

Salinity, photosynthesis, and leaf growth

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Manipulation of the plant's environment to reduce salinity will continue to be the principal management strategy in the future. Competition for limited quantities of high-quality water, however, may eventually force growers to use lower quality water, such as municipal and irrigation return flows. Development of new, more salt-tolerant crops and crop varieties will therefore provide an important supplemental means of managing salinity.

A necessary first step in breeding salt-resistant plants is to learn how salinity restricts growth. There are two hypotheses to explain salinity-induced growth reductions: that salinity decreases the water available to the plant by decreasing the osmotic potential at the root surface, and that an excess of certain ions such as sodium or chloride directly exerts toxic effects ("specific ion effects").

Plant biomass production depends on the accumulation of carbon products in photosynthesis. This in turn is determined by two main components: the rate of photosynthesis per leaf area and the area of leaf surface available for photosynthesis. Our experimental approach is to investigate the effects of salinity on these two physiological components of yield — photosynthesis and leaf expansion — when both are measured under the same growing conditions. The question is to what extent salinity-caused growth reductions are due to a decrease in photosynthesis as opposed to decreases in leaf expansion.

The answers require an integrated study of whole-plant behavior along with determination of biochemical and biophysical responses at cellular and subcellular levels. Changes in whole-plant behavior are determined by analysis of plants grown in controlled-environment chambers. This analysis involves measurements of the dry weights of individual plant parts, leaf areas and numbers, cell numbers and

volumes, as well as chemical contents of leaf, stem, and roots.

Because we perceive changes in leaf growth to be a key factor in understanding the mechanism of salinity damage, we have developed the capability of monitoring leaf growth with high resolution over time. Using linear displacement electronic transducers, we are following the minute-by-minute changes in leaf extension, width, and thickness in response to changes in salinity, humidity, and temperature.

The influence of salinity on photosynthesis is being explored with a wide range of techniques. We are measuring *in vivo* photosynthesis by monitoring the rate of photosynthetic carbon dioxide uptake by leaf gas exchange. Using a transparent chamber to enclose a leaf that remains attached to the plant, we are able to measure continuously the carbon dioxide uptake, water vapor output, and leaf temperature in a carefully controlled environment of light, temperature, carbon dioxide concentration, and humidity. In this way we can determine the effects of salinity on photosynthesis, transpiration, and stomatal conductance in specific leaf environments.

Leaf gas exchange measurements separate the effects of salinity on stomatal conductance from its effects on other components of the photosynthetic apparatus. Photosynthesis occurs in chloroplasts, the subcellular organelles that give the green color to leaves. The chloroplasts are assayed to determine which enzymes are being affected by salinity.

In sugarbeet, a fairly salt-tolerant plant, growth and leaf area expansion were reduced even at very low salinity levels. Total plant dry matter and total leaf area were decreased at levels as low as 25 moles/m³ (1,460 mg/L) sodium chloride (supplied hydroponically in half-Hoagland's solution); the reductions in these attributes became progressively greater with each additional increment of salt. On the other hand, the rate of photosynthesis per unit of leaf area was not reduced until sodium chloride con-

centrations reached 200 or 300 moles/m³ (11,700 or 17,500 mg/L), and leaf respiration was not affected even at 500 moles/m³ (29,200 mg/L). The primary effect of salinity on growth thus appeared to occur through an effect on leaf expansion rather than through changes in the rates of photosynthesis or respiration per leaf area.

Salinity affected the expansion of the plant's total leaf surface through the expansion of individual leaves rather than through the rate of production of new leaves. When we investigated leaf extension with linear displacement transducers, we found that the effect of salinity on leaf growth was strikingly dependent on the time of day. Leaf extension in control plants was on average three to six times faster at night than during the day: in one sugarbeet experiment, for example, the extension rate was 1.40 mm per hour in the dark and 0.41 mm in the light. In salinized plants, the ratio was greater: leaf extension in darkness (0.41 mm per hour) was 7.7 times that in the light (0.053 mm). Typically in our experiments, more than 90 percent of the leaf extension by saline-treated plants occurred in darkness.

Another striking aspect of these results was the speed with which growth changed with change in environment. For example, when the growth chamber lights came on in the morning, leaf extension slowed or ceased within seconds. In contrast, stomatal opening occurred over many minutes, requiring up to half an hour to become complete. Similarly, when the growth chamber lights went off, leaf extension accelerated to very high rates, again within seconds.

In general, our results point to the idea that salinity effects on leaf growth are mediated very largely by changes in the plant's water status, particularly that of the leaf. For example, it is our interpretation that leaf extension slowed when the lights came on in the growth chamber because leaf water status was diminished: as the radiant heat load increased, the evaporative demand would have been greater so that water losses would outstrip supply and reduce leaf water potential. An increase in root zone salinity would exacerbate this effect by lowering the overall plant water status. When salinity was imposed for 48 hours, leaf growth and leaf water potential measured hygrometrically declined; when the plant was restored to a nonsaline condition, leaf extension and water potential returned to presalinized levels. The rapidity and complete reversibility of these changes also suggest that the effect of



Even low salinity inhibited leaf expansion of sugarbeet grown in nutrient solution with salt added, compared with one grown in nonsaline solution (right).

of leaf area did not diminish. Probably the increased amount of photosynthetic apparatus per unit area of the thicker leaves compensated for the lowered internal carbon dioxide concentration.

Conclusion

Our main conclusion is that salinity-induced plant growth reduction in sugarbeet is due principally to a diminished surface area available for photosynthesis rather than to a reduced rate of photosynthesis per leaf area.

Measurements with linear displacement transducers showed that leaf extension growth occurred mainly in darkness, especially under salinized conditions.

Imposition of short-term root zone salinity (48 hours) reduced the leaf extension rate and leaf water potential. Removal of root zone salinity led to complete recovery of leaf extension rates and the return of leaf water potentials to their presalinized levels. These and other results suggest that salinity growth reductions were mediated largely by changes in plant water status.

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Despite the obvious implication that salinity effects are coupled with leaf water relations, it is very difficult to establish this relationship experimentally. When sugarbeet plants are exposed to salinity, they osmoregulate by absorption and transport of salts to leaves. This in turn lowers the osmotic potential of leaves so that turgor pressures remain as high as those of control plants. Thus, even though leaf extension rates of salinized plants in darkness were typically only half those of control plants, we found turgor pressures of salinized plants to be equal to or slightly higher than those in control plants.

Salinity affects the form as well as the growth rate of leaves. They may become considerably thicker with greater amounts of photosynthetic apparatus per leaf area than on nonsalinized plants. Salinized plants commonly had more chlorophyll, photochemical reaction centers, and electron carriers (P_{700} and cytochrome f), soluble protein, and extractable ribulose biphosphate carboxylase activity per unit of leaves than did control plants. Our studies on sugarbeet and mangrove have shown that salinity does not adversely affect thylakoid membranes of the photosynthetic apparatus; thylakoid lipid and protein contents, permeability, and the activities of their electron transport systems (photosystem II or photosystem I + II) were unaffected by salt up to 500 moles/ m^3 (29,200 mg/L)

sodium chloride. It is not surprising that photosynthetic rate is so tolerant of salinity.

Salinity significantly impaired stomatal conductance, causing a reduction in transpiration rate and an elevation of leaf temperature. Although photosynthetic rates expressed per unit of chlorophyll decreased, photosynthesis per unit

Measurements with a special instrument showed that sugarbeet leaf growth occurred mainly in darkness, especially under salinized conditions.

