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Carbon translocation patterns associated with new root proliferation during episodic growth of transplanted *Quercus rubra* seedlings†

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Summary Patterns of carbon allocation in northern red oak (*Quercus rubra* L.), characterized by episodic growth through recurrent single-season flushing, vary by growth stage. To examine post-transplant timing and carbohydrate sources for new root growth, dormant, bare-root, half-sibling northern red oak seedlings were transplanted to pots and placed in a favorable growth chamber environment. Unlabeled seedlings were harvested at transplant and at the bud swell stage. After leaf emergence, seedlings were exposed to $^{14}CO_2$ at the linear shoot, linear leaf or lag growth stages. Seedlings were then placed in a growth room for 48 h to allow for translocation of ^{14}C-labeled current photosynthate and its stabilization in sink component plant parts. Seedlings were subsequently harvested and tissue ^{14}C:^{12}C ratio analyzed. New root growth began during the linear shoot growth stage. However, no increase in ^{14}C:^{12}C ratio was found in new roots until the linear leaf and lag growth stages, indicating a downward shift in translocation of current photosynthate to fuel new root growth. In old roots, ^{14}C:^{12}C ratio increased at the lag stage. Our results indicate that both stored carbohydrates and current photosynthate contribute to new root growth of transplanted northern red oak seedlings; stored carbohydrates promote initial new root proliferation, whereas current photosynthate assumes a greater role as new leaves mature and the flush terminates. Optimizing nursery practices to increase carbohydrate reserves may reduce the time required to establish root–soil contact and facilitate early post-planting survival.

Keywords: carbohydrate reserves, carbon allocation, Quercus morphological index, root growth.

Introduction

Relatively few studies have examined carbon allocation in temperate deciduous forest tree species exhibiting episodic growth patterns (Dickson et al. 1990, 2000*a*, 2000*b*). True episodic flushing, as exhibited by northern red oak (*Quercus rubra* L.), is characterized by the endogenously controlled recurrent development of flushes throughout the growing season during periods of suitable environmental conditions; such growth involves the expansion of new stem and leaf material from a resting bud before formation of a new resting bud (Dickson 1994).

To faciliate studies examining the association of physiological status and activity with physical growth of *Quercus* seedlings, Hanson et al. (1986) developed the *Quercus* morphological index (QMI). The QMI divides a flush of growth into stages that are readily identifiable by a series of simple morphological measurements. Several studies have successfully used the QMI in conjunction with ^{14}C labeling techniques to quantify allocation and partitioning patterns of current photosynthate at various developmental stages and across a number of flushes (Dickson et al. 1990, 2000*a*, 2000*b*). Patterns of allocation of current photosynthate in northern red oak seedlings vary greatly across QMI growth stages, with the greatest downward translocation to roots typically occurring during the lag stage when the resting bud is set at the end of a flush (Dickson et al. 2000*a*).

Research on northern red oak has focused on the carbon allocation patterns during the first growing season growth flushes (Dickson et al. 1990, 2000*a*, 2000*b*). Several studies have been conducted with coniferous species to examine post-transplant allocation of current photosynthate (van den Driessche 1987, Philipson 1988, Maillard et al. 2004). New root growth following transplanting depends at least partially on current photosynthate in Douglas-fir (*Pseudotsuga menziessii* (Mirb.) Franco), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and Corsican pine (*Pinus nigra* Arn. ssp. *laricio* var. *corsicana*) (van den Driessche 1987, Philipson 1988, Maillard et al. 2004). Despite information relating seedling root morphology to planting success of *Quercus* spp., few studies have examined physiological aspects of root growth in relation to transplanting. Andersen et al. (2000) hypothesized that loss of coarse roots before transplanting had a more negative effect on post-transplant root growth than loss of fine roots, and that new root growth following transplanting is likely reliant on nonstructural carbohydrates and nutrients stored in coarse roots. To test the hypothesis that new root growth following transplanting relies on stored carbohydrates, and to assess the degree to which current photosynthate contributes to new root

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growth following transplanting of northern red oak sedlings, we used the QMI in conjunction with established techniques for labeling of current photosynthate with ^{14}C and examined patterns of new root proliferation across the QMI stages along with the ratio of ^{14}C:^{12}C in new and old roots.

Materials and methods

Plant material

Northern red oak acorns were collected from a single open-pollinated tree near the Purdue University campus in West Lafayette, IN, USA (40° 25′ N, 86° 55′ W) in fall 2003 and cold stratified (2 °C) over winter. In May 2004, acorns were sown in 2.8-l Treepots (Stuewe and Sons, Corvallis, OR) containing Metro-Mix 360 growing medium (Sun Gro Horticulture Canada CM, Vancouver, BC) in a greenhouse at the Purdue University Department of Horticulture and Landscape Architecture (HLA) Plant Growth Facility. Seedlings were grown in an ambient photoperiod with a mean day/night temperature of 24/20 °C and fertilized with a commercial water-soluble fertilizer (N,P,K; 15,5,15 plus other macro- and micro-nutrients) to apply 75 mg N per seedling exponentially throughout the growing season, starting the second week following planting and continuing for 16 weeks (Salifu and Jacobs 2006). Seedlings were irrigated to container capacity (determined gravimetrically) at time of planting and twice weekly thereafter throughout the growing season. Containers were rearranged every 2 weeks to minimize edge effects. In October 2004, seedlings were transferred from the greenhouse to a cooler at 2 °C for over-winter storage.

In April 2005, 25 northern red oak seedlings exhibiting two flushes were randomly selected and removed from cold storage. Medium was carefully washed from roots to leave fine roots intact. After washing, any new roots were removed to simulate a minimal loss of fine roots under ideal bare-root transplant conditions. Initial shoot height (cotyledon scar to base of terminal bud) and root volume (by water displacement) were measured and 21 seedlings were randomly selected and repotted in 6.2-l TPOT2 Treepots containing a 1:1 (v/v) mixture of sphagnum peat and sand. The remaining four seedlings served as a pre-transplant sample for immediate harvest (FIH).

Repotted seedlings were placed in a growth chamber (Model EY15, Controlled Environments, Winnipeg, MB) providing a 16-h photoperiod, a day/night temperature of 27/21 °C, and a photosynthetic photon flux of 300–400 μmol m^{-2} s^{-1} at seedling top height. Seedlings were watered to container capacity with tap water and measured every 2 days. Seedlings were randomly rearranged weekly to minimize edge effects.

Measurements and treatment

The FIH seedlings were separated by shoot flush and organ. Roots were further separated into old roots and new (white) roots. New roots were tallied by length class (0.25–5 cm, 5–10 cm or > 10 cm). All plant parts were dried for 1 h at 100 °C followed by 48 h at 70 °C and ground to pass a 20-mesh screen (Dickson and Isebrands 1991).

Measurements of repotted seedlings, which were made every 2 days, included shoot height, length of the first new internode subtending a normal leaf, and length of the second to the topmost leaf. These measurements were used to identify the key growth stages within the flush as delineated by the QMI, with bud swell stage (BUD), linear shoot growth stage (SL), linear leaf growth stage (LL) and lag stage (LAG) being identified by a swollen bud, cessation of growth of the first new internode subtending a normal leaf, cessation of growth of the total shoot, and cessation of elongation of the second to topmost leaf of the flush, respectively (Hanson et al. 1986, Dickson et al. 2000*a*).

A growth stage for treatment (BUD, SL, LL or LAG) was randomly assigned to each of the 21 seedlings, each serving as a biological replicate. One seedling from the BUD group and one seedling from the LL group failed to break bud during the experiment and both were consequently removed from the study, leaving $n = 4$ for FIH, BUD and LL, and $n = 5$ for SL and LAG. When measurements indicated a seedling had reached its assigned growth stage, it was removed from the growth chamber at 1300 h, solar time, and transferred to a greenhouse bench in the HLA Plant Growth Facility. Removed seedlings were allowed 2 h to acclimate before placement in a gas-tight closed-loop labeling system on the same bench. Seedlings were left to further acclimate to chamber conditions for 45 min at ambient temperature and in ambient light (24 °C, mean photosynthetic photon flux 500 μmol m^{-2} s^{-1}). Because of a lack of leaves, seedlings of the BUD group were not labeled but were transferred to a growth room (16-h photoperiod, mean day/night temperature of 23/23 °C, photosynthetic photon flux of 300–400 μmol m^{-2} s^{-1}) to mimic the post-labeling translocation environment of seedlings of the SL, LL and LAG groups. Following a translocation period of 48 h, the labeled seedlings were harvested, final root volumes were measured, and seedlings were processed as described for the FIH group. Because seedling flushes were synchronous, all seedlings of the SL, LL and LAG groups were labeled as groups by growth stage.

Labeling design and isotopic analysis

The gas-tight closed-loop labeling system consisted of a main treatment chamber (76.2 × 76.2 × 106.7 cm) and a reaction chamber (15.3 × 15.3 × 20.3 cm) constructed of 0.64 cm acrylic and connected by 1.3-cm inside diameter PVC tubing. The reaction chamber was fitted with a port containing closed-cell foam to allow for reagent injection. Two fans within the main treatment chamber acted to mix the air and a battery-operated pump served to circulate the chamber air through the system. A pair of valves on the tubing between the reaction chamber and main treatment chamber allowed for routing of the circulating chamber air volume through a soda lime scrubber to remove CO_2 from the chamber air. Following reaction of a sodium bicarbonate solution with an excess of 0.1 M hydrochloric acid in the reaction chamber, CO_2 concentration in the system was measured with an LI-6200 portable photosynthesis system (Li-Cor, Lincoln, NE) attached to the

closed-loop system in such a way as to allow sampling of circulating gases without routing the entire circulating chamber air volume through the LI-6200. Measurements indicated that CO_2 concentration within the system equilibrated within 60 s of addition of CO_2 and equilibrated near 0 ppm within 90 min following routing of the circulating chamber air volume through the soda lime scrubber.

Following the acclimation period, a vial containing 250 nCi of ^{14}C in an aqueous solution of sodium bicarbonate was reacted via injection of an excess of 0.1 M hydrochloric acid (5 ml) to release $^{14}CO_2$ and begin the labeling session. Each labeling session lasted 1 h from the time of reaction of the label until the circulating chamber air volume was diverted through the soda lime scrubber to end the labeling session. An LI-6200 portable photosynthesis system monitored CO_2 concentration within the chamber as previously described and confirmed the completion of the scrubbing procedure. Following the labeling session, seedlings were removed from the chamber and transferred to a growth room for a 48 h translocation period as previously described. Following the translocation period, seedlings were processed as described for the BUD group.

After processing, the dried and ground samples were sent to the Purdue Rare Isotope Measurement Laboratory at Purdue University for determination of ^{14}C:^{12}C ratio by accelerator mass spectrometry (AMS).

Data analysis

A one-way analysis of variance (ANOVA) ($P < 0.05$) followed by Tukey's multiple pairwise comparison ($\alpha = 0.05$) was used to detect significant effects within a given plant part across growth stages. Means (± SE) were calculated for new root mass, number of new roots in the root length classes 0.25–5 cm, 5–10 cm and > 10 cm, change in root volume from planting to time of labeling or harvest, or both, ^{14}C:^{12}C ratio of new roots, mass of old roots and ^{14}C:^{12}C ratio of old roots for the initial sample and at each growth stage.

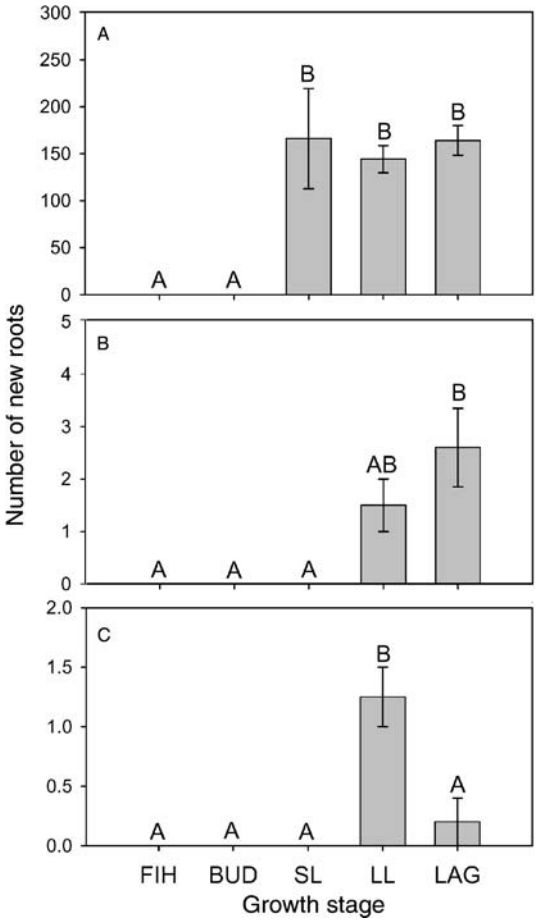

Figure 1. Mean (± SE) number of new roots by length class ((A) 0.25–5 cm, (B) 5–10 cm and (C) >10 cm) for northern red oak seedlings harvested immediately on removal from storage (FIH) or at the bud swell growth stage (BUD), or labeled and harvested at the linear shoot growth stage (SL), linear leaf growth stage (LL) or lag stage (LAG). Bars marked with the same letter are not significantly different as determined by Tukey's multiple pair-wise comparison ($\alpha = 0.05$).

Results

Counts of new white root tips indicated that significant new root growth began at SL for roots in the 0.25–5 cm length class, with the number of new roots in this length class remaining constant thereafter throughout the flush (Figure 1). Number of new white root tips in the 0.25–5 cm root length class was greater at SL, LL and LAG than at FIH or BUD ($P < 0.01$). New white roots in the 5–10 cm length class appeared in significantly greater numbers at LAG than at FIH, BUD or SL ($P < 0.001$), whereas new white roots in the >10 cm length class appeared in significant numbers only at LL ($P < 0.0001$ in all comparisons involving LL) (Figure 1). Despite trends of increasing new root dry mass after the SL phase, no significant differences were detected ($P = 0.054$) over the course of the first flush after transplanting (Figure 2A). The only significant increase in root volume during the first flush occurred at LL ($P < 0.01$ in all comparisons involving LL) (Figure 2B). The ^{14}C:^{12}C ratio of new roots at SL was similar to that of unlabeled plant tissue from FIH and BUD, suggesting no downward translocation of current photosynthate at this growth stage (Figure 2C). Despite high variability between seedlings, the ^{14}C:^{12}C ratio of new roots at LL was significantly greater than at FIH, BUD or SL ($P < 0.01$); similarly, the ^{14}C:^{12}C ratio of new roots at LAG was significantly greater than at FIH, BUD or SL ($P < 0.01$) (Figure 2C). These findings suggest labeled current photosynthate contributes to new root growth at LL and LAG.

Dry mass of old roots exhibited a decreasing trend over the course of the flush, although no significant change in the mass of old roots occurred (Figure 3A). The ^{14}C:^{12}C ratio of old roots was greater at LAG than at FIH, BUD or SL ($P < 0.01$), indicating downward translocation of labeled current photosynthate to old roots at LAG (Figure 3B).

Discussion

Inadequate natural regeneration of northern red oak has stimu-

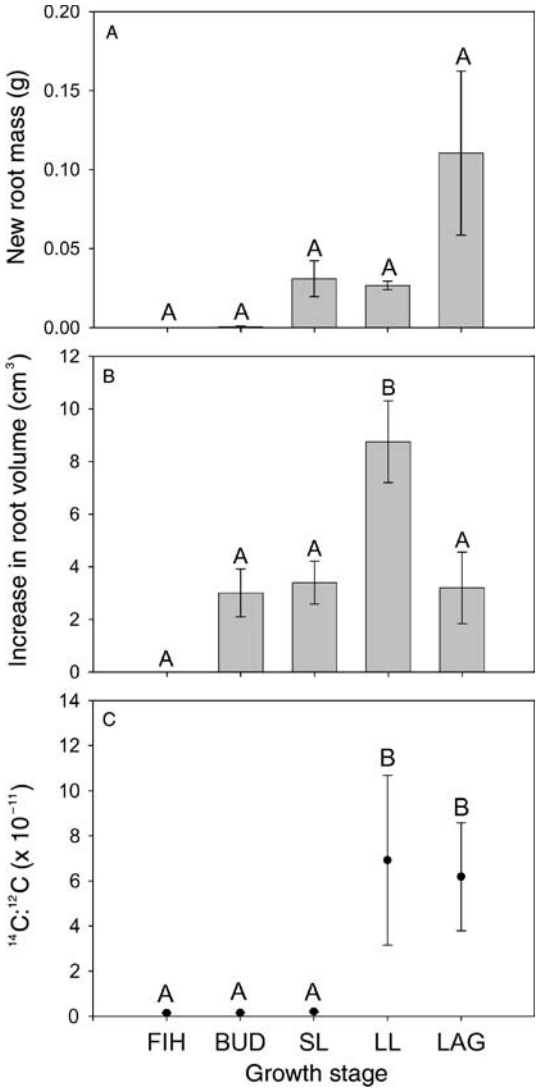

Figure 2. Mean (± SE) (A) dry mass of new roots, (B) changes in root volume and (C) ^{14}C:^{12}C ratio in new roots. Growth stages indicate northern red oak seedlings harvested immediately on removal from storage (FIH) or at the bud swell growth stage (BUD), or labeled and harvested at the linear shoot growth stage (SL), linear leaf growth stage (LL) or lag stage (LAG). Within the same graph, bars or points marked with the same letter are not significantly different as determined by Tukey's multiple pairwise comparison ($\alpha = 0.05$).

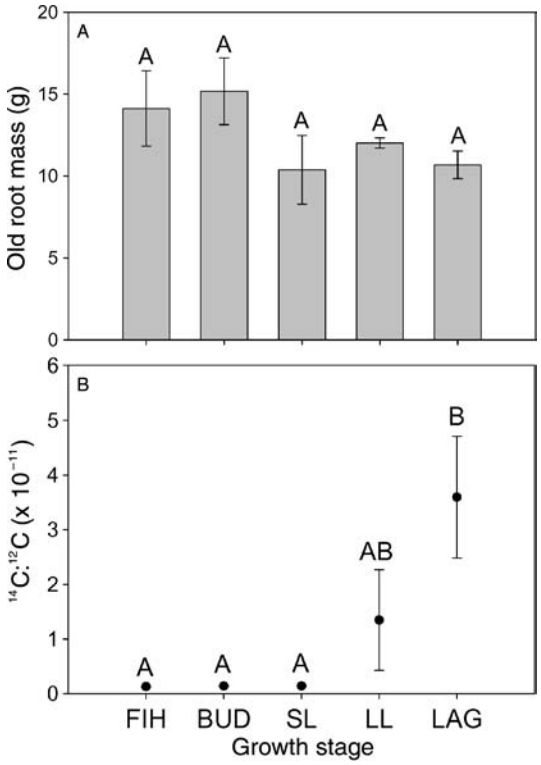

Figure 3. Mean (± SE) (A) dry mass and (B) ^{14}C:^{12}C ratio of old roots at the time of harvest. Growth stages indicate northern red oak seedlings harvested immediately on removal from storage (FIH) or at the bud swell growth stage (BUD), or labeled and harvested at the linear shoot growth stage (SL), linear leaf growth stage (LL) or lag stage (LAG). Within the same graph, bars or points marked with the same letter are not significantly different as determined by Tukey's multiple pairwise comparison ($\alpha = 0.05$).

lated interest in artificial regeneration of this species by planting seedlings (Johnson 1994). Impairment of physiological processes and loss of fine roots during lifting, handling, storage and transport of nursery seedlings, however, often results in a period of growth impairment following planting and before establishment (Grossnickle 1988, 2005, Struve and Joly 1992, Johnson 1994). Pre-transplant loss of fine roots significantly decreased stem dry mass in *Quercus robur* one season after transplanting, suggesting the importance of fine roots during post-transplant recovery (Andersen et al. 2000). Post-transplanting root growth plays a major role in alleviating transplant stress and resumption of normal seedling physiological activity by reestablishing root–soil contact, which is necessary for efficient water and nutrient uptake (Grossnickle 1988, 2005).

Cerasoli et al. (2004) found that 2-year-old cork oak (*Quercus suber* L.), an evergreen oak that assimilates carbon throughout winter, re-translocated carbon from stored winter assimilates to new root growth in early spring. Cork oak stores carbohydrate reserves in leaves over winter for use during the spring flush; subsequently, the spring flush relies on both stored carbohydrates and current photosynthate (Cerasoli et al. 2004). However, phenological patterns of evergreen cork oak differ from those of deciduous oaks, and the source–sink relationships found by Cerasoli et al. (2004) are distinct from those of northern red oak.

We found that counts of new white root tips provided the most sensitive measure of early post-transplanting root proliferation; measurements of root mass and volume revealed no change in fine root material in all cases (Figures 1, 2A and 2B). New root growth occurred at all growth stages following bud break and did not appear closely linked to growth stage as would be expected based on the results of Reich et al. (1980)

showing dependence of root growth on developmental stage, and of Dickson et al. (2000*a*), demonstrating dependence of root growth on current photosynthate in first-year seedlings. In our study, loss of new roots at the time of transplanting disrupted endogenous patterns of new root growth in a manner analogous to that caused by transplanting from nursery to forest plantation. Similar independence of root growth on developmental stage was reported in first-season northern red oak and *Q. robur* seedlings (Harmer 1990, Dickson 1994).

In our study, the ^{14}C:^{12}C ratio in new roots did not increase significantly until the linear stage of leaf growth, whereas significant new root proliferation began earlier at the linear stage of shoot growth (Figures 1 and 2C). This indicates that initial post-transplanting root proliferation relied on stored carbohydrates, with current photosynthate contributing as the flush progressed and leaves matured. Similarly, Cerasoli et al. (2004) found that cork oak relied on both stored carbohydrates and current photosynthate for growth during the spring flush. Our results support those of Isebrands et al. (1994) in that leaves of northern red oak seedlings do not fully mature and carbon exchange rate does not reach a maximum until about one full flush after expansion. Dickson et al. (2000*a*) found that only 20–25% of current photosynthate was translocated from source leaves at the lag stage during the first flush of growth in first-season northern red oak seedlings; about 40% of exported photosynthate was translocated downward to roots. Although Dickson et al. (2000*a*) did not report carbon translocation values from the linear stage of leaf growth, our results confirm their finding that a given flush of leaves exports current photosynthate on reaching lag stage and we show that this pattern holds for seedlings after transplanting.

The ^{14}C:^{12}C ratio in new roots increased at the linear stage of leaf growth and remained elevated through the lag stage, indicating downward translocation of current photosynthate to fuel new root growth at these stages (Figure 2C). New roots in the > 10 cm root length class and root volume increased significantly at the linear stage of leaf growth concurrently with initiation of downward translocation of current photosynthate to new roots, with changes in root volume corresponding to changes in number of new roots > 10 cm in length (Figures 1 and 2B). The significant decreases in number of new roots > 10 cm and root volume from the linear stage of leaf growth to lag stage are consistent with the brief spike in root growth that Dickson et al. (2000*a*) observed followed initiation of downward translocation of current photosynthate.

The decreasing trend in old root mass, although non-significant, suggests initial and possibly continued dependence of new root growth on stored carbohydrates (Figure 3A). Dickson et al. (2000*b*) demonstrated repeated depletion of starch and sugars in taproots and lateral roots following periods of root growth in first-season northern red oak seedlings; our finding of elevated ^{14}C:^{12}C in old root tissue at the lag stage indicates downward translocation of current photosynthate to old roots at this stage and suggests allocation to root energy reserves, which may have been depleted over the course of the flush (Figures 3A and 3B).

Our results emphasize the importance of carbohydrate reserves in the successful establishment of planted red oak seedlings. Starch concentration of roots at the time of lifting was not strongly correlated with root growth after transplanting or survival in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Omi and Rose 1990), and conifers apparently rely more heavily on current photosynthate to fuel root growth after transplanting than does northern red oak (van den Driessche 1987). Consequently, it remains to be determined how various nursery cultural practices alter chemical pools in *Quercus* spp. and the degree to which establishment after transplanting are thereby affected.

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