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Sucrose metabolism, growth and transplanting stress in sweetgum seedling taproots and stems

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Abstract

One-year-old nursery-grown bare-root sweetgum (*Liquidambar styraciflua* L.) seedlings were lifted and transplanted into a nearby nursery bed or a cleared forest field in late January 1994. Seedlings remained in the same bed for the second year were the nontransplanted controls. Seedlings growing in beds were watered regularly and those in field received only rain. Specific activities of sucrose synthase (SS), pyrophosphate-dependent phosphofructokinase (PPi-PFK), ATP-dependent PFK (ATP-PFK), fructokinase (FK), and glucokinase (GK) were determined in the xylem-side cambial tissues of control and transplanted seedling taproots and stems from April through November 1994. Stem and taproot SS activity of control seedlings exhibited similar seasonal patterns with stem SS higher than root most of the time. Low SS activity was observed during early leaf expansion in the spring with resumption of taproot SS activity occurring 2 weeks later than stem SS. Seedling SS activity peaked in June and September and decreased sharply near leaf abscission in fall. Seasonal patterns of PPi-PFK in control seedlings were similar to those of SS except that PPi-PFK peaked only in June. Taproots of nontransplanted seedlings had similar level of PPi-PFK to that of stems. From late April to mid-June, there were 35–75% and 20–45% decreases in SS and PPi-PFK activities in transplanted seedlings, respectively, as compared with the controls. Moreover, seedlings transplanted into the forest field had much less growth and lower activities of SS and PPi-PFK than seedlings transplanted into the nursery beds. Activities of ATP-PFK and FK were generally lower in transplanted seedlings than controls.

During spring and early summer, some transplanted seedling stems had tip dieback or black mottling and scars or both. These seedlings usually had small reddish leaves, little new root growth, and very low SS and PPi-PFK activities as compared with healthy transplanted seedlings of the same site. Some of the black mottling/scare areas on discolored seedlings were infected with *Botryosphaeria dothidea* (Moug.:Fr.) Ces. De Not. At the end of the first year, about 10% mortality was observed with seedlings transplanted into the nursery bed or the forest site. No further mortality occurred on the forest site for the following 3 years. It is concluded that transplanting stress, based on sucrose metabolism, lasted at least through late June for sweetgum seedlings planted in January.

Abbreviations: ATP-PFK – ATP-dependent phosphofructokinase; FK – fructokinase; GK – glucokinase; PPi-PFK – pyrophosphate-dependent phosphofructokinase; SG – sweetgum; SS – sucrose synthase

Introduction

Sucrose is the major translocated form of carbohydrates in trees (Zimmermann and Brown, 1971). The central roles of sucrose in plant cell growth, storage, and gene regulation have been investigated intensively in recent years (for review, see Koch, 1996). For example, in addition to being the starting and end points of sucrolysis and sucroneogenesis, sucrose can modulate genes for starch synthesis, storage protein synthesis, sucrose cleavage, and nitrate

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reductase (Koch, 1996, and references cited therein). In the sucrose metabolic pathway, sucrose synthase (SS) and pyrophosphate-dependent phosphofructokinase (PPi-PFK) are active in actively growing and storing tissues and inactive in dormant tissues (Sung et al., 1989; Xu et al., 1989). Activities of the alternative enzymes to SS and PPi-PFK, such as invertases and ATP-dependent PFK, usually remain at low levels regardless of the physiological status of plants (Sung et al., 1989; Xu et al., 1989). Sucrose synthase has been identified as a stress indicator for *Pinus taeda* seedlings and trees (Sung et al., 1993b, 1996) and for *P. jeffreyi* trees (Otrosina et al., 1996). It took transplanted loblolly pine seedlings 8 months to resume their cambial growth and SS activities similar to those of the nontransplanted ones (Sung et al., 1993b).

In contrast to conifers, most hardwoods do not appear to suffer as much from transplanting stress. It was reported that transplanted sweetgum (SG, *Liquidambar styraciflua* L.) seedlings have delayed root growth compared to leaf growth (Kormanik, 1986b). Moreover, 41–89% of transplanted SG seedlings had mid-June stem dieback during the first year of transplanting (Kormanik, 1986a). It is critical for transplanted seedlings to establish, as quickly as possible, root–soil contacts for water and nutrient uptake. These processes require energy from stored carbohydrate reserves, current photosynthates, or both (Johnsen et al., 1988; Philipson, 1988). Moreover, before leaves become photoautotrophic, they live off sucrose. Elongation and diameter growth of stems also require sucrose. Seasonal sucrose metabolism was reported in 2- and 3-year-old nursery grown, nontransplanted SG seedlings (Sung et al., 1989). No reports, however, have been made on the biochemical characteristics of transplanting stress experienced by SG seedlings in controlled environments or on forest sites. The objectives of this study were: (1) to follow seasonal patterns of SS, PPi-PFK, ATP-PFK, FK, and GK in nontransplanted and transplanted SG seedling taproots and stems; and (2) to relate SS activity and growth with transplanting stress or other stresses in SG seedlings.

Materials and methods

In April 1993 stratified sweetgum seeds of mixed seed lots were sown in a raised concrete block nursery bed (18.3×1.2×1.2 m) at the Whitehall Experiment Forest (Athens, GA, USA). Seedlings were grown at a density of 66 m^{-2} following the nursery protocol of Kormanik (1986b) except that soil P level was 100 ppm and no vesicular-arbuscular-mycorrhizae were added to the beds. In late January 1994, seedlings from half of the bed were lifted, tagged, and measured prior to transplanting to a nearby nursery bed at the Whitehall Experiment Forest or to a cleared forest field on the Savannah River Site, National Environmental Research Park (New Ellenton, SC). A total of 225 seedlings were transplanted into the nursery bed at a density of 33 m^{-2}. Another 300 seedlings were planted in the forest field at 3×3 m spacing. Seedlings remained in the same nursery bed for the second year were thinned to 33 m^{-2} and served as the nontransplanted controls. Thinning was accomplished by cutting off every other seedlings at the root collar level in later January. The controls and transplanted seedlings in the nursery beds were water regularly. Transplanted seedlings in the forest field received only rain. Seedling condition was evaluated for the presence of stem tip dieback or disease in August, 1994. First year seedling survival was assessed in December 1994. In December 1996 and July 1998, growth measurements and mortality were recorded for plants in the forest field.

The nursery seedlings were lifted periodically from April through November of 1994 for enzyme activities. From June to August, discolored transplanted seedlings also were lifted. Because of the variable cambial SS and PPi-PFK activities among first-order lateral roots of young sweetgum trees during active growing seasons (Sung et al., 1993a), only taproot cambial tissues were analyzed for enzyme activities. At each sampling time, four nontransplanted, four healthy transplanted, or eight discolored transplanted were lifted from nursery beds or the field. Diameter and weight growth of each lifted seedling was recorded. Protocols for sampling and extracting taproot and stem cambial tissues and for enzyme assays and protein determination were based on the procedures of Sung et al. (1993b). Briefly, after bark peeling, xylem-side cambial tissues were scraped into a weight boat. Tissues from two seedlings were composited into a stem or a root sample. Duplicate samples were collected and analyzed each time. Samples were immediately frozen with liquid nitrogen and extracted with extraction buffer, at a 10:1 ratio (weight:volume), containing 200 mM Hepes/NaOH (pH 7.8), 3 mM Mg acetate, 5 mM dithiothreitol (DTT), 1% (w/v) soluble polyvinylpyrrolidone-40, and 10% (v/v) glycerol. After centrifugation at 34 000×g for 20 min at 4°C, supernatant was analyzed for enzyme assays and pro-

tein determination. Changes of OD at 340 nm in all enzyme assays were monitored with a Beckman DU-70 spectrophotometer at 25°C. Sucrose synthase was assayed with 100 mM sucrose, 0.5 mM UDP, and 1 mM PPi as substrates. Pyrophosphate-dependent PFK was assayed with 10 mM fructose-6-P and 1 mM PPi. Enzyme specific activities between duplicate samples varied less than 15%. Average values are reported here.

Results

Nontransplanted SG seedlings started bud break and new root growth near the end of March. Bud break and new root growth of transplanted seedlings began near the end of April. There existed a clear seasonal pattern for SS specific activity in nontransplanted SG stem cambial tissues (Fig. 1A). Stem SS activity was at the lowest level in early April when mean leaf size was about 8 cm^2 (Fig. 1A). Near the end of April, stem SS activity increased more than 4-fold and peaked in June followed by decreases in July and August. The second peak SS activity was observed in September. By November SS activity was low (Fig. 1A). Sweetgum leaf abscission occurred in early December at this nursery. Generally, taproot cambial SS activity tracked that of the stem throughout the year with delayed resumption of activity in the spring (Fig. 1A). Except for May, taproot SS was lower than stem SS. The SS activity in transplanted seedling taproots and stems was at much lower level than the nontransplanted controls from April to June except for SS in transplanted stems sampled in May (Fig. 1B). Transplanting related losses of SS activity were more obvious and lasted longer with taproots than with stems. Maximal loss of SS was 75% for taproots in June and 60% for stems in April. In August, stem and taproot SS in transplanted seedlings were greater than controls (Fig. 1). Nevertheless, transplanting did not alter the spatial pattern of SS activity. Transplanted taproot had lower SS than stem except in November (Fig. 1).

Peak PPi-PFK activity in nontransplanted and transplanted seedling stems and taproots was greater than SS in corresponding organs (Figs. 1 and 2). In contrast to SS, taproot had similar PPi-PFK activity to that of stem in nontransplanted seedlings (Fig. 2A). Nevertheless, the seasonal patterns of seedling taproot and stem PPi-PFK activity (Fig. 2A) were similar to those of SS (Fig. 1A) with only one peak PPi-PFK activity in June. Losses of PPi-PFK activity, about 20–45%, in transplanted seedlings occurred from April through June (Fig. 2B). Sweetgum seedling taproots and stems did not exhibit any seasonal or spatial patterns for ATP-PFK, FK, and GK activities (data not shown). Furthermore, transplanting related losses of ATP-PFK, FK, and GK activities in taproot and stem cambial tissues were minimal compared to those of SS or PPi-PFK (Fig. 3 vs. Figs. 1 and 2).

In this study, about 25% of seedlings transplanted to the nursery bed or the forest field had both stem dieback and black mottling or scars on stems or branches. Another 25% of transplanted seedlings had black mottling or scars on stems or branches. Some of the discolored areas were verified to be infected with the fungus *Botryosphaeria dothidea* (Moug.:Fr.) Ces. De Not (WJ Otrosina, personal communication). Most of the discolored seedlings had small, reddish purple colored leaves. Only a few nontransplanted controls had the above-mentioned symptoms in 1994. At the end of the first year after transplanting, nearly 90% of seedlings survived (Table 1). The dead seedlings generally had fewer first-order lateral roots (FOLR) at transplanting than those survived: 6.9±0.8 (mean±S.E.) vs. 9.3±0.3 for nursery beds

Table 1. Growth (mean±S.E.) and survival of sweetgum seedlings transplanted into a nursery bed or a forest field. Seedlings (1–0) were lifted and transplanted in late January 1994

	Nursery bed	Forest field
January 1994		
Seedling number	225	300
First-order later root number	9.3±0.3	9.0±0.3
Height (cm)	94.5±1.1	91.3±1.2
Root collar diameter (mm)	11.9±0.2	11.7±0.1
December 1994		
Survival (%)	94.0	88.7
December 1996		
Survival (%)[a]	–	89.1
Height (m)	–	2.4±0.04
Diameter at breast height (mm)	–	21.3±0.7
July 1998		
Survival	–	88.4
Height (m)	–	4.9±0.04
Diameter at breast height (mm)	–	55.3±1.1

[a]All nursery bed seedlings were discarded in December 1994. Some dead seedlings in the field sprouted by December 1996.

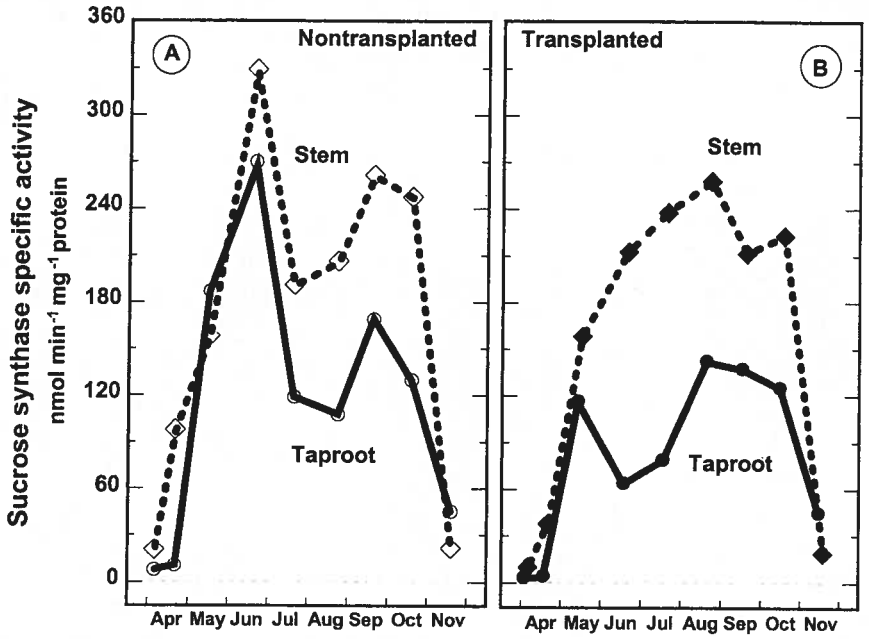

Figure 1. Seasonal patterns of sucrose synthase specific activity in taproot and stem cambial tissues of (A) nontransplanted and (B) transplanted sweetgum seedlings during 1994. Seedlings were lifted and transplanted into a nearby nursery bed in late January 1994. Seedlings remained in the same nursery bed were the nontransplanted controls.

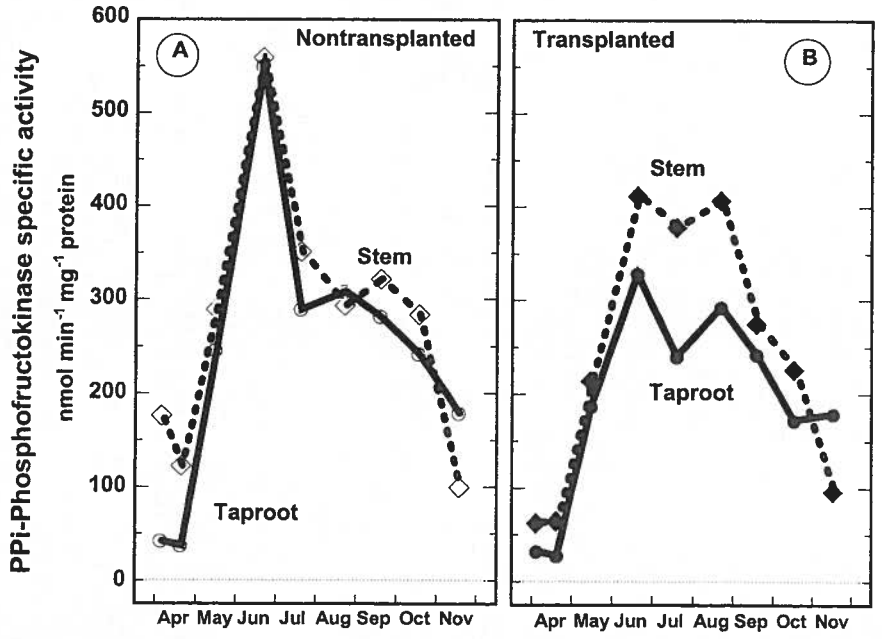

Figure 2. Seasonal patterns of pyrophosphate-dependent phosphofructokinase specific activity in taproot and stem cambial tissues of (A) nontransplanted and (B) transplanted sweetgum seedlings during 1994. Seedlings were lifted and transplanted into a nearby nursery bed in late January 1994. Seedlings remained in the same nursery bed were the nontransplanted controls.

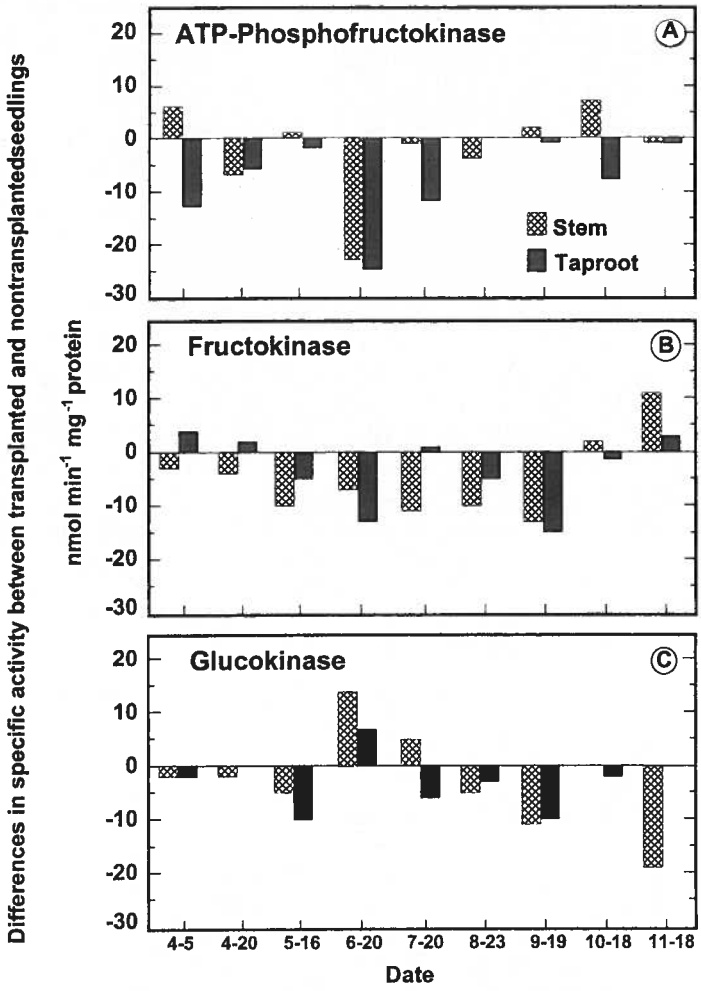

Figure 3. Differences in (A) ATP-dependent phosphofructokinase, (B) fructokinase and (C) glucokinase specific activities between transplanted and nontransplanted sweetgum seedlings during 1994. Seedlings were lifted and transplanted into a nearby nursery bed in late January 1994. Seedlings remained in the same nursery bed were the nontransplanted controls.

and 8.2±0.8 vs. 9.0±0.3 for the forest site. No further mortality occurred for the forest field plants for the following 3 years (Table 1).

Diameter and weight growth of healthy or discolored transplanted SG lifted in the months of June through August were presented in Table 2. Enzyme activities of these seedlings were presented in Table 3. In general, the discolored seedlings had fewer FOLR and smaller diameter at transplanting than the healthy ones (Table 2). The discolored seedlings had little root, stem or leaf growth but greater amounts of stem dieback, compared to the healthy seedlings of the same site (Table 2). Seedlings in the forest field grew much less than those transplanted into the nursery bed. Moreover, SS activity of healthy seedlings in the forest field remained low even in August when transplanted seedlings in the nursery beds had greater SS activity than controls (Table 3, Fig. 1A). Generally, SS and PPi-PFK activities in discolored seedling taproots and stems were much lower than those of the healthy seedlings (Table 3). Again, activities of ATP-PFK, FK, and GK were constant regardless of seedling condition or transplanting site.

Discussion

Results in Figure 1 and Tables 2 and 3 indicated that there exists a close relationship between SS activity

Table 2. Growth of healthy and discolored sweetgum seedlings in a nursery bed or a forest field during the first year after transplanting. Seedlings in the nursery bed were watered regularly but those in the forest field received rain only

Date	Site	At transplanting		Ater transplanting (fresh weight, g)							
		FOLR[a] (#)	RCD (mm)	Seedling Condition[b]	RCD (mm)	New root[c]	Total root	Stem/ branch	Dieback stem	Leaf	Seedling
6-3	Forest	10	13.1	Healthy	14.1	6.5	68	60	2.6	34	162
		6	10.9	Discolored	11.0	0.1	34	26	7.1	4	64
6-20	Nursery	7	11.1	Healthy	13.4	8.8	60	77	0.8	62	199
		5	10.5	Discolored	10.9	1.1	30	27	9.2	17	74
7-20	Nursery	11	11.3	Healthy	18.3	31.1	173	192	0	234	599
		5	10.0	Discolored	13.5	2.4	61	57	10.0	52	170
8-10	Forest	9	11.6	Healthy	15.5	–	69	58	0.4	40	167
		7	10.2	Discolored	13.4	–	57	42	0.6	17	116
8-23	Nursery	9	12.9	Healthy	20.7	–	216	320	0.5	290	826
9-19	Nursery	17	12.4	Healthy	25.9	–	347	534	0.1	396	1277
10-18	Nursery	12	13.4	Healthy	26.1	–	276	441	0	244	961
11-18	Nursery	12	12.6	Healthy	28.5	–	304	593	7.4	203	1100

[a]FOLR and RCD: first-order lateral root number and root collar diameter of seedlings lifted from the nursery bed in January 1994. Values presented were means from four healthy or eight discolored seedlings.
[b]Same seedlings lifted at each sampling date were analyzed for enzyme activities. Discolored seedlings had black mottling or scars on stems or branches. Some discolored areas were infected with *Botryosphaeria dothidea*. Leaves of discolored seedlings were generally small and reddish purple in color.
[c]New lateral roots were non-suberized and white in color. They were not distinguishable from the original roots by August.

Table 3. Sucrose metabolic pathway enzyme activities in the cambial tissues of taproots and stems of healthy and discolored sweetgum seedlings during the first year after transplanting. Seedlings in the nursery bed were watered regularly but those in the forest field received rain only

Date	Site	Seedling condition[a]	Taproot enzyme specific activity (nmol min^{-1} mg^{-1} protein)					Stem enzyme specific activity (nmol min^{-1} mg^{-1} protein)				
			SS[b]	PPi-PFK	ATP-PFK	FK	GK	SS	PPi-PFK	ATP-PFK	FK	GK
6-3	Forest	Healthy	4	183	30	38	28	62	264	21	34	19
		Discolored	6	76	46	24	12	1	68	7	14	16
6-20	Nursery	Healthy	65	329	33	51	50	213	413	35	58	48
		Discolored	48	225	30	50	34	94	346	29	49	21
7-20	Nursery	Healthy	80	241	24	52	27	238	380	46	50	33
		Discolored	16	170	18	40	21	35	163	16	47	26
8-10	Forest	Healthy	27	151	30	51	23	65	188	25	40	18
		Discolored	8	40	23	23	22	1	20	35	19	11

[a]Same seedlings were measured for growth as presented in Table 2. Two healthy or four discolored seedlings were composited into a sample. Duplicate samples were analyzed. Discolored seedlings had black mottling or scars on stems or branches. Some discolored areas were infected with *Botryosphaeria dothidea*. Leaves of discolored seedlings were generally small and reddish purple in color.
[b]SS, sucrose synthase; PPi-PFK, pyrophosphate-dependent phosphofructokinase; ATP-PFK, ATP-dependent PKF; FK, fructokinase; GK, glucokinase. Values presented were means of two samples.

and tissue growth: low SS activity in early spring prior to full leaf expansion, increasing SS activity as more leaves exporting sucrose in the summer and early fall, and low SS activity toward leaf abscission. Furthermore, healthy transplanted seedlings had higher SS level than the discolored seedlings of the same site. And, transplanted seedlings receiving regular watering had higher SS activity and grew more than those planted in the forest field and received only rain. These lines of evidence further support results of studies on tree and crop species: that SS activity is closely related to growth (Otrosina et al., 1996; Ross and Davies, 1992; Sun et al., 1992; Sung et al., 1989, 1993b, 1994, 1996; Xu et al., 1989). In other words, SS activity can be used as a stress indicator for plant tissues. In this study, transplanting stress only lasted through June with sweetgum seedlings transplanted into nursery beds and watered regularly. However, most plantation establishment for trees does not have irrigation facility. Thus transplanting stress can be longer, as in the case of forest field seedlings, depending on weather conditions. The enhancing effects of irrigation on photosynthesis rate and fertigation on leaf area, as reported by Samuelson (1998), were assessed beginning in June. It is not known the effect of fertilization on sucrose metabolism of these transplanted SG.

Activity of PPi-PFK more or less tracked that of SS in sweetgum seedlings of different environments. However, this enzyme is not as responsive to growth/stress as SS (Figs. 1 and 2, Table 3). Activities of the other sucrose metabolic pathway enzymes remained constant and were only slightly affected by stress (Fig. 3, Table 3). These results were similar to studies with other crops and trees of different environments where ATP-PFK and GK were identified as the maintenance enzymes for being constant and low in activity (Sung et al., 1989, 1993b; Xu et al., 1989).

Stem dieback and delayed resumption of root growth (as compared to that of leaf) was reported for transplanted sweetgum seedlings (Kormanik, 1986a,b). In fact, initial stem dieback was considered 'common' for sweetgum plantation by foresters. It is not clear whether stem dieback is directly associated with infection by *B. dothidea*. Since no discolored symptom was observed with SG seedlings at transplanting, there exist two possibilities. The first is that *B. dothidea* infected and stayed latent during the first year in the nursery and became aggressive later when transplanted sweetgum are under other stress such as drought. In other words, it was possible that transplanting exacerbated the discolored/disease problem. The second possibility is that the inferior seedlings, those with fewer FOLR and smaller diameter, were infected more often by the disease in the field. Discolored seedlings sampled in this study for growth and enzyme activity have fewer FOLR and smaller diameter at transplanting as compared to healthy transplanted seedlings. Kormanik (1986a) reported that SG seedlings with greater FOLR number also had greater diameter at lifting from the nursery. These seedlings outperformed those with fewer FOLR in the field. Similarly, in this study dead transplanted seedlings had fewer FOLR, at transplanting, than those survived. More study is needed to correlate extents of stem discoloration or stem dieback to seedling FOLR. No *B. dothidea* related symptoms have been observed in trees of the forest field at least for the fourth year after transplanting.

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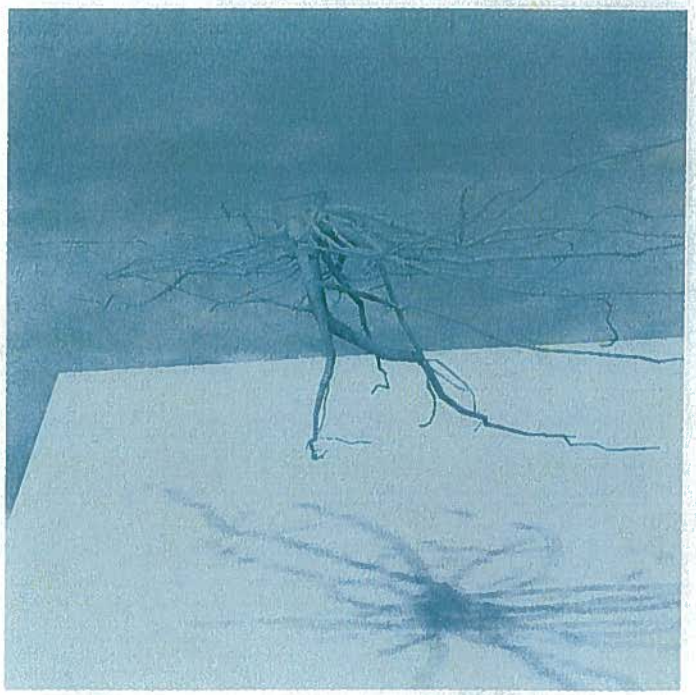

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