Evidence That Root Pressure Flow Is Required for Calcium Transport to Head Leaves of Cabbage

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ABSTRACT

Young cabbage plants (Brassica oleracea L. var. capitata) that were exposed to an atmosphere at 50\% relative humidity transpired freely and accumulated significant quantities of \(^{45}\)Ca in the leaves. Plants that were enclosed by plastic bags to stop transpiration from all leaves exhibited guttation with the development of root pressure and also accumulated significant quantities of \(^{45}\)Ca in the leaves. \(^{45}\)Ca accumulation increased in the leaves and tended to decrease in roots and stems with increasing quantities of water transpired or guttated by the plant. When plants were only partially enclosed so that some leaves were covered and the remainder exposed, only the exposed leaves that were transpiring accumulated significant quantities of \(^{45}\)Ca. The covered leaves of partially enclosed plants exhibited no guttation and accumulated little \(^{45}\)Ca with no measurable \(^{45}\)Ca at the margins of the leaves. The results demonstrate that root pressure flow is required to transport adequate amounts of Ca to those tissues in plants that are not undergoing transpirational water loss.

It is recognized that Ca movement in plants occurs primarily through transport in the xylem (1, 2, 5). The movement of Ca has been found to be principally acropetally toward leaves of the plant at a rate that can be correlated with the water moving to the tissues. Thus, rapidly transpiring tissues obtain more Ca than low transpiring tissues (4). It has been shown that Ca can also be moved in the xylem with water movement driven by root pressures (3). However, root pressures have not been recognized as serving a vital function for Ca movement to tissues until the recent research with cabbage (8). This report demonstrates that inner head leaves of cabbage cannot receive adequate amounts of Ca unless root pressure flow is occurring over some portion of each daily cycle. This paper provides details of the distribution of Ca in leaves and other organs of the plant with transport by both transpirational water movement and root pressure flow and relates amounts of Ca accumulation with rates of water movement.

MATERIALS AND METHODS

Cabbage plants, Brassica oleracea L. var. capitata, ‘Sanibel’, were grown to a seven-leaf stage in nutrient solution containing Na, K, Mg, Ca, NO\(_3\), SO\(_4\), H\(_2\)PO\(_4\), and Cl at 0.5, 3, 2, 5, 7.5, 2, 0.5, and 0.5 meq/l, respectively; and Fe, B, Mn, Zn, Cu, and Mo at 2.3, 0.25, 0.25, 0.0025, 0.01, and 0.005 \(\mu\)g/ml, respectively. Fe was added as FeEDTA. They were maintained in a growth chamber under 21.5 klx (31.0 mE sec\(^{-1}\) cm\(^{-2}\)), 20 C, and 60 to 70\% relative humidity. They then were placed in either an illuminated chamber at 21.5 klx, 20 C and 50 relative humidity, or a darkened chamber at the same temperature and relative humidity. The inner four to seven leaves numbered acropetally of four plants in both the illuminated and darkened chambers were covered with sheets of polyethylene film overlayed with aluminum foil to prevent transpiration from the inner leaves but not from the outer leaves (Fig. 1). Inner leaves of four additional plants in the darkened chamber were covered, then the plants were entirely covered with a polyethylene bag to minimize transpiration from the entire plant and encourage root pressure flow. Four plants in each chamber remained without covers to encourage transpiration from all leaves.

After a 2- to 3-hr period under the conditions indicated above, the nutrient solution for each plant was replaced with 400 ml of fresh nutrient solution containing 10 \(\mu\)Ci of \(^{45}\)Ca as CaCl\(_2\). The plants were kept for an additional 4 hr under the treatment conditions to allow absorption and translocation of the \(^{45}\)Ca, and then harvested. Treatment conditions are summarized in Table I.

At harvest, the stems were severed at the base of the cotyledonary node. Roots were washed twice in 100 ml of cold 0.1 m CaCl\(_2\) for a 5-min period, then blotted dry. Each leaf removed from the stem was divided into a central portion and two marginal portions by parallel cuts made on each side of the midrib, halfway between the midrib and the leaf edge. The marginal and central portions of the outer and inner leaves of each plant were analyzed for radioactivity separately. The stem, and all leaves less than 1 cm in length were retained as a separate sample. All tissue was dried at 70 C for 2 days, and dry wt were determined. Tissue was then wet-ashed, and brought to a known volume with H\(_2\)O, as described previously.

Fig. 1. Cabbage plant with covering over inner leaves to prevent transpiration from inner leaves.

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CALCIUM TRANSPORT BY ROOT PRESSURE FLOW

Table I. Accumulation of $^{45}\text{Ca}$ in separate organs of cabbage plants maintained under different humidity and light conditions.

<table>
<thead>
<tr>
<th>Leaf Covering</th>
<th>Light Conditions</th>
<th>$^{45}\text{Ca}$ Accumulation $^2$</th>
<th>Plant Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Outer Leaves</td>
<td>Inner Leaves</td>
<td>Roots</td>
</tr>
<tr>
<td>A</td>
<td>covered</td>
<td>covered</td>
<td>dark</td>
</tr>
<tr>
<td>B</td>
<td>uncovered</td>
<td>covered</td>
<td>dark</td>
</tr>
<tr>
<td>C</td>
<td>uncovered</td>
<td>uncovered</td>
<td>dark</td>
</tr>
<tr>
<td>D</td>
<td>uncovered</td>
<td>covered</td>
<td>lighted</td>
</tr>
<tr>
<td>E</td>
<td>uncovered</td>
<td>uncovered</td>
<td>lighted</td>
</tr>
</tbody>
</table>

(Average dry weight in mg)

(163 $\pm$ 26) (22 $\pm$ 4) (869 $\pm$ 119) (1054 $\pm$ 141)

$^2$Mean separation within columns by Duncan's multiple range test at 5% level.

RESULTS AND DISCUSSION

Comparison of $^{45}\text{Ca}$ accumulation under the different treatment conditions provides evidence that root pressure flow transported substantial quantities of Ca to leaves of cabbage that were prevented from transpiring (Table I, treatment A). With root pressure flow, the quantity of $^{45}\text{Ca}$ transported was nearly 50% of that which was transpired to leaves of plants which were transpiring freely (Table I, treatment E). Root pressure flow occurred in completely covered plants as indicated by guttation from the leaf margins. The data from these two treatments provide evidence that both root pressure flow and transpiration can move Ca to leaves of cabbage.

$^{45}\text{Ca}$ translocation to leaves increased with increasing quantities of water translocated through the plants, but it was not directly proportional since the ratio of $^{45}\text{Ca}$ transported to water use decreased with increasing amounts of water moving through the plants (Table II). The large amount of $^{45}\text{Ca}$ accumulated by plants in the dark (treatment B) correlated with the large amount of water found to be transpired by these plants. The amounts of $^{45}\text{Ca}$ accumulated and water transpired by plants in the dark were nearly equal to the amounts from plants in the light (treatment D). Transpiration in the dark was apparently due to stomates remaining open. Loftfield (6) reported that stomata of cabbage are open most of the night. Measurements made in the course of these studies with a diffusion porometer also indicated that the stomates are open in the dark, for the diffusion resistance of both the upper and lower surfaces of the cabbage leaves was only slightly less in the dark than in the light.

In all treatments, stem tissue accumulated more $^{45}\text{Ca}$ on a dry wt basis than other tissues (Table I). A possible reason for this is that the stem contains a large proportion of vascular tissue with a high cation exchange capacity; and, as solution containing $^{45}\text{Ca}$ passed from the root to the shoot, large amounts of $^{45}\text{Ca}$ would be bound to the negatively charged sites. The accumulation of $^{45}\text{Ca}$ in the stems, and also in the roots was inversely related to water use of plants in the different treatments.

$^{45}\text{Ca}$ accumulation in the different leaves of the plant was significantly altered when part of the plant was covered and part was left exposed. The leaves which were exposed and transpiring had significant accumulation of $^{45}\text{Ca}$ but leaves that were covered had very little accumulation of $^{45}\text{Ca}$ (Table III, treatments B and D). This demonstrates that Ca will be distributed unequally in plants when only some of the plant leaves are transpiring, because the Ca taken up by the roots will be translocated primarily to the transpiring leaves. Those leaves that are not transpiring will accumulate very little Ca.

Differences in accumulation of $^{45}\text{Ca}$ in the marginal area of the leaves under the different transpiration conditions were especially dramatic. Essentially, no $^{45}\text{Ca}$ accumulated in the marginal areas of inner leaves that were covered when the outer leaves were exposed to 50% relative humidity (Table III, treatments B and D); however, substantial amounts of $^{45}\text{Ca}$ accumulated in the marginal area of the inner leaves when all of the leaves were covered and root pressure flow occurred (Table III, treatment A). Large amounts of $^{45}\text{Ca}$ also accumulated in the marginal area of inner leaves when they were uncovered and exposed to 50% relative humidity so that they transpired freely (Table III, treatments C and E). The accumulation of Ca in marginal areas of leaves is of most interest and concern.
Table III. Accumulation of $^{45}$Ca in leaves of cabbage plants maintained under different humidity and light conditions.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaf Covering</th>
<th>Light Conditions</th>
<th>$^{45}$Ca Concentration* (cpm/mg dry wt ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>covered</td>
<td>dark</td>
<td>822a ± 110, 366a ± 108, 1400b ± 110, 1082b ± 96</td>
</tr>
<tr>
<td>B</td>
<td>uncovered</td>
<td>dark</td>
<td>1321b ± 167, 840b ± 188, 286b ± 60, -1a ± 3</td>
</tr>
<tr>
<td>C</td>
<td>uncovered</td>
<td>dark</td>
<td>1233b ± 115, 774b ± 196, 1853c ± 251, 1579b ± 535</td>
</tr>
<tr>
<td>D</td>
<td>uncovered</td>
<td>lighted</td>
<td>1666c ± 218, 1405c ± 227, 171a ± 40, 7a ± 16</td>
</tr>
<tr>
<td>E</td>
<td>uncovered</td>
<td>lighted</td>
<td>1604c ± 160, 1373c ± 164, 1358 ± 207, 1642b ± 616</td>
</tr>
</tbody>
</table>

(Average dry weight in mg)

(423 ± 63) (332 ± 40) (67 ± 22) (47 ± 19)

*Mean separation within columns by Duncan's multiple range test at 5% level.

since it is in this area of the leaf that Ca-related disorders of several plants as tipburn of cabbage, tipburn of lettuce, and blackheart of celery are initiated (8, 9).

The Ca level of enclosed heading leaves is known to be at very low levels, 0.2 to 0.4%, compared to the Ca level of expanded outer leaves, 2 to 3% (7, 10).

The necessity for root pressure flow to provide Ca to covered leaves of cabbage to prevent leaf injury is evidence that this process is required for adequate movement of Ca to the inner leaves of heading plants (8). These results also suggest that root pressure may be required to move Ca to low transpiring organs of other crops that sometimes develop Ca deficiency injuries. Partially enclosed organs such as inner leaves of leaf lettuce, celery, and endive may depend upon root pressure flow for sufficient Ca to prevent injury because of the reduced transpiration rates of the partially enclosed leaves. Fruits are known to have low transpiration rates and may also depend upon root pressure flow for adequate amounts of Ca when growth is rapid and demand for Ca is high. The transport of other substances acropetally such as boron, and certain pesticides, which are transported primarily in the xylem, may also be affected by conditions which affect root pressure flow.

LITERATURE CITED

3. CURTIS, L. C. 1944 The influence of guttation fluids on pesticides. Phytopathology 34: 196-205