SHORT COMMUNICATIONS

POLAR AND LATERAL TRANSPORT OF WATER IN AN APPLE TREE*

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An apparent polar movement of nutrients associated with polar water transport has been demonstrated for plants with a particular arrangement of vascular tissues. Rinne and Langston (1960) studied the movement and distribution of ^{32}P in peppermint (*Mentha piperita* L.) and showed polar transport to occur when half the root system was fed with ^{32}P. In the short term ^{32}P was even confined to half leaf blades of leaves in the median orthostichies. Caldwell (1961), who used a split-root technique to grow *Coleus* sp., demonstrated the apparent polar transport of nutrients to be maintained over a long period when half the root system was grown in nutrient-rich soil and half was grown in nutrient-deficient sand. Much less growth occurred in the side of the plant supplied by the roots in the nutrient-deficient sand.

Both *Coleus* sp. and peppermint have vascular tissues situated at the corners of a square stem with connecting tissues between the vascular bundles to provide a means of lateral transport under certain conditions. In further work with *Coleus* sp. grown by the split-root technique (Baker and Milburn 1965), it was shown that no specific polar transport of phosphorus occurred when half the root system was supplied with water at a low tension while the other half of the root system was in dry sand. The change from a normal, apparently polar, transpiration stream, to a non-polar stream occurred in response to increased lateral gradients in water potential within the plant when part of its root system was in an environment of increasing soil moisture stress.

In contrast to the work cited for plants having specialized arrangements in their vascular tissue, the work reported here was a study of the water transport phenomenon in a plant with a complete cylinder of vascular tissue in response to a soil moisture stress on part of the root system.

Material and Methods

The three test plants used were 2-year-old apple trees, cv. Red Gravenstein, on MM104 rootstock. The root systems and lower 20 cm of the trunks, which were about 10 cm in circumference, were divided into four parts by two saw cuts normal to each other. Each part of a tree's root system was established in a separate container of soil until the roots were fully extended throughout the soil volume. Two of the trees were supplied frequently with water to all four parts of their root systems to maintain the soil at or near field capacity throughout the experimental period. These control trees were housed in an open-sided, roofed shelter and provided a measure of the potential water use. The soil of the four root zones of the third tree was initially maintained at field capacity to provide a period for calibration of water loss by this tree against the control trees (see Fig. 2). The soil moisture content in each zone was allowed to fall (through

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loss by transpiration) to a low level. At this stage the soil in all four containers was again increased to field capacity, normal tap water being added to three and tritium-enriched tap water to the fourth. The soil in the latter container was maintained at field capacity while the soil in the other containers was allowed to dry out under the action of the plant's transpiration. Surface evaporation from the containers was prevented by covering the soil with polyethylene film and with stones (1-cm mesh) to a depth of 5 cm.

The trees were weighed at intervals of 1 or 2 days during the experimental period to determine the amounts of water lost by transpiration, and the amounts of water added to maintain the soil at field capacity in the appropriate root zones were recorded.

A minimum of 0·5 ml of transpired water vapour was condensed from one branch on either side of the tree two to four times each day and analysed for tritium activity with a scintillation spectrometer. The condensation was effected by sealing the selected branch in a clear polyethylene film bag with a condensing coil cooled with liquid CO_2. The bag was purged with dry air and transpiration was allowed to proceed for about 10 min before condensation was commenced. The branches used were selected, according to a polar transport hypothesis, to provide one branch which would be supplied from the tritium-enriched quarter and one from a non-enriched quarter. Soil moisture was determined gravimetrically in samples taken daily from the drying zones. The time after application of tritium-enriched water could then be correlated with the pF values for the soil (see Fig. 1). Thus the fifth day corresponded to a pF value of 3·25 and the sixteenth day to a value of 4·1.

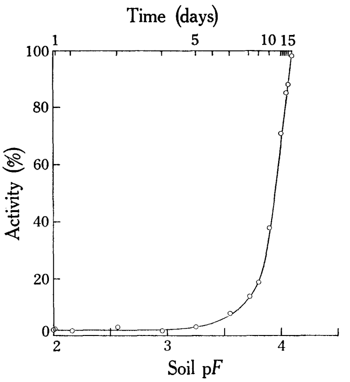

Fig. 1.—Tritium activity in transpired water above unenriched roots (expressed as a percentage of the activity in transpired water above enriched roots) as a function of soil pF in the unenriched root zone. The correlation of time after application of tritium-enriched water with soil pF is also shown.

Results

For the first 5 days after treatment was commenced the tritium level in the transpired water above the unenriched root system remained at about 2% of the level found on each day above the enriched zone (Fig. 1). Thereafter the percentage activity increased with time until by the sixteenth day the tritium level above the untreated side was 98% of the level above the treated side.

Parallel with this effect, the level of activity above the treated root system reached about 50% of the final level within 4 hr after the treatment was imposed, and remained at this level for the first 6 days. A rapid increase in activity occurred over the next 5 days and a maximum level was reached after 11 days.

Variable patterns occurred in the tritium levels from the different sides of the tree both within and between days as the soil dried out above the untreated parts of the root system. For the first 9 days after treatment, samples taken above the enriched quarter in the afternoon of any day had a higher activity than those taken in the morning of the same day. Thereafter the tritium levels were unchanged between morning and afternoon samples. An opposite pattern occurred above the unenriched side for the first 9 days and the highest activity for each day occurred in samples taken in the mornings. From the ninth day onwards, the afternoon samples showed a higher level of activity. The changed patterns of activity occurred at a soil p*F* value of 3·7 in the drying root zones.

Water supplied to the tree by the root zone which later received tritium-enriched water accounted for 20–25% of the total loss from the tree in the period of calibration. After the treatment was started, this proportion increased progressively to 100% by 16 days (Fig. 2, curve *A*). Figure 2, curve *B*, shows the loss over the same period of time of water by the tree relative to the control trees as the proportion of the root system able to supply water to the tree decreases to one-quarter of that available at the commencement of the experiment. During the period of calibration the mean water loss from the treated tree was 88% of the water loss of the control trees. For the first 2 days of treatment water loss from the drying zones continued at this level then dropped steadily until the sixteenth day when the soil reached wilting point (p*F* 4·1). After this the water loss stabilized at a level of 55–60% of the loss of the control trees (mean 56%).

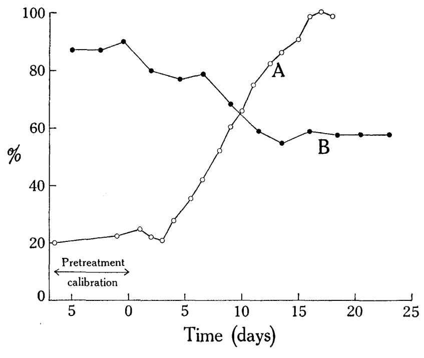

Fig. 2.—*A*, water loss (running mean) from the tritium-enriched root zone (expressed as a percentage of the total water loss by the tree) as a function of time. *B*, water loss (running mean) by the tritium-supplied tree (expressed as a percentage of the mean amount of water lost by the two control trees) as a function of time. The pretreatment calibration period is indicated.

Discussion

The plot of tritium activity above the untreated root zone, expressed as a percentage of the level of activity above the treated zone, against soil p*F* in the drying quarters (Fig. 1) suggests that polar transport of water predominated in the apple tree for the first 5 days after treatment started. It was maintained against a lateral potential gradient in the soil of 2 atm (p*F* 3·3) and was little affected until the lateral potential gradient in the soil approached 5 atm (p*F* 3·7).

The daily pattern of activity in samples from either side of the tree and the change in activity from the branch above the enriched root zone as the p*F* exceeded 3·7 in the unenriched zones supports this suggestion. Until the p*F* of the drying soil reached 3·7, diffusive mixing or lateral transport occurred at night, when the polar gradients from transpirational stress were removed, but during each day an increasing proportion of the water required to meet the transpirational stress was supplied by the roots in polar contact with the branches concerned. Above p*F* 3·7 in the drying root zones, lateral transport was more evident and the enriched roots at p*F* 2·0 supplied an increasingly high proportion of the water needs of the whole tree.

The increase in activity in the branch above the treated roots as the pF around the untreated roots exceeded $3 \cdot 3$ suggests that part of the water supply to this branch was initially derived from untreated roots and that the potential gradient of about 2 atm within (or across) the soil required to produce lateral transport over the tree as a whole also applied within a branch which, in this case, was only about 1 cm in diameter.

The change from polar to lateral transport of water is also demonstrated by the values for water uptake for the treated tree. With a tree restricted to polar water transport the change from a fully watered tree to one receiving water through one-quarter of its root system would result in a decrease in water loss from 100 to 25% while the water uptake rate in the root zone supplied with water would remain unchanged. In this tree, water use fell by only 37% relative to the control trees while the uptake rate increased from 1 to $2 \cdot 56$ in the tritium-supplied zone as this zone supplied an increasing proportion of the total water lost.

Although the absence of a geometrical arrangement of the vascular bundles increases the problem of determining the specific branch–root relationship, polar transport of water has been shown to occur in the apple tree and to be maintained against a soil water potential gradient on different parts of the root system of the order of 2 atm. At higher soil water potential gradients lateral transport within the plant becomes more important in supplying the water needs of the whole plant.

References

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