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Photosynthate Partitioning in Split-Root Citrus Seedlings with Mycorrhizal and Nonmycorrhizal Root Systems[1]

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ABSTRACT

Photosynthate partitioning was examined in seedings of sour orange (*Citrus aurantium* L.) and Carrizo citrange (*Poncirus trifoliata* [L.] Raf. × C. *sinensis* [L.] Osbeck) grown with split root systems inoculated on one side with vesicular-arbuscular mycorrhizal fungus (*Glomus intraradices* Schenck and Smith). Source-sink relations were studied without mitigating differences in mineral content or physiological age that can occur in separate plant comparisons, because phosphorus was evenly distributed between leaves on opposite sides of the seedlings. Aboveground portions of each plant were exposed to $^{14}CO_2$ for 8.5 minutes and ambient air for 2 hours, followed by extraction and identification of labeled assimilates. Mycorrhizal halves of root systems accumulated 66 and 68% of the ^{14}C-labeled photosynthates translocated to roots of sour orange and 'Carrizo' citrange, respectively, as well as an average of 77% greater disintegrations per minute per gram fresh weight. Distribution of ^{14}C-labeled assimilates was independent of phosphorus effects on photosynthate partitioning in leaves and did not reflect fresh or dry weights of roots or degree of mycorrhizal dependency of the species. Differences in radioactivity between mycorrhizal and nonmycorrhizal root halves after 2 hours indicated at least 3 to 5% of the whole plant ^{14}C-labeled photosynthates were allocated to mycorrhizae-related events on one side and that twice this amount, or 6 to 10%, might be expected if the entire root system was infected.

Vesicular-arbuscular mycorrhizae are believed to benefit both host and fungi in most situations; however, the cost of this association in terms of photosynthate demand is not clear. Many studies have compared dry matter partitioning within mycorrhizal and nonmycorrhizal plants measured with different environmental conditions (3, 15), with different species (4, 8, 20), or at various stages of development. VAM[2] plants tend to grow taller than uninoculated controls in most experiments, produce greater total dry matter, and often partition more C to below-ground tissues (8, 19). In addition, inoculation can stimulate N assimilation (5), raise levels of tissue P, Zn, and Cu (2, 21), and increase resistance to moisture stresses (28).

The beneficial effects of colonization by mycorrhizal fungi may not always outweigh the cost to the host. In some situations, the proportion of carbon diverted to the fungi is apparently great enough to decrease plant growth (2, 3). Fungal dependence on photosynthate supply can be further seen in the decreased rate of infection and VAM development when alternate sinks are present on host plants (1, 14) or when light intensity is lowered (9, 12). Dry matter distribution and long term allocation of ^{14}C-labeled photosynthates have also been compared in mycorrhizal and nonmycorrhizal plants. Resulting estimates of mycorrhizal demand for carbohydrates range from nearly zero up to 12% of the total plant C (3, 4, 29, 30). These may vary among species (4), and few include CO_2 losses due to fungal respiration (24).

The basis for sink strength of VAM has not been determined. Several possible factors have been suggested, which include fungal respiration (4, 11, 29), conversion of host photosynthates to glycogen and/or lipids in the fungus (4, 7, 19), root exudation of assimilate (10, 15, 30) growth regulators from fungi, sucrose hydrolysis (18, 23), and others (11, 18). Vesicular-arbuscular mycorrhizal fungi could also indirectly affect partitioning of photosynthates by altering phosphorus levels of source leaves. Phosphate in leaf mesophyll cells is known to have striking effects on the partitioning of photosynthate between translocatable assimilates and stored starch (13). Increased phosphate uptake by VAM-infected plants would favor allocation of carbon to sucrose and subsequent export to roots. Such effects have not been considered in the past, and previous comparisons of mycorrhizal and nonmycorrhizal plants have been confounded by lower phosphorus content in the uninfected plants. This can be countered to varying degrees by phosphorus fertilization, yet the rate and pattern of host plant development often still differ (29).

Split-root citrus seedlings, half mycorrhizal and half uninfected, provide a valuable method for quantifying sink strength independent of phosphate effects on source leaves. The uniform phosphorus content between sides of the shoot obtained in the present study allows control of this important variable. Furthermore, short term $^{14}CO_2$-labeling experiments are used to minimize the amount of ^{14}C lost through respiration or translocation into those soil hyphae not sampled with roots. The purpose of this research was first, to distinguish sink strength of mycorrhizal fungi from phosphorus effects on photosynthate partitioning in leaves, and second, determine the cost of the symbiosis in terms of host photosynthate utilized.

MATERIALS AND METHODS

Plant Material. Split-root seedlings were grown in a greenhouse using sour orange (*Citrus aurantium* L.) and Carrizo citrange (*Poncirus trifoliata* × *Citrus sinensis* [L.] Osbeck). Two pots were used for one plant so that separate mycorrhizal and nonmycorrhizal root systems could be grown. Split-root systems were initiated by removing tap roots of seedlings at the three-leaf stage, and dipping remaining segments into 2500 mg L^{-1} IBA

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[2] Abbreviations: VAM; vesicular-arbuscular mycorrhizae; PPFD, photosynthetic photon flux density; RuBP, ribulose bisphosphate; IBA, indolebutyric acid.

solution. Treated seedlings were placed under mist in perlite-vermiculite medium for 3 to 4 weeks and those with two uniform, adventitious roots were selected for split-root studies. Seedlings with split root systems were transplanted into paired 500-ml square plastic containers. Potting medium consisted of a 1:4 ratio of Canadian peat and fired ceramic particles (a combination of attapulgite and montmorillinite clay; Mid-Florida Mining Co. Lowell, FL). Dolomitic limestone was used to adjust pH to 6.0 and micronutrients were added as commercial mix (Perk; Estech Chemical Co. Winter Haven, FL). Low levels of superphosphate were incorporated at a rate of 0.3 kg m^{-3} of medium. Nitrogen (17.79% NH_4 and 7.21% NO_3) and potassium (25% K_2O) were applied weekly at a rate of 200 mg L^{-1} each.

One side of the split-root seedlings was inoculated at transplanting with mycorrhizal fungus *Glomus intraradices* (Schenk and Smith) using a 5 g mixture of chlamydospores (250 spores g^{-1} soil), hyphae, and infected roots. The other half was drenched with an inoculum filtrate to provide the bacterial component. Sour orange and Carrizo citrange plants were grown to a height of approximately 25 cm or for 14 to 16 weeks, respectively. Experiments on a given species were conducted within an 8-d period. Six small root segments were taken from each side of the root system after $^{14}CO_2$ labeling to determine VAM infection levels using a procedure described by Phillips and Hayman (26). From 45 to 50% infection occurred on inoculated sides, levels considered typical for mycorrhizal associations. No hyphae were observed in control roots.

Labeling Studies. The above-ground portion of four sour orange and six Carrizo citrange plants was equilibrated for 24 h in a 1.146-L Plexiglas cuvette prior to each experiment. Ambient air flowed continuously through the apparatus during the period and temperature was maintained at 30.4 ± 1.1°C during the 10-h photoperiod. PPFD at midplant level was 790 μmol m^{-2} s^{-1}. Experiments were initiated the following day between 1100 and 1200 h for Carrizo citrange and from 900 to 1000 h for sour orange. The chamber and associated IR gas analysis system were first purged with N_2 for approximately 60 s, then refilled with a bottled gas mixture of 312 μl L^{-1} $^{14}CO_2$ containing 311 μl/l total CO_2 and a balance of dry air (Golob Analytical Service, Berkeley Heights, NJ). A total of 17.2 μCi was utilized in each experiment. The apparatus was then immediately converted from an open, flow-through air stream to a closed, gas-tight cycle. Levels of CO_2 could therefore be measured during each experiment and were maintained between 118 and 270 μl/l. The system was reopened after photosynthesis in $^{14}CO_2$ for 8.5 min to an ambient air supply for an additional 2 h before extracting tissues for ^{14}C-labeled assimilates.

Extraction and Analysis of ^{14}C-Labeled Assimilates. Experiments were terminated by separating plant parts, freezing them in liquid N_2, and extracting assimilates in 80% (v/v) ethanol. Each seedling was divided into source leaves, stem wood, stem bark, and mycorrhizal and nonmycorrhizal halves of the root system. Stem components were separated along the vascular cambium so that wood samples contained primarily xylem and bark contained the phloem. Outermost xylem surface was removed and discarded to minimize contamination from phloem or vascular cambium. The thick fleshy citrus root systems allowed potting media to be rinsed away with little tissue loss, although hyphae extending into the medium were undoubtedly removed.

Plant samples were ground to a coarse powder in a mortar and pestle after a second freezing. Particulate material was further extracted with 80% (v/v) ethanol, followed by filtration through Whatman No. 1 paper in a Büchner funnel. Insoluble fractions were rinsed again with 95% (v/v) ethanol which resulted in 93 to 96% release of radioactivity to pooled washings from nonleafy tissues. Insoluble materials accounted for approximately one-quarter (23 to 25%) of the label in leaves and was identified as 81 to 90% starch by treatment with amyloglucosidase (Sigma Chemical Co.). Ethanol-soluble extracts and insoluble residues were sampled for determination of ^{14}C content using liquid scintillation spectrometry.

Leaf and root tissue phosphorus levels were determined for Carrizo citrange plants using the molybdenum blue procedure (7).

RESULTS AND DISCUSSION

Phosphorus Distribution. Phosphorus levels were not significantly different between mycorrhizal or nonmycorrhizal halves of split-root seedlings or between opposite sides of the shoot (Table I). Variations in mineral uptake by roots of full-sized trees often appear in branches directly above them (27), but uniform mineral distribution would be more likely in small seedlings due to their smaller stem diameter. Lateral transfer in xylem is restricted to vertical ranks in young plants of some species, but not in others (27). Microscopic analysis of sour orange stems at this stage of development shows pith and xylem ray parenchyma make up large portions of the stem, and vascular gaps at leaf insertions substantially alter xylem patterns (J. Soule, unpublished data). Anatomy of young citrus seedlings therefore facilitates lateral transfer of minerals.

An even distribution of phosphorus between sides of above-ground plant parts (Table I) makes it possible to distinguish between the influence of P nutrition on photosynthate partitioning and that of sink demand by mycorrhizal or nonmycorrhizal roots. Variations in phosphorus content between seedlings has been a source of difficulty in past comparisons between mycorrhizal and nonmycorrhizal plants (3, 16, 36). Numerous attempts to remedy this situation with phosphorus fertilization of nonmycorrhizal plants have met with variable success (3, 29). Similar size can sometimes be obtained among groups of plants, but physiological age will not necessarily be the same (29). In addition, developmental patterns differ such that plants may be comparable for only a limited period during their growth (29). Higher levels of phosphorus in leaves of mycorrhizal plants could conceivably be the basis for translocation of more photosynthate to roots of these plants. Increased phosphorus content in source leaves often results in more rapid photosynthesis (13) and greater allocation of carbon to translocatable assimilates *versus* starch (13). Photosynthetic rates may change through indirect effects of phosphorus on ATP/ADP ratios or a direct action of Pi on RuBP carboxylase activity (13). Changes in photosynthate partitioning may also be based on actions of a Pi translocator in the chloroplast membrane which controls the rate of triose-P movement out of this organelle (13). These three carbon sugars are exported from chloroplasts and used in subsequent steps of sucrose synthesis when cellular Pi levels are high. This in turn can be loaded into phloem for translocation. Conversely, decreased levels of Pi tend to favor retention of triose-P within the chloroplast where they are utilized in formation of hexoses and eventually starch. Phosphorus was uniformly distributed between sides of shoots in the present study so that any related differences in photosynthate

Table I. *Phosphorus Levels in Tissues of Carrizo Citrange Seedlings*
Values are means from measurements of 10 plants.

Tissues	Mycorrhizal Side	Nonmycorrhizal Side
	% phosphorus g^{-1} dry wt	
Leaves	0.108 ± 0.004 NS[a]	0.092 ± 0.013
Roots	0.068 ± 0.004 NS	0.050 ± 0.010

[a] Not significantly different from nonmycorrhizal sides of plants based on a paired *t* test.

partitioning were minimized among source leaves.

Photosynthate Partitioning in Source Leaves. Accumulation of ^{14}C-labeled photosynthates in individual source leaves was also examined in relation to stage of development and position above respective halves of the root system (Fig. 1). A direct vertical path between source and sink does not necessarily occur, because a twist in the stem or more complex patterns of vascular distribution could link mycorrhizal roots to specific source leaves other than those directly above them (27). If so, then phosphorus and/or photosynthate accumulation in leaves may differ markedly from those patterns normally related to leaf development. Instead, accumulations of radioactivity observed in leaves during the present study were associated most closely with changes in leaf size and development along the length of the plant (Fig. 1). Leaves on the upper half of the plant were much larger, and those in positions 3 to 9 from the apex contained the vast majority of labeled photosynthates. Some irregularities in this pattern of ^{14}C-labeled assimilate distribution occurred, but these were restricted to one or two leaves without apparent correlation to position above or near different sides of the root system. Likewise, ^{14}C-labeled photosynthate partitioning between soluble and insoluble fractions of leaves was relatively constant. Variations were not associated with vertical alignment of leaves or phyllotaxy.

Partitioning between Split Root Systems. Mycorrhizal halves of root systems accumulated significantly greater percentages of ^{14}C-labeled photosynthates translocated to roots, with 66 and 68% of the root total recovered from tissue in sour orange and Carrizo citrange, respectively (Table II). Root samples included endophytic hyphae and fungal material appressed to roots, but ^{14}C-labeled assimilates were not examined in those hyphae which extended into the soil. Amounts of radioactivity translocated to mycorrhizal sides of the root system may therefore have been still greater than measured values because soil biomass was not included in ^{14}C samples. These results in combination with those shown in Table I indicate the degree of sink strength for the VAM side of the root system which is determined independently of phosphorus effects on photosynthate partitioning in source leaves. The total photosynthate available for export may still be related to phosphorus nutrition, but the preferential translocation of these assimilates to a mycorrhizal symbiont *versus* other tissues is influenced by factors within the sink.

There are several possible reasons for increased sink strength of VAM roots. A larger root mass typically accompanies mycorrhizal infections (8, 14, 20) and this might be expected to produce a greater total demand for photosynthates. Our results show no significant differences in fresh or dry weight between infected and uninfected halves, yet average radioactivity per unit fresh weight was still 63 and 85% greater in mycorrhizal sides for the two root stocks (Table II). Respiratory losses from both host and symbiont could raise the demand for photosynthates and account for differences between ^{14}C-labeled assimilate allocation and dry matter accumulation. Recently, Snellgrove *et al.* (29) measured losses of labeled CO_2 from below-ground portions of leek which

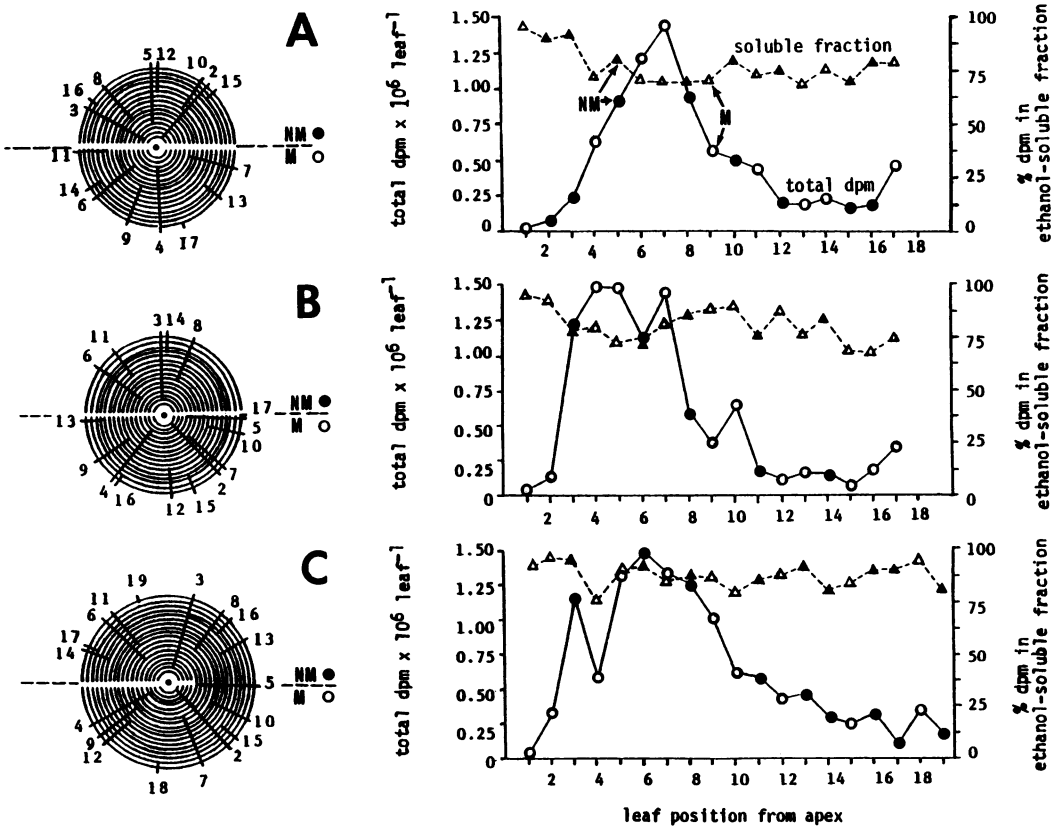

FIG. 1. Accumulation and partitioning of ^{14}C-labeled photosynthates in individual source leaves of split-root Carrizo citrange seedlings. Concentric circles represent nodes in descending order from the plant apex (center point of each diagram). Radial lines indicate direction of leaf extension from respective nodes and are numbered from youngest to oldest. A horizontal line divides each diagram into plant parts above mycorrhizal or nonmycorrhizal root halves. Graphs show ^{14}C distributions within and between source leaves positioned as shown in adjacent figures. Total dpm recovered from each leaf are indicated by (——) for tissues above mycorrhizal (bottom half of diagram [○]), and nonmycorrhizal (top half of diagram [●]) root systems. Percentages of ^{14}C-labeled photosynthates recovered in ethanol-soluble fractions from leaves are indicated by (- - -) for tissues above mycorrhizal (△) and nonmycorrhizal root systems (▲), respectively. A, B, and C represent separate experiments on different seedlings.

Table II. *Comparison of Accumulated ^{14}C and Fresh and Dry Matter in Mycorrhizal and Nonmycorrhizal Halves of Root Systems*

*, $P < 0.05$ significantly different from nonmycorrhizal halves of roots based on a paired t test. **, $P < 0.01$. Total amounts of radioactivity recovered from below-ground tissues were 1.0, 2.8, 0.8, and 3.4×10^6 dpm, respectively, for sour orange seedlings and 2.4, 1.6, 3.4, 3.1, 4.6, and 7.2×10^6 dpm, respectively, for Carrizo citrange seedlings. Values represent replicate seedlings. Additional data from other tissues of these same plants are expressed in Table III.

Mycorrhizal Status of Half-Root System	^{14}C Recovered from Below-Ground Tissues		Fresh Wt		Fresh Wt		Ethanol-Insoluble Dry Matter	
	+	−	+	−	+	−	+	−
			dpm g^{-1}		*mg*		*mg*	
Sour orange	60.2	39.8	244	194	1815	1501	361	283
	59.6	40.4	1841	651	907	1743	188	332
	75.1	24.9	371	351	1617	563	289	109
	70.7	29.3	1195	859	2003	1153	401	240
Mean	66.4*	33.6	913 NS	514	1585 NS	1240	309 NS	241
Carrizo citrange	53.8	46.2	984	595	1301	1141	186	212
	61.7	38.3	1844	1171	2246	2198	412	368
	65.7	34.3	1859	772	1184	1491	215	238
	69.7	30.3	845	588	2534	1586	488	299
	79.7	20.3	1489	702	2455	1325	507	268
	75.6	24.4	2485	1291	2191	1350	463	294
Mean	67.7**	32.3	1584**	853	1985 NS	1515	379 NS	280

were great enough to account for a considerable portion of increased translocation to VAM roots. Respiratory rates of mycorrhizal fungi can be substantially greater than those of root tissue (11).

In addition to affecting respiration rates and root biomass, VAM could contribute to sink demand through storage of fungal end-products and/or uptake of assimilates exudated from roots. Ectomycorrhizal fungi store carbohydrates as trehalose or mannitol, thus producing a gradient of sucrose from host to fungus (4). Although VAM fungi appear to store glycogen and lipids instead (4, 7, 19), they may still compartmentalize sucrose and/or hexoses away from the host prior to use in synthetic reactions. Nemec and Guy (23) have also reported that levels of reducing sugars relative to sucrose are greater after mycorrhizal infection of citrus roots. Differences in root exudation between infected and noninfected roots may too be related to sink strength. Considerable 'leakage' of assimilated C has been measured from the latter and is believed to aid mycorrhizal infection and establishment (9, 10, 30). Some authors have speculated that photosynthate loss from the host before and after infection may be similar and that active uptake by mycorrhizal membranes may maintain this flux and hence sink strength (10, 30). The observation in the present study that lesser amounts of ^{14}C-labeled photosynthates move to uninfected sides of root systems (Tables I and II) does not necessarily contradict this hypothesis because earlier studies demonstrated that leakage was more closely related to membrane permeability than concentrations of soluble photosynthate within the root (10). Finally, the effects of growth regulators as mediators of mycorrhizal sink strength must be considered because their balance is believed to change in symbiotic or parasitic associations (18). Auxins and cytokinin-like substances have been found to increase in mycorrhizal plants (18, 22) and the effect of growth regulators on photosynthesis and distribution of assimilates has received considerable attention (13).

Partitioning of ^{14}C-labeled photosynthates between mycorrhizal and nonmycorrhizal roots in a 2:1 ratio is strikingly similar in both cultivars (Table II). This does not correspond to the degree of mycorrhizal dependency, because optimal growth of sour orange seedlings is highly dependent on mycorrhizal infection, while that of trifoliate orange hybrid rootstocks is not generally as sensitive (20). The amount of carbohydrate made available for VAM-related processes therefore appears to be independent of the host requirement for phosphorus or other materials from the fungal symbiont.

Table III. *Distribution of ^{14}C-Photosynthates among Tissues of Split-Root Citrus Seedlings*

Total amounts of radioactivity recovered from seedlings were 1.1, 2.4, 1.4, and 2.4×10^7 dpm, respectively, for sour orange and 1.2, 2.6, 4.0, 2.7, 4.3, and 3.4×10^7 dpm, respectively, for Carrizo citrange. Values represent replicate seedlings. Additional data on below-ground tissues of these same plants is expressed in Table II.

Leaves	Stem		Roots	
	Phloem	Xylem	Mycorrhizal	Nonmycorrhizal
	% total ^{14}C recovered			
Sour orange				
79.86	10.28	1.15	5.25	3.46
82.89	4.60	1.21	6.73	4.57
78.79	13.36	2.65	3.91	1.29
70.26	14.38	2.01	9.44	3.91
Mean 77.75	10.60	2.04	6.31	3.30
Carrizo citrange				
62.75	14.45	3.22	10.53	9.05
53.39	15.72	4.64	16.19	10.06
74.66	14.71	2.23	5.52	2.88
64.60	18.13	5.93	7.90	3.44
63.95	20.26	5.10	8.52	2.17
59.51	15.60	3.73	16.03	5.13
Mean 63.14	16.48	4.14	10.78	5.46

Distribution of ^{14}C-Labeled Assimilates in the Whole Plant. Table III shows that the percentage of total carbon allocated to

mycorrhizal halves of root systems is greater in Carrizo citrange, but this corresponds to a change in partitioning between shoot and root rather than between root halves. Sour orange, presumably the more mycorrhizal dependent of the two, partitioned only 9.9% of its total ^{14}C-labeled photosynthate to roots, compared to 16.3% in Carrizo citrange.

The majority of labeled photosynthates remained in source leaves of both rootstocks, with 78 and 63% in sour orange and Carrizo citrange, respectively (Table III). Comparable percentages of ^{14}C-labeled assimilates also remain in leaves of other species (17), because complete translocation of labeled photosynthates out of a source leaf may be delayed by starch storage in chloroplasts. In the present study, 23 to 25% of the ^{14}C-labeled photosynthates which remained in citrus leaves were ethanol-insoluble and amylase digestion indicated 81 to 90% of this fraction was starch.

Stem samples of bark (phloem) contained mean percentages of 16.5 and 10.6 of the total ^{14}C recovered from sour orange and Carrizo citrange seedlings, respectively. Comparable root stock differences are also evident in below-ground samples (16.3 and 9.9%) for the same plants. Only 2 to 4% of the labeled assimilates were detected in stem xylem samples, however. Small amounts of ^{14}C-labeled assimilates may have been transferred directly from phloem, since evidence exists for phloem-to-xylem transfer of photosynthates in woody plants (25) much like a reverse of the xylem-to-phloem transfer which occurs in legumes. Movement of ^{14}C-labeled photosynthates to roots and back up the xylem stream is also possible, especially since amino acids have been shown to move from roots to shoots in citrus xylem after NH_4^- assimilation (16). This redistribution of recently labeled C out of roots of other species can occur within only 2 h and so could have been evident here (K. Koch, unpublished data).

Carbon Cost of the Symbiosis. Carrizo citrange seedlings partitioned 10.8 and 5.5% of labeled photosynthates between mycorrhizal and nonmycorrhizal sides of the root system, while a comparable allocation of 6.3 and 3.3% was observed in sour orange. The presence of mycorrhizae therefore accounted for an additional translocation of 5.3 and 3.0% of ^{14}C-labeled assimilates to half-root systems. These differences were significant at the 1 and 5% levels in the two species when half-roots were compared as in Table III. A whole mycorrhizal root system would be expected to double these differences so that about 10 and 6% of the total carbon assimilated by Carrizo citrange and sour orange seedlings may be diverted to mycorrhizae-related functions within 2 h. Localization of ^{14}C-labeled assimilates within mycorrhizal hyphae is not shown in these data. However, consistent increases in translocation to this portion of the plant are likely to have their basis in metabolic changes either directly or indirectly related to the symbiosis.

This 6 to 10% C cost of the citrus mycorrhizal symbioses over 2 h is similar to a recent approximation of 7% for VAM in leek based on differences between infected and uninfected plants 48 h after $^{14}CO_2$ assimilation (29). Even greater C loss to mycorrhizal hyphae has been indicated in nodulated legumes (3). Two symbioses were present, but 12% of the total photosynthates were believed to be allocated to mycorrhizal fungi alone at the time of infection in broadbeans (24).

CONCLUSIONS

Results presented in this paper show the degree of sink strength created by mycorrhizal fungi independent of possible VAM effects on source leaves through the known relationship between phosphorus and photosynthate partitioning. The approach used here also demonstrates that at least 3 to 5% of the total ^{14}C-labeled photosynthates were allocated to mycorrhizae-related events of a half-root system in 2 h and that twice these amounts or more might be expected for an entire mycorrhizal root system.

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