Table 3. Effect of soil compaction on early plant growth and yield of ‘Dixie’ squash.

<table>
<thead>
<tr>
<th>Compaction treatment</th>
<th>Spring Dry wt (mg/plant)</th>
<th>Fall Fruit wt (kg/ha)</th>
<th>Fruit/m² no.</th>
<th>Fruit wt kg/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noncompacted</td>
<td>245a</td>
<td>1910a</td>
<td>12.2a</td>
<td>2110a</td>
</tr>
<tr>
<td>Compacted</td>
<td>152b</td>
<td>810b</td>
<td>7.8b</td>
<td>1140b</td>
</tr>
</tbody>
</table>

2Plant dry wt data collected May 27 (14 days after planting).
3Mean separation, within columns, by Duncan’s multiple range test, 5% level.

NO₃-N/kg of soil for all treatments at this date. Petiole NO₃ of squash grown in noncompacted soil receiving Ca(NO₃)₂ was 51% greater than that receiving NH₄NO₃; however, petiole NO₃ of squash receiving Ca(NO₃)₂ was 33% lower than squash receiving NH₄NO₃ when the soil was compacted.

The data shows that soil compaction resulting from tractor traffic on the seedbed area after moldboard plowing restricted squash root growth and reduced yield. Soil atmosphere analyses indicate that O₂ and CO₂ concn were not greatly affected by soil compaction, and that these factors do not explain differences in root growth and yield of squash grown in sandy soil. Increases in soil strength due to soil settling from rainfall appeared to have less effect on squash yield than mechanical soil compaction. Soil compaction reduced N use efficiency as indicated by both petiole NO₃ analyses and yield, and the efficiency reduction was greater with CaNO₃ than with NH₄NO₃ N source.

Table 4. Interaction of soil compaction and nitrogen source on petiole NO₃ and marketable yield of ‘Dixie’ squash (spring 1976).

<table>
<thead>
<tr>
<th>Compaction treatment</th>
<th>N source</th>
<th>Petiole NO₃ (ppm)</th>
<th>Yield (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noncompacted</td>
<td>NH₄NO₃</td>
<td>350b</td>
<td>1770b</td>
</tr>
<tr>
<td></td>
<td>Ca(NO₃)₂</td>
<td>5310a</td>
<td>2050a</td>
</tr>
<tr>
<td>Compacted</td>
<td>NH₄NO₃</td>
<td>2810c</td>
<td>880c</td>
</tr>
<tr>
<td></td>
<td>Ca(NO₃)₂</td>
<td>1887d</td>
<td>730d</td>
</tr>
</tbody>
</table>

2Petiole NO₃ fresh wt basis, sample collected June 23.
3Mean separation, within columns, by Duncan’s multiple range test, 5% level.

The addition of carbohydrates to water taken up by cut flowers results in an enhancement of floral longevity (1, 5, 6, 9). Previous investigators who have studied the movement of exogenously-fed sucrose, generally agree that active phloem transport plays a role in movement of the sugar to the stem base (3, 4, 7). The extent of that role, however, has been difficult to determine in rose stems, and because designs of various girdling experiments often prevent valid comparison of data, much work remains inconclusive (4, 7). In addition, there is little information concerning the location in the cut flower stem of possible lateral transport from xylem to phloem, although based on girdling studies, Katacker and Steponkus (4) suggest that little phloem-mediated transport of exogenously-fed sucrose occurs in rose stems below the first 5 leaflet leaf. It was assumed that transfer of such exogenously-fed sugar from the xylem to phloem occurred in the leaf tissues (4). Ho and Nichols (3) however, working with leafless carnation flowers, reported that transfer from the xylem to phloem occurred within 10 cm of the basal portion of the stem. They further proposed that the amount of lateral transport is dependent upon the concentra-

Metabolism of Sucrose in Cut Roses. II. Movement and Inversion of Sucrose Absorbed by Cut Rose Stems¹

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Additional index words. flower storage, postharvest physiology, Rosa hybrida

Abstract. ¹⁴C-sucrose, when taken up into the xylem, moved rapidly into leaves and flower heads of cut roses (Rosa hybrida L.). Outward lateral movement of ¹⁴C occurred rapidly along the entire length of stem at a uniform rate, regardless of ¹⁴C-sucrose concentration within the xylem and associated tissues. The quantity of ¹⁴C inverted sugars found in xylem tissue after uptake of ¹⁴C sucrose, and the rapid hydrolysis of sucrose passing through xylem of isolated stem segments suggests the involvement of invertase located in the xylem.

The addition of carbohydrates to water taken up by cut flowers results in an enhancement of floral longevity (1, 5, 6, 9). Previous investigators who have studied the movement of exogenously-fed sucrose, generally agree that active phloem transport plays a role in movement of the sugar to the stem base (3, 4, 7). The extent of that role, however, has been difficult to determine in rose stems, and because designs of various girdling experiments often prevent valid comparison of data, much work remains inconclusive (4, 7). In addition, there is little information concerning the location in the cut flower stem of possible lateral transport from xylem to phloem, although based on girdling studies, Katacker and Steponkus (4) suggest that little phloem-mediated transport of exogenously-fed sucrose occurs in rose stems below the first 5 leaflet leaf. It was assumed that transfer of such exogenously-fed sugar from the xylem to phloem occurred in the leaf tissues (4). Ho and Nichols (3) however, working with leafless carnation flowers, reported that transfer from the xylem to phloem occurred within 10 cm of the basal portion of the stem. They further proposed that the amount of lateral transport is dependent upon the concentra-

Determination of sugars in freshly-harvested roses. Freshly-harvested roses were cut to a stem length of 37 cm and divided into leaves, petals, and stems; receptacles were discarded. The stems were further separated by peeling the bark consisting of phloem, cortex and outer tissues, from the inner tissues consisting of xylem and pith. Wherever reference is made to xylem (xy), pith is also included. Similarly, periderm and cortex are included wherever reference is made to phloem (ph) or bark.

Each rose portion was cut into small pieces and extracted twice with 80% ethanol by reflux, with each extraction lasting 30 min. The 2 extracts were combined and evaporated to dryness, and then redissolved in water to a convenient volume. Anthocyanin pigments in the extracts were removed by passing extracts through a Polyclar-AT (G.A.F., New York, N.Y.) column. Sugars were separated by TLC and quantitatively determined as previously described (8).

Uptake of 14C-sucrose. A freshly-harvested rose was cut to a stem length of 35 cm and all foliage was removed, except for one 5-leaflet leaf situated 15 cm from the cut end. The bark covering the basal 5 cm of stem was peeled so only the xylem and pith would remain exposed to the sucrose solution. The rose was allowed to take up a 2% 14C-U-sucrose solution (5 μC/ml) for 45 min. Upon removal from the feeding solution the rose was separated into petal, receptacle, leaf, and stem portions. After removing and discarding the basal 5 cm of peeled stem which was exposed to the feeding solution, the stem was cut into 6 segments of equal length. The bark from the lower 5 segments was peeled from the inner tissue, and bark from the highest segment, being difficult to remove, was left intact. Each of the various rose portions was extracted and the sugars separated by TLC. Radioactivity of sugar was determined as described previously (8).

Hydrolysis of sucrose during movement through xylem. Phloem was excised from 5 cm rose internode stem segments by slipping and peeling. Five segments consisting of xylem and phloem were connected with rubber tubing to a reservoir containing 2% sucrose (Fig. 1). The reservoir solution level was 60 cm above the stem segment bases, and hydraulic pressure allowed the 2% sucrose to pass through the xylem of the segments. Effluent was collected with a fraction collector, and sugars in each fraction were separated by TLC and the quantities determined (8).

Results and Discussion

Distribution of sucrose, glucose, and fructose of freshly-harvested roses. Determination of sugars in leaves of freshly-harvested roses indicated that the predominant sugar was sucrose (Fig. 2). Quantities of glucose and fructose per unit fresh wt in leaves were each about 13% that of sucrose. Conversely, petals contained greater levels of both glucose and fructose, on a fresh wt basis, than of sucrose. Sucrose in petal tissue was more abundant than that found by Kaltaler and Steponkus (4) in 'Red American Beauty' rose petal tissue. The differences may have been due to dissimilarities between the 2 cultivars, since Weinstein (11) found glucose to be the predominant sugar present in petals of 'Better Times' roses. Stem tissue of freshly-harvested roses contained at least double the sucrose quantity as either glucose or fructose. Phloem and associated tissues contained a greater proportion of sucrose than did inner xylem tissues.

Distribution of 14C in roses taking up 14C-sucrose. Determination of radioactivity in dissected rose portions after allowing uptake into the xylem of 14C-sucrose for 45 min, revealed the greatest amount of 14C in the petal tissue (Fig. 3). Slightly less 14C was found in the single leaf, which was left intact during the uptake period. The preferential movement of 14C immediately to the flower head might appear to conflict with prior reports of immediate movement of 14C to the leaves of roses pulsed with 14C-sucrose (7) but since most leaves were removed in the present experiment, thereby materially reducing the leaf sink area, the flower head assumed a greater relative role as a sink for exogenously-fed sugars than in other tests where leaves were left intact.

During uptake of 14C-sucrose, the removal of bark from the basal portion of the cut rose stem resulted in entry of most 14C-sucrose via the xylem, since only the xylem and pith were exposed to the feeding solution. Most 14C recovered from the phloem area, therefore, was concluded to be present there as a
result of movement from the xylem. Comparison of $^{14}C$ levels recovered from inner and outer portions of each stem segment revealed an interesting pattern. Although a diminishing gradient of $^{14}C$ of great magnitude occurred in xylem from segments 1 to 5, $^{14}C$ in the phloem of each of these segments appeared to remain relatively constant. This suggests that lateral movement of label from the xylem to the phloem occurs at a constant rate throughout the entire length of the stem, which may possibly be mediated by a transfer mechanism functioning at capacity. Operation of such a system could result in a constant transfer rate of label from xylem to phloem throughout the stem, regardless of the quantity of $^{14}C$ in the xylem at any particular level within the stem, so long as the concn of $^{14}C$ available in the xylem is not rate limiting. Since $^{14}C$ levels in the stem were not monitored during the 45-min uptake period, however, one cannot rule out the possibility that lateral transport may be dependent upon a concn gradient between the xylem and phloem.

Ho and Nichols (3), based on data obtained with carnations, have proposed that the rate of radial transfer of sugars from the xylem to phloem is dependent upon the concentration of sugars in the xylem. Further work is required to resolve this question.

The equal distribution of $^{14}C$ throughout the entire length of phloem of the stem, suggests that the leaf, which has a high intensity of radioactivity, may not be the sole source of $^{14}C$ found in the stem phloem. If the latter were the case, one might expect the stem phloem to display a gradient of $^{14}C$, with the highest concn close to the axil of the leaf. Furthermore, any active transport downward would have caused $^{14}C$ to accumulate in the phloem of segment 1. In all probability movement of $^{14}C$-sugar from the xylem to phloem occurs to some extent in the leaf, but the data suggest that such sugars also move laterally at all points in the stem to a considerable degree.

**Distribution of $^{14}C$ sucrose, glucose, and fructose.** Determination of relative amounts of labeled sucrose, glucose and fructose after uptake of $^{14}C$ sucrose revealed that $^{14}C$-glucose and $^{14}C$-fructose were present in fairly high proportions in all flower parts (Fig. 4). The proportion of $^{14}C$-sucrose, relative to the combined proportions of $^{14}C$-glucose and $^{14}C$ fructose varied, depending upon which portion of rose was being examined. The relative proportion of $^{14}C$-sucrose to $^{14}C$-glucose and $^{14}C$-fructose was lower in petal tissue than in the receptacle. This suggests that hydrolysis of sucrose may occur as the sugars move from the receptacle to the petals. It is also possible that inversion of sucrose is essential for optimal movement of sugars into the petal tissue. If movement into the petal tissue is dependent upon the action of an invertase, as is suggested here, the hydrolyzing enzyme might possibly play a regulatory role in the movement of sugars into petal tissue. This indeed appears to be the case in the movement of sugars into the kernels of sugar cane and maize (2, 10). In the present study, no attempt was made to ascertain whether there are specific sites of sucrose hydrolysis. Further study is necessary to

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Fig. 3. Distribution of $^{14}C$ in various cut rose portions after a 45 min uptake of $^{14}C$-sucrose.

Fig. 4. Relative percentages of $^{14}C$-glucose, $^{14}C$ fructose and $^{14}C$-sucrose recovered from various cut rose portions 45 min after uptake of $^{14}C$-sucrose by the cut rose flower.
determine the ability of intact sucrose to gain entrance to rose petals cells via the plasmalemma.

About 50% of the $^{14}$C-sugars tested in the rose leaf was recovered as $^{14}$C-sucrose (Fig. 4). This was a percentage similar to that found in the receptacle. The % $^{14}$C-sucrose in phloem areas of segment 1 through 5 was almost constant, about 50%. That in xylem areas of these same segments, however, changed inversely with the distance of the segment from the base of the stem, about 20% $^{14}$C-sucrose in xylem of segment 5, the highest segment, to about 33% $^{14}$C-sucrose in xylem of segment 1, the basal segment.

Hydrolysis of sucrose during movement through xylem. $^{14}$C-reducing sugars were abundant in the xylem areas of all stem segments (about 67% $^{14}$C-hexoses from the xylem area of the basal segment), even though only $^{14}$C-sucrose was in the feeding solution (Fig. 4). This finding suggests that rapid hydrolysis of sucrose occurs within the xylem. In order to more closely examine the possibility of rapid sucrose inversion during movement through the xylem, bark was slipped and peeled from rose stem internode segments in order to remove phloem tissue. A sucrose solution was then forced through the xylem under hydraulic pressure as described (Fig. 1). It was found that although only sucrose was present in the feeding solution, inversion products appeared in the effluent. The effluent was fractioned by collecting at hourly intervals, during an 8 hr period. During the collection time, the flow rate declined, while the quantity of reducing sugars in each fraction remained relatively constant (Fig. 5). This suggests that sucrose inversion occurs within the xylem independently of flow rate, and that invertase activity may be rate limiting. Under such conditions, dynamic equilibrium would not be attained since the substrate is moving at varying velocities through the xylem. The role of invertase within the xylem, possibly bound to inner walls, is not presently well understood. The usual role of invertase is to convert sucrose to fructose and glucose, which are subsequently metabolized in order to provide the tissue with necessary energy. Although this role of providing metabolic substrates may not be discounted, it is possible that xylem-bound invertase may also function as a regulatory mechanism. Large amounts of sucrose are not normally found in xylem of intact plants, and when sucrose is taken up into the xylem of cut roses, the invertase might aid in rapid removal of sucrose from the xylem, especially if inversion is a prerequisite for optimum lateral movement through vascular parenchyma. Once reaching the phloem, the reducing sugars could be reconverted to sucrose, which would be translocated to other areas.

It is apparent from the data presented here that sucrose taken up by cut roses undergoes a complex pattern of hydrolysis. Invertase may possibly assume a role of regulatory control in 2 areas. First, in the stem xylem, where hydrolysis takes place at a constant rate, and secondly, in the receptacle or petals, where reducing sugars are predominant. Whether or not hydrolysis is requisite for movement in either area has not been demonstrated here. It is, however, a question which is central to understanding the utilization of carbohydrates by cut roses, and one which will be dealt with more freely in the third paper of this series.

Literature Cited