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# VASCULAR PATHWAYS CONSTRAIN $^{13}C$ ACCUMULATION IN LARGE ROOT SINKS OF *LYCOPERSICON ESCULENTUM* (SOLANACEAE)[1]

TARA M. BLEDSOE AND COLIN M. ORIANS[2]

Department of Biology, Tufts University, Medford, Massachusetts 02155 USA

While carbon transport and partitioning is largely determined by phloem source–sink relationships, it may be constrained by vascular connections. Tomato (*Lycopersicon esculentum*) plants exhibit a high degree of sectoriality, with restricted movement of nutrients from particular roots to orthostichous leaves. In this experiment we investigated the manner in which sectoriality influences source–sink phloem partitioning from shoots to roots in tomatoes and whether the size of the sink (root) modifies the pattern of carbon movement outside sectored pathways. Using $^{13}C$, we determined that shoot-to-root carbon transport in tomatoes is sectored even from upper leaves. Sink size also influenced carbon partitioning. Specifically, when a lateral root was grown in isolation (using a split-pot technique), it grew more and acquired significantly more $^{13}C$ from an orthostichous, exposed leaf than did any other single root. Vascular constraints were evident. $^{13}C$ accumulation in a large, isolated lateral root was very low when a leaf opposite the isolated lateral root was exposed. Thus sink size did not overcome vascular constraints. Because carbon assimilates are needed for nutrient acquisition and assimilation, these vascular constraints may affect the ability of sectored plants to utilize heterogeneously distributed soil resources. If so, future studies should compare species that differ in sectoriality to determine whether vascular constraints affect competitive hierarchies when soil resource availability is patchy.

**Key words:** carbon-13; partitioning; sectoriality; sink size; Solanaceae; tomato; vascular architecture.

Fixed carbon is transported long distances and partitioned to actively growing sinks, above- and belowground. Partitioning, however, also is affected by vascular architecture, which places constraints on the movement of carbon throughout a plant (Watson and Casper, 1984; Watson, 1986; Marshall, 1996; Preston, 1998). Studies show that orthostichous leaves or leaves and roots—those vertically aligned on the stem—have the greatest amount of resource sharing (Murray et al., 1982; Stieber and Beringer, 1984; Watson and Casper, 1984; Murphy and Watson, 1996; Vuorisalo and Hutchings, 1996; Orians et al., 2000, 2002). Although many studies have documented sectorial transport within shoots, very few have examined transport to roots. If carbon transport to roots is highly sectored, spatial heterogeneity in carbon acquisition could limit root responses to patchy soil nutrient availability.

Sink strength is a key determinant of carbon partitioning. Within the phloem, long-distance transport occurs through mass flow along a positive pressure gradient created by the loading and unloading of sucrose (Dickson, 1991). This movement occurs from source areas, where photosynthate is created, to sink areas, where photosynthate is used at a higher rate than it can be made (Tschaplinski and Blake, 1989; Wardlaw, 1990; Dickson, 1991; Taiz and Zeiger, 2002). Sink strength depends upon sink size and sink activity (Taiz and Zeiger, 2002). Sink size (carbohydrate uptake per mass of tissue) reflects the fact that larger tissues are likely to import more carbohydrates than smaller tissues (e.g., Reekie et al., 1998). Activity (rate of carbohydrate uptake per mass of tissue) reflects the fact that more metabolically active tissues import more carbohydrates per unit time (e.g., Singleton and Van Kessel, 1987). Although sink size and activity are not always positively correlated (e.g., when comparing woody tissues with actively growing tissues), Liang et al. (2001) found that the two are correlated in actively growing sinks.

While vascular architecture has been shown to constrain carbon partitioning, there is evidence that sectorial transport in the phloem may be broken down after modification of source–sink relationships via defoliation or inflorescence removal (Shea and Watson, 1989; Price et al., 1992, 1996). Shea and Watson (1989) found that the removal of orthostichous leaves from fireweed, *Chamaenerion angustifolium*, did not reduce fruit development within that sector. Thus, phloem constraints on carbon movement are not fixed, and under certain conditions whole-plant resource sharing can occur. Because vascular bundles can come in and out of contact with each other up and down the stem, lateral movement of assimilate through plasmodesmata is likely to occur, especially as the distance between two tissues increases (Dimond, 1966; Zwieniecki et al., 2003). To our knowledge, no studies have examined whether sectored, long-distance transport of carbon from leaves to roots is modified by distance or by source–sink dynamics. If sectored transport is not modified, then nutrient acquisition and assimilation (both carbohydrate-demanding processes) by roots in nutrient-rich hot spots may be constrained by a restricted supply of carbon.

Tomato plants (*Lycopersicon esculentum* Mill) are sectored and therefore are an excellent system for examining the interactions of vascular architecture and source–sink dynamics on long-distance carbon transport. In tomato, orthostichous leaves and roots share connections while opposite leaves and roots are less connected (Dimond, 1966; Orians et al., 2002). Using rhodamine B dye, Orians et al. (2002) mapped xylem flow from roots to shoots in tomatoes, finding leaves positioned on the stem within 45° of a lateral root placed in rhodamine B received the most dye, while leaves on the opposite side of the stem received none. This indicates that the movement of solutes in the xylem remained within a defined pathway and no sharing occurred outside of the sector. Although Orians et al. (2002)

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[2] Author for correspondence (Colin.Orians@tufts.edu), fax: 617-627-3805

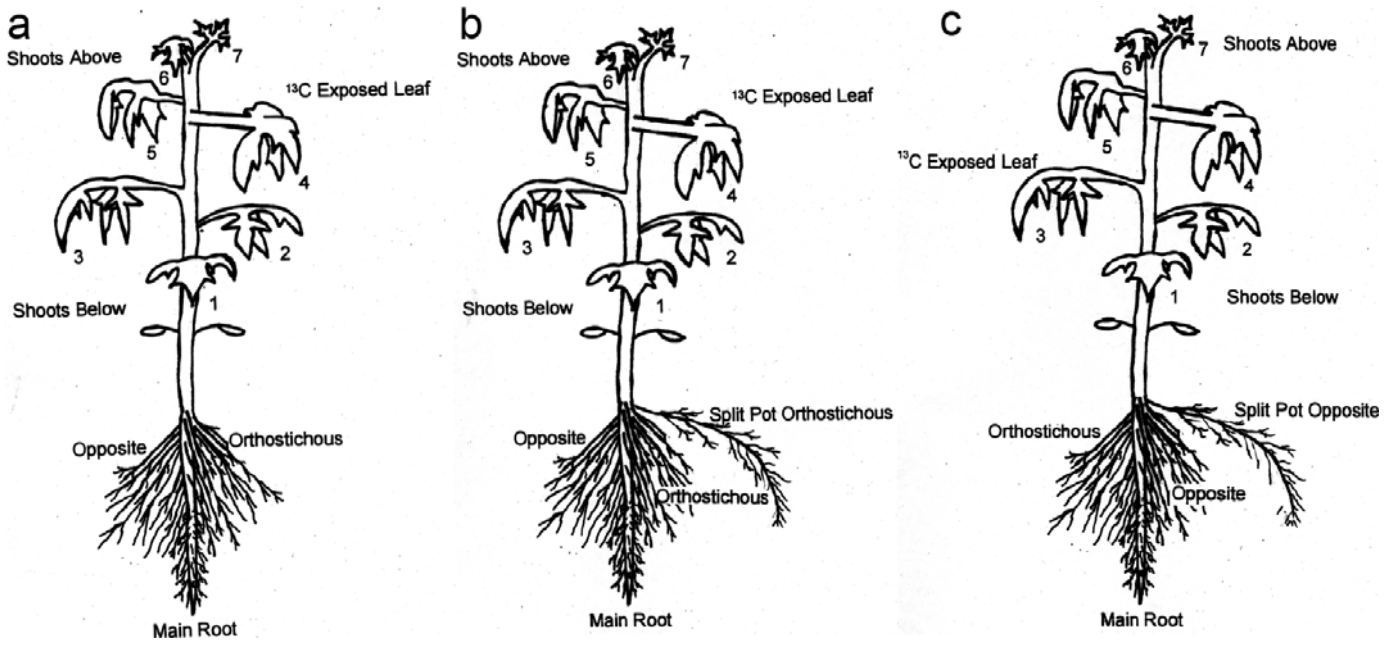


Fig. 1. Diagrams of experimental designs to determine where carbon-13 accumulated in tomato seedlings (c. 3 wk old). Plants were divided into various shoot and root sections: (a) single-pot tomato, (b) split-pot tomato with isolated lateral root orthostichous to exposed leaf, and (c) split-pot tomato with isolated lateral root opposite to exposed leaf. Shoots above are leaves plus stem above labeled leaf and shoots below are leaves plus stem below labeled leaf.

focused on xylem transport, phloem transport appears to be similarly restricted to vascular bundles along the stem (Orians et al., 2000; and reviewed by Orians et al., 2005).

In this study, we used tomato plants to observe vascular connections from leaves to roots in the phloem using carbon-13 as a tracer, to look at distance effects from leaves to roots on vascular connections, and to examine the combined effects of vascular architecture and the size of the sink (root) on long-distance carbon transport and partitioning. Although we did not measure root (sink) activity, we expect root size to be positively correlated with root activity in this study because plants were harvested within 4–6 wk of growth, leaving little time for the development of physiologically less active coarse roots (see Materials and Methods). In fact, all the lateral roots appeared to be fine roots (T. Bledsoe, personal observation). We hypothesized that (1) roots orthostichous to the exposed leaf would accumulate the greatest amount of $^{13}C$ while those on the opposite side accumulate very little, keeping carbon transport within a defined sector; (2) $^{13}C$ photosynthate from upper leaves would exhibit greater partitioning to non-orthostichous root sectors than lower leaves because vascular bundles from different sectors come in and out of contact along the length of the stem; (3) $^{13}C$ photosynthate concentration in roots would increase with greater sink size; and (4) sink size would override vascular constraints and result in an increase in carbon partitioning from leaves to non-orthostichous roots.

## MATERIALS AND METHODS

***Plants***—Tomato seeds (*Lycopersicon esculentum* cv. Celebrity F1; Johnny's Selected Seeds, Albion, Maine, USA) were planted and grown in Metro Mix Growing Medium-200 (Scotts, Marysville, Ohio, USA), in the Tufts University greenhouse, continuously from the spring through the fall of 2003. Seeds were sown in trays and watered daily, and natural light was supplemented with 400W sodium halide lights (16 h light : 8 h dark).

At the three- to four-leaf stages (~3 wk), tomato plants were replanted using either single pots or split pots. All root systems were washed before repotting, regardless of experimental design. Those in single pots were transferred to individual 0.1 × 0.1 m square pots to determine the baseline pattern of $^{13}C$ movement from shoots to roots. In the split-pot design, all but one lateral root (chosen due to its orthostichous alignment with leaf 4 along the stem) was placed in the main pot (0.1 × 0.1 × 0.13 m), while the isolated lateral root had its own smaller pot (0.06 × 0.06 × 0.13 m). In side pots (competition-free space), a single lateral becomes a strong sink (it grows faster and becomes larger) compared to other lateral roots.

After repotting, all plants were watered daily and fertilized weekly with Peters Professional fertilizer (0.5 g 20-20-0 N-P-K/L; Scotts, Marysville, Ohio, USA). Plants were fertilized for 2–3 wk (experiments 1, 3–5) or 4–5 wk (experiment 2). Plants grown in a single pot received 25 mL of fertilizer. Plants grown in split-pot treatments (experiments 3–5) received one of two fertilization regimes: equal fertilization (experiments 3 and 4, 25 mL of fertilizer applied to the main pot and 14.5 mL to the lateral pot; equal in that each pot is given an amount proportionate to its size) or patchy fertilization (experiment 5, 25 mL of fertilizer applied to the lateral pot only). Experiment 5 was designed to test whether $^{13}C$ transport is less sectored when an isolated root is the sole source of nutrients for the entire plant.

***Carbon-13 exposure and analysis***—Sunny days with temperatures between 20° and 30°C were chosen for $^{13}CO_2$ exposure. One leaf of each plant was placed in a sealed chamber with 30 mg of $^{13}C$-labeled $NaHCO_3$ (99 atom% $^{13}C$; Aldrich Chemicals, Milwaukee, Wisconsin, USA), with $^{13}CO_2$ released by the addition of 500 μL 20% lactic acid to the labeled sodium bicarbonate. Exposure lasted for 4 h, after which the chamber was moved outside of the greenhouse to prevent contamination. Twenty-four hours after exposure, the tomato roots were harvested. We chose 24 h based on the work of Khan and Sagar (1969). They exposed tomato plants to $^{14}C$ and harvested the plants at different time points. Within 4 h, $^{14}C$ moved from the leaf to the roots and back up to the stem, demonstrating that vertical reallocation of carbon occurs rapidly. Therefore our 24-h chase method should be sufficient to test for differential accumulation as a function of vascular architecture and sink strength.

After the experiment, plants were washed and divided into shoot and root sections (Fig. 1). Each section was dried at 60°C, weighed, and ground using a Kleco pulverizer (Kinetic Laboratory Equipment, Visalia, California, USA). Ground samples were stored at −20°C until analysis. To determine $^{13}C$ accumulation in each section of the plant, 2-mg samples were analyzed at the

TABLE 1. Relative biomass measurements for experiments 1, 3–5 in (A) all major tissue sections and (B) within lateral root sections (divided into groups based on orientation relative to exposed leaf) of tomato plants. Superscript letters denote significant differences within experiments ($P < 0.05$). See Materials and Methods for a detailed description of experiments. Values are means with standard errors in parentheses.

| | Experiment | | | |
|---|---|---|---|---|
| | 1 | 3 | 4 | 5 |
| Tissue | Baseline relative biomass | Orthostichous sink relative biomass | Non-ortho sink equal nutrients relative biomass | Non-ortho sink patchy nutrients relative biomass |
| A) Major tissue sections | | | | |
| Shoots above | 0.318 (0.044)$^{A}$ | 0.433 (0.059)$^{A}$ | 0.553 (0.026)$^{A}$ | 0.582 (0.020)$^{A}$ |
| Exposed leaf | 0.160 (0.008)$^{B}$ | 0.099 (0.016)$^{B}$ | 0.053 (0.007)$^{B}$ | 0.048 (0.006)$^{B}$ |
| Shoots below | 0.352 (0.038)$^{A}$ | 0.253 (0.035)$^{C}$ | 0.173 (0.021)$^{C}$ | 0.173 (0.018)$^{C}$ |
| Roots | 0.169 (0.006)$^{B}$ | 0.215 (0.017)$^{C}$ | 0.222 (0.007)$^{C}$ | 0.196 (0.006)$^{C}$ |
| B) Lateral root sections | | | | |
| Sp root | no root | 0.029 (0.004)$^{A}$ | 0.033 (0.005)$^{A}$ | 0.039 (0.003)$^{A}$ |
| Ortho roots | 0.036 (0.002)$^{A}$ | 0.033 (0.007)$^{AB}$ | 0.048 (0.010)$^{A}$ | 0.041 (0.009)$^{A}$ |
| Opp roots | 0.038 (0.004)$^{A}$ | 0.051 (0.008)$^{B}$ | 0.041 (0.006)$^{A}$ | 0.044 (0.006)$^{A}$ |

*Notes:* SP, split pot; Ortho, orthostichous; Opp, opposite.

Stable Isotope Facility at the University of California at Davis, California, USA.

To compare $^{13}C$ accumulation among sections of each plant, $\delta^{13}C$ was converted into mass percentage $^{13}C$ following equations given in Scrimgeour and Robinson (2004). Total $^{13}C$ in the tissues was calculated as: Total μg $^{13}C$ in tissue = total C (sample) × biomass (section) × (mass% × 0.01). Background $^{13}C$ from unexposed tissues was subtracted from each section total. Because plants differed in biomass and in the amount of $^{13}C$ fixed, we calculated relative biomass (section biomass/whole-plant biomass) and relative $^{13}C$ accumulation (section $^{13}C$/whole-plant $^{13}C$). From these values, we calculated the biomass-specific $^{13}C$ accumulation (relative $^{13}C$ accumulation/relative biomass). Tissues with higher biomass-specific accumulation values are greater sinks for $^{13}C$.

*Experiment 1: baseline shoot–root carbon movement*—Tomatoes grown in single pots ($N = 8$) to the eighth leaf stage were used in this experiment to determine whole-plant patterns of $^{13}C$ transport and partitioning. Leaf 4 of each plant was exposed to $^{13}CO_2$, and $^{13}C$ accumulation was measured in six different tissues: shoots above exposed leaf, exposed leaf, shoots below exposed leaf, main root, all lateral roots orthostichous to exposed leaf, and all lateral roots opposite exposed leaf (Fig. 1a).

*Experiment 2: distance effects on baseline carbon movement*—Tomatoes grown in single pots to the 10th leaf stage were used to determine whether $^{13}C$ accumulation in non-orthostichous roots was greater as distance to the root increased. Two plants were assigned to each $^{13}C$ exposure regimen: exposing leaf 4 (L4), leaf 5 (L5), leaf 6 (L6), leaf 7 (L7), or leaf 8 (L8). In a 10-leaf tomato plant these leaves are fully expanded. $^{13}C$ accumulation was measured in lateral roots that were either orthostichous or opposite to the leaf. This required that we determine, based on vascular pathways, the roots to which each leaf position was connected. A sectoriality index was created by subtracting the accumulation in opposite roots from that in orthostichous roots and dividing by the accumulation in the orthostichous roots. A sectoriality index of 1 indicates that $^{13}C$ accumulated only in the orthostichous roots, while values <1 provide an estimate of the extent of partitioning to opposite roots.

*Experiment 3: $^{13}C$ transport to orthostichous sinks*—Tomatoes grown in split pots with equal fertilization ($N = 5$) were used to test whether sink size influences the partitioning of $^{13}C$. Again, plants were grown to the eighth leaf stage, after which the fourth leaf, which was orthostichous to the split-pot lateral root, was exposed to $^{13}CO_2$. In addition to the six tissue types described in experiment 1, we also measured $^{13}C$ accumulation in the single orthostichous lateral root that was growing in the split pot (Fig. 1b).

*Experiment 4: $^{13}C$ transport to non-orthostichous sinks (equal fertilization)*—Tomatoes, eighth leaf stage, grown in split pots with equal fertilization ($N = 4$) were used to test whether a lateral root that is non-orthostichous but is a large sink can accumulate $^{13}C$ from a leaf on the opposite side of the stem. In this experiment, leaf 3 was exposed to $^{13}CO_2$, and $^{13}C$ accumulation was measured in the same seven tissue types as described in experiment 3 (Fig. 1c). In this experiment the split-pot lateral root was now opposite to the exposed leaf. We tested leaf 3 (as opposed to leaf 4 as in experiments 1, 3, and 5) because all plants were initially split so that the lateral root was orthostichous to leaf 4 and therefore opposite leaf 3. Based on the results in experiment 2 (see Results—*Experiment 2: distance effects on baseline carbon movement*), we expect that the results would have been the same if carbon had been fed to leaf 4 and quantified in roots opposite that leaf.

*Experiment 5: $^{13}C$ transport to non-orthostichous sinks (patchy fertilization)*—Tomatoes grown in split pots with patchy fertilization ($N = 3$) were used in this experiment, and like experiment 4, a leaf opposite the split-pot lateral root was exposed to $^{13}C$. This experiment differed from experiment 4 in that

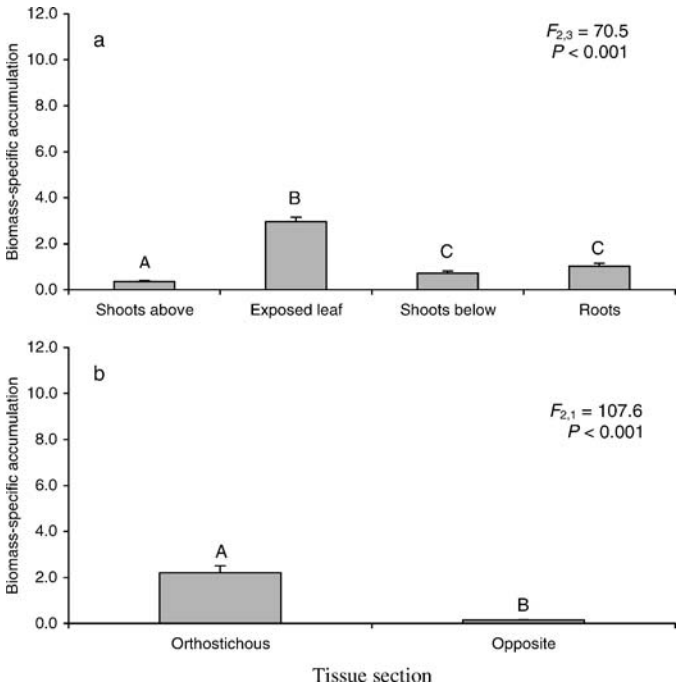


Fig. 2. Biomass-specific $^{13}C$ accumulation in plants in experiment 1 (grown in a single pot) for (a) all major tissues and (b) lateral root sections ($N = 8$, means + 1 SE). Difference in lettering indicates significant differences in biomass-specific $^{13}C$ accumulation based on Tukey's test ($P < 0.05$). Labels for lateral root sections were based on positions along stem relative to exposed leaf 4.

TABLE 2. Relative $^{13}C$ accumulation measurements for experiments 1, 3–5 in (A) all major tissue sections and (B) within lateral root sections (divided into groups based on orientation relative to exposed leaf) of tomato plants. Superscript letters denote significant differences within experiments ($P < 0.05$). See Materials and Methods for a detailed description of experiments. Values are means with standard errors in parentheses.

| | Experiment | | | |
|---|---|---|---|---|
| | 1 | 3 | 4 | 5 |
| Tissue | Baseline relative accumulation | Orthostichous sink relative accumulation | Non-ortho sink equal nutrients relative accumulation | Non-ortho sink patchy nutrients relative accumulation |
| A) Major tissue sections | | | | |
| Shoots above | 0.121 (0.026)$^{A}$ | 0.240 (0.037)$^{A}$ | 0.298 (0.033)$^{A}$ | 0.286 (0.033)$^{AB}$ |
| Exposed leaf | 0.473 (0.039)$^{B}$ | 0.387 (0.032)$^{B}$ | 0.350 (0.055)$^{A}$ | 0.418 (0.073)$^{A}$ |
| Shoots below | 0.233 (0.012)$^{C}$ | 0.143 (0.023)$^{A}$ | 0.185 (0.033)$^{A}$ | 0.154 (0.024)$^{B}$ |
| Roots | 0.173 (0.019)$^{AC}$ | 0.230 (0.039)$^{A}$ | 0.166 (0.019)$^{A}$ | 0.143 (0.026)$^{B}$ |
| B) Lateral root sections | | | | |
| SP root | no root | 0.116 (0.033)$^{A}$ | 0.011 (0.003)$^{A}$ | 0.010 (0.001)$^{A}$ |
| Ortho roots | 0.078 (0.010)$^{A}$ | 0.045 (0.014)$^{B}$ | 0.064 (0.016)$^{B}$ | 0.055 (0.011)$^{B}$ |
| Opp roots | 0.005 (0.001)$^{B}$ | 0.006 (0.001)$^{BC}$ | 0.010 (0.002)$^{A}$ | 0.015 (0.004)$^{A}$ |

*Notes:* SP, split pot; Ortho, orthostichous; Opp, opposite.

fertilizer was only applied to the lateral root in the split pot. Theoretically, this should create an even larger sink in the isolated lateral root. $^{13}C$ accumulation was measured in the same seven tissue types as described in experiments 3 and 4 (Fig. 1c).

***Statistical analysis***—One-way analyses of variance (ANOVA) were performed on the arcsine square-root-transformed data for relative biomass among all plant sections and root sections. A Tukey's test was performed to determine differences among sections. ANOVAs also were performed on log-transformed, biomass-specific $^{13}C$ accumulation data both among all plant sections and among root sections with a Tukey's test to determine differences among sections.

## RESULTS

***Experiment 1: baseline shoot–root carbon movement***—At the time of $^{13}CO_2$ exposure, biomass of shoots above and below the exposed leaf was significantly greater than the biomass of the root (Table 1). Leaf 4 exported more carbon to roots than to the shoot above (Table 2). Also, biomass-specific accumulation was greater in roots than in the shoots above (Fig. 2a). Relative biomass of each lateral root section was similar (Table 1), but they differed significantly in their relative $^{13}C$ accumulation (Table 2). Of the total $^{13}C$ accumulation in the roots, 45% went to the orthostichous roots below the exposed leaf and only 3% went to the opposite roots (the rest remained in the main root). Moreover, biomass-specific $^{13}C$ accumulation was greater in orthostichous roots than in opposite roots (Fig. 2b).

***Experiment 2: distance effects on baseline carbon movement***—Lateral roots orthostichous to the exposed leaf always had higher biomass-specific $^{13}C$ accumulation compared to roots opposite the exposed leaf, regardless of the leaf exposed (Fig. 3). Our index of sectoriality did not decrease as the number of intervening leaves increased ($F_{1,8} = 0.03$, $P = 0.86$, $R^2 = 0.004$). In fact, all indices were close to one (~0.95), indicating that accumulation was always highly sectored (data not shown).

***Experiment 3: $^{13}C$ transport to orthostichous sinks***—Although shoots above the exposed leaf had significantly higher biomass than both shoots and roots below the exposed leaf (Table 1), $^{13}C$ accumulation was similar in all tissues (Table 2). Roots, however, had higher biomass-specific $^{13}C$ accumulation than did shoots above and below the exposed leaf (Fig. 4a). Within the root sections, the single lateral root placed in the split pot grew as large, or nearly as large, as the 10–15 lateral roots that remained in the main pot (Table 1), and this root accumulated significantly more $^{13}C$ than all other root sections (Table 2, Fig. 4b), obtaining 50% of all the $^{13}C$ in the roots. The multiple lateral roots on the opposite side of the stem accumulated only 3%. Even within the main pot, the multiple lateral roots orthostichous to the exposed leaf had significantly greater biomass-specific $^{13}C$ accumulation than the opposite roots (Fig. 4b).

***Experiment 4: $^{13}C$ transport to non-orthostichous sinks (equal fertilization)***—Plants had greater biomass in shoots above the exposed leaf (Table 1), and all tissues had similar $^{13}C$ accumulations (Table 2). As before, shoots and roots below the exposed leaf had higher biomass-specific $^{13}C$ accumulations than shoots above the exposed leaf (Fig. 5a). Again the single lateral root in the split pot grew as large as the multiple

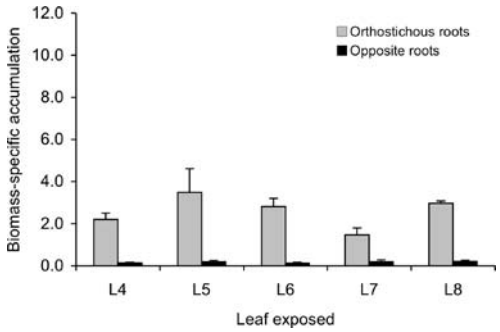


Fig. 3. Biomass-specific $^{13}C$ accumulation (means + 1 SE) in lateral root sections of plants in experiment 2 (grown in single pots) looking at the effects of distance from shoots to roots on the patterns of $^{13}C$ movement. Each group of plants had a single leaf exposed to $^{13}C$ where groups were distinguished by which leaf was exposed (leaf 4, $N = 8$; leaves 5, 6, 7, or 8, $N = 2$). Labels below bars indicate exposed leaf (number increases with distance from the roots), and labels for lateral root sections were based on positions along the stem relative to the exposed leaf.

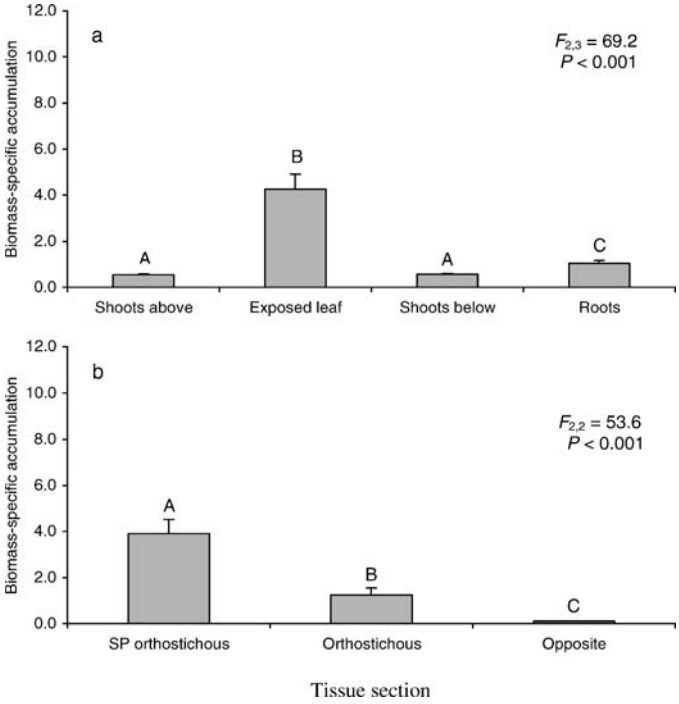


Fig. 4. Biomass-specific $^{13}C$ accumulation for plants in experiment 3 (grown in a split-pot design having equal fertilization, with an isolated lateral root orthostichous to the exposed leaf) for (a) all major tissues and (b) lateral root sections ($N = 5$, means + 1 SE). Labels for lateral root sections were based on positions along the stem relative to the exposed leaf (SP = split pot).

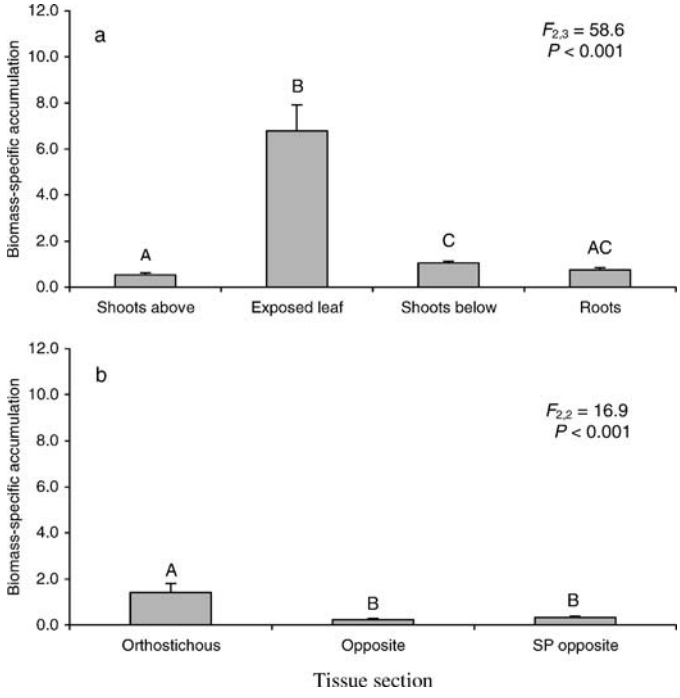


Fig. 5. Biomass-specific $^{13}C$ accumulation for plants in experiment 4 (grown in a split-pot design having equal fertilization, with an isolated lateral root opposite to the exposed leaf) for (a) all major tissues and (b) lateral root sections ($N = 4$, means + 1 SE). Labels for lateral root sections were based on positions along the stem relative to the exposed leaf (SP = split pot).

lateral roots within the main pot, with each section having similar biomass (Table 1), but very little $^{13}C$ accumulated in this root. Roots on the same side of the stem as the exposed leaf accumulated six times more $^{13}C$, and the two opposite root sections, the single root in the split pot, and the multiple roots in the main pot did not differ in percentage of root $^{13}C$ in each section (7% and 6%, respectively; Table 2). Moreover, the multiple orthostichous roots had significantly greater biomass-specific $^{13}C$ accumulation than the opposite root sections, which did not differ from one another (Fig. 5b).

***Experiment 5: $^{13}C$ transport to non-orthostichous sinks (patchy fertilization)***—Shoots above the exposed leaf had significantly greater biomass than did shoots and roots below the exposed leaf (Table 1). However, there were similar relative $^{13}C$ (Table 2) and biomass-specific $^{13}C$ accumulations (Fig. 6a) in all three tissues. Within the roots, the biomass of the single lateral root in the split pot was similar to the multiple roots in the orthostichous and opposite sections within the main pot (Table 1). Again this split-pot opposite root had low levels of $^{13}C$. The orthostichous lateral roots accumulated five times more $^{13}C$ than the two opposite root sections, the single root in the split pot and the multiple roots in the main pot, and these opposite root sections did not differ in the percentage of root $^{13}C$ in each section (7% and 10%, respectively; Table 2). Also, biomass-specific $^{13}C$ accumulation of main-pot orthostichous roots was significantly higher than both main-pot roots and the split-pot opposite root, which did not differ from one another (Fig. 6b).

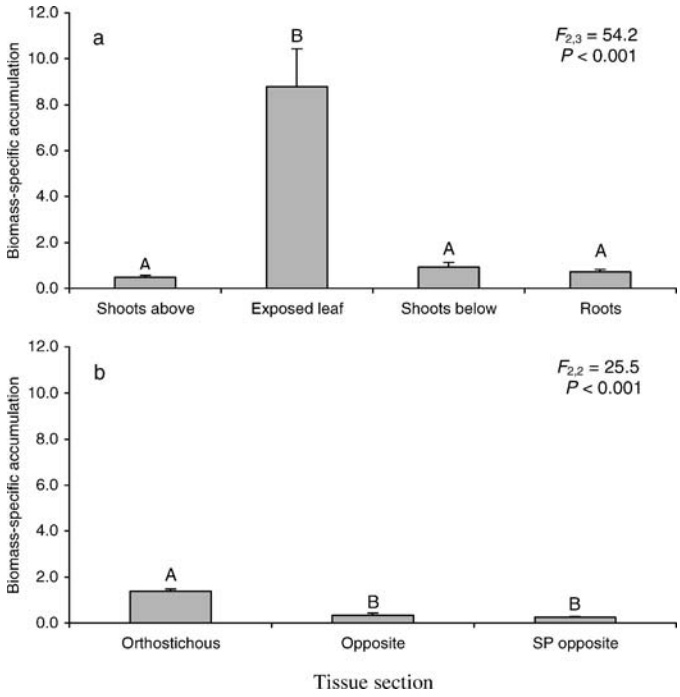


Fig. 6. Biomass-specific $^{13}C$ accumulation for plants in experiment 5 (grown in a split-pot design having patchy fertilization, with an isolated lateral root opposite to the exposed leaf) for (a) all major tissues and (b) lateral root sections ($N = 3$, means + 1 SE). Labels for lateral root sections were based on positions along the stem relative to the exposed leaf (SP = split pot).

## DISCUSSION

Phloem partitioning of carbon assimilates in tomato is greatly affected by vascular architecture. As hypothesized, lateral roots orthostichous to the exposed leaf had higher biomass-specific $^{13}C$ accumulation than roots opposite to the exposed leaf (hypothesis 1). Contrary to our prediction, no decrease in sectoriality was detected when $^{13}C$ movement occurred over longer distances from shoots to roots (hypothesis 2). Carbon from both the lowest leaf (leaf 4) and the highest leaf (leaf 8) exhibited similar patterns of sectoriality. Also, as expected, larger roots were larger sinks and accumulated more $^{13}C$ (hypothesis 3) but, contrary to our hypothesis, only when those roots were orthostichous to the exposed leaf (hypothesis 4). These results indicate that within-crown heterogeneity in carbon acquisition could severely limit the availability of carbon to actively growing roots in high-nutrient patches.

Sectored transport of carbon in our study agrees with previous research (Shea and Watson, 1989; Murphy and Watson, 1996; Preston, 1998; Li et al., 2000; Alkio et al., 2002). For example, Murphy and Watson (1996) showed in *Coleus rehneltianus* that carbon assimilate movement occurred only within specific orthostichous sectors from leaves to roots. We expected sectored transport to be weaker from upper leaves because there is extensive apoplastic (outside the plasma membrane) release and retrieval of phloem constituents along the vascular pathway (Eschrich et al., 1972; Minchin and Thorpe, 1984, 1987; van Bel, 2003; van Bel et al., 2002; Thorpe et al., 2005) and in tomato, vascular bundles come in and out of contact along the length of the stem (Dimond, 1966). Although this could facilitate increased lateral resource sharing as the area for vascular contact increases, we found no evidence that photosynthate from upper leaves results in increased $^{13}C$ accumulation in non-orthostichous roots.

We found that sink size had a significant effect on $^{13}C$ partitioning in tomato. An isolated lateral root grew rapidly, often obtaining a mass similar to all other lateral roots combined (>10% of root mass). As might be expected from a strong sink, this root accumulated more $^{13}C$ than other lateral roots (50% of all the $^{13}C$ was partitioned to the single lateral root in experiment 3). Moreover, the biomass-specific $^{13}C$ accumulation, an indicator of the amount of $^{13}C$ per tissue mass, in this lateral root was much greater. This suggests that these roots not only accumulated more $^{13}C$ because they were larger but also because they were more active.

Surprisingly, sink size did not modify vascular connectivity in our study. Split-pot lateral roots positioned opposite to exposed leaves (experiments 4, 5) were as large as in experiment 3, but accumulated significantly less $^{13}C$. The relative $^{13}C$ accumulation was similar in both opposite root sections and 5–6 times less than the orthostichous roots. Thus, we did not detect a breakdown in sectoriality of carbon transport as other researchers have reported. (Shea and Watson, 1989; Price et al., 1992). If a non-orthostichous root is the only source of nutrients (experiment 5), could this promote partitioning to that root? As expected, the relative biomass of the split root in experiment 5 (0.039) was larger than in experiment 4 (0.033), but the relative $^{13}C$ accumulation and biomass-specific accumulation were similar in both experiments. This implies that leaves orthostichous to a root in a nutrient-rich patch can supply all the carbon necessary to promote root proliferation in that patch. Perhaps carbon will only be drawn from other sectors following localized leaf area loss (sensu Shea and Watson, 1989; Price et al., 1992). Defoliation may increase the integrated movement of carbon (breaking down sectoriality) by decreasing the pressure inside the phloem connected to the removed leaf, allowing for carbon assimilate to move laterally via apoplastic and symplastic pathways from higher-pressure phloem vessels in the non-orthostichous sector (reviewed by Orians et al., 2005).

***Implications***—When studying the effects of carbon partitioning in plants, both source–sink dynamics and vascular architecture must be taken into consideration. Our results suggest that, within sectored plants, source leaves with higher photosynthetic rates could provide more carbon assimilates to growing organs within their sectors, but provide minimal photosynthate to roots in other sectors, even when the other roots are in nutrient-rich hot spots. This may constrain the ability of plants to utilize nutrient-rich patches. If, for example, defoliation by herbivores is concentrated on leaves above roots in a nutrient-rich patch, this may prevent the plant from being able to forage for and efficiently utilize a nutrient patch. There is also evidence that species differ in sectoriality (Orians et al. 2005) and integrated, less sectored, species may be able to outcompete more sectored species when soil nutrient availability is heterogeneous, either by partitioning more carbon to promote root proliferation or to increase specific uptake rates. To our knowledge no studies have compared the competitive ability of more sectored species with more integrated species.

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