

Relative Evaluation of Water Stress Indicators for Soybeans¹

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ABSTRACT

The understanding of the relationships between changes in crop foliage to variations in the amount and status of soil water is at best incomplete. Since plant growth is directly affected by deficits of water in plants, and only indirectly by soil-water deficits and atmospheric stresses, the importance of using plant measurements, rather than soil indices, is warranted and has led to this investigation. Field studies were conducted during 1976 on Ida silt loam [fine, silty, mixed (calcareous) mesic family of Typic Udorthents] at the Western Iowa Experimental Farm, Castana, Iowa, to evaluate three plant measurements (viz., stomatal conductance, leaf-water potential, and leaf area) as water stress indicators for soybeans [*Glycine max* (L.) Merr.]. Stomatal conductance and leaf water potential were measured at 2-hour intervals from 0600 to 2000. Stomatal resistance was measured with a diffusion porometer, with stomatal conductance taken as the reciprocal of leaf resistance. Leaf-water potential was measured using a pressure chamber. Leaf area was measured with an electronic leaf-area integrator.

Daily means of stomatal conductance and leaf-water potential measured several times during the growing season were closely related to changes in soil-water potential. "Rate of leaf-area expansion" which is defined as the change in average leaf area (leaf area/number of leaves) per plant over a period of time, also showed a close correspondence with soil-water potential.

Relative growth rates of soybeans showed a negative correlation with stomatal conductance, leaf-water potential, and rate of leaf-area expansion. The three plant measurements should prove useful in explaining water-deficit effects quantitatively under field conditions.

Additional index words: Stomatal conductance, Leaf-water potential, Leaf area, Soil-water potential, Relative growth rate.

THE response of crop foliage to changes in the amount and status of soil water in the root zone is far from completely understood. Recent research emphasizes the importance of using plant measurements, rather than soil indices, in evaluating crop water status (Kramer, 1974). Plant growth is controlled directly by water deficits in plants and only indirectly by soil-water deficits and atmospheric stresses (Ritchie, 1974). The variance in the reported results between field tests and greenhouse, or growth chamber tests, point out the need for studying the growth response of plants to water deficits in the field (Jordan and Ritchie 1971). An inspection of the available literature points to the possibility of using several plant measurements as water-stress indicators. The most promising ones under field conditions are leaf water

potential (Clark and Hiler, 1973; Brady et al., 1974; Gandar and Tanner, 1976) and stomatal resistance (Kanemasu et al., 1973; Brady et al., 1975; Al-Ani and Bierhuizen, 1971). Seasonal and diurnal changes in the plant measurements in response to changes in soil-water status have been reported, but few attempts have been made to relate plant growth directly to plant-water status.

Fischer and Hagan (1965) concluded that leaf area is very sensitive to water stress. Similar conclusions prompted Shawcroft et al. (1970) to suggest that rate of development of leaf area could be used as a plant parameter to evaluate the water status of a crop under field conditions. Very little research has been done in this area because of the tedious work involved in measuring leaf area. Recent developments on leaf-area integrators however, have made the measurements of leaf area easier.

Because of the concepts just described, the present study was conducted to evaluate three plant measurements (viz., stomatal conductance, leaf-water potential, and leaf area) as water-stress indicators for soybeans (*Glycine max* (L.) Merr.) under field conditions.

MATERIALS AND METHODS

The experiment was conducted during 1976 on Ida silt loam soil [fine, silty, mixed (calcareous) mesic family of Typic Udorthents] at the Western Iowa Experimental Farm, Castana, Iowa. The plot areas faced west, with about an 8% slope. Soil chemical and physical characteristics for the experimental site have been described in an earlier paper (Sivakumar et al., 1977).

The experiment was laid out in a randomized block design with four replications of two treatments. For one treatment the interrow strips of soil were covered with a 4-mil black, plastic film; for the other treatment the soil was left uncovered. Steel staples were used at 1-ft intervals to firmly secure the plastic film on the ground. The purpose of the plastic cover was to alter the soil-water status under field conditions primarily by preventing the rainfall from seeping into the ground, although at the same time it would reduce the evaporative losses of soil water. Individual plots were 50 m long and 7 rows (row spacing 100 cm) wide. The uncovered plots were given two 5- to 6-cm irrigations, one on 12 July and the second on 21 July. Irrigation provided a range of moisture stress conditions on the soybean growth.

Inoculated "Wayne" soybeans were planted in east-west rows on 12 May. Immediately after planting, Chloramben herbicide was sprayed on the soil surface at the recommended rate.

Leaf-water potential and stomatal resistance measurements were taken twice weekly during the growing season beginning at the V4 stage (four nodes above the unifoliate node). Measurements on each day were taken from 0600 to 2000 hours at 2-hour intervals. At each time interval, measurements were taken in two replicates on four, uppermost, fully expanded trifoliate leaves to avoid mutual shading and senescent effects that may occur in the lower leaves. Stomatal resistance was measured with a diffusion porometer (Kanemasu et al., 1969). The porometer was calibrated before field measurements. Adaxial (R_{ad}) and abaxial (R_{ab}) measurements were taken on the same center leaflet of a trifoliate leaf. The leaf stomatal resistance (R_{leaf}) was calculated as:

$$\frac{1}{R_{leaf}} = \frac{1}{R_{ad}} + \frac{1}{R_{ab}} \quad [1]$$

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Table 1. Meteorological parameters during the 1976 growing season at the Western Iowa Experimental Farm.

Month	Avg. temp.		Precipitation cm	Avg. 24-hour winds km	Avg. solar radiation ly/day	Total pan evaporation cm
	Maxi- mum	Mini- mum				
	C					
May	22.4	7.4	11.4	104.8	-	18.4
June	28.3	13.6	0.9	107.8	600	23.9
July	31.3	17.0	1.1	66.3	559	24.1
Aug.	31.6	15.6	0.8	74.8	530	23.2
Sept.	26.7	11.1	4.1	71.8	-	17.0

Stomatal conductance was taken as the reciprocal of leaf resistance.

Leaf-water potential was measured always in conjunction with the stomatal resistance measurements on the same leaf by use of a pressure chamber (Scholander et al., 1965). The measurement was accomplished by placing a freshly cut, center leaflet of a trifoliate leaf into the pressure chamber with the cut end protruding, and then applying pressure to the chamber. The pressure necessary to balance the internal stress of the leaf and to force liquid from the xylem to the cut surface was considered equal to the water potential of leaf cells, assuming that the osmotic effect of the solutes in the xylem sap is negligibly small. Only occasionally was there a problem with foam formation on the petiole. In these cases another leaflet was sampled.

For relative growth rate measurements, whole plants, except roots, were sampled at weekly intervals beginning at the V 4 stage. On each sampling date, 10 plants were selected randomly from each replicate. Each plant was cut off at the ground surface and separated into leaves, stem, petioles, pods, and seeds. Leaf area of each plant was measured with a LI-COR portable leaf-area meter (LAMBDA Instruments Corporation, Lincoln, Nebr.).³ The number of leaves on each plant also was counted at the same time. Plant parts were dried to constant weight in a forced-draft oven at 65 C and then weighed. Relative growth rates (Radford, 1967) were calculated by using the data on dry matter accumulation.

To assess the water deficit effects on soybean leaf growth, an index, which can be termed "rate of leaf-area expansion" was developed. Rate of leaf-area expansion is the difference in average leaf area (total area/number of leaves) per plant over a period of time, 7 days in the present study. The average leaf area obtained at any time was the mean of 40 plants; and hence the sampling errors affecting the index were considerably reduced. The choice of this index over other growth analysis terms was dictated by two main considerations: first, the overwhelming evidence available supporting the sensitivity of leaf expansion to water deficits; second, the accuracy with which leaf area could be measured with the use of leaf area integrators.

Soil moisture was measured gravimetrically at weekly intervals to a depth of 180 cm. Measurements were taken at 15-cm intervals to the 30-cm depth, and at 30-cm intervals down to 180 cm. An average of five cores were obtained in each plot at each sampling time by means of a core sampler. Volumetric soil-moisture values represented an average of 20 cores at any time. Soil-water potential values were obtained by using the volumetric soil-water content-pressure relationships for various depths described by Willatt and Taylor (1977). Reported soil-water potentials of the root zone were estimated by averaging the soil-water potential measured for each depth in the effective root zone. Effective rooting depth during the growing season was estimated from the root samples taken in an earlier study (Sivakumar et al., 1977).

RESULTS AND DISCUSSION

A summary of the meteorological parameters measured during the growing season is presented in Table 1. Very little precipitation was received during the months of June, July, and August. A range of soil-

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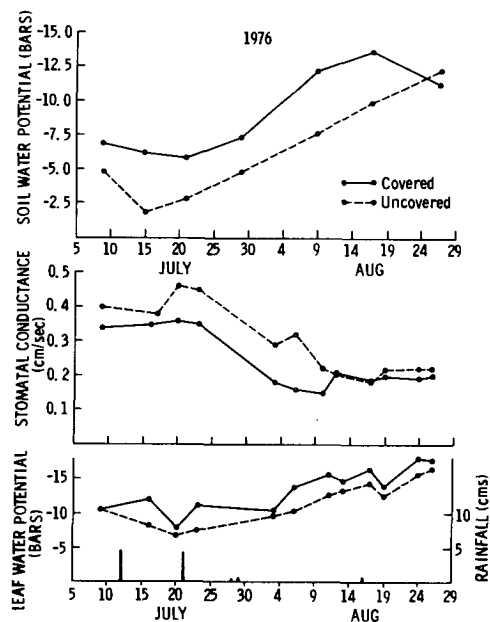


Fig. 1. Seasonal changes in soil-water potential, overall daily means of stomatal conductance, and leaf-water potential.

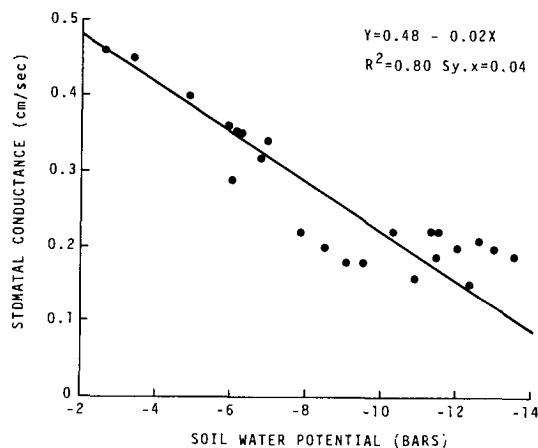


Fig. 2. Stomatal conductance as a function of soil-water potential.

water potential values was obtained under field conditions by the addition of two irrigations on the uncovered plots. The hot, dry weather conditions during the season resulted in severe moisture stress, especially during the month of August. The moisture stress patterns showed an increasing trend with time, as evidenced by the seasonal changes in soil-water potential, stomatal conductance, and leaf-water potential (Fig. 1). Because the purpose of this study was to examine the relative changes in stomatal conductance and leaf-water potential with changes in soil-water potential, only daily mean values of plant measurements averaged over the seven time periods during the observational day were used. In general, there was a 3- to 4-bar difference in soil-water potential between the plastic covered and no-cover treatments. This difference in soil-water potential values is corroborated by the differences in the daily mean values of stomatal conductance and leaf-water potentials between the two treatments.

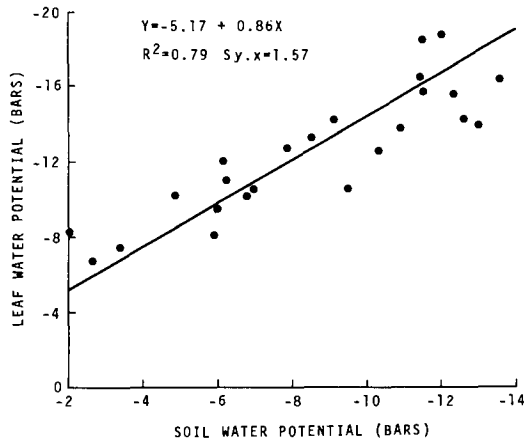


Fig. 3. Response of leaf-water potential to changes in soil-water potential.

The availability of water to the plants is closely related to soil-water potential and the potential gradient between the soil and the plant. Although the atmospheric evaporative demand mediates the range of potential gradient that develops between the soil and the plant, the importance of a base soil-water potential in altering the plant response to water stress cannot be overlooked. Hence, the evaluation of any plant measurement used to indicate water stress should begin with an examination of the relative changes in the plant measurements in response to changes in soil water.

For the purpose of discussion, the data from the two treatments have been pooled to provide more data for the elucidation of various relationships. The daily means of stomatal conductance in relation to soil-water potential are plotted in Fig. 2. It is evident that the stomatal conductance shows a linear decline with increasing soil-water deficits. This reduction in the stomatal conductance when the soil water potential decreases shows how the plants respond to restrict transpiration to a low rate. Denmead and Miller (1976) suggest that under severe water stress stomatal control is very strong.

The response of leaf-water potential to changes in soil-water potential is shown in Fig. 3. When the soil-water potential decreased, leaf-water potential also decreased. The relative scatter of daily means of leaf-water potential at any given soil-water potential is at least partially due to the different atmospheric evaporative demand prevailing during the observational days. As the soil becomes progressively drier, a plant is subjected to stress earlier in the day and recovers more slowly during periods of low evaporative demand. Under the conditions of the severe water deficits, the leaves showed low leaf-water potentials even at 0600 CST, suggesting the inability of the plants to regain full turgidity during the following night. Gandar and Tanner (1970) reported that the nighttime water potential recovery of stressed plants was much slower than that of well watered plants. As Boyer (1971) observed, the nighttime recovery of plant water could be retarded by increased plant hydraulic resistance associated with severe desic-

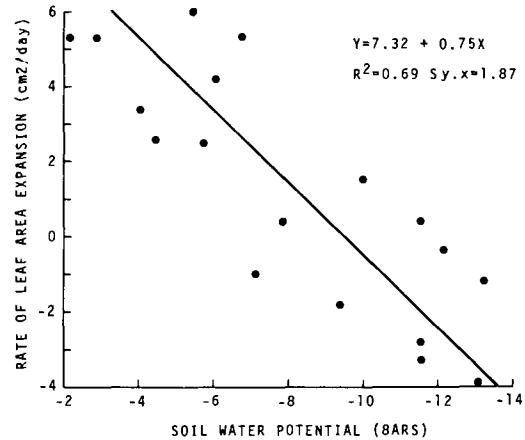


Fig. 4. Rate of leaf-area expansion as a function of soil-water potential.

cation. Plant turgidity is important in relation to the opening and closing of stomata, expansion of leaves and flowers, and movement of water and nutrients to various parts of the plant (Kramer, 1969).

It has been shown that leaf enlargement is strongly reduced by water stress (Boyer, 1970, Acevedo et al., 1971). The index, "rate of leaf-area expansion" could be tested for its sensitivity through a plot against soil-water potential (Fig. 4). There is a wide scatter around the regression line, but it is apparent that at low soil-water potential values, the leaves show very little expansion. In fact, the rate of expansion showed negative values because of the onset of senescence brought about by higher water deficits. Gandar and Tanner (1970) observed that over the growing season, diminished leaf enlargement caused by short periods of water deficits could result in a substantial reduction in total leaf growth.

From the discussion up to this point, it is obvious that an extended drying cycle decreases the stomatal conductance, leaf-water potential, and rate of leaf-area expansion. With the decreasing stomatal conductance for CO_2 , it is reasonable to expect a decrease in photosynthetic activity, resulting in a reduced rate of dry matter accumulation. Also, it seems that turgor pressure directly regulates cell division and cell enlargement so as to render the cell number and cell size compatible with the rate of assimilation (Gardner, 1970). Any change in the plant measurements affected by water deficits should be closely linked to the plant growth rates.

The relative growth rate of soybeans is shown as a function of daily mean values of stomatal conductance in Fig. 5. Relative growth rates show a linear decline with decrease in stomatal conductance. The indirect effect of loss of turgidity on the regulation of stomatal conductance and hence on net photosynthesis is evidenced by the reduced growth rates. Kanemasu and Tanner (1969) attributed the large decrease in transpiration and growth rates at modest soil-water potentials to the increased stomatal resistance. Hence maintenance of high stomatal conductivity through effective water management practices seems to have an important bearing on the growth rates of field plants.

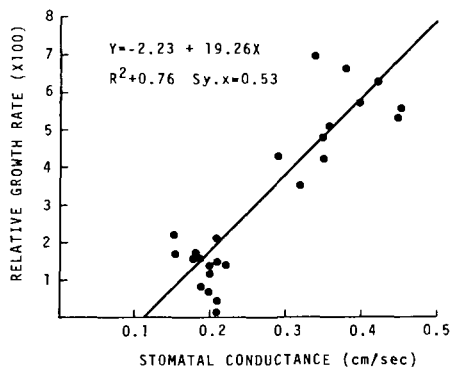


Fig. 5. Relative growth rate of soybeans as a function of stomatal conductance.

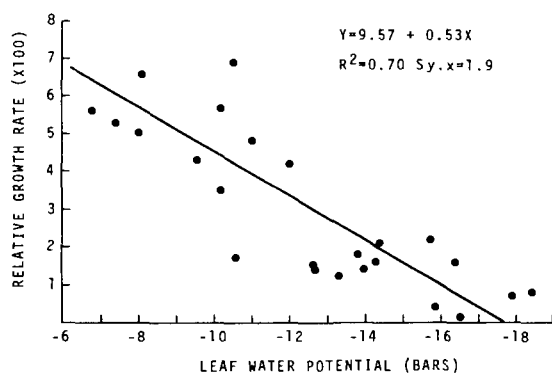


Fig. 6. Relative growth rate of soybeans as a function of leaf-water potential.

In greenhouse studies, Jordan (1970) observed that although potentials determined by the pressure-chamber technique represent only instantaneous values, these values may be correlated with growth response. The relation between relative growth rates and the daily means of leaf-water potential is shown in Fig. 6. There is considerable scatter around the regression line but the trend shows that relative growth rates increase as leaf-water potential increases. Jordan (1970) observed a trend towards reduced rate of dry matter production with increasing water stress. Using the data of Kanemasu and Tanner (1969), Gardner (1970) showed that relative growth rate of soybeans decreased with decreasing leaf-water potential. Adjei-Twum and Splittstoesser (1976) also observed that the dry weight, plant height, and leaf area of soybean seedlings decreased sharply as leaf-water potential decreased. Observed reductions in growth rates with low leaf-water potentials could have been brought about by increased respiration rates associated with increased plant temperatures; and reduced photosynthetic rates resulting from reduced CO_2 intake.

Because leaf area is an important factor in C assimilation, it follows that changes in leaf area are related to changes in growth rates. Relative growth rate as a function of the index, rate of leaf area expansion, is shown in Fig. 7. The decrease in growth rates appears linear. The fact that rate of leaf-area expansion and growth rates as stomatal conductance and showed as good a relationship with the soil-water po-

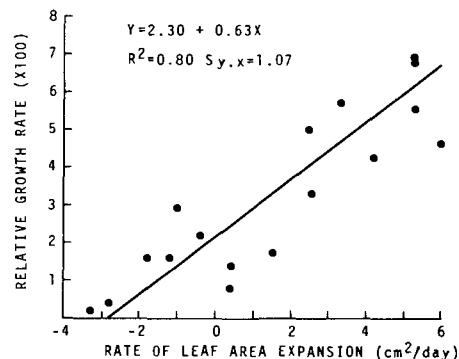


Fig. 7. Response of relative growth rate of soybeans to rate of leaf area expansion.

leaf-water potential indicates that it is one of the potential plant parameters which could be used to quantify the water deficit effects.

The results of this study demonstrate the usefulness of the plant measurements in addition to soil-water measurements to indicate and quantify water stress effects under field conditions. This of course, involves frequent sampling and monitoring of plant growth in addition to obtaining plant measurements that would be used as water-stress indicators. Different cultivars would have to be compared. Weather conditions during the growing season in the present study were sufficiently conducive to delineate a uniform moisture stress pattern throughout the growing season. It seems that plant measurements would prove very useful under a prolonged drying period. Further investigations would be needed to answer the question as to what would happen if the moisture stress pattern was cyclical under field conditions.

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