

Although we do not know the complete details of the mechanism of the enzyme-catalyzed reaction of CO<sub>2</sub> with ribulose-1,5-diphosphate yielding two moles of 3-phosphoglyceric acid (19), we can assume that the overall reaction is similar, if not identical, in the many organisms that carry out photosynthesis. We are, therefore, faced with a situation in which the same or a very similar reaction is catalyzed by an enzyme in at least three quite different molecular forms. Additional experiments are required to determine whether the three carboxylases (6S, 13S, and 18S) are indeed chemically similar or chemically unrelated proteins.

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#### References and Notes

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## Sensors Monitor Tensions in Transpiration Streams of Trees

Abstract. *Resistance of implanted sensors fluctuated predictably with up-takes and loss of water by plants, and correlated positively with coincidental measurements of leaf-water potential when transpiration was minimized. Preliminary results indicate that transmission of change in tension may be almost instantaneous, regardless of transpirational flow rates. Rates of relaxation of tension were very rapid after precipitation, but only after water had percolated to root surfaces.*

According to the transpiration-cohesion theory of the ascent of (xylem) sap, the sap stream should be subjected to varying tension that depends on relative rates of water absorption and transpiration. I now describe sensors that permit continuous monitoring of stream tension in woody plants.

Each sensor consisted of a pair of stainless steel electrodes, spaced by fiberglass wrapping around one of them, embedded in a gypsum (plaster-of-Paris) cylinder (Fig. 1). Both ends of each sensor were "sealed" and strengthened with epoxy resin, and short leads were soldered to the electrodes before implantation of the sensor.

The amount of water in such a sensor depends, of course, on the relative water potential ( $\psi$ ) of moisture in its environment; thus sensor resistance is determined by this volume of water and the concentration of electrolytes in solution. Since the concentration of sap solutes does not fluctuate greatly—over short periods, at least—and since the CaSO<sub>4</sub> component would quickly saturate any water held in the sensor matrix, changes in sensor resistance are thought to reflect primarily changes in the volume of water held. The xylem matrix  $\psi$  should be relatively constant, so that changes in external  $\psi$  must be due to changes in tension. Thus change in sensor resistance is a result of change in sap tension.

Sites for implantation of sensors were selected on stems, branches, and shallow roots that were at least 2 cm in diameter and not exposed to direct sunlight. The bark was removed from a small area, and a hole slightly larger in diameter than the dry sensor was bored in the wood to sufficient depth to accommodate the entire length of the gypsum cylinder. Sensors were then gently inserted, and the outer tissue that had been removed was replaced

with putty; only the sensor leads protruded from the plant. Sensor resistance was then measured with either portable a-c resistance bridges or (for the most part) a Bristole Dynamatic high-resistance recorder; the latter permitted automatic monitoring of from 1 to 24 sensor points, with intervals of 10 to 15 seconds between consecutive readings.

Implantation obviously disrupted the transpiration stream in the area of the wound. After implantation, however, the gypsum swelled markedly when it absorbed moisture from the wood. The ensuing high degree of contact between sensor and tissue resulted in formation of a continuous liquid-water phase between the sensor and adjacent intact portions of the stream. Such moisture "bridges" probably account for the great sensitivity of the sensors, because of the exchange of water by bulk flow (1).

The amount of contact between sensor and stream, however, differed between implants, so that any preinsertion standardization or calibration of readings was precluded. This problem was overcome by correlation of sensor readings with pressure-bomb estimates of leaf  $\psi$  (2) during relatively static transpirational conditions. Tensions under such conditions should be equivalent to the vector sum of forces in any one direction.

I produced static conditions in saplings growing in pots by placing them in darkness long enough (usually overnight) to minimize transpiration. Tensions were varied in these trees by drying or wetting of the soil to different degrees. Satisfactory localized "static" conditions were also produced by enclosure, in opaque black plastic bags for a sufficient length of time, of only the foliage to be sampled (3). Saplings used included sour cherry (*Prunus cerasus* L. var. Montmorency) and two species of *Eucalyptus*.

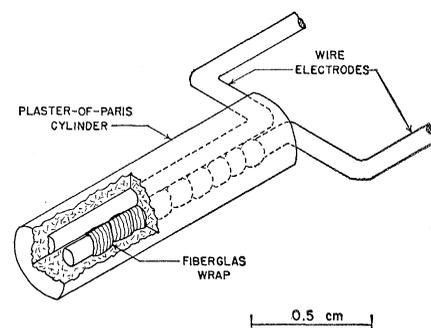


Fig. 1. Diagram of the moisture-tension sensor for plants.

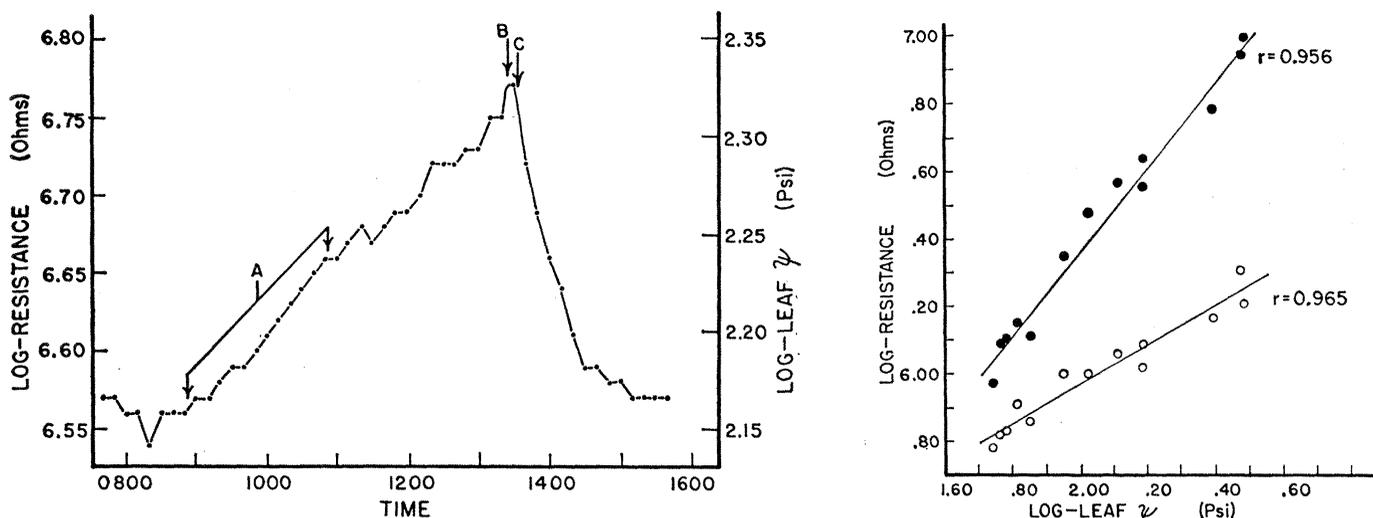


Fig. 2 (left). Sensor readings in a *Eucalyptus* sapling at 10-minute intervals. Foliage was exposed to diffuse daylight from approximately 0800 hours, with a period (A) of added radiation from a 1000-watt incandescent spotlight approximately 50 cm above the canopy. The relatively dry soil was wetted with 250 ml of distilled water applied to the surface at 1326 (B). The initial drop in resistance was noted by 1332 (C). Fig. 3 (right). Coincidental readings of two sensors in a *Eucalyptus* sapling, plotted against measured leaf  $\psi$ . These data represent four cycles of wetting and drying of the soil. In similar plots for other sensors, regression lines were usually more nearly parallel to the upper line in the figure.

Additional information about sensor performance and tensions was obtained by use of uncalibrated sensors in mature forest trees. In some instances, sets of sensors were implanted various distances apart along the axes of individual trees (up to 5.8 m between two consecutive sensors and 9.5 m between the two farthest apart). Species most used in field studies were beech (*Fagus grandifolia* Ehrh.) and black cherry, *Prunus serotina* Ehrh. Among the several other woody species tried, a few such as *Acer saccharum* Marsh. and *Pinus sylvestris* L. were found unsuitable because exudates produced in response to wounding interfered with exchange of moisture between sensor and stream.

In the field, general environmental conditions within the canopy (about 18 m above ground) were recorded by instruments on an abandoned windmill tower; factors determined included air temperature, humidity, precipitation, and relative cloud cover.

After 1 or 2 days, resistance in most implanted sensors began to fluctuate predictably on the basis of prevailing environmental conditions that regulate moisture exchange and so affect tensions. Resistances were particularly sensitive to changes in availability of soil moisture and in radiation (Fig. 2). In addition, linear relations were found between log-resistance and log-leaf  $\psi$  values (Fig. 3), with correlation coefficients usually exceeding 0.95 (4). These data generally support the contention that the sensors do measure tensions in the transpiration stream.

Responses of separate sensors in the

same tree were nearly parallel, and there was usually no measurable lag (limit of measurement, within 10 to 15 seconds) between relative maxima or minima of consecutive readings, especially during periods of grosser environmental changes affecting moisture exchange. By use of the maximum distance between consecutive sensors (5.8 m in beech), changes in tension appeared to be transmitted through the tree at a minimum rate of 5.8 m in 15 seconds—nearly 1400 m/hour.

Tentatively one might conclude from these results that change in tension was not transmitted by simple transpirational flow, since the rate was at least 200 to 300 times greater than flow rates reported for beech (5) and remained essentially the same regardless of transpirational conditions. This finding also implies that changes in tension may be "felt" almost immediately throughout even large trees.

Resistance changes of sensors in adjacent trees also were similar but less so than of sensors in the same tree. The lower correspondence between coincidental readings probably reflects differences in root and canopy size, structure, and exposure.

In field studies, tension was not relieved by precipitation before rain penetrated the soil and reached root surfaces. In a mature forest with a closed canopy and accumulation of litter, this meant a lag of 1 to 2 hours between the start of rainfall and the relaxation of tension, depending on the rate of precipitation. Rapid relaxation rates after delivery of water to root sur-

faces, on the other hand, indicate that there is relatively little resistance to flow into roots once the water is available (6).

Thus these new sensors appear to be useful tools for investigation of many ecologic and physiologic questions about tensions in woody plants.

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#### References and Notes

1. More direct evidence of this possibility was obtained with sensors in water-soaked pine blocks that were subjected to pressure changes in a pressure-membrane extractor of soil moisture. If the grain of these blocks was oriented normal to the membrane so that water in the lumina could be forced out through the membrane, the resistance of the sensor increased immediately as pressure was applied, and decreased when pressure was released. No significant changes in resistance were noted, however, when the grain was parallel to the membrane. Moreover, in the former orientation, loose-fitting sensors displayed less sensitivity and narrower ranges of response.
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3. Corrections for weight of water columns should be made if significant differences exist between heights of sensor and foliage used.
4. The statistic for computation of the correlation coefficient ( $r$ ) was (slope of regression line)  $\times$  [(variance of log-leaf  $\psi$ )/(variance of log-resistance)] [W. J. Dixon and F. J. Massey, Jr., *Introduction to Statistical Analysis* (McGraw-Hill, New York, 1957)].
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