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Leaf Response to Water Deficits in Soybeans

By

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Abstract

Soybeans [*Glycine max* (L.) Merrill cv. Wayne] plants were subjected to an extended drying cycle in the field to investigate the leaf sensitivity to water deficits. Soybeans in irrigated plots were superior to those in non-irrigated plots in the average size and number of leaflets per plant. Apparent differences in the leaf area distributions in the canopy seemed to be mediated by moisture stress effects associated with leaf senescence and light penetration in the lower depths of the canopy. A major decrease in leaf enlargement occurred near a leaf-water potential of −8 bars, and at −12 bars, the growth was completely halted. Similar decreases were observed at a stomatal conductance of 0.4 cm/s and at 0.2 cm/s no enlargement was observed.

Introduction

Many experiments have been conducted on the short-time effects of water stress and growth. Little data are available on the long-time effects. Both cell division and cell enlargement have been shown to be sensitive to water stress (Slatyer 1967, Hsiao *et al.* 1970). A progressive decline in the rates of cell enlargement was observed as water deficits developed, with enlargement ceasing at moderate water deficit levels (Stransky and Wilson 1964, Boyer 1968, 1970).

The effect of water stress on growth tends to be especially pronounced in those tissues that are in rapid stages of development (Williams and Shapter 1955, Gates 1968). The fact that cell growth is generally more sensitive to water stress than the stomatal opening and CO_2 assimilation (Hsiao 1973) has a direct implication in the analysis of water-deficit effects on leaf growth. Mare and Palmer (1976) noted that the total number of leaves produced by the primary stem of sunflower was reduced when the water stress was imposed over a period of 10 days. Studies involving short-term drying cycles under constant conditions in an environmental chamber (Boyer 1970) and in the field (Gandar and Tanner 1976) have shown that leaf growth is extremely sensitive to water stress.

Shawcroft *et al.* (1970) has suggested that leaf area could be used as a crop parameter to evaluate water stress. The present study is aimed at investigating leaf sensitivity to water deficits under an extended drying cycle in the field.

Abbreviation: LAI, Leaf-area index (leaf area per unit land area).

Materials and Methods

The experiment was conducted during 1976 on a deep loess silt-loam soil 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 study (Sivakumar *et al.* 1977).

The experiment was laid out in a randomized block design with four replications. Each replicate consisted of two plots, one plot in which the interrow strips of soil were covered with a 0.1 mm thick black-plastic film, and the other plot which was left uncovered. Steel staples were used at 30 cm intervals to firmly secure the plastic film on the ground. For simplicity, the treatments will be referred to as "covered" and "uncovered" to identify the black plastic and bare plots respectively. The purpose of the plastic cover was to alter the soil-water status under field conditions by preventing the rainfall from seeping into the ground. Individual plots were 50 m long and seven rows (100 cm apart) wide. The uncovered plots were given irrigations of 5–6 cm on July 12 and July 21. Irrigations facilitated the provision of a range of moisture-stress conditions on soybean growth.

Inoculated 'Wayne' cultivar soybeans [*Glycine max* (L.) Merrill] were planted in east–west rows on May 12. Weed control was obtained by use of a herbicide (Chloramben, 2-amino-2,5-dichlorobenzoic acid) sprayed on the soil surface immediately after the soybeans were planted. Above-ground

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whole plants were sampled at weekly intervals beginning at the four-node stage. On each sampling date, 10 plants were randomly selected from each replicate. Leaf area of each plant was measured with a LI-COR portable leaf-area meter (LAMBDA Instruments Corporation, Lincoln, Nebraska). The number of leaflets on each plant was also counted at the same time. From the data on the weekly changes in the average leaflet area (leaf-area per plant or number of leaflets per plant), leaf enlargement has been calculated.

Leaf-water potential and stomatal-conductance measurements were taken twice weekly during the growing season. Measurements were taken on each day from 0600 to 2000 hours at 2-h intervals. At each time interval, measurements were taken in two replicates, on four uppermost, unrolled, trifoliate leaves to avoid mutual shading and senescent effects that may occur in the lower leaves. Leaf-water potential was measured by placing a freshly cut center leaflet of a trifoliate leaf into a pressure chamber (Scholander *et al.* 1965), with the cut end protruding, and applying pressure to the chamber.

Stomatal resistance was measured with a diffusion porometer (Kanemasu *et al.* 1969). The porometer was calibrated before field measurements. Adaxial (Rad) and abaxial (Rab) resistance measurements were taken on the center leaflet of a trifoliate leaf and leaf stomatal resistance (R leaf) was calculated as: 1/R leaf = (1/Rad) + (1/Rab). Stomatal conductance is taken as the reciprocal of leaf resistance.

Results and Discussion

Average size and number of leaflets

In a review of water-deficit effects on plant growth, Fischer and Hagan (1965) concluded that leaf growth was very sensitive to water stress. In Figure 1 the average leaflet size is plotted against days after planting. The advantage in leaf area that the uncovered plots maintained over the covered plots occurred after the two irrigations in July. The largest value of average leaflet area, 39.5 cm^2, was recorded 85 days after planting for the covered plots. Uncovered plots had the largest leaflet area of 46.9 cm^2 at 92 days after planting. The decrease in average leaflet area observed during the later part of the growing season is due to dropping of relatively large leaflets.

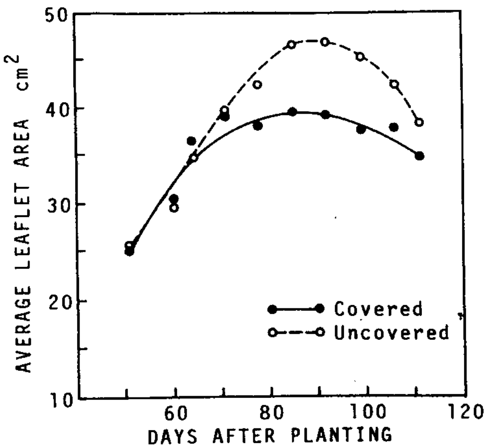

Figure 1. *Average size of soybean leaflets per plant as a function of days after planting.* Covered designates where ground between rows was covered with plastic film, uncovered is natural ground cover.

From the number of the leaflets remaining on the plant and the number of nodes on the plant, an estimate of the number of leaflets that had fallen was obtained at eight times during the growing season (Table 1). An analysis of variance of the data indicated highly significant differences in the number of leaflets between the two treatments. The uncovered plots maintained their superiority in the number of leaflets per plant over the covered plots. The differences between the two treatments were very evident during the later part of the growing season.

An analysis of variance for the fallen leaves showed no significant differences between the two treatments. There was however, a significant ($P < 0.05$) treatment interaction with time. Soybean plants were under severe water stress in the covered plots for a major portion of the growing season and leaf senescence was greater. Uncovered plots were only under moderate stress until early in August, and the

Table 1. *Number of leaflets on the plant, estimated number of fallen leaves and percentage senescence as a function of time for the two treatments.* Each observation is the mean of 40 plants.

Days after planting	Number of leaflets		Number of fallen leaves		% Senescence	
	Covered	Uncovered	Covered	Uncovered	Covered	Uncovered
64	29.1	31.9	4.1	4.1	12.4	11.4
71	37.0	39.4	3.1	2.8	7.8	6.7
78	42.6	46.9	5.6	4.6	11.7	9.0
85	40.4	50.7	11.2	9.2	21.7	15.4
92	42.7	52.8	11.3	11.6	21.0	18.1
99	37.4	47.8	14.8	16.1	28.4	25.2
106	29.3	42.0	16.8	20.4	36.5	32.7
111	28.1	35.6	18.8	24.0	40.1	40.3

Table 2. *Leaf-area index (leaf area per unit land area) in different strata of the crop canopy for the covered and uncovered plots.* Each observation is the mean of 40 plants.

Days after planting	Canopy depth from the top, cm — Covered plots						Uncovered plots					
	0–15	15–30	30–45	45–60	60–75	Total	0–15	15–30	30–45	45–60	60–75	Total
71	2.1	1.0	0.4	0.2	—	3.7	2.2	1.1	0.7	0.5	—	4.5
78	1.9	1.2	0.7	0.2	—	4.0	2.4	1.2	0.9	0.6	0.3	5.4
85	1.5	1.2	0.8	0.4	0.1	4.0	2.3	1.2	1.2	0.9	0.5	6.1
92	1.5	1.2	1.1	0.5	0.1	4.4	2.1	1.5	1.2	1.1	0.6	6.5
99	1.4	1.0	0.8	0.5	0.2	3.9	1.7	1.4	1.2	1.0	0.5	5.8
106	1.3	0.9	0.6	0.2	—	3.0	1.7	1.2	1.1	0.7	0.4	5.1
111	1.1	0.8	0.6	0.2	0.2	2.9	1.4	1.0	0.8	0.5	0.4	4.1

percentage senescence was lower than for the covered plots until that time. With progressive soil drying, the uncovered plots showed as much senescence as the covered plots by 111 days after planting.

From the previous discussion, it is evident that moisture-stress effects are apparent on leaf size, as well as on number of leaves and leaf senescence.

Leaf-area distribution

Leaf-area distributions with height for the covered and uncovered plots, respectively, are presented in Table 2. Analysis of variance for the data showed that there were significant ($P < 0.01$) differences in the leaf-area index between the treatments in all canopy layers except the 15–30 cm layer. Most of the leaves in the soybean plants were concentrated in the top layers of the canopy. Uncovered plots showed a larger leaf-area index in the top layers than did the covered plots. Leaf-area index values in the bottom layers of the canopy substantiate the observations on differences in leaf senescence. In the covered plots, leaf senescence was responsible for lower leaf-area index values.

Using the data in Table 2, the fraction of total leaf area between the top of the canopy and different depths of penetration into the canopy were calculated as a function of total leaf-area index. Smooth curves drawn through these data points are shown in Figure 2. For the sake of clarity, only curves for 71, 99, and 111 days after planting are shown. The cylindrical distribution of leaf area, which assumes that leaves are uniformly distributed around the plant with depth, is shown in the figure for the sake of comparison. Moisture-stress effects on leaf-area distribution are observable from the shape of the curves. Leaf area in the covered plots is more concentrated in the top layers, and deviation from the cylindrical distribution is significant. For the uncovered plots, at 99 days after planting, the leaf area approaches the closest to a uniform pattern, as shown by the cylinder pattern. Blad and Baker (1972) attributed the differences in leaf-area distribution they found to plant age,

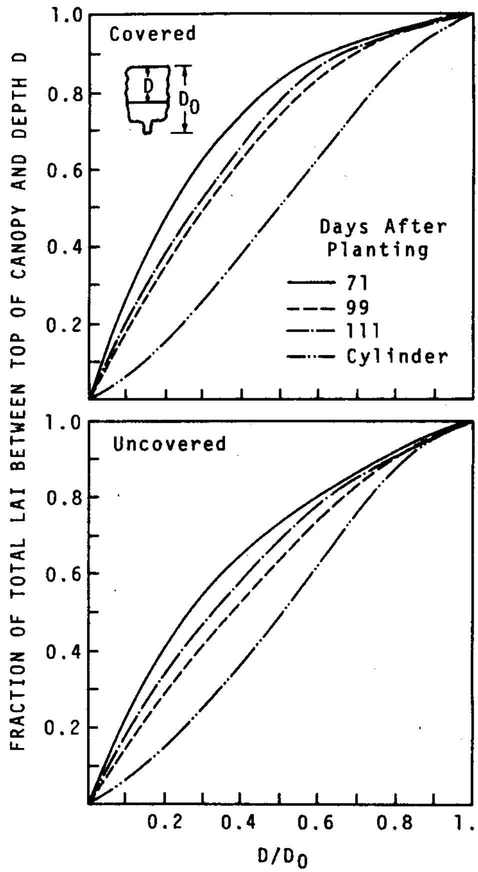

Figure 2. *Leaf-area distribution with height for the two treatments at three times during the season.* LAI, leaf-area index; D_0, height of the crop canopy; D, depth in the canopy from the top for which the fractional leaf-area index was calculated.

leaf size, row width and orientation, and other factors that influence the distribution of light in the soybean canopy. The differences in the leaf-area distributions in the present case seem mediated by moisture-stress effects associated with leaf senescence and light penetration in the lower depths of the canopy. Preferential flow of water to the young developing leaves at the top of the plant could have caused leaf senescence in the bottom layers.

Leaf enlargement as a function of water potential and stomatal conductance

Boyer (1970) showed that as leaf-water potential decreased, leaf enlargement was inhibited earlier, and more severely, than photosynthesis or respiration. This suggests that a minimal leaf turgor must be present before rapid leaf enlargement will occur. Growth was completely halted by a drop of leaf-water potentials to about –4 bars in sunflower (Boyer 1968), –7 bars in maize (Acevedo *et al.* 1971), and –12 bars in soybean (Boyer 1970).

The leaf enlargement rates (% increase in average leaflet areas) as a function of leaf-water potential and stomatal conductance are presented in Figure 3. Data points on the figure represent the pooled data from both treatments. From the figure, it seems that leaf enlargement is more closely related to changes in leaf-water potential than to stomatal conductance. This difference in response was probably associated with different roles of water in the two cases (Boyer 1970). Leaf-water potential represents the changes in water status of the growing cells themselves, whereas stomatal conductance relates to the diffusion of both CO_2 and water vapour. Under constant environment chamber conditions, Boyer (1970) found that leaf enlargement was 25% of the observed maximum at –4 bars, and at –12 bars the leaf enlargement dropped to zero. In the present experiment, a major decrease in leaf enlargement occurred near –8 bars, and at a leaf-water potential of –12 bars the growth was completely halted, indicating an adaptation of soybean plants to continuous moisture stress conditions in the field. This also agrees with the results shown by Jordan and Ritchie (1971).

A rapid reduction of leaf enlargement occurred near a stomatal conductance of 0.4 cm/s, and at 0.2 cm/s no enlargement was observed.

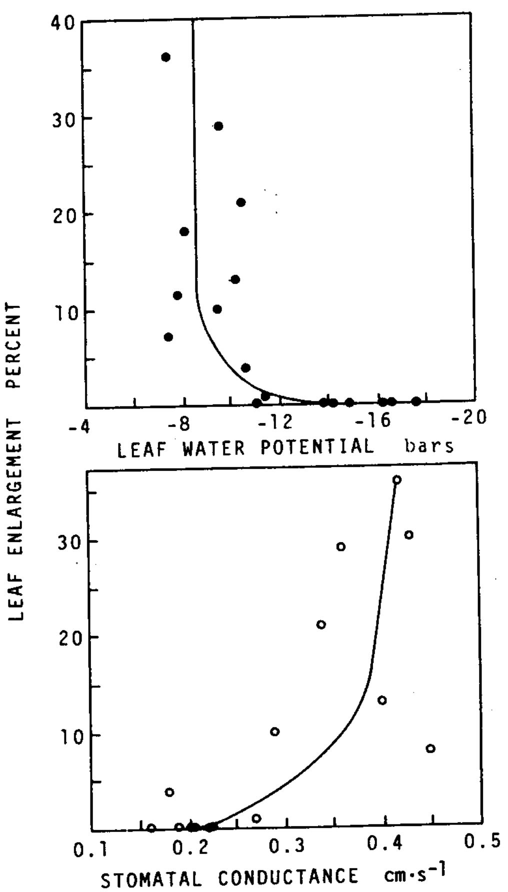

Figure 3. *Leaf enlargement rates for soybeans as a function of leaf-water potential and stomatal conductance.*

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