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Temporal and spatial aspects of root and stem sucrose metabolism in loblolly pine trees

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Summary We studied root and stem sucrose metabolism in trees excavated from a 9-year-old artificially regenerated loblolly pine (*Pinus tueda* L.) plantation. Sucrose synthase (SS) activities in stem and taproot vascular cambial tissues followed similar seasonal patterns until they peaked during September. After September, stem SS activity disappeared quickly, whereas taproots exhibited SS activity even in January. Pyrophosphate-dependent phosphofructokinase (PPi-PFK) activity tracked SS activity. The activities of ATP-dependent PFK and several other glycolytic enzymes (e.g., phosphoglucomutase and phosphoglucoisomerase) remained relatively constant in cambial tissues of stem, taproot, and all first-order lateral roots (FOLRs) throughout the year. However, during the growing season, individual FOLRs exhibited variable sucrose metabolic activities that were independent of root diameter or position on the taproot. The FOLRs with low or no SS activity also had low PPi-PFK activity. We propose that when intense competition for sucrose occurs among different organs of a tree, the variable activities of the sucrose metabolic enzymes in FOLRs ensure that enough sucrose is allocated to the stem and taproot for growth. For a tree's long-term survival and growth, second or higher-order roots can be sacrificed, whereas FOLRs, stem and taproot are essential.

Keywords: first-order ***lateral root, glycolysis,*** *phosphofructokinase,* ***Pinus taeda, sucrolysis, sucrose synthase,*** *taproot,* ***vascular cambium enzymes.***

Introduction

A distinct aspect of tree biology is the strong seasonal growth patterns. Because these patterns must be linked with the supporting biochemical processes, we have studied seasonal patterns of sucrose metabolism (sucrolysis) and glycolysis in nursery-grown loblolly pine (*Pinus taeda* L.) seedlings (Sung et al. 1993a). Although forest seedlings differ in many respects from mature trees and trees may also have a juvenile phase of growth that is different from that of both seedlings and mature trees (Hutchison and Greenwood 1991, Hanson et al. 1994), our working hypothesis is that the fundamental processes involved in sucrolysis and glycolysis are similar in all higher plants, irrespective of plant age. This hypothesis is supported by our finding that sucrose metabolism is similar in nursery seedlings and 9-year-old trees of sweetgum (*Liquidambar styraciflua* L.) (Sung et al. 1993b).

What is unique to a given species is how the temporal and spatial aspects of sucrolysis are expressed. For example, evergreen conifers have the potential to produce sucrose year round (Smith and Paul 1988, Kuhns and Gjerstad 1991), which could support a unique sucrose metabolism in their roots (Sung et al. 1993*a*). In potato (*Solanum tuberosum* L.), fast changes (in a few days) in sucrose synthase (SS) activity in any given tuber indicate that sucrose is allocated among the tubers in a fashion not associated with tuber size or position along a stolon (Sung et al. 19896, 1990, Ross and Davies 1992). Sung et al. (1993b) also observed a seemingly random distribution of SS activity in first-order lateral roots (FOLRs) of sweetgum.

Based on these observations and our previous studies showing that the cambial tissues of stems, taproots, and woody lateral roots of trees compete for sucrose throughout each season's growth (Sung et al. 1989*a*, 1993*b*), we hypothesized that both the temporal and spatial aspects of sucrose metabolism differ between stems and roots. The specific objectives of this study were to: (1) identify the sucrose metabolic pathway and glycolysis in vascular cambial tissues of 9-year-old loblolly pine tree taproots, FOLRs, and stems; (2) determine the temporal and the spatial patterns of sucrose metabolism in these organs; and (3) deduce the roles and importance of various types of roots in sucrose metabolism.

Materials and methods

From May 1994 to January 199.5, trees from a 9-year-old loblolly pine plantation, located at the Department of Energy's Savannah River Site, Aiken, South Carolina, were sampled monthly. At each sampling, an 8-10 m^2 area was selected where there was little mortality and there were trees of three stem diameter classes, namely large, average (medium), and small. Ranges of stem diameter at breast height for large, medium, and small classes were 9.0 to 12.5 cm, 7.0 to 9.0 cm, and 4.0 to 6.5 cm, respectively. Except for May and June, one tree from each stem diameter class was excavated each month. One large tree was excavated in May, and one large tree and one medium tree were excavated in June. After the selected

trees were felled, a commercial tree spade was used to extract the stump and roots in a soil cone of 1.22 x 1.37 m. Roots within the soil cone averaged 79% of the total root fresh weight (PP. Kormanik, personal communication). Mean growth data for all the trees in each stem diameter class are presented in Table 1.

Vascular cambial tissue samples were collected immediately following tree excavation. One or two 15 x 5 cm strips of bark were removed from each stem at breast height and near ground level. Xylem-side vascular cambial tissues were scraped from the debarked stem area and immediately frozen in liquid N_2. Cambial tissues were scraped from a 10 x 5 cm debarked area on the taproot located 5 cm below the soil surface. The whole length of the FOLRs within the soil cone was sampled for cambial tissues and each FOLR was processed and analyzed separately. For some large-diameter FOLRs, a subsample of total cambial tissues was used for protein extraction. For some small-diameter FOLRs, two or three FOLRs of similar diameter were combined to obtain enough cambial tissues. At each sampling, a few FOLRs were not included in the protein extraction and enzyme assays because the barks were impossible to peel. Within 24 h of tree excavation, tissues were processed for enzyme analysis. We used the procedures for protein extraction and enzyme assays described previously (Sung et al. 1993*a*). We assayed sucrose synthase (SS), pyrophosphate-dependent phosphofructokinase (PPi-PFK), ATP-dependent PFK, fructokinase, glucokinase, UDP-glucopym -phosphorylase, phosphoglucoisomerase, and phosphoglucomutase in each sample extract. In all of the enzyme assays, activities were proportional to the amount of each extract and time. The protein concentration of each extract was determined with Bradford reagents using bovine serum albumin as the standard. Enzyme specific activities are expressed on a mg protein basis.

Table 1. Growth data for 9-year-old loblolly pine trees in three stem diameter size classes. Values presented are means ± SD of all the trees excavated for each size class.

	Large tree	Medium tree	Small tree
Height, m	6.5 ± 0.7	4.9 ± 0.6	4.4 ± 0.8
Stem DBH[1], cm	11.1 ± 1.2	7.9 ± 1.1	5.7 ± 1.2
FOLR diameter range[2], mm	7.8 ± 1.7 to 37.8 ± 9.5	9.0 ± 4.8 to 27.2 ± 5.7	8.6 ± 4.0 to 16.8 ± 8.2
FOLR number	18.0 ± 3.0	11.0 ± 4.0	7.0 ± 6.0
Tree fresh weight[3], kg	66.8 ± 12.7	27.7 ± 8.7	16.8 ± 8.2
Fresh weight allocation[3], %			
Stem	47.7 ± 4.4	45.6 ± 2.9	45.6 ± 5.9
Branch/Needle	3 1.6 ± 4.2	30.9 ± 3.8	30.8 ± 5.5
Taproot	18.7 ± 2.6	21.6 ± 2.8	21.7 ± 4.5
FOLR	2.0 ± 0.6	1.9f.0.8	1.9 ± 1.1

[1] Stem diameter at breast height.
[2] Diameters taken in two directions perpendicular to each other at 5 cm from the taproot on each FOLR.
[3] Fresh weights of second- and higher-order lateral roots and their mycorrhizae were not included.

Results

and fresh weight allocation of loblolly pine trees

Stem diameter size had no effect on fresh weight allocation patterns (Table 1), which remained essentially constant throughout the study period (Figure 1). Fresh weight allocation to stems, taproots, and first-order lateral roots (FOLRs) ranged between 40 and 50%, 18 and 22%, and 1.8 and 2.1%, respectively. Large-diameter trees had greater ranges in FOLR diameter and more FOLRs than medium- and small-diameter trees (Table 1); hence more FOLRs were sampled for enzyme activities from large-diameter trees than from medium- or small-diameter trees.

Temporal and spatial patterns of sucrolysis in vascular cambial tissues of loblolly pine trees

Because there were no differences in enzyme activities of stem vascular cambial tissues collected near ground level and at breast height, enzyme activities from these stem cambial tissues were averaged. Stem diameter size had no effect on amounts of enzyme activity. Activity of SS in stem, taproot, and FOLR cambial tissues fluctuated with the season (Figure 2). In all tissues, SS activity increased from May through September. Decreases in SS activity occurred after September in all tissues, with SS activity of stems decreasing faster than that of roots and approaching zero in December and January (Figure 2). Seasonal patterns of SS activity in taproots and FOLRs were similar, with some SS activity remaining in taproots during the winter.

Phosphofructokinase and other glycolytic enzymes in vascular cambial tissues of loblolly pine trees

The temporal and spatial patterns of PPi-PFK activity followed similar trends to those of SS activity (cf. Figures 2 and 3).

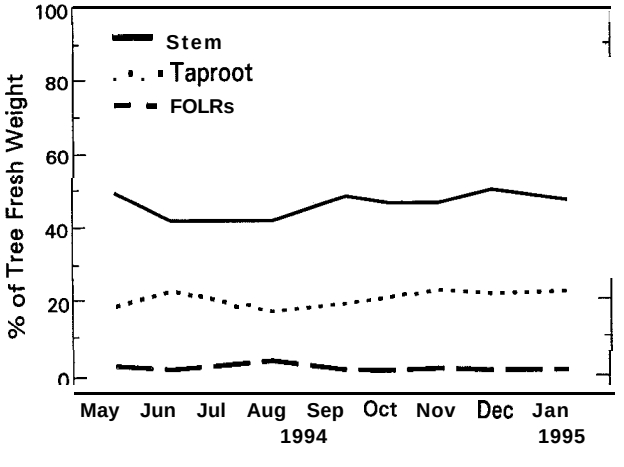

Figure 1. Percents of fresh weight allocation within 9-year-old plantation loblolly pine trees. Fresh weights from second- and higher-order lateral roots with their mycorrhizae were not included. At each sampling, except for May and June, values from a large-diameter tree, a medium-diameter tree, and a small-diameter tree were averaged. In June, values from a large tree and a medium tree were averaged. Only one large tree was sampled in May.

However, unlike stem SS activity, some PPi-PFK activity was present in stems in January. Activity of PPi-PFK decreased 4- to 5-fold from fall to winter and increased earlier in the spring than SS activity (cf. Figures 2 and 3). Activity of PPi-PFK in May was almost as high as in the summer, whereas SS activity had only just begun to increase in May. The patterns for ATP-PFK activity exhibited little change either at a temporal or a spatial level (Figure 4).

Other glycolytic enzymes measured were all active in the cambial tissues of loblolly pine tree stems, taproots, and FOLRs (Table 2), but showed little seasonal or spatial change (data not shown).

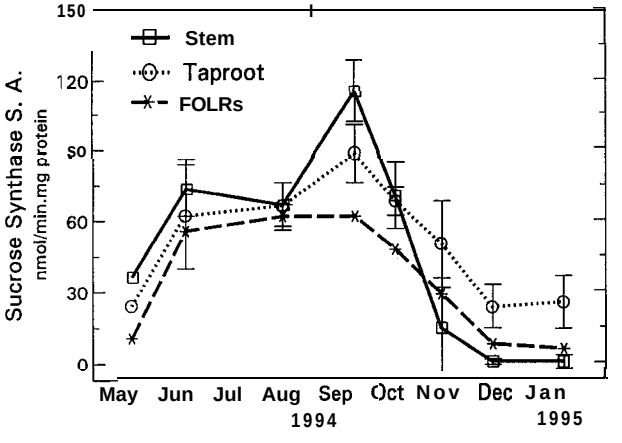

Figure 2. Temporal and spatial patterns of sucrose synthase activity in vascular cambial tissues of 9-year-old loblolly pine trees. The same trees as measured for Figure 1 were used for enzyme analysis. Means ± standard deviation for all trees determined at each sampling are presented for stems and taproots. Values for FOLR are means for all the FOLRs analyzed at each time.

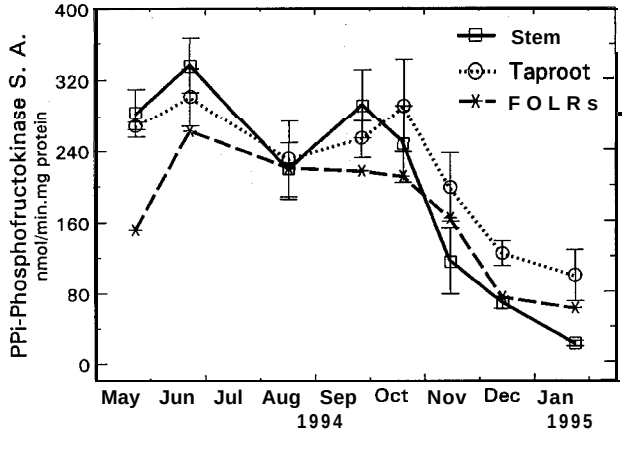

Figure 3. Temporal and spatial patterns of PPi-phosphofructokinase activity in vascular cambial tissues of 9-year-old loblolly pine trees. The same extracts as used for Figure 2 were assayed. Means ± standard deviation for all trees determined at each sampling are presented for stems and taproots. Values for FOLR are means for all the FOLRs analyzed at each time.

FOLR vascular cambial tissues of loblolly pine trees

A plot of SS activity from individual FOLRs against root diameters showed that there was little correlation between lateral root diameter and SS activity (Figure 5). There were also no correlations between root position and SS activity (Table 2). Furthermore, none of the glycolytic enzyme activities in FOLRs were correlated with lateral root diameter or root position on the taproots (Table 2).

Low amounts of SS activity in FOLRs (e.g., root positions 10 to 13 in Table 2) were correlated with low amounts of PPi-PFK activity (r = 0.95). In general, r values between FOLR SS and PPi-PFK at each sampling time ranged from 0.54 to 0.89, except for May when r = 0.35. There were no correlations between SS and ATP-PFK activities (r values between 0.004 and 0.28) for individual FOLRs throughout the year, except for one tree that had a value of 0.78 (Table 2).

Discussion

Temporal and spatial patterns of sucrose metabolism in cambial tissues and its relations to growth of loblolly pine trees

Sucrose synthase activity is positively related with sucrose sink activity (e.g., growth and storage) in many trees and annuals, including developing needles (Claussen et al. 1986, Sung et al. 1989*a*, 1989*b*, Ross and Davies 1992, Williams et al. 1992, Sung et al. 1993*a*, 1994, Hampp et al. 1994, Godt et al. 1995, Pfeiffer and Kutschera 1995). The reported periodicity in growth of loblolly pine tree stems and Sitka spruce (*Picea sitchensis* (Bong.) Carribre) tree stems and roots paralleled the seasonal patterns of SS activity in loblolly pine tree stems and roots, with roots becoming the major sucrose sink in late fall and winter (Figure 2) (Deans and Ford 1986, Blanche

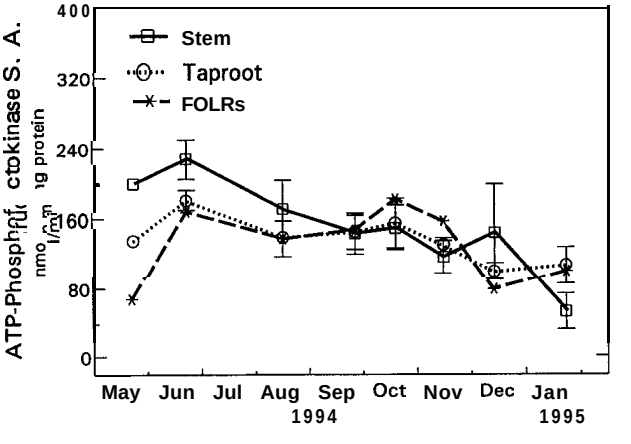

Figure 4. Temporal and spatial patterns of ATP-phosphofructokinase activity in vascular cambial tissues of 9-year-old loblolly pine trees. The same extracts as used for Figure 2 were assayed. Means ± standard deviation for all trees determined at each sampling are presented for stems and taproots. Values for FOLR are means for all the FOLRs analyzed at each time.

Table 2. Sucrolytic and glycolytic enzyme activities in individual first-order lateral roots (FOLRs) of a large 9-year-old loblolly pine tree excavated in June 1994. Abbreviations are as follows: sucrose synthase, SS; pyrophosphate-dependent phosphofructokinase, PPi-PFK, ATP-dependent PFK, ATP-PFK; fructokinase, FK; glucokinase, GK; phosphoglucomutase, PGM; phosphoglucoisomerase, PGI; and UDP-glucopyrophosphorylase, UDPG.

Position[1]	Diameter (mm)	Specific activity, nmol mg^{-1} min^{-1}								PFWSS ratio[2]
		ss	PPi-PFK	ATP-PFK	FK	GK	PGM	PGI	UDPG	
1	29.3	58	320	154	69	53	1644	807	1989	8.2
3 and 4	22.3	92	379	217	68	71	3880	1019	4330	6.5
6	40.8	95	399	233	82	81	3376	1027	4996	6.7
7	61.6	52	273	218	62	50	3029	929	4067	9.4
8	36.6	91	357	231	87	71	3141	1014	4617	6.5
10, 11 and 12	16.3	23	124	103	28	21	1670	495	1982	9.9
13	26.4	31	190	132	35	28	3318	839	3247	10.4
14	28.5	77	287	142	50	72	2813	838	3435	5.6
16	30.5	78	337	183	71	68	3134	923	5008	6.7

[1] Positions of FOLRs on taproot, with 1 near the soil surface and 16 deep in the soil profile. The FOLRs at positions 2, 5, 9 and 15 had diameters of 13.0, 8.5, 14.8 and 18.4 mm, respectively. Barks of these roots were not peelable and these FOLRs were not included in protein extraction and enzyme assays.

[2] Ratio = sum of PPi-PFK and ATP-PFK specific activities over SS specific activity.

et al. 1992). In winter, loblolly pine seedlings and trees photosynthesize and increase in belowground biomass (Adams et al. 1990, Kuhns and Gjerstad 1991). Thus, it is reasonable to conclude that SS activity is also an indicator for sucrose sink activity in loblolly pine trees.

Further insights on the spatial competition for sucrose within trees and seedlings are provided in Figure 6. Figure 6a was derived from the data published on loblolly pine seedlings in Figures 1 and 3 of the paper by Sung et al. (1993*a*) and Figures 6b and 6c were derived from the data on 9-year-old loblolly pine trees presented in Figure 2 of this study. Loblolly pine seedlings had 60 to 80% of their sucrose metabolizing activity in the stem between May and early November (Figure 6a). During the fall, seedling taproots increased their share of sucrose metabolizing activity from 40 to 90% and maintained this share of activity over winter. In the 9-year-old loblolly pine trees, taproot and FOLRs had more than 50% of the total sucrose metabolizing activity beginning in June and this share increased to more than 80% by November (Figure 6b).

Sucrose synthase activity in FOLRs of loblolly pine trees ranged between 20 and 30% of the total sucrose metabolizing activity throughout the year (Figure 6c). The almost three-way division of SS activity among stems, taproots, and FOLR from June through mid-October was not correlated with the percents of fresh weight allocation within trees (Figures 1 and 6c, Table 1). First-order lateral roots and the taproot represented only 2 and 20%, respectively, of the total tree fresh weight. Although on a total SS activity per organ basis, stems were the most competitive organ for sucrose in spring and summer? on a per unit cambial tissue protein basis, taproots, FOLRs, and stems were equally competitive for sucrose from June through October (Figure 6c). In several forest tree species, 24 to 80% of current photosynthates are invested belowground annually (Cannell 1985, Sheriff and Rook 1990). It is possible that, unlike stems and taproots that metabolize sucrose for biomass accumulation, FOLRs use sucrose mainly for energy to develop higher-order lateral roots, tine roots, mycorrhizae, and water uptake (Haussling et al. 1988, Nambiar 1990, VanRees and Comerford 1990, MacFall et al. 1991, Sung et al. 1995).

Phosphofructokinases in cambial tissues loblolly pine trees

Although we found positive correlations between SS and PPi-PFK activities in loblolly pine trees (e.g., Table 2) and seedlings (Sung et al. 1993*a*), PPi-PFK activity was less indicative of sink activity than SS activity (Figures 1 and 3, Sung et al. 1993*a*). No correlations existed between SS and ATP-PFK activities.

The sum of the activities of PPi-PFK plus ATP-PFK in a tissue represents its maximum potential for phosphorylating fructose 6-P Theoretically, a 2/1 ratio of total PFK to SS activity (PFK/SS) is necessary for the glycolysis of sucrose. (Sung et al. 1993a). This PFK/SS ratio provides another indication of sink strength because sucrose cleavage and fructose 6-P phosphorylation are rate-limiting steps in sugar metabolism. The PFK/SS ratio ranged between 5.6/1 and 10.4/1 in FOLRs of a single tree during an active-growing month (Table 2). Generally, trees had PFK/SS ratios between 3/1 and 10/1 from June through October in stems, taproots, and in most FOLRs. In slow-growing months, the PFK/SS ratio increased to 10/1. Furthermore, a greater percent of FOLRs had a PFK/SS ratio $> 10/1$ in the slow-growing months than in the active-growing months.

Sucrose synthase activity in FOLR cambial tissues of loblolly pine trees

The tight developmental control of annual plants over their reproductive sinks, e.g., seeds and fruits, is evidenced by the positive correlation between sink strength and SS activity in

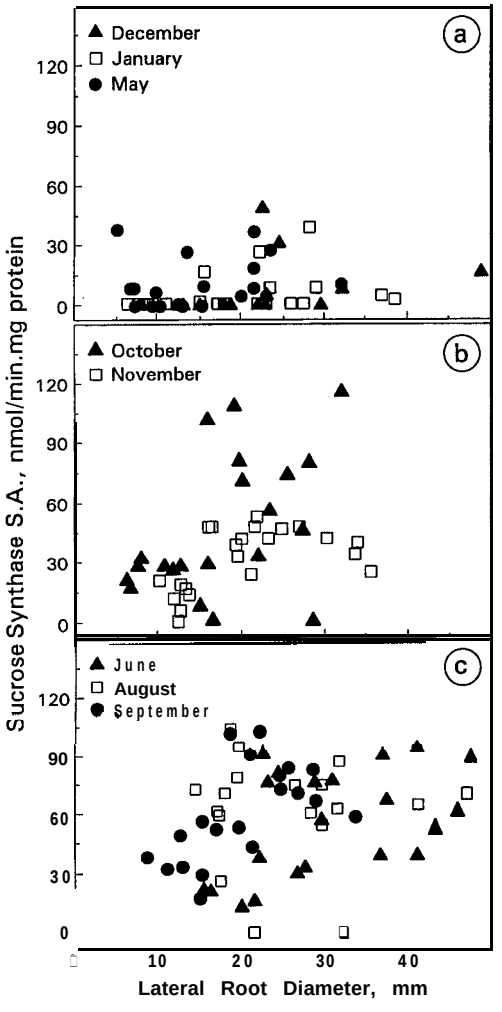

Figure 5. Scattergram of cambial tissue sucrose synthase activity versus diameters of first-order lateral roots of 9-year-old loblolly pine trees throughout a growing season. For clarity, data presented are grouped as (a) low overall activity in winter and spring, (b) medium overall activity in fall, and (c) high overall activity in summer and early fall.

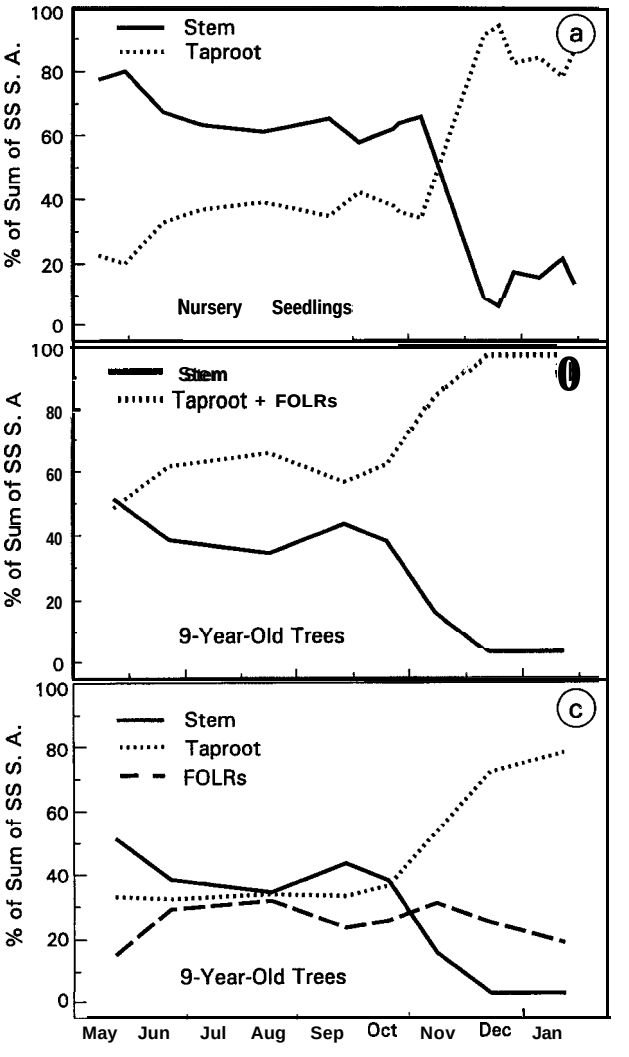

Figure 6. Seasonal patterns for percent of sucrose synthase activity in (a) stems and taproots of 2-year-old nursery-grown loblolly pine seedlings grown in 1991 and 1992 (data derived from Sung et al. 1993*a*), (b) stems and taproots plus first-order lateral roots of 9-year-old plantation loblolly pine trees, and (c) stems, taproots, and first-order lateral roots of 9-year-old plantation loblolly pine trees.

these organs throughout the developmental stage, and by little variation in SS activity in these sinks at similar developmental stages (Sung et al. 1994). In contrast, an independence of SS activity among FOLRs of a loblolly pine tree was observed at all sampling times. The non-linear relationships between SS activity and FOLR diameter and position on the taproot (Figure 5, Table 2) were similar to the non-linear relationship observed by Sung et al. (1989b) between potato tuber SS activity and tuber size and position on a stolon. It appears that, at any particular time, plants allocate their photosynthates among vegetative sinks in a less regular pattern than among reproductive organs. It is possible that the quick response of SS activity to the presence and absence of imported sucrose results in the non-synchronization of SS activity among FOLRs (Figure 5, Table 2) (cf. Sung et al. 1990, Ross and Davies 1992, Williams et al. 1992, Black et al. 1995).

The low SS activity of some FOLRs could affect the functioning of their higher-order roots. Thus, when competition for sucrose is strong among different organs of a tree, the variable rates of sucrose metabolism in FOLRs probably ensure that enough sucrose is allocated to stem and taproot for growth at the expense of the higher order roots. In other words, second- or higher-order roots can be sacrificed but FOLRs can not. The variable amounts of SS activity, and thus growth, in FOLRs have implications for tree root research, i.e., the results of any natural variation in conditions (e.g., seasons or environment) or imposed treatments (e.g., fertilization or irrigation) might be concealed if sampling is restricted to only a few roots of a tree. We conclude that trees species have similar sucrolytic and glycolytic enzymes that are under similar developmental control (cf. Sung et al. 1989*a*, Sung et al. 1993*a*, 1993*b*), but that

there is an apparently random distribution of SS activity among individual FOLRs of a tree.

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