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Photosynthate distribution patterns in cherrybark oak seedling sprouts†

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Summary We used ^{14}C tracers to determine photosynthate distribution in cherrybark oak (*Quercus pagoda* Raf.) seedling sprouts following release from competing mid-story vegetation. Fall acquisition of labeled photosynthates by seedlings followed expected source–sink patterns, with root and basal stem tissues serving as the primary sinks. Four months after the seedlings had been labeled with ^{14}C, they were clipped to induce sprouting. First-flush stem and leaf tissues of the resulting seedling sprouts were the primary sinks for labeled photosynthates stored in root tissues. Second-flush stem and leaf tissues, and first-flush stem and leaf tissues the following growing season, were not primary sinks for labeled photosynthates stored in root tissues despite the high radioactivity in root tissues. Root tissues appeared to deposit photosynthates in a layering process whereby the last photosynthates stored in new xylem were the first to be depleted during the initiation of a growth flush the following spring. There were more labeled photosynthates in roots of released seedling sprouts compared with non-released seedling sprouts, indicating increased vigor of released seedling sprouts in response to greater light availability. In contrast, stem and source leaf tissues of non-released seedling sprouts contained greater percentages of labeled photosynthates compared with released seedling sprouts, indicating either greater sink strength or poorly developed xylem and phloem pathways that created inefficiencies in distribution to root tissues. The ^{14}C distribution coefficients confirmed the distribution patterns and provided additional information on the important sinks in released and non-released cherrybark oak seedling sprouts.

Keywords: ^{14}C labeling, carbon allocation, mid-story control, oak reproduction, Quercus pagoda, release.

Introduction

Cherrybark oak (*Quercus pagoda* Raf.) occurs throughout the southeastern USA on river and stream floodplains, adjacent terraces, and uplands (Braun 1950, Krinard 1990). Its rapid growth and high-quality wood make it a desired timber species (Putnam 1951), and its mast is preferred by various wildlife species including white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and squirrels (*Sciurus* spp.) (Lotti 1957). Though a highly desired species in bottomland hardwood forests of the southeastern USA (Putnam et al. 1960), regeneration efforts are often unsuccessful (Hodges 1987, Hodges and Janzen 1987).

Numerous natural regeneration problems have been reported in oak-dominated forests (Putnam 1951, McKnight 1968, Johnson 1979*b*, Watt 1979, McGee 1984, 1986, Lorimer 1989, Cho and Boerner 1991) even when silvicultural prescriptions designed to increase the oak component are implemented (Sander and Clark 1971, Johnson and Krinard 1976, Sander 1977, Loftis 1983). Three forms of oak reproduction are recognized (Aust et al. 1985): (1) new seedlings (those that germinate just before or soon after a harvest); (2) advance reproduction (seedlings and seedling sprouts that develop beneath an existing overstory canopy; Smith 1986); and (3) stump sprouts. New seedlings are considered the least competitive form of reproduction, whereas advance reproduction and stump sprouts are considered the most reliable forms of oak reproduction. In this paper, we focus on seedling sprouts, which are new shoots arising from older root stock where the previous stem dbh (diameter at breast height, 1.37 m) was < 2.5 cm (Merz and Boyce 1956).

Little is known about the physiology of oak seedling sprout growth and development. In general, oak seedlings have numerous dormant buds at the stem base that sprout prolifically

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in response to stem clipping (Matsubara and Hiroki 1985). Subsequent sprouts, especially stump sprouts, are characterized by rapid early height growth (Sander 1972, Johnson 1975, 1979*a*, McQuilkin 1975, Wendel 1975, Cobb et al. 1985, Gardiner and Helmig 1997). Reasons for rapid sprout growth are not fully understood, but may include favorable root/shoot ratios (Janzen 1985), increased photosynthetic capacity (Kruger and Reich 1989, 1993) and increased water transport capabilities (Blake and Tschaplinski 1986). Understanding oak seedling sprout growth and development is therefore important for increasing the success of naturally regenerating oak forests. Our study objective was to determine carbon allocation patterns in cherrybark oak seedling sprouts. To meet this objective, we compared carbon allocation patterns of seedling sprouts growing beneath an intact forest canopy with seedling sprouts growing beneath a partial forest canopy.

Materials and methods

Study site description

The study site was located on a terrace near the Noxubee River on the Noxubee National Wildlife Refuge, Oktibbeha County, Mississippi, USA (33.3° N, 88.8° W). Stand composition was mixed loblolly pine (*Pinus taeda* L.) and broadleaf species consisting primarily of cherrybark oak, water oak (*Quercus nigra* L.) and sweetgum (*Liquidambar styraciflua* L.) in the overstory and sweetgum, oaks, hornbeam (*Carpinus caroliniana* Walt.) hophornbeam (*Ostrya virginiana* Mill.) and red maple (*Acer rubrum* L.) in the middle and lower canopy. Overstory stand age was about 48 years. Soil is a Stough fine sandy loam (course-loamy, siliceous, semiactive, thermic Fragiaquic Paleudults). Though this soil is poorly drained, the site rarely floods. Site index for cherrybark oak was 25 m at base age 50 years (Baker and Broadfoot 1979). The climate is warm and moist, with mean annual precipitation of 1300 mm and mean annual temperatures ranging from 27 °C in July to 8 °C in January.

Treatments

Forty cherrybark oak seedlings (seedling morphological characteristics are summarized in Table 1) were selected in fall 1989. Twenty seedlings were located in a plot of about 0.1 ha, where the mid-story canopy had been removed the previous year (released seedlings). The remaining 20 seedlings were located in an adjacent plot where the mid-story canopy was left intact (non-released seedlings); see Lockhart et al. (2000) for a complete description of the mid-story canopy removal treatment. All sample seedlings were in the Lag stage (stage between flushing events) of seedling development (Hanson et al. 1986) to minimize between-seedling variability. The plots were fenced to minimize herbivory of the seedlings.

Labeling with ^{14}C

Seedlings were labeled with ^{14}C between 1200 and 1400 h on clear to partly cloudy, warm days over a 2-week period in September and October 1989 as described by Isebrands and Nelson (1983). A plastic cup and tygon tubing were taped to the stem of each seedling. A CO_2-impermeable mylar bag was then placed over the seedling and fastened at the lower end with a twist-tie and cellophane tape. The bag was filled with ambient air from a hand-held air pump. Five ml of 5.55 MBq (150 μCi) $Na_2H^{14}CO_3$ was then injected through the mylar bag into the cup with a syringe. A second syringe was used to add 5 ml of 20% lactic acid to the cup and the syringe hole was immediately sealed with cellophane tape. The reaction of sodium bicarbonate with lactic acid produced $^{14}CO_2$, which the seedlings were allowed to fix for 30 min. During this time, ambient air was periodically introduced. After fixation, the remaining liquid was withdrawn with the second syringe, and the bag was removed from the seedling.

Plant harvesting and stem clipping

Two seedlings per treatment were harvested on February 25, 1990 to determine distribution of labeled photosynthates during the dormant season. Harvested seedlings were divided into taproot, lateral root, stem and leaf tissues. Leaves that had abscised between labeling and harvesting were located near the seedling with a Geiger counter and combined with leaves removed from each seedling prior to excavation. During this harvesting period, the shoots of the remaining seedlings (18 per treatment) were clipped 2.5 cm above the ground surface to induce sprouting the following growing season. Subsequent seedling sprouts therefore received labeled photosynthates from root tissues only.

Table 1. Morphological characteristics of cherrybark oak seedlings before labeling with ^{14}C. Values are means ± 1 SE; $n = 20$ unless noted otherwise.

Morphological characteristic	Mid-story intact	Mid-story removed	*P*-value
Height (cm)	32 ± 2	31 ± 2	0.8859
Root-collar diameter (mm)	3.2 ± 0.2	3.9 ± 0.2	0.0151
Number of flushes	1.4 ± 0.1	2.5 ± 0.2	0.0001
Number of leaves	5.3 ± 0.4	10.7 ± 1.1	0.0001
First-flush length (mm)	3.2 ± 0.4	3.1 ± 0.5	0.8728
Second-flush length (mm)	6.8 ± 1.2 ($n = 8$)	4.2 ± 0.7 ($n = 17$)	0.0655
Third-flush length (mm)	– ($n = 0$)	5.4 ± 0.9 ($n = 10$)	–
Fourth-flush length (mm)	– ($n = 0$)	9.3 ± 3.8 ($n = 2$)	–

Five seedling sprouts from each treatment were harvested on June 1, 1990, the first growing season after seedling clipping, during their 1-Lag developmental stage (Hanson et al. 1986). Harvested plants were separated into taproot, lateral roots, stool (stump of original stem), dead stool, first-flush stems and first-flush leaves. Five released seedling sprouts and one non-released seedling sprout were harvested on July 13, 1990 during the 2-Lag developmental stage (only one seedling sprout in the mid-story intact treatment had a second flush at this time) (Hanson et al. 1986). Plants were harvested and processed as described previously, except that second-flush leaves and stems were separated. A final harvest was made of the remaining seedling sprouts on May 15, 1991. Five released seedling sprouts and three non-released seedling sprouts were in their 1-Lag developmental stage. Plants harvested during this time were in their second growing season after labeling and seedling-sprout induction. Plants were harvested and separated into root and stool tissues as previously described. The remaining shoot tissues were divided into 1990 first-flush stems, 1990 second-flush stems, 1991 first-flush stems and 1991 first-flush leaves. Three released seedling sprouts contained a third flush from the 1990 growing season. These stem tissues were combined with the second-flush stem tissues. All tissues were placed in individual plastic bags, transported to the laboratory in ice, and stored at –2 °C until analyzed.

Laboratory analyses

Following 1 to 3 months in cold storage, seedling sprout tissues were oven-dried at 105 °C for 48 h and weighed. Three subsamples (about 0.10 to 0.20 g for leaves and new stem growth, 0.15 to 0.50 g for roots, or 0.30 to 0.60 g for older woody material) were taken from each seedling tissue, unless the whole tissue could be used, and oxidized at 900 °C for 4 min in an OX-600 Biological Oxidizer (Harvey, Hillsdale, NJ) to convert the tissue subsample to CO_2 and water vapor. These gases were forced through a series of catalysts and then into a glass trap containing 15 ml of liquid scintillation cocktail. The carbon from the CO_2 in the bubbling gases was trapped in cocktail solution and radioactivity in each sample was determined five times with a liquid scintillation spectrometer.

Statistical analyses

Total ^{14}C in each tissue was determined by multiplying the mean ^{14}C per gram (specific activity) from subsamples, corrected for oxidation and counting efficiencies, by the total dry mass of that tissue. The ^{14}C content of each tissue was then summed for respective root and shoot tissues and further summed for total seedling ^{14}C content (we note that respiratory losses of ^{14}C may have occurred in the field and in cold storage). Percentage ^{14}C exported was calculated by subtracting leaf tissue ^{14}C content from total seedling ^{14}C content for seedlings harvested during the dormant season. Export for seedling sprouts harvested during each growing season following clipping was calculated by subtracting root tissue ^{14}C content from seedling sprout total ^{14}C content. Because seedling tissue size may influence the distribution of ^{14}C in a plant, a ^{14}C distribution coefficient was calculated for recovered and exported ^{14}C between roots and shoots and between individual tissues. The ^{14}C distribution coefficient is a measure of the specific activity (MBq g^{-1}) of a given tissue divided by the specific activity of the whole seedling, thus providing a means of expressing the sink strength of individual components independently of their size (Edwards et al. 1992). We evaluated mid-story treatments differences in ^{14}C distribution, ^{14}C export from root sources, and ^{14}C distribution coefficients for both recovered and exported ^{14}C in seedling sprouts with *t*-tests (level of significance was $P \leq 0.05$).

Results

Dormant season

Although the released seedlings had one full growing season to respond to mid-story competition control, there was no significant difference in mean dry mass between released and non-released dormant seedlings harvested in February 1990 (Table 2). The lack of statistical differences was probably a result of the small number of seedlings harvested per treatment ($n = 2$) and the high variability associated with seedling biomass. The root/shoot ratio (dry mass basis) for non-released seedlings was < 1, whereas the ratio was > 1 for released seedlings (Table 2).

There were no differences between released and non-released dormant seedlings in the percentage of labeled photosynthates in roots ($P = 0.1617$) and shoots ($P = 0.1617$). Among specific tissues, there were more labeled photosynthates in lateral roots of released seedlings ($P = 0.0052$) compared with non-released seedlings (Figure 1A), whereas the percentage of labeled photosynthate in stem tissue tended to be greater in non-released seedlings than in released seedlings ($P = 0.0519$). It was evident from the samples harvested in the dormant season before stem clipping that labeled photosynthates were exported from source leaves (Figure 1B). Ninety percent of exported labeled photosynthates were found in the root systems of released seedlings compared with only 47% for non-released seedlings.

The ^{14}C distribution coefficients confirmed the observed distribution patterns of labeled photosynthates in the dormant

Table 2. Dry mass (g) for non-released and released cherrybark oak seedlings harvested on February 25, 1990. Values are means ± 1 SE ($n = 2$).

Tissue	Non-released	Released	*P*-value
Taproot	1.34 ± 0.43	2.49 ± 1.13	0.4934
Lateral roots	0.16 ± 0.07	0.55 ± 0.26	0.3681
Stems	1.32 ± 0.42	1.90 ± 1.18	0.7163
Leaves	0.68 ± 0.23	0.88 ± 0.51	0.7745
Root	1.50 ± 0.50	3.04 ± 1.39	0.4652
Shoot	2.00 ± 0.65	2.77 ± 1.68	0.7334
Total	3.50 ± 1.15	5.81 ± 3.07	0.5935
Root/shoot ratio	0.75:1 ± 0.01	1.25:1 ± 0.26	0.3015

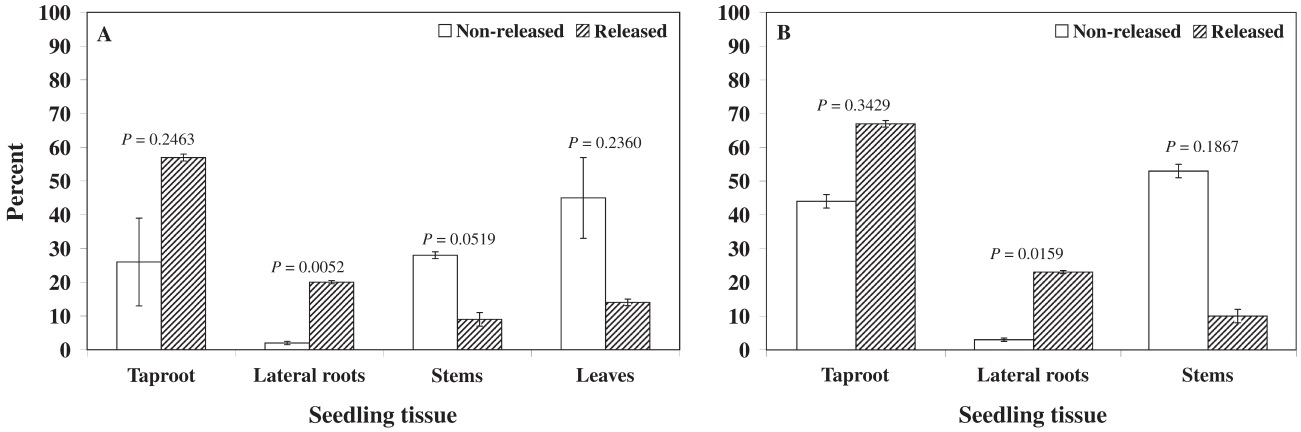

Figure 1. Percentage of ^{14}C-labeled photosynthates distributed (A) and exported from (B) roots in non-released and released cherrybark oak seedlings harvested on February 25, 1990 (dormant season). Bars denote ± 1 SE.

seedlings (Table 3). Taproot and lateral root tissues of released seedlings and leaf tissues of non-released seedlings had greater than average specific activities (values > 1). For released seedlings, the greatest sink for exported ^{14}C was lateral root tissues (Table 3), whereas for non-released seedlings, it was stem tissue. Taproot tissues were also considered sinks.

First growing season 1-Lag

No differences were found in the distribution of labeled photosynthates between released and non-released 1-Lag (first-flush) seedling sprouts during their first growing season after labeling, despite differences in dry mass (Figure 2A and Table 4). Dry mass of roots and shoots was nearly three times greater for released seedling sprouts than for non-released seedling sprouts (Table 4). These differences were particularly noticeable for lateral root, first-flush stem and first-flush leaf tissues (Table 4). In the field, released seedling sprouts produced more and larger leaves on the first flush than non-released sprouts. First-flush stem and leaf tissues of released seedling sprouts contained appreciable amounts of exported labeled photosynthates (Figure 2B). The stool also contained appreciable amounts of labeled photosynthates as a result of its connection between the root and the remainder of the shoot.

The ^{14}C distribution coefficients confirmed the distribution of labeled photosynthates in 1-Lag seedling sprouts (Tables 5 and 6). First-flush tissues had coefficients greater than 1, especially first-flush stem tissues (Table 5). Lateral root tissue of released seedling sprouts also had a coefficient greater than 1. Taproot tissues had values less than 1 despite having the greatest mean distribution percentage of labeled photosynthates (Figure 2A). First-flush stem and leaf tissues were also the greatest sinks for exported labeled photosynthates (assuming that root tissues served as the source), with first-flush stems being greater sinks than first-flush leaves (Table 6).

First growing season 2-Lag

Statistical comparisons between 2-Lag released and non-released seedling sprouts could not be made because only one non-released seedling sprout had a second flush in the 2-Lag stage of development by mid-July; therefore, labeled photosynthate distribution patterns are described for released seedling sprouts only. Labeled photosynthate distribution in 2-Lag seedling sprouts was similar between the whole root and shoot (41 and 59% and 46 and 54%, respectively, for non-released and released seedling sprouts). The taproot contained considerably more labeled photosynthates than the lateral roots (Figure 3A). Among specific tissues, stool tissues contained < 5% of distributed labeled photosynthates, whereas first-flush stem and leaf tissues contained about 40% of the distributed photosynthates, indicating that first-flush tissues were the greatest sinks for ^{14}C exported from root tissues (Figure 3B). Although second-flush tissues contained less labeled photosynthates than first-flush tissues, second-flush leaf tissues contained appreciable amounts of labeled photosynthates, whereas second-flush stem tissues, especially for released seedling sprouts, contained relatively little exported ^{14}C.

In released seedling sprouts, all tissues, except the taproot and second-flush stems and leaves, had ^{14}C distribution coefficients greater than 1, similar to the 1-Lag seedling sprouts (Ta-

Table 3. The ^{14}C distribution coefficients (MBq (g tissue)$^{-1}$/MBq (g whole plant)$^{-1}$) for recovered and exported labeled photosynthates for non-released and released cherrybark oak seedlings harvested on February 25, 1990. Values are means ± 1 SE (n = 2).

Tissue	Non-released	Released	P-value
Recovered ^{14}C			
Taproot	0.68 ± 0.34	1.28 ± 0.10	0.3241
Lateral roots	0.40 ± 0.03	2.07 ± 0.19	0.0698
Stems	0.73 ± 0.02	0.28 ± 0.03	0.0249
Leaves	2.31 ± 0.65	0.97 ± 0.15	0.2802
Root	0.65 ± 0.30	1.42 ± 0.12	0.2186
Shoot	1.26 ± 0.22	0.50 ± 0.04	0.1785
Exported ^{14}C			
Taproot	0.92 ± 0.30	1.27 ± 0.07	0.4522
Lateral roots	0.62 ± 0.17	2.05 ± 0.13	0.0325
Stems	1.12 ± 0.27	0.27 ± 0.02	0.1974

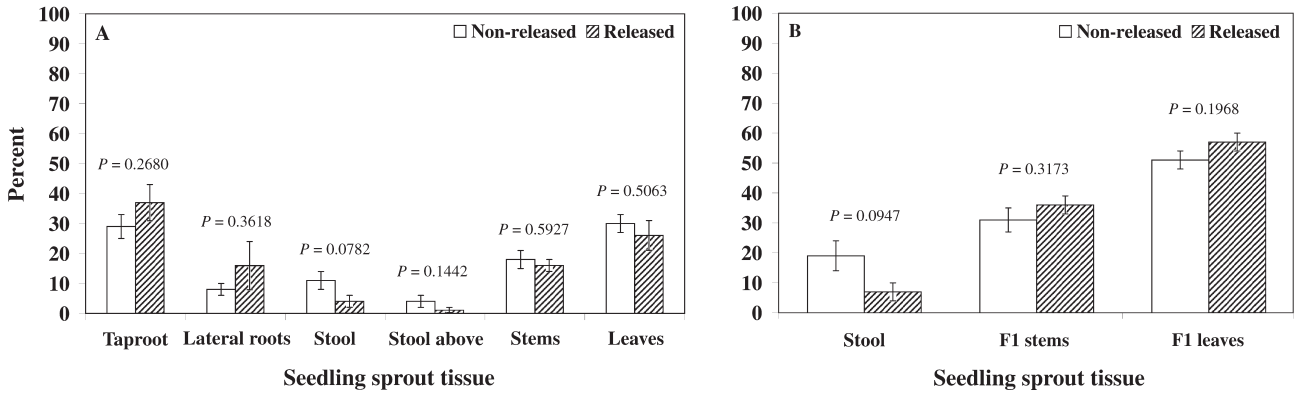

Figure 2. Percentage of ^{14}C-labeled photosynthates distributed (A) and exported (B) from roots in non-released and released cherrybark oak seedling sprouts harvested at 1-Lag on June 1, 1990. Bars denote ± 1 SE. No standard error bars are shown for non-released seedling sprouts because only one seedling sprout had a second flush.

ble 5). Second-flush stem and leaf tissues had ^{14}C distribution coefficients less than 1, indicating low demand for labeled photosynthates (Table 6). Although second-flush leaf tissues contained 19% of exported labeled photosynthates (Figure 3B), the ^{14}C distribution coefficient of 0.46 (Table 6) indicates that this tissue was not a major sink for labeled photosynthates. The low ^{14}C distribution coefficient probably reflects a dilution effect caused by the higher dry mass associated with this tissue (Table 4).

Second growing season 1-Lag

Released seedling sprouts harvested at 1-Lag in the second growing season following labeling tended to have a greater mass than non-released seedling sprouts, but there was high variability among the released seedlings sprouts (Table 4).

Labeled photosynthates were nearly three times higher in root tissues of released seedling sprouts compared with non-released seedling sprouts, particularly in lateral root tissue (Figure 4A). Conversely, shoots of non-released seedling sprouts contained more labeled photosynthates, particularly in the stool and first-flush stem tissues, than shoots of released seedling sprouts. For all sprouts, little ^{14}C was found in the first-flush stem and leaf tissues initiated in the second growing season after labeling despite relatively high radioactivity in root tissues. Although stool and 1990 stem tissues contained appreciable amounts of exported labeled photosynthates (Figure 4B), similar to the second-flush tissues harvested at 2-Lag in 1990 (Figure 3B), 1991 1-Lag leaf tissues contained more labeled photosynthates than associated first-flush stem tissues.

The ^{14}C distribution coefficients confirmed that root tissues of released seedling sprouts and shoot tissues of non-released seedling sprouts contained appreciable amounts of labeled

Table 4. Dry mass (g) for non-released and released cherrybark oak seedlings harvested at 1-Lag on June 1, 1990, 2-Lag on July 13, 1990 and 1-Lag on May 15, 1991. Abbreviations: F1 = first flush and F2 = second flush. Values are means ± 1 SE.

Tissue	1-Lag (June 1, 1990)			2-Lag (July 13, 1990)		1-Lag (May 15, 1991)		
	Non-released (n = 5)	Released (n = 5)	P-value	Non-released (n = 1)	Released (n = 5)	Non-released (n = 3)	Released (n = 5)	P-value
Taproot	1.09 ± 0.12	2.62 ± 0.68	0.0569	2.86[1]	1.43 ± 0.15	1.09 ± 0.37	3.40 ± 1.48	0.1969
Lateral root	0.18 ± 0.03	0.56 ± 0.13	0.0237	0.20	0.26 ± 0.05	0.09 ± 0.02	0.62 ± 0.26	0.1878
Stool	0.22 ± 0.04	0.55 ± 0.25	0.2405	0.13	0.15 ± 0.05	0.16 ± 0.03	0.30 ± 0.07	0.1249
Stool above	0.09 ± 0.03	0.10 ± 0.03	0.7382	0.55	0.20 ± 0.06	0.07 ± 0.04	0.08 ± 0.03	0.8087
F1 Stems	0.11 ± 0.03	0.37 ± 0.07	0.0161	0.63	0.23 ± 0.05	0.04 ± 0.01	0.27 ± 0.13	0.2289
F1 Leaves	0.37 ± 0.06	1.03 ± 0.16	0.0123	1.18	0.40 ± 0.05	0.46 ± 0.08	1.88 ± 0.62	0.1397
F2 Stems	–[2]	–		0.18	0.15 ± 0.02	–	–	
F2 Leaves	–	–		0.45	0.69 ± 0.09	–	–	
1990 F1 Stems	–	–		–	–	0.15 ± 0.02	0.96 ± 0.72	0.4271
1990 F2 Stems	–	–		–	–	–	0.29 ± 0.15	
Total roots	1.27 ± 0.13	3.18 ± 0.72	0.0311	3.06	1.68 ± 0.16	1.18 ± 0.39	4.02 ± 1.74	0.1817
Total shoots	0.79 ± 0.08	2.05 ± 0.42	0.0189	3.12	1.82 ± 0.21	0.87 ± 0.08	3.78 ± 1.64	0.2326
Total seedling sprout	2.07 ± 0.21	5.23 ± 1.08	0.0203	6.18	3.50 ± 0.32	2.05 ± 0.46	7.80 ± 3.38	0.2506
Root/shoot ratio	1.61:1 ± 0.04	1.60:1 ± 0.19	0.9470	0.98:1	0.95:1 ± 0.09	1.31:1 ± 0.34	1.24:1 ± 0.24	0.8807

[1] No standard errors because only one seedling was harvested.
[2] No tissues were available for analyses.

Table 5. The ^{14}C distribution coefficients (MBq (g tissue)$^{-1}$/MBq (g whole plant)$^{-1}$) for total recovered labeled photosynthates for non-released and released cherrybark oak seedlings harvested at 1-Lag on June 1, 1990, 2-Lag on July 13, 1990, and 1-Lag on May 15, 1991. Abbreviations: F1 = first flush and F2 = second flush. Values are means ± 1 SE.

Tissue	1-Lag (June 1, 1990)			2-Lag (July 13, 1990)		1-Lag (May 15, 1991)		
	Non-released (n = 5)	Released (n = 5)	P-value	Non-released (n = 1)	Released (n = 5)	Non-released (n = 3)	Released (n = 5)	P-value
Taproot	0.55 ± 0.07	0.81 ± 0.21	0.2859	0.81[1]	0.88 ± 0.13	0.44 ± 0.22	1.14 ± 0.17	0.0496
Lateral root	0.89 ± 0.18	1.21 ± 0.29	0.3688	1.03	1.33 ± 0.27	0.33 ± 0.14	2.84 ± 0.37	0.0015
Stool	0.99 ± 0.13	0.74 ± 0.39	0.5837	0.51	1.36 ± 0.19	1.81 ± 0.93	1.27 ± 0.39	0.6334
Stool above	0.86 ± 0.13	0.53 ± 0.16	0.1683	0.55	1.35 ± 0.44	3.88 ± 2.08	2.04 ± 1.20	0.4948
F1 Stems	3.57 ± 0.25	2.33 ± 0.49	0.0663	1.95	1.58 ± 0.15	0.56 ± 0.05	0.13 ± 0.04	0.0025
F1 Leaves	1.70 ± 0.15	1.30 ± 0.27	0.2307	0.97	1.77 ± 0.21	0.29 ± 0.13	0.10 ± 0.03	0.1043
F2 Stems	–[2]	–		4.66	0.35 ± 0.09	–	–	
F2 Leaves	–	–		0.20	0.46 ± 0.16	–	–	
1990 F1 Stems	–	–		–	–	2.76 ± 1.10	1.42 ± 0.23	0.1702
1990 F2 Stems	–	–		–	–	–	0.33 ± 0.16	
Total roots	0.60 ± 0.07	0.90 ± 0.17	0.1489	0.83	0.96 ± 0.14	0.43 ± 0.22	1.41 ± 0.13	0.0234
Total shoots	1.64 ± 0.11	1.21 ± 0.22	0.1382	1.17	1.04 ± 0.13	1.62 ± 0.15	0.58 ± 0.10	0.0044

[1] No standard errors because only one seedling was harvested.
[2] No tissues were available for analyses.

photosynthates (Table 5). First-flush stem tissues developed during the 1990 growing season also contained above average amounts of labeled photosynthates (coefficients greater than 1), whereas first-flush stem and leaf tissues developed during the 1991 growing season had coefficients less than 1. The ^{14}C distribution coefficients for exported labeled photosynthates were greater than 1 for first-flush stem tissues developed during the 1990 growing season (Table 6), similar to the seedling sprouts harvested at 1-Lag and 2-Lag in 1990. In contrast to 1-Lag seedling sprouts harvested in 1990, stool tissues of 1-Lag seedling sprouts harvested in 1991 had coefficients greater than 1.

Discussion

Distribution of labeled photosynthates

Oak seedlings exhibit a recurrent or episodic pattern of shoot growth where rapid stem and leaf growth is followed by a quiescent period (Borchert 1975, Reich et al. 1980, Hanson et al. 1986, Dickson 1991, 1994, Kozlowski and Pallardy 1997). Rapid stem growth precedes rapid leaf growth following the initiation of a flush. Under ideal growing conditions, oak seedlings can attain five to seven flushes in a growing season (Crow 1988). Under heavily shaded conditions (< 5% full sunlight), oak seedlings will typically produce only one flush of shoot growth. Comparative data on flush development between oak seedlings and oak seedling sprouts are lacking, but field observations indicate that seedling sprouts also exhibit an episodic pattern of flush growth where rapid stem growth precedes rapid leaf growth (authors' unpublished observation).

There are many studies on source–sink relationships in trees (e.g., Geiger 1987, Turgeon 1989, Dickson 1991). In general, sources, such as mature leaves, are exporters of assimilated photosynthates, whereas active sinks are net importers of these photosynthates (Dickson 1991). Recent work on carbon allocation patterns in oak seedlings has focused on distribution of

Table 6. The ^{14}C distribution coefficients (MBq (g tissue)$^{-1}$/MBq (g whole plant)$^{-1}$) for exported labeled photosynthates for non-released and released cherrybark oak seedlings harvested at 1-Lag on June 1, 1990, 2-Lag on July 13, 1990, and 1-Lag on May 15, 1991. Abbreviations: F1 = first flush and F2 = second flush. Values are means ± 1 SE.

Tissue	1-Lag (June 1, 1990)			2-Lag (July 13, 1990)		1-Lag (May 15, 1991)		
	Non-released (n = 5)	Released (n = 5)	P-value	Non-released (n = 1)	Released (n = 5)	Non-released (n = 3)	Released (n = 5)	P-value
Stool	0.56 ± 0.06	0.48 ± 0.21	0.7283	0.42[1]	1.34 ± 0.20	1.45 ± 0.44	2.82 ± 1.11	0.3018
F1 Stems	2.04 ± 0.15	1.88 ± 0.21	0.5551	1.63	1.54 ± 0.10	0.91 ± 0.52	0.23 ± 0.05	0.1299
F1 Leaves	0.97 ± 0.06	1.03 ± 0.09	0.5748	0.81	1.71 ± 0.10	0.24 ± 0.05	0.17 ± 0.04	0.3889
F2 Stems	–[2]	–		3.89	0.36 ± 0.11	–	–	
F2 Leaves	–	–		0.17	0.43 ± 0.12	–	–	
1990 F1 Stems	–	–		–	–	2.71 ± 0.42	2.90 ± 0.67	0.8229
1990 F2 Stems	–	–		–	–	–	0.81 ± 0.41	

[1] No standard errors because only one seedling was harvested.
[2] No tissues were available for analyses.

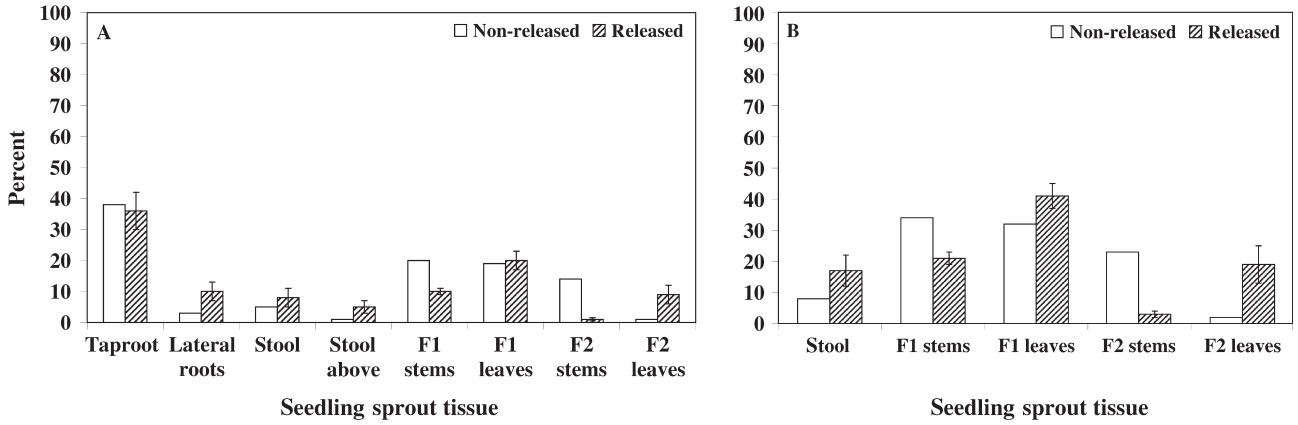

Figure 3. Percentage of ^{14}C-labeled photosynthates distributed (A) and exported (B) from roots in non-released and released cherrybark oak seedling sprouts harvested at 2-Lag on July 13, 1990. Bars denote ± 1 SE.

^{14}C-labeled photosynthates from source leaf tissues (Isebrands et al. 1994, Dickson et al. 1990, 2000*a*, 2000*b*). Carbon allocation from source leaf tissues is strongly influenced by the stage of oak seedling development. First- and second-flush leaf tissues of northern red oak (*Quercus rubra* L.) allocate carbon acropetally during the development of subsequent flushes (Dickson et al. 2000*a*). During lag periods, carbon allocation from source leaf tissues shifts basipetally to lower stem and root tissues. Furthermore, carbon allocation from source leaf tissues is partitioned to different chemical fractions depending on the stage of oak seedling development (Dickson et al. 2000*b*). During flush development, carbon allocation from source leaves is partitioned primarily to structural carbohydrates, whereas during the lag stage of development carbon is partitioned primarily in starch and sugar fractions of basal stem and root tissues. These starch and sugar fractions support the development of subsequent flushes of stem and root growth.

Before stem clipping, root tissues were the primary importers of labeled photosynthates during the fall labeling period (Figures 1A and 1B). In response to stem clipping, roots of dormant seedlings serve as the primary source of labeled photosynthates during the development of the first flush of seedling-sprout growth. All labeled photosynthates found in the shoots of seedling sprouts could be traced back to root tissues, and to a lesser extent, stool tissues. Because rapid first-flush stem development precedes rapid first-flush leaf development, the stem tissue was the first major sink of photosynthates stored in the root (Figure 2B, Table 6), and early first-flush leaf growth was the second major sink for root-stored photosynthates (Figure 2B, Table 6). Labeled material found in first-flush leaves could also be attributed to root sources, although internal cycling of labeled non-structural carbohydrate chemical fractions could have occurred in the first-flush stem with subsequent distribution to developing first-flush leaves.

Distribution of labeled photosynthates following harvest of 2-Lag seedling sprouts was similar to that in 1-Lag seedling sprouts. First-flush stem and leaf tissues were strong sinks for labeled photosynthates. In contrast, second-flush tissues were minor sinks for labeled photosynthates from root or first-flush stem and leaf tissues (Tables 5 and 6), indicating that photosynthates used to support second-flush stem and leaf tissues

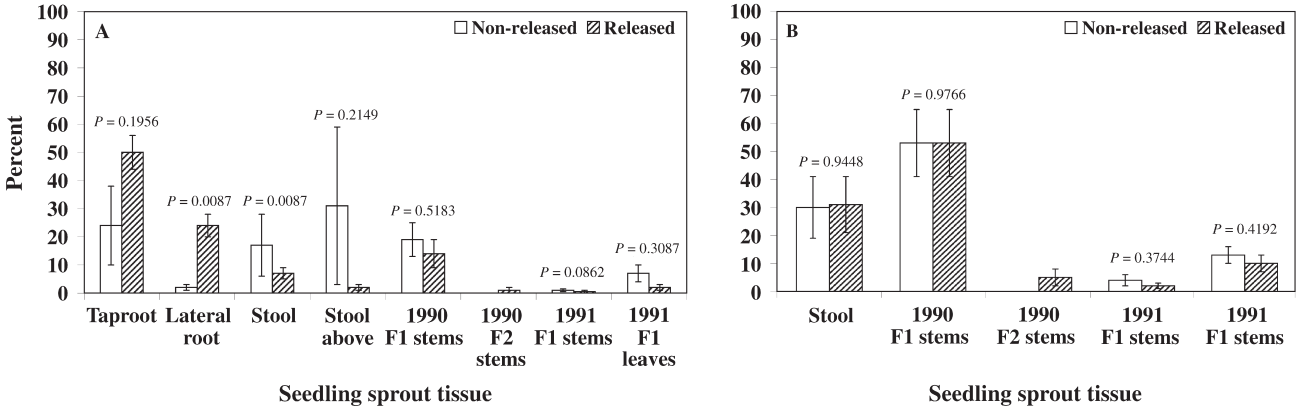

Figure 4. Percentage of ^{14}C-labeled photosynthates distributed (A) and exported (B) from roots in non-released and released cherrybark oak seedling sprouts harvested at 1-Lag on May 15, 1991. Bars denote ± 1 SE.

came from either recently assimilated photosynthates from first-flush source leaf tissues or non-labeled fractions from the root tissues. Hanson et al. (1988*a*, 1988*b*) showed that first-flush leaf tissues in northern red oak seedlings increased their photosynthetic rates in response to the development of the second flush. Dickson et al. (2000*a*) demonstrated that carbon assimilated by first-flush source leaf tissues in northern red oak moved acropetally to the strong sink created by the developing second flush. Although first-flush leaf tissues are probably the primary source of photosynthates for development of the second flush, use of stored photosynthates from root tissues cannot be excluded.

Wargo (1979) showed that distribution of photosynthates in roots of sugar maple (*Acer saccharum* Marsh.) followed a layering pattern—the last photosynthates stored in new xylem were the first to be depleted on initiation of a growth flush the following spring. During maturation and lag in first-flush cherrybark oak seedling sprouts and before the development of the second flush, non-labeled carbon assimilated by first-flush leaf tissues is allocated to root tissues in addition to growth of first-flush stem and leaf tissues (Dickson et al. 2000*a*). Based on the layering concept, these unlabeled photosynthates allocated to root tissues would be the first used by the developing second flush. We note that high amounts of labeled photosynthates remained in the taproot during the second flush (Figure 3A); however, some of these labeled photosynthates were used in root structure (Table 5).

Distribution of labeled photosynthates following harvest of 1-Lag seedling sprouts during the second growing season after labeling provided further evidence that layering of stored photosynthates may occur in root tissues. First-flush stem and leaf tissues relied primarily on stored reserves in the lower stem and root tissues for initial growth. Although first-flush stem tissue from the 1990 growing season and root tissues contained high percentages of labeled photosynthates, first-flush stem and leaf tissues initiated during the second growing season contained low percentages of labeled photosynthates (Figures 4A and 4B) and had a low demand for these photosynthates (Tables 5 and 6). Thus, labeled photosynthates stored in the root tissues following labeling in fall 1989 were not required for the development of either second-flush tissues in 1990 or first-flush tissues in 1991.

Released versus non-released seedling sprouts

The primary effect of controlling competing mid-canopy trees is to increase the irradiance that reaches seedlings. The mid-story release treatment increased light availability from < 50 μmol m^{-1} s^{-1} (< 5% of full sunlight) to 200–300 μmol m^{-1} s^{-1} (40 to 60% of full sunlight) (Jenkins and Chambers 1989, Lockhart et al. 2000); however, prominent short-periods of increased sunlight (sunflecks) > 300 μmol m^{-1} s^{-1} occurred in the control treatment (Lockhart 1992). Gardiner and Hodges (1998) demonstrated that moderate light availability resulted in the best growth of cherrybark oak seedlings. Although control of competing mid-story vegetation alone will not result in optimum oak seedling growth, clipping the seedlings to induce sprouts, in addition to releasing them from competing mid-story canopy vegetation, may increase seedling survival and growth rate.

Carbon distribution of our cherrybark oak seedling sprouts was influenced by light availability. Before the seedlings were clipped, photosynthate allocation to root tissues was greater for released seedlings than for non-released seedlings (Figure 1A). Furthermore, released seedlings had more flushes and leaves at the time of labeling than non-released seedlings, indicating greater seedling vigor in response to increased irradiance following mid-story competition control (Table 1). Labeled photosynthates in non-released seedlings prior to clipping were primarily located in the shoot, especially source leaves. Because these leaves were inactive in February (when the seedlings were harvested) and had either abscised or were about to abscise, these photosynthates represent lost potential food reserves for future seedling growth.

The non-released seedlings may have had little demand for newly acquired photosynthates from source leaves because of reduced growth or inefficiencies in the xylem and phloem pathways. Evidence in favor of the latter explanation includes the slow growth response of oak seedlings to release from mid-story competition. Released oak seedlings eventually responded to increased light availability after 3–5 years (Deen et al. 1993, Lockhart et al. 2000). Graney (1989) also reported height growth of about 3 m in northern red oak, black oak (*Quercus velutina* Lam.) and white oak (*Quercus alba* L.) 5 years after mid-story competition control. Likewise, released northern red oak grew about 0.3 m in height 2 years after release and only 0.72 m after 6 years (Beck 1970).

A greater percentage of labeled photosynthate was maintained in the root tissues of released seedling sprouts compared with non-released seedling sprouts (Figures 2A, 3A and 4A). This finding may indicate that the enhanced growth exhibited by released seedling sprouts (Table 4) allowed increased allocation to and export from root tissues of non-labeled photosynthates. That is, as a result of the layering pattern, these non-labeled photosynthates were utilized preferentially when shoot tissue demands could not be met by photosynthates from source leaf tissues, especially at the beginning of a growing season. Greater root growth of released seedling sprouts could also account for a greater distribution of labeled photosynthates to the root tissues if labeled photosynthates one and two growing seasons following allocation reside primarily in structural carbohydrates.

Non-released seedling sprouts maintained lower growth rates than released seedling sprouts (Table 4, Lockhart et al. 2000). Non-released seedlings and seedling sprouts typically flushed only once per growing season (Lockhart 1992), and long-term observations indicate that survival of non-released seedling sprouts is low (Lockhart et al. 2000). The non-released seedling sprouts relied heavily on photosynthates stored in the root system for survival, with growth and development being secondary. Second-flush stem tissues (note that only one seedling sprout contained a second flush) contained a relatively high percentage of labeled photosynthates from root sources, an indication that first-flush leaves were unable to generate sufficient photosynthates to meet second-flush demands. Lockhart (1992) observed that cherrybark oak seed-

lings growing in < 5% full sunlight have photosynthetic rates of less than 1 μmol CO_2 m^{-2} s^{-1}.

The ^{14}C distribution coefficients

Large tissues may mask relative sink strengths within a plant simply because of their greater biomass. Edwards et al. (1992) used a ^{14}C distribution coefficient to compare sink strength of plant tissues independently of their size. The ^{14}C distribution coefficient is a dimensionless expression comparing tissue specific activity (MBq g^{-1}) to plant specific activity (MBq g^{-1}). This coefficient is similar to the normalized specific radioactivity used by Dickson et al. (1990) and to Mor and Halevy's (1979) relative specific activity. The ^{14}C distribution coefficient also corrects for differences in total plant radioactivity when comparing the ^{14}C concentration of specific tissues (Edwards et al. 1992). A value greater than 1 indicates a greater than average concentration of ^{14}C in a specific tissue, thus indicating a sink for labeled photosynthates (Edwards et al. 1992).

Based on ^{14}C distribution coefficients, we found that 1-Lag taproot tissues harvested in 1990 contained 29 and 37% of recovered ^{14}C for non-released and released seedling sprouts, respectively (Figure 2A). These percentages were similar to those for first-flush leaf tissues and greater than those for first-flush stem tissues (Figure 2A). The ^{14}C distribution coefficients for taproot tissues had values less than 1, whereas the first-flush stem and leaf tissues had values considerably greater than 1 (Table 5). Therefore, although taproot tissues contained the largest percentage of recovered ^{14}C, stem and leaf tissues were greater sinks for stored labeled photosynthates (Tables 5 and 6). Similar values were found in 2-Lag leaf tissues for released seedling sprouts (Figure 3A, Table 5) and taproot and first-flush leaf tissues for non-released seedling sprouts harvested in 1991 (Figure 4A and Table 5).

We conclude that distribution of stored photosynthates from root tissues is critical to the development of the first flush of shoot growth following seedling clipping. Although first-flush stem and leaf tissues are dependent on these stored photosynthates, subsequent flushes rely more on photosynthates recently produced or stored by first-flush leaf tissues. Cherrybark oak carbon allocation patterns are similar to those of northern red oak. Carbon allocation was similar between seedlings and seedling sprouts. Increased light availability (from < 50 μmol m^{-2} s^{-1} in the non-release treatment to 200–300 μmol m^{-2} s^{-1} in the mid-story release treatment) resulted in increased carbon assimilation and storage. Further research is needed to determine critical irradiances for survival and subsequent growth of oak seedlings and seedling sprouts.

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