Transport of Sodium into the Xylem Exudate of Tobacco

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ABSTRACT

When tobacco (Nicotiana tabacum L. var. Virginia Gold) plants were pretreated with Na (22Na) several days before detopping, from 2.3 to 4.9% of Na previously accumulated in roots appeared in the xylem exudate in 7 days after detopping. Na from the external medium, however, was readily transported to the xylem. Moreover, the amount of the pretreatment Na that was transported to the exudate was not influenced by the presence of Na in the external medium. When Na was present in the external medium after detopping, about 4% (with an NaNO3 post treatment) to 10% (with an NaCl post treatment) of the Na transported to the xylem in the 7 days following detopping originated in the vacuoles. Nitrate salts of K or Na in the external medium after detopping resulted in transport of large quantities of the respective cation to the exudate, but not in increased transport of the pretreatment Na. A much larger percentage of the K that was accumulated after detopping than of the Na similarly accumulated was transferred to the xylem exudate.

Sodium is not readily transported to the shoots of some plant species (11, 13, 16, 17, 21). Rather, nearly all the Na is retained in the roots. Tobacco and bush beans, under at least some conditions, are two such species (11, 19, 20). Sodium retention in roots of tobacco and bush beans may be regulated at the tonoplast with Na being retained in the vacuoles (17, 19, 20). In bush beans any manipulation which interferes with metabolism (inhibitors, low temperature, high temperature, nutrient-element deficiencies, anaerobiosis) resulted in release of some Na from the vacuoles and its translocation to shoots (16, 17, 20, 21). The primary objective of this study was to investigate the effect of K and Na in the outer solution on the transfer to the xylem exudate of Na which had been previously accumulated in roots.

MATERIALS AND METHODS

Seeds of Nicotiana tabacum L. var. Virginia Gold were sown on the surface of fine vermiculite in 15-cm pots in a humid chamber in a glasshouse. They were irrigated with water and germination occurred in about 5 days. The pots were then transferred to a glasshouse bench and watered on alternate days with water and with one-half strength nutrient solution (full strength solution was in mmole/liter: 5 Ca(NO3)2, 2.5 K2SO4, 2 MgSO4, 2 NH4H2PO4, 0.1 MnSO4, 0.04 H3BO3, 0.0025 ZnSO4, 0.003 H2MoO4, and 0.1 Fe as FeEDDHA). About 5 weeks after planting, the plants were transferred from vermiculite to one-fourth strength nutrient solution in 8-liter crocks with four plants per cock. After 2 weeks the plants were transferred to 8-liter crocks in one-half strength nutrient solution with one plant per cock. After an additional 2 weeks, the solutions were changed to full strength solution.

The tobacco plants were then pretreated with 10 mm 22NaCl in the presence of nutrient solution for a period of 3 weeks. Initial radioactivity was 1960 cpm/ml nutrient solution as determined with a scintillation well-counter. The plants were then transferred to nutrient solution without 22Na for another 3 weeks. They were then detopped and placed in 7 liters of 10 mm KCl, KNO3, NaCl, NaNO3 or in water. All media contained CaCl2 at 1 mm (13). Xylem exudate was collected daily for 7 days. Similar tobacco plants have been shown to exude with diurnal rhythm for as many as 19 days with uniform volume and uniform concentration of ions (18). The exudate was assayed for 22Na (scintillation well-counter), and Na and K (flame photometer), and the volume of exudate was measured. Roots also were assayed for 22Na, Na, and K. Calculations of percentages of Na, 22Na, and K in roots and in exudate were made from these data. Four separate experiments were conducted with 15 plants for each experiment.

RESULTS AND DISCUSSION

The data in Table I represent the effects of both Na and K salts in the solution about roots of detopped plants on transfer of previously accumulated Na (22Na in this case) from roots to the xylem exudate. Sodium and K, particularly from the nitrate source, were readily transported from the external solution to the xylem exudate. The previously accumulated Na was transported to the xylem exudate in reasonably uniform and small amounts regardless of the presence or absence of Na in the external medium. The results in general indicate extremely slow mixing of the recently absorbed Na with that absorbed during the pretreatment. Most of the pretreatment 22Na remained in the roots and apparently was not exchanged by stable Na added later. This result could obtain only if the pathway of Na transport from the external solution to the exudate did not pass through the pool of previously accumulated 22Na. This was the case with both NaNO3 and NaCl. There indeed was a pathway, however, to the xylem exudate for the previously accumulated Na. The magnitude of Na transport from the vacuoles to the xylem exudate was only 4 to 10% of that coming from the outer solution when Na was in the outer solution (see footnote to Table I).

These results are consistent with the idea of the Na ions passing from the outer solution to the xylem without first passing through the vacuoles. Several workers (7-10, 12, 13, 18) have suggested that other ions largely bypass the vacuoles in

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transport to xylem vessels via cytoplasmic connections as first suggested by Munch (14). This concept of a symplasm was further elaborated by Broyer (5, 6), Arisz (2, 3), and more recently by Fried and Broeshart (8) and Anderson and House (1).

The potassium nitrate treatment decreased slightly the amount of previously accumulated \(^{22}\text{Na}\) that was transported to the xylem exudate. Perhaps more pronounced was the effect of the Na treatments in decreasing the amount of K in the exudate (Table II).

The large quantities of Na and K transported to the xylem exudate when the respective nitrate salt was in the outer solution (Table I and II) have been described in previous reports (14, 17). The percentage increase in transport of Na or K to the xylem caused by nitrate was greater than the percentage increase in root Na or K caused by the nitrate even though the majority of K or Na that was accumulated remained in roots (Tables I and II).

The reason why Na is retained in roots of some species (11, 13, 16, 21, 22) is not satisfactorily explained by these studies. When Na was applied as a single salt (but with 1 mm \(\text{CaCl}_2\)), it was readily transported to the xylem vessels, more so with the nitrate than with the chloride source. Once Na had been transported to the vacuoles, relatively little of it was transported to xylem vessels (Table I). The vacuoles were not saturated by the pretreatment \(^{22}\text{Na}\) application, however, and considerable Na continued to accumulate in them during the exudation period. About five times as much Na was retained in roots as was transported to the xylem exudate (Table I). In contrast, about two-thirds of the K accumulated from the nitrate source was transported to the xylem exudate (Table II); the vacuoles evidently were essentially saturated with K at the time of detopping. Even so, one could conclude that Na was more tightly bound in roots than was K as suggested by Lauchli et al. (13). A hypothesis to explain the preferential retention of Na in roots in contrast to K must recognize that the symplasmic route is usually largely unavailable for Na in intact plants and for Na previously accumulated in vacuoles of detopped plants.

The 7 days involved in this study do not present a serious problem in interpretation. Neither should the contention of Ben Zioni et al. (4) concerning the role of tobacco shoots on nitrate transport cause any problem in interpretation. They suggest that nitrate reduction in the shoots results in formation of malic acid which is cycled to roots as potassium malate which exchanges, after oxidation to KHC\(_2\)O\(_3\), for more KNO\(_3\), at the root surface which then is transported to shoots where nitrate is reduced. Cycling of K would result in a build-up of Na in shoots but not of K. If their hypothesis is fully correct, the molar concentration of Na in tobacco leaves should greatly exceed that of the cations, which it does not.

### Table I. Comparison of the Amount and Proportions of Na from Internal and External Sources in the Xylem Exudate in 7 Days of Exudation

<table>
<thead>
<tr>
<th>External Medium</th>
<th>Na in Exudate + Final Na in Roots</th>
<th>Na in Exudate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total (\mu)C/plant &amp; 1000 cpm/plant &amp; From pretreatment to root</td>
<td>Total (\mu)C/plant &amp; 1000 cpm/plant &amp; %</td>
</tr>
<tr>
<td>1 mm CaCl(_2)</td>
<td>2400 &amp; 312 &amp; 134</td>
<td>15.3</td>
</tr>
<tr>
<td>10 mm KCl + 1 mm CaCl(_2)</td>
<td>2450 &amp; 311</td>
<td>2250 &amp; 302</td>
</tr>
<tr>
<td>10 mm KNO(_3) + 1 mm CaCl(_2)</td>
<td>6370 &amp; 274</td>
<td>463</td>
</tr>
<tr>
<td>10 mm NaCl + 1 mm CaCl(_2)</td>
<td>7470</td>
<td>253</td>
</tr>
<tr>
<td>10 mm NaNO(_3) + 1 mm CaCl(_2)</td>
<td>9205</td>
<td>114</td>
</tr>
</tbody>
</table>

\(^1\) Column 2  
\(^2\) Column 3  
\(^3\) As calculated from the specific radioactivity, 10\% of Na in the exudate came from the labeled source when NaCl was in the external medium and 4\% when NaNO\(_3\) was in the external medium.

### Table II. K Contents in the Root and in the Xylem Exudate in 7 Days of Exudation

| External Medium | Total K \(\mu\)C/plant & K in Exudate | Prop. of Total K in Exudate |  
|-----------------|-----------------|-----------------|-----------------|  
| 1 mm CaCl\(_2\) | 9280 & 543 | 5.9 |  
| 10 mm KCl + 1 mm CaCl\(_2\) | 10730 & 697 | 6.5 |  
| 10 mm KNO\(_3\) + 1 mm CaCl\(_2\) | 10750 & 1998 | 14.9 |  
| 10 mm NaCl + 1 mm CaCl\(_2\) | 9205 | 114 | 1.2 |  
| 10 mm NaNO\(_3\) + 1 mm CaCl\(_2\) | 8635 | 311 | 3.6 |  

LITERATURE CITED


