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Short Communication

Removal of Salt from Xylem Sap by Leaves and Stems of Guttating Plants[1]

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Summary. Although root pressure and guttation presumably result from a high concentration of salt in the root xylem, the guttation fluid is very dilute. Measurements of the osmotic potential of the guttation liquid and of exudates at various levels in guttating plants indicate that salt is removed from the xylem in the upper part of plants, particularly in the leaves. The concentration of salt solutions forced through individual leaves by an artificial root pressure has no influence on the osmotic potential of the guttation fluid. This suggests that leaves play an important role in removing salt from the xylem of guttating plants.

It is generally agreed that guttation is caused by root pressure (2) and that root pressure occurs because the accumulation of salt in the root xylem causes osmotic uptake of water and development of hydrostatic pressure in the xylem sap (10). Although the development of root pressure depends on the accumulation of salt in the root xylem, the salt concentration of the liquid produced by guttation is very low. For example, Eaton (4) found the guttation liquid from leaves of tomato plants to have an osmotic potential higher than -1 bar while the exudate from stem stumps near the soil level had an osmotic potential of -1.5 to -2.4 bars. Eaton attributed this decrease to removal of salt from the ascending sap stream as it passes up the stem. However, no direct measurements of the osmotic potential at various levels in the plant have been made to determine how much salt is removed in the stems and how much in the leaves. The possibility of measuring the osmotic potential of samples as small as 3 μl with a modified Richards and Ogata psychrometer (3) made it feasible to measure the osmotic potential of single drops of exudate.

The first experiments were performed on 1-month-old tomato plants (*Lycopersicon esculentum* Mill. var. Manalucie) growing in soil. The leaves were rinsed with water to remove surface contaminants and kept overnight in a dark moist chamber. In the morning samples were taken of the guttation fluid, of the exudate from the distal ends of petioles from which the leaf blades had been removed, and then of exudate from the main stem cut at various levels. Since guttation did not begin until 1 or 2 hours before sampling, little change in concentration of the guttation fluid could have occurred as a result of water exchange with the humid air. Cut surfaces were blotted before sampling to reduce contamination from cut cells. Table I shows the results from 1 of the 4 plants sampled. The relative values are similar for the other 3 plants, but the absolute values and position in the plants differed so much that averages are not meaningful. These results show that the osmotic potential of the xylem sap at the end of the petiole is much lower than that of the guttation fluid at the leaf margins. This indicates that a considerable amount of salt is removed from the xylem sap as it passes through the leaves. Similar results were obtained with pepper plants (*Capsicum frutescens* L. var. California Wonder). It is not surprising that the leaf cells remove salt from the xylem sap in view of the observation by Smith and Epstein (9) that leaf discs accumulate salt. There is generally a measurable gradient of increasing osmotic potential in the upper part of the stem which causes the osmotic potential of the exudates from the petioles of upper leaves to be higher.

A method was devised to produce pressure in the xylem of detached leaves in order to study the effects of xylem sap concentration and pressure on the concentration of artificially-produced guttation fluid. The leaf petiole was inserted through the seal in a pressure chamber similar to that used by Scholander et al. (8) with the cut end immersed in a beaker containing water or any desired solution. The leaf blade could be kept in a dark moist chamber or exposed to light and air, according to the needs of a particular experiment.

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In experiments with pepper leaves, a pressure of 0.1 to 0.2 bar for 0.5 to 2 hours caused guttation resembling that of intact plants. However, a pressure to 0.3 to 0.4 bar caused abnormal injection of the base of the leaf blades, without normal guttation. In sharp contrast to pepper leaves, a pressure of 2.0 bars for 2 hours or of 1.0 bar for 4 hours was required to produce guttation from a branch of white pine (*Pinus strobus* L.) about 10 cm in length. A high resistance to water flow through the xylem probably explains why guttation is never seen in pine. This artificially-induced guttation (fig 1) probably is the first observation of this phenomenon in pine. Pressures from 0.2 to 1.0 bar applied to the base of the stem of pepper plants caused normal guttation from the leaves; a pressure of 1.5 or 2.0 bars resulted in rapid guttation from nodes and from cracks in the stem and petioles and in abnormal injection of the center of leaves. O'Leary (6) found that pressures of less than 1.0 bar produced normal guttation in several species.

This method was used for further study of guttation in pepper leaves. After leaves had been detached under water, the cut ends were immersed in Hoagland's solutions (5) of various concentrations and allowed to transpire for 2 hours so that the xylem sap presumably was replaced by the solutions. They were then placed in a humid dark chamber overnight. The petioles were sealed in the pressure chamber the next morning and subjected to a pressure of 0.2 bar. To measure the osmotic potential of solutions entering and leaving the leaf, samples of the guttated fluid were collected, the leaf blade was excised and petiole exudate was collected. Leaf tissue was sampled from near the midvein and along the margin, and water potentials and osmotic potentials were measured in a Richards and Ogata psychrometer (7) and corrected for tissue respiration (1). Similar measurements were made on control leaves not subjected to pressure.

The results (table II) indicate that both the petiole and the leaf blade removed salt from the xylem sap except at very low concentrations of introduced solution. The osmotic potential of the petiole exudate tended to decrease with increase in concentration of the solution supplied to the leaf, but the concentration of the guttation fluid and the water potential of the leaf tissue were not affected by the concentration. Neither is there a clear difference between the osmotic potential of the controls and that of the leaves subjected to pressure, although the data suggest a slight increase at the margin, possibly caused by dilution in the infiltrated tissue. However, water potential at the margin of the leaves subjected to pressure was as much as 1.0 bar higher than that of the controls, doubtless the result of infiltration in this area.

Table I. *The Osmotic Potentials (OP) of Stem and Petiole Exudates and of Guttation Fluid at Various Levels in the Stem of a Tomato Plant*

After sampling the guttation fluid, leaf blades were removed for sampling of petiolar exudate, and finally successive cuts were made below the base of 2 petioles for collecting stem exudate.

Distance above soil level (cm)	OP of stem exudate (bars)	OP of petiolar exudate (bars)	OP of guttation liquid (bars)
21	...	—0.88	—0.09
20	—1.25	...	...
17	...	—1.01	—0.09
13	—1.31	—1.35	—0.25

Table II. *Osmotic Potential (OP) of Petiole Exudate and Guttation Fluid and the Osmotic Potential and Water Potential of the Center and Margin of Pepper Leaves*

The various solutions were pushed through leaves with a pressure of 0.2 bar. All values are in bars.

OP of introduced solution	OP of petiole exudate	OP of guttation fluid	OP of leaf margin		OP of leaf center		Water Potential of leaf margin	
			Test	Control	Test	Control	Test	Control
0	—0.27	—0.13	—8.0	—10.9	—8.6	—9.9	—0.9	—1.9
	—0.25	—0.19	—9.1		—8.4		—1.2	
—0.31	...	—0.18	—8.7	—9.4	—8.6	—8.9	—0.8	—2.0
	—0.40	—0.25	—9.3		—9.3		—0.9	
—0.80	—0.78	—0.12	—7.8	—7.7	—8.1	—7.7	—0.9	—1.5
	—0.61	—0.08	—9.2		—9.8		—0.9	
—1.42	—0.63	—0.06	—7.1	—9.8	—7.0	—9.3	—1.1	—1.7
	—0.66	—0.32	—8.3		—8.8		—0.8	
—1.86	—1.24	—0.23	—7.9	—8.0	—8.4	—8.0	—1.2	—1.4
	—0.84	—0.10	—8.9		—9.9		—0.7	

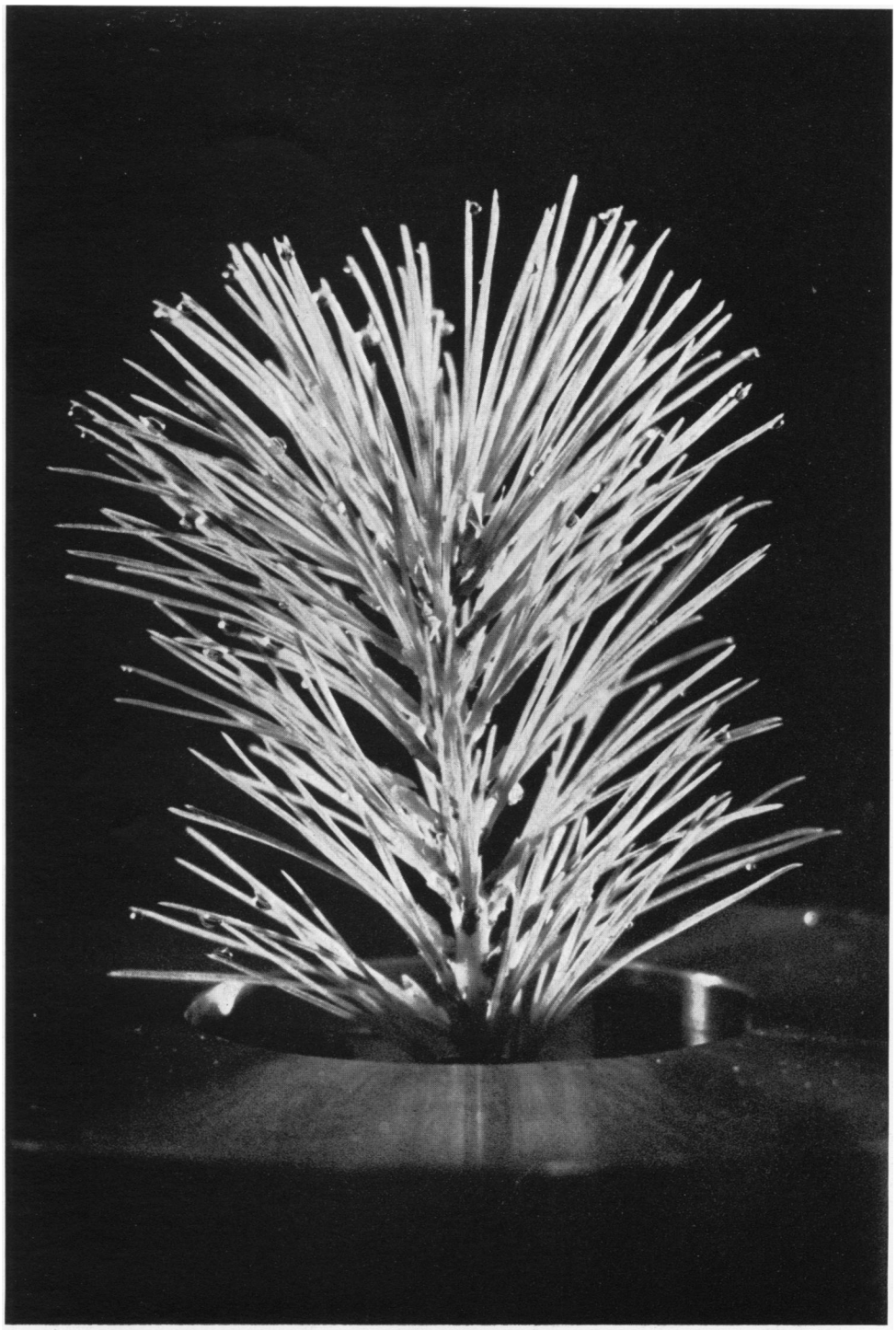

FIG. 1. White pine shoot showing guttation with a pressure of 1.0 bar applied to the cut stem.

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