Water Potential and Stomatal Resistance of Sunflower and Soybean Subjected to Water Stress during Various Growth Stages

Received for publication March 24, 1976 and in revised form June 17, 1976

Nasser Sionit* and Paul J. Kramer
Department of Botany, Duke University, Durham, North Carolina 27706

ABSTRACT

Plants of two varieties of soybean (Glycine max (L.) Merr.) and two varieties of sunflower (Helianthus annuus L.) were grown in controlled environments and subjected to water stress at various stages of growth. Leaf resistances and leaf water potentials were measured as stress developed. In soybeans the upper leaf surface had a higher resistance than the lower surface at all leaf water potentials and growth stages. Resistance of the upper surface began to increase at a higher water potential and increased more than the resistance of the lower surface. Resistances returned to prestress values 4 days after rewatering. In sunflowers upper and lower leaf surfaces had similar resistances at all water potentials and growth stages. Leaf resistances were higher in sunflower plants stressed before flowering than in those stressed later. Sunflower plants stressed to −16 bars recovered their prestress leaf resistance and water potential a few days after rewatering, but leaves of sunflower plants stressed to −23 bars died. Leaves of soybean and sunflower plants stressed before flowering suffered less injury than those of older plants and sunflowers stressed after flowering suffered more injury than soybeans.

The objective of this research was to investigate the behavior of stomata of soybeans and sunflower plants subjected to water stress at various stages of development. It has been reported that the critical water stress causing stomatal closure varies with the growing conditions (6, 8, 10, 14), the position of the leaves in the canopy (17), and the stage of development (7). Differences in the behavior of stomata on the upper and lower surfaces of leaves also have been reported (5, 9). Some discrepancies among the findings of various investigators can be attributed to differences in the species studied, and to differences in stage of development and environmental conditions under which the plants were grown. The results reported here were obtained from plants grown under controlled conditions and subjected to measured levels of leaf water stress at several stages of growth.

MATERIALS AND METHODS

Soybean (Glycine max (L.) Merr.), variety Ransom, was grown in a mixture of one part by volume of Vermiculite and one part gravel in 25-cm plastic pots in a growth chamber of the Duke University phytotron (13). The temperature was 28 C during the 9-hr day, and 17 C during the dark period which corresponded to the average of maximum day temperature and minimum night temperature outdoors during the summer of 1974. The light intensity was 450 hectolux or over 600 µm in -1 as measured with a Lambda PAR sensor. The dark period was interrupted by illumination for 1 hr with incandescent lamps except for a period of 7 days, starting 30 days after emergence, to induce flowering. The relative humidity was maintained at 80% during the day. Except when subjected to water stress, the plants were watered every day with half strength Hoagland solution No. 1 in the morning and demineralized water in the afternoon until liquid dripped from the bottoms of the pots. Groups of five plants were subjected to water stress by withholding irrigation during one of the following stages of growth to produce a minimum of −23 bars leaf water potential: flower induction (T1), flowering period (T2), pod formation (T3), and pod filling (T4).

One group of plants, considered as the control, received the normal irrigation schedule during the entire growing period. The experiment was repeated later on the Bragg variety of soybean in similar conditions. The plants were grown to maturity to obtain seed yields which will be reported elsewhere.

A similar experiment was conducted on two varieties of sunflower (Helianthus annuus G.). Record and Krasnodarets, grown in the phytotron greenhouse at 26/20 C and 70% daytime relative humidity, with natural summer illumination. Groups of five sunflower plants were subjected to water stress by withholding irrigation during one of the following stages of growth: before heading (T1), during formation of heads (T2), during anthesis (T3), and during formation of seeds (T4).

Two levels of water stress were imposed on two different groups of sunflower plants, such that the minimum leaf water potential reached was either −16 or −23 bars. Total water potentials of both soybean and sunflower leaves stressed early in the season decreased more slowly than those stressed later. This was because the younger plants were smaller and transpired more slowly.

The osmotic and total water potentials of leaves were measured on leaf discs with thermocouple psychrometers of a modified Peltier type (18). The psychrometers were attached to an automatic scanning and recording system. The osmotic potential was determined after freezing the leaf discs used to measure the water potential. The pressure potential was obtained by subtracting the osmotic potential from the total leaf water potential. A preliminary experiment showed that the water potential of well watered soybean and sunflower plants in the phytotron approached constant values early in the afternoon. Therefore, samples were taken for measurements of water status between 1 and 2 PM from fully expanded leaves of approximately the same age. Stomatal resistances were measured with a diffusion porom...
eter (11) early in the afternoon. Transpiration was determined by weighing the pots daily.

RESULTS AND DISCUSSION

The stomatal resistance of soybean was consistently higher for the upper leaf surface than for the lower leaf surface but there was no important change with increasing age on either surface. Brady et al. (3) also reported no differences in stomatal resistance of upper or lower surfaces of soybean during different physiological stages of growth.

Slatyer (16) suggested that water deficit may not greatly affect the stomatal resistance until a critical leaf water potential is reached. In the present experiment the stomatal resistances of both surfaces of soybean leaves began to increase as soon as water stress began to develop, but the resistance of the lower surface increased more slowly and remained lower than the resistance of the upper surface during every stress period. In other experiments we have found the stomata on the lower surface of soybean leaves to be less sensitive to both light and water than those on the upper surface. This differs from the behavior of corn reported by Sanchez-Diaz and Kramer (15), where the differences between upper and lower surfaces decreased as the leaf water potential decreased. Kanemasu and

Fig. 1. Total leaf water potential and stomatal resistance of soybean plant stressed to −23 bars during flower induction (T1, ▼), flowering (T2, ○), pod formation (T3, □), and pod filling (T4, ×). Plants attained the desired degree of stress sooner when stress was applied later in development because the larger plants exhausted the soil water more rapidly.

Fig. 2. Transpiration rate of soybean plants stressed during different stages of growth as a function of leaf total water potential. Stress during flower induction (T1), stress during flowering (T2), stress during pod formation (T3), and stress during pod filling (T4). The low rate of transpiration at flowering (T3) is puzzling, but has been observed by other workers (4).

Fig. 3. Total leaf water potential and upper surface stomatal resistance of sunflower plants stressed to −16 bars during vegetative growth (T1, ▼), heading (T2, ○), flowering (T3, □), and seeding (T4, ×). These plants recovered when rewatered.
Tanner (9) found that the resistance of the lower surface of snapbeans was not significantly affected at leaf water potentials above -11 bars, but the stomatal resistance of the upper surface increased sharply at a leaf water potential of -8 bars. In the present experiment the sharp increase in the lower surface resistance began at a leaf water potential of -10 bars and the upper surface resistance increased rapidly from the beginning up to the end of the stress periods (Fig. 1). After rewatering, the resistances of both surfaces of soybean leaves decreased rapidly and in 4 days were back approximately to their prestress values.

Transpiration/unit of leaf area was considerably higher in plants stressed before flowering than in those stressed after flowering (Fig. 2). Stomatal resistances were also lower at this stage of development than later (T1, Fig. 1). The very low transpiration of flowering plants is puzzling because the stomatal resistance was no higher at this time than in other treatments (T2, Fig. 1). However, stomatal resistances were measured on the youngest fully expanded leaves and do not represent the average behavior of all leaves while the transpiration measurements represent averages of all leaves on the plants. Dennison (4) reported a sharp drop in water absorption by turkish tobacco plants just as flower buds were forming and cited several other examples of decreased water uptake at the time of flower bud initiation. This problem deserves further study.

The response of sunflower to water stress differed from that of soybean. The two sunflower varieties have similar numbers of stomata and similar resistances on both leaf surfaces and the stomata on both surfaces responded equally promptly to increasing stress and to rewatering (Figs. 3 and 4). However, the resistance of plants stressed before flowering was higher than that of plants stressed at later stages of development (T1 of Figs. 3 and 4). Also leaves of plants stressed to lower than -20 bars at flowering or later failed to recover and eventually died, although those stressed before flowering recovered (T1, Fig. 4). Boyer (1) also reported that sunflower leaves stressed to -20 bars seldom recovered. The main cause for the absence of recovery was shown to be the high resistance to water uptake by roots and to

![Graph](image-url)

**Fig. 4.** Total leaf water potential and upper and lower surface stomatal resistance of sunflower plant stressed to -23 bars during vegetative growth (T1, ▼, ▽), heading (T2, ○), flowering (T3, □), and seeding (T4, ×). Note that upper and lower surface resistances are similar. There are no points for treatments T3 to T4 after rewatering because only the plants stressed before flowering recovered.

![Graph](image-url)

**Fig. 5.** Variations in the total and osmotic potentials of nonstressed soybean leaves (var. Ransom) during the growing season.
water transport through the stem xylem. Kramer (12) pointed out that the degree of recovery from severe stress depends on the plant's capability to produce new roots, the vigor of the plant, and the duration and intensity of wilting. In the present experiment, soybean leaves, despite having higher root resistance than sunflower (2), were less injured by low leaf water potential than sunflower leaves.

There is a progressive decrease in the osmotic and total water potential of the leaves of nonstressed soybean plants during the early part of the growing season (Fig. 5). Total water potential decreased somewhat more slowly causing an increase in the pressure potential of the leaves until 65 days after emergence. This reflects an increasing ability of the plant to maintain turgor at low leaf water potential.

Wilting was observed at leaf water potentials of −12 bars on lower leaves of the soybean plants stressed during pod filling, and at −16 bars on lower leaves of the plants stressed during flower induction or flowering. Figure 1 shows that dehydration of soybean leaves to −23 bars in all the growth stages induced a similar lag of recovery in leaf water potential after rewetting. In sunflower plants, wilting was observed at a leaf water potential of −6 bars on lower leaves stressed during any stage of growth.

These experiments indicate that sunflowers differ from soybeans in several respects. Leaf resistances are similar for upper and lower surfaces of stressed and unstressed sunflower leaves but they are consistently higher for the upper than the lower surfaces of stressed and unstressed soybeans. The stomata on the upper surface of soybean leaves are more sensitive to water stress than those on the lower surface, but there was no difference between upper and lower surfaces of sunflower. In general sunflower leaves wilted sooner and were injured more by severe water stress than soybean leaves.

Acknowledgments—We wish to acknowledge the assistance of G. N. Fick of the Agricultural Research Service, North Dakota State University, in providing seed of suitable varieties of sunflower and of D. T. Patterson in revising the manuscript.

LITERATURE CITED