

# Leaf Enlargement and Metabolic Rates in Corn, Soybean, and Sunflower at Various Leaf Water Potentials<sup>1</sup>

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## ABSTRACT

Rates of photosynthesis, dark respiration, and leaf enlargement were studied in soil-grown corn (*Zea mays*), soybean (*Glycine max*), and sunflower (*Helianthus annuus*) plants at various leaf water potentials. As leaf water potentials decreased, leaf enlargement was inhibited earlier and more severely than photosynthesis or respiration. Except for low rates of enlargement, inhibition of leaf enlargement was similar in all three species, and was large when leaf water potentials dropped to about  $-4$  bars.

Intact sunflower leaves were held for 4 days at leaf water potentials which permitted maximal photosynthesis and respiration, but which inhibited leaf enlargement. Although leaf enlargement did not occur initially, enlargement resumed toward the end of the desiccation period. However, the rate of enlargement was not as rapid as in the well watered control, nor did it return to the control rate when the plant was rewatered.

The present study is concerned with the ways in which leaf enlargement, photosynthesis, and respiration respond to reduced leaf water potentials in three plant species. It has been suggested that cell enlargement may be more sensitive than photosynthesis to reduced leaf water potential (2). In sunflower, at least, leaf enlargement is reduced at water potentials as high as  $-2.5$  bars, and ceases at potentials of  $-4$  bars (2). Photosynthesis in other species is usually unaffected at these levels (5). However, a recent study (18) of carbon fixation and leaf elongation in *Lolium* has shown that photosynthesis and leaf enlargement are affected similarly at moderate leaf desiccation and that elongation is inhibited more strongly than photosynthesis only at low leaf water contents. The work with *Lolium* suggested that conclusions regarding leaf enlargement in sunflower (2) may have been premature. Consequently, a comparison of the response of photosynthesis and leaf enlargement to low leaf water potentials was made in sunflower and also in corn and soybean.

## MATERIALS AND METHODS

Corn (*Zea mays*, var. GSC 50 single cross), soybean [*Glycine max* (L.) Merr. var. Harosoy], and sunflower (*Helianthus annuus* L.) plants were soil-grown from seed in a constant environment

chamber [temperature was  $29 \pm 1$  C during the day and  $21 \pm 1$  C at night; relative humidity was  $70 \pm 5\%$ ; light intensity was 2500 ft-c (fluorescent and incandescent); photoperiod was 14 hours].

Rates of net photosynthesis and respiration were measured daily in shoots of 4- to 5-week-old intact plants with the use of an infrared gas analyzer and assimilation chamber in a semi-closed system (3). Chamber temperature was  $25 \pm 0.25$  C, relative humidity was  $77 \pm 2\%$ , and wind speed was 1.7 m sec<sup>-1</sup>. Under these conditions, leaf temperatures were within 0.6 C of chamber temperature. For photosynthesis, seven 300-w incandescent spotlights provided a light intensity of 1.6 cal cm<sup>-2</sup> min<sup>-1</sup> (measured with a Moll thermopile) at leaf height, which was saturating for soybean and sunflower. The rate of photosynthesis was determined at approximately 10-min intervals by measuring the time required for the shoot to decrease the CO<sub>2</sub> concentration in the assimilation chamber from 270 to 230  $\mu$ l/liter. Respiration rate was determined similarly by measuring the time required for an increase in CO<sub>2</sub> concentration from 230 to 270  $\mu$ l/liter in the dark. Between measurements of photosynthetic or respiratory rates, the CO<sub>2</sub> concentration was held constant at  $250 \pm 7$   $\mu$ l/liter.

After steady rates of gas exchange were obtained, the assimilation chamber was opened and a leaf disc was rapidly removed from a lower leaf and placed in a thermocouple psychrometer chamber for isopiestic measurement of leaf water potential (1, 4).

The rate of leaf enlargement was determined by measuring the differences in leaf area (soybean and sunflower) or leaf length (corn) before and after a growth period of 24 hr. The soil in which the plants were growing was permitted to dry to varying degrees before the growth period. The plants were then placed in a dark, humid chamber to grow for 24 hr. Tests indicated that weight loss from the plant-soil system was negligible during the growth period and that leaf water potentials did not change. At the end of the growth period, a disc was removed from the experimental leaf and was placed in a thermocouple psychrometer for isopiestic measurement of leaf water potential (1, 4).

## RESULTS

Figure 1 shows the response of leaf enlargement and net photosynthesis in corn, soybean, and sunflower as leaf water potential decreased after water had been withheld from the soil. Over the entire range of potentials, leaf enlargement was considerably more inhibited than photosynthesis by low leaf water potentials. When rapid enlargement was occurring, a small lowering of the leaf water potential caused considerable inhibition of enlargement. At  $-4$  bars, leaf enlargement was 0% in sunflower, 25% of the observed maximum in soybean, and 20% of maximum in corn. In corn it is likely that part of this enlargement was associated with meristematic activity at the base of the leaf.

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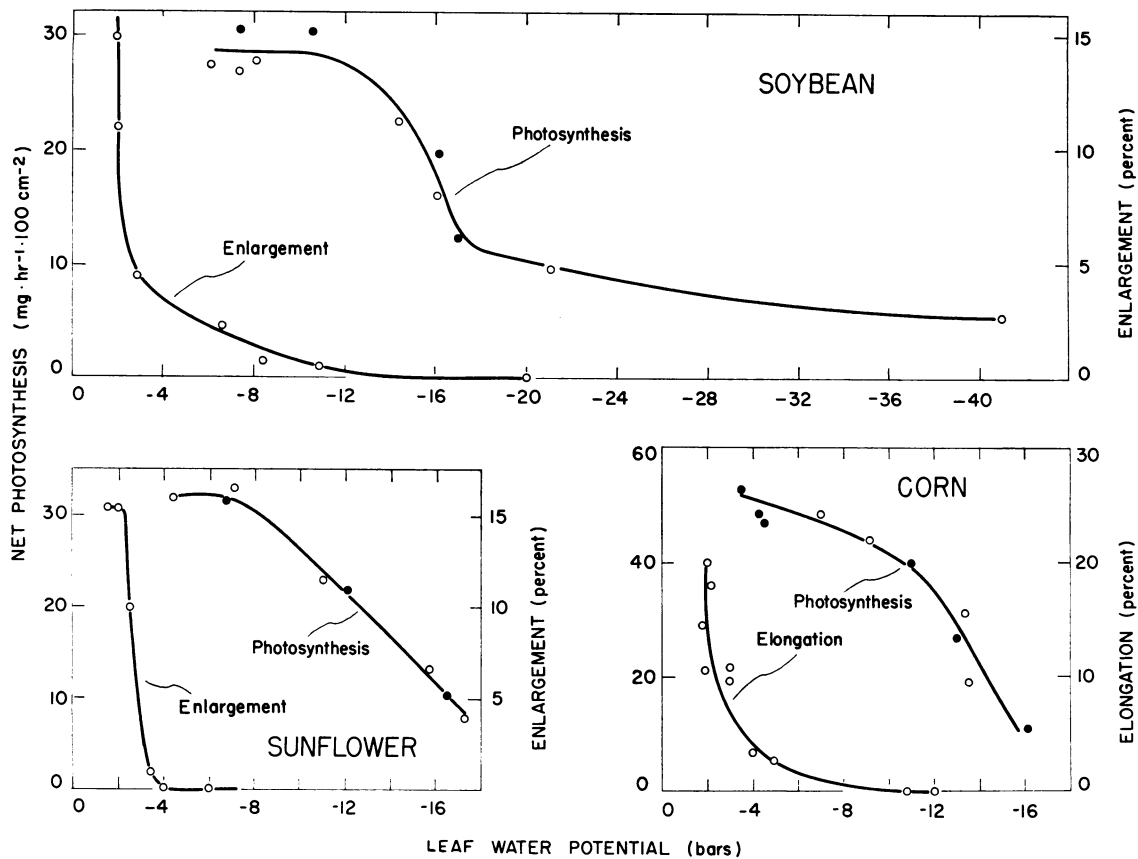


FIG. 1. Rates of leaf enlargement and net photosynthesis in corn, soybean, and sunflower plants at various leaf water potentials. The photosynthesis data were collected from two different plants for each species (●: Plant 1; ○: Plant 2). The plants were 45 to 60 cm tall. The growth data for soybean and sunflower represent enlargement of the fourth and sixth leaves from the base of the plant, the leaves having an area of about 20 and 60 cm<sup>2</sup>, respectively, at the beginning of the 24-hr growth period. For corn, growth was determined as elongation of the sixth leaf blade. The corn leaf blades were initially 25 to 35 cm long.

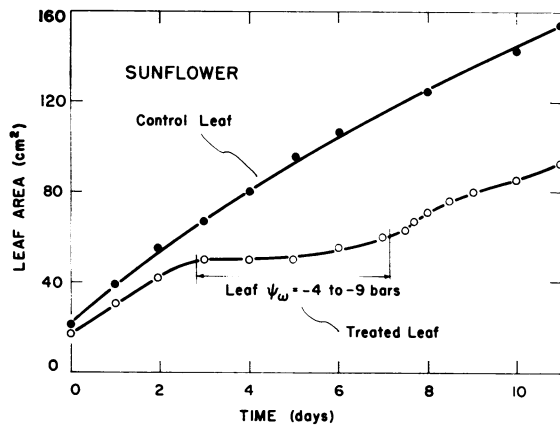


FIG. 2. Leaf enlargement during a period of moderate leaf desiccation. Control was well watered throughout the experiment. Water was withheld from the treated plant at the time indicated, and sufficient water was added to the soil in small amounts to keep leaf water potentials between -4 and -9 bars. At the end of the treatment period, the soil was well watered, and subsequent leaf enlargement was followed.

The response of leaf enlargement to reduced water potentials suggests that a minimal turgor must be present before rapid enlargement will occur. Osmotic potentials were -16 to -17, -13, and -10 bars in well watered corn, soybean, and sunflower, respectively. Thus, the lowest turgor associated with growth was about 7 to 8 bars in corn, soybean, and sun-

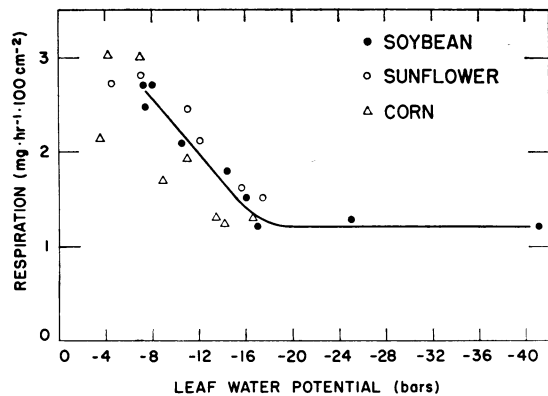


FIG. 3. Rates of dark respiration in corn, soybean, and sunflower plants at various leaf water potentials. The data were collected from two different plants for each species.

flower, respectively. At no time was growth observed in the absence of turgor, and rapid growth rates occurred only when turgor was high.

The difference in the response of leaf enlargement and photosynthesis suggests that desiccation does not limit enlargement due to lack of photosynthate, unless, perhaps, desiccation promotes translocation away from sites of leaf enlargement. During moderate desiccation, photosynthate should accumulate, if not in the leaf, then in other portions of the plant. With such an

accumulation, growth might be more vigorous after a period of water deficiency than before (9, 12, 13).

This idea was tested by following the enlargement of a sunflower leaf growing on a plant that was subjected to a period of low leaf water potentials in the light. Small quantities of water were added to the soil during the 4-day stress period, but leaf water potentials remained between  $-4$  and  $-9$  bars. At these potentials, leaf enlargement should have been negligible. Figure 2 shows that enlargement did not occur initially but began toward the end of the 4-day stress period. After rewatering, there was an increase in enlargement rate, although not enough to represent complete recovery to the control rate. Thus, in spite of high availability of photosynthate, some other factor limited growth after rewatering.

Dark respiration rates were similar in the three species (Fig. 3) and were roughly proportional to water potential down to  $-16$  bars. Below  $-16$  bars, soybean showed no change in respiration rate. As opposed to the strong inhibition of photosynthesis at low water potentials, respiration was not inhibited by more than 50%.

### DISCUSSION

The inhibition of leaf enlargement by declining leaf water potential was more severe than that of photosynthesis and respiration in every case. The major changes occurred within a 2- to 3-bar interval, with maximal rates of enlargement at about  $-1.5$  to  $-2.5$  bars and with strongly inhibited rates at  $-4$  to  $-5$  bars. The difference in response of the two processes was probably associated with the different roles of water in each one. Reductions in rates of photosynthesis are often brought about by stomatal closure (5, 16, 17), whereas changes in rates of cell enlargement are the result of changes in the water status of the growing cells themselves. Turgor determines the response of stomata (19) and appears to be involved in cell enlargement (2, 7, 8, 10, 11, 14; see 6 for dissenting view). If photosynthetic inhibition was a stomatal phenomenon in the present study, the data suggest that there may be considerable differences in the response of stomata and cell enlargement to reduced turgor.

Although rapid leaf enlargement was uniformly sensitive to low leaf water potentials in the three species, there were differences between species when growth rates were low. At leaf water potentials below  $-4$  bars, enlargement was completely suppressed in sunflower, but continued at low rates in soybean and corn. The large inhibition in sunflower at such potentials may result in little leaf growth during the day, even in well watered soil (2). For corn and soybean under these conditions, leaf enlargement would probably occur at moderate rates during the day.

The photosynthetic response to reduced leaf water potential also may have been different in the three species. Photosynthesis in corn was reduced whenever leaf water potentials decreased, whereas photosynthesis in soybean was unaffected by leaf water potentials as low as  $-11$  bars. In corn, however, the percentage of inhibition of photosynthesis was still much less than that of leaf enlargement. The behavior of respiration during desiccation was not significantly different for the three species (5, 15).

The growth data are in agreement with the idea that a minimal turgor is required for rapid cell enlargement (11). Small increases in turgor result in large increases in rates of enlargement. Similar results have been found in intact *Nitella* (10), in isolated

cell walls of *Nitella* (14), and in oat coleoptiles (7). The resumption of leaf growth during moderate desiccation, which was found in the present work for sunflower, has also been observed in *Nitella* (10), but after a much shorter time. In sunflower, recovery of normal rates of leaf enlargement did not occur upon rewatering. Complete recovery, and even rates exceeding control rates, has been noted in other species (9, 12, 13).

Regardless of how much water was supplied to the plant, it was not possible to obtain leaf tissue having a water potential of zero (2). During the growth experiments, transpiration was negligible, and as a result, the potential of the leaf cells could not be attributed to gradients occurring during transpiration. The highest leaf water potentials obtained in the three species were associated with rapid rates of leaf growth. Apparently, water entry during growth caused a yielding of the cell wall so that turgor did not increase to a value high enough to produce a leaf water potential of zero. Consequently, there was a potential gradient of about 1.5 to 2.5 bars between the growing cells and their water supply (2). Such a gradient implies that leaf cells have a resistance to water entry during growth.

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### LITERATURE CITED

- BOYER, J. S. 1966. Isopiestic technique: measurement of accurate leaf water potentials. *Science* 154: 1459-1460.
- BOYER, J. S. 1968. Relationship of water potential to growth of leaves. *Plant Physiol.* 43: 1056-1062.
- BOYER, J. S. AND B. L. BOWEN. 1970. Inhibition of oxygen evolution by chloroplasts isolated from leaves with low water potentials. *Plant Physiol.* 45: 612-615.
- BOYER, J. S. AND E. B. KNIPLING. 1965. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. *Proc. Nat. Acad. Sci. U.S.A.* 54: 1044-1051.
- BRIX, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. *Physiol. Plant.* 15: 10-20.
- BURSTRÖM, H. G., I. UHRSTRÖM, AND R. WURSCHE. 1967. Growth, turgor, water potential, and Young's modulus in pea internodes. *Physiol. Plant.* 20: 213-231.
- CLELAND, R. 1959. Effect of osmotic concentration on auxin action and on irreversible and reversible expansion of the *Avena* coleoptile. *Physiol. Plant.* 12: 809-825.
- CLELAND, R. 1967. A dual role of turgor pressure in auxin-induced cell elongation in *Avena* coleoptiles. *Planta* 77: 182-191.
- GATES, C. T. 1955. The response of the young tomato plant to a brief period of water shortage. I. The whole plant and its principal parts. *Aust. J. Biol. Sci.* 8: 196-214.
- GREEN, P. B. 1968. Growth physics in *Nitella*: a method for continuous *in vivo* analysis of extensibility based on a micromanometer technique for turgor pressure. *Plant Physiol.* 43: 1169-1184.
- LOCKHART, J. A. 1965. Cell extension. In: J. Bonner and J. E. Varner, eds., *Plant Biochemistry*. Academic Press, New York. pp. 826-849.
- MILLER, L. N. 1965. Changes in radiosensitivity of pine seedlings subjected to water stress during chronic gamma irradiation. *Health Phys.* 11: 1653-1662.
- OWEN, P. C. AND D. J. WATSON. 1956. Effect on crop growth of rain after prolonged drought. *Nature* 177: 847.
- PROBINE, M. C. AND R. D. PRESTON. 1962. Cell growth and the structure and mechanical properties of the wall of internodal cells of *Nitella opaca*. *J. Exp. Bot.* 13: 111-127.
- SCHNEIDER, C. W. AND N. F. CHILDERS. 1941. Influence of soil moisture on photosynthesis, respiration, and transpiration of apple leaves. *Plant Physiol.* 16: 565-583.
- TROUGHTON, J. H. AND R. O. SLATYER. 1969. Plant water status, leaf temperature, and the calculated mesophyll resistance to carbon dioxide of cotton leaves. *Aust. J. Biol. Sci.* 22: 815-827.
- VAADIA, Y., F. C. RANEY, AND R. M. HAGAN. 1961. Plant water deficits and physiological processes. *Ann. Rev. Plant Physiol.* 12: 265-292.
- WARDLAW, I. F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. *Aust. J. Biol. Sci.* 22: 1-16.
- ZELITCH, I. 1969. Stomatal control. *Ann. Rev. Plant Physiol.* 20: 329-350.