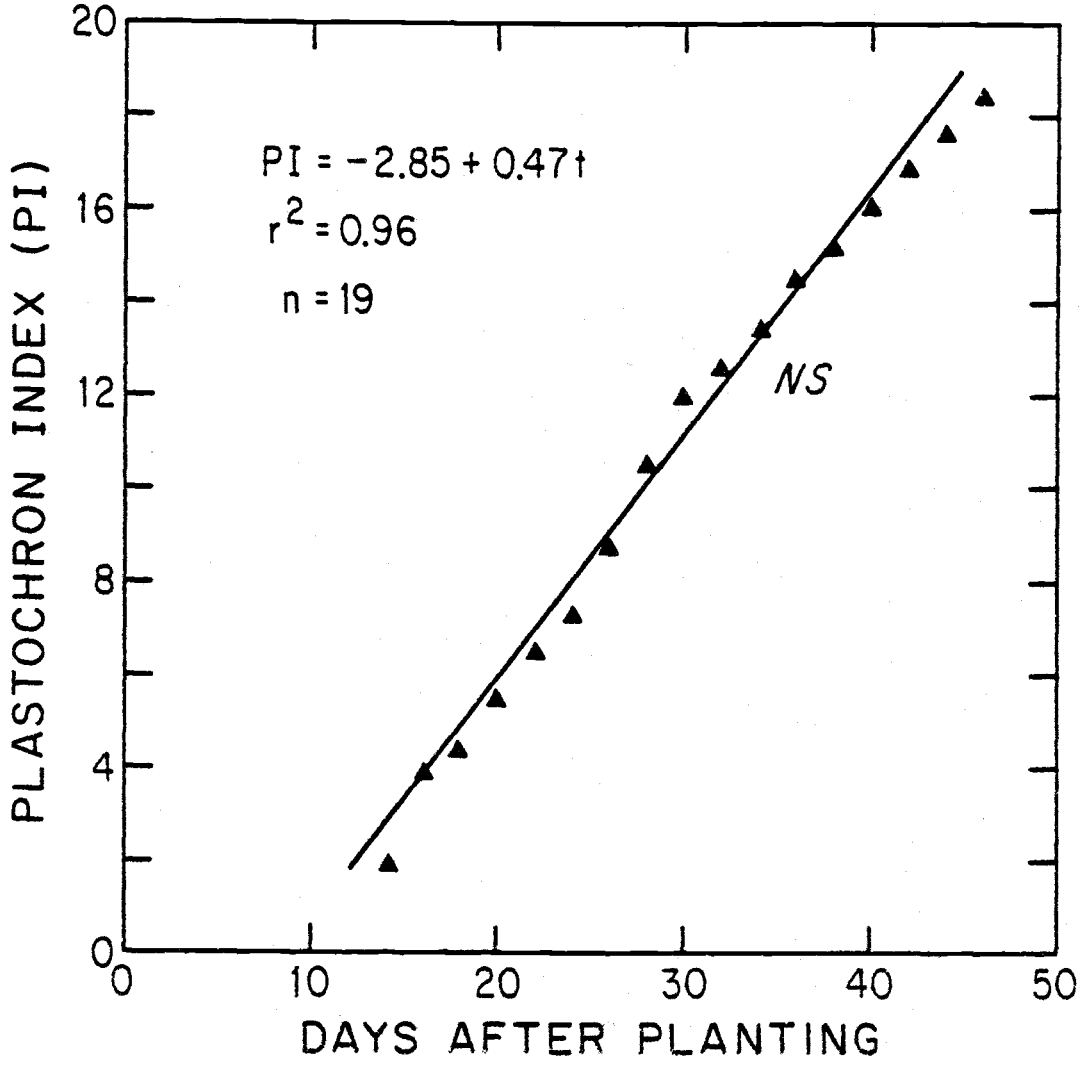

Figure 53. Plastochron index as a function of DAP. Based on data shown in Table 7.

Applications of PI and LPI

The practicality of the use of the PI was discussed by Michelini (1958). He demonstrated that the use of the PI offers many advantages over the use of chronological time in the interpretation of certain physiological processes during plant growth and development. His study showed a linear relationship between the PI and dry weight, fresh weight, and chlorophyll content, while extreme variability existed when these measurements were plotted against chronological time. Maksymowych et al. (1973) raised an appropriate question about the necessity of using the PI for developmental studies under highly controlled environmental conditions. Suntaree (1976) conducted an experiment in the growth chamber to characterize the development of two soybean cultivars by determining the PI as a function of time. The results showed that the Dare cultivar had longer but thinner leaves with a bigger leaf surface area at the same chronological age than the Hood cultivar which had a slightly higher PI value at the same age. However, the differences were not significant statistically. These results contradict the findings of Michelini (1958) about the superiority of the PI over the chronological age. For the purpose of the experiment, Suntaree (1976) selected the leaf chronological age to represent the developmental stage of the leaf rather than the PI. In another study under controlled conditions, Larson and co-workers (1971) developed a statistical model for the relationships between LPI and leaf length, leaf area and leaf dry weight for seedlings of different sizes of cottonwood. Results of their study showed that the number of primary vessels per internodi and per petiole was shown to be

linearly related to LPI. They theorized that it should be possible to predict such growth correlations as leaf area, leaf dry weight, number of vessels, and transitions from primary to secondary vessel formation. In a study of the differentiation process for the lamina in Xanthium Italicum, the LPI was used as the time scale (Maksymowych, 1959). The study concluded that the lamina of the tip of the 9th leaf was mature with the LPI of 2.3 and fully differentiated with the LPI of 4.2. However, its elongation proceeded until the LPI was 6.75. In another study of the same plant, it was concluded that the leaf was completely differentiated with LPI of 9.2 (Maksymowych et al., 1960). The concept of PI has also been used in the study of hormonal regulations (Maksymowych, 1973), chloroplast growth in Xanthium (Holowinsky et al., 1965), flower induction in Xanthium (Jacobs, 1972), to develop information needed for the construction of plant growth models for leaves and stem growth of soybeans (Hofstra et al., 1977), and to study the growth characteristics of Coenocytic Marine Algae Coulerpa (Chen, 1971, 1972). A very thorough and valuable review of two decades of PI use was published by Lamareaux et al. (1978).

The plastochron index has been productively applied to a wide variety of situations. However, its use in the study of the effects of soil water deficits on growth and development of higher plants has not been reported. The intent of this experiment was to test the index and its applicability in water stress studies conducted under growth chamber as well as under field conditions. The author hopes to stimulate discussion about the use of this valuable research tool and to contribute, if possible, to the vast amount of information concerning

water stress effects on plant growth and development.

Water Stress Effects on the Plastochron Index

The growth curves of bean leaves under conditions of adequate water supply can be represented by those of the control treatment (NS). Figures 54 and 55 show the leaf length as a function of the chronological age of plants from treatments NS and SS, respectively. Both figures show that the shape of the growth functions seem to change with age with a slower rate of elongation for the younger leaves. The leaflets of the stressed plant (SS) grew slower and showed greater variation than those of the NS treatment presumably as a result of water stress (Figure 55). The logarithms of length of leaflets of irrigated (NS) and non-irrigated (SS) plants were also plotted as a function of DAP (Figures 56 and 57). The growth curves shown in Figures 56 and 57 are parallel for the early part of growth. The leaves appear at approximately equal intervals. The leaflets of the stressed treatment appear with longer intervals. The reference length was chosen equal to 2.718 mm so that $\ln(L_r) = 1.0$. This value is smaller than the value of 10 to 20 mm suggested by Erickson et al. (1957).

The plastochron indexes of treatments NS, GS, and SS are plotted as a function of DAP in Figure 58. The lines shown in Figure 58 are linear with r^2 values exceeding 0.99. Departure from linearity generally occurs when the plants enter the reproductive stage. Deviation from linearity during the vegetative growth stage can be attributed to the fact that some leaves appear together and have nearly equal lengths

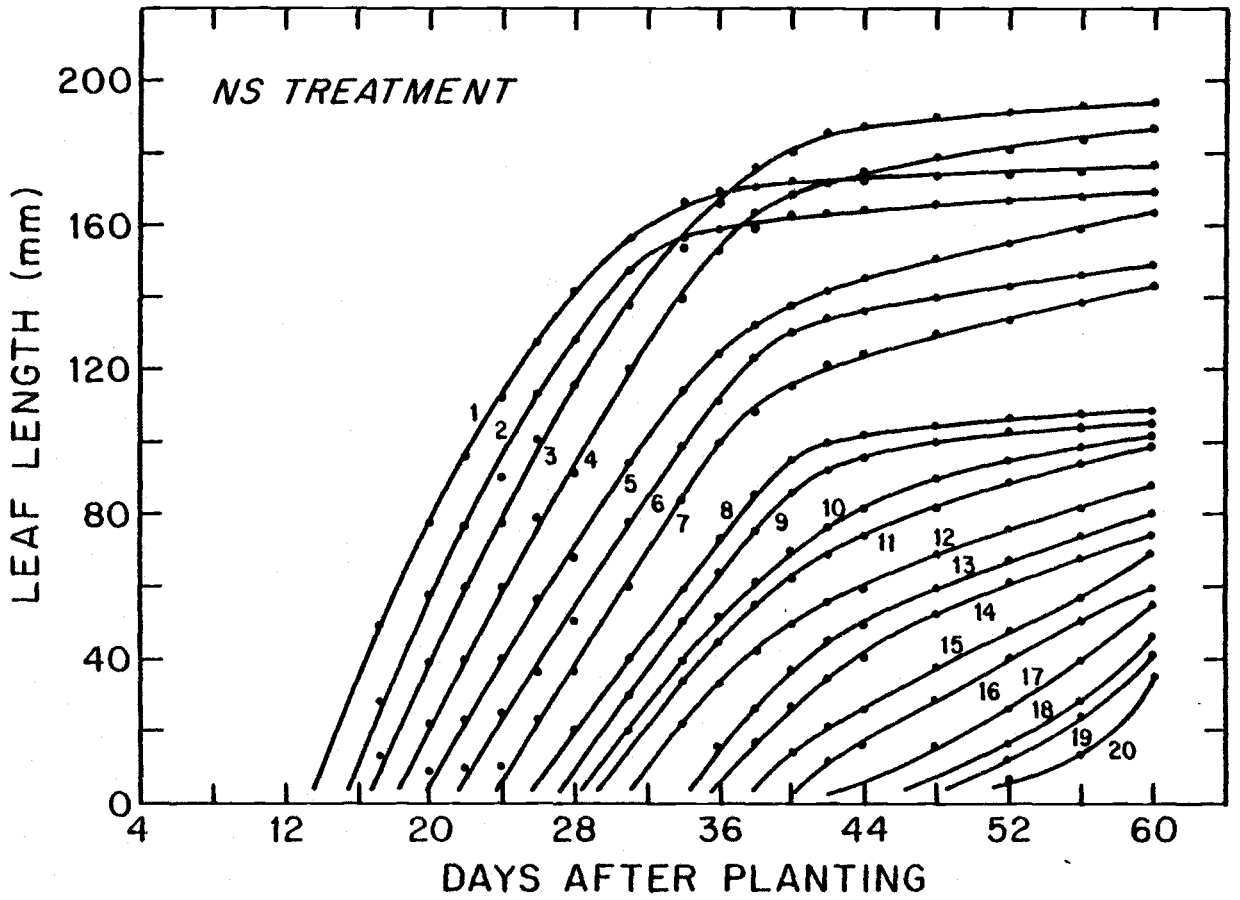

Figure 54. Lengths of successive leaves of a plant from the NS treatment plotted against days after planting. Each curve applies to a single leaf of the same plant.

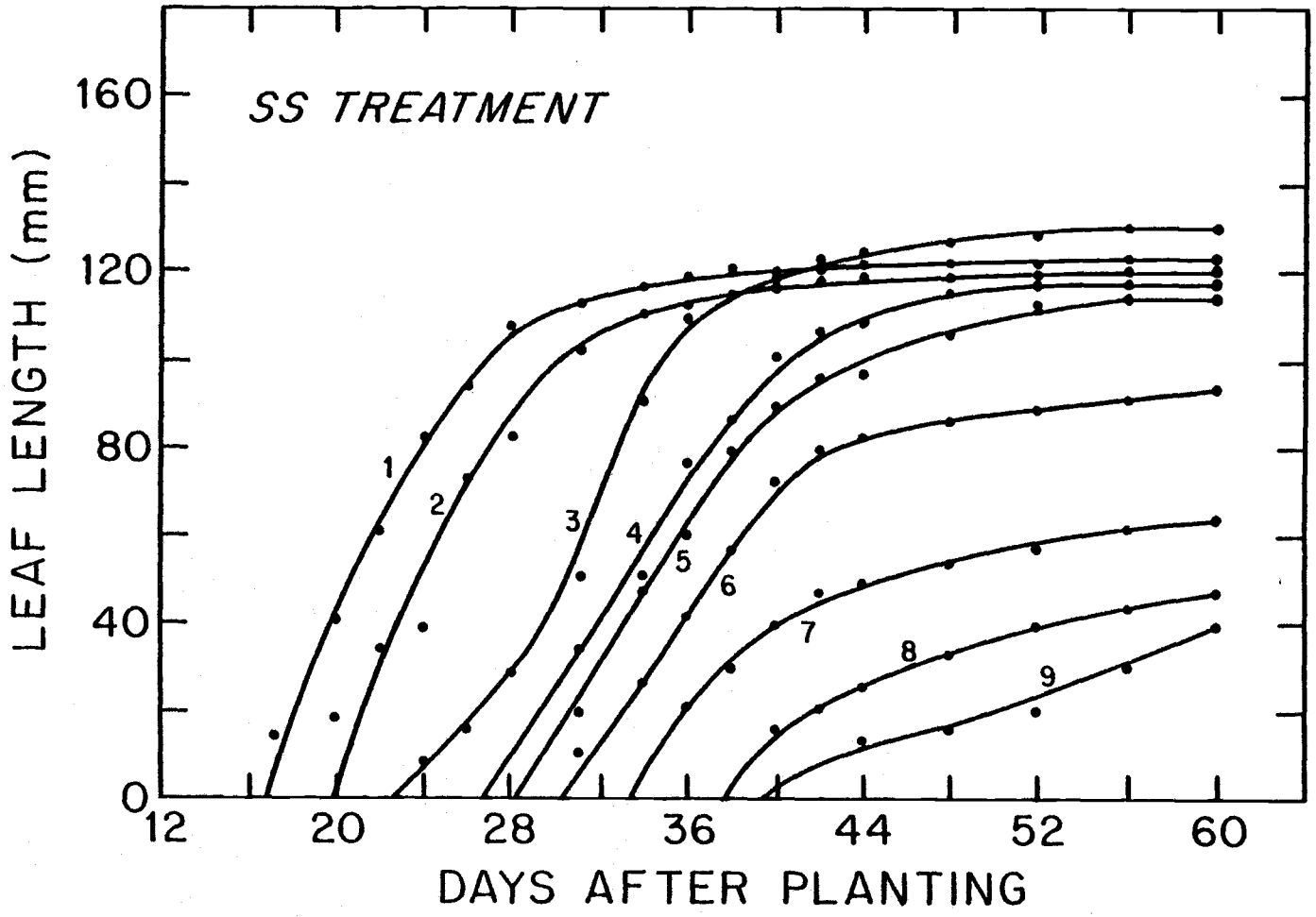

Figure 55. Length of successive leaves of a plant from the SS treatment plotted against days after planting. Each curve applies to a single leaf of the same plant.

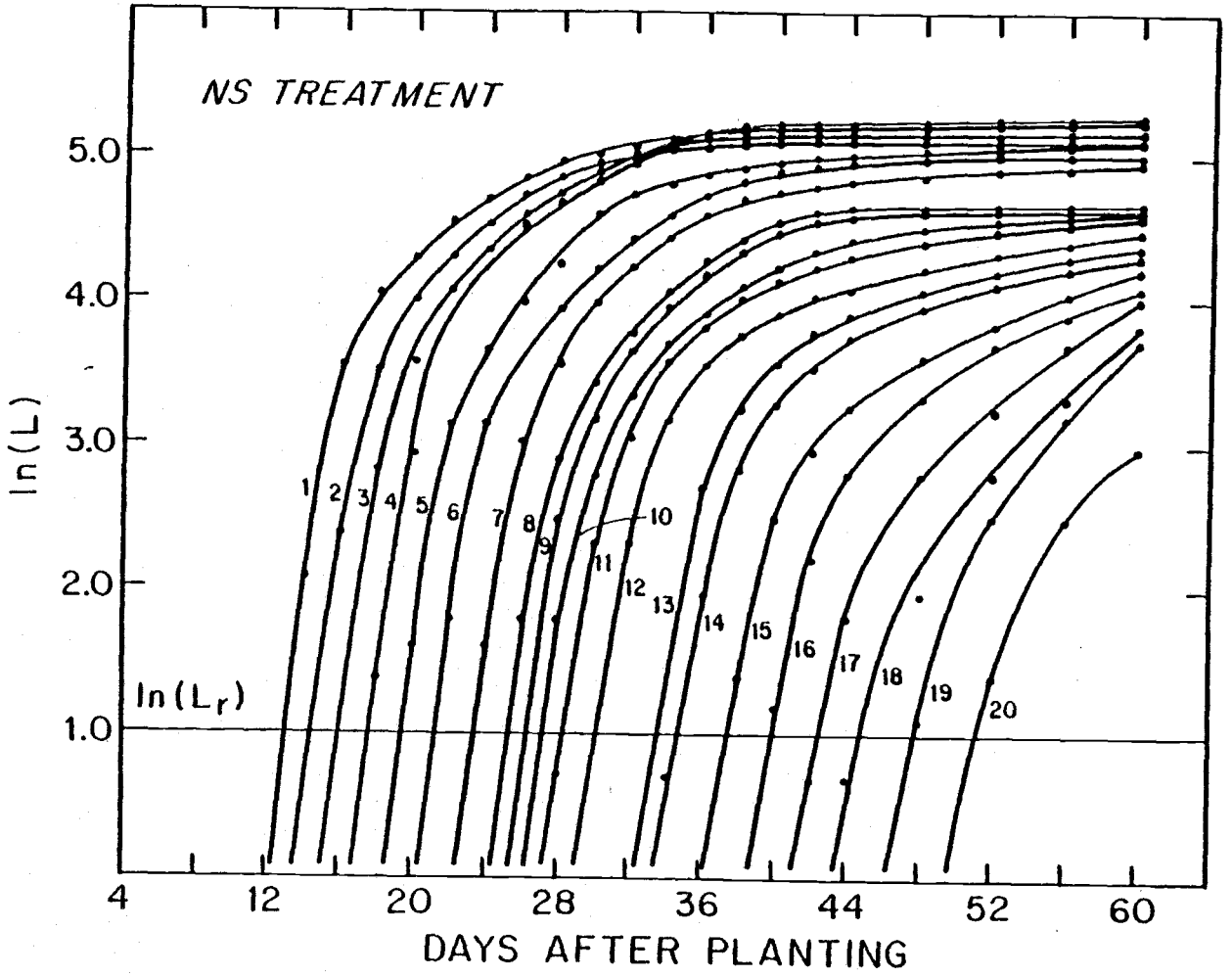

Figure 56. Logarithms of leaf lengths shown in Figure 54 plotted against time.

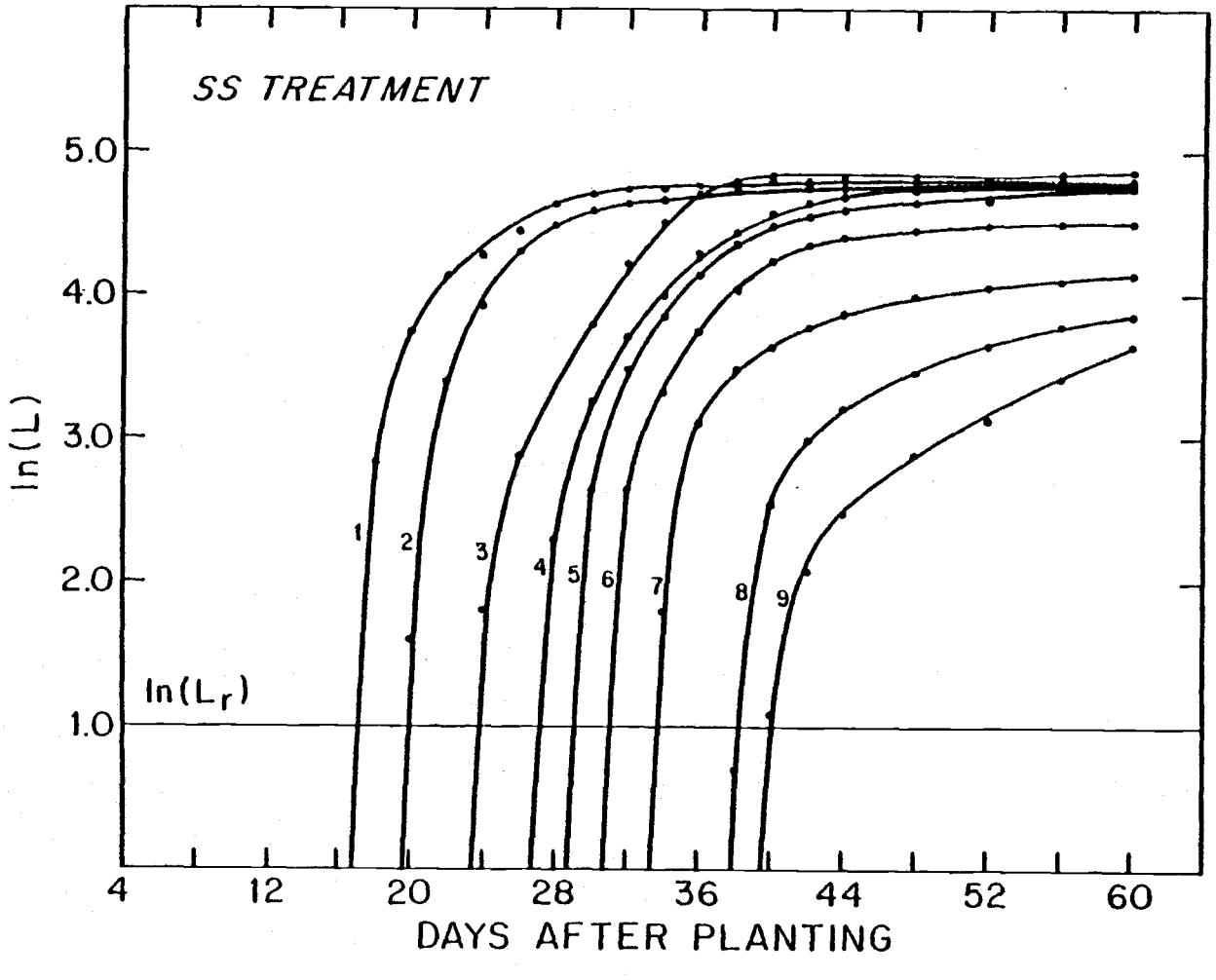

Figure 57. Logarithms of leaf lengths shown in Figure 55 plotted against time.

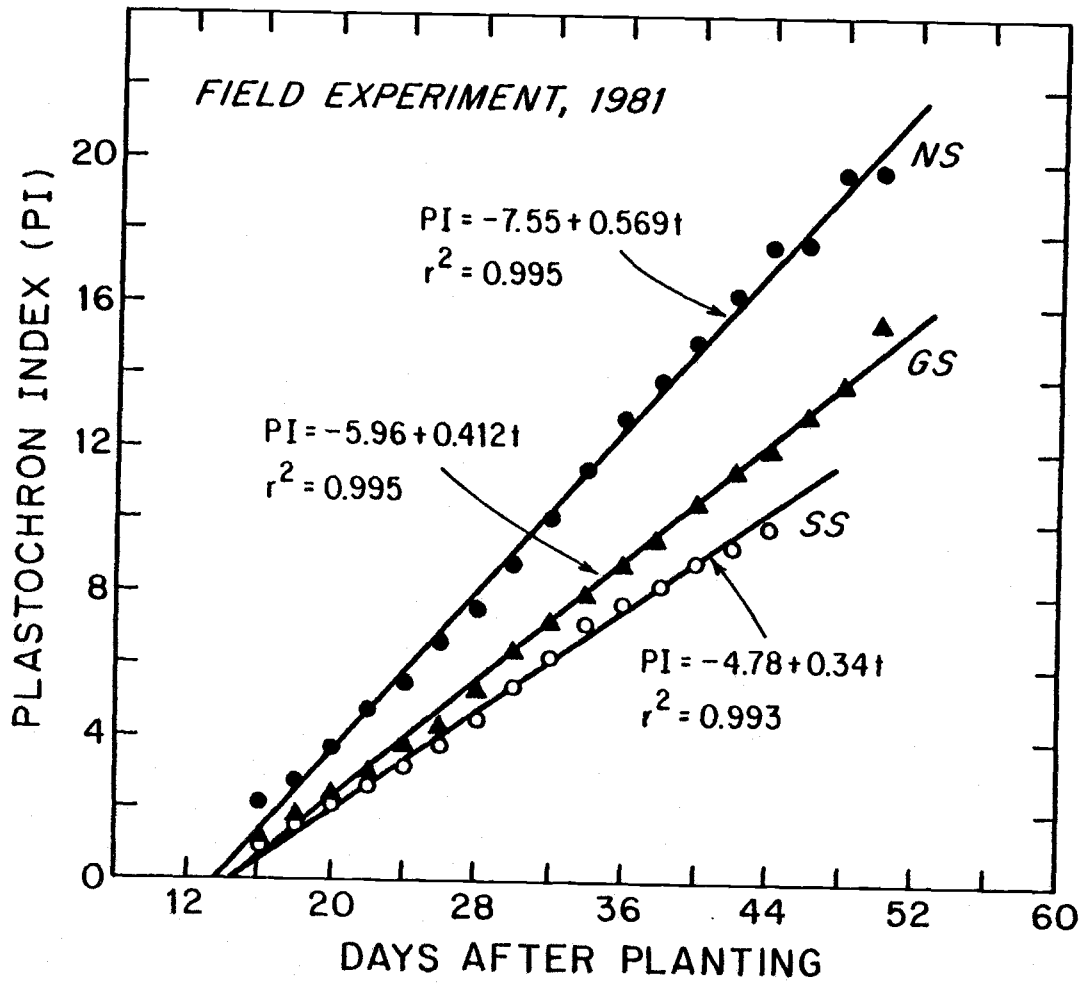

Figure 58. Plastochron index PI as a function of days after planting for treatments NS, GS, and SS. Data points represent an average of 12 measurements of the 1981 field experiment.

throughout their development. Also, some leaflets may have a plastochron duration shorter than the ones before and after it. Slopes of the curves in Figure 58 are 0.559, 0.412, and 0.340 plastochrons/day for treatments NS, GS, and SS, respectively. Slopes of similar graphs pertaining to the growth chamber experiments (Figure 59) are much lower, namely 0.165 and 0.104 plastochron/day for the non-stressed (NS) and severely stressed (SS) treatments, respectively. These results indicate that water stress reduces the value of the slope drastically both in the field and the growth chamber.

Table 8 summarizes the values of the slope for both growth chamber and field experiments. The plastochron durations are the reciprocals of the slopes of the lines given in Figures 58 and 59. The plastochron duration values were 42 $\pm$ 11.6, 58 $\pm$ 11.4, and 71 $\pm$ 8.8 hours for treatments NS, GS, and SS, of the field experiment, respectively. The plastochron duration of the SS treatment was 1.65 times greater than that of the NS treatment. In the growth chamber, the severely stressed (SS) treatment had a plastochron duration 1.59 times greater than the non-stressed treatment. These results indicate that water stress delays leaf initiation and also decreases the rate of cell enlargement and cell division after initiation. This has been documented frequently (Hsiao, 1973). Erickson et al. (1957) reported a standard error of 0.018 plastochrons or 0.018 x 24 = 0.43 hr, another study reported an error of a few hours (Coleman and Greyson, 1976). In our study, the results show standard error values of 11.64, 11.42, and 8.78 hours for the NS, GS, and SS treatments of the field experiment, respectively. However, for the growth chamber experiment, the standard

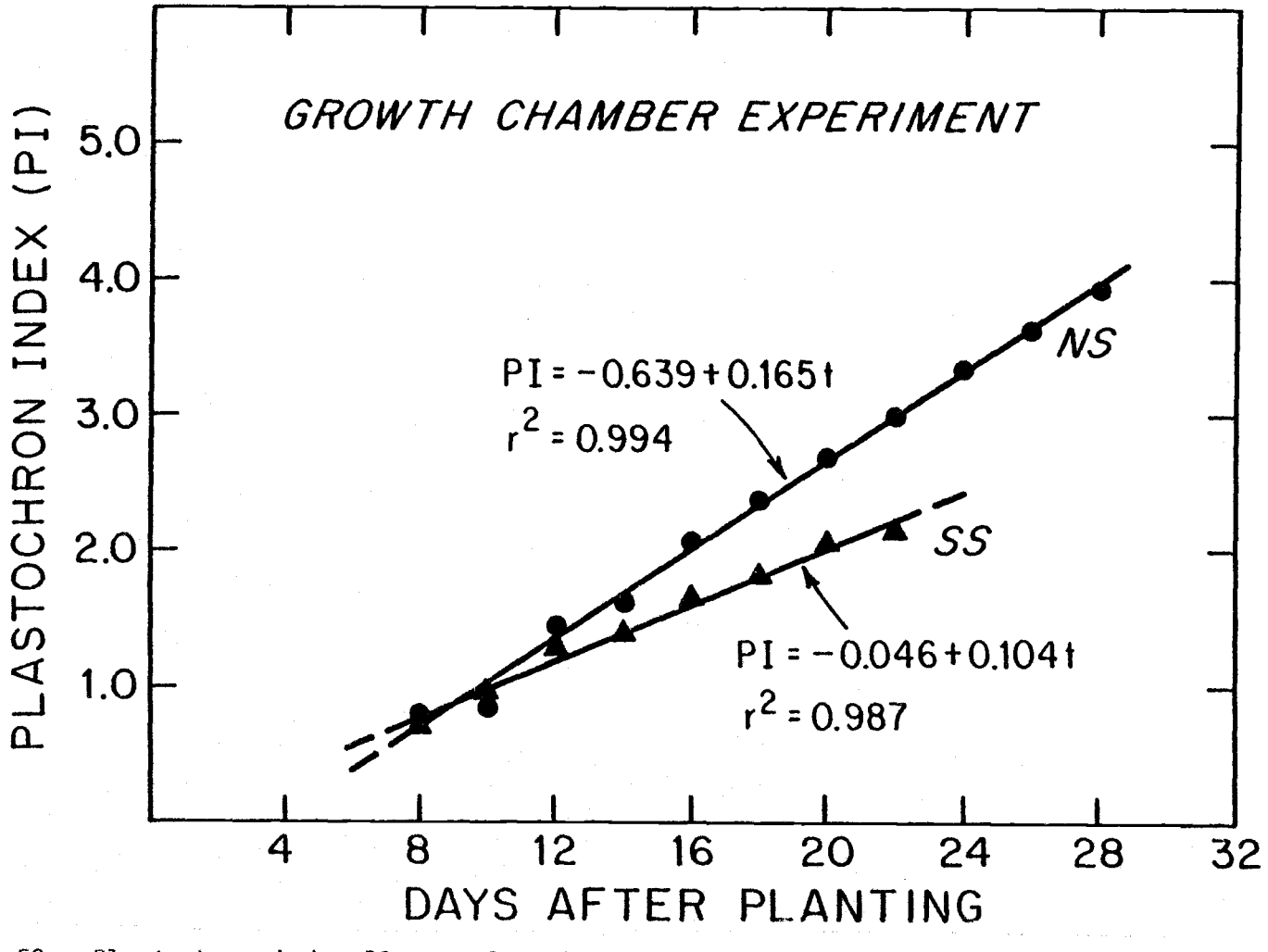

Figure 59. Plastochron index PI as a function of days after planting for treatments NS and SS of the growth chamber experiment. Data points represent an average of three measurements for NS and six measurements for SS treatments.

TABLE 8. Comparisons of indexes derived from plots of PI vs time for irrigation treatments of field experiment and growth chamber experiment.

	Slope (r/p)	Intercept	Plastochron Duration		Standard Error	
			days	hours	days	hours
Field Experiment						
NS	0.559	-7.55	1.79	42	0.485	11.64
GS	0.412	-6.76	2.43	58	0.476	11.42
SS	0.340	-4.78	2.94	71	0.366	8.78
Growth Chamber Experiment						
NS	0.165	-0.67	6.06	145	0.137	3.29
SS	0.104	-0.05	9.60	230	0.130	3.12

errors are 3.29 and 3.12 hours for NS and SS treatments, respectively. The values of the standard error in the growth chamber are much lower than those of the field, which points out that the accuracy is greater under controlled conditions environment as compared to a constantly changing environment in the field.

Effects of Water Stress on LPI

The development of a particular leaf may be better understood by plotting its length against its LPI calculated by equation 29. Figure 60a shows these plots for leaflets 1, 3, and 5 of the NS treatment. Leaflets 1, 3, and 5 achieved about the same final length although the slopes of the graph differed somewhat between leaves. On the other hand, results of treatment SS (Figure 60b) show that leaflet 5 was much shorter than leaflet 1 throughout their growth and the final length attained at the same LPI was also shorter. Leaflet 5 achieved about 80 percent of the final length of leaflet 1. This is an indication of the cumulative effects of water stress which became more severe as time elapsed. The younger leaflets of treatment NS, namely 11 and 13, were much different from 1 or 5 in their growth patterns. The L vs. LPI curves of leaflets 11 and 13 were linear. These leaves did not appear in the SS treatment.

The development of a particular leaf growing in a growth chamber is shown in Figure 61 where the graphs for the second trifoliate of both NS and SS treatments are shown. The leaflets had similar growth patterns only during the early part of growth. The severely stressed leaflets had a lower elongation rate after LPI = 1.0. The well

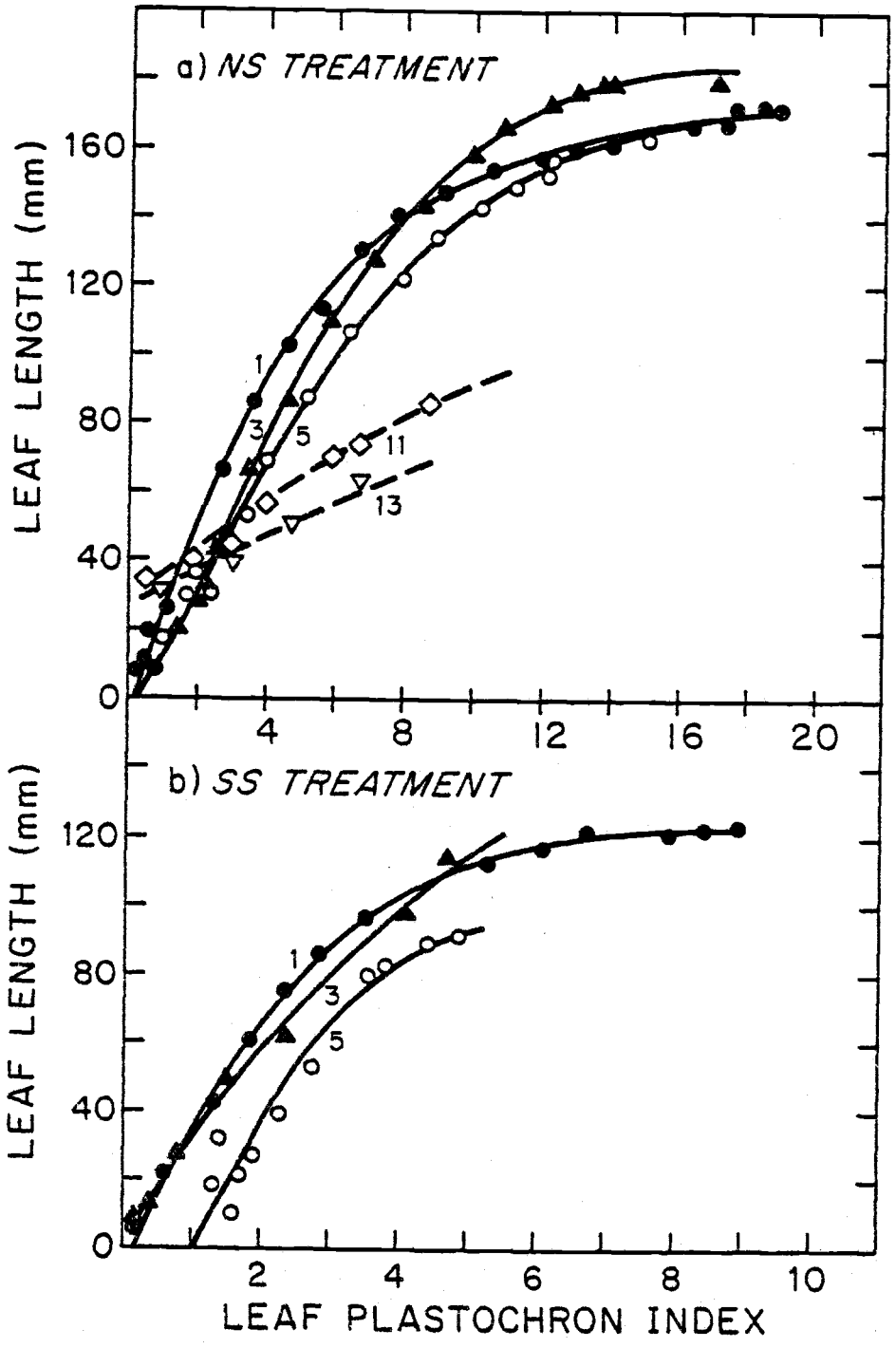

Figure 60. Length of leaves 1, 3, and 5 as a function of leaf plastochron index for leaves of treatment NS (a) and leaves of SS treatment (b). Leaves 11 and 13 of NS treatment are also shown. Data were obtained from 1981 field experiment.

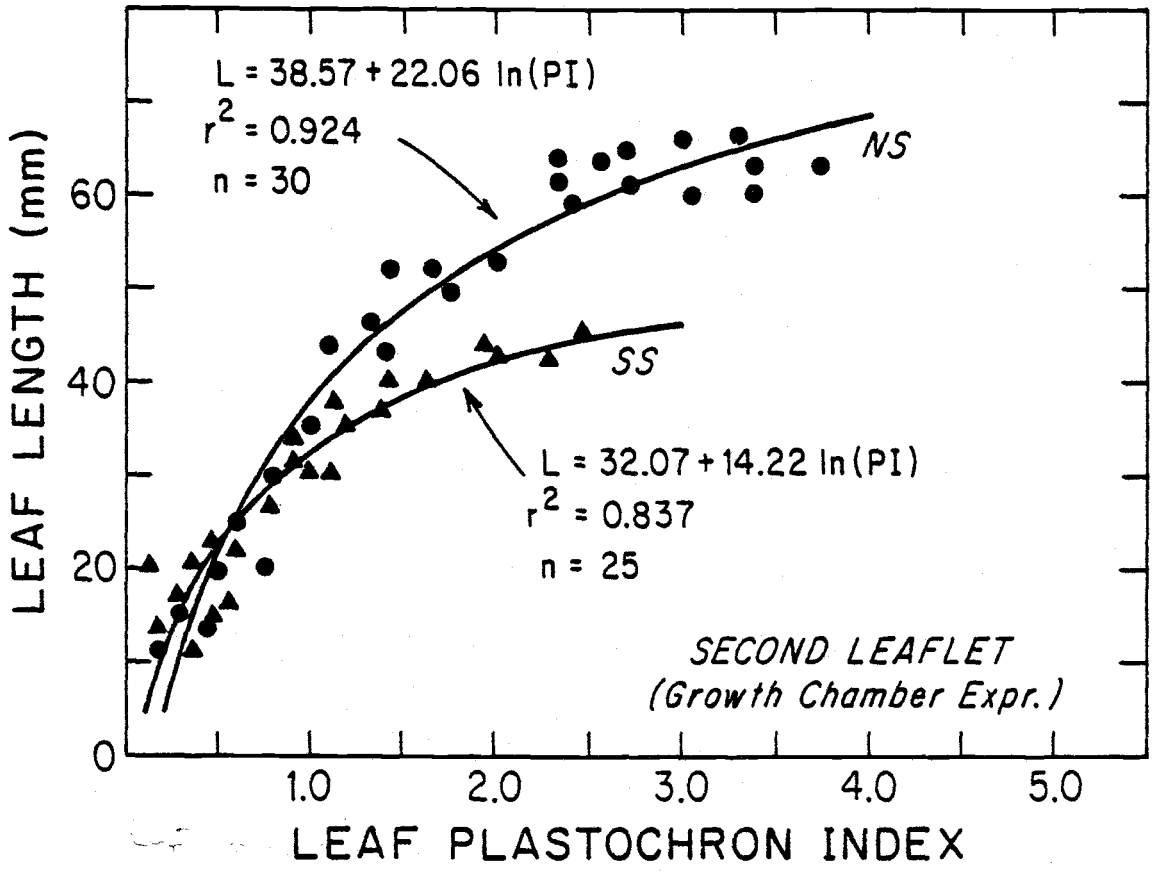

Figure 61. Length of the second trifoliate leaves of NS and SS treatments as a function of leaf plastochron index (LPI). Data obtained from growth chamber experiment.

watered leaflets attained 1.4 times the length of the stressed leaflets.

Correlation of the PI with Some Growth Parameters

Attempts were made to establish relationships between the developmental index and certain growth measures of the plant such as total fresh weight, total dry weight, and LAI of the crop. Figure 62 shows the total fresh weight of the plant on a function of PI for treatments NS, GS and SS. The total fresh weight increases exponentially with PI for all treatments. The NS treatment was different from the other stressed treatments with a lower fresh weight of all values of PI. Treatments GS and SS show similar fresh weights at the same plastochron index. Treatments GS and SS had a higher fresh weight per plant at any given PI than treatment NS. This observation can be explained by the fact that even though the stressed plants have fewer and smaller leaves, their leaves are succulent, thicker and heavier. These results are different from those which are obtained when chronological age is used as the time scale (Figure 63b). Figure 63b shows that the plants from the NS treatment have greater fresh weight per plant than those of the GS and SS treatments, throughout the growing season. It will be shown later (Figure 81b) that the leaves of the stressed treatments, GS and SS, have a greater specific leaf weight than those of the irrigated treatment NS, which implies thicker leaves or leaves which weigh more per unit leaf area.

Effects of water stress are more pronounced when dry weight per plant is plotted versus PI (Figure 64). The SS treatment had greater

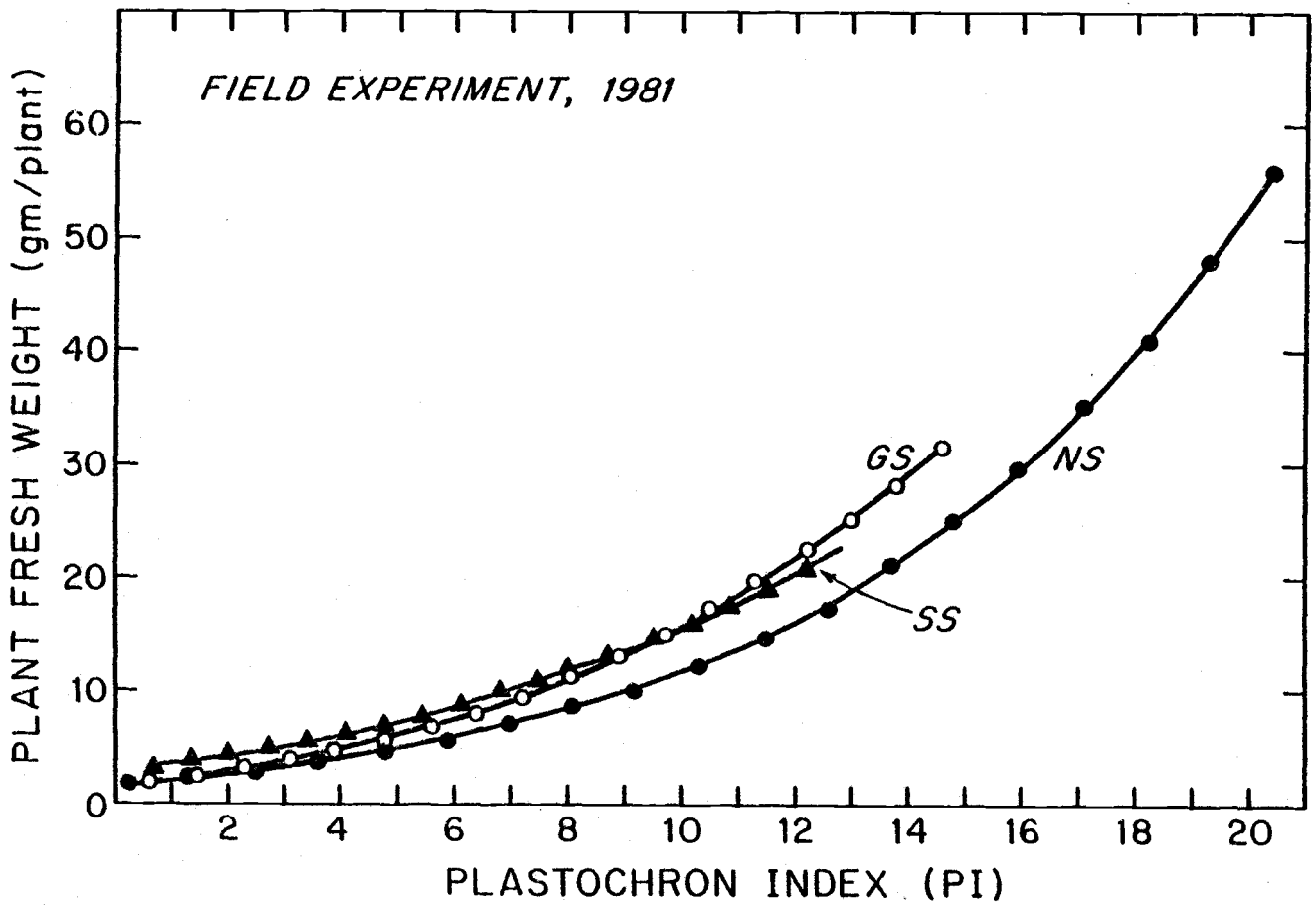

Figure 62. Plant fresh weight as a function of plastochron index for treatments NS, GS and SS. Data obtained from field experiments, 1981.

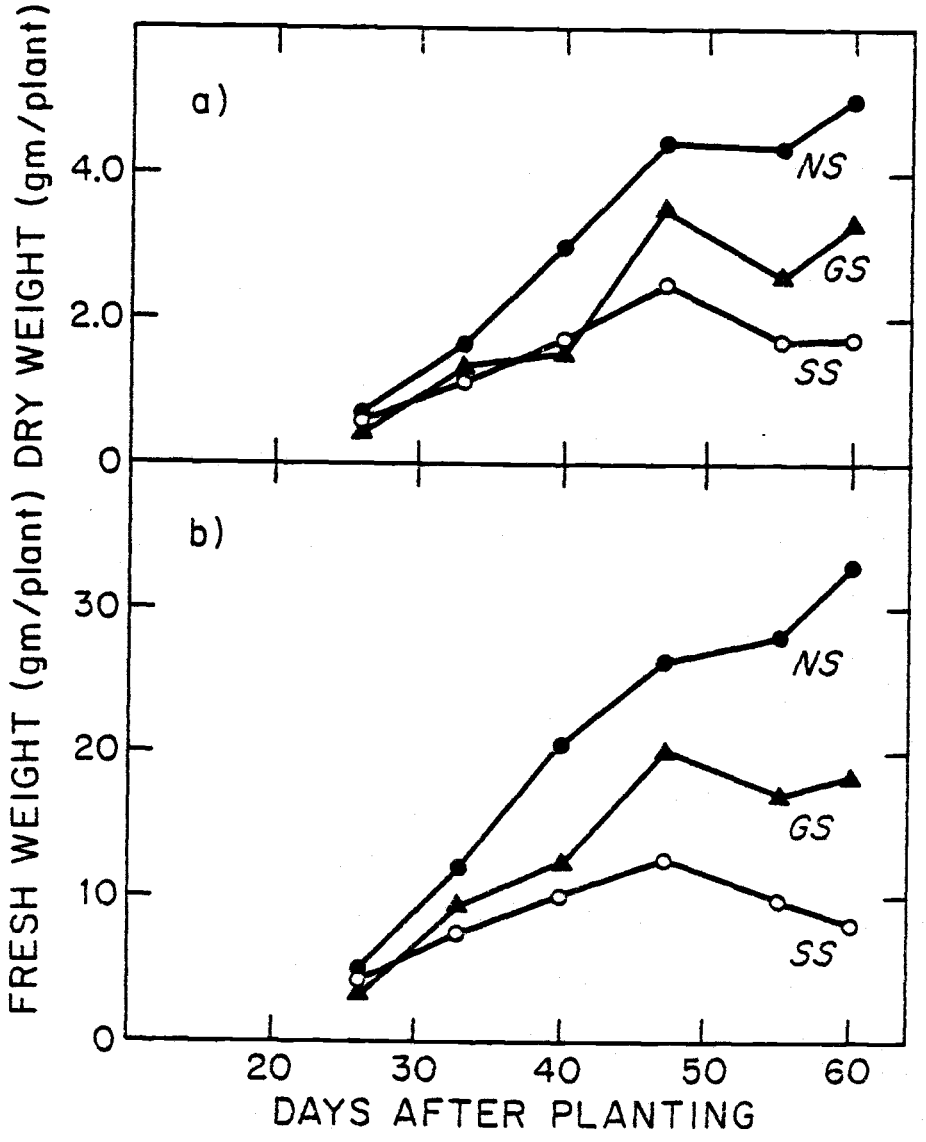

Figure 63. Dry weight (a) and fresh weight (b) of plants from treatments NS, GS and SS as a function of days after planting. Each point is the average of four measurements.

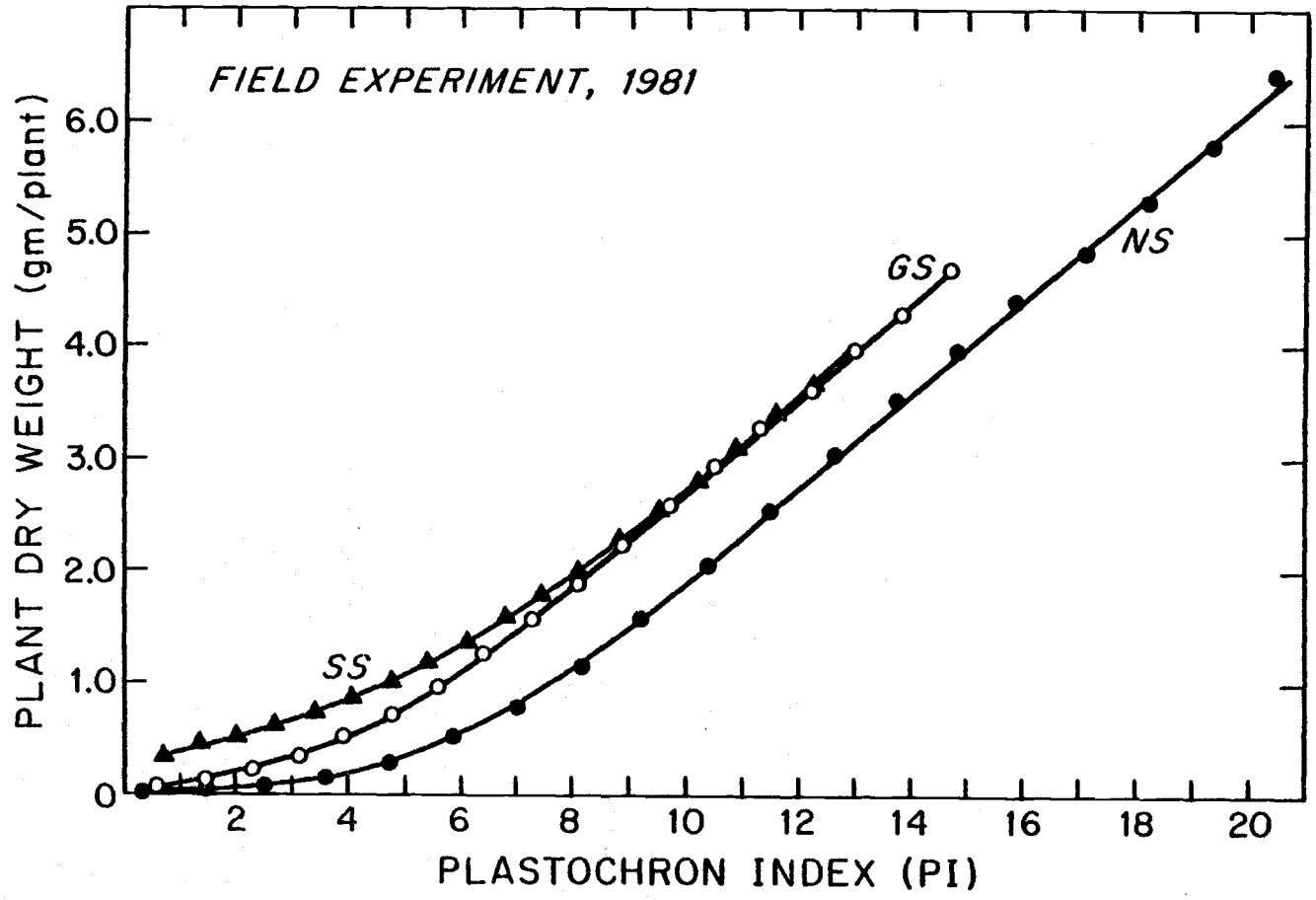

Figure 64. Plant dry weight as a function of Plastochron index of NS, GS and SS treatments of the 1981 field experiment.

dry weight per plant at any given plastochron age than the NS treatment. This supports previous observations, namely that stressed plants have produced more dry matter at the same plastochron age. The degree of stress did not seem to be very critical, as indicated by the fact that graphs from the two stressed treatments fairly coincide. Figure 65 shows the ratio of the dry weight to fresh weight of the above ground biomass as a function of the PI of the three treatments. This ratio is a measure of the water content of the plants in the field. That is

$$\frac{\text{Dry weight}}{\text{Fresh weight}} = \frac{\text{Fresh weight - water}}{\text{Fresh weight}} = 1 - \left(\frac{\text{Water}}{\text{Fresh weight}}\right) ,$$

As the value of water content decreases, the ratio increases and vice versa. In other words, a higher ratio means that the water content of the tissues was lower.

Figure 65 shows that the ratios of dry to fresh weight increase with increasing plastochron age to a maximum value and decrease gradually. The ratio increases with age may be because of the accumulation of dry matter (i.e. lignin) as plants grow. The severely stressed plants show a greater ratio because of lower water content of the tissues. The maximum value of the ratio is obtained by a maximum accumulation of dry matter per unit fresh weight or by a minimum water content of the tissues. Results in Figure 65 indicate that all treatments reached a maximum ratio of 17.5 percent or a minimum water content of 82.5 percent. This observation indicates that the point of maximum of dry weight to fresh weight ratio is indpendent of water stress; it may be determined by other physiological factors such as

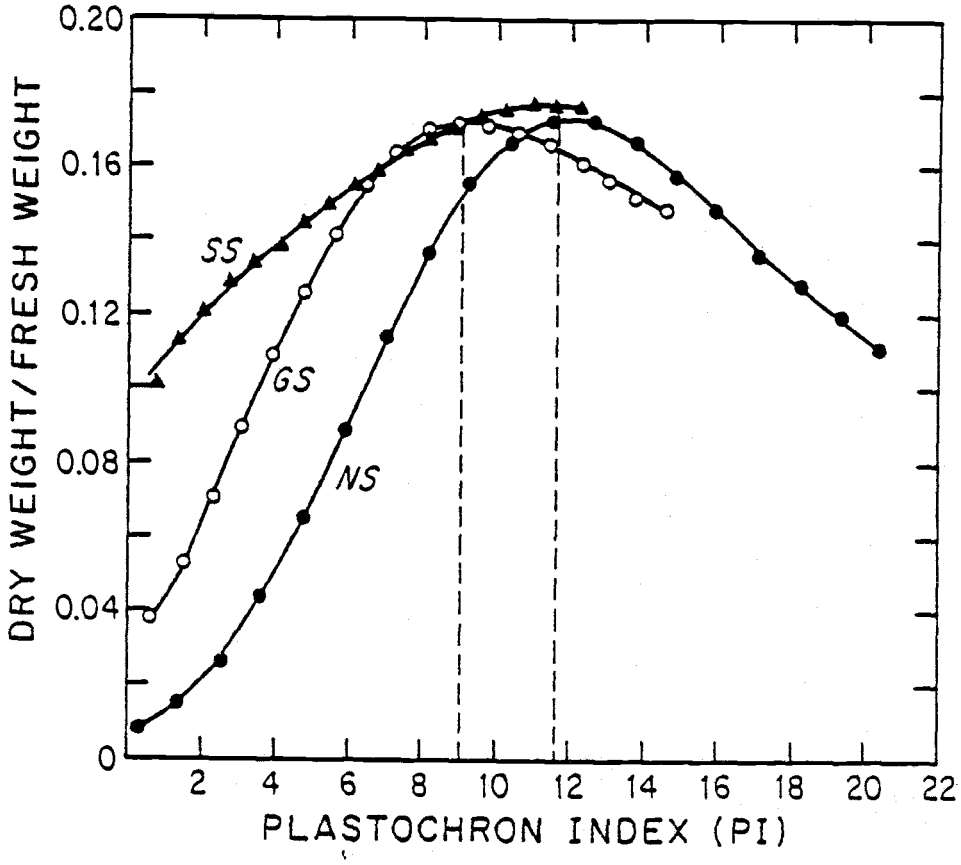

Figure 65. The ratio of dry weight to fresh weight of the plant for NS, GS, and SS treatments as a function of plastochron index. Data obtained from Figures 63 and 64.

the crop maturity. The ratio decreases when there is less water for the same fresh weight, this is where leaves no longer grow and senesce. The value of the PI at which the ratio is maximum and below and above which the ratio decreases is affected by water stress. For the moderately stressed treatment, the maximum value of the ratio was reached around PI of 9, where the NS treatment reached the maximum value at the 11.6 plastochrons. The maximum ratio for treatment GS occurred at 9.0 plastochrons which is about 36 days after planting. However, the maximum value occurred around day 34 after planting. This period might be associated with the time of changing the source-sink relationship, where the assimilates movement were mainly to the reproductive organs rather than the vegetative organs.

Figure 66 shows the relationship between LAI and the PI of the three treatments. The stressed treatments, GS and SS, had higher LAI than the NS treatment at the younger plastochron ages. At the age of 6 plastochrons, the leaf area indexes were approximately 0.15, 0.40, and 0.50 for the NS, GS, and SS treatments, respectively. These results indicate that at PI = 6 plants have 6 leaves but those of the SS treatments were older and therefore bigger. The rate of increase in LAI was the highest for treatment NS, was parallel to NS until later in the season for the GS treatment, and was the lowest for the severely stressed treatment. The shift of the LAI for GS treatment occurred at PI 12.5 (45 DAP) and at PI 10.2 (44 DAP) for the SS treatment. This period coincides with the time of movement of assimilates from the leaves to the pod formation sites.

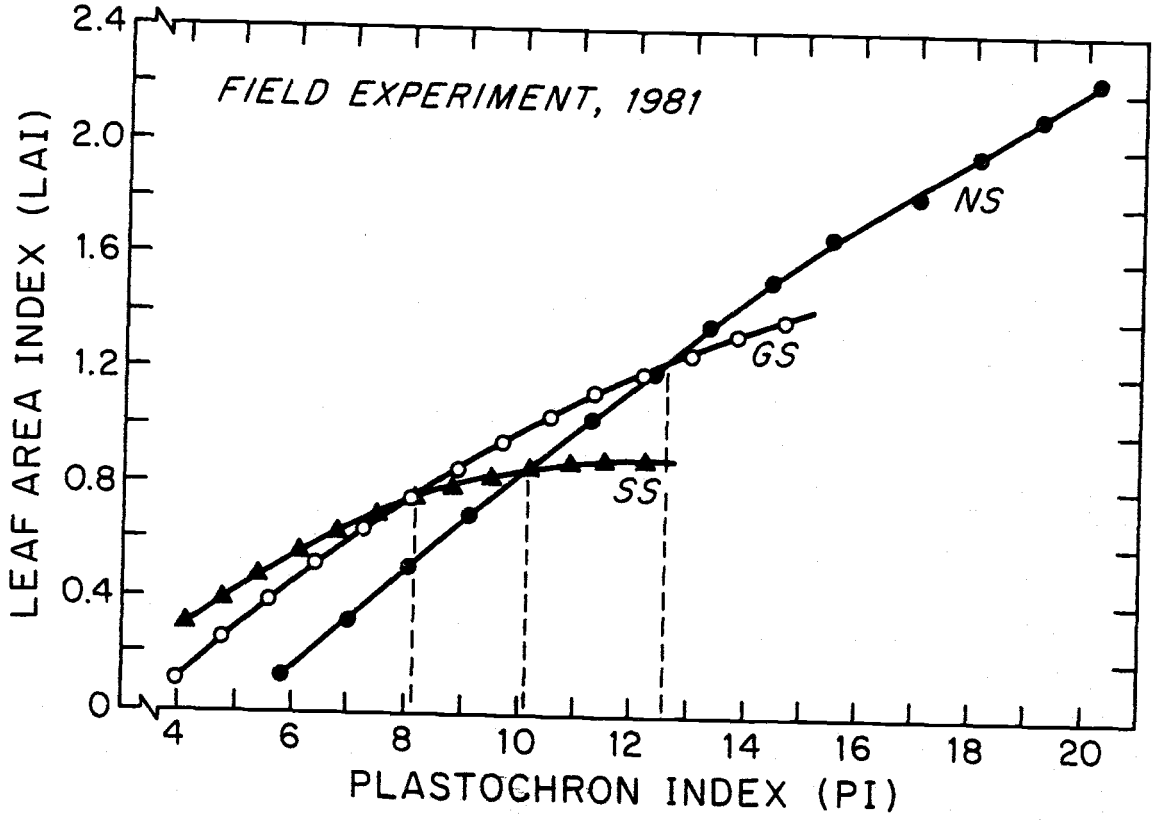

Figure 66. Leaf area index (LAI) as a function of plastochron index (PI) for treatments NS, GS and SS of the 1981 field experiment.

Treatment Effects on Growth of Leaves

Leaf lengths were measured with a ruler hourly for leaflets of the NS treatments during a few days early in the season. Measurements were taken four times during the daytime. The leaf measurements suggested that the use of a ruler for leaf length measurements was not accurate enough to detect the hourly changes. The increase of leaf length was observed to be greatest during the nighttime and minimal during the daytime hours. The hourly measurements of leaf lengths were not considered in this analysis, because of the imprecise nature of the methods.

For long term growth of leaves, leaf lengths were measured every other day and at the same time of the day. The leaves were from three plants selected randomly from each replicate. At the end of the growing season, the average number of leaves per plant were 20, 14, and 9 for the NS, GS, and SS treatments, respectively.

Figures 67 and 68 show the growth curves of the odd-numbered leaflets for treatments NS and SS, respectively. The final number of leaves were 21, 16, and 11 for treatments NS, GS, and SS, respectively. Detailed comparisons between leaflets of the three irrigation treatments are shown in Figure 69. The water supply clearly affected the time of leaf initiation. Leaves of the frequently irrigated treatment (NS) appeared sooner than corresponding leaflets of the stressed treatments (GS and SS).

The delay in leaf appearance is magnified by the severity and length of the stress period. The 7th leaf appeared about eight days later on the GS treatment than on the NS treatment, as shown in

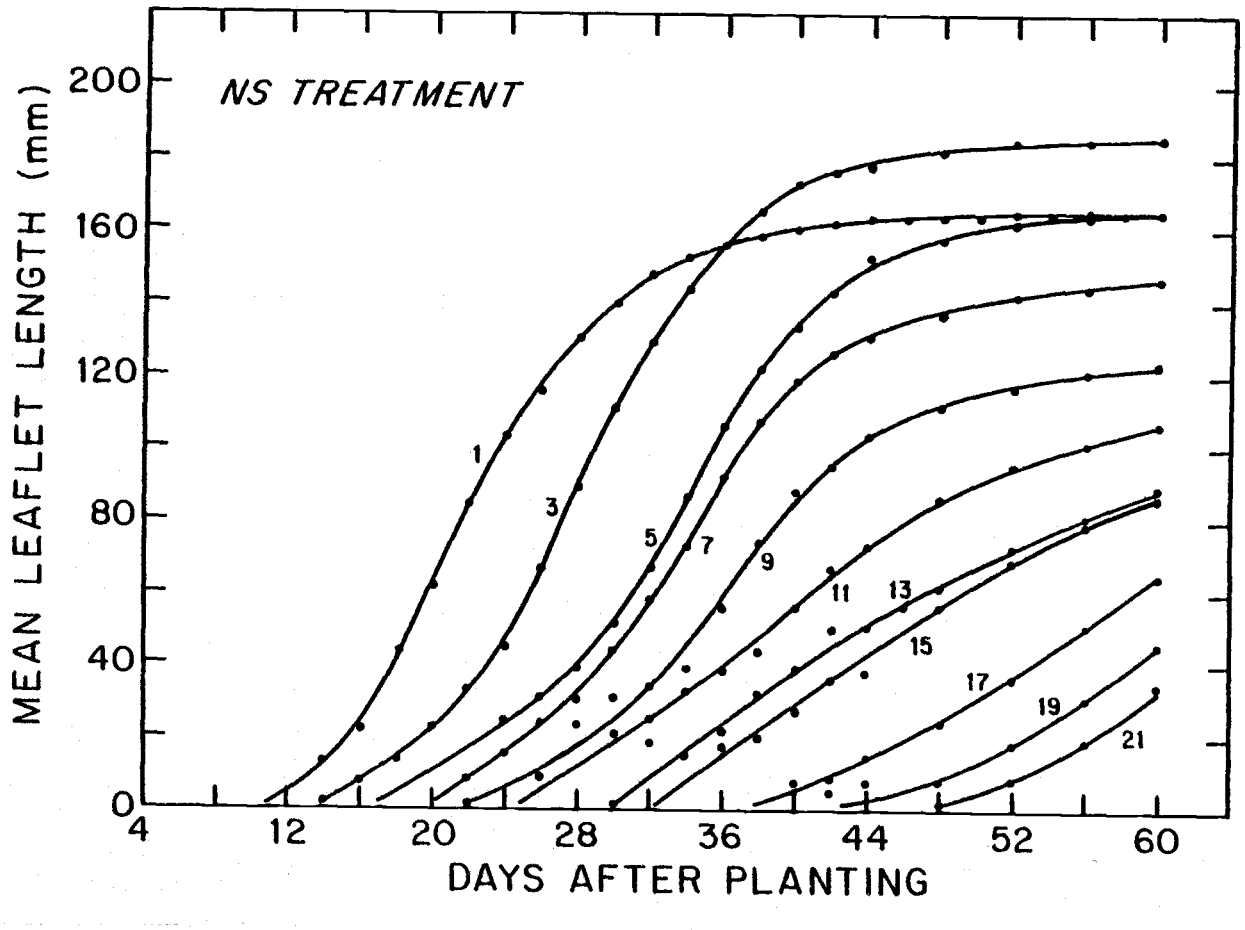

Figure 67. Average lengths of alternate leaves of the NS treatment as a function of days since planting. Each growth curve represents the average of 12 leaves on 12 different plants.

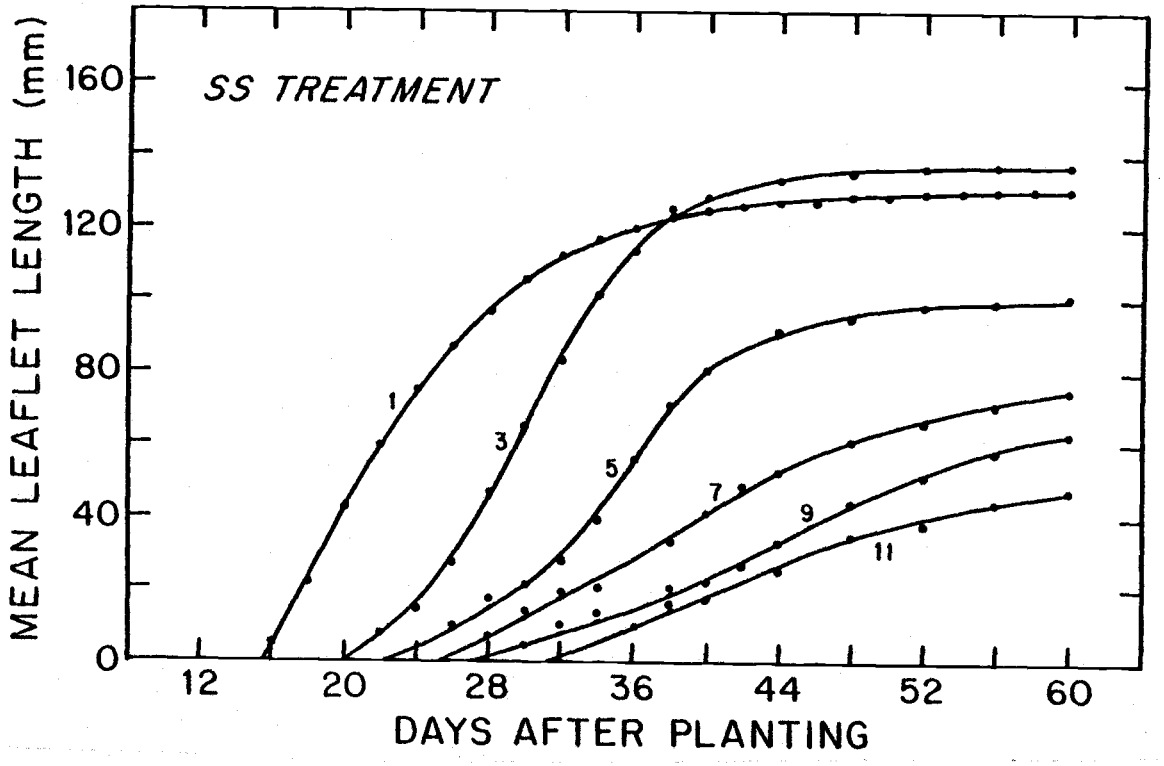

Figure 68. Average lengths of alternate leaves of the SS treatment as a function of days since planting. Each growth curve represents the average of 12 leaves on 12 different plants.

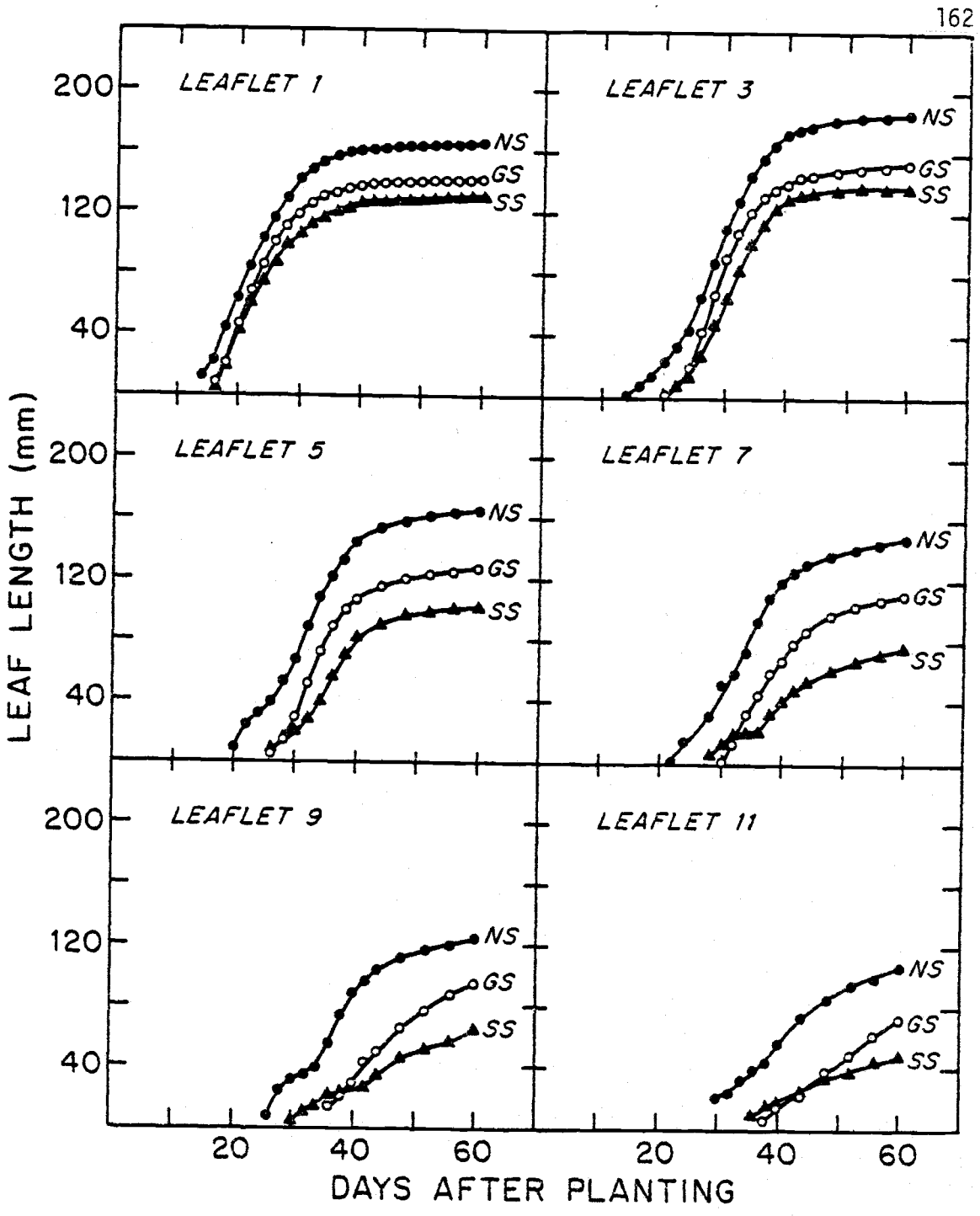

Figure 69. Average leaf lengths of alternate, successive leaves of NS, GS and SS treatments expressed as a function of days since planting. Each growth curve represents the average of 12 leaves on 12 different plants.

Figure 69. Leaf initiation on the non-irrigated (SS) plants was usually earlier than on the GS treatment, but the rate of elongation was much slower. The difference in appearance of the GS and SS treatments were smaller, however, and not significant. The leaves of the same plant did not reach the same final growth, as shown in Figures 67 and 68. However, water stress reduced leaf length of all leaves in all of the stressed plants. Compared with the NS treatment, the final lengths attained by the 1st, 3rd, and 5th leaflets were reduced by 24, 31, and 38 mm with the GS treatment, and by 36, 50, and 66 mm with the SS treatment, respectively. Table 9 summarizes the differences between treatments for the oldest five leaves. The delay of leaf appearances in comparison with NS treatment ranged from four days for the 1st leaf to eight days for the 5th leaf for the SS treatment. This delay increased as plants aged. The reduction in the final leaf length as percent of the NS treatment ranged from 21.7 percent for the 1st leaflet to 39.8 percent for the 5th leaflet.

The growth curves shown in Figure 52 were fitted and analyzed with polynomial regression functions of the form $L = a + bt + ct^2 + dt^3$, where L is the leaf length in mm, t is time in days, and a, b, c, and d are regression constants. The regression coefficients, r^2, of the fitted functions range from 0.993 to 0.997. The elongation rates of the leaves were obtained from the first derivative of the regression equations. The elongation rates (dL/dt) were in the form of $dL/dt = b^1 + c^1t + d^1t^2$, where b^1, c^1 and d^1 are constants.

The growth characteristics of bean leaves under favorable water supply conditions indicated that growth rates for all leaves decreased

TABLE 9. Comparisons between treatments of the estimated time of appearance and final length attained by the oldest five leaves of plants from the NS, GS and SS treatments. Treatment NS is considered a standard for comparison.

		1	2	3	4	5
Approximate time of appearance (days after planting)	NS	12	12	14	16	19
	GS	15	18	20	23	25
	SS	16	19	21	25	27
Delay in appearance in comparison with the NS treatment (days)	GS	3	5	6	7	5
	SS	4	6	7	9	8
Final length attained (mm)	NS	166	150	186	176	166
	GS	142	133	155	135	128
	SS	130	119	136	116	100
Reduction of final length in percent of NS treatment	GS	14.5	11.3	16.7	23.3	22.9
	SS	21.7	20.7	26.9	34.1	39.8

with age (Figure 70). Variations between individual leaves could be due to the dynamic nature of the growth process under natural environmental conditions. The leaves were exposed to different sets of growing conditions and these conditions are changing with time.

The relative growth rate (dL/dtL) can be expressed in the form [d(lnL)/dt], which can be obtained by fitting the functions between lnL and t, then differentiating the regression functions. The functions between lnL and t were best fitted by a third degree polynomial equation with r^2 values ranged from 0.990 to 0.998. The first derivative of these regression functions produced a family of curves of the relative growth rate as a function of time (Figure 71). The results of the relative growth rates versus time show that the older leaves usually appear with a relatively high growth rate with decreases with age reaching low values after flower initiation. Figure 72 shows elongation rates plotted as a function of leaf plastochron index (LPI). At the same LPI, the stressed leaflets have lower elongation rates than those of the NS treatment. The differences between treatments became greater as plants grew older and stress became more severe. Patterns of growth were different for leaflets 3 and 5.

It is unfortunate that the daily growth patterns were not monitored in this study. This prevented the correlation of the growth rate with the diurnal changes of water status. The seasonal growth curves can only be useful in reaching general conclusions. Generally speaking, the leaf elongation rate is highly sensitive to water stress. Effects of water stress changes with length of stress period,

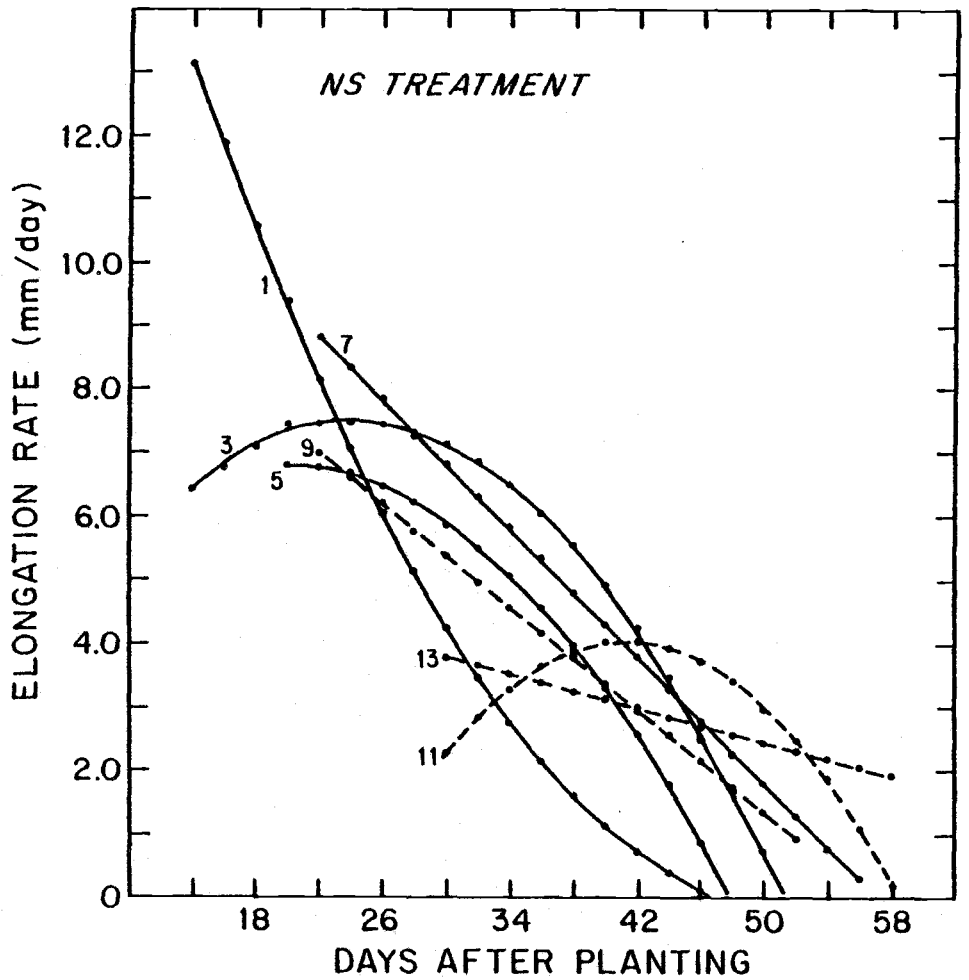

Figure 70. The elongation rates of the alternate leaves of the NS treatment expressed as a function of days after planting.

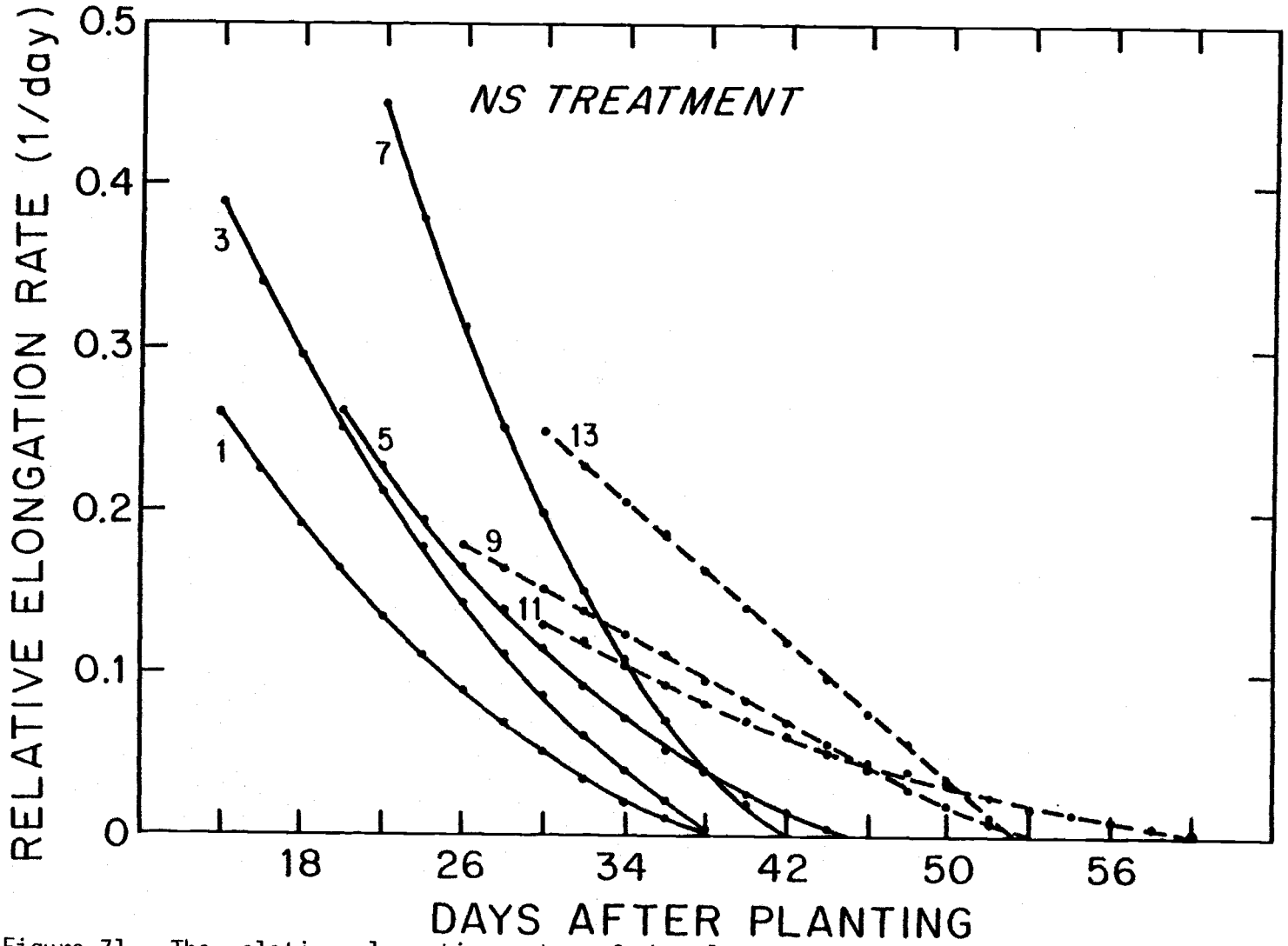

Figure 71. The relative elongation rates of the alternate leaves of the NS treatment expressed as a function of days after planting.

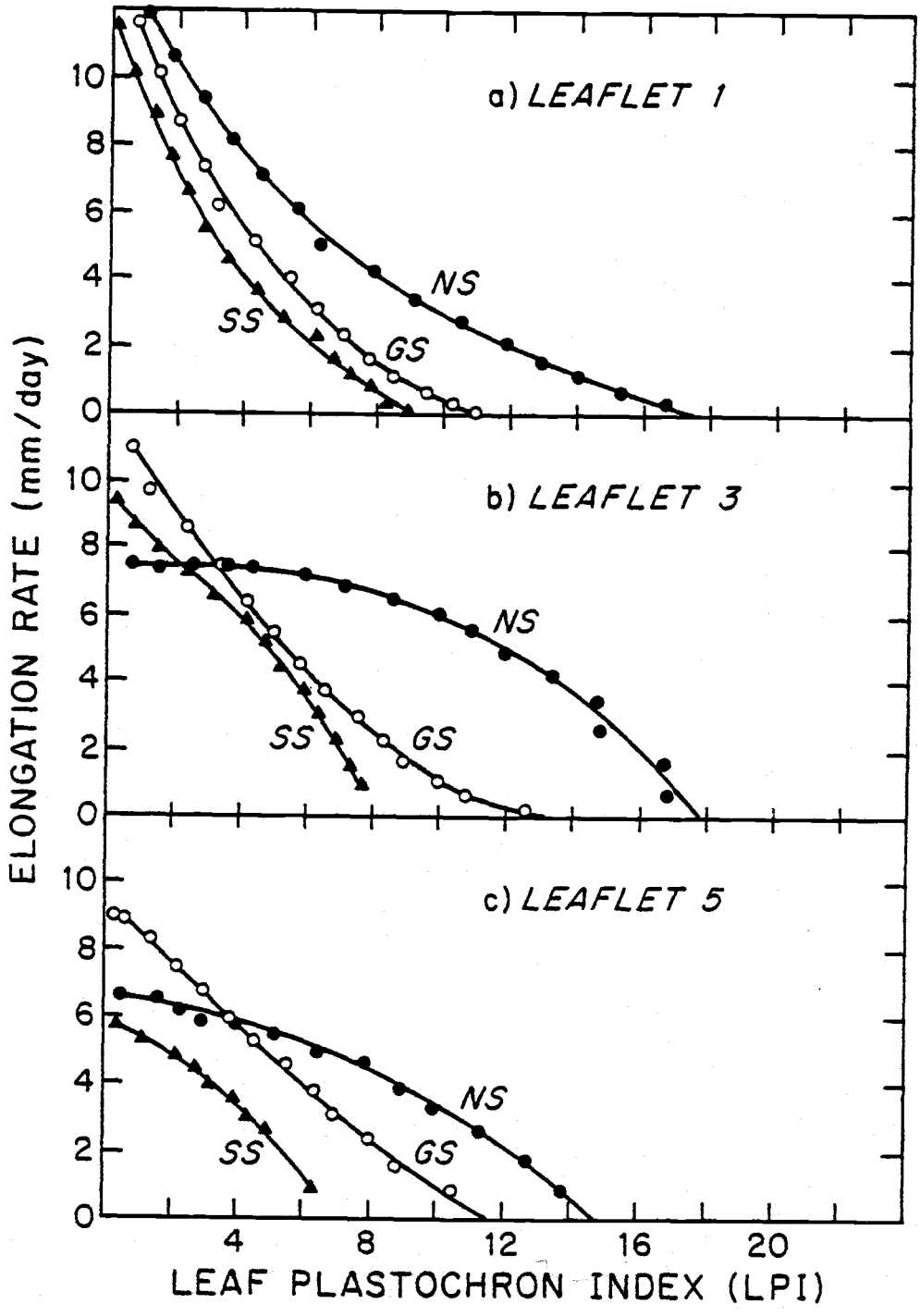

Figure 72. Elongation rates of alternate leaves as function of leaf plastochron index for leaflet 1 (a), leaflet 3 (b), and leaflet 5 (c) from the NS, GS, and SS treatments, respectively.

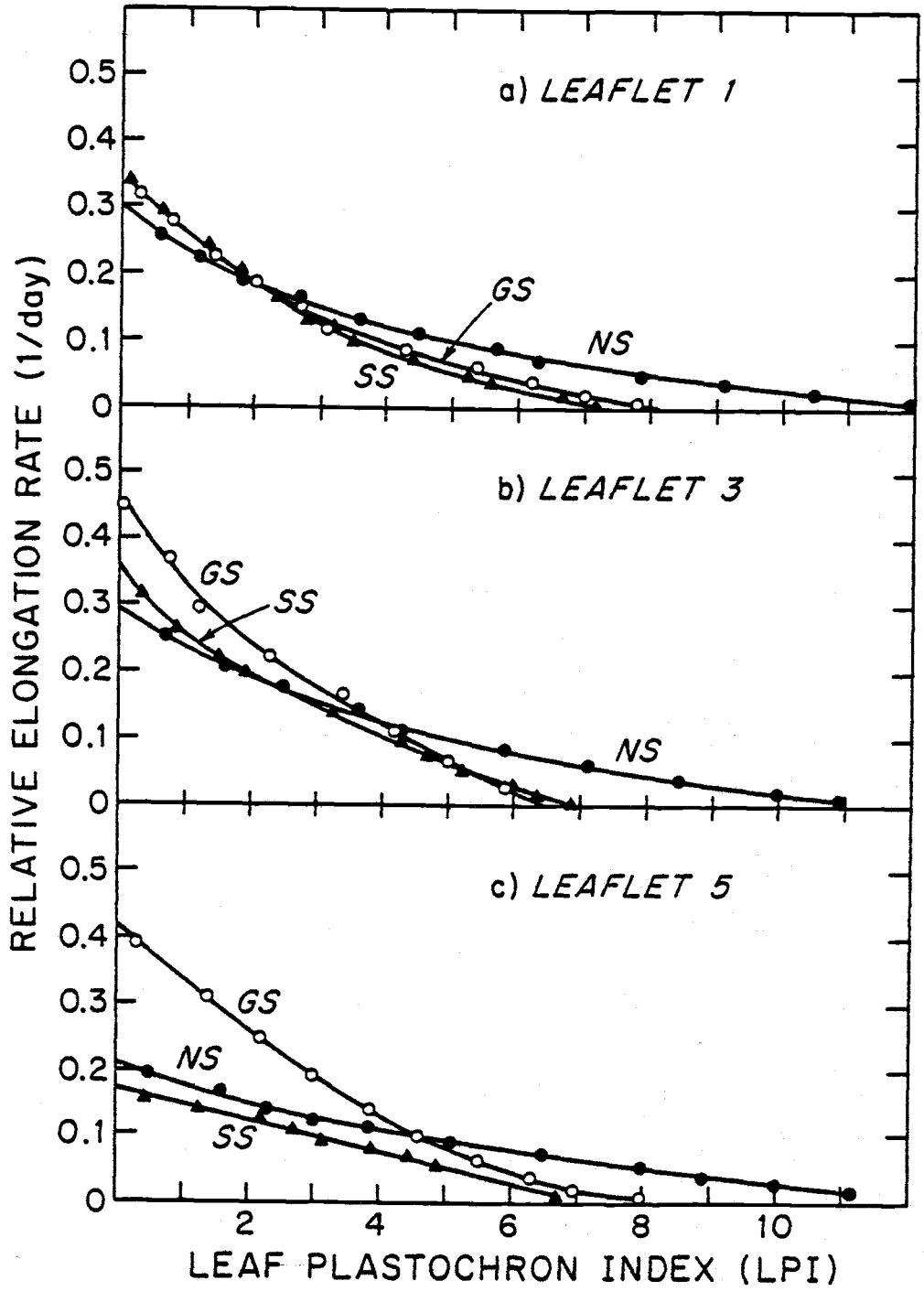

Figure 73. Relative elongation rates of alternate leaves as a function of leaf plastochron index for leaflet 1 (a), leaflet 3 (b), and leaflet 5 (c) from the NS, GS, and SS treatments, respectively.

that is, leaf elongation is severely reduced under conditions of prolonged, severe stress.

In a preceding chapter, we made the observation that the SS treatment has a higher Ψ_p on a seasonal basis (see Figure 49) and on a diurnal basis (see Figure 33), yet the growth rates of SS leaves were much lower than those of the irrigated treatment (NS). The interpretations of these data are complicated by the fact that the effects of Ψ_p can be responsible for short-term effects. However, long-term effects may not be attributable to a reduction in Ψ_p. Possible causes of the long-term effects of water stress on rate of leaf elongation are retardation of cell wall synthesis (Cleland, 1967), alteration of growth regulators, such as IAA (Green and Cummings, 1974), and ABA (Zabadel, 1974), and inhibition of cell division (Wenkert et al., 1978a).

The growth rate as described by equation 24 is a function of E_g, Ψ_p, and $\Psi_{p,th}$. These parameters are not constant at different degrees of water stress. The combination of E_g and $(\Psi_p - \Psi_{p,th})$ is more important than the absolute value of tissue Ψ_p. The data contained in this study are not complete enough to estimate the value of $\Psi_{p,th}$ for each treatment (see Figure 44). It has been reported that $\Psi_{p,th}$ value is not constant but rather decreased to near zero as Ψ_p was lowered. This made $(\Psi_p - \Psi_{p,th})$ more favorable in rye coleoptile (Green and Cummings, 1974). Therefore, we might conclude that even though the SS leaves have greater bulk Ψ_p, this does not mean that their growth rate should be higher than those of control treatment. Cutler et al. (1980) reported that the rate of leaf elongation increased with increasing pressure to about 5 bars above which no further increase was observed.

They concluded that the rate of water uptake normally limits the rate of leaf elongation.

Treatment Effects on Leaf Area Development

The photosynthetic area can be estimated in terms of the number of leaves that plants can bear and leaf area index as the season progresses. Figure 74 presents counts of fully expanded leaves per plant against time. Data from both years are plotted on the graph for treatments NS and GS. Water stress has negative effects on the number of leaves a plant can bear. The well-irrigated treatment (NS) had the highest number of leaves throughout the season and the SS treatment had the lowest number throughout. The SS treatment achieved its maximum number of leaves about 50 days after planting. The number of leaves then remained constant. This result could be due to the enhancement of leaf senescence due to water stress. The older leaves of the SS treatment were observed to become yellowish in color and drop much earlier than those of other treatments.

Figure 75 shows the seasonal development of the LAI. The difference between treatments became noticeable around 45 days after planting in the 1980 experiment. These differences between treatments were significant beyond day 33 in the 1981 experiment. On day 50 after planting, the difference in LAI between treatments and the control treatment (NS) were in the order of 1.5 and 0.5 units of LAI for the SS and GS treatments of the 1981 experiment, respectively. During the 1980 experiment, the LAI of the NS treatment did not develop as well as it did during the 1981 experiment (Figure 75). This may be because

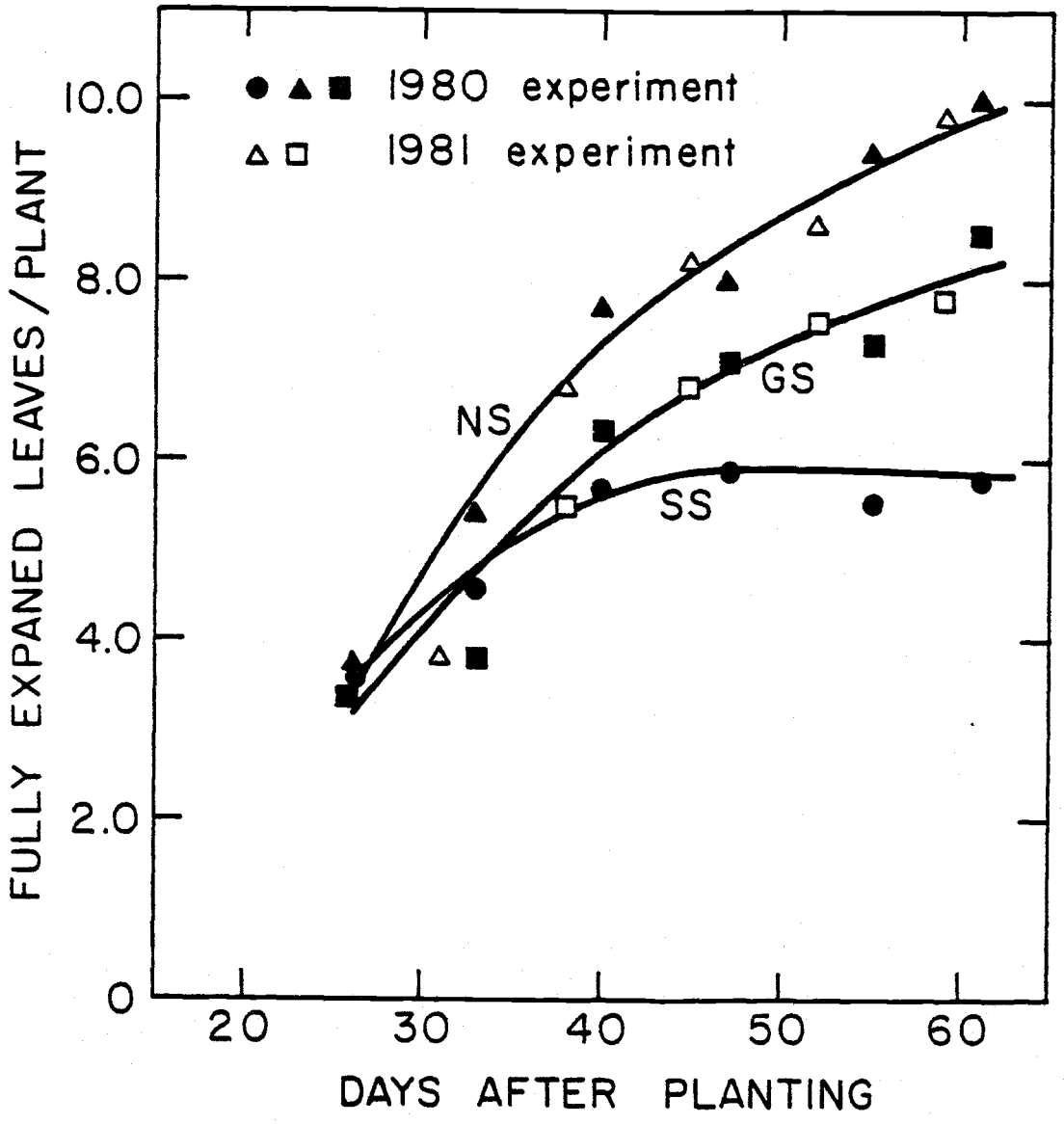

Figure 74. Number of fully expanded leaves as function of days after planting for treatments NS, GS and SS of the 1980 and 1981 experiments. Each data point represents an average of four measurements. Lines fitted using "eye balling" technique.

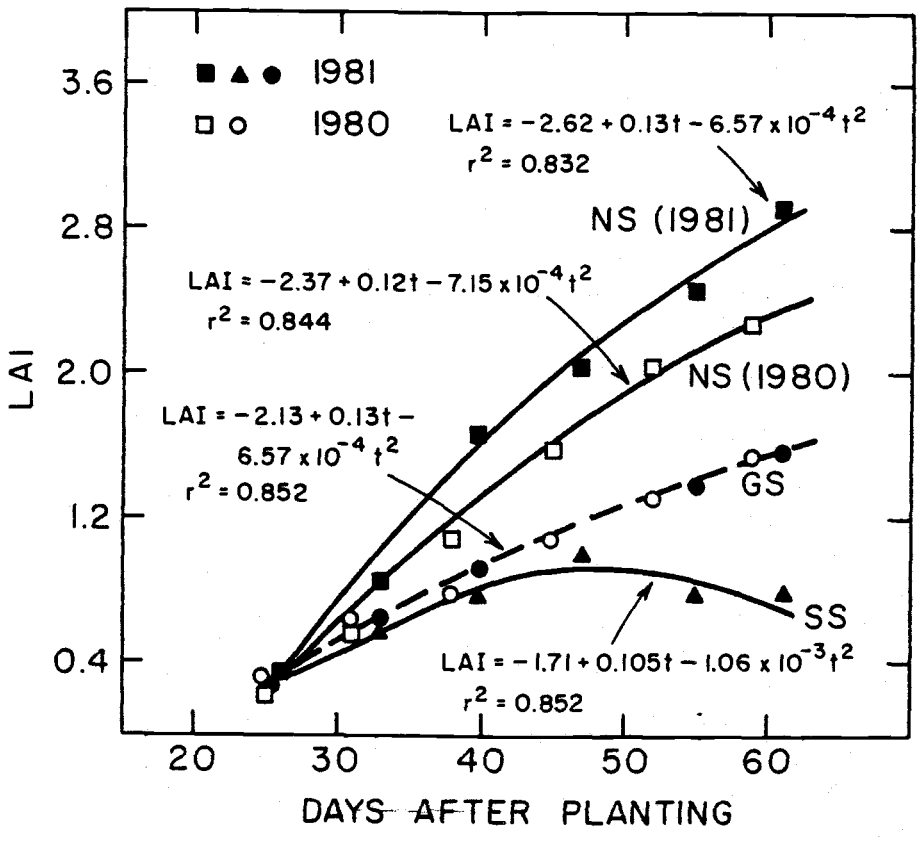

Figure 75. Leaf area index (LAI) as a function of days since planting for the indicates treatments.

better monitoring of the soil water status during the 1981 experiment provided better timing for the irrigations. The effect of the degree of the stress can be evaluated by comparing the three irrigation regimes shown in Figure 76. This figure compares the most stressed treatments of the two field experiments and shows the effect of irrigation timing on development of leaf area.

The LAI seems to decrease in all treatments after a maximum value was reached. The maximum value appears at about the same time in all treatment but the rate of decrease differs between treatments being largest with the SS treatment. Irrigation dates are indicated by the arrows along the DAP scale of Figure 76. Treatment SF was irrigated very frequently until 10 days before flowering, after which date plants were not irrigated for 22 days. This provided an exposure to water stress throughout the flowering stage. On the other hand, treatment GS was irrigated three times during this period, namely on days 29, 40, and 52. This difference in irrigation timing might explain the difference in LAI after day 40 between the GS and SF treatments. Therefore, the single irrigation on day 40 of treatment GS had a greater effect on increasing the LAI. More precisely, the absence of an irrigation on day 40 on the SF treatment was responsible for the shift of its rate of development of LAI.

Treatment Effects on Dry Matter Accumulation

The accumulation of dry matter on the various treatments was followed through periodic sampling. Approximately every 6 to 7 days, 10 plants were harvested from each of the four replicates of each

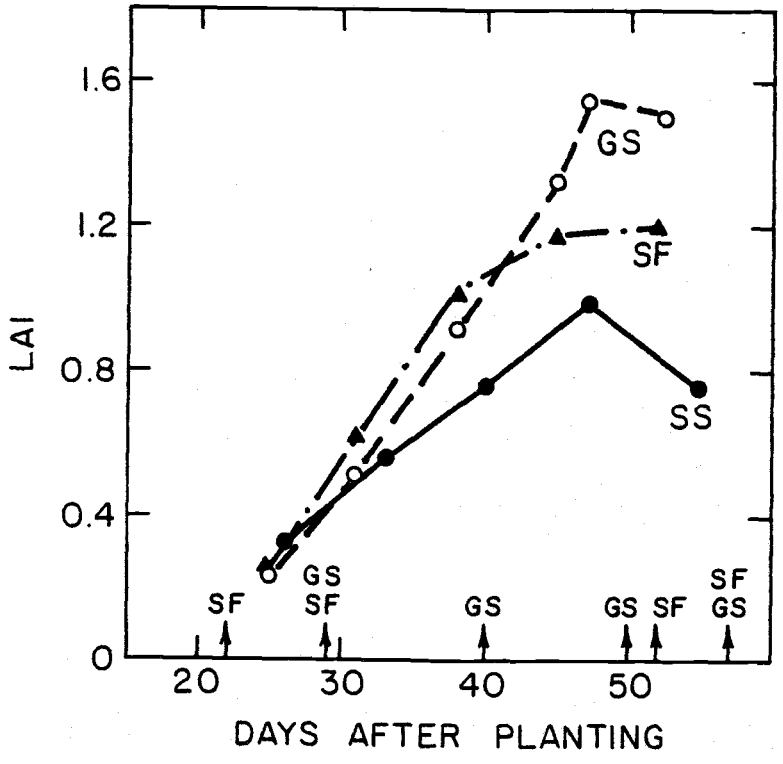

Figure 76. Leaf area index (LAI) as a function of days after planting for three stressed treatments (GS, SF and SS). Arrows at the bottom of the diagram indicate irrigation times of the indicated treatments.

treatment. The plants were separated into leaves, stems, and pods, dried in an oven at 65°C for at least 48 hours and weighed.

Figures 77a and 77b show the total above-ground dry matter at different times throughout the season for all the treatments. The frequently irrigated NS treatment accumulated the most dry matter through the season. The SS treatment had the lowest amount of dry matter throughout the season (Figure 77b).

The difference between the NS and SS treatments in total dry matter production increased as time progressed. This might be explained by the increase of water stress severity and by the increase of complexity of effects and after effects of stress. As time progressed, the dry matter accumulation was affected directly by reducing leaf area and probably the rate of photosynthesis. Indirect effects such as smaller ground coverage and lower light interception could also result in lower dry matter accumulation. Exposing the plants to severe water stress during flowering as in the case of SF (Figure 77a) had a great impact on the production of dry matter. The SF treatment started to deviate from the NS treatment a few days after the last irrigation before flowering. Resuming irrigation on day 52 did not lead to a full recovery to the NS treatment yield. Treatment SF accumulated about 72 percent of the NS treatment at the end of the season.

In the 1981 experiment, there was a slight decline of dry matter production for the GS and SS treatment at the end of the season when compared to the results of the 1980 experiment. This decline could be attributed to the enhancement of leaf senescence and reduction in

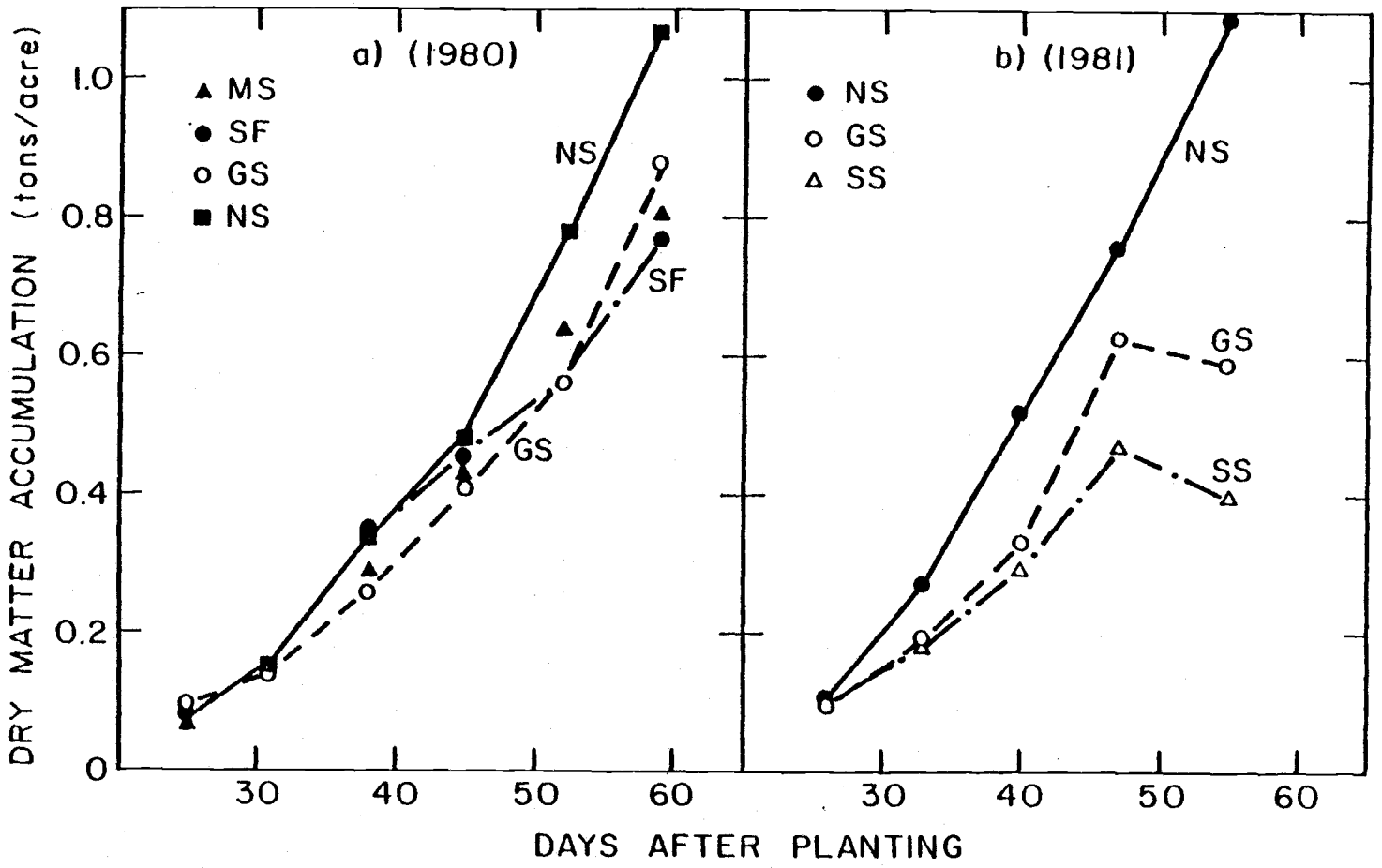

Figure 77. Dry matter accumulation as function of days since planting for the 1980 experiment (a) and the 1981 experiment (b).

the LAI. The final above-ground biomass in GS and SS were about 55 percent and 37 percent that of NS treatment. However, treatment GS produced about 82 percent that of NS treatment in the previous year.

To get some insight into the nature of the effect of the treatments on dry matter accumulation, it is of interest to examine the evolution of the growth components such as stems and leaves. Figures 78a, 78b, and 78c present these results for the period from day 26 to harvest. A comparison of the figure shows an early effect of water stress on dry matter production of stem and leaf. This evidenced by lower weights for the GS and SS treatments than those of NS treatment throughout the season.

It is of interest to note that in all treatments the leaf and stem weights started to decline after 47 days. This might correspond to the movement of assimilates from those organs to the pods which start to form at that time. On day 47, the stem and leaf dry weights of GS treatment were 81 percent and 85 percent of those of NS treatment, respectively. For severely stressed treatment (SS), their weights were only 62 percent and 61 percent of those of NS treatment, respectively.

The data presented in Figures 79 and 80 show that there is a unique relationship between LAI and dry matter accumulated. The accumulation of dry matter increases exponentially with increasing the area of the photosynthetic tissues. It is of interest to note that the frequently irrigated treatment (NS) requires more photosynthetic tissues per unit area of land to accumulate the same level of dry matter when compared to the SF or SS treatments. The severely

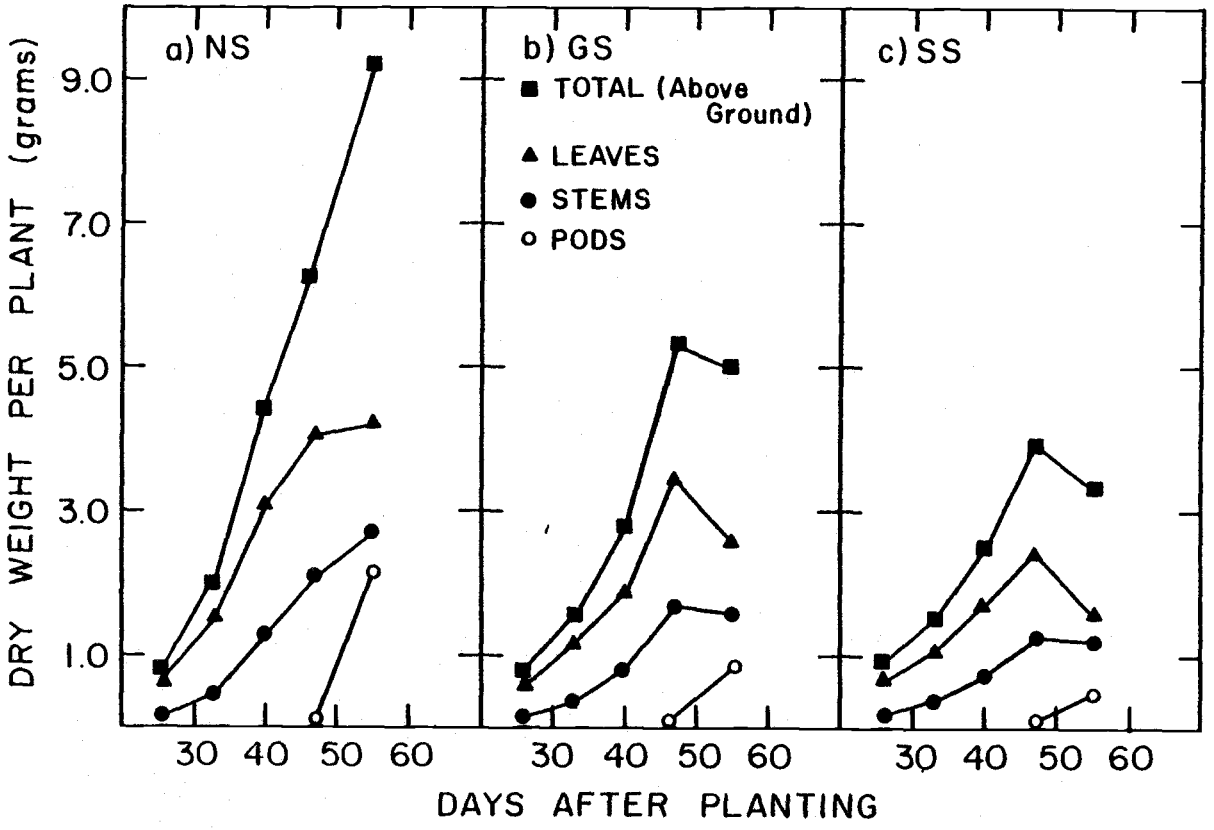

Figure 78. Dry weight accumulation of stems, leaves, and total above ground biomass as function of days after planting for treatment NS (a); treatment GS (b); and treatment SS (c).

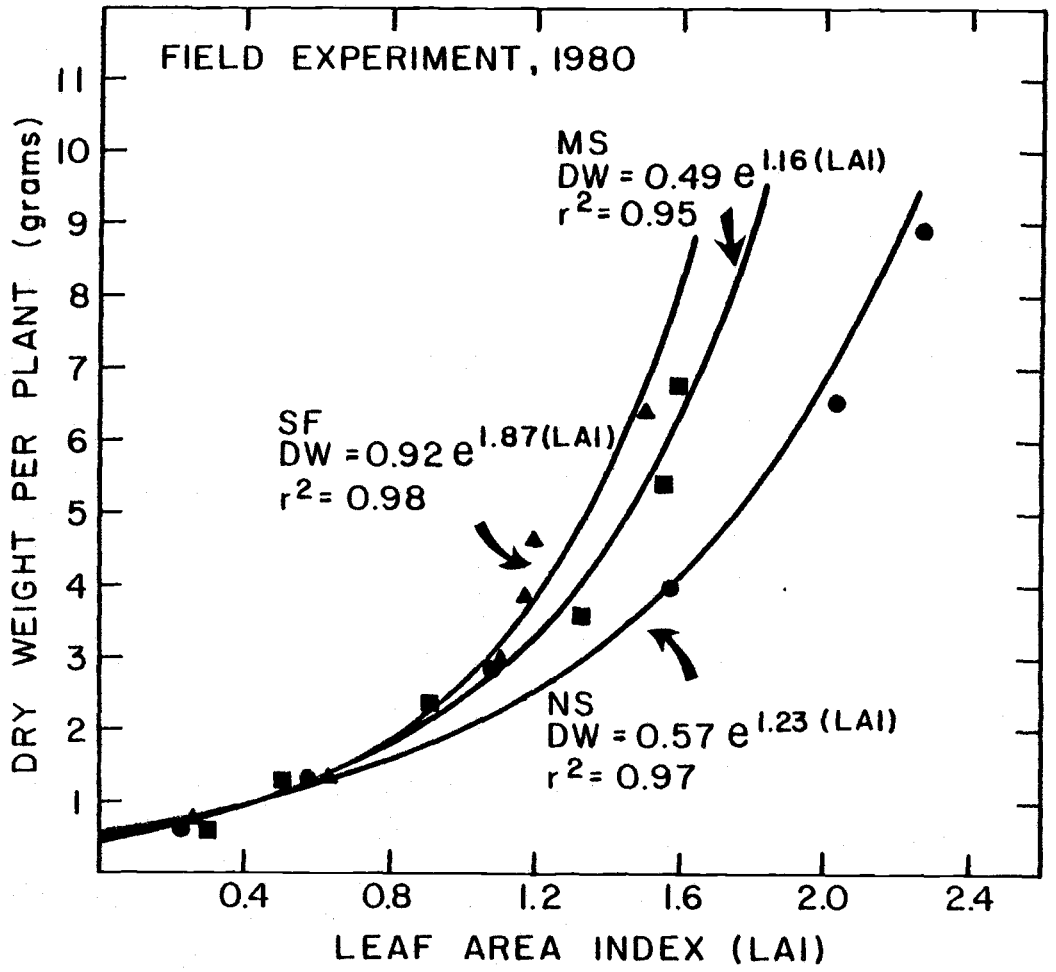

Figure 79. Dry weight per plant as function of leaf area index (LAI) for NS, MS and SF treatments of 1980 experiment.

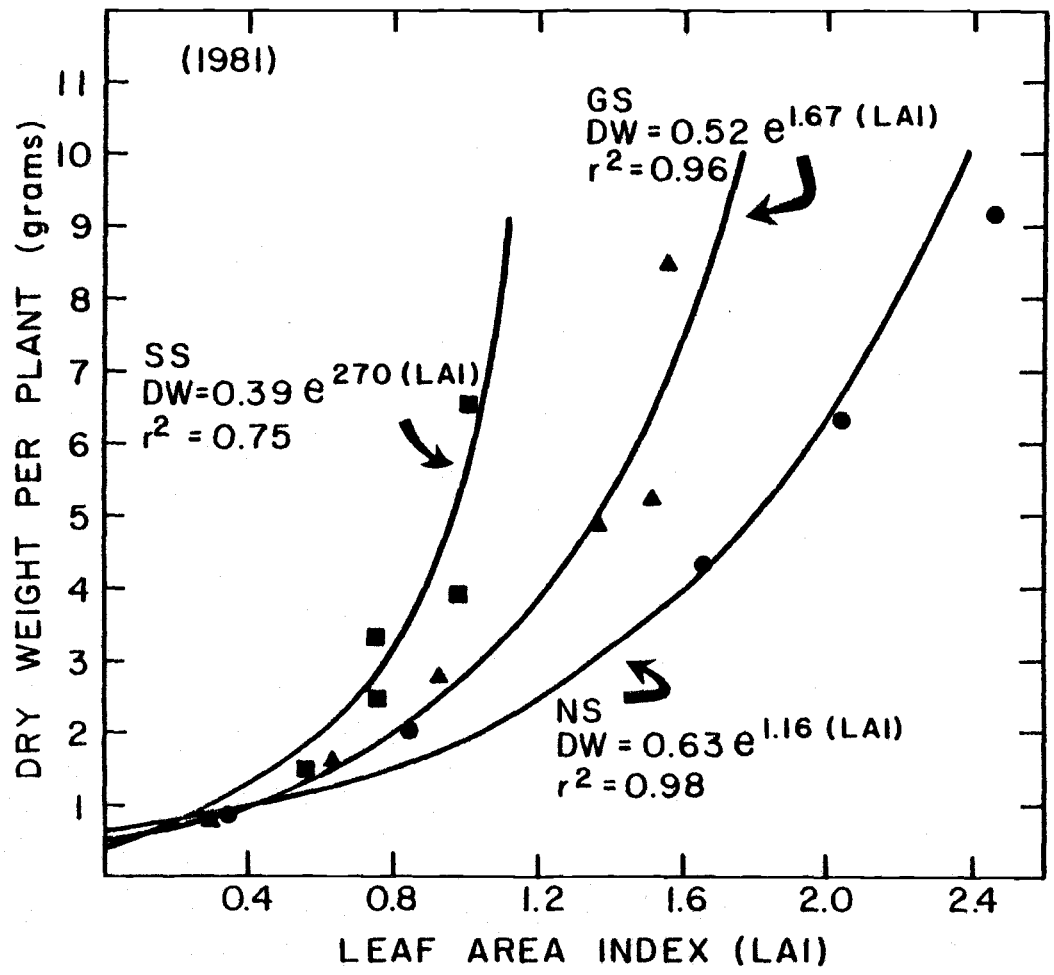

Figure 80. Dry weight per plant as function of leaf area index (LAI) of NS, GS and SS treatments of 1981 experiment.

stressed treatment show higher efficiency of a unit area of photosynthetic tissues per unit land area than those of the NS treatment. This may be explained partially by the effect of water stress on the morphology and thickness of the leaf. This can be discussed by looking at a well-known parameter which describes the dry weight of the leaf per unit area and called specific leaf weight (SLW). Higher SLW implies thicker tissues per unit leaf area. Figure 81b shows the changes of this parameter with plant age.

The data in Figure 81b show that the specific leaf weight of the SS treatment was greater than those of GS and NS treatment throughout the season, reaching a maximum level on day 47 after planting. This period corresponds to the time of movement of assimilates from the leaves to the pod formation sites. These results indicate that water stress increases the thickness of the leaf and this becomes more pronounced under severe water stress. The SS and GS treatments had about 80 and 90 percent of the maximum specific leaf weight of NS treatments. Results of Figures 79 and 80 may also be explained by the fact that the severely stressed treatment had smaller ground coverage and experienced less self-shading throughout the day. However, in the case of the NS treatment, the canopy reached full coverage a few days after flowering and self-shading was common throughout the rest of the growing season. This difference in self-shading might provide some differences in utilizing direct solar radiation.

Figures 81a shows an increase of the leaf area ratio with age of the plant. Statistical analysis shows no significant difference between treatments throughout the season.

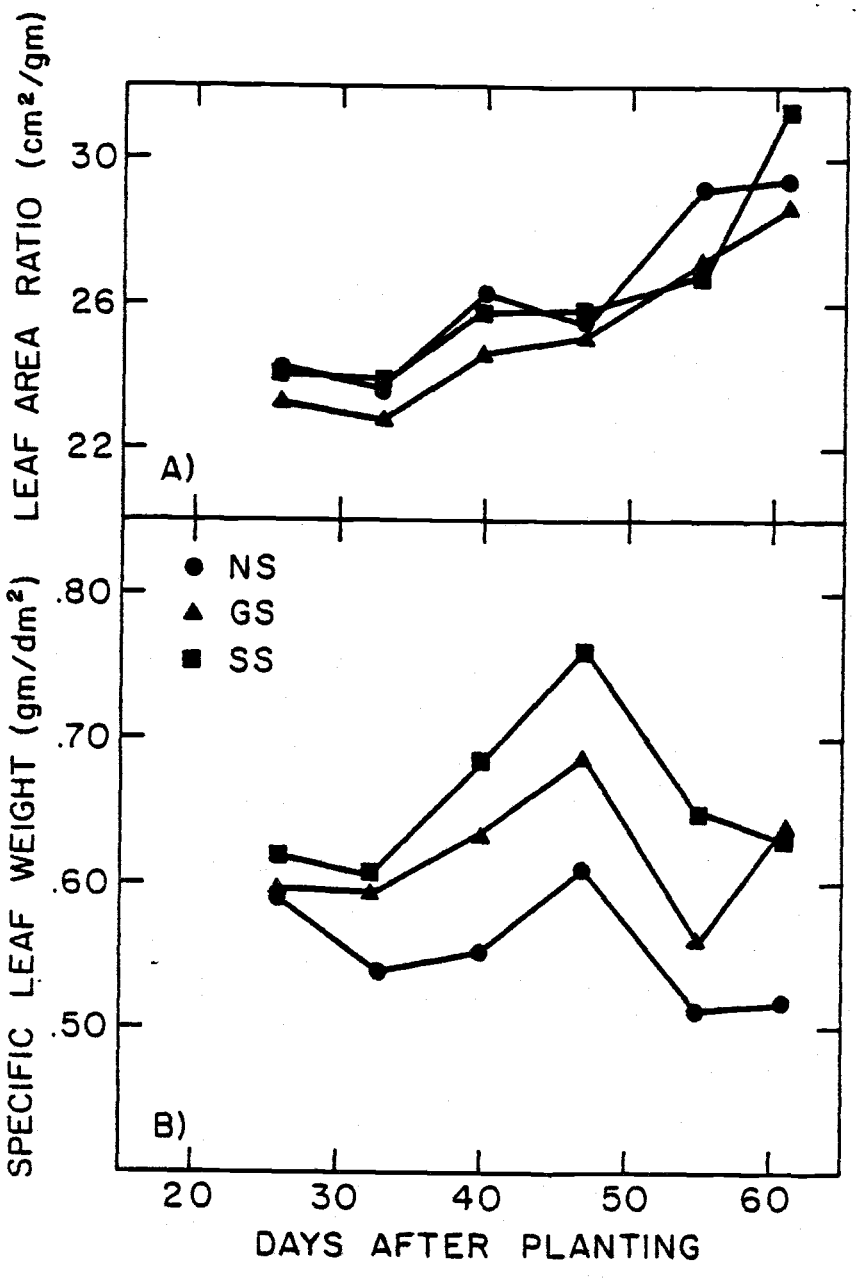

Figure 81. Leaf area ratio (a) and specific leaf weight (b) as functions of days after planting for treatments NS, GS, and SS of the 1981 experiment.

Treatment Effects on Yield and Yield Components

The treatment effects on the above-ground biomass production resulted in the GS and SS treatments producing 50 and 33 percent of the control treatment, respectively (Figure 77b). It would be more important to analyze the treatment in terms of pod yield. Tables 10 and 11 give the yield data for all treatments of the two experiments along with the number of pods per plant and weight of pods.

The analysis of variance of these parameters showed highly significant F values at the 5 percent and 1 percent levels of significance. Severe water stress reduced the weight per pod and the number of pods per plant. Hence, these two parameters determined the differences in yield among the treatments.

Treatment GS of the 1980 experiment was superior to the frequently irrigated NS treatment in pod weight, number of pods per plant and pod yield. This could be attributed to a better timing of irrigation at different growth stages. Treatment SF of 1980 was significantly lower than all other treatment in pod yield and number of pods per plant (Table 12). This treatment provided moderate stress during the flowering stage. This stage of bean development clearly is very sensitive to water stress in terms of pod yield. Reduction in the number of pods per plant due to water stress can be attributed to many possible causes such as abortion of fertilized ovules (Panelsos, 1961). Once the pod number per plant is fixed, the pod weight is determined by the ability of the plant to provide assimilates during the pod filling period. Results from the 1981

TABLE 10. Comparisons between treatments of yield and yield components of the 1980 experiment. The symbols *, ** and *** denote significance according to the analysis of variance at the 10%, 5%, and 1% level of significance, respectively. Any two means in the same horizontal row did not differ significantly if followed by the same letter.

Yield Components	MS	SF	GS	NS
Weight of pod (gm/pod)***	5.75b	4.88a	5.91b	5.17a
No. of pods/m^2 **	275.1a	183.5b	325.8a	294.8a
No. of pods/plant**	9.16a	6.12b	10.86a	9.84a
Pod yield (Kg/ha)***	15864a	9093b	19348a	15270a
Total yield (Kg/ha)**	31085a	27199b	35063a	29627a
Harvest index*	0.506ab	0.410b	0.550a	0.518a

TABLE 11. Comparisons between treatments of yield and yield components of the 1981 experiment. The symbols *, **, and *** denotes significance according to the analysis of variance at the 10%, 5%, and 1% level of significance, respectively. Any two means in the same horizontal row did not differ significantly if followed by the same letter.

Yield Components	NS	GS	SS
Weight of pod (gm/pod)***	5.14a	4.06a	2.47c
No. of pods/m^2 ***	361a	344a	164b
No. of pods/plant***	11.94a	11.48a	5.47b
Pod yield (Kg/ha)***	18557a	14109a	4052b
Total yield (Kg/ha)***	33580a	21967b	8278c
Harvest index**	0.553ba	0.538a	0.490b

TABLE 12. Comparisons of pod yield, number of pods per plant, and weight per pod for the 1980 experiment.

Treatments	NS	MS	GS	SF
Pod yield (Kg/ha)	15270	15863	19348	9093
% Relative to NS	100	103	127	59
No. of pods per plant	9.84	9.16	10.86	6.12
% Relative to NS	100	93	110	62
Weight per pod (gm)	5.17	5.75	5.91	4.88
% Relative to NS	100	111	114	94

TABLE 13. Comparison of pod yield, number of pods per plant, and weight per pod for the 1981 experiment.

Treatments	NS	GS	SS
Pod yield (Kg/ha)	18557	14109	4052
% Relative to NS	100	76	22
No. of pods per plant	11.94	11.48	5.47
% Relative to NS	100	96	46
Weight per pod (gm)	5.14	4.06	2.47
% Relative to NS	100	79	48

experiment showed that the pod yield for the GS and SS treatments were 24.0 percent and 78.0 percent less than the yield of NS treatment for the 1981 experiment, respectively (Table 13).

Water stress may have a negative effect on rate of photosynthesis during pod filling, by stomatal closure or by altering related biochemical processes. Water stress may also affect the plant by reducing the leaf area duration (integral of LAI vs. time curve). Water stress may accelerate leaf senescence and hence reduce leaf area duration (Figure 76). Reduction in the leaf area duration may cause shortening of the pod filling period and consequently produce smaller pods. It can be generally concluded that reduction in rate of photosynthesis and in leaf area duration contributed significantly to the reduction in the yield of the water stressed crops.

An important parameter in crop production is the harvest index which is the ratio of dry weight of economic product to total biomass dry weight. Tables 10 and 11 show that the GS treatment produced the highest HI level both years. In this treatment the higher proportions of total dry matter was allocated to the pods. The SS treatment had a much lower HI. The SF treatment produced a lower HI than the SS treatment. The differences between GS and NS could be attributed to the poor canopy architecture and the mutual self-shading of leaves of the NS treatment. Another possible explanation is that in the case of NS the root growth might have acted as an alternative sink which competed for assimilates with the developing pod during pod filling stage. The data obtained in this experiment are not sufficient to evaluate this possibility.

Results shown in Figure 82 might provide a possible explanation for the difference in HI between treatments listed in Tables 10 and 11. The number of pods per plant, which is considered as an indication of sink strength, was well-correlated with the harvest index. The correlation r^2 value was 0.806. The diagram suggests that under conditions of mild water stress, plants might be able to efficiently mobilize and translocate substances from many parts of the plant into the harvestable yield. However, under conditions of severe water stress, translocation of these accumulated substances will be impaired as in the case of the SS treatment of the 1981 experiment.

Severe water stress reduces the number of pods to be filled and then reduces translocation of assimilates from other plant parts to the pod, reducing the final pod weight.

The Water Production Function of Snap Beans

A water production function is generally defined as the relationship between water applied and yield. In this experiment it was assumed that other inputs (fertility, weed control, ...) held constant and at levels adequate for high yields (Stewart et al., 1973).

There are many expressions for the input units. Many research workers use crop evapotranspiration (ET_c) as the input and consider the function in terms of ET_c vs Y. Stewart et al. (1973, 1974) showed that plotting the water applied versus yield results in a curvilinear relationship. However, plotting yield versus total evapotranspiration of the crop produces a linear relationship. Cuenca (1978) argued that the ET versus yield function can be related

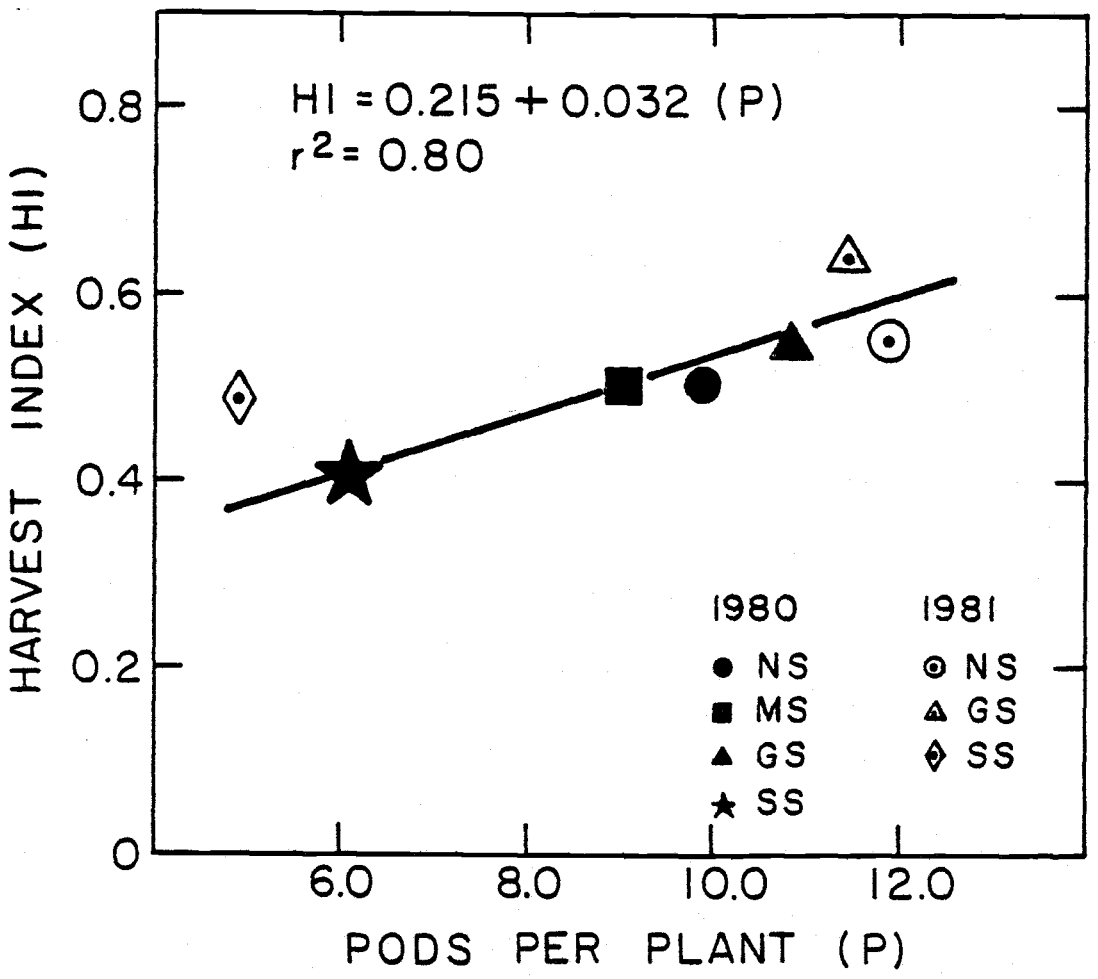

Figure 82. Harvest index (HI) as function of number of pods per plant. The line represents the linear regression over the experimental points of both field experiments. Each data point represents the average of four replications.

indirectly to different climatic conditions. On the other hand, the applied water versus yield relationship does not take into consideration soil water depletion that reflects the soil and climatic conditions. This linear characteristic of the ET_c vs Y relationship makes it more useful and informative for our study.

In this study, the crop ET is estimated by employing a modified water balance method. It considers the variation of soil water in the root zone in addition to the amount of water applied by irrigation or rainfall. Deep percolation was not measured, but water in excess of the estimated field capacity was considered to be lost to deep percolation. The change of soil water content was monitored by the use of a neutron probe. It is used to measure the water content on a volume basis and was calibrated in the field as shown in Figure 83. This instrument is considered by many as satisfactory (Tanner, 1967; Hillel, 1980).

Neutron probe measurements were performed one day before and one day after irrigation. Soil wetness was monitored at depths of 15, 30, 45, 60, 90, 120, 150, and 180 cm. Water applied during irrigation was assumed to be sufficient to completely wet the soil profile to field capacity. The level of field capacity was estimated by determining the water content in a fallow area two to three days after irrigation. Field capacity was determined early in the season in each plot of the experiments to minimize the variation due to spatial variability.

The ET of the crop was estimated by using the following expression of the water balance equation

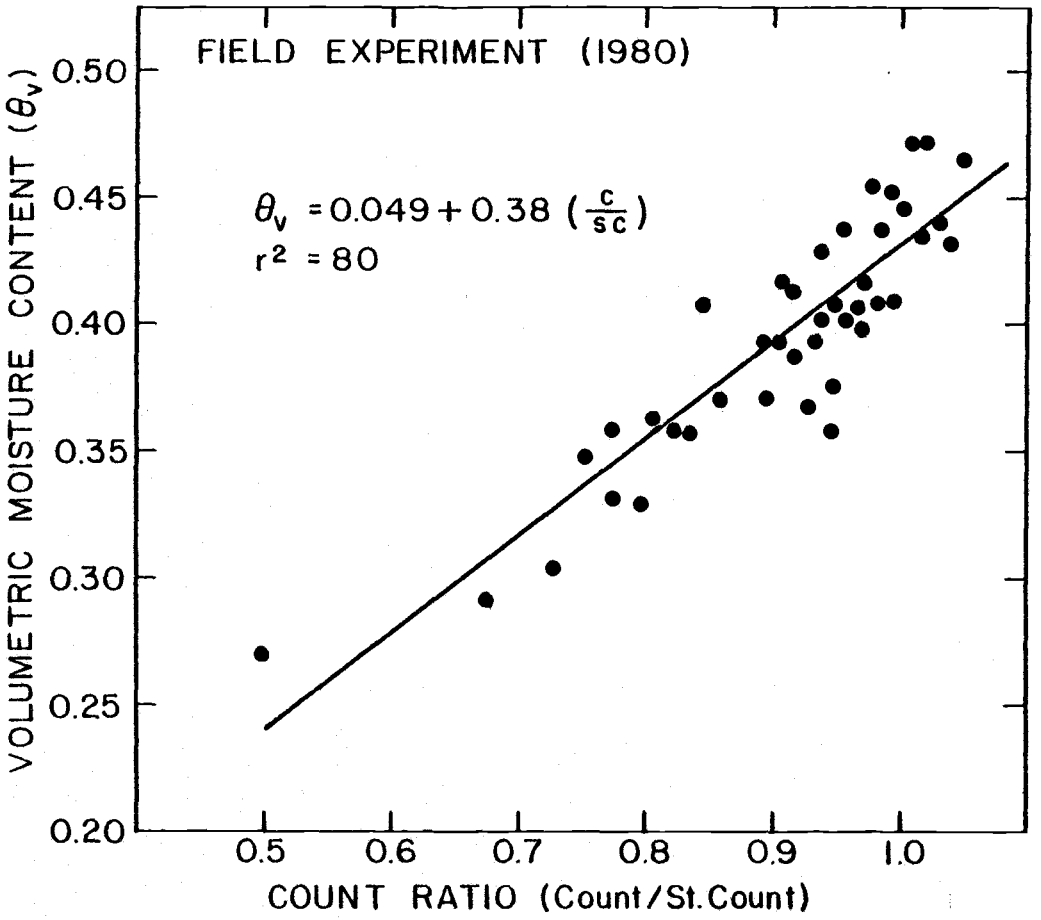

Figure 83. Neutron probe calibration curve relating the volumetric water content with count ratio (the ratio of the counts to the standard counts). The instrument is made by Troxler Electronic Laboratories, Inc., Moisture Gauge Model 104A and Scaler Model 2601.

$$\theta_{i-1} + I_i + R_{i-j} = (ET_c)_{i-j} + \theta_{j-1}$$

where θ_{i-1} is the soil water content in the profile directly before the i^{th} irrigation, I_i is the amount of irrigation water applied in the i^{th} irrigation, R_{i-j} is the amount of rainfall between the i^{th} and the j^{th} irrigation, $(ET_c)_{i-j}$ is the amount of crop evapotranspiration during the period between irrigations i and j, θ_{j-1} is the soil water content in the profile directly before the j^{th} irrigation,

and $i = 1,2,3,4,5,\ldots,n$, $j = i+1 = 2,3,4,5,\ldots n+1$

therefore

$$(ET_c)_{i-j} = \theta_{i-1} + I_i + R_{i-j} - \theta_{j-1} \qquad (31)$$

and seasonal $ET_c = \sum_{i=1}^{n} (ET_c)_{i-j} \quad j = i+1$

When water applied during irrigation plus rainfall does not fill the profile to the level of field capacity, deep percolation will be neglected and ET_c can be estimated by equation (31). However, if the water applied (irrigation + rainfall) is greater than the field capacity estimated, crop ET can be estimated by the following equation

$$(ET_c)_{i-j} = FC + R_i - \theta_{j-1} \qquad (32)$$

where FC is the estimate of field capacity in the soil profile, R_i is the amount of rainfall during the period two days after the i^{th} irrigation to the j^{th} irrigation.

The seasonal crop ET can be computed by making use of the available information on evaporation of water from a standard class A evaporation pan. Total evaporation from a class A pan was calculated to be 367.5 and 374.4 mm during the 1980 and 1981 experiments, respectively. Doorenbos and Pruitt (1977) have recommended the use of the equation,

$$ET_r = k_p \cdot E_{pan} , \qquad (33)$$

where E_{pan} is the pan evaporation in mm, and k_p is the pan coefficient. This coefficient was estimated to be equal to 0.65 for the conditions of light winds and medium humidity that was common throughout the growing season of the two field experiments (see Doorenbos and Pruitt, 1977), and ET_r is the reference evapotranspiration which was given by Jensen et al. (1970) and refined later by Doorenbos and Pruitt (1977). This parameter was extracted from the original concept of potential evapotranspiration (ET_p). Penman (1956) defined ET_p as "the amount of water transpired in unit time by a short green crop, completely shading the ground, of uniform height, and never short of water." Many researchers discussed and provided many definitions of ET_p (Penman, 1956; Van Bavel, 1966; Jensen, 1974; Doorenbos and Pruitt, 1977; Burman et al., 1980).

The reference ET values estimated from equation 33 for the 1980 and 1981 experiments were 238.9 mm and 243.3 mm, respectively. The mean daily values for the two seasons were 3.85 and 3.92 mm/day, respectively. The actual crop evapotranspiration (ET_c) can be related to ET_r as follows

$$ET_c = k_c \cdot ET_r \qquad (34)$$

where k_c is the crop coefficient, and ET_c and ET_r were defined previously. The crop coefficient incorporates the effects of crop density, growth stage, and crop physiology in general terms. It relates the ET of a disease-free crop growing in large fields under optimum soil, water, and fertility conditions which achieve the full production potential under the given growing environment (Doorenbos and Pruitt, 1977). In our study we estimated the k_c value of the well watered treatment (NS) for comparison purposes. The k_c varies during the growing season depending on the growth stage. Figure 84 shows the variation of k_c of the NS treatment with plant age. This figure is constructed by the procedure described by Doorenbos and Pruitt (1977). For the other irrigation treatments, a family of k_c curves would be needed, with a different curve for each irrigation treatment. Equation 34 provided ET_c values of 19.42 mm and 19.86 mm for the NS treatment during the 1980 and 1981 experiments, respectively. Table 14 shows a comparison between the ET_c calculated from the water balance method and that estimated from climatic data.

TABLE 14. Comparison of crop evapotranspiration (ET_c) calculated from the water balance method [$(ET_c)_{soil}$] and that calculated from the climatic data [$(ET_c)_{climate}$] for 1980 and 1981 experiments.

	E_{pan}	k_p	ET_r	$(ET_c)_{soil}$	$(ET_c)_{climate}$
1980	367.5	0.65	238.9	155.7	194.2
1981	374.4	0.65	243.3	176.3	198.6

The water production function of the combined data of the 1980 and 1981 experiments is shown in Figure 85. It can be seen that the relationship between evapotranspiration and pod yield appears to be a linear one, as has been reported for other crops by researchers elsewhere. Table 15 shows some of those functions for sorghum, corn, cotton, tomato, and two bean varieties. It can be noted that the data show great scattering. This would be expected due to unavoidable variation in field studies in addition to the errors produced in the monitoring of the soil water depletion by the neutron probe. Figure 86 shows the relationship between percent yield reduction ($\Delta Y = 100\ (Y_m - Y/Y_m)$) and percent evapotranspiration deficit, $\Delta ET = 100\ (ET_m - ET/ET_m)$. The slope of the line represents the yield reduction ratio

$$YRR = \frac{\Delta EY}{\Delta ET} .$$

This ratio represents the impact on yield from each increment of ET (Cuenca et al., 1978). It is a characteristic of a particular crop. It may differ between crop varieties as well as species.

Stewart (1975) reported figures of 0.98, 1.26 and 2.33 as yield reduction ratios for grain sorghum, maize, and pinto beans, respectively. This ratio is considered by many researchers as a good indicator of drought tolerance of crops. The smaller the ratio, the higher the drought tolerance. Therefore, a low value of this ratio should be sought when breeding for drought tolerance. Results in Figure 86 shows that snap beans have a yield reduction ratio (YRR = 1.23) comparable to that of maize. This value might imply that snap beans do not respond so critically to water deficits. However, from

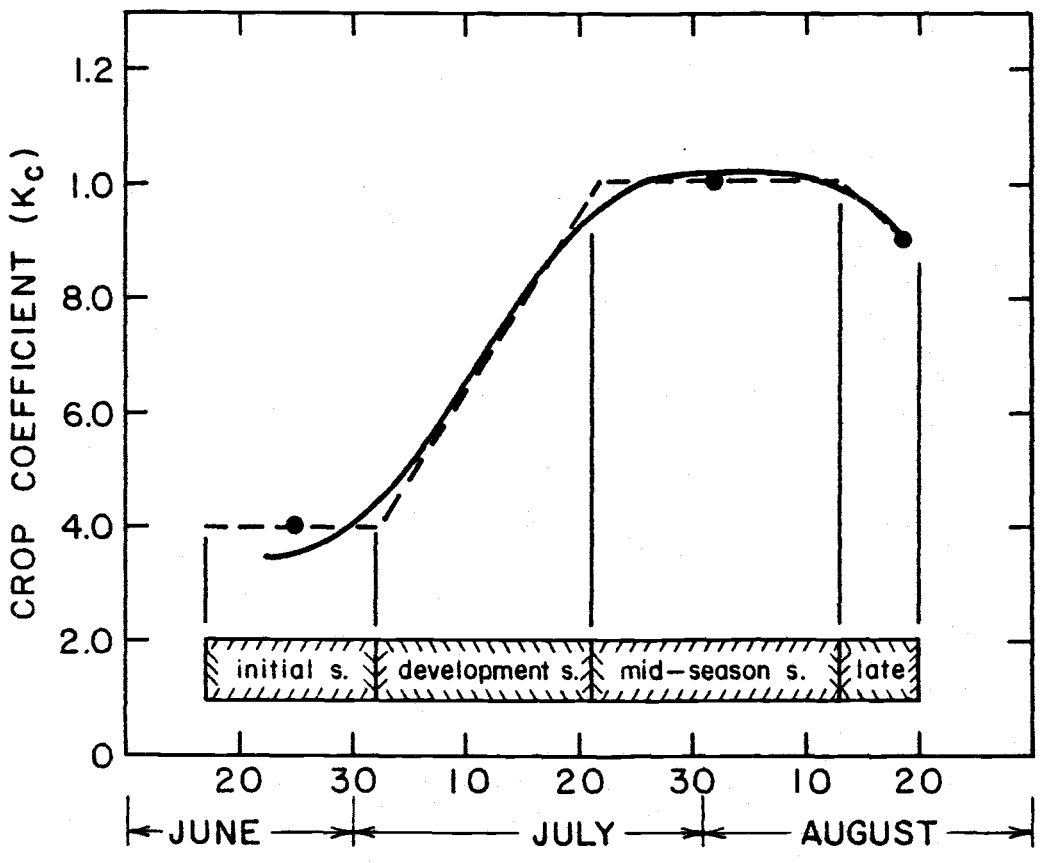

Figure 84. The crop coefficient curve for beans grown in Corvallis, Oregon. K_c values relates to a reference crop of grass. Curve constructed according to procedure described by Doorenbos and Pruitt (1977).

TABLE 15. Water production functions, Y vs ET, for different cultivars.

Cultivars	Functions	References
Grain Sorghum	$Y^{\bigstar} = 541 + 144.8\ ET$	Stewart et al. (1973)
SJ2 Cotton	$Y = -499 + 31.2\ ET$	Cuenca (1978)
Corn	$Y = -3979 + 261.5\ ET$	Stewart & Hagan (1973)
UC82 Tomato	$Y = 125 + 12.5\ ET$	Cuenca et al. (1978)
Light Red Kidney Bean	$Y = -916 + 91.84\ ET$	Cuenca et al. (1978)
Gloria Pink Bean	$Y = -730 + 114\ ET$	Cuenca et al. (1978)

★ Y expressed in kgm/ha and ET in cm.

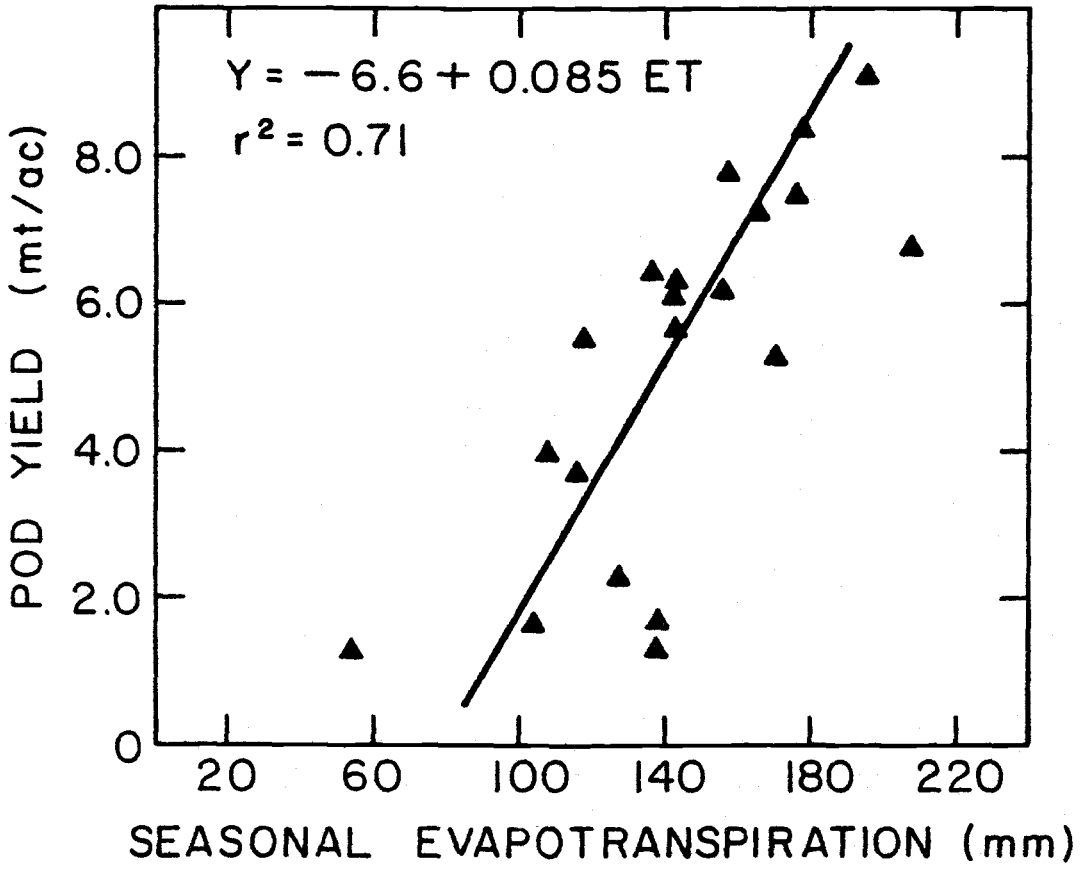

Figure 85. Pod yield as a function of seasonal evapotranspiration. Data points represent an average of two plots of 1980 experiment and a single plot of 1981 experiment.

the evidences demonstrated throughout the text of this discussion it appears that snap beans respond to water deficits in many ways which led eventually to lower yield of the crop. Stewart (1975) pointed out that yield of beans does not respond so critically to water deficit because of their ability to produce a new set of pods when moisture becomes favorable. Unfortunately, this was not studied in many details in this experiment.

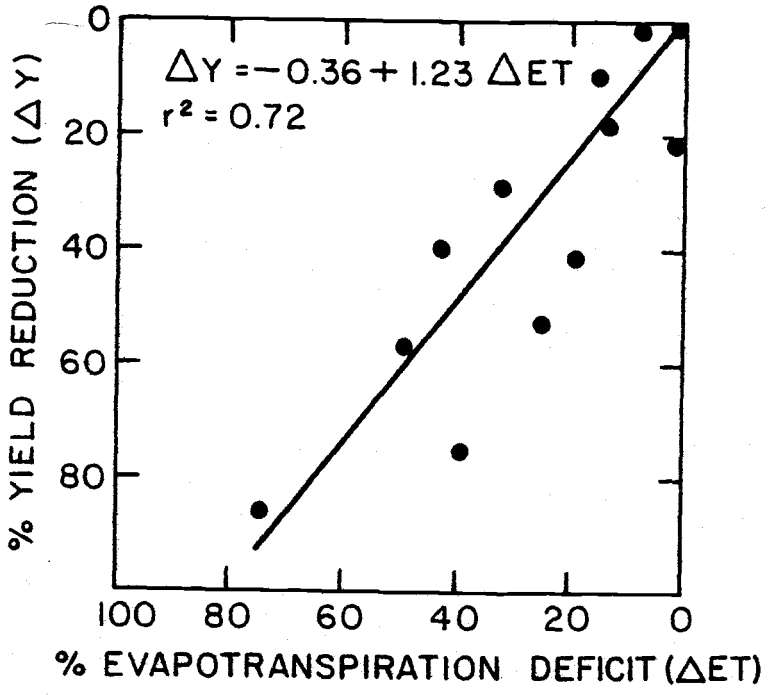

Figure 86. Relative yield reduction as a function of evapotranspiration deficit.

SUMMARY AND CONCLUSIONS

Some physiological and agronomic responses to water stress of snap beans were investigated in two field experiments. Additionally, a simple experiment was conducted in the controlled environment of the growth chamber to study the concept of Plastochron Index in monitoring the changes in the growth of the leaves under variable water supply.

P-V Curves

Observations

The Pressure-Volume method was used to study plant water relations at the cellular level and to determine the parameters required for correction of osmotic potential of the leaf sap. The mean values of osmotic potential at full turgor, $\Psi_{s,100}$, of fully expanded bean leaves were -5.39 $\pm$ 0.34 and -6.72 $\pm$ 1.33 bars for the NS and SS treatments, respectively, and -8.84 bars for leaves of the controlled environment experiment. The mean values of osmotic potential at zero turgor were -8.02 $\pm$ 0.53, -10.66 $\pm$ 2.36, and -11.10 bars for the NS, SS, and CE treatments, respectively. The mean values of the relative water content at zero turgor were 76.0 $\pm$ 2.0, 79.7 $\pm$ 5.1 and 82.5 percent for NS, SS, and CE treatments, respectively. The apoplastic water content ranged from 12.1 to 16.9 percent of the total volume with a mean value of 14.9 $\pm$ 2.5 percent for the leaves of the irrigated treatment. Value of the apoplastic water content for the SS leaves ranged from 22.4 to 25.4 percent with a mean value of 23.7 $\pm$ 1.52

percent. The leaves of the controlled environment had an apoplastic fraction of 9.9 percent. The elastic modulus of the tissues increased linearly with increasing turgor pressure from 0 to 2.5 bars. The decrease in Ψ_s by going from full turgor to zero turgor status was from 1.5 to 3.0 bars in the NS treatment and from 2.5 to 6.0 bars in the SS treatment. There was no significant difference between treatments in the degree of change of Ψ_s with respect to change in hydration level (RWC). The ratio of symplastic water to total water volumes (V_s/V_t) of the severely stressed treatment (SS) was consistently lower by about 7.0 percent than that of the NS treatment. There was no significant difference in the volume ratio of symplastic water at zero turgor to that at full turgor.

Conclusions

Severe and prolonged water stress condition reduced the values of $\Psi_{s,0}$, $\Psi_{s,100}$, and Ψ_0. The apoplastic water fraction increased with water stress as did the RWC_0. Changes in the modulus of elasticity varied within treatments as much as between treatments.

Plastochron Index

Observations

Plastochron Index measurements revealed information about responses of vegetative growth to water stress. Water stress reduced the value of the slope of PI versus time drastically both in the field and in the growth chamber experiments. The values of the slope of the

curves of PI vs. time after planting were 0.559, 0.412, and 0.340 for treatments NS, GS, and SS of the field experiments, respectively. Slopes for the growth chamber experiment were 0.165 and 0.104 for the NS and SS treatments, respectively. The plastochron durations of the SS treatment were 1.65 and 1.69 times that of the control treatments of the field and growth chamber experiment, respectively.

Conclusion

The plastochron index and the leaf plastochron index can be applied to an individual plant sampled over specific time interval or to a large number of plants sampled simultaneously at different times of the growing season. The use of PI for the water stress studies seems promising and encouraging, which suggests that similar studies with more precise and specific objectives for the use of PI are needed for snap beans and commercial plants.

Plant Water Potentials

Observations

Measurements of the diurnal and seasonal changes of water potentials showed that it is very difficult to establish an accurate threshold level of Ψ at which stomata close. When plants were detached and exposed to higher rates of stress development, the threshold value of Ψ for stomatal closure was estimated to be in the range from -10.5 to -12.5 and from -13.0 to -15.0 bars for the SS and the NS treatments, respectively. Estimation of threshold turgor

pressure was not possible from the available measurements.

Conclusion

The slow development of water stress under field conditions showed that the leaves of the well watered treatment had higher (less negative) leaf Ψ than those of the severely stressed treatment throughout the daytime hours. Measurements showed diurnal as well as seasonal changes in the potential components. There was some evidence of partial closure of stomatas during mid-day hours. This closure was more pronounced under severe water stress.

Responses to Water Stress

Observation

The agronomic responses to water stress were represented by the seasonal changes in LAI, fresh weight, and dry weight of the plant. The maximum difference of LAI at the end of the vegetative growth period were in the order of 0.9 and 1.1 units for the GS and SS treatments, respectively. The control treatment (NS) accumulated the most dry matter through the season and (SS) treatment gave the lowest dry matter yield through the 1981 season. Exposing the plants to prolonged severe stress during flowering as in the case of the treatment SF had great impact on the production of dry matter. Treatment SF accumulated only 72 percent of that of the NS treatment. The final above ground biomass in GS and SS treatments were about 55 and 37 percent that of the NS treatment in the 1981 experiment. Specific

leaf weight of plants on the severely stressed treatment was greater than those of the GS and NS treatments throughout the season, reaching a maximum value about day 47 after planting.

Conclusion

It appears that water stress causes delay of leaf initiation, the reduction of cell division and cell enlargement, the reduction of leaf area development, the reduction of dry matter accumulation, and the enhancement of leaf senescence. The specific leaf weight is reduced by water stress. The flowering stage seems to be very sensitive to water stress conditions.

Yield Components

Observations

The maximum value of dry weight to fresh weight ratios was 0.107 for all irrigation treatments. These maximum ratios occurred at an age of 11.6 and 9.0 plastochron for NS and GS treatments, respectively.

The maximum numbers of leaves per plant were 21, 16, and 11 for the NS, GS, and SS treatments, respectively. The leaves of the same plant did not reach the same final lengths. Leaves of the stressed plants had slower growth rates and did not attain the same final length as those of the well watered plants. The delay in leaf appearances due to water stress ranged from four days for the 1st leaf to eight days for the 5th leaf. The elongation rates of all leaves decreased with age. This effect became more pronounced with increasing severity of water stress. The pod yield for the GS and SS treatments

were reduced by 24.0 and 78.0 percent of that of the NS treatments, respectively. Treatments SS and GS produced smaller pods weighing 48 and 79 percent of those produced by the NS treatment, respectively. Irrigation timing played a major role in determining the yields of treatment GS of the 1980 experiment. Treatment GS was superior to all other treatments including the frequently irrigated treatment. It gave higher pod yields, heavier pods and greater number of pods per plant. Treatment GS had the highest Harvest Index (HI) in both field experiments and treatment SF had the lowest value of HI.

Conclusion

Severe water stress reduced the growth rates and the final length attained by leaves. Irrigation timing may play a major role in minimizing the damages of water stress. Severe water stress reduced the pod yield, number of pods, and the weight per pod.

Summary

This study of soil-water plant relations of beans under water deficit under field conditions was most revealing. Within the limitations imposed by our methodology and type of measurements taken, some important general conclusions could be drawn from the results of these experiments. These are tabulated below.

1. The pressure-volume technique seems to be very useful in studying the internal characteristics of water relations of plants and in obtaining the apoplastic water content necessary for correcting osmotic potential data determined

by the hygrometric method. This method cannot be used to obtain osmotic and turgor pressure for plants capable of undergoing osmotic adjustment. The use of this method is restricted by the limited number of measurements that can be made.

2. The relationship between total water potential and relative water content is not unique and was altered by water deficit conditions. The relationship changes in space and time.
3. The water deficit conditions produced water stress that reduced the value of $\Psi_{s,0}$, Ψ_0, and $\Psi_{s,100}$. The bound water fraction increased with water stress as did the relative water content at zero turgor.
4. Results indicate that the modulus of elasticity was not altered by water stress. However, it is the author's belief that this parameter is ambiguous and needs to be defined more accurately and clearly.
5. The leaf water status expressed as Ψ, Ψ_s, and Ψ_p is not constant, rather it changes diurnally and seasonally due in part to the plants ability to osmoregulate. Bean plants seem to be capable of adjusting the osmotic component partially which allows for maintenance of the turgor component at low water potential.
6. Results of the effects of water stress on the growth rate of leaves lead to the conclusion that the relationship between growth rate and turgor pressure is not simple. Differences in growth rates between non-stressed and stressed treatments

could not be explained on the basis of turgor pressure alone. The Ψ_p seems to be responsible for the short term effects. However, long term effects might be attributable to factors other than turgor pressure.

7. The plastochron index concept seems to be very useful in water relation studies. It allowed an accurate and reproducible description of the shoot and leaf ontogeny in quantitative terms. This index, however, cannot be applied to all growth stages indiscriminently. A different index should be developed for the reproductive stage where the growth of a reproducible organ is measured rather than the leaf length.
8. It appears that water stress causes delay of leaf initiation in addition to its effect on cell division and cell enlargement. A reduction in vegetative growth and in leaf area induced by water stress may be critical in terms of yield, but the most critical growth stage to water stress is the flowering stage.
9. The irrigation timing according to the growth stages indicated in treatment GS of the 1980 experiment produced the highest level of crop yield pointing to a possible water management strategy.
10. The pod yield was drastically reduced under conditions of severe, prolonged, water stress. Reduction of pod yield was expressed in terms of smaller number of pods per plant and lighter pods produced.

11. Overall it can be concluded that bean crop is highly sensitive to water stress. The crop may adapt partially against a changing environment, but not to overcome the drastic effects of severe water stress.

12. Finally, it is reasonable to conclude that even though field conditions are quite variable and very dynamic and the obtained results were based on a discrete measurements of a continuously changing system. Yet these kinds of studies proved to be informative and valuable to integrative research approaches.

BIBLIOGRAPHY

Acevedo, E. 1975. The growth of maize (Zea mays L.) under field conditions as affected by its water relations. Ph.D. Dissertation. University of California, Davis. 253 pp.

Acevedo, E., E. Fereres, T. C. Hsiao, and D. W. Henderson. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. Plant Physiol. 46:476-480.

Acevedo, E., T. C. Hsiao, and D. W. Henderson. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.

Arnon, I. 1981. Physiological principles of crop production. In: Physiological aspects of dry land farming. U.S. Gupta (ed.) pp. 3-124. 4th Printing. Oxford and IBH Publishing Co. New Delhi.

Barlow, E. W. R. 1979. Physiological effects of water stress on young corn plants. Ph.D. Dissertation. Oregon State University. 128 pp.

Barlow, E. W. R., L. Boersma, and J. L. Young. 1976. Root temperature and soil water potential effects on growth and soluble carbohydrate concentration of corn seedlings. Crop Science 16:59-62.

Barrs, H. D. 1968. Determination of water deficit in plant tissues. In: Water deficits and plant growth, I. (T. T. Kozlowski, ed.) Academic Press, New York.

Baughn, J. W., and C. B. Tanner. 1976. Leaf water potential: Comparison of pressure chamber and in situ hygrometer on five herbaceous species. Crop Science 16:181-184.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

Bernstein, L. 1961. Osmotic adjustment of plants to saline media. I. Steady State. Amer. J. Bot. 48:909-918.

Blum, A. 1974. Genotypic responses in sorghum to drought stress. II. Leaf tissue water relations. Crop Science 14:691-692.

Boyer, J. S. 1967a. Leaf water potentials measured with a pressure chamber. Plant Physiol. 42:133-137.

Boyer, J. S. 1967b. Matric potential of leaves. Plant Physiol. 42:213-217.

Boyer, J. S. 1968. Relationship of water potential to growth of leaves. Plant Physiol. 43:1056-1062.

Boyer, J. S. 1969. Measurement of the water status of plants. Ann. Rev. Plant Physiol. 20:351-364.

Boyer, J. S. 1970a. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46: 236-239.

Boyer, J. S. 1970b. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at low leaf water potentials. Plant Physiol. 46:233-235.

Boyer, J. S. 1971. Recovery of photosynthesis in sunflower after a period of low water potential. Plant Physiol. 47:816-820.

Boyer, J. S. 1974. Water transport in plants: Mechanism of apparent changes in resistance during absorption. Planta 117:187-207.

Boyer, J. S. 1976. Photosynthesis at low water potentials. Phil. Trans. R. Soc. Lond. B 273:501-512.

Brevedan, E. R., and H. F. Hodges. 1973. Effect of moisture deficits on ^{14}C translocation in corn (Zea mays L.). Plant Physiol. 52:436-439.

Brix, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiologia Pl. 15:10-20.

Brown, K. W. 1974. Calculations of evapotranspiration from crop surface temperature. Agric. Meteorol. 14:199-201.

Brown, K. W., W. R. Jordan, and J. C. Thomas. 1976. Water stress induced alteration of the stomotal response to decreases in leaf water potential. Physiol. Plant 37:1-5.

Bunce, J. A. 1977. Leaf elongation in relation to leaf water potential in soybean. J. Exp. Bot. 28:156-161.

Bunce, J. A. 1978. Effects of water stress on leaf expansion, net photosynthesis, and vegetative growth of soybeans and cotton. Can. J. Bot. 56:1492-1498.

Burman, R. B., P. R. Nixon, J. L. Wright, and W. D. Pruitt. 1980. Water requirements. In: Design and operation of farm irrigation systems (M. E. Jensen, ed.). ASAE.

Campbell, G. S., and M. D. Campbell. 1974. Evaluation of a thermocouple hygrometer for measuring leaf water potential in situ. Agron. J. 66:24-27.

Campbell, G. S., R. I. Papendick, E. Rabie, and A. J. Shayo-Ngowi. 1979. A comparison of osmotic potential, elastic modulus, and apoplastic water in leaves of dryland winter wheat. Agron. J. 71:31-36.

Catsky, J. 1974. Direct methods of water content determination. In: Methods of studying plant water relations (J. Jacobs et al., eds.). Springer-Verlag, New York.

Chen, J. C. W. 1971. Effects of continuous illumination on the rhizome of caulerpa prolifera. Plant Cell Physiol. 12:895-905.

Chen, J. C. W. 1972. Effects of continuous illumination on the rhizoide cluster of caulerpa prolifera. Plant Cell Physiol. 13:875-884.

Cheung, Y. N. S., M. T. Tyree, and J. Dainty. 1975. Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. Can. J. Bot. 53:1342-1346.

Cheung, Y. N. S., M. T. Tyree, and J. Dainty. 1976. Some possible sources of error in determining bulk elastic moduli and other parameters from pressure-volume curves of shoots and leaves. Can. J. Bot. 54:758-765.

Christensen, N. W., R. G. Taylor, T. L. Jackson, and B. L. Mitchell. 1981. Chloride effects on water potential and yield of winter wheat infected with take-all root rot. Agron. J. 73:1053-1058.

Cleland, R. 1967. Inhibition of cell elongation in avena coleptyle by hydroxiproline. Plant Physiol. 42:271-274.

Cleland, R. 1971. Cell wall extension. Ann. Rev. Plant Physiol. 22:197-222.

Coleman, W. K., and R. I. Greyson. 1976. The growth and development of the leaf in tomato (Lycopersicon esculentum). I. The plastochron index, a suitable basis for description. Can. J. Bot. 54: 2421-2428.

Cuenca, R. H. 1978. Transferrable simulation model for crop soil water depletion. Ph.D. Dissertation, University of California, Davis. 310 pp.

Cuenca, R. H., J. I. Stewart, W. O. Pruitt, J. Tosso, and R. M. Hagan. 1978. Impacts on crop yields of different irrigation amounts and development of guidelines for efficient irrigation management. Interim report to state of California, Department of Water Resources, Department of Land, Air and Water Resources, University of California, Davis, 27 pp.

Cummings, W. R., H. Kende, and K. Raschke. 1971. Specifity and reversibility of the rapid stomatal response to abscisic acid. Planta (Berl.) 99:347-351.

Cutler, J. M., D. W. Rains, and R. S. Loomis. 1977. Role of changes in solute concentration in maintaining favorable water balance in field grown cotton. Agron. J. 69:773-779.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1979. Characterization of internal water relation of rice by a pressure-volume method. Crop Science 19:681-685.

Cutler, J. M., P. L. Stepnkus, M. J. Wach, and K. W. Shahan. 1980. Daynomic aspects and enhancement of leaf elongation in rise. Plant Physiol. 66:147-152.

Doorenbos, J., and W. O. Pruitt. 1977. Crop water requirements, Irrigation and Drainage Paper No. 24. Revised, Food and Agricultural Organization of the United Nations, Rome. 144 pp.

Doss, B. D., R. W. Pearson, and H. T. Rogers. 1974. Effect of soil water stress at various growth stages on soybean yield. Agron. J. 66:297-299.

Dubetz, S., and P. S. Mahalle. 1969. Effect of soil water stress on bush beans Phaseolus vulgaris L. at three stages of growth. Am. Soc. of Hort. Sci. 94:479-481.

Duniway, J. M. 1971. Water relations of fussarium wilt in tomato. Physiol. Plant Pathol. 1:537-546.

Ehrler, W. L. 1973. Cotton leaf temperature as related to soil water depletion and meteorological factors. Agron. J. 65:404-409.

Ehrler, W. L., S. B. Idso, R. D. Jackson, and R. J. Reginato. 1978. Wheat canopy temperature: relation to plant water potential. Agron. J. 70:251-256.

Ekasingh, M. 1982. Translocation of photosynthesis in soybeans (Glycine max. (L.) Merr. cv. Wilkin) as affected by soil water potential and soil temperature. Ph.D. Dissertation. Oregon State University, 184 pp.

El-Nadi, A. H., R. Browner, and J. Locker. 1969. Some responses of the root and the shoot of Vicia faba plants to water stress. Neth. J. Agric. Sci. 17:133-142.

Elston, J., A. J. Karamanos, A. H. Kassam, and R. M. Wadsworth. 1976. The water relations of the field bean crop. Phil. Trans. R. Soc. Lond. B. 273:581-591.

Erickson, R. O. 1948. Cytological and growth correlations in the flower bud and anther of Lilium Longiflorum. Amer. J. Bot. 35: 729-739.

Erickson, R. O. 1960. Nomogram for the plastochron index. Amer. J. Bot. 47:350-351.

Erickson, R. O., and F. J. Michelini. 1957. The plastochron index. Amer. J. Bot. 44:297-305.

Fereres, E. 1976. Growth, development and yield of sorghum in the field under variable water supply. Ph.D. Thesis, University of California, Davis. 247 pp.

Fereres, E., E. Acevedo, D. W. Henderson, and T. C. Hsiao. 1978. Seasonal changes in water potential and turgor maintenance in sorghum and maize under water stress. Physiol. Plant. 44:261-267.

Fischer, R. A., T. C. Hsiao, and R. M. Hagan. 1970. After effects of water stress on stomatol opening potential. I. Techniques and magnitude. J. Exp. Bot. 21:371-385.

Ford, C. W., and J. R. Wilson. 1981. Changes in levels of solute during osmotic adjustment to water stress in leaves of four tropical pasture species. Aust. J. Plant Physiol. 8:77-91.

Frank, A. B., J. F. Power, and W. O. Willis. 1973. Effect of temperature and plant water stress on photosynthesis, diffusion resistance, and leaf water potential in spring wheat. Agron. J. 65:777-780.

Gale, J., H. C. Kohl, and R. M. Hagan. 1966. Mesophyll and stomatol resistances affecting photosynthesis under varying conditions of soil water and evaporative demand. Israel J. Bot. 15:64-71.

Green, P. B. 1968. Growth physics in Nitella: a method for continuous in viro analysis of extensibility based on a micro-manometer technique for turgor pressure. Plant Physiol. 43:1169-1184.

Green, P. B., R. O. Erickson, and J. Buggy. 1971. Metabolic and physical control of cell elongation rate. In viro studies in Nitella. Plant Physiol. 47:423-430.

Green, P. B., and N. R. Cummings. 1974. Growth rate and turgor pressure. Auxin effect studies with an automatic apparatus for Coleophle. Plant Physiol. 54:863-870.

Gonzalez, A. R., and J. W. Williams. 1979. Effect of water stress during pod development on yield and quality of raw and canned snap beans. Hort. Sci. 14:125.

Hammel, H. T. 1968. Measurement of turgor pressure and its gradient in the phloem of oak. Plant Physiol. 43:1042-1048.

Hartt, E. E. 1967. Effect of moisture supply on translocation and storage of ^{14}C in sugar cane. Plant Physiol. 43:338-346.

Heathcote, D. G., J. R. Etherington, and F. L. Woodward. 1979. An instrument for nondestructive measurement of the pressure potential (Turgor) of leaf cells. J. Exp. Bot. 30:811-816.

Hellkvist, T., G. P. Richards, and P. G. Jarvis. 1974. Vertical gradients of water potential and tissue water relations in sitka spruce trees measured with a pressure chamber. J. App. Ecol. 11:637-667.

Hiler, E. A., C. H. M. van Bavel, M. M. Hossain, and W. R. Jordan. 1972. Sensitivity of Southern Peas to plant water deficit at three growth stages. Agron. J. 64:60-64.

Hillel, D. 1980a. Fundamentals of soil physics. Academic Press. New York.

Hillel, D. 1980b. Applications of soil physics. Academic Press. New York.

Hoffman, G. J., and J. A. Jobes. 1978. Growth and water relations of cereal crops as influenced by salinity and relative humidity. Agron. J. 70:765-769.

Hofstra, G., Hesketh, J. D., and D. L. Myhre. 1977. A plastochron model for soybean leaf and stem growth. Can. J. Plant Sci. 57:167-175.

Holowinsky, A. W., P. B. Moore, and J. B. Torrey. 1965. Regulatory aspects of chloroplast growth in leaves of Xanthium pennsylvanicum and etiolated red Kidney bean seedling leaves. Protoplasma 60:94-110.

Hsiao, T. C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.

Hsiao, T. C., and E. Acevedo. 1974. Plant responses to water deficits, water use efficiency and drought resistance. Agric. Meteorol. 14:59-84.

Hsiao, T. C., E. Acevedo, E. Fereres, and D. W. Henderson. 1976. Water stress, growth and osmotic adjustment. Phil. Trans. R. Soc. Lond. B. 273:479-500.

Humble, G. D., and K. Raschke. 1971. Stomotal opening quantitatively related to potassium transport: Evidence from electron probe analysis. Plant Physiol. 48:447-453.

Idso, S. B., R. J. Reginato, D. C. Reicosky, and J. L. Hatfield. 1981. Determining soil induced plant water potential depressions in alfalfa by means of infrared thermometry. Agron. J.

Iljin, W. S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. Plant Physiol. 8:257-274.

Jackson, R. D., S. B. Idso, R. J. Reginato, and P. J. Pinter, Jr. 1981. Canopy temperature as a crop water stress indicator. Water resources research 17:1133-1138.

Jacobs, N. P. 1972. Rhythm of leaf development and sensitivity to photoperiodic floral induction. Amer. J. Bot. 59:437-441.

Jensen, M. E. (Ed.). 1974. Consumptive use of water and irrigation water requirements. Rep. Tech. Com. on Irrig. Water Requirement. Am. Soc. Civ. Eng., Irrig. Drain. Div., 227 pp.

Jensen, M. E., D. C. N. Robb, and C. E. Franzoy. 1970. Scheduling irrigations using climate - crop - soil data. Proc. Am. Soc. Civ. Engr., J. Irrig. and Drain. Div. 96:25-38.

Jones, M. M., and H. M. Rawson. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency, and osmotic potential in sorghum. Plant Physiol. 45:103-111.

Jones, M. M., and N. C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61: 122-126.

Jones, M. M., and N. C. Turner. 1980. Osmotic adjustment in expanding and fully expanded leaves of sunflower in response to water deficits. Aust. J. Plant Physiol. 7:181-192.

Jones, M. M., C. B. Osmond, and N. C. Turner. 1980. Accumulation of solutes in leaves of sorghum and sunflower in response to water deficits. Aust. J. Plant Physiol. 7:193-205.

Jordan, W. R. 1970. Growth of cotton seedlings in relation to maximum daily leaf water potential. Agron. J. 62:699-701.

Jordan, W. R., K. W. Brown, and T. C. Thomas. 1975. Leaf age as a determinant factor in stomatal control of water loss from cotton during water stress. Plant Physiol. 56:595-599.

Kanemasu, E. T. 1975. The parameter of Kanemasu, Thurtell, and Tanner. In: Measurement of stomal aperture and diffusive resistance. Wash. State University, Agric. Sta. Bull. 809.

Kanemasu, E. T., and C. B. Tanner. 1969. Stomatol diffusion resistance of snap beans. I. Influence of leaf-water potential. Plant Physiol. 44:1547-1552.

Kanemasu, E. T., G. W. Thurtell, and C. B. Tanner. 1969. Design, calibration and field use of a stomatol diffusion parameter. Plant Physiol. 44:881-885.

Kappen, L., T. T. Oertli, O. L. Lange, E. O. Schutze, M. Erenari, and J. Buschborn. 1975. Seasonal and diurnal courses of water relations of the arido-active plant Hammada scoparia in the Neger Desert. Oleol. 21:175-192.

Kassam, H. H., and J. F. Elston. 1974. Seasonal changes in the status of water and tissue characteristics of leaves of Vicia faba L. Ann. Bot. 38:419-429.

Keatinge, J. D. H., and C. F. Shaykewich. 1977. Effect of the physical environment on the growth and yield of field beans (Vicia faba minor) in the Canadian prairie. J. Ag. Sci. UK 89:349-353.

Knipling, E. G. 1967. Effect of leaf aging on water deficit - water potential relationships of dogwood leaves growing in two environments. Physiol. Plant 20:65-72.

Kozlowski, T. T., (Ed.) 1968. Water deficits and plant growth. Vol. I. New York: Academic. 390 pp.

Kramer, P. J. 1969. Plant and soil water relationships. McGraw-Hill, New York. pp. 482.

Kramer, P. J. 1974. Fifty years of progress in water relations research. Plant Physiol. 54:463-471.

Kramer, P. J. 1980. Drought, stress and the origin of adaptations. In: Adaptation of plants to water and high temperature stress. N. C. Turner, and P. J. Kramer (Eds.). A Wiley-Interscience publication. John Wiley and Sons. New York.

Kramer, P. J., E. B. Knipling, and L. N. Miller. 1966. Terminology of cell water relations. Science 153:889-890.

Lamareaux, R. J., W. R. Chaney, and K. M. Brown. 1978. The plastochron index: A review after two decades of use. Amer. J. Bot. 65:586-593.

Larson, K. L., and J. D. Eastin (Eds.). 1971. Drought injury and resistance in crops. Crop Sci. Soc. Am. Madison, Wis.

Lawlor, D. W., and G. F. Milford. 1973. The effect of Na on growth of water stressed sugar beets. Ann. Bot. 37:597-604.

Lawlor, D. W. 1969. Plant growth in polyethylene glycol solutions in relation to the osmotic potential of the root medium and the leaf water balance. J. Exptal. Bot. 20:895-911.

Lechtenberg, V. L., D. A. Holt, and H. W. Youngberg. 1971. Diurnal variation in nonstructural carbohydrates, in vitro digestibility, and leaf to stem ratio of alfalfa. Agron J. 63:719-724.

Lechtenberg, V. L., D. A. Holt, and H. W. Youngberg. 1973. Diurnal variation in nonstructural carbohydrates of Sorghum sudanese (Stapf) as influenced by environment. Agron. J. 65:579-583.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press. New York. pp. 697.

Levitt, J. 1980. Responses of plants to environmental stresses. II. Water, radiation, salt and other stresses. Academic Press. New York.

Lockhart, J. A. 1965. An analysis of irreversible plant cell elongation. J. Theoret. Biol. 8:264-275.

Loomis, R. S., W. A. Williams, and A. E. Hall. 1971. Agricultural productivity. Ann. Rev. Plant Physiol. 22:431-468.

Ludlow, M. M., and T. T. Ng. 1976. Effect of water deficit on carbon dioxide exchange and leaf elongation rate of Panicum maximum var. trichoglume. Aust. J. Plant Physiol. 3:401-413.

Ludlow, M. M., and T. T. Ng. 1977. Leaf elongation rate in Panicum maximum var. trichoglume following removal of water stress. Aust. J. Plant Physiol. 4:263-272.

Maksymowych, R. 1959. Quantitative analysis of leaf development in Xanthium pennsylvanicum. Am. J. Bot. 46:635-644.

Maksymowych, R. 1973. Analysis of leaf development. Cambridge University Press. Cambridge.

Maksymowych, R., and R. O. Erickson. 1960. Development of the lamina in Xanthium italicum represented by the plastochron index. Am. J. Bot. 47:451-459.

Maksymowych, R., and A. B. Maksymowych. 1973. Induction of morphogenetic changes and acceleration of leaf initiation by gibberellic acid in Xanthium pennsylvanicum. Am. J. Bot. 60:901-906.

Mansour, N. S. 1975. Commercial production of bush beans in Oregon. Ext. Circ. 862. Oregon State University Extension Service.

Martin, J. H., W. H. Leonard, and D. L. Stamp. 1976. Principles of field crop production. Third Edition. pp. 722-739. Macmillan Publishing Co., Inc. New York.

McCree, K. J. 1974. Changes in the stomatol response characteristics of grain sorghum produced by water stress during growth. Crop Sci. 14:273-278.

Meidner, H., and M. Edwards. 1975. Direct measurements of turgor pressure potentials of guard cells. I. J. Exp. Bot. 26:319-330.

Melkonian, J. J., J. Wolfe, and P. L. Steponkus. 1982. Determination of the volumetric modulus of elasticity of wheat leaves by pressure-volume relations and the effect of drought conditioning. Crop Sci. 22:116-123.

Meyer, R. F., and J. S. Boyer. 1972a. Sensitivity of cell division and cell elongation to low water potential in soybean hypocotyls. Planta 105:77-87.

Meyer, R. F., and J. S. Boyer. 1972b. Sensitivity of cell division and cell elongation to low water potentials in soybean hypocotyls. Planta 108:75-78.

Michelena, V. A., and J. S. Boyer. 1982. Complete turgor maintenance at low water potentials in the elongation region of maize leaves. Plant Physiol. 69:1145-1149.

Michelini, F. J. 1958. The plastochron index in developmental studies of Xanthium italicum moretti. Am. J. Bot. 45:525-533.

Millar, A. A., M. E. Duysen, and G. E. Wilkinson. 1968. Internal water balance of barley under soil moisture stress. Plant Physiol. 43:968-972.

Millar, A. A., M. E. Duysen, and E. B. Norum. 1970. Relationships between the leaf water status of barley and soil water. Can. J. Plant Sci. 50:363-370.

Millar, B. D. 1971. Improved thermocouple psychrometer for the measurement of plant and soil water potential. I. Thermocouple psychrometry and an improved instrument design. J. Exp. Bot. 22:875-890.

Millar, B. D., and G. K. Hansen. 1975. Exclusion errors in pressure chamber estimates of leaf water potential. Ann. Bot. 39:915-920.

Millar, B. D., and O. T. Denmead. 1976. Water relations of wheat leaves in the field. Agron. J. 68:303-307.

Moldau, H. 1973. Effects of various water regimes on stomatol and mesophyll conductance of bean leaves.

Morgan, J. M. 1980. Differences in adaptation to water stress within crop species. In: Adaptation of plants to water and high temperature stress. N. C. Turner and P. J. Kramer (Eds.). Wiley Interscience. New York.

Munns, R., C. J. Brady, and E. W. Barlow. 1979. Solute accumulation in the apex and leaves of wheat during water stress. Aust. J. Plant Physiol. 6:379-389.

Namken, L. N., J. F. Bartholic, and J. R. Runkles. 1969. Monitoring cotton stem radius as an indication of water stress. Agron. J. 61:891-893.

Nagaraja, R. C. R., T. Y. Lee, W. Bradley, and G. Dorsch. 1981. Solar radiation and related meteorological data for Corvallis, Oregon.

Neumann, H. H., G. W. Thurtell, and K. R. Stevenson. 1973. In situ measurements of leaf water potential and resistance to water flow in corn, soybean and sunflower at several transpiration rates. Can. J. Plant Sci. 54:175-184.

Nobel, P. S. 1974. Biophysical plant physiology. W. H. Freeman. San Francisco. 488 pp.

O'Toole, J. C. 1975. Photosynthetic responses to water stress in Phaseolus vulgaris L. Dissertation Abstracts International, B. 36:505.

Parker, J. 1968. Drought-resistance mechanisms. In: "Water deficits and plant growth." Vol. I. T. T. Kozlowski (Ed.). Academic Press, Inc. New York.

Peet, M. M., A. Bravo, D. H. Wallace, and J. L. Ozburn. 1977. Photosynthesis, stomatol resistance, and enzyme activities in relation to yield of field-grown dry bean varieties. Crop Sci. 17:287-292.

Penman, H. L. 1956. Evaporation: An introductory survey. Netherlands. J. Agri. Sci. 1:9-29.

Pinter, P. J., and R. J. Reginato. 1981. Thermal infrared techniques for assessing plant water stress. Proceedings of the Am. Soc. Agri. Engr., Irrigation Scheduling Conference. ASAE Publication 23-81.

Popisilova, J., I. Ticha, J. Catsky, and J. Solarova. 1978. Carbon dioxide exchange in primary bean leaves as affected by water stress. Biol. Plant. 20:368-372.

Raschke, K. 1975. Stomatol action. Ann. Rev. Plant Physiol. 26: 309-340.

Rawson, H. M., N. C. Turner, and J. E. Begg. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. IV. Photosynthesis, transpiration, and water use efficiency of leaves. Aust. J. Plant Physiol. 5:179-194.

Reicosky, D. C., D. E. Deaton, and J. E. Parsons. 1980. Canopy air temperature and evapotranspiration from irrigated and stressed soybeans. Agric. Meteorol. 27:21-35.

Scholander, P. F., H. T. Hammel, E. A. Hemmingsen, and E. A. Bradstreet. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Natl. Acad. Sci. U.S.A. 52:119-125.

Scholander, P. F., H. T. Hammel, E. O. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339-346.

Sionit, N., and P. J. Kramer. 1977. Effect of water stress during different stages of growth of soybean. Agron. J. 69:274-277.

Slatyer, R. O. 1967. Plant water relationships. London Academic. 366 pp.

Slatyer, R. O. 1969. Physiological significance of internal water relations to crop yield. In: Physiological aspects of crop yield. J. D. Eastin (Ed.), Amer. Soc. Agron., Madison, Wis. pp. 53-83.

Slatyer, R. O., and W. R. Gardner. 1965. Overall aspects of water movement in plants and soils. Symp. Soc. Exp. Biol. 19:113-129.

Slatyer, R. O., and S. A. Taylor. 1961. Terminology in plant and soil water relations. Nature 197:922.

Slavik, B. 1974. Methods of studying plant water relations. Academia Publishing House. Prague and Springer-Verlag. Berlin.

Statfelt, M. G. 1966. The role of the epidermal cells in the stomatol movements. Physiol. Plant 19:241-256.

Steudle, E., U. Zimmerman, and U. Luttge. 1977. Effect of turgor pressure and cell size on the wall elasticity of plant cells. Plant Physiol. 59:285-289.

Stewart, J. I. 1975. Report of East African food crops research project. (Marginal rainfall areas subproject). April. Univ. of California at Davis.

Stewart, J. I., and R. M. Hagan. 1973. Functions to predict effects of crop water deficits. J. Irrig. and Drain. Div., Am. Soc. Civ. Engr. 99(IR4):421-439.

Stewart, J. I., R. M. Hagan, and W. O. Pruitt. 1974. Functions to predict optimal irrigation programs. J. Irrig. and Drain Div., Am. Soc. Civ. Engr. 100(IR2):179-199.

Stone, J. F. (Ed.). 1974. Plant modification for more efficient water use. Agric. Meteorol., Special Issue.

Sullivan, C. Y., and J. D. Eastin. 1974. Plant physiological responses to water stress. Agric. Meteorol. 14:113-127.

Suntaree, Y. 1976. Ozon inhibition of transpiration and photosynthesis of two soybeans (Glycine max. [L.] Merr.) cultivars. Master Thesis. Oregon State University.

Tanner, C. B. 1967. Measurement of evapotranspiration. In: Irrigation of agriculture lands. R. M. Hagan et al. (Eds.). pp. 534-574. Amer. Soc. Agron., Madison, Wis.

Thomas, J. C., K. W. Brown, and W. R. Jordan. 1976. Stomatol responses to leaf water potential as affected by preconditioning water stress in the field. Agron. J. 68:706-708.

Thorne, G. N. 1966. Physiological aspects of grain yield in cereals. In: The growth of cereal and grasses. Milthrope, F. L. and J. D. Ivins (Eds.). London.

Turner, N. C. 1974. Stomatol behavior and water status of maize, sorghum, and tobacco under field conditions. II. At low soil water potential. Plant Physiol. 53:360-365.

Turner, N. C. 1975. Concurrent comparisons of stomatol behavior, water status, and evaporation of maize in soil at high or low water potential. Plant Physiol. 55:932-936.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. In: Stress physiology in crop plants. H. Mussell and R. C. Staples (Eds.). Wiley Interscience, New York.

Turner, N. C. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil 58:339-366.

Turner, N. C., and J. E. Begg. 1973. Stomatol behavior and water status of maize, sorghum, and tobacco under field conditions. I. At high soil water potential. Plant Physiol. 51:31-36.

Turner, N. C., and J. E. Begg. 1978. Responses of pasture plants to water deficits. In: Plant relations in pastures. J. R. Wilson (Ed.). pp. 50-66.

Turner, N. C., and J. E. Begg. 1981. Plant-water relations and adaptation to stress. Plant and Soil 58:97-131.

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustment. A review and evaluation. In: Adaptation of plants to water and high temperature stress. N. C. Turner, and P. J. Kramer (Eds.). Wiley Interscience, New York and London.

Turner, N. C., and P. J. Kramer. 1980. Adaptation of plants to water and high temperature stress. Wiley Interscience. New York.

Turner, N. C., J. E. Begg, and M. L. Tonnet. 1978. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water-potential at which stomata close. Aust. J. Plant Physiol. 5:597-608.

Turner, N. C., J. E. Begg, J. E. Rawson, H. M. English, and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance, $^{14}CO_2$ photosynthesis, and adaptation to water deficits. Aust. J. Plant Physiol. 5:179-194.

Tyree, M. T. 1976. Negative turgor pressure in plant cells: fact or fallacy? Can. J. Bot. 54:2738-2746.

Tyree, M. T., and H. T. Hammel. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. J. Exp. Bot. 23:267-282.

Tyree, M. T., M. E. Macgregor, A. Petrov., and M. I. Upenieks. 1978. A comparison of systematic errors between the Richards and Hammel methods of measuring tissue water relations parameters. Can. J. Bot. 56:2153-2161.

Van Bavel, C. H. M. 1966. Potential evaporation: The combination concept and its experimental verification. Water Resources Res. 2:455-467.

Van Bavel, C. H. M., F. S. Nakayama, and W. L. Ehrler. 1965. Measuring transpiration resistance of leaves. Plant Phys. 40:535-540.

Watts, W. R. 1974. Leaf extension in Zea mays. III. Field measurements of leaf extension in response to temperature and water potential. J. Exp. Bot. 25:1085-1096.

Weatherly, P. E. 1965. Contribution to the general discussion. In: Water stress in plants (B. Slavik, Ed.). Dr. W. N. V. Junk Publishers, The Hague.

Weatherly, P. E. 1970. Some aspects of water relations. Adv. Bot. Res. 3:171-206.

Wenkert, W. 1980. Measurement of tissue osmotic pressure. Plant Physiol. 65:614-617.

Wenkert, W., E. R. Lemon, and T. R. Sanclair. 1978a. Leaf elongation and turgor pressure in field grown soybean. Agron. J. 70:761-764.

Wenkert, W., E. R. Lemon, and T. R. Sinclair. 1978b. Changes in component potentials for mature and immature leaves under field conditions. Ann. Bot. 42:295-307.

Wenkert, W., E. R. Lemon, and T. R. Sinclair. 1978c. Changes in water potential during pressure bomb measurement. Agron. J. 70:353-355.

Wilson, J. R. 1977. Variation of leaf characteristics with levels of insertion of a grass tiller. III. Tissue water relations. Aust. J. Plant Physiol. 4:733-743.

Wilson, J. R., M. J. Fisher, E. D. Schulze, G. R. Dolby, and M. M. Ludlow. 1979. Comparison between pressure-volume and dewpoint-hygronomy techniques for determining the water relations characteristics of grass and legume leaves. Oceologia (Berlin) 41:77-88.

Wilson, J. R., M. M. Ludlow, M. J. Fisher, and E. D. Schulze. 1980. Adaptation to water stress of the leaf water relations of four tropical forage species. Aust. J. Plant Physiol. 7:207-220.

Wright, S. T. C., and R. W. P. Hiron. 1969. Abscisic acid, the growth inhibitor induced in detached wheat leaves by a period of wilting. Nature 244:719-720.

Zabadel, T. J. 1974. A water potential threshold for the increase of abscisic acid in leaves. Plant Physiol. 53:125-127.

Zelitch, I. 1969. Stomatol control. Ann. Rev. Plant Physiol. 20: 329-350.

Zimmerman, U., and E. Steudle. 1976. Turgor pressure regulation in valonia utricularis. Plant Physiol. 58:608.